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TROPICAL ECOLOGY

Termites mitigate the effects of drought in tropical rainforest

L. A. Ashton^{1,2,3*}, H. M. Griffiths^{4,*,†}, C. L. Parr^{4,5,6}, T. A. Evans⁷, R. K. Didham^{7,8}, F. Hasan², Y. A. Teh⁹, H. S. Tin¹⁰, C. S. Vairappan¹⁰, P. Eggleton²

Termites perform key ecological functions in tropical ecosystems, are strongly affected by variation in rainfall, and respond negatively to habitat disturbance. However, it is not known how the projected increase in frequency and severity of droughts in tropical rainforests will alter termite communities and the maintenance of ecosystem processes. Using a large-scale termite suppression experiment, we found that termite activity and abundance increased during drought in a Bornean forest. This increase resulted in accelerated litter decomposition, elevated soil moisture, greater soil nutrient heterogeneity, and higher seedling survival rates during the extreme El Niño drought of 2015–2016. Our work shows how an invertebrate group enhances ecosystem resistance to drought, providing evidence that the dual stressors of climate change and anthropogenic shifts in biotic communities will have various negative consequences for the maintenance of rainforest ecosystems.

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 droughts predicted to increase in coming decades (2, 3). Research has shown that extreme droughts cause increased tree mortality (4), which has implications for forest structure and functioning. Microbial decomposition and the movement of nutrients through soil are also thought to decrease during droughts because dry conditions reduce activity of microorganisms (5). Together, these disturbances suggest ecosystem-wide effects of increasing drought frequency and severity. However, we know little about how drought-mediated changes in invertebrate communities 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 subtropical distribution, from 50°N to 45°S (7). All termite groups have mutualistic relationships with microbes (i.e., groups of bacteria, archaea, protists, and/or fungi), which enable them to digest cellulose (8). These mutualistic relationships have helped termites become dom-

inant invertebrate leaf litter and dead wood decomposers. Termites are major ecosystem engineers (6, 8) that change the soil physical environment through bioturbation, decomposition of soil organic matter (e.g., wood and leaf litter) (9), and facilitation of nutrient cycling (8), but their contributions to these ecosystem functions have not yet been experimentally quantified. Termites also regulate soil moisture (and hence the movement of nutrients through mass flow) by transporting water upward through the soil and decreasing transpiration with their “sheeting” (temporary aboveground protective structures) (10). These processes are likely to affect plant communities, especially during drought, because soil nutrient availability and heterogeneity influence plant growth and community structure (11) and promote species diversity (12). Moreover, soil moisture is a key factor determining the magnitude of water stress experienced by plants, which directly influences plant mortality (13). Termites are sensitive to changes in soil moisture and, counterintuitively, they may be more active and abundant in rainforests during droughts (14). Given their key role in modifying soil environments, an increase in termite activity during extended dry periods could help to maintain soil moisture and soil nutrient flow and could 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 (15).

To investigate this potential mitigation, we carried out a large-scale in situ manipulation (16) of 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), and monitored termite communities in control plots. This experimental approach 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. The suppression reduced termite feeding activity on plots by 45% [Δ AIC = 59 (AIC, Akaike information criterion)] (table S2 and figs. S3B and S4) and significantly altered termite community composition (Monte Carlo permutation test within a redundancy analysis: pseudo F = 23.6, P = 0.001) (fig. S5) by reducing the activity of large wood-feeding termites (fig. S6) over 2 years (17). The targeted suppression did not, however, affect other invertebrate groups (table S1 and figs. S3A, S7, and S9). This experimental manipulation allowed us to partition the effects of termites from those of other organisms and to test the hypothesis that termites play a crucial role in maintaining ecosystem processes in rainforests during periods of drought.

Termite abundance in standardized survey transects (18) in control plots was more than twice as high during drought than in post-drought conditions (Fig. 1, inset). This drought-induced change in termite abundance 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 compensated to maintain litter decomposition on the termite suppression plots (fig. S8).

Contrary to previous findings (19), which have focused on microbial decay, we found that leaf litter decomposition rates of a locally abundant species [*Shorea johorensis* (Dipterocarpaceae)] increased, rather than decreased, on our control plots during the drought (Fig. 2A). We attribute this higher litter decomposition rate to the increased abundance and activity of termites during the drought. We found that the leaf litter decomposition rate increased by 41% on the control plot versus the suppression plot during drought conditions, with termite suppression contributing substantially to model fit (Δ AIC = 6), whereas termite suppression did not influence model fit under post-drought conditions (Δ AIC < 2) (Fig. 2A, table S3D, and fig. S8). Microorganisms are typically assumed to be the main drivers of litter decomposition (20), perhaps owing to a temperate bias in ecology, as termites are usually absent in temperate climates. Additionally, there is generally a microbial focus in tropical studies where termite effects are not considered (21, 22); in studies where termites have been included, they have not been well discriminated from other non-termite macroinvertebrates (23). Here, we show that termites are important decomposers in tropical rainforest systems and can actually accelerate litter decomposition during dry periods.

