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RESEARCH ARTICLE

Drivers of wood decay in tropical ecosystems: Termites versus microbes along spatial, temporal and experimental precipitation gradients

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Abstract

1. Models estimating decomposition rates of dead wood across space and time are mainly based on studies carried out in temperate zones where microbes are dominant drivers of decomposition. However, most dead wood biomass is found in tropical ecosystems, where termites are also important wood consumers. Given the dependence of microbial decomposition on moisture with termite decomposition thought to be more resilient to dry conditions, the relative importance of these decomposition agents is expected to shift along gradients in precipitation that affect wood moisture.
2. Here, we investigated the relative roles of microbes and termites in wood decomposition across precipitation gradients in space, time and with a simulated drought experiment in tropical Australia. We deployed mesh bags with non-native pine wood blocks, allowing termite access to half the bags. Bags were collected every 6 months (end of wet and dry seasons) over a 4-year period across five sites along a rainfall gradient (ranging from savanna to wet sclerophyll to rainforest) and within a simulated drought experiment at the wettest site. We expected microbial decomposition to proceed faster in wet conditions with greater relative influence of termites in dry conditions.
3. Consistent with expectations, microbial-mediated wood decomposition was slowest in dry savanna sites, dry seasons and simulated drought conditions. Wood blocks discovered by termites decomposed 16–36% faster than blocks

undiscovered by termites regardless of precipitation levels. Concurrently, termites were 10 times more likely to discover wood in dry savanna compared with wet rainforest sites, compensating for slow microbial decomposition in savannas. For wood discovered by termites, seasonality and drought did not significantly affect decomposition rates.

4. Taken together, we found that spatial and seasonal variation in precipitation is important in shaping wood decomposition rates as driven by termites and microbes, although these different gradients do not equally impact decomposition agents. As we better understand how climate change will affect precipitation regimes across the tropics, our results can improve predictions of how wood decomposition agents will shift with potential for altering carbon fluxes.

KEYWORDS

Australia, carbon flux, decomposition, microbe, precipitation gradient, termite, tropical, wood decomposition

1 | INTRODUCTION

Up to 78% of global forest carbon flux occurs in tropical ecosystems (Harris et al., 2021). In these ecosystems, dead wood represents around 10% of the total carbon stock (Pan et al., 2011) and contributes substantially to carbon fluxes through decomposition. At present, estimates of these dead wood fluxes across all forest ecosystems are largely based on temperate zone studies (Harmon et al., 2020; Hu et al., 2018); however, 80% of dead wood is found in tropical ecosystems (Pan et al., 2011). Estimates of such fluxes based on temperate forests may not apply in the tropics due to differences in climate, with higher rainfall seasonality (Tan et al., 2020), and different communities of decomposers, such as the high prevalence of termites (Griffiths et al., 2019; Zanne et al., 2022). As predictions are made to estimate future carbon fluxes in forest ecosystems, it is critical to have a better understanding of the drivers of decomposition across climatic gradients in tropical ecosystems.

Two of the most important biotic decomposition agents of dead wood are wood-dwelling microbes, which are important globally, and wood-feeding termites, which are important in the tropics. In some locations, termites consume ~50% of dead wood and significantly accelerate decomposition rates in relation to microbes (Cheesman et al., 2018; Griffiths et al., 2019; Seibold et al., 2021; Wu et al., 2021; Zanne et al., 2022). It is expected that these two decomposer groups will differentially impact the decomposition process depending on precipitation and moisture availability in the wood substrate due to their different strategies to acquire and process dead wood. Saprobic microbes colonize dead wood via spores and hyphae and can be present in living trees before they die. Microbes decompose dead wood via extracellular enzymes (Allison et al., 2007) that require moisture to deliver the enzymes to the substrates, and therefore, their activity is enhanced when more moisture is available (Brischke & Alfredsen, 2020). However, too much moisture may lead to anoxic conditions with lower decomposition rates (Piaszczyk et al., 2022).

Termites decompose wood in a two-step process. First, as mobile invertebrates, they must discover the dead wood and recruit other workers to help consume it. Then, termites physically remove pieces of dead wood and digest it using endogenous cellulases and symbiotic microbes either within their guts (Brune, 2014) or in their mounds (Nobre et al., 2011). Termites have adapted to consume wood under low moisture conditions by altering their nest structure and location to retain water (Korb, 2011; Wijas et al., 2022) and building clay structures around and between their food sources (King Jr & Spink, 1969) allowing them to process dead wood under dry ambient conditions.

Microbes are more dependent on moisture being available within their substrate, whereas termites are better able to engineer their environment to maintain suitable conditions. Therefore, precipitation is a key environmental driver that is expected to lead to differing responses between termite and microbial decomposers. The moisture of the substrate within which organisms feed is largely determined by precipitation (Duan, Chavez Rodriguez, Hemming-Schroeder, et al., 2023), which can vary spatially, for example, with distance from water bodies, or on either side of mountain ranges. Additionally, precipitation can vary temporally, for example, across seasons, ENSO cycles and climate change. To date, most studies examining microbe and termite decomposition responses to variation in precipitation examine spatial contrasts (Seibold et al., 2021; Veldhuis et al., 2017; Zanne et al., 2022) or temporal contrasts among years (e.g. shifts between La Niña and El Niño years; Ashton et al., 2019), but not both. These studies found that the relative importance of termites in dead wood decomposition increased with lower precipitation, in contrast to microbial decomposition (Taylor et al., 2017). However, in some studies, termite-mediated decomposition also decreased during extreme droughts, suggesting that even termites can be sensitive to extreme dry conditions (Cheesman et al., 2018).

In tropical ecosystems, precipitation can also vary intra-annually with well-defined dry and wet periods throughout the year (Tan et al., 2020). In dry seasonal tropical ecosystems such as savannas, termite activity increased during transitional and wet periods (Davies et al., 2015; Dawes-Gromadzki & Spain, 2003); however, the opposite trend occurred in wet rainforest sites, with termite activity declining in wet seasons (Ashton et al., 2019; Dibog et al., 1998). Microbial activity consistently increased with rainfall during wet seasons (Liu et al., 2013) leading to higher decomposition of grass and leaf litter in these periods (Davies et al., 2013; Ngatia et al., 2014; Peña-Peña & Irmler, 2016). Little is known of the influence of seasonality on dead wood decomposition rates and the relative importance of biotic decomposition agents through time.

