

Correspondence

Termites can decompose more than half of deadwood in tropical rainforest

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Globally, an estimated 73 ± 6 Pg of carbon is contained in deadwood, representing roughly 30 times the amount of carbon sequestered by forests annually [1]. Decomposition transfers this carbon to the soil, other organisms or the atmosphere [2], but it is not clear how different biological agents contribute to the decomposition process. Using a novel large-scale termite suppression experiment in old growth tropical forest, we quantify, for the first time, the relative contribution of microbes and termites to deadwood decomposition. Contrary to prevailing understanding, we demonstrate that termites can be responsible for the majority of wood mass loss. Using a dead wood decomposition assay, we found termites were responsible for 58–64% of total mass loss, while microbes carried out 36–42%. Tropical forests are globally important for biodiversity and ecosystem service provision, yet climate change and habitat conversion [3] threaten the functioning of these forests with repercussions for the global biosphere [4]. Our study demonstrates that termite-mediated deadwood decay must be included in global carbon models. These findings will consequently help improve the accuracy of Earth-system models and climate forecasts in the face of global change.

Dead wood is a huge store of carbon because few organisms have evolved to digest its main components, cellulose and lignin, the most abundant biomolecules on earth. Microbes are often cited as the primary drivers of wood decomposition, with invertebrates frequently considered secondary in wood decay [2,5].

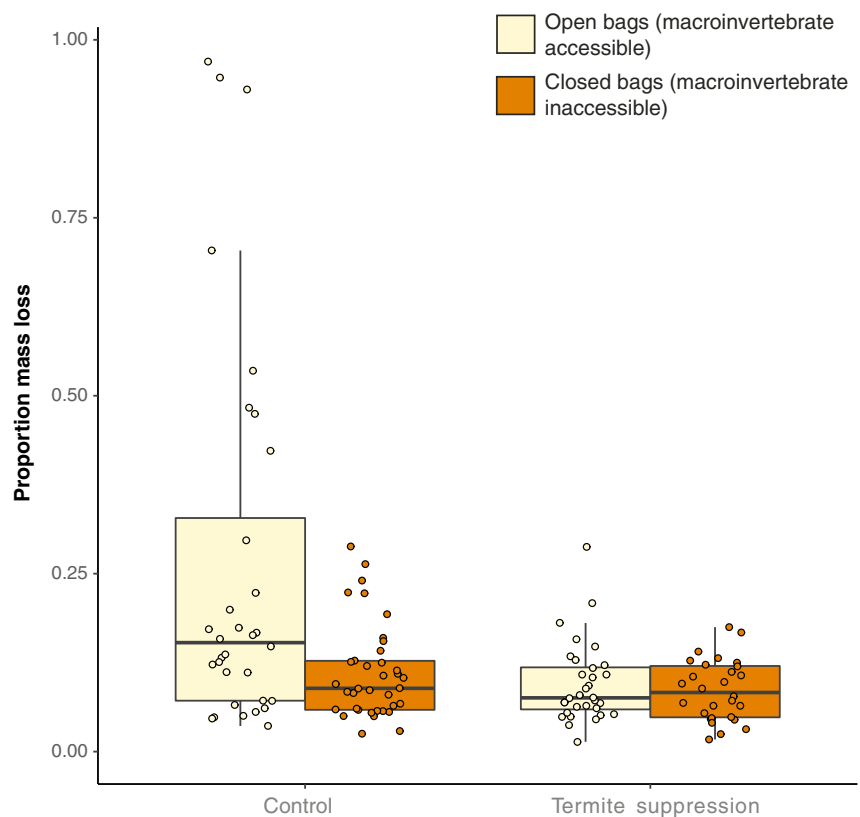


Figure 1. Effect of termites on dead wood decomposition.

The median plus interquartile range for mass lost from macroinvertebrate accessible (yellow bars) or macroinvertebrate inaccessible (brown bars) wood blocks within control and termite suppression plots. The termite suppression had a significant effect on decomposition (control open bags vs. termite suppression open bags: z value = -2.7 , $P = 0.03$). Raw data are displayed over the boxes to show variability in mass loss.

Termites are known to be important for wood decomposition (reviewed in [5]), and can be highly abundant, reaching densities of up to 10,000 individuals per m^2 [6]. However, despite an extensive body of literature into the role of termites and other invertebrates as decomposers, their specific contribution to wood decomposition is yet to be quantified within an experimental framework that specifically manipulates the abundance of termites. Factors involved in wood decomposition are poorly understood at a global scale [7], although it is known termites are sensitive to climatic variability [8] and habitat disturbance [9]. Therefore, a more precise understanding of the role of termites in tropical deadwood decomposition is essential to better predict the consequences of anthropogenic disturbances for global carbon budgets and climate feedback.

