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Title: Termites mitigate the effects of drought in tropical rainforest

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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% (ΔAIC = 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.

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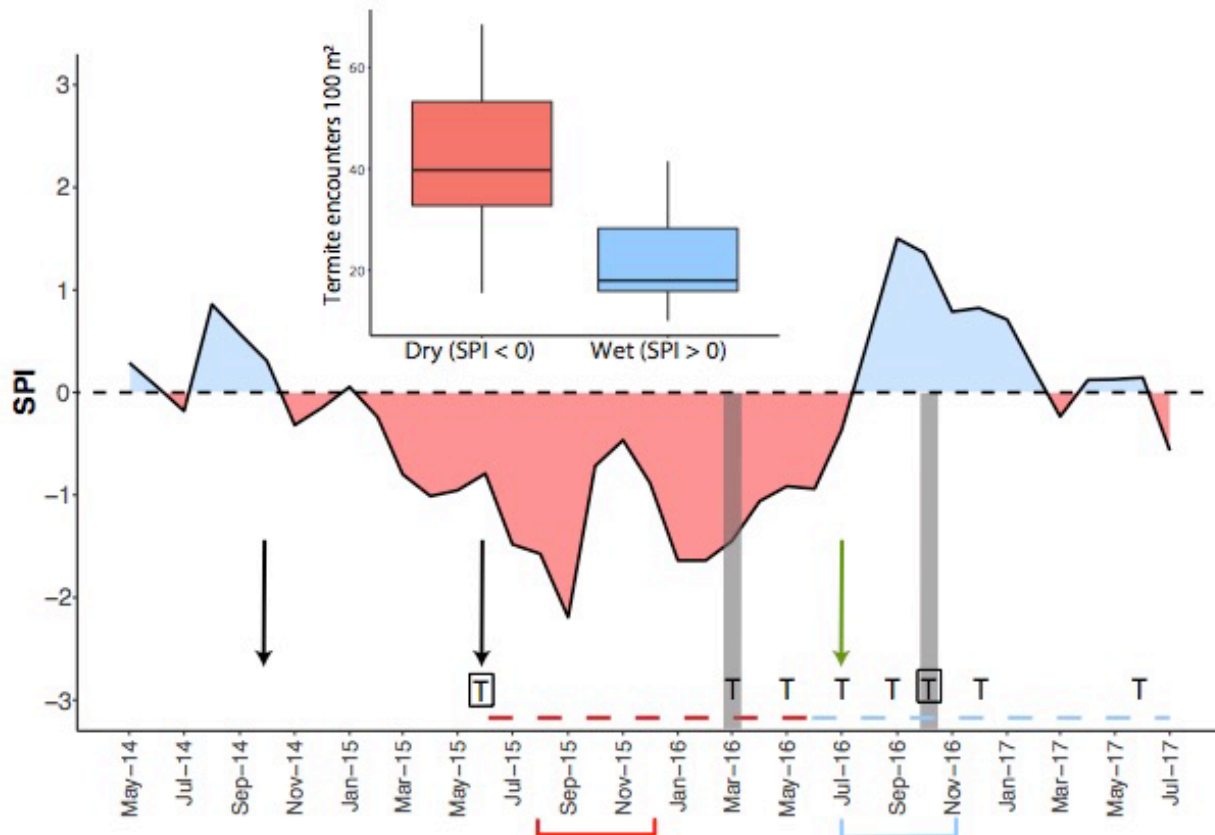
Fig. 1: Three-month Standardised Precipitation Index (SPI) calculated using rainfall data from

Danum Valley Conservation area for one year preceding, and the two-year duration of the study

(2014 – 2017). SPI is climatic proxy used to quantify and monitor drought; negative values

indicate drier than average conditions, while positive values are wetter than average. See

Figure S1 for a 20-year SPI plot of the region. Brackets below the x-axis show the duration of

the litter decomposition experiments in the drought (red) and post-drought (blue), which were in

place for 4 months during the drought and post-drought period; the horizontal dashed lines

show the duration of the seedling survival assessment periods during the drought (red line) and

post-drought (blue line) periods; "T" symbols show repeated termite transect sampling events on

the control plots only to assess the effect of drought on termite communities, "T" symbols

encased in boxes represent termite transects that were carried out on control as well as the

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).
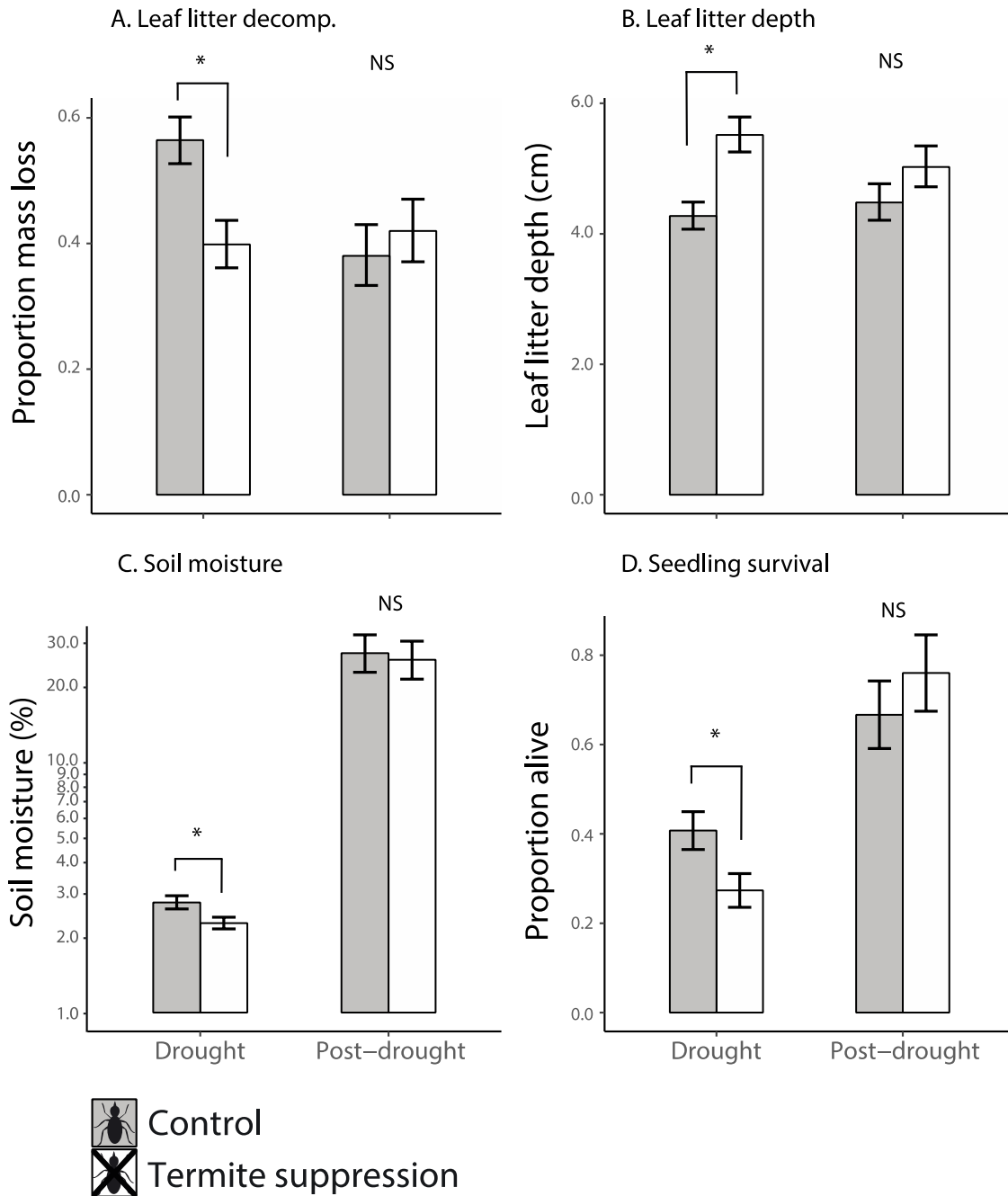
110

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 (Dipterocarpacae)) 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 (ΔAIC = 6), whereas

128 termite suppression did not influence model fit under post-drought conditions (ΔAIC < 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

A. Leaf litter decomp.

B. Leaf litter depth

C. Soil moisture

D. Seedling survival

Control

Termite suppression

138

Fig. 2: The effect of drought and termite suppression on: A. proportion mass loss from open-mesh leaf litter decomposition bags (assessed after remaining on the forest floor for four months); B. forest floor leaf litter depth; C. soil moisture; D. probability of seedling survival. Grey bars are control plots, white bars are termite suppression plots and all bars display mean values ± 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, ΔAIC = 7) but not during post-

153   drought conditions (suppression effect model, ΔAIC < 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.

