

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

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

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**Abstract:** Termites perform ecological functions in tropical ecosystems, are affected by variation in rainfall, and respond negatively to habitat disturbance. Yet it is not

known how the projected increase in frequency and severity of drought in tropical rainforests will alter termite communities and the maintenance of ecosystem processes. Using a large-scale suppression experiment, combined with regular monitoring of termite communities, we found that termites increased in activity/abundance during drought in Bornean forest. This resulted in accelerated decomposition, increases soil moisture, soil nutrient heterogeneity, and seedling survival during the El Niño drought of 2015-2016. This work shows how an invertebrate group enhances ecosystem resistance to drought, providing evidence that the dual stressors of climate change and shifts in biotic communities will have negative consequences for the maintenance of rainforest ecosystems.

**Main text:**

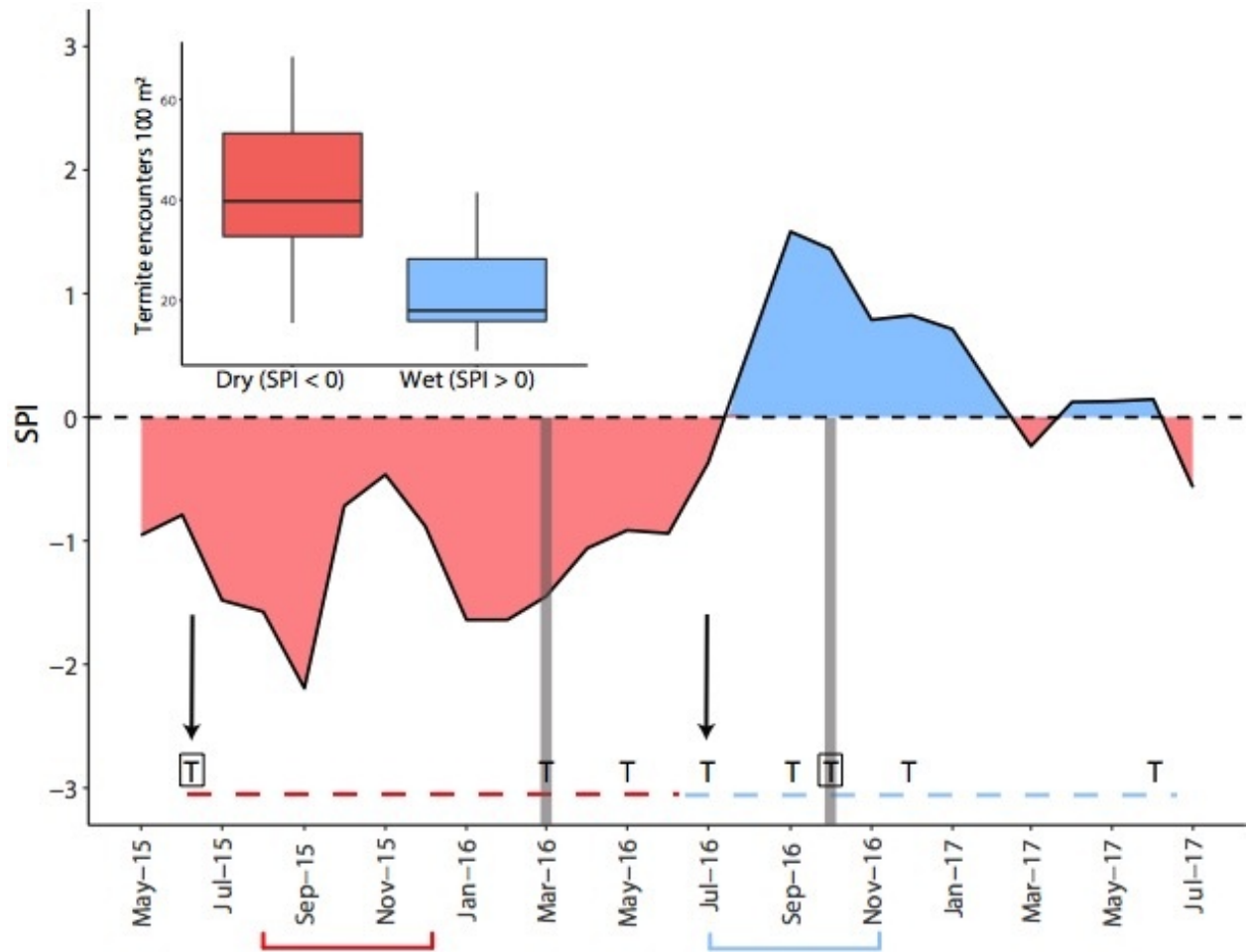
Tropical forests have the highest productivity and biodiversity of any terrestrial system (1). Climate change poses a threat to these ecosystems, with the frequency and intensity of drought events predicted to increase in coming decades (2, 3). Recent research has showed that extreme drought events result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