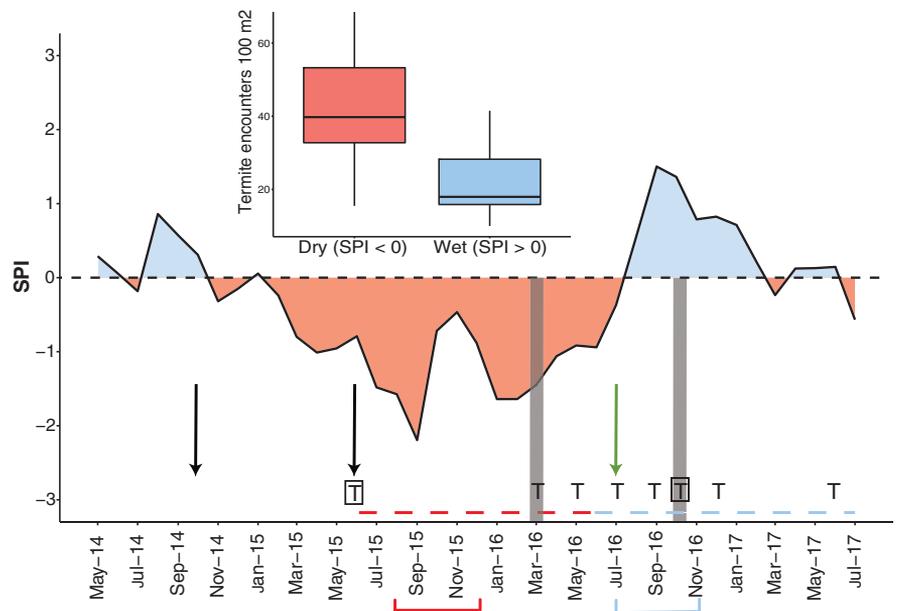
As might be predicted from the observed increase in decomposition rates during the drought period, leaf litter depth was lower, by 22%, on the control plots (where intact termite communities were present) compared with suppression plots (Fig. 2B, table S4A, and fig. S3D). This greater

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Fig. 1. Drought status during the study and timings of experiments. Three-month standardized precipitation index (SPI) calculated using rainfall data from Danum Valley Conservation Area for 1 year preceding and the 2-year duration of the study (2014–2017). SPI is a climatic proxy used to quantify and monitor drought; negative values indicate drier-than-average conditions and positive values indicate wetter-than-average conditions. See fig. S1 for a 20-year SPI plot of the region. Brackets below the x axis show the duration of the litter decomposition experiments during the drought (red) and post-drought (blue), which were in place for 4 months during the drought and post-drought periods. 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 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 black arrows indicate invertebrate sampling pre-drought and pre-termite suppression (2014) and during the drought and suppression (2015). The green arrow represents invertebrate sampling post-drought during the suppression (2016), as well as the collection of soil and leaf material for pesticide residue analysis. The gray bars indicate the soil moisture, soil nutrient analysis, and leaf litter depth sampling events. The 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 termite transects, which provide relative abundance data).



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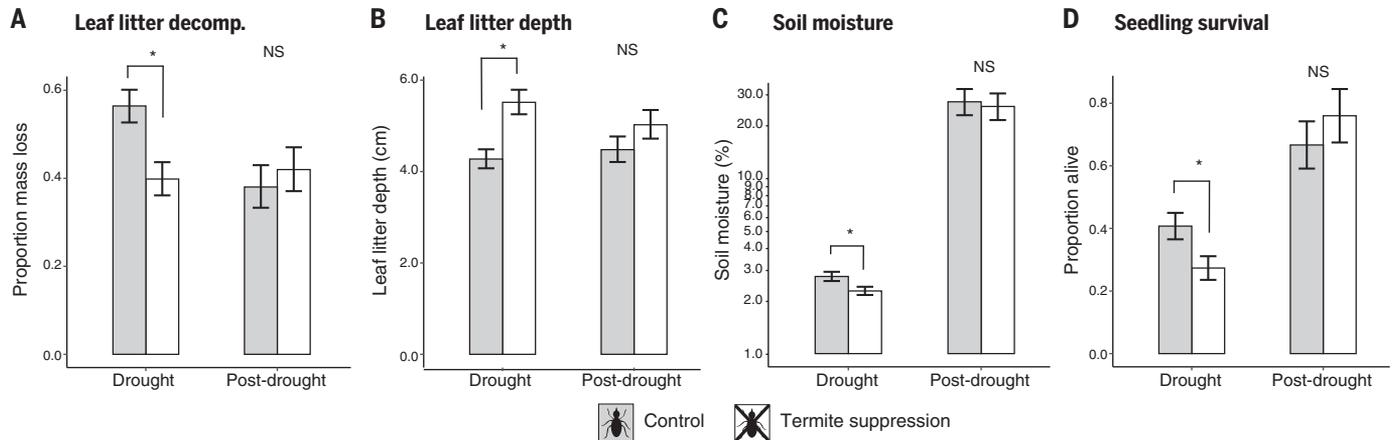