Because most decomposition studies come from cooler temperate ecosystems where microbes dominate decomposition, we have a better empirical understanding of the microbial decomposition process than the termite one at ecosystem scales (Harmon et al., 2020; Mackensen et al., 2003; Zell et al., 2009). Additionally, carbon cycling models including the Yasso model (Liski et al., 2005) or the soil module of the Community Land Model Version 5 (Lawrence et al., 2019) use assumptions from leaf litter studies to model dead wood decomposition. These models assume that all dead wood decomposition occurs through the lens of microbial responses to climate and edaphic variables, for example, precipitation and soil moisture. Given the differences in how termites and microbes find and process dead wood, it seems unlikely that existing microbe-centric decomposition models will accurately depict the carbon consequences of termite decomposition for several reasons. First, microbial decomposition models do not account for the two steps in termite decomposition (Zanne et al., 2022), discovery followed by decomposition. Second, decreasing precipitation should favour termite over microbial decomposition, meaning current models should be less accurate in dry conditions. For instance, Bonan et al. (2013) found that leaf litter decomposition rates are underestimated by the Community Land Model in drier ecosystems, but it is currently unknown if this is the case for dead wood as well.

Finally, most models predicting dead wood decomposition through time assume the data follow a Weibull function with two parameters or a negative exponential function (specialized case of the Weibull) with one parameter. There is an emerging consensus that two-parameter functions, such as the Weibull, better capture the decomposition process of dead wood because they allow a lag phase at the start of the decomposition process (Cornwell & Weedon, 2014; Lee et al., 2022); however, both functions assume that the discovery of wood blocks occurs equally at the start of decomposition leading to relatively low variability in decomposition rates through time among pieces of wood. Given the initial discovery phase by termites can be sporadic and occur anytime throughout the decomposition process, it is possible that these typical functional forms, Weibull and negative exponential, used to capture microbial decomposition do not translate well to termites. Considering the potential limitations of these commonly used wood decomposition models and the lack of knowledge on their application in termite-dominated systems, it is important to test their applicability.

Through this study, our aim was to explore the impact of different precipitation gradients (spatial, temporal and experimental) on the relative contributions of wood-dwelling microbes and wood-feeding termites to dead wood decomposition across five sites in tropical Queensland, Australia. To address our aim, we deployed pine wood blocks and manipulated access to termites over a 4-year period. To provide different views of the contributions of these biotic decomposers, we examined decomposition responses in three ways. First, we quantified overall rates of decomposition of wood blocks accessible to all decomposers whether these were discovered by termites or not (= all-accessible decomposition) which amounts to the decomposition rates of wood at the site level by explicitly weighting by the frequency of discovered and undiscovered wood blocks. For spatial variation in precipitation (with the 5 sites spanning dry savanna to wet rainforest), following classic models of decomposition (Adair et al., 2008), we expected that decomposition of dead wood accessible to termites and microbes would be faster in wet sites (i.e. lower time to 50% mass loss; Figure 1b). Second, we examined the influence of termites on dead wood through two steps: We quantified the number of wood blocks discovered by termites (= termite discovery; Figure 1a) and we investigated the decomposition rates of those discovered blocks (= termite discovered decomposition) which underwent a termite-plus-microbe decomposition pathway (Figure 1b). Finally, we explored decomposition rates under a microbial-only pathway (= termite undiscovered decomposition). These steps allowed us to quantify the relative contributions of termites and microbes to decomposition. We predicted that for termite decomposition, we would find higher discovery (Figure 1a) and termite discovered decomposition (Figure 1b) at dry sites, whereas microbial decomposition (i.e. in wood undiscovered by termites) would be higher at wet sites (Figure 1b). Furthermore, we investigated decomposition rates of dead wood temporally across wet and dry seasons at each site, as well as with an experimental manipulation simulating drought conditions at the wettest site. We expected our predictions about the impact of precipitation on decomposition to apply across spatial, temporal and experimental variation in precipitation (Figure 1) and under experimental drought at the wet site. Finally, we expected that a two-parameter Weibull model would better fit decomposition processes for undiscovered blocks (microbes only) than discovered blocks (microbes and termites).

2 | METHODS

2.1 | Study sites

We carried out our study in tropical Far North Queensland, Australia, along a rainfall gradient ranging from 776 to 2973 mm/year. The sites in order of decreasing rainfall include a lowland rainforest at the James Cook University's Daintree Rainforest Observatory