167

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 (ΔAIC = 3), but not under post-drought

173   conditions (ΔAIC < 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

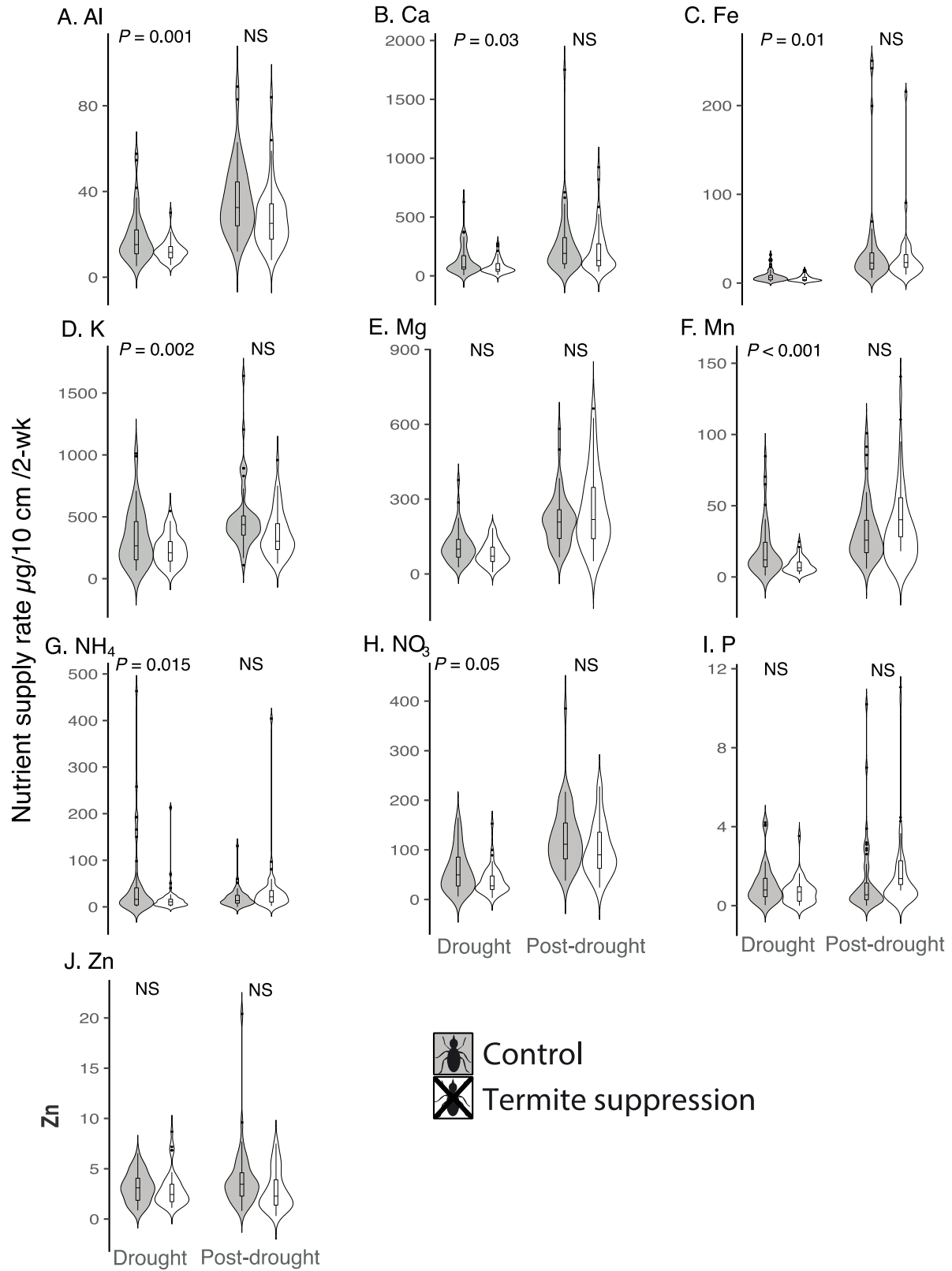175   into the influence of invertebrates on soil processes during drought (*28*).

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 % ± 0.1 during drought compared with ca 25.2 % ± 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 (ΔAIC = 3). Termite

201   suppression had no effect on model fit under post-drought conditions (ΔAIC < 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.

A. Al $P = 0.001$ NS

B. Ca $P = 0.03$ NS

C. Fe $P = 0.01$ NS

D. K $P = 0.002$ NS

E. Mg NS NS

F. Mn $P < 0.001$ NS

G. NH$_4$ $P = 0.015$ NS

H. NO$_3$ $P = 0.05$ NS

I. P NS NS

J. Zn NS NS

Nutrient supply rate μg/10 cm /2-wk

Zn

Drought Post-drought

Control
Termite suppression

208

12

Fig. 3: Extent of variability in A. Al; B. Ca; C. Fe; D. K; E. Mg; F. Mn; G. NH_4; H. NO_3; I. P; J. Zn soil nutrient supply over a 2-week period in control (grey violins) and termite suppression plots (white violins) during drought and post-drought conditions. Plots display (i) density of data estimated by kernel method (shaded areas); (ii) median values (horizontal line in the centre of the boxplots); and (iii) interquartile range (between the top and bottom of the box). Differences in heterogeneity between treatments were assessed using Flinger-Killen test of homogeneity of Variances carried out on the residuals from linear mixed effects models. *P* values denote significant differences between values.

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

13

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

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Termites mitigate the ecosystem-wide effects of drought in tropical rainforest

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Materials and Methods

Experimental design and termite suppression

Our study sites were located in primary tropical lowland rainforest within the Maliau Basin Conservation Area, Sabah, Malaysia. We established four exclusion and four control plots, randomly placed within a 42-ha area (4°44′35″ to 55″ N and 116°58′10″ to 30″E; Fig S2). On the termite suppression plots we added 15 m buffer zones, so the total area treated with insecticide was 80 x 80 m. In order to avoid any edge effects, sampling occurred only within core 50 x 50 m plots. The plots were established in October 2014 and termite suppression was maintained until July 2017. When establishing the termite suppression plots, we physically removed all termite mounds and applied 23ppm (0.00235) imidacloprid (a neonicotinoid motor neuron blocker) solution to the area of soil the mounds had covered. In total we applied between 8 and 38 L of imidacloprid solution to between 0.3 and 5.9 m^2 (0.004-0.091% of the total treated area of each plot), according to the size and number of termite mounds present. Standard domestic toilet paper rolls (TPRs) have been used as baits to monitor termite activity temporally and spatially in the field (*39, 40*). Therefore, to target and suppress termites, we expanded on previous work that tested the efficacy of fipronil treated TPR (*41*) incorporating a novel combination of treated tea bags and TPR, mound destruction and integrated pest management to provide the first large-scale suppression of termite activity in a natural system. We used TPRs sawn in half, and tea bags (TBs, containing *Camillia sinensis*), dunked in 5.7ppm of fipronil solution (a phenylpyrazole insecticide nerve blocker). TPRs absorbed ca. 83ml and TBs absorbed ca. 4ml of solution. We deployed 289 treated half TPRs six times (ca. six monthly), and 500 TBs twice (first year only), applied evenly in a grid across each of the four termite suppression plots; in total we applied ca. 148 L of fipronil solution to the total area over the duration of the experiment (ca. $8mL.m^{-2}.y^{-1}$). After the initial removal of mounds from the plots and application of poison TPRs, we re-poisoned using TPRs every 6 months.

We monitored termite feeding activity on the plots using untreated TPRs, which provide a direct link between the termite suppression and termite resource use. Sixteen untreated TPRs were placed on each plot and were scored for termite attack on a 0 to 5 scale, where 0 is untouched and 5 is completely eaten. After one month, TPR were scored and replaced with a new TPR, in order to have the same baseline starting point for assessment in the subsequent month. Before they were replaced, we recorded the cumulative amount of TPR consumed on each plot and calculated the plot-level cumulative mean attack scores. Using the mean scores from each monitoring event, we calculated a slope for the control and treatment line (using a regression through the origin in each case). From this we estimated consumption rate per month, which was 0.87 units of TPR per month in the control and 0.48 units per month in the treatment. This is the equivalent of 22% toilet roll consumption per month for control plots and 12% per month in the termite suppression plots. This amounts to a steady suppression of activity of 45% (Table S2; Fig. S3B and Fig. S4). To test this difference in cumulative attack rate between the termite suppression and control plots, we carried out an analysis using a linear mixed effect model (lmer) with the interaction between treatment and month as explanatory variables, and square-root transformed cumulative TPR score as the dependent variable. A random slopes model was used (time | plot was specified as the random factor) to account for the lack of temporal and spatial independence caused by repeatedly sampling the same plots.

By applying poisoned TPRs to our termite suppression plots, we were able to target termites without suppressing or poisoning other elements of the ecosystem. This is because termites are amongst the few invertebrate groups that are able to digest cellulose (via their mutualist microbes) (42, 43). Xylophagous beetles do also consume cellulose, but most species utilise the resource in a different way to termites, burrowing into large pieces of deadwood at the larval stage. Therefore, small pieces of poisoned TPR baits are unlikely to attract other invertebrates as a food source (41, 44) and are therefore extremely unlikely to be affected

directly by the termite suppression treatment. To assess this, we sampled non-target leaf litter invertebrates using Winkler bag extractions and tested for the presence of pesticide residues in soil and leaf material on plots using gas chromatography mass spectrometry (GC-MS). In October 2014 June 2015, July 2016 (prior to poisoning and one and two years after initial poisoning), fifteen 1 m^2 leaf litter samples were collected from each plot, and suspended in Winkler bags for three days to extract invertebrates. Generalised linear mixed models (glmer: 'lme4' package) with a Poisson error structure were used to test for any effect of termite suppression on non-target invertebrate abundance within leaf litter samples. Random slopes models were performed on each major taxonomic group with year | plot included as random factors. Poisoning did not have an effect on any of the 14 most common invertebrate groups with mean abundances of > 0.5 individuals per square metre (Table S1, Fig. S3A). However, given that invertebrate groups were not identified to a finer taxonomic scale than order, we cannot rule out the possibility that our treatment had indirect and opposing effects on taxa within the same order.

We sampled soil and seedling material on our termite suppression and control plots to test for environmental contamination associated with our selected pesticides, imidicloprid and fipronil. Five 5 cm^3 soil samples, taken from the top soil layer were collected per plot. Soils were air-dried for 24 hours, homogenised and sieved (2 mm mesh size). In preparation for chemical extraction, a 10 g sub-sample of homogenized soil was extracted using 120 ml methanol:acetonitrile (1:1) and sonicated for 15 minutes. Five seedlings, < 30 cm tall, were also collected per plot. Leaves were shredded and soaked in methanol overnight. Validation soil samples, spiked with fipronil and imidacloprid, were prepared to show that GC-MS analysis was able to detect these pesticides at the doses used in the field. The GC-MS analyses were performed on a Shimadzu 2010 gas chromoatograph coupled to a QP2010 Plus mass spectrometer detector (Shimadzu, Kyoto). An RTX-5MS (30 m × 0.25 mm i.d.) (Restek, Pennsylvania) fused silica capillary column with a 0.25 μm film thickness was used

with helium as carrier gas at a constant linear velocity adjusted to 47.2 cm/sec. One microliter of the sample (1mg/ml) was injected in the high pressure splitless mode at 250 °C with a splitless time before opening the injector valve of 1.5 min. The total run time was 47 min, the interface was kept at 250 °C, the ion source at 200 °C and the mass spectra were obtained at an electron energy of 70 eV. Shimadzu Class VP software (version 2.1) was used to integrate peak areas. In validation analyses, both imidacloprid and fipronil were successfully detected in sim scan mode (Fig. S8A and B). No pesticides were detected in environmental soil or leaf samples from any of the experimental plots (Fig. S8C – F).