Fig. 2. The effect of drought and termite suppression on four ecosystem responses. (A) Proportion mass loss from open-mesh leaf litter decomposition bags (assessed after remaining on the forest floor for 4 months), (B) forest floor leaf litter depth, (C) soil moisture, and (D) proportion of seedlings surviving. Gray bars and white bars represent control plots and termite suppression plots, respectively,

and all bars display mean values \pm SE. Asterisks denote significant differences between values (see tables 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 (C) is presented on a \log_{10} scale for ease of interpretation. NS, not significant.

accumulation of leaf litter on suppression versus 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 2015–2016 El Niño drought showed a net increase in tropical forest carbon flux compared with post-drought conditions (24), indicating that the increased termite-mediated carbon cycling is not offset by increased carbon uptake by plants. We estimate that termite-driven decomposition of leaf litter could contribute up to $1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ during drought periods (17). These findings suggest that present models may underestimate future carbon flux from tropical rainforests (25, 26). Given

that termites have also been shown to contribute measurably to decomposition in the New World tropics (27), these results point to termites acting as a major component 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. At 5 cm (a depth

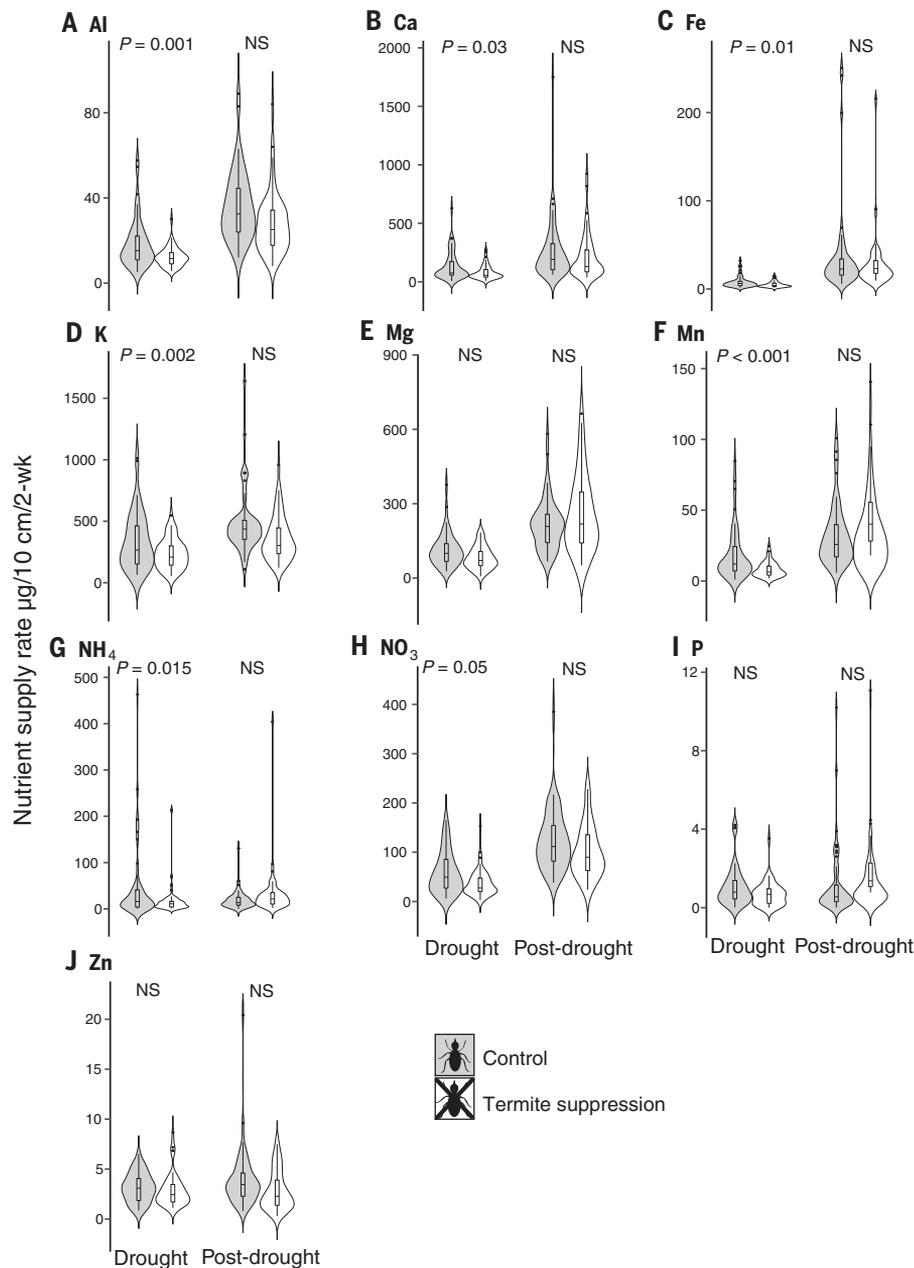


Fig. 3. The effect of drought and termite suppression on soil nutrient heterogeneity. Extent of variability in (A) Al, (B) Ca, (C) Fe, (D) K, (E) Mg, (F) Mn, (G) NH₄, (H) NO₃, (I) P, and (J) Zn soil nutrient supply over a 2-week period in control (gray violins) and termite suppression plots (white violins) 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 center of the boxplots), and (iii) interquartile range (between the top and bottom of the box). Differences in heterogeneity between treatments were assessed using Fligner-Killeen test for homogeneity of variances carried out on the residuals from linear mixed effects models. *P* values denote significant differences between values.

relevant for shallow rooted plants and seedlings), control plots displayed a 36% increase in soil moisture compared with the termite suppression plots during the drought ($\Delta\text{AIC} = 3$) but not under post-drought conditions ($\Delta\text{AIC} < 2$) (Fig. 2C, table S4B, and fig. S3D). 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 (28).

Soil nutrient availability (29, 30) and heterogeneity (12) 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 and 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 aluminum (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. This could be a direct effect of the movement of organic material and/or an indirect effect of termite activity increasing soil moisture content. These data imply that termites facilitate the movement of soil nutrients when soil moisture is very low ($\sim 2.1\% \pm 0.1$ during drought, compared with $\sim 25.2\% \pm 0.8$ under post-drought conditions) (Fig. 2C), leading to a more heterogeneous soil environment.