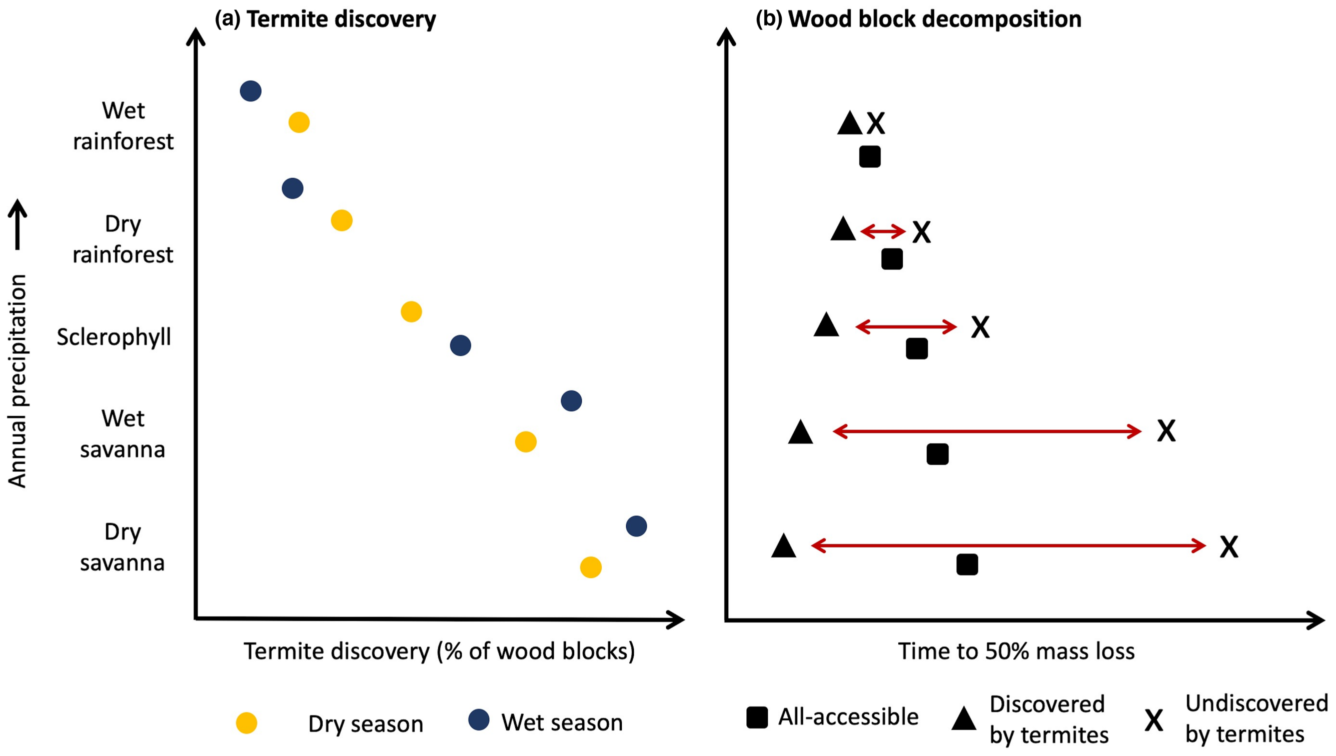

FIGURE 1 Expectations for (a) discovery frequencies of wood blocks by termites during dry (yellow dot) and wet (blue dot) seasons and (b) decomposition rates of all-accessible (square), termite discovered (triangle) and termite undiscovered (x) dead wood across the study sites. Note the red arrows indicate the overall amount termites were predicted to increase decomposition rates relative to just microbes, calculated as decomposition rates of [(Discovered) − (Undiscovered)]/(Undiscovered). Decomposition rates of all-accessible dead wood will depend on the relative importance of termites in decomposition at those sites as determined by discovery frequencies of blocks and termite discovered decomposition rates.

(wet rainforest) and four sites in Australian Wildlife Conservancy's Brooklyn Sanctuary including an upland rainforest on Mount Lewis (dry rainforest), a wet sclerophyll eucalypt forest on Mount Lewis (sclerophyll), an open Eucalyptus woodland/savanna (wet savanna) and a dry savanna (dry savanna), (Figure 2). All sites had unmanipulated natural vegetation. Additionally, a drought experiment was set up in the lowland rainforest site at the Daintree Rainforest Observatory in May 2015 (described in Tng et al., 2018; hereafter experimental drought plot). All sites experience a distinct wet and dry season, with sites receiving between 80% and 94% of rainfall between November and April (Table S1, Figure 2a; Cheesman et al., 2018). The appropriate permits and authorizations were obtained from the Australian Wildlife Conservancy and James Cook University.

2.2 | Weather data

The amount of rainfall at sites across our experiment was estimated by Duan, Chavez Rodriguez, Flores-Moreno, et al. (2023) using a combination of local weather stations and satellite-derived precipitation data. In addition, we assessed the long-term average annual rainfall for each site using the gridded annual precipitation product provided by the Australian Bureau of Meteorology (Table S1). We applied a buffer zone of 5 km around each site and calculated the average of all rainfall values within the area. Average daily temperatures ranged between 25.8°C and 19.7°C in the wet season and 24.1°C and 17.6°C in the dry season; long-term annual precipitation ranged between 776 and 2973 mm (Table S1).

2.3 | Decomposition experiment

Given that our goal was to compare the relative roles of different decomposition agents with changing precipitation, and there were no overlapping native tree species across our five sites, we used wood blocks (9 cm × 5 cm × 5 cm) of a non-native pine species, *Pinus radiata*, to standardize measurements of dead wood decomposition rates (Zanne et al., 2022). Of note, our study design with a single species of non-native wood allowed us to standardize measurements across wide precipitation gradients and target questions around the response of different decomposition agents to changing environmental conditions; however, extrapolation of our results to other systems should be done with caution as the results from the pine blocks may not always apply to other species of wood (Law et al., 2023).

Blocks were dried at 105°C to a constant mass and measured for initial mass before wrapping in 280 μm lumite® mesh (BioQuip) bags that were sealed by sewing the ends shut. At each site, in

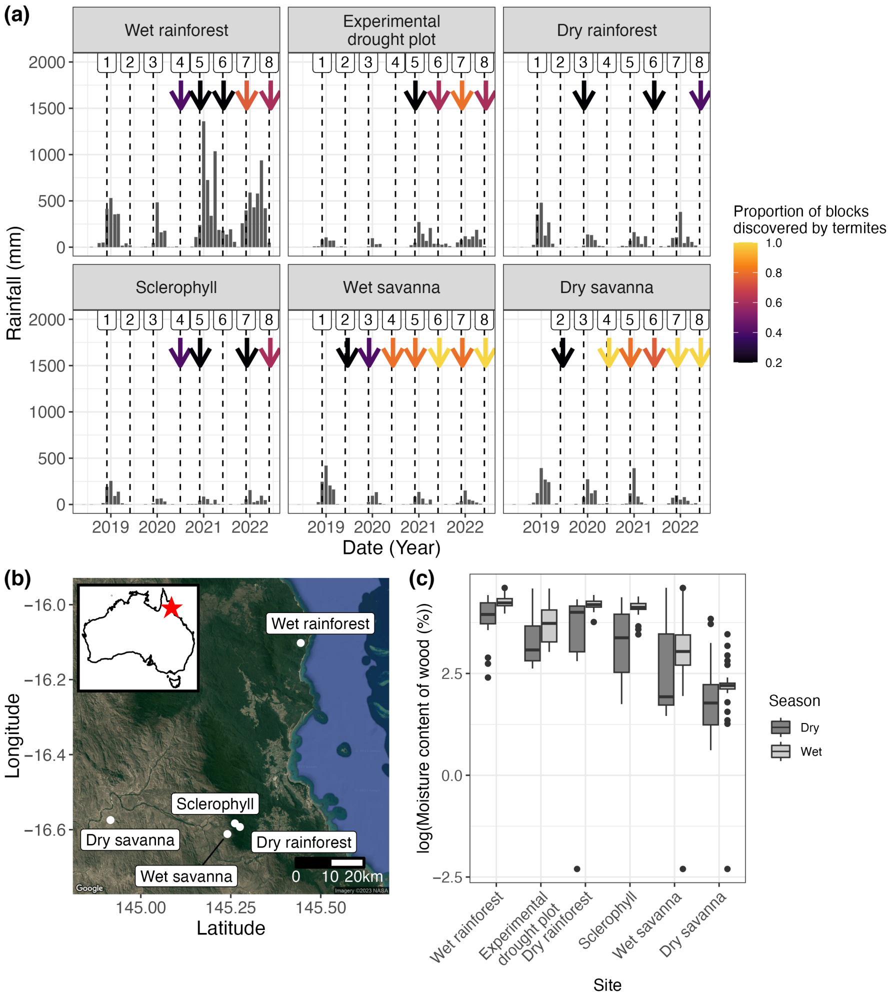

FIGURE 2 (a) Monthly rainfall from 2018 to 2022 (grey-filled bars) from Duan, Chavez Rodriguez, Flores-Moreno, et al. (2023) at our sites in Far North Queensland, Australia, as shown in the satellite map (b). For (a), the numbers in square boxes above the dashed lines refer to the number of the harvest at each site and the coloured arrows represent the proportion of wood blocks discovered by termites at each harvest across sites. (c) Median, quartiles and minimum/maximum values for the $\log_{10}$ of the moisture content of wood blocks (%) across sites and seasons (light grey = wet, dark grey = dry).