Measuring termite abundance and ecosystem processes

To quantify the effect of the suppression treatment on termite community composition, we sampled termites on suppression and control plots in June 2015 and October 2016 using the Jones and Eggleton transect method (*18*). This method uses a 100 m x 2 m belt transect, which is divided into 20, 5m x 1m sections. Each section is sampled for thirty minutes by two trained collectors searching for termites in 12, 12 cm x 12 cm x 10 cm soil pits, and examining all dead wood, leaf litter and trees for the presence of termites. When encountered, termite specimens are collected in 80% ethanol. We placed two, 50 m x 2 m transects diagonally across each plot, totalling 20 hours of human effort for each transect sampling occasion. The species abundances were then weighted by species-specific biomasses and these data were used in a redundancy analysis (RDA) to determine if there was a shift in the termite communities between the control and termite suppression plots. Significance differences between the communities within the termite suppression and control plots were tested using a Monte Carlo permutation test. To assess the relationship between rainfall and termite abundance, we carried out termite transects on control plots every 2 months from March 2016 to December 2016 and also at the beginning and the end of the experimental period in June 2015 and June 2017 (See Fig 1. for sampling dates). Daily total rainfall was collected from Danum Valley forest reserve (4°57′53″ to 55″ N and 117°48′14″ to 30″E) from November 2010 to March 2017. Daily values were used to

calculate total monthly rainfall in the region, and this was used to calculate 3-monthly Standardised Precipitation Index (SPI) (*45*) using the 'SPI' package in R. The SPI is a climatic proxy used to quantify and monitor drought; negative values indicate drier than average conditions that occurred serendipitously during our field-experiment in 2015-2016, while positive values represent wetter than average conditions.

Decomposition rate was assessed using leaf litter decomposition bags. A recent cross site-study of decomposition suggests that leaf chemistry/leaf traits are not a major driver of decay rates in the study region (*46*). Therefore, we used a single-species leaf litter bag approach as we wanted to use a standardized leaf litter across all treatments. We collected freshly abscised *Shorea johorensis* (Dipterocarpaceae) leaf litter from trees close to our experimental plots for use in the decomposition bags. *Shorea johorensis* was selected because it is a common species at the study site and is therefore likely to be broadly representative of decomposition rates. The leaf litter was dried at 60 degrees Celsius until it reached a constant weight. We used 300-micron nylon mesh to produce macroinvertebrate exclusion bags, the closed-bag treatment, and created an open-bag treatment by cutting 10, 1 cm holes in each side of the 300-micron mesh bags to allow access to the material by termites and other macroinvertebrates. This approach avoided any bias due to the 'mesh effect' or microclimate effects from using different mesh sizes (*47*). Each leaf litter bag contained on average 10.5 g ± 0.6 g of dried *Shorea johorensis*. We used three closed-bag and three open-bag treatments on each plot, a total of 48 samples. We left litter bags on the forest floor for 112 days before collection. Bags were placed on plots at the beginning of the 2015 drought (August 2015) and again during the post-drought period (July 2016). The combination of open and closed decomposition bags on termite suppression and control plots allowed us to determine the relative contributions of microbes, termites and other macroinvertebrates to decomposition rates during the drought and post-drought period (Table S3; Fig. S3C and Fig. S8). Proportion mass loss from each bag was logit transformed (because the data were bounded continuous proportions) before performing linear mixed

effect model analyses (lmer from the "lme4" package) to assess if the interaction between plot treatment (termite suppression vs. control) and mesh treatment (open and closed bags) affected the proportion mass loss from decomposition bags. In these models, plot was included as a random factor. In termite suppression plots, litter mass loss did not differ between the open and closed decomposition bags in either the drought or post-drought periods (Table S3; Fig. S8). However, in the control plots, open vs. closed bag treatment did influence leaf litter mass loss, with more mass lost from the open than the closed bags. Given that there was no negative effect of termite suppression on non-termite macro-invertebrates (Table S1), we conclude that other detritivorous invertebrates did not contribute substantially to decomposition of the leaf litter over the time-course of the experiment, nor did they compensate in the absence of termites.

Leaf litter depth: an *in situ* assay of ecosystem-level decomposition was carried out by measuring leaf litter depth during the drought (March 2016) and post-drought (October 2016) periods. Sampling was carried out by research assistants, unaware of treatment type, who used a ruler, placed vertically in the leaf litter, and recorded the highest point the leaf litter reached. Forty leaf litter depth measurements were taken in total per plot in March 2016, with 10 measurements spaced every 3 m across four 30 m transect lines, with each transect being separated by 10 m. In October 2016, a total of sixty measurements were taken per plot, similarly spaced out across a total of six 30 m transect lines. We assessed the effect of treatment on plot-wide *in situ* leaf litter depth using linear mixed effect models (lmer, 'lme4' package); transect was nested within plot and included as random factors. Litter depth was $\log_{10}$ transformed.

Soil moisture was measured using a Delta-T Devices HH2 moisture metre (precise to 0.01 %) in March and October 2016. Soil moisture was recorded at 25 points, spread evenly across each plot in a grid, with each sampling point separated by 5 m from the next point.

Measurements were obtained by instantaneous readings from the top 10 cm of soil. Because rainfall events most commonly occurred in the afternoon, evening and during the night, measurements were taken between 9:00 and 12:00 to standardise, as far as possible, time since rainfall when taking the measurements. No soil moisture measurements were taken if it was raining or had been raining in the morning prior to sampling. Linear models were used to assess the influence of plot treatment on soil moisture during the drought and post-drought conditions. Soil moisture percentage was divided by 100 to give a proportion before logit transformation and plot was included as a random factor.

Plant available soil nutrients: We used Plant Root Simulator (PRS®) resin probes to assess mineralization rates of plant available soil nutrients (NO_3^-, NH_4^+, P, K, Ca, Mg, Mn, Al, Fe, Zn) over a two-week period, during drought and post-drought conditions. In March 2016, we buried two anion and cation probe pairs at a random subsample of 12 points within the 25 sampling grid used to measure soil moisture. In October 2016, four probe pairs were placed at each point of the complete 25 sampling grid. We buried the probe membranes to a depth of 10 cm and left them *in situ* for two weeks, after which they were removed from the soil, cleaned with de-ionized water and analysed by Western Ag Innovations, Saskatoon, Canada. To account for the differences in the number of sampling points used in the different time periods, we resampled 12 points (without replacement) from the full 25 points taken in October and carried out statistical analyses on only these 12 points. We carried out this resampling 10 times and calculated mean test statistics for each soil nutrient. The mean test statistics calculated from models carried out 10 times on 12 resampled points (taken from the full 25 sampling points) are presented in the main text (Fig. 3). The results from the full 25 points and the sub-sampled points are largely the same, with the exception of a significant treatment effect on Manganese in the post-drought period when including all sample points (the non-significant mean subsampled results are presented in the main text). See Table S5 for the mean subsampled and full sample results from the post-drought

period, as well as the results obtained during the drought. Because readings from the probe pairs at each of the sampling points were pooled, we were unable to resample to account for the differences in the number of probe pairs (two versus four) used at each sampling point in drought versus post-drought periods. However, this difference in the number of probes used in each time period does not compromise the validity of our results because we are testing for differences in mineralisation rates between treatments within the same sampling period. In each sampling event (during the drought compared with the post-drought) the number of probes used in each treatment was consistent. We investigated the influence of treatment on plot level mean nutrient supply using linear mixed effect models (lmer, 'lme4' package). Each soil nutrient was analysed in a separate model and plot was included as a random factor. Following (48), we carried out Flinger-Killeen tests of homogeneity of variances to assess if heterogeneity in soil nutrients was equal between the control and termite suppression treatments. To account for our nested experimental design, we first carried out separate linear mixed effects models on each of the soil nutrients, including plot as a random factor, then carried out the Flinger-Killeen tests on the residuals of each model.

Seedling experiment: Seedling mortality was assessed using a seedling transplant experiment. In July 2015, 200 individuals of a leguminous liana, *Agelaea borneensis*, were collected from the forest matrix surrounding our plots. Seedlings were selected from seedling mats resulting from a masting event in 2014. We selected individuals that had only their cotyledons, had not yet developed their first true leaves, and were roughly the same height. We are therefore confident that individuals were all of the same age and developmental stage and that we minimised confounding influences of genetic variability by using individuals from the same conspecific seedling mat. Seedlings were planted in the ground in July 2015 in the same grid of 25 used to assess soil moisture (n = 25 per plot), which was located within the central 50 m sampling area of experimental plots. Each seedling was separated by at least 5 m from the next closest seedling. To minimise the effect of stochastic disturbance-induced mortality as a result of transplantation shock, we

used the number of individuals alive one month after the initial transplant as the baseline abundance. Survival of seedlings during the drought was assessed 11 months after transplantation, in June 2016. Following this assessment, the number of live individuals in June 2016 was used as a new baseline abundance. Survival during post-drought conditions was assessed 12 months later in June 2017. We used two separate binomial generalised linear mixed effects models (glmer: 'lme4' package) to assess if termite suppression affected the likelihood that seedlings survived during the drought year and subsequently during the post-drought year. Seedlings were assigned a 1 if they were alive one year after transplantation and a 0 if they died. In the second glmer, the seedlings that survived the initial year were assigned a 1 if they remained alive in the final assessment and a 0 if they died. Plot was included as a random factor. All analyses were carried out in R version 3.4.3 (*49*); see Fig. 1 for details of all sampling events.