Termites are an important macroinvertebrate group for ecosystem function (6), with a wide tropical and sub-tropical distribution, from 50° north to 45° south (7). All termite groups have mutualistic relationships with microbes (i.e. groups of bacteria, archaea, protists and/or fungi) allowing them to digest cellulose (8). These mutualistic relationships have helped them to become the dominant invertebrate decomposers. Termites are major ecosystem engineers (6, 8), changing the soil physical environment through bioturbation, decomposing soil organic matter (SOM), wood and leaf litter (9), and facilitating nutrient cycling (8), but their precise contributions to these ecosystem functions have not yet been experimentally quantified at a whole system scale. Termites also regulate soil moisture (and hence the movement of nutrients through mass flow) by transporting water upwards through the soil and decreasing transpiration with their 'sheeting' (temporary above-ground protective structures) (10). These processes are likely to have important effects on plant communities, especially during drought, because soil nutrient availability and heterogeneity influence plant growth and community structure (11), promote plant species diversity (12) and can modulate plant responses to global change drivers (13). Moreover, soil moisture is a key factor determining the magnitude of water stress experienced by plants, directly influencing plant mortality (14). Termites are sensitive to changes in soil moisture and, counter-intuitively, they may be more active and abundant in rainforests during droughts (15). Given their key role in modifying soil environments, an increase in termite activity during extended dry periods could act to maintain soil moisture and soil nutrient flow and have indirect consequences for plant survival. Termites could therefore mitigate the ecological

effects of drought in rainforest systems, as has been shown theoretically for drylands (16).

To address this, we carried out a large scale *in-situ* manipulation (17) of whole termite communities. We suppressed termite activity in old-growth tropical rainforest in Malaysian Borneo, during and after the El Niño drought of 2015-2016 (Fig. 1 and, Fig. S1), alongside regular monitoring of termite communities in control plots.

Critically, this allowed us to assess the relative contribution of termites to ecosystem functioning in drought versus post-drought conditions. Termite suppression was achieved through a targeted approach within quarter-hectare plots by physically removing termite mounds and using poisoned cellulose baits. This reduced termite feeding activity on suppression plots by 45% over the experimental period ( $\Delta AIC = 59$ ; Table S2; Fig. S3 B and S4)) and significantly altered termite community composition (Monte Carlo permutation test within an RDA:  $pseudoF = 23.6$ ,  $P = 0.001$ ; Fig. S5) by reducing the activity of large wood-feeding termites (Fig. S6) over two years (see Methods (18)). The targeted suppression approach reduced termite activity and/or abundance, while other ecosystem components were not directly affected by the poisoning (Table S1, Fig. S3 A). The ability to experimentally manipulate termite activity allowed us to partition the effects of termites from those of other organisms, and test the hypothesis that termites play a crucial role in maintaining ecosystem processes in rainforests during periods of drought.