TABLE 1 Replication statement.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Spatial gradient: Wood blocks	Site (×5), harvest (×8) and termite treatment (×2)	5 replicates per treatment per site, per harvest. Total of 400 blocks
Drought experiment: wood blocks	Site (×2), harvest (×8) and termite treatment (×2)	5 replicates per treatment, per site, per harvest. Total of 160 blocks. Note that of these 160 blocks, 80 were also used in the spatial gradient experiment
Temporal gradient: harvest	Site (×6), harvest (×8), season (×2)	4 wet seasons and 4 dry seasons over 4 years

June 2018, we placed the wood blocks in five stations separated by 5 m. The area around the stations at the savanna and sclerophyll eucalypt sites was burned prior to deployment to protect blocks from fire damage. At each station, we randomly placed 16 blocks, each separated by 15 cm. Half of the blocks were assigned to a termite excluded (TE) treatment and the other half to a termite accessible (TA) treatment. Termite accessibility was achieved by punching 10 holes with a holepunch of 5 mm diameter on the bottom of each bag.

One randomly assigned block from each treatment was collected every 6 months at each station between December 2018 and June 2022 amounting to eight harvests totalling four at the end of every wet and every dry season (Figure 2). Once the blocks were harvested, the bags were cut open and the remaining wood was brushed to remove soil. Any termite, fungi or other invertebrate damage was noted before blocks were placed into paper bags until they could be transported to the lab for processing. In the lab, we separated carton (organic material produced by termites; Lee & Wood, 1971) and soil that was imported by termites before weighing the remaining wood. We considered blocks discovered by termites if we found termites, imported soil, carton or termite galleries and undiscovered (regardless of treatment TE or TA) if they lacked these signs. Each wood block was dried at 105°C for 72 h before it was weighed again to assess harvest dry mass. We calculated the proportional mass remaining of each block using the following equation:

$$\text{Proportional Mass Remaining} = 1 - \frac{(\text{Harvest dry mass})}{(\text{Initial dry mass})}$$

We also calculated the moisture content of wood using the following equation:

$$\text{Moisture content} = \frac{(\text{Harvest wet mass} - \text{Harvest dry mass})}{(\text{Harvest dry mass})} * 100$$

The number of wood block replicates is detailed in Table 1 and the proportion of discovered and undiscovered blocks at each site and harvest is shown in Figure 2a.

2.4 | Analysis

2.4.1 | Spatial gradient, temporal gradient and drought experiment: Termite discovery

We modelled the discovery frequency of termites using a generalized linear model with a binomial logit function. For this, we only considered blocks accessible to termites in the TA treatment with termite discovery (Yes/No) as a response variable. We used time since a given block was deployed in the field, site and season harvested as predictor variables. We examined models with all two-way and three-way interactions and used a model selection approach to remove interactions and predictor variables that did not provide additional explanatory power when included in the model. The model with the best fit was selected based on the lowest Akaike information criterion value (Wagenmakers & Farrell, 2004).

2.4.2 | Spatial gradient and drought experiment: Dead wood decomposition

We modelled the decomposition rates of blocks by using the package *'litterfitter'* in R (v 4.1.2), (Cornwell & Weedon, 2014) with the *'fit_litter'* function; this function generates parameters to fit a Weibull model (two parameters) or a negative exponential model (one parameter) to replicated values of mass remaining through time. Model fitting was performed using constrained optimization with the 'L-BFGS-B' algorithm implemented in the *'optim'* function in base R (Cornwell & Weedon, 2014). Given Weibull models are typically better at capturing the dead wood decomposition process than negative exponential models (Cornwell & Weedon, 2014), we present results from Weibull models in the main text from which we extracted time to 50% mass remaining as a proxy for decomposition rates. *K*-values from the negative exponential models can be found in the Supporting Information (Tables S2 and S3).

We have considerable variation in our system, both within and across our different factors of interest (harvest, site, termite discovery; Figure 3). To explicitly explore different effects of microbes and termites on dead wood decomposition, we examined decomposition rates in two ways. First, we modelled the decomposition of termite accessible (TA) treatment blocks at each site to quantify the decomposition rates in relation to all biotic pressures in the system (all-accessible), (Figure 3a). This analysis inherently considers the joint contributions of termites and microbes to decomposition. These models were based on data from 40 wood blocks across eight harvests at each site. Next, we modelled the decomposition of blocks at each site separately for termite discovered and termite undiscovered blocks (Figure 3b). This partitioning allowed us to quantify the decomposition for just those blocks experiencing a microbial decomposition pathway versus a microbes-plus-termites pathway.

For the decomposition rates of termite discovered blocks, we used proportion mass loss from undiscovered blocks across each harvest at each site until the first harvest at which a block was discovered after which only proportion mass loss from discovered blocks was included to fit the model. Because the number of discovered wood blocks varied by site, the models were based on differing numbers of blocks (Table S4). To statistically evaluate the difference in decomposition rates among sites and termite discovery treatments, we generated 95% confidence intervals using a parametric bootstrap method with 1000 iterations on the optimal parameters of our model. We considered that the time to 50% mass remaining was statistically different if there was no overlap among the 95% confidence intervals (Wood, 2004).

To evaluate the goodness of fit of the Weibull decomposition model for mass loss through time separately for termite discovered and undiscovered blocks, we computed the R^2 for each model.

To quantify the proportion of variation explained across replicates in each factor versus means across factors, we used a variance components analysis on a linear regression using the *'POV'* package in R. Mass remaining was used as a response variable with harvest, site and termite discovery as factors.

2.4.3 | Temporal gradient: Dead wood decomposition

To measure the influence of seasonality on decomposition for discovered and undiscovered dead wood, we averaged the percentage mass remaining separately for each wood category. We computed the difference in average mass remaining between each pair of harvests to get an average over four dry seasons and four wet seasons for blocks that were undiscovered or discovered by termites. We did not include all dry and wet seasons for blocks discovered by termites because for many harvests no blocks were discovered, especially during the early harvests (Figure 2a). To evaluate differences in mass loss between seasons and among sites, we used a linear model with average mass remaining of either discovered or undiscovered blocks as a response variable and season harvested, site, their interaction and harvest number as fixed factors.