In order to determine the likely impact on carbon dynamics of the observed change in termite-facilitated leaf litter decay, we conducted a simple ecosystem-scale extrapolation using plot-level data on leaf litterfall combined with mass loss rates observed from the leaf litter decomposition experiment. If we assume leaf litterfall in this ecosystem is approximately 5 MgC/ha/yr (*50*) and that all of this leaf litter input is mineralized to CO_2 on an annual basis (*50*), then the amount of leaf litter C emitted as CO_2 during the ENSO was approximately 2 MgC/ha/yr in the termite suppression treatments compared to 2.9 MgC/ha/yr in the controls. This translates into a difference between treatments of almost 1 MgC/ha/yr. Arguably, this simple calculation underestimates the overall contribution of termites to organic matter decay and ecosystem respiration, because our suppression did not remove all termites, and this calculation does not account for the role of termites in wood decay nor the decomposition of soil organic matter, all of which are major components of the terrestrial C cycle.
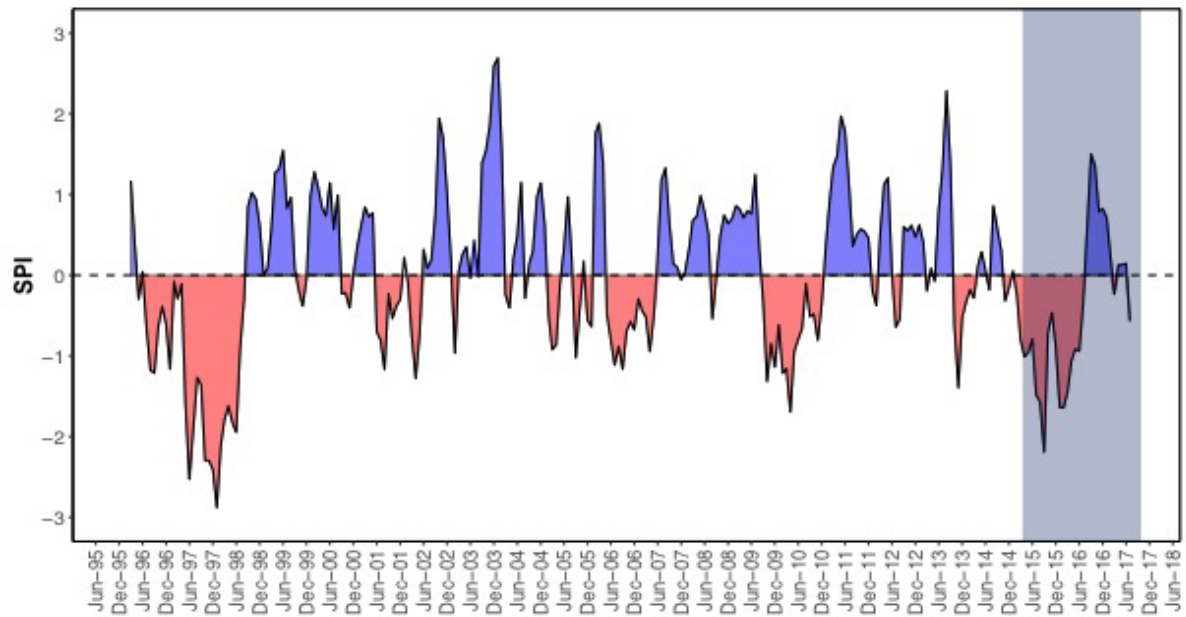
Fig. S1: Three-month standardised precipitation index (SPI) calculated using rainfall data from Danum Valley Conservation Area from 1995-2017. The shaded area shows the experimental period for this investigation, demonstrating that drought is a regular event in the study region.
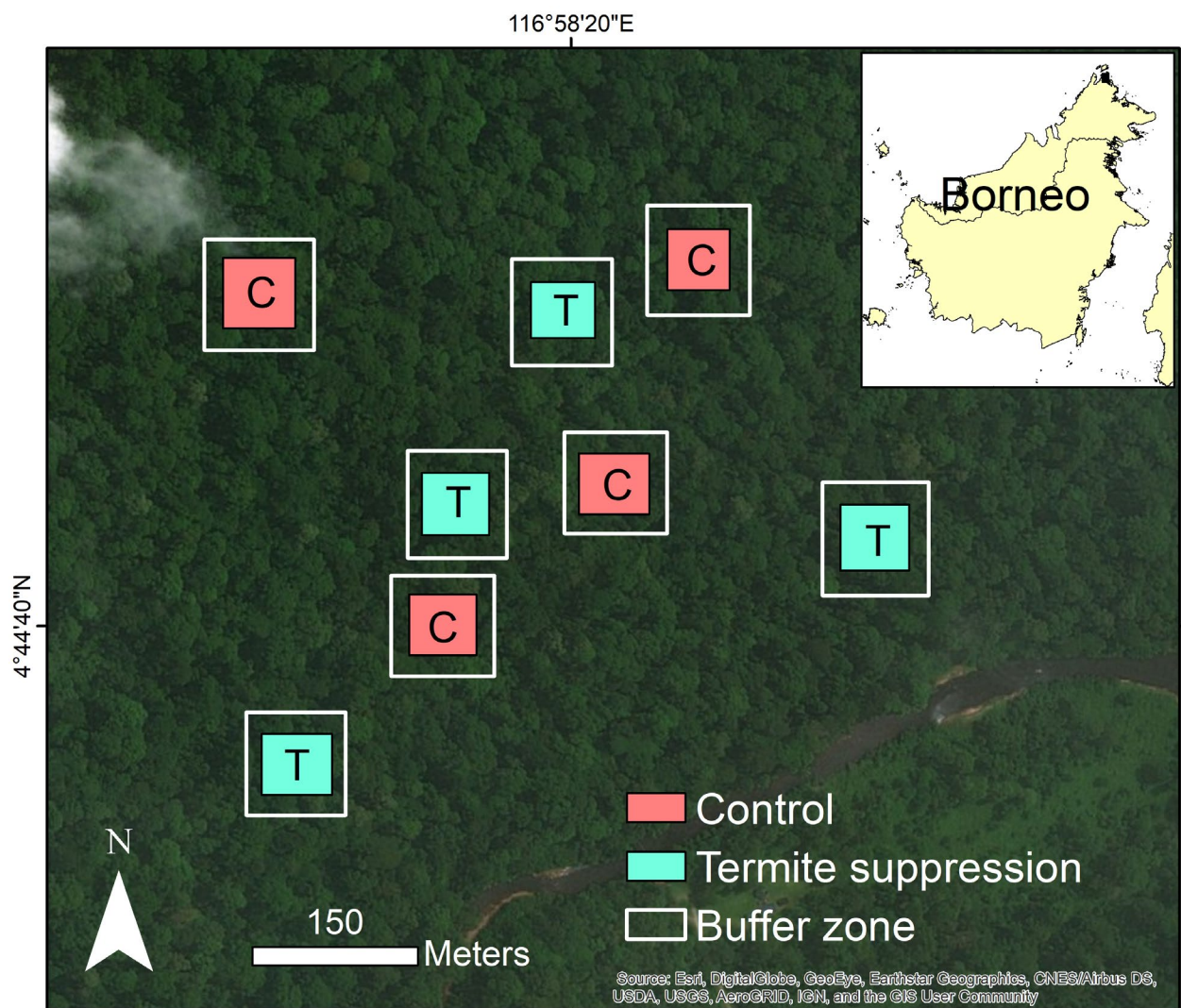
Fig. S2: Schematic layout map of 50 x 50 m (with 15m buffer strips) experimental plots located at Maliau Basin (4°44′35″ to 55″ N and 116°58′10″ to 30″E). Control plots are in red, termite suppression plots are in blue.
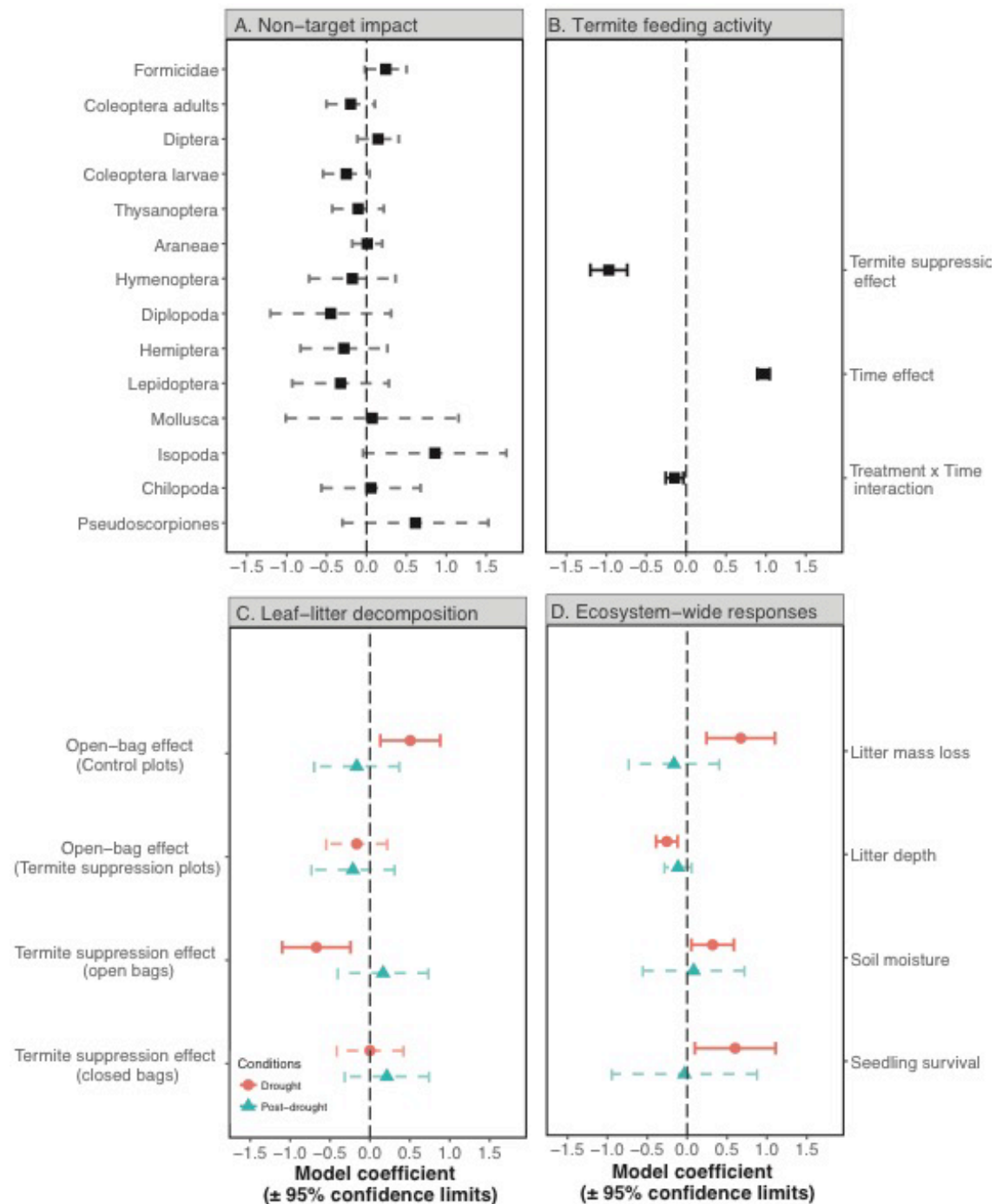
Fig. S3. Results of mixed effects models testing experimental treatment effects on a range of ecological response variables. A. Random slopes, generalised linear mixed effects models (glmer) with a Poisson error distribution, testing the effect of the termite suppression treatment on non-target responses of the 14 dominant leaf litter macroinvertebrate groups. Fifteen, 1 m² litter samples were collected from each of the eight plots in 2015 and 2016 and invertebrates were extracted using Winkler bags over a three-day period. Symbols represent