To quantify the relative contributions of microbes and termite decomposition, we established a large-scale manipulation experiment in primary lowland Dipterocarp rainforest at Maliau Basin, Sabah, Malaysia, between October 2014 and July 2017, using a novel targeted suppression approach to reduce the abundance of termites. Within a 42 ha area ($4^{\circ}44'35''$ to $55''$ N and $116^{\circ}58'10''$ to $30''$ E), four 80 x 80 m plots were created in which we physically removed termite mounds and used poisoned cellulose baits (which no other invertebrates consume) to reduce termite numbers. In addition, four control plots with no termite suppression were established. Decomposition was assessed using untreated *Pinus radiata* blocks contained within mesh bags. We used 300 micron nylon mesh to produce a combination of ‘closed’ wood bags, with no holes, accessible



only to microbes, and ‘open’ wood bags with ten 1 cm holes on each side of the bags (macroinvertebrate and microbe accessible). We used these closed and open treatment mesh bags in combination with our termite suppression manipulation to partition the contributions of termites and microbes to decomposition. In order to capture decomposition rates across different climatic conditions, we repeated the study on two consecutive years, deploying one set of wood blocks in August 2015 and a second set in July 2016. Wood blocks were left on the forest floor for 12 months, after which they were removed from the forest, dried and weighed. Across each plot, we placed five closed and five open wood block bags for each time period, in a grid pattern, at least 10 m apart ([10] and see Supplemental Information, published with this article online, for a full description of the methods).

Closed bags (macroinvertebrate inaccessible) on the control plots lost an average of $11 \pm 2\%$ of their mass, compared with $26 \pm 8.3\%$ mass loss from open bags (macroinvertebrate accessible) on the control plots. This is a $58 \pm 4\%$ reduction of mass loss where macroinvertebrates did not have access to the wood resource (LMER random slopes model on logit transformed proportion data: $z = -4.21$, $P < 0.001$), indicating that microbes were responsible for $42 \pm 4\%$ of the total wood decomposition. By comparing the open bags on the control plots to the open bags on the termite suppression plots we can assess the specific contribution of termites to decomposition. The average total mass lost from the macroinvertebrate accessible blocks on the control plots was $26 \pm 8.3\%$ compared with $9.4 \pm 1.7\%$ on the termite suppression plots: $64 \pm 7\%$ less mass was removed where termites did not have access to the wood ($z = 4.22$, $P < 0.001$; Figure 1).

Overall our results indicate that microbes contribute between 36 and 42% of wood decomposition over a 2 year period in tropical rainforest, while termites are responsible for 58–64%. These patterns are consistent in not only the first year, which was exceptionally dry, but also in the second year, which was

wetter and had more variable rainfall patterns. Our study demonstrates the consistent importance of termites for wood decomposition in a variety of climatic conditions (see Supplemental Information for wood decay presented for each year).

Our results are based on an artificial assay of decomposition (*Pinus radiata*), which we chose to allow for standardization and ease of comparison across our experimental plots. Although our study revealed no compensation by other macroinvertebrate groups in the absence of termites, this may be because phloem feeders and large wood-boring beetles were not attracted to our wood blocks due to their small size and lack of bark [5]. Therefore, our estimates of dead wood decomposition are conservative. Our results highlight the large proportion of decomposition driven by termites, rather than the lack of any apparent decomposition by other macroinvertebrate groups. Additionally, *Pinus radiata* as a decomposition assay is unlikely to represent decomposition rates of other wood which differs in traits such as density. The next step to fully understand the roles of other macro-invertebrates should be decomposition assays that include different wood sizes, wood traits, as well as fresh wood with intact bark [5]. Our estimates are based on the decomposition of low density wood; therefore, exploring how wood density influences decomposer taxon would also be useful.

Over the two-year period, we suppressed the activity of termites by an average of 45% (see Supplemental Information). Given that we were only able to suppress part of the termite assemblage, our estimates of termite-mediated decomposition are conservative. This is the first study to partition the relative contribution of microbes and termites to wood decay, allowing us to disentangle a key component of nutrient and carbon cycling in tropical forests. We found that over the course of our experimental period, termites were responsible for over half of the mass lost from wood blocks, demonstrating that termites can represent a large, and frequently overlooked, portion of the global carbon cycle.

SUPPLEMENTAL INFORMATION

Supplemental Information contains one figure, one table, and experimental procedures, and can be found with this article online at <https://doi.org/10.1016/j.cub.2019.01.012>.

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