3 | RESULTS

3.1 | Spatial precipitation gradient

Termites were over 10 times more likely to discover dead wood in the dry sites (dry savanna and wet savanna) compared with the

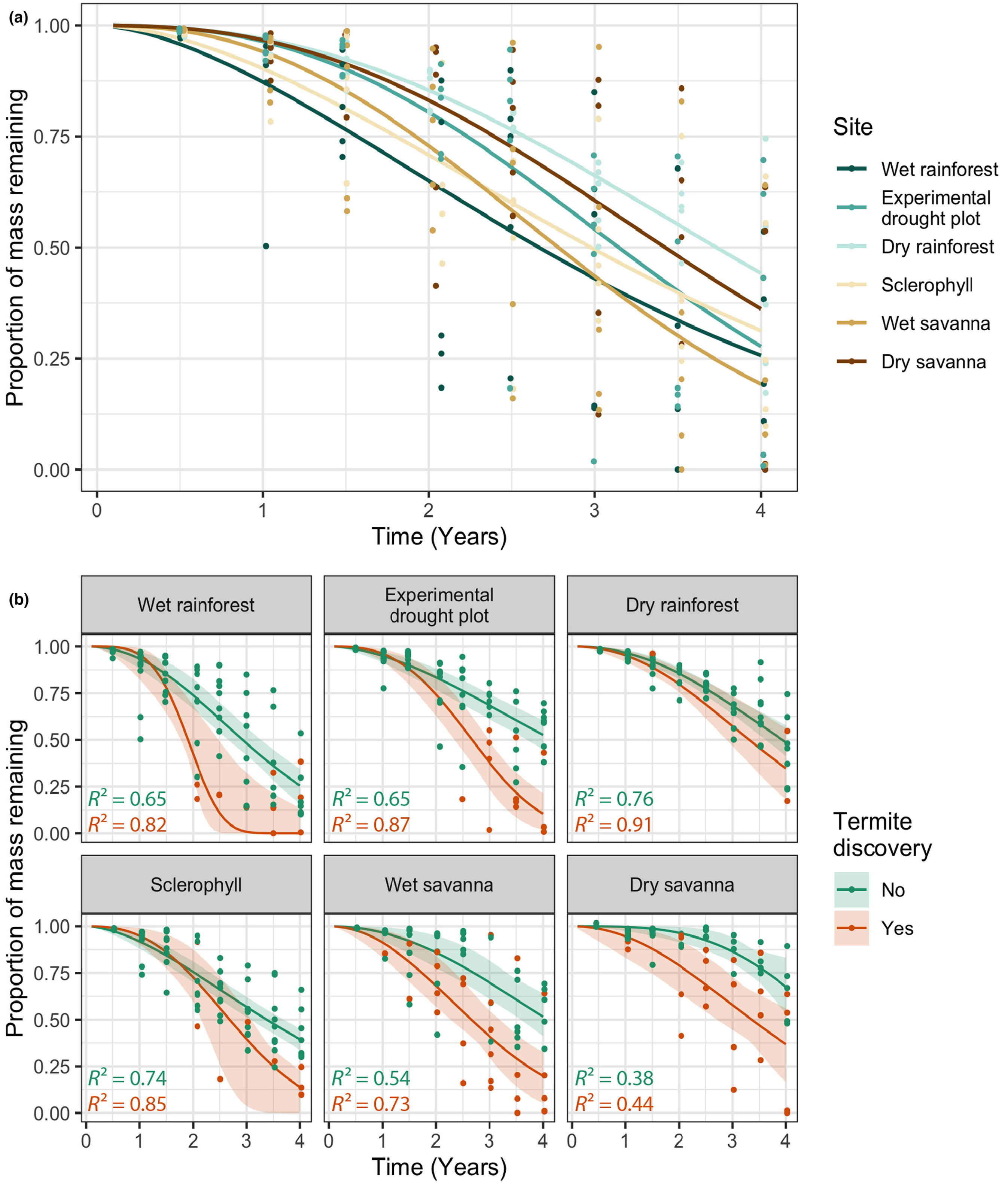

FIGURE 3 Modelled proportion mass remaining through time using Weibull models (solid lines) of (a) site-level decomposition including all biotic pressures and (b) blocks discovered by termites (orange) or not (green), (±95% CI) across sites. Each solid point represents an individual wood block. R^2 values denote model fits for termite undiscovered blocks (green) and termite discovered blocks (orange) at each site.

wet sites (wet rainforest, dry rainforest and sclerophyll), (Figure 4, Table S5). There was a 20% lower rate of discovery in the dry rainforest compared with the wet rainforest (Figure 4, Table S5). The proportion of blocks discovered by termites increased with time (Figure 4, Table S5). Over 95% of blocks were discovered by termites within 4 years in the savanna sites while 75% of blocks were discovered in the wet rainforest, 56% in sclerophyll and 36% in the dry rainforest.

Moisture content of wood blocks was similar between the wet rainforest and dry rainforest but decreased steadily from the sclerophyll to the dry savanna (Figure 2c, Table S6). All-accessible decomposition rates (from the TA treatment) were similar among the wettest site (wet rainforest), the wet savanna and the sclerophyll (Table S8, Figure 5a). Slower all-accessible decomposition rates were observed in the dry savanna and dry rainforest compared with the wet rainforest sites (Table S8). In variance partitioning from linear regression, most of the variation in mass remaining of wood blocks was explained by harvest (53.5%) followed by termite discovery (8.5%) (Table S7). Variation across sites explained 5.2% of model fit compared with 3.5% within sites (Table S7).