the glmer model coefficient (± 95% confidence limits) for the difference in mean (log) abundance in termite suppression plots versus control plots (i.e. termites present). Positive values represent higher abundance in suppression plots than control plots. On all panels, solid lines represent effects for which the 95% confidence interval does not overlap zero, indicating a significant treatment effect. B. A linear mixed effects model (lmer) testing the effect of plot treatment (control versus termite suppression) and time on termite feeding activity at cellulose baits. Symbols represent the lmer model coefficients (± 95% confidence limits) for the difference in cumulative toilet paper roll consumption in termite suppression plots versus control plots, and through time (as the experimental period progressed). Negative values represent lower consumption rates in suppression plots than control plots, whereas the positive effect of time demonstrates that more toilet roll was consumed as the experiment progressed through time. C. Lmer testing the effects of plot treatment (control versus termite suppression) and bag treatment (open: macroinvertebrate accessible versus closed: macroinvertebrate inaccessible) on leaf litter mass loss from leaf litter decomposition bags during drought (red symbols) and post-drought (blue symbols) conditions. By comparing the open and closed mesh bags on the control plots (Open bag effect: Control plots), we can assess the contribution of all macroinvertebrates to decomposition. Under drought conditions macroinvertebrates contributed substantially to litter mass loss. Comparison of the open and closed bags on the termite suppression plots demonstrates the contribution of non-termite macroinvertebrates to decomposition (Open bag effect: Termite suppression plots). Because non-termite-macroinvertebrates did not contribute substantially to litter mass loss in either the drought or post-drought conditions, we can compare the open bags on the control plots with the open bags on the termite suppression plots (Termite suppression effect: open bags) to assess the contribution of termites to decomposition. This demonstrates that during drought conditions, termites were responsible for all macroinvertebrate driven decomposition and that this effect disappears during wetter periods. D. Mixed effects models testing the effect of termite presence (control versus termite suppression) on leaf litter mass loss (lmer), leaf litter depth on the forest floor (lmer),

soil moisture (lmer), and seedling survival (glmer) under contrasting drought and post-drought conditions. Symbols represent model coefficients (± 95% confidence limits) and in this case significant positive values show higher litter mass loss, soil moisture retention and seedling survival where termites were present in the drought, while significant negative values show reduced forest floor leaf litter depth where termites were present in the drought.
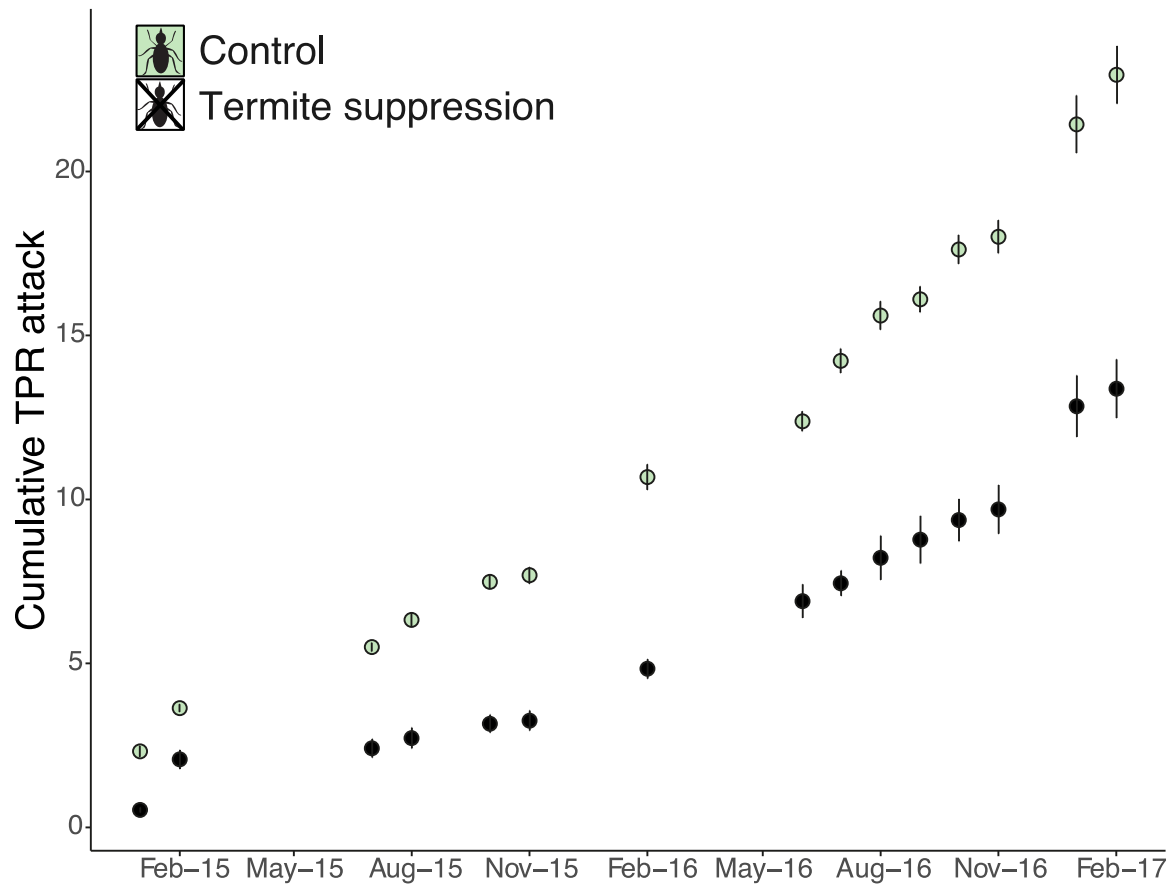
Fig. S4. Cumulative consumption of standardised toilet paper rolls (TPR) by termites in control versus termite suppression plots over the duration of the suppression experiment. Error bars are standard errors for replicate plots in each treatment group. See methods for calculation of attack rates.
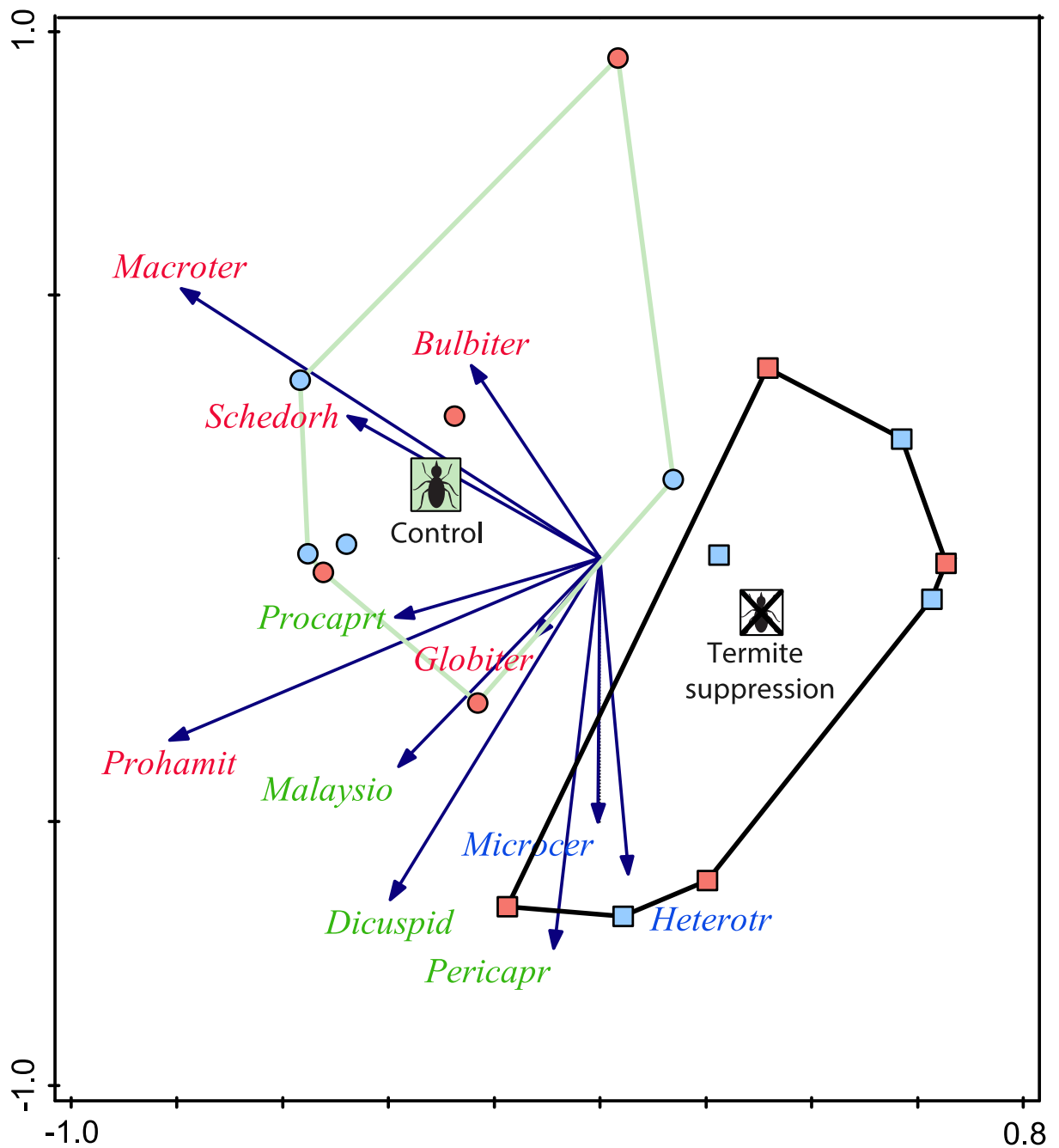
Fig. S5. Principal Components Analysis biplot showing the distribution of termite genera (arrows indicating increasing encounter rates) in relation to control versus termite suppression treatments. Control plots are shown with circles and termite suppression plots with squares (for termite transects conducted in each of the two years; see Methods), and treatment icons indicate the plot centroids in each treatment category. Sampling was carried out once during the drought (June 2015 – red symbols) and once in post-drought conditions (October 2016: blue symbols). The treatment effect was tested using a permutation test