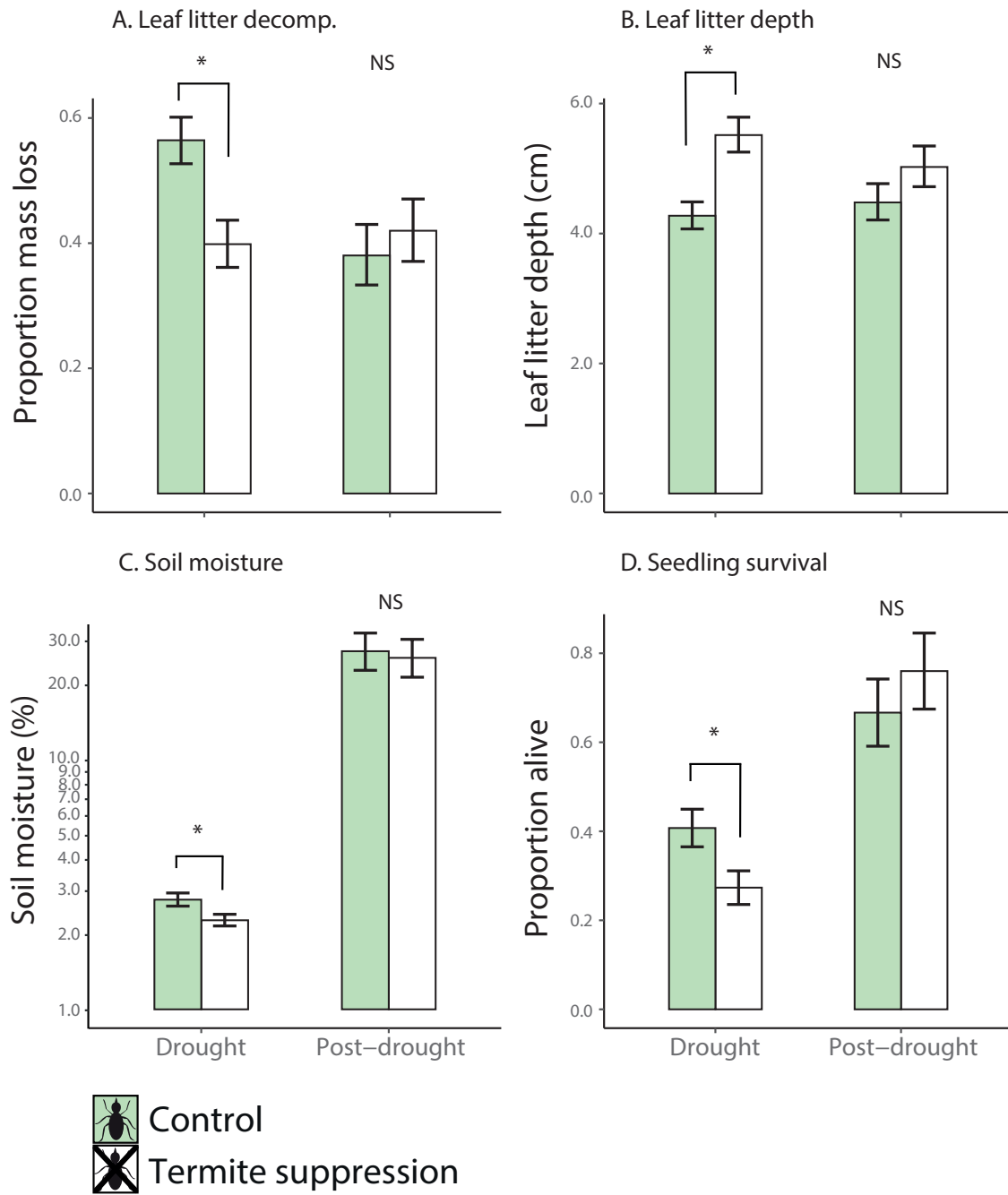
**Fig. 1:** Three-month Standardised Precipitation Index (SPI) calculated using rainfall data from Danum Valley Conservation area for the duration of the study (2015 – 2017). SPI is climatic proxy used to quantify and monitor drought; negative values indicate drier than average conditions that occurred during 2015-2016, while positive values represent wetter than average conditions. 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) conditions, 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 communities; the arrows indicate the non-target invertebrate sampling and collection of soil and leaf material for residue analysis (soil and leaf litter were collected only once, in July 2016); the grey vertical lines indicate the soil moisture, soil nutrient analysis and leaf litter depth sampling events; inset, shows the higher termite encounter rate (median plus interquartile range) during the dry period ( $SPI < 0$ ) compared with the wet period ( $SPI > 0$ ) (assessed using termites transects, which provide relative abundance data).

Termite abundance in standardised survey transects (19) was more than 100% higher during drought compared with post-drought conditions (inset Fig. 1). This drought-induced change in termite abundance in control plots influenced a number of key ecosystem processes and properties, resulting in higher leaf litter decomposition rates, soil nutrient heterogeneity and soil moisture. Termites were responsible for all of the measured macroinvertebrate-driven leaf litter decomposition (See Table S3 and Fig. S3C for a detailed breakdown of microbial, macroinvertebrate and termite contributions to litter decomposition): no other invertebrate group (such as beetles or millipedes) compensated to maintain litter decomposition rates on the termite suppression plots (Fig. S7).