The microbe-driven decomposition pathway (undiscovered decomposition) broadly followed the expected pattern (Figure 1b). Dead wood undiscovered by termites had higher decomposition rates in the wet rainforest and sclerophyll, compared with the savannas. The dry rainforest site had a similar decomposition rate to the two savannas (Figure 5b; Table S8). The decomposition patterns under a termite-plus-microbe pathway (discovered decomposition) contradicted our hypothesis that termites would accelerate the decomposition of dead wood more in dry compared with wet sites (Figure 5b). Dead wood discovered by termites had similar decomposition rates across sites but higher decomposition rates than undiscovered dead wood at most sites irrespective of rainfall, except the dry rainforest and dry savanna sites (Figure 5b; Table S8). Time to 50% mass remaining of discovered compared with undiscovered

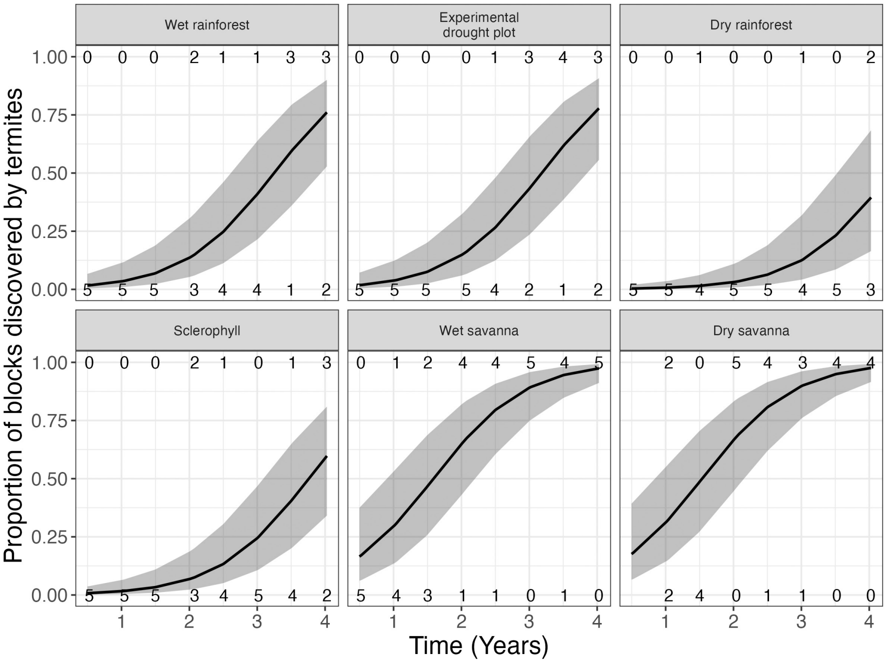

FIGURE 4 Proportion of blocks discovered by termites through time (starting at the first harvest which is 6 months into the experiment) and across sites with number of wood blocks discovered (top of each plot at $Y=1$) and undiscovered (bottom of each plot at $Y=0$) within the all-accessible wood blocks.

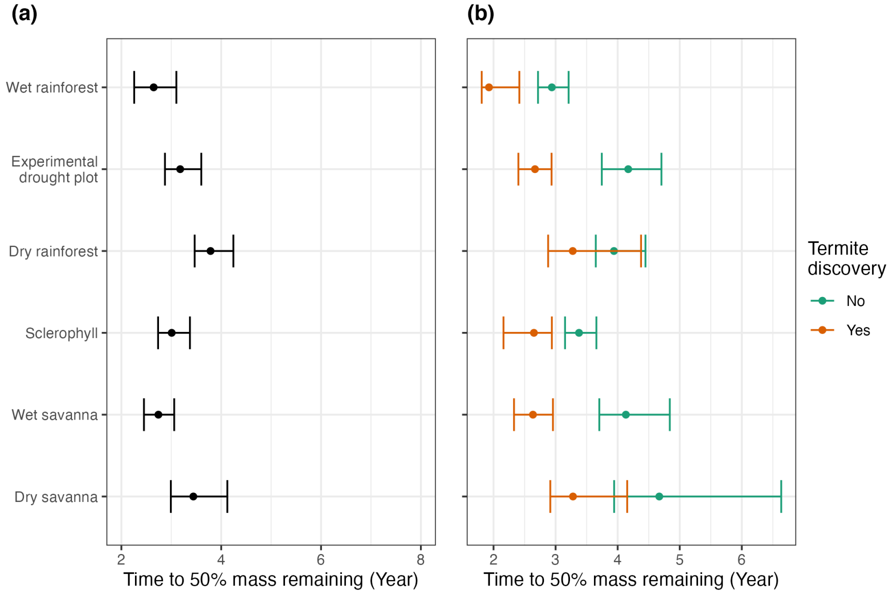

FIGURE 5 Time to 50% mass remaining (±95% CI) for (a) all-accessible blocks (TA) and (b) blocks either discovered (orange) or undiscovered (green) by termites across sites. The number of replicated wood blocks used for each model estimate can be found in Table S4 and the Weibull models used are shown in Figure 3.

blocks was 36% faster in the wet rainforest and wet savanna sites while these dropped to 30% in dry savanna, 21% in sclerophyll and 16% in dry rainforest. The model performance (R^2) of generalized Weibull models predicting decomposition was similar for discovered and undiscovered dead wood across all sites (Figure 3b).

3.2 | Temporal gradient

The moisture content of wood blocks was lower during the dry than the wet season regardless of site (Figure 2c, Table S6). Across the study, mass loss of undiscovered blocks was 17% higher during the wet than dry seasons (95% CI [6.00–26.86], $p=0.003$; Figure 6a) regardless of the site (Table S9), while mass loss of discovered blocks did not differ between seasons (95% CI [−18.37–70.94], $p=0.232$; Figure 6b) regardless of the site (Table S10). Seasonality also did not significantly influence termite discovery of dead wood (Table S5, Table S11).

3.3 | Experimental drought

The moisture content of wood blocks was lower in the experimental drought plot than in the wet rainforest (Figure 2c, Table S6). Overall decomposition (all-accessible) rates did not differ between the wet rainforest and the experimental drought plot (Table S8, Figure 5a). Decomposition rates for undiscovered blocks were higher in the wet rainforest than in the experimental drought plot although the decomposition of discovered blocks was similar between the two (Figure 5b). Furthermore, termites increased decomposition compared to just microbially decomposed dead wood; discovered blocks decomposed 37% faster than undiscovered blocks in the experimental drought plot compared to 36% in the wet rainforest. However, there were no significant differences in termite discovery between the wet rainforest and the experimental drought plot (Figure 4, Table S5).

Within the experimental drought plot, mass loss was higher in undiscovered blocks during the wet as compared to the dry seasons (Table S9, $p=0.003$) while no differences in mass loss were found for discovered blocks across seasons (Table S10).

4 | DISCUSSION

Contrary to common assumptions from vegetation decomposition models, we found that all-accessible (termites and microbes) decomposition rates did not increase with higher precipitation (Figure 5a) and associated increases in wood moisture (Figure 2c). Although surprising, the decomposition rates of dead wood discovered by termites were statistically similar along the precipitation gradient (Figure 5b). However, in line with our predictions, termite discovery was 10× higher at dry sites (Figure 4), meaning the overall termite impact on decomposition increased. Together, greater termite discovery under dry conditions in conjunction with higher decomposition rates of discovered dead wood compensated for reduced microbial activity. Contrary to our predictions, termite discovery was not seasonally higher but rather termites compensated for decreased microbial activity by promoting similar decomposition rates of dead wood across seasons and between the experimental drought plot and the wet rainforest. Finally, we demonstrated that a Weibull function can accurately predict termite-driven wood decomposition despite randomness in termite discovery.