within a Redundancy Analysis (see text). Only axis 1 and 2 are shown, which together explain 55% of the total variation in the data. Genera are colour-coded by feeding guild: Red are wood-feeders; Green are soil feeders and Blue are small-bodied, twig dwelling species. The arrows pointing into the control envelope show that genera that declined with the suppression treatment (e.g. Macroter: *Macrotermes*, Prohamit: *Prohamitermes*) are large-bodied wood feeding termites. Arrows pointing into the treatment envelope show that genera that increased in abundance in response to the suppression treatment (e.g. Microcer: *Microcerotermes*, Heterotr: *Heterotermes*) are small-bodied twig dwelling species. Bulbiter: *Bulbitermes*-group, Dicuspid: *Dicuspiditermes*, Globiter: *Globitermes*, Malaysio: *Malaysiotermes*, Pericapr: *Pericapritermes*, Procaprt: *Procapritermes*, Schedorh: *Schedorhinotermes*
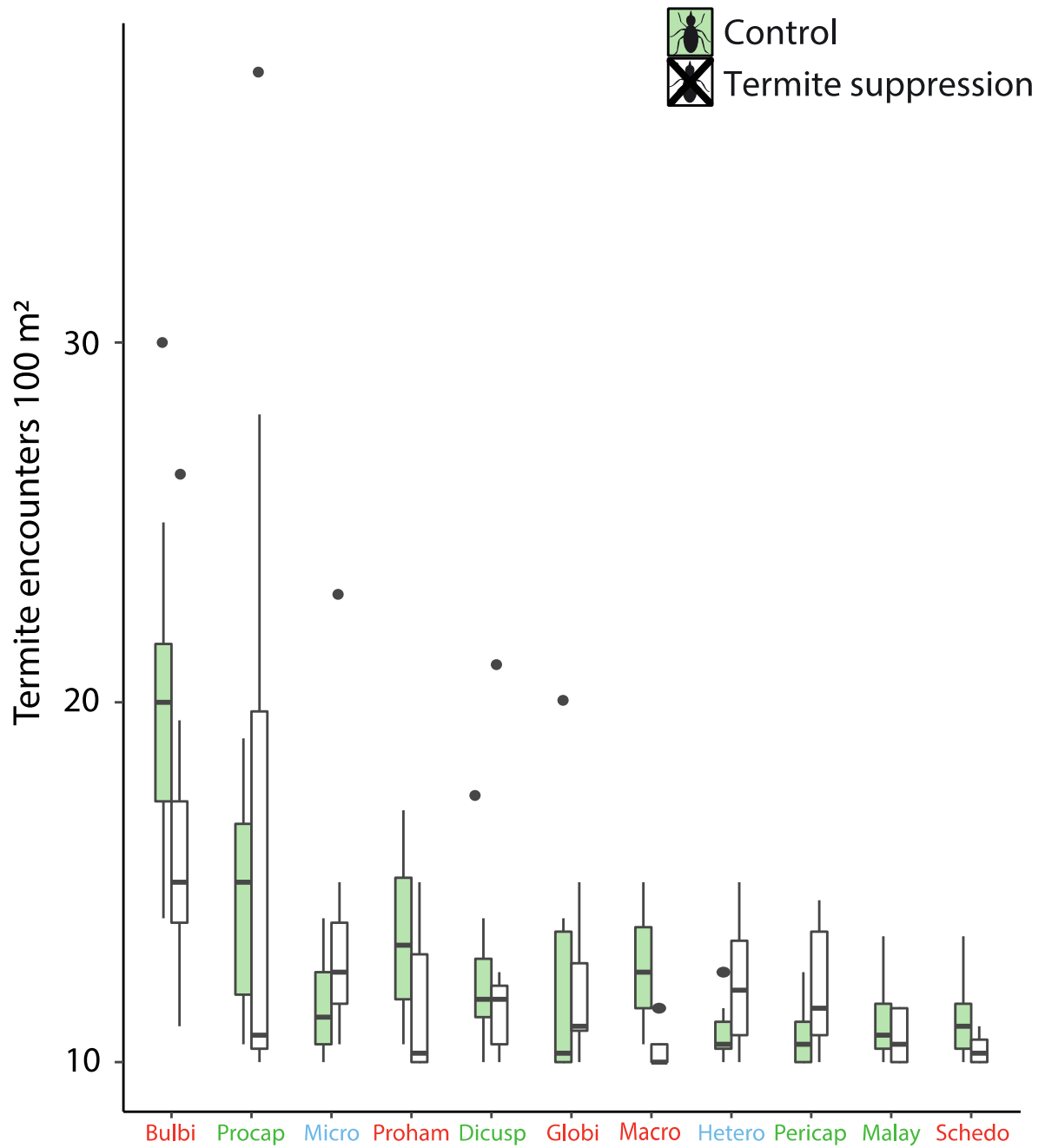
Fig. S6. Median termite genera encounter rates plus interquartile range on control (green boxes) and termite suppression plots (white boxes). Genera are colour-coded by feeding guild: wood-feeders (red); soil feeders (green) and small-bodied twig-dwelling wood feeders (blue).
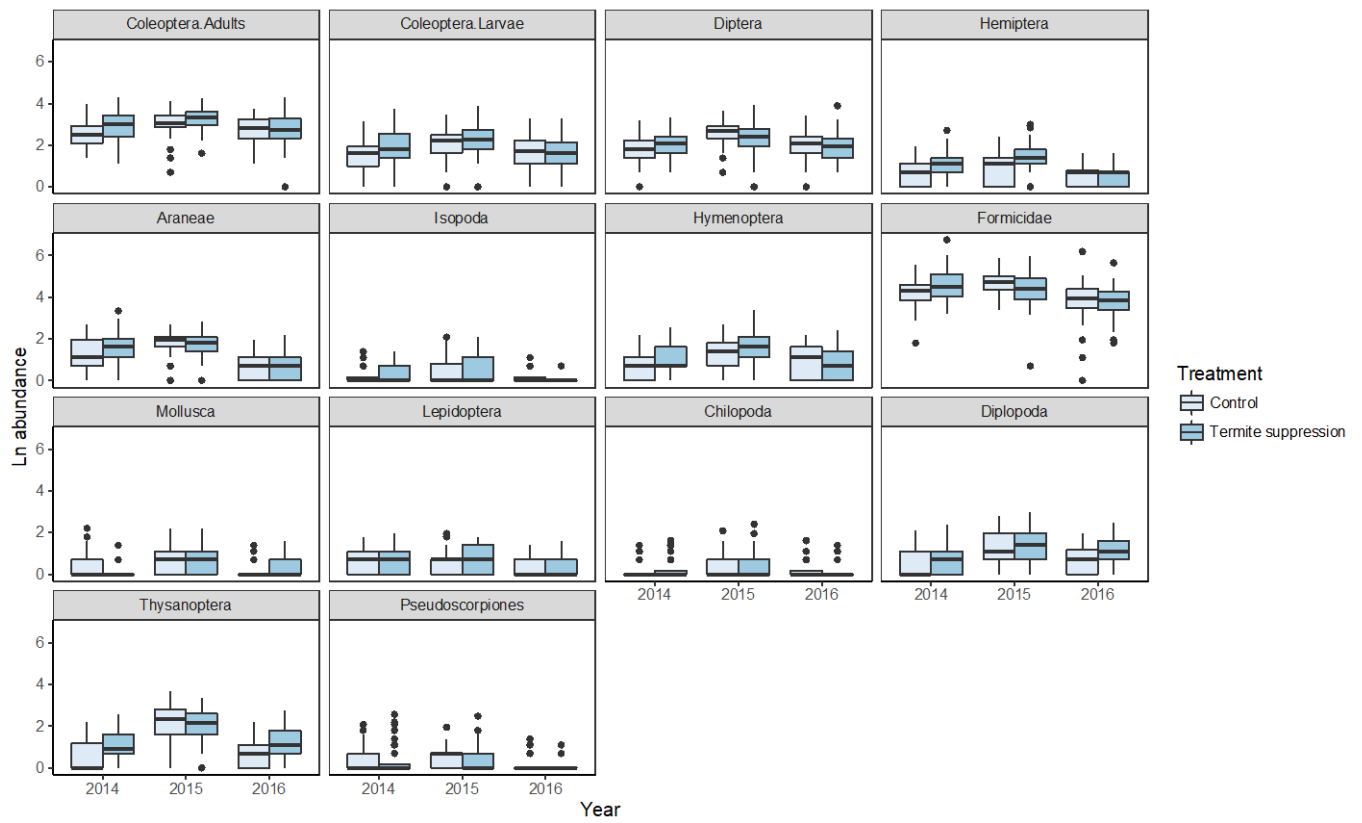
Fig. S7: Ln-transformed median abundances plus interquartile and range of non-target invertebrates sampled from 1 m² leaf litter samples in 2014 (pre-drought and pre-suppression), 2015 (during the drought and the suppression) and 2016 (post-drought).
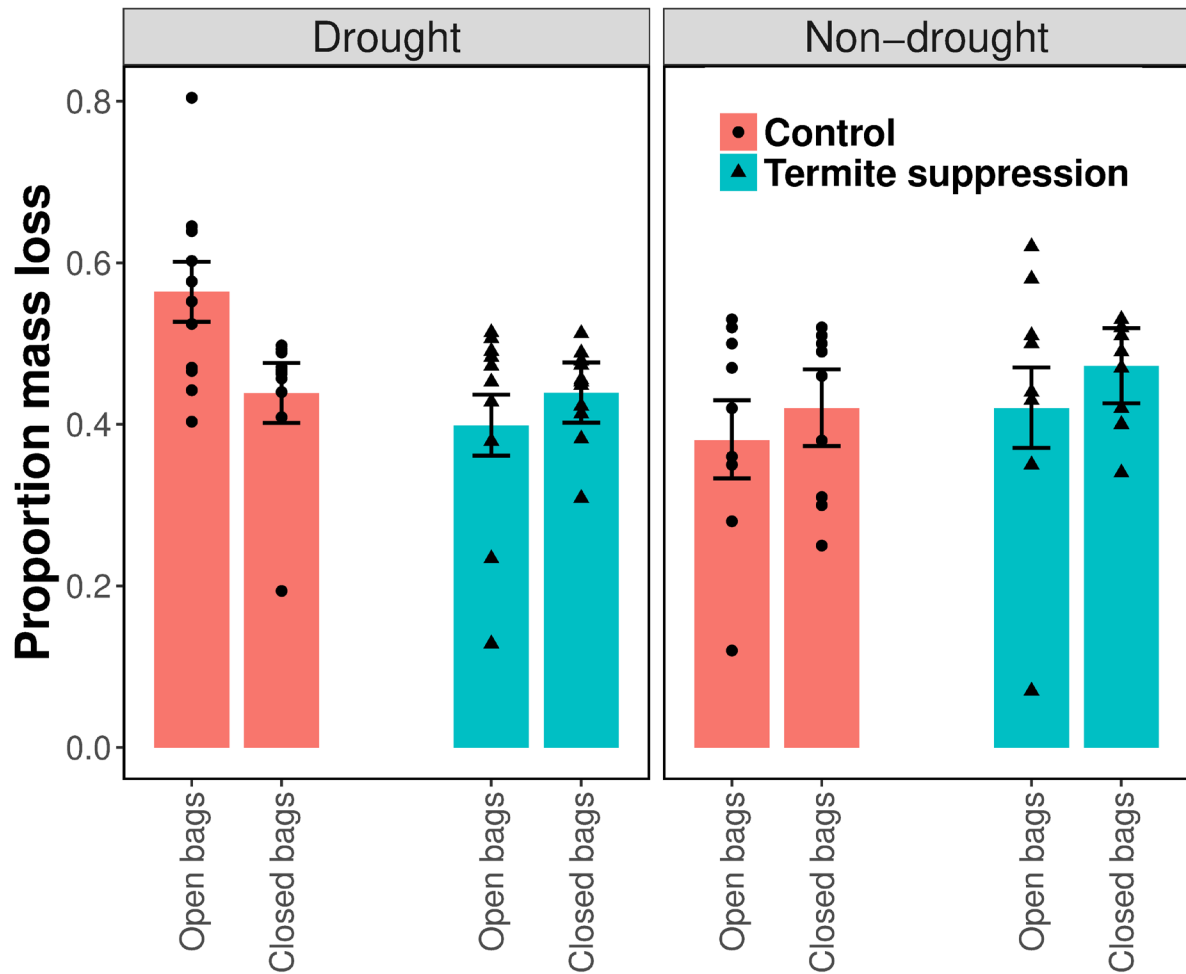
Fig. S8: Mean ± SE proportion mass loss from leaf litter decomposition bags that were accessible (open bags) or inaccessible (closed bags) to macroinvertebrates in control (red bars) and termite suppression (blue bars) plots. The bars show back-transformed mean predicted values from linear mixed effects model outputs using logit-transformed proportion data, and error bars are the back-transformed model SE estimates. The raw data are shown as circles for the control plots and triangles for the termite suppression plots.