Contrary to previous findings (20), which have focused on microbial decay, we found that the leaf litter decomposition rates of a locally abundant species (*Shorea johorensis* (Dipterocarpaceae)) increased, rather than decreased, during the drought on our unmanipulated control plots (Fig. 2A). We attribute this higher litter decomposition rate to the increased abundance and activity of termites during the drought. We found a 41% higher leaf litter decomposition rate on the control vs. the

suppression plots during drought conditions, with termite suppression contributing substantially to model fit ( $\Delta AIC = 6$ ), whereas termite suppression did not influence model fit under post-drought conditions ( $\Delta AIC < 2$ ; Fig. 2A; Table S3D and Fig. S7). Microorganisms have been seen as the main drivers of decomposition (21), perhaps due to a temperate bias in ecology, where termites are usually absent. Additionally, there is generally a microbial focus in tropical studies where termite effects are not considered (22, 23), and when termites have been included they have not been well discriminated from other non-termite macroinvertebrates (24). Here, we show that termites are also important decomposers in tropical rainforest systems and can actually accelerate litter decomposition during dry periods.



**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. Green bars are control plots, white bars are termite suppression plots and all bars display mean values  $\pm$  SE. Asterisks denote significant differences between values (see Table S3 and S4 for model outputs). Data presented are back-transformed mean predicted values



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

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

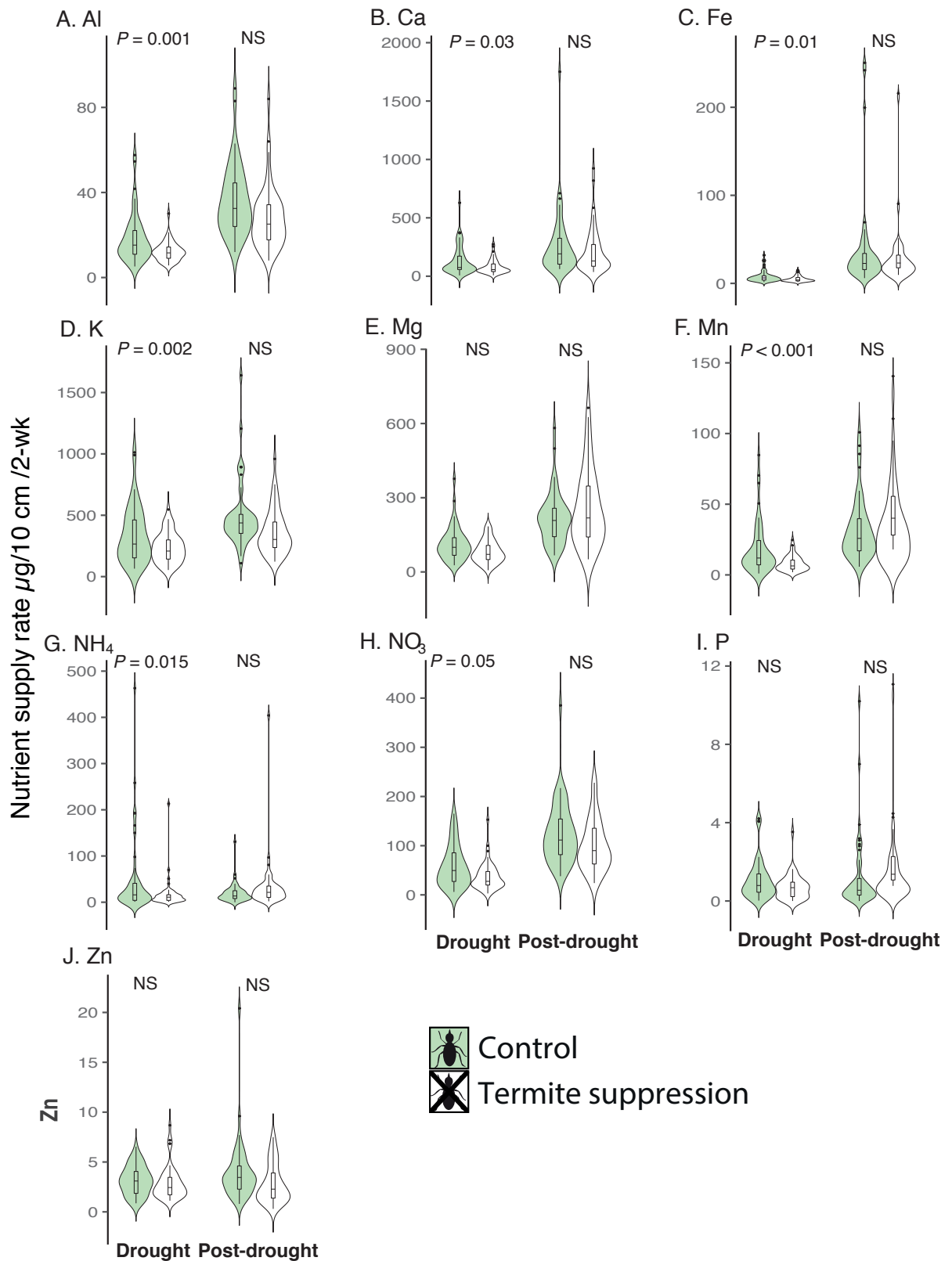
This observed increase in litter cycling represents a previously unmeasured and potentially large contribution by termites to terrestrial carbon flux during drought conditions. Evidence from the 2015-16 El Niño drought has shown a net increase in tropical forest carbon flux compared with post-drought conditions (25), indicating that the increased termite-mediated carbon cycling is not offset by increased carbon uptake from plants. We estimate that termite-driven decomposition of leaf litter could contribute up to 1 MgC/ha/yr during drought periods (18). These findings suggest that present models may underestimate future carbon flux from tropical rainforests (26, 27). Given that termites have also been shown to contribute significantly to decomposition in the New World tropics (28), these results point to termites acting as major components of carbon cycling globally.