4.1 | Importance of termites in the decomposition process

Termites play a critical role in decomposition across our rainfall gradient. Across most sites, the time to 50% mass remaining was between 16% and 36% longer without termites (Figure 5b); this is despite greater richness and abundance of termites in the savannas as compared to the rainforests (Clement et al., 2021).

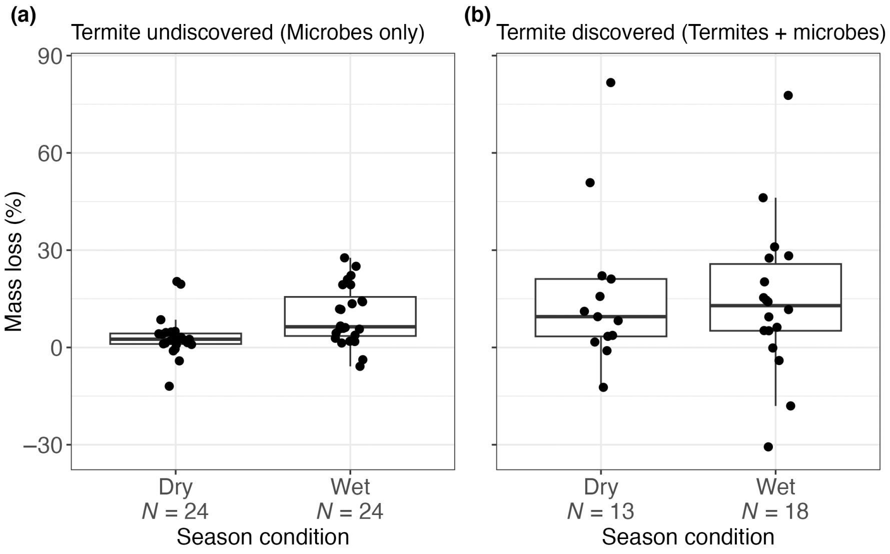

FIGURE 6 Median, quartiles and minimum/maximum values for percentage mass loss of blocks between wet (December–May) and dry (June–November) seasons across all sites including the experimental drought plot for (a) undiscovered by termites or (b) discovered by termites.

Additionally, termites discovered up to 95% of the dead wood in the savanna sites and 75% in the wet rainforest by the end of our study, further highlighting their importance in a range of tropical ecosystems across Australia. These findings align with studies from Africa (Collins, 1981; Schuurman, 2005) and Asia (Griffiths et al., 2019; Wu et al., 2021), which is interesting given that the diversity of termites in tropical Australian rainforests is low compared to other continents (Clement et al., 2021). While our study was carried out in the tropics, studies from temperate warm forests also highlight the importance of termites in the decomposition process, extending the relevance of our results to temperate systems (Bradford et al., 2021; Ulyshen, 2014).

Despite our expectation that the idiosyncratic nature of termite discovery would mean termite-driven decomposition is problematic to predict with statistical models, the Weibull model, in particular, provided adequate predicted fits of the observed decomposition data in the presence of termites (Figure 3). The large sample size in this experiment likely provided enough data to accurately model termite-induced stochasticity. This result is promising for larger scale modelling of termite effects on ecosystems using Weibull models that allow for a lag phase at the start of the decomposition process (Cornwell & Weedon, 2014).

4.2 | Influence of precipitation on the decomposition process

Whether in savanna or wet rainforest ecosystems, all-accessible decomposition rates were statistically similar across spatial precipitation gradients. Therefore, contrary to commonly used decomposition models in Earth system models (Lawrence et al., 2019), we did not find that higher precipitation led to higher overall decomposition rates of dead wood. Instead, biotic decomposition agents were differentially sensitive to precipitation, compensating for one another as precipitation changed spatially, temporally and with a simulated drought; microbes played a larger role in wet environments and termites played a larger role in dry environments. However, the finding that microbial decomposition is fastest in wet sites, with fivefold more precipitation, is consistent with leaf litter studies from the tropics (Taylor et al., 2017). This similarity between leaf and wood decomposition is interesting given the greater complexity in three-dimensional structure and morphology and higher carbon content of wood compared to leaves. The importance of moisture as a mediator of microbial activity is further corroborated by the drought experiment and through seasonal variation in precipitation and moisture content of the wood. Decomposition rates due to microbes were significantly reduced in the experimental drought plot and overall decomposition rates of dead wood was higher during the wet season (~17%) regardless of the ecosystem considered. It is important to note that there was also large variation in microbial decomposition rates within each site (Figure 3, Table S7) similar to findings from temperate ecosystems (Bradford et al., 2014). This decomposition variation may be driven by within-site differences in fungal communities (Maynard et al., 2017), as well as microclimatic conditions of the wood blocks themselves. Using the same wood blocks as in the current study, Duan, Chavez Rodriguez, Hemming-Schroeder, et al. (2023) demonstrated large within- and across-site variation in moisture content, which was strongly predictive of mass loss, especially for microbial decomposition.

The equally high all-accessible rate of decomposition at the wet savanna and wet rainforest sites is likely due to the higher discovery of dead wood by termites (>10×) in the savanna. With higher discovery, termites compensated for a reduction in microbial-mediated decomposition and accelerated overall decomposition at these dry sites. Our results agree with a global study showing that in tropical ecosystems with high temperatures, termites have high discovery of blocks resulting in elevated dead wood decomposition (Zanne et al., 2022). Our findings also provide novel evidence that sites which had high termite abundance, species richness (Clement et al., 2021) and discovery frequencies do not always lead to high decomposition rates of dead wood following discovery. For instance, although the wet savanna and wet rainforest sites had different discovery frequencies of blocks, the decomposition of discovered blocks was similar. This result may be attributable to variation in recruitment or consumption abilities of termites among ecosystems or to shifting environmental conditions post discovery. For instance, we know that there is almost complete turnover in termite (Clement et al., 2021) and fungal communities (M. Barrett, pers. comm) between rainforest and savanna sites, with more species and feeding guilds of termites in the savanna.