A. Imidicloprid
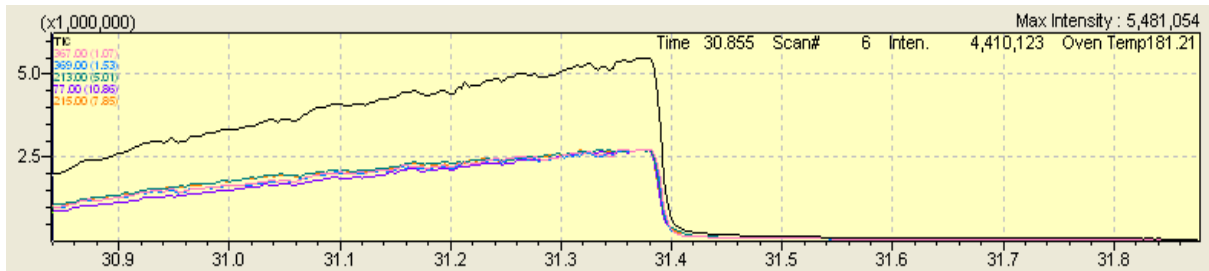
B. Fipronil
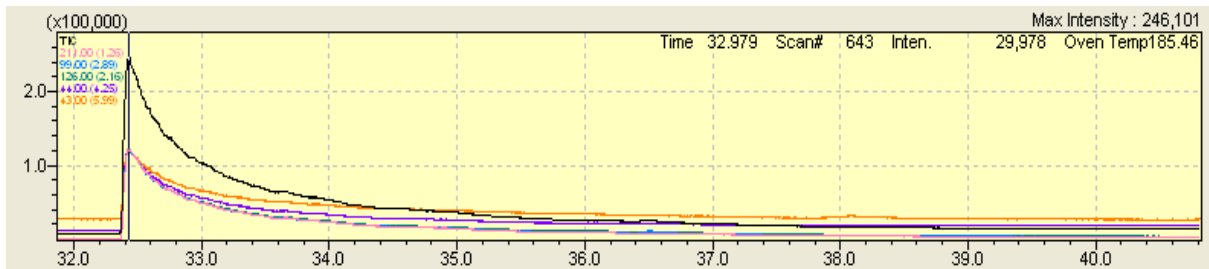
Soil sample example:

C. Imidicloprid
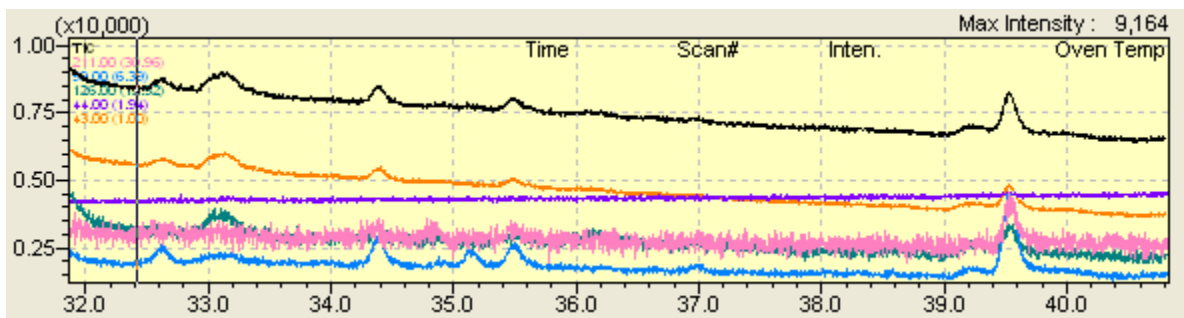
D. Fipronil
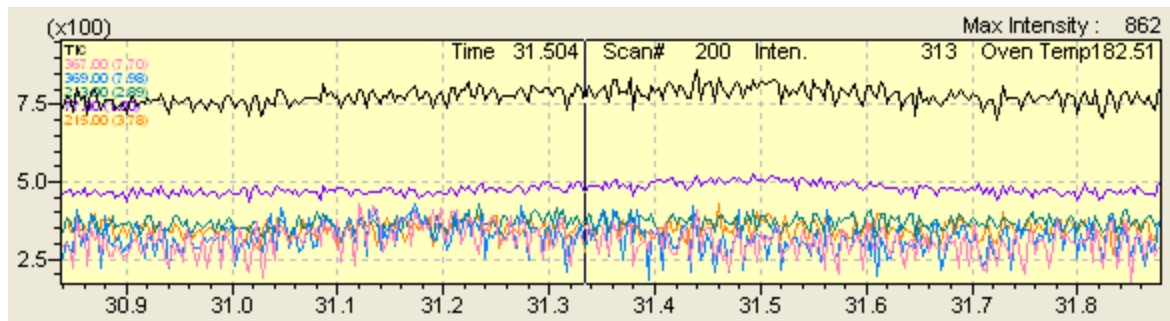
Seedling example:

E. Imidicloprid

F. Fipronil

Fig. S9: A sensitivity analysis demonstrating successful detection in validation analysis of Imidicloprid (A) and Fipronil (B) in soil spiked with known concentrations of compounds, and some example figures of unsuccessful detection of both pesticides in soil (C – D) and seedlings (E – F) taken from both control and treatment plots.