As expected, soil moisture was lower on all plots during the drought compared with post-drought conditions. However, the presence of termites contributed substantially to soil moisture retention during the drought. Control plots displayed 36% greater soil moisture than the termite suppression plots at 5 cm (a depth relevant for shallow rooted plants and seedlings) during the drought ( $\Delta AIC = 3$ ), but not in post-drought conditions ( $\Delta AIC < 2$ ; Fig. 2C; Table S4B and Fig. S3D). Strikingly, these termite-driven increases in soil moisture are more than double the effect size reported by previous investigations into the influence of invertebrates on soil processes during drought (29).

Soil nutrient availability (30, 31) and heterogeneity (12) along with other factors (such as light, for example) all contribute to plant productivity, distribution and diversity in rainforest ecosystems. By measuring plant available soil nutrients from multiple subsamples across each plot in the drought and post-drought periods, we show that an increase in termite activity also had consequences for the spatial heterogeneity of soil nutrients (although not for mean plot-level nutrient concentrations, which did not differ significantly between control vs suppression plots under either drought or post-drought conditions, Fig. 3). In the drought, soil nutrient heterogeneity was significantly lower in the termite suppression plots compared with the control plots for nitrate, ammonia, calcium, potassium, iron, manganese and aluminium (Fligner-Killeen test for heterogeneity of variances; Fig. 3). Under post-drought conditions, the suppression of termites did not influence heterogeneity of any of the soil nutrients (except manganese; Fig. 3). This could be a direct effect of the movement of organic material, or an indirect effect of termite activity increasing soil moisture content (or

both). These data imply that termites facilitate the movement of soil nutrients when soil moisture is very low (ca 2.1 %  $\pm$  0.1 during drought compared with ca 25.2 %  $\pm$  0.8 under post-drought conditions, Fig. 2C), leading to a more heterogeneous soil environment.

Seedling survival is often negatively affected by drought and soil desiccation (32). The positive impacts of termites on soil moisture and nutrient heterogeneity could therefore have positive effects for seedling survival. We investigated the possible indirect effects of termite-mediated processes using a transplant experiment to quantify the survival of liana seedlings (*Agelaea borneensis* (Fabaceae)) on our plots during and after the drought. During the drought year, we found 51% higher seedling survival on the control, compared with the termite suppression plots, with the termite suppression treatment contributing substantially to model fit ( $\Delta\text{AIC} = 3$ ). Termite suppression had no effect on model fit under post-drought conditions ( $\Delta\text{AIC} < 2$ ; Fig. 2D; Table S4C and Fig. S3D). Our findings show that termites may buffer seedlings against the negative effects of drought by enhancing soil moisture content and nutrient heterogeneity. Given that extreme droughts are projected to become more frequent and severe with climate change (3), these results suggest that termites will play an increasingly important role in structuring tropical plant communities and maintaining plant productivity and diversity in the future.