The relative increase of the termite role in the decomposition process in dry sites is corroborated by decomposition results from the experimental drought plot and during dry seasons. In contrast with our results of higher discovery at dry sites across our spatial gradient, termite discovery did not increase in dry seasons or the experimental drought plot. However, despite this lack of elevated discovery, termites still played a strong role in decomposition. The discovered blocks exhibited no difference in mass loss between the wet and dry seasons and between the experimental drought plot and the wet rainforest, although the undiscovered blocks did. Taken together, these results indicate that while microbial decomposition was lower in dry conditions, that of termites was not, hence, termites were consuming a greater amount of dead wood than microbes under the experimental drought plot and during the dry season compared with wet rainforest site and the wet season, respectively. While we know of no other such study for wood, similar results were found by Ashton et al. (2019) in which termites enhanced the decomposition of leaf litter during a drought period in a tropical rainforest. The potential compensatory impacts of termites and microbes on decomposition rates suggest that environmental conditions (here precipitation) and direct biotic interactions between termites and microbes affect the decomposition process. The role and process of such interactions remain outstanding research questions.

Our findings also suggest that termite communities within each site forage for dead wood resources year-round which contrasts with other studies which showed that termites are more active during wet seasons in the savanna (Davies et al., 2015; Dawes-Gromadzki & Spain, 2003) or dry seasons in the rainforest (Dibog et al., 1998). We already know that there are strong continental differences in termite richness and abundance (Clement et al., 2021), and these results suggest that there may also be strong differences in termite behaviours.

4.3 | Beyond precipitation: Other abiotic influences on decomposition rates

Although precipitation varied fivefold along our gradient, other factors such as temperature and fire frequency also vary across our study sites and likely affected decomposition rates. Indeed, in the dry rainforest, both termite discovery frequencies and microbial-mediated decomposition rates were slower than in the wet rainforest. As the dry rainforest was at higher elevation than the wet rainforest, it was also cooler (Table S1). Given the known sensitivity of both termites and microbes to low temperatures (A'Bear et al., 2014; Clement et al., 2021; Zanne et al., 2022), it is not surprising that this site had lower decomposition rates despite its relatively high rainfall.

There were also differences in decomposition between the two savanna sites. At the dry savanna site, while termites discovered blocks at similarly high rates to the wet savanna site, they were slower at consuming them with even lower decomposition than the wet rainforest site. We believe this lower decomposition may be due to differences in fire occurrence. Two fires swept through the dry savanna during our study period which did not occur at the other sites. Fires likely led to low abundances and activity of termites (Dawes-Gromadzki, 2007; Ferrar, 1982) and hence slowed their capacity to consume dead wood even when they did discover it. Given that most studies are arrayed along a nexus of intersecting gradients, it will be useful to understand the relative influences of these different environmental pressures in shaping ecosystem processes via organisms' sensitivities to these pressures.

5 | CONCLUSIONS

As climate change alters precipitation patterns (Trenberth, 2011), it is important to understand the drivers of decomposition across precipitation gradients to better predict future carbon emissions from tropical ecosystems. Our results make a step in that direction by showing that variation in moisture availability through space and time as driven by precipitation did not alter all-accessible decomposition rates across sites, but rather caused dead wood to tip decomposition towards different pathways. Termite communities within each site used dead wood resources regardless of shifts in precipitation. However, while microbes decomposed dead wood faster in wet sites and wet periods, termites increased their influence on decomposition at dry sites, within an experimental drought and during dry seasons. Given the important differences in how termites and microbes process and release carbon in dead wood, future carbon models should include the termite effect on dead wood decomposition. For instance, termites lack decomposition enzymes to break down lignin (although some in Africa and Asia cultivate fungus in their mounds that can), which may lead to less carbon released to the atmosphere (Brune, 2014) as carbon dioxide from a given piece of dead wood than when it undergoes decomposition via microbes with lignolytic capabilities (Cline et al., 2018). However, most termite species also produce methane, in addition to carbon dioxide, during the decomposition process (Brune, 2014). As methane has a greater warming potential than carbon dioxide (Carmichael et al., 2014), the gasses termites do release may have larger impacts on the Earth system. Given the differences in how and when termites and microbes decompose dead wood, it is likely that the rates and forms of carbon emissions will shift as termites play a greater role in dead wood decomposition.

AUTHOR CONTRIBUTIONS

Baptiste J. Wijas analysed the data and drafted the manuscript. Habacuc Flores-Moreno, Marc Rosenfield, Rebecca Clement and Amy E. Zanne set up the experiment. Baptiste J. Wijas, Abbey R. Yatsko, Habacuc Flores-Moreno, Rebecca Clement, Marc Rosenfield, Alexander W. Cheesman, Lucas A. Cernusak, Elizabeth S. Duan, Luciana Chavez Rodriguez and Amy E. Zanne collected the data. Steven D. Allison, Habacuc Flores-Moreno, Lucas A. Cernusak, Amy E. Zanne, Alexander W. Cheesman and Paul Eggleton contributed to experimental design. All authors edited and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

We declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.0rxwdbs5r (Wijas et al., 2023).

STATEMENT OF INCLUSION

Local collaborators from Northeast Queensland in Australia were integral to develop the protocol from the start including with the collection of pilot data to the finish with the editing of the paper. We also work with the local NGO Rainforest Rescue and are disseminating results with them.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Temperature and precipitation across the study period during wet and dry seasons as recorded by site weather stations and average long-term rainfall with data taken from the Australian Bureau of Meteorology (BOM).

Table S2. Parameters from negative exponential models and Weibull models of decay across sites for wood blocks discovered by termites. Note that *k* refers to exponential decay rate per year.

Table S3. Parameters from negative exponential models and Weibull models of decay across sites for wood blocks which were undiscovered by termites. Note that *k* refers to exponential decay rate per year.

Table S4. Number of wood blocks used in model fits of decay rates on mass remaining through time. Numbers differed by treatment (Figure 2) depending on natural discovery of blocks by termites at the sites.

Table S5. Model output of generalized linear model of termite discovery against time since the wood blocks were deployed, site and season. CI corresponds to confidence interval. *p*-values marked in bold are <0.05 with odds ratios significantly different from 1.

Table S6. Linear model output for moisture content of wood blocks against site, season and their interaction. *p*-values marked in bold are <0.05.

Table S7. Variance partitioning analysis investigating mass remaining against site, harvest and termite discovery.

Table S8. Time to 50% mass remaining in years (95% CI) across all sites and whether the wood blocks were exposed to all biotic pressures, discovered or undiscovered by termites.

Table S9. Linear mixed effects model output for mass loss of wood blocks which were undiscovered by termites (%) against season, site and their interaction. *p*-values marked in bold are <0.05.

Table S10. Linear mixed effects model output for mass loss of wood blocks which were discovered by termites (%) against season, site and their interaction. *p*-values marked in bold are <0.05.

Table S11. Model selection process using the Akaike information criterion for termite discovery against explanatory variables as specified in the first column.

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