Table S1. Results of random slopes generalised linear mixed effects models testing the effect of termite suppression on the 14 dominant non-termite leaf litter macroinvertebra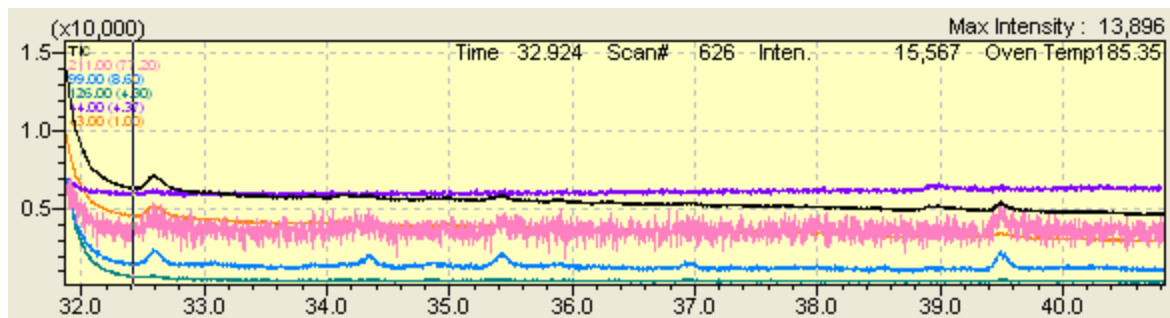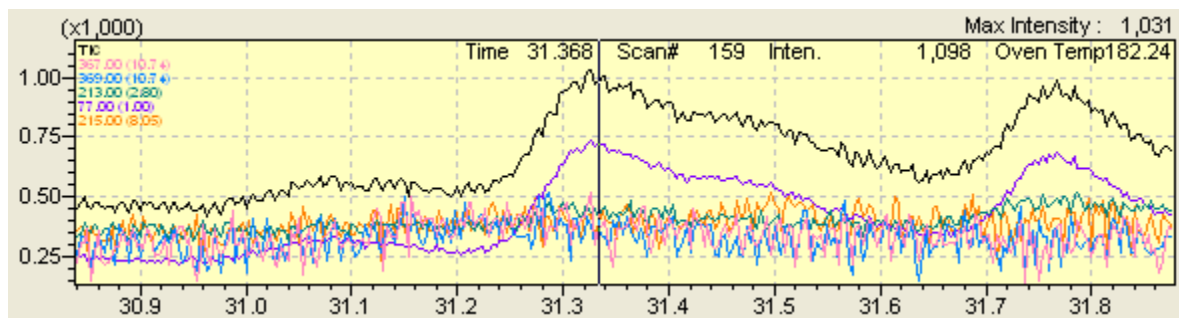te groups (with average abundances of > 0.5 individuals per m^2). Year | plot was specified as a random factor and a Poisson error distribution was used in each model. Fifteen, 1 m^2 litter samples were collected from each of the eight plots in 2015 and 2016 and invertebrates were extracted using Winkler bags over a three-day period. N: total abundance of each taxon across all 240 samples; Mean: mean number of individuals per 1 m^2 leaf litter sample; SE: standard error of the mean from each 1 m^2 sample; Estimate: glmer model coefficient representing the difference in mean (log) abundance in termite suppression plots versus control plots (i.e. termites present); SE: standard error of the estimate. The termite suppression treatment did not have a significant effect on the abundance of any of the non-target organisms.

Group	N	Mean	SE (of mean)	Estimate	SE	z-value
Formicidae	20746	86.4	4.45	-0.241	0.133	-1.819
Coleoptera adults	5364	22.4	0.91	0.199	0.155	1.288
Diptera	2492	10.4	0.51	-0.145	0.132	-1.098
Coleoptera larvae	1879	7.8	0.44	0.253	0.149	1.694
Thysanoptera	1528	6.4	0.48	0.106	0.165	0.638
Araneae	794	3.3	0.20	-0.01	0.096	-0.933
Hymenoptera	769	3.2	0.23	0.178	0.276	0.645
Diplopoda	717	3.0	0.22	0.449	0.387	1.159
Hemiptera	497	2.1	0.19	0.282	0.278	1.014
Lepidoptera	235	1.0	0.08	0.325	0.309	1.049
Mollusca	211	0.9	0.10	-0.071	0.553	-0.128
Isopoda	161	0.8	0.09	-0.857	0.459	-1.867
Chilopoda	159	0.7	0.08	-0.056	0.317	-0.176
Pseudoscorpiones	123	0.5	0.08	-0.613	0.467	-1.311

Table S2. Results of linear mixed effects model (lmer) testing the effect of plot treatment (control versus termite suppression) on termite feeding activity at cellulose baits (see Fig S3B). A random slopes model was used (time | plot was specified as a random factor) to account for the lack of temporal and spatial independence caused by repeatedly sampling the same plots.

	Estimate	SE	df	t value
Intercept (Control)	3.3434	0.0834	110	40.070
Treatment (Termite suppression)	-0.9696	0.1180	6	-8.220
Time	0.9693	0.0402	110	24.120
Termite suppression × Time	-0.1453	0.0568	110	-2.560

Table S3. Results of linear mixed effects models (lmer) testing the effects of plot treatment (control versus termite suppression) and bag treatment (open: macroinvertebrate accessible versus closed: macroinvertebrate inaccessible) on leaf litter mass loss from leaf litter decomposition bags during drought and post-drought conditions.

	Estimate	SE	df	t value
Drought model				
Intercept (Termite suppression; open bags)	-0.4122	0.1576	33	-2.615
Treatment (Control)	0.6715	0.2187	6	3.070
Mesh (closed bags)	0.1666	0.1963	33	0.849
Treatment (Control) × Mesh (closed bags)	-0.6730	0.2741	33	-2.455
Post-Drought model				
Intercept (Termite suppression; open bags)	-0.3233	0.2052	29	-1.575
Treatment (Control)	-0.1649	0.2907	6	-0.567
Mesh (closed bags)	0.2127	0.2666	29	0.798
Treatment (Control) × Mesh (closed bags)	-0.0480	0.3816	29	-0.126

Table S4. Results of mixed effects models testing the effect of plot treatment (control versus termite suppression) on A. forest floor leaf litter depth, B. soil moisture, and C. seedling survival under contrasting drought and post-drought conditions. Linear mixed effects models (lmer) were used for litter depth and soil moisture models, while generalised linear mixed effects models (glmer) with a binomial error distribution were used for seedling survival models.

A. Litter depth

	Estimate	SE	df	t value
Drought model				
Intercept (Termite suppression)	1.7075	0.0487	288	35.100
Treatment (Control)	-0.255	0.0688	6	-3.710
Post-Drought model				
Intercept (Termite suppression)	1.6143	0.0623	431	25.910
Treatment (Control)	-0.114	0.0881	6	-1.302

B. Soil moisture

	Estimate	SE	df	t value
Drought model				
Intercept (Termite suppression)	-4.385	0.0963	191	-45.520
Treatment (Control)	0.3188	0.1360	6	2.340
Post-Drought model				
Intercept (Termite suppression)	-1.2254	0.2306	192	-5.313
Treatment (Control)	0.0813	0.3262	6	0.249

C. Seedling survival

	Estimate	SE	z value
Drought model			
Intercept (Termite suppression)	-0.9775	0.1903	-5.137
Treatment (Control)	0.6028	0.2586	2.331
Post-Drought model			
Intercept (Termite suppression)	0.6932	0.3397	2.041
Treatment (Control)	-0.0339	0.4653	-0.073

Table S5. Results of Fligner-Killeen tests of homogeneity to assess if termite suppression treatment influenced heterogeneity in plant available soil nutrients carried out on all 25 sample points collected in October 2016 (left panel); the mean results from tests carried out 10 times on 12 sub-sampled points (without replacement) from the full 25 sampling points in October 2016 (middle panel); and results from tests carried out on 12 sample points (the full amount sampled during this period) in March 2016 (right panel). The results highlighted in bold indicate where there are differences in the results obtained from using the full and subsampled data; subsampling does not affect the results of any element, except Mn: there was a significant effect of treatment during the post-drought period when using all 25 points, but this disappeared when using the subsampled data.

	October 2016: post-drought				March 2016: drought	
	Results from full 25 sample points		Mean results from 12 sub-sampled points		Results from full 12 sampling points	
Nutrient	Chisq	p	Chisq	p	Chisq	p
Al	2.716	0.099	4.457	0.066	10.45	0.001
Ca	1.387	0.239	2.672	0.291	4.48	0.034
Fe	1.069	0.301	1.172	0.417	6.23	0.013
K	0.278	0.598	0.383	0.634	9.88	0.002
Mg	3.808	0.051	1.702	0.333	1.90	0.168
Mn	**6.281**	**0.012**	**0.440**	**0.597**	18.11	<0.001
NH4.N	2.104	0.147	0.961	0.524	5.97	0.015
NO3.N	1.978	0.160	1.892	0.372	3.71	0.054
P	0.638	0.425	1.298	0.568	3.64	0.056
Zn	0.621	0.431	0.764	0.499	1.24	0.266

Termites Mitigate The Effects Of Drought

Tropical Rainforest in Drought
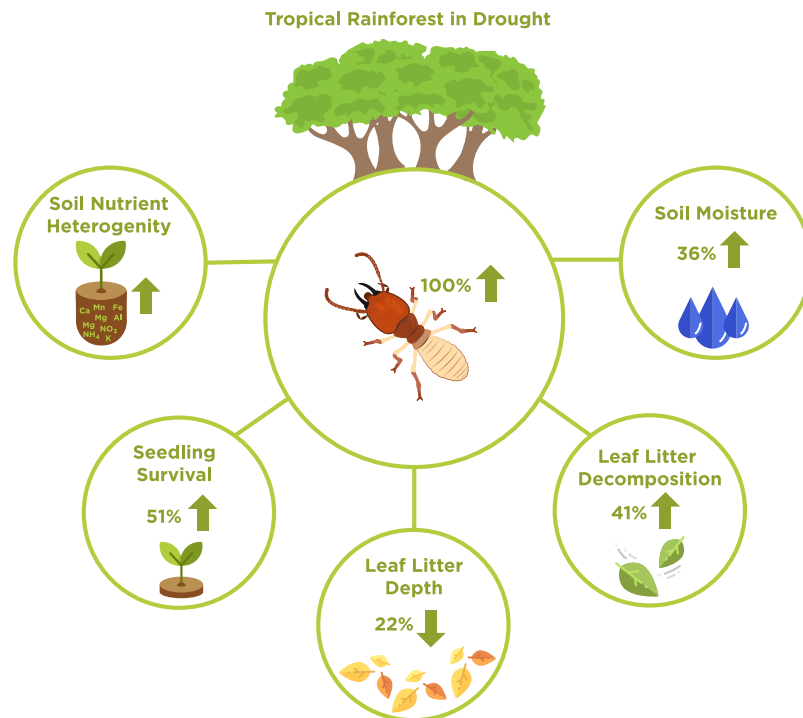
Graphical abstract summarising the results of the investigation. In a tropical rainforest the abundance of termites increased by 100% during drought conditions compared with post-drought conditions. An experimental suppression of termites spanning drought and post-drought conditions showed that this increase in termite abundance had consequences for multiple ecosystem processes and properties. During the drought, intact termite communities on control plots caused increased soil moisture, leaf litter decomposition, soil nutrient heterogeneity and seedling survival compared with termite suppression plots. During post-drought conditions, there were no such differences in these ecosystem processes between control and suppression plots.

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