**Fig. 3:** Extent of variability in A. Al; B. Ca; C. Fe; D. K; E. Mg; F. Mn; G.  $\text{NH}_4$ ; H.  $\text{NO}_3$ ; I. P; J.

Zn soil nutrient supply over a 2-week period in control (green violins) and termite

suppression plots (white violins) during drought and post-drought conditions. Plots display (i)

the density of data estimated by kernel method (shaded areas); (ii) the median value (horizontal line in the centre of the boxplots); and (iii) the 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. the *Bulbitermes*-group, *Macrotermes*, and *Prohamitermes*, were the genera 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. The mechanisms driving the observed increase in termite activity during droughts are yet to be established, possible explanations could include favourable environmental conditions for tunnelling (such as 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 perception that biota and ecological processes in tropical rainforests are generally negatively affected by drought (e.g. (4)). We show that termites form an essential link between dead plant material and the rest of the ecosystem during dry periods, and no other decomposer

group compensates for the functions they perform. However, it is important to consider the possibility that compensatory post-drought dynamics and legacy effects in system recovery following the severe drought (e.g. 33) could have influenced the post-drought patterns we observed in our measured ecosystem processes. To explore this, future investigations could expand the manipulative termite suppression approach to include multifactorial environmental manipulations (e.g. drought and litter addition experiments) and monitor ecosystem functioning and recovery over longer-term annual cycles. This would allow us to disentangle the role of termites in ecosystem processes following periods of system stress from other confounding environmental factors.

While there have been small-scale manipulative experiments showing the importance of invertebrates in alleviating the effects of drought (29), our large-scale data show that a major invertebrate group maintains ecosystem functioning during periods of drought, with potentially cascading consequences for plant survival during times of environmental perturbations. Forest disturbance is known to reduce termite abundance and diversity (34, 35) and globally, more than 50 % of tropical rainforests have been modified by humans, representing a land area of over 10 million square kilometres (36). Human-modified tropical landscapes are likely to be less resistant to drought, because of a reduction in termite-mediated buffering of ecosystem processes. Our findings indicate that climate change along with human disturbance to biotic communities will have negative, and interacting (37) consequences for the maintenance of functioning rainforest ecosystems. Biodiversity is positively associated with the functioning and stability of ecosystems (36, 37). This study

provides further evidence of the importance of conserving natural ecosystems by showing that intact biological communities can safeguard ecosystem processes in a time of rapid environmental change.

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## Supplementary Materials:

### Materials and Methods

**Fig S1:** Three-month standardised precipitation index (SPI) calculated using rainfall data from Danum Valley Conservation Area from 1995-2017.

**Fig S2:** Map showing the location of experimental plots.

**Fig S3:** Results of mixed effects models testing experimental treatment effects on a range of ecological response variables.

**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.

**Fig. S5:** Principal Components Analysis biplot showing the distribution of termite genera in relation to control versus termite suppression treatments.

**Fig. S6:** Median encounter rates of termite genera sampled in control and termite suppression plots.

**Fig. S7:** Mean  $\pm$  SE proportion mass loss from leaf litter decomposition bags that were accessible or inaccessible to macroinvertebrates in control and termite suppression plots.

**Fig. S8:** A sensitivity analysis demonstrating successful detection of Imidicloprid and Fipronil in soil spiked with known concentrations of compounds, and examples of unsuccessful detection of both pesticides in soil and seedlings taken from both control and treatment plots.

**Table S1:** Results of generalised linear mixed effects models (glmer) with a Poisson error distribution, testing the effect of termite suppression on the 14 dominant non-termite leaf litter macroinvertebrate groups

**Table S2:** Results of linear mixed effects model (lmer) testing the effect of plot treatment on termite feeding activity at cellulose baits.

**Table S3:** Results of linear mixed effects models (lmer) testing the effects of plot treatment and bag treatment on leaf litter mass loss from leaf decomposition bags during drought and post-drought conditions.

**Table S4:** Results of mixed effects models testing the effect of plot treatment on forest floor leaf litter depth, soil moisture, and seedling survival under contrasting drought and post-drought conditions.

**Table S5:** The mean subsampled and full sample results from the post-drought period, as well as the results obtained during the drought from Fligner-Killeen tests carried out to assess the heterogeneity of soil nutrients on experimental plots.