Seedling survival is often negatively affected by drought and soil desiccation (31). The positive impacts of termites on soil moisture and nutrient heterogeneity could therefore have positive effects for seedling survival. We investigated this 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 a 51% increase in 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 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.

This study shows that termite activity increases in rainforests during dry conditions and that termites buffer important soil processes of consequence to 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., species belonging to *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 favorable environmental conditions for tunneling (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 perception that biota and ecological processes in tropical rainforests are negatively affected by drought (4). We show that termites form an essential link between dead plant material and the rest of the ecosystem during dry periods and that no other decomposer group compensates for the functions that termites perform.

This study is constrained by a relatively short duration, and it is possible that legacy effects in system recovery after the severe drought (32) could have influenced the post-drought patterns we observed. However, pre-drought abundances of non-termite invertebrates were comparable to post-drought abundances (fig. S7), indicating that our post-drought data are likely to be representative of the non-drought-stressed system. Future investigations could expand the manipulative termite suppression approach to include multifactorial environmental manipulations (e.g., drought and litter addition experiments) and monitoring of 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.

Although small-scale manipulative experiments have shown the importance of invertebrates in alleviating the effects of drought (28), our large-scale data show that a major invertebrate group maintains ecosystem functioning during periods of drought, with potentially cascading consequences for plant survival. Forest disturbance is known to reduce termite abundance and diversity (33, 34) and, globally, more than 50% of tropical rainforests have been modified by humans: an area of more than 10 million square kilometers (35). Tropical landscapes that are heavily modified by human disturbance are likely to be less resistant

to drought, because of a reduction in termite-mediated buffering of ecosystem processes. Our findings suggest that climate change, along with human disturbance to invertebrate communities, will have negative and interacting (36) consequences for the maintenance of functioning rainforest ecosystems. 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

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Forest termites mitigate the effects of drought

In many tropical regions, where drought is predicted to become more frequent in the coming years, termites are key components of ecosystem function. Ashton *et al.* experimentally manipulated termite communities to quantify their role during the 2015–2016 "super El Niño" drought in a Malaysian tropical rainforest. Termite relative abundance more than doubled in control plots during drought, maintaining three major ecosystem processes: decomposition, nutrient heterogeneity, and moisture retention. Seedling mortality increased where termites were suppressed.

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