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RESEARCH ARTICLE

Wood traits explain microbial but not termite-driven decay in Australian tropical rainforest and savanna

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Abstract

1. Variation in decay rates across woody species is a key uncertainty in predicting the fate of carbon stored in deadwood, especially in the tropics. Quantifying the relative contributions of biotic decay agents, particularly microbes and termites, under different climates and across species with diverse wood traits could help explain this variation.
2. To fill this knowledge gap, we deployed woody stems from 16 plant species native to either rainforest ($n = 10$) or savanna ($n = 6$) in northeast Australia, with and without termite access. For comparison, we also deployed standardized, non-native pine blocks at both sites. We hypothesized that termites would increase rates of deadwood decay under conditions that limit microbial activity. Specifically, termite contributions to wood decay should be greater under dry conditions and in wood species with traits that constrain microbial decomposers.
3. Termite discovery of stems was surprisingly low with only 17.6% and 22.6% of accessible native stems discovered in the rainforest and savanna respectively. Contrary to our hypothesis, stems discovered by termites decomposed faster only in the rainforest. Termites discovered and decayed pine blocks at higher rates than native stems in both the rainforest and savanna.
4. We found significant variation in termite discovery and microbial decay rates across native wood species within the same site. Although wood traits explained

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85% of the variation in microbial decay, they did not explain termite-driven decay. For stems undiscovered by termites, decay rates were greater in species with higher wood nutrient concentrations and syringyl:guiacyl lignin ratios but lower carbon concentrations and wood densities.

5. *Synthesis*. Ecosystem-scale predictions of deadwood turnover and carbon storage should account for the impact of wood traits on decomposer communities. In tropical Australia, termite-driven decay was lower than expected for native wood on the ground. Even if termites are present, they may not always increase decomposition rates of fallen native wood in tropical forests. Our study shows how the drivers of wood decay differ between Australian tropical rainforest and savanna; further research should test whether such differences apply world-wide.

KEYWORDS
decomposition, ecosystem function and services, fungi, microbes, savanna, soil carbon, termites, tropical forest, wood traits

1 | INTRODUCTION

Globally, deadwood accounts for approximately 8% of the carbon stored in forests (Pan et al., 2011), most of which is ultimately released to the atmosphere via decomposition or combustion. Deadwood carbon stocks and emissions vary substantially among biomes and forest types with the largest quantities found in tropical forests (Delaney et al., 1998; Harris et al., 2021; Palace et al., 2012; Seibold et al., 2021). Understanding the mechanisms that determine the rate of carbon release from wood decomposition, in both tropical forests and savannas, is crucial for improving predictions of carbon fluxes under present and future climates.

Climate has a large impact on the biological agents that drive wood decay. In temperate regions, fungi are generally the primary wood decay agents with a smaller role for macroinvertebrates (Cornwell et al., 2009; Seibold et al., 2021; Ulyshen, 2016). However, in tropical and subtropical regions, macroinvertebrates may account for almost one third of carbon emissions from deadwood decay (Seibold et al., 2021). Wood-feeding termites, largely tropical in their distribution (Jones & Eggleton, 2011), are the key macroinvertebrates responsible for this decomposition (Griffiths et al., 2019; Law et al., 2019; Liu et al., 2015; Seibold et al., 2021; Wu, Ulyshen, et al., 2021; Zanne et al., 2022). In some tropical ecosystems, termites may contribute more to deadwood decay than microbes (Griffiths et al., 2019; Wu, Ulyshen, et al., 2021).

Termites and microbes may be constrained by different environmental variables, such that termites compensate for low rates of microbial decay. In dry climates, termites are vulnerable to desiccation (Woon et al., 2019), but they can forage in dry conditions through behavioural adaptations such as building protective tunnels and sheeting. Because they can circumvent water limitation, termites may contribute more to wood decomposition in dry compared to wet ecosystems. Indeed, termite abundance increased during an El-Niño drought period in tropical rainforest (Ashton et al., 2019), and a global analysis found that termite discovery of *Pinus radiata* blocks was 1.8 times higher in semi-arid than in humid sites (Zanne et al., 2022).

Prior studies suggest that variation in wood traits can also affect rates of decomposition by microbes and termites (Guo et al., 2021; Liu et al., 2015). For example, wood with high density may resist termite mastication (Liu et al., 2015; Wu, Pietsch, et al., 2021). On the other hand, termites might circumvent some of the chemical constraints facing microbial decomposers. Higher carbon concentrations and lower concentrations of nitrogen, phosphorus and calcium—which are required for decomposer biomass growth—might constrain termites less than fungal decomposers (Weedon et al., 2009).

Across diverse tropical ecosystems, variation in climate and woody species composition makes it difficult to predict rates of deadwood decay. It remains unclear how climate and wood traits interact to affect the biotic agents that drive these rates. Because previous global studies have tested only one or a few wood species (Seibold et al., 2021; Zanne et al., 2022), we do not yet know how termite versus microbial decomposition varies among ecosystems and wood species in the tropics.

To address this knowledge gap, we aimed to quantify how termites and microbes impact decay rates in two globally relevant ecosystem types, tropical rainforest and dry savanna, in northeast Australia. We tested three main hypotheses in these systems. First, we hypothesized that termites should make greater relative contributions to deadwood decay in drier savanna compared to wetter rainforest. Second, we hypothesized that wood traits would explain variation in microbial decay across native wood species, but that termite-driven decay would be less constrained by wood traits. As no native woody species are shared between rainforest and savanna, to separate wood traits from environmental drivers, we also included non-native pine blocks as a common substrate in both sites.

We hypothesized that pine block decomposition would be greater in the rainforest compared to the savanna due to greater microbial activity in the wetter climate of the rainforest.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

We conducted our experiment from June 2018 to December 2021 at two sites with contrasting rainfall in Far North Queensland, Australia (Figure S1): (1) lowland rainforest located at James Cook University's Daintree Rainforest Observatory (−16.1012°N, 145.4444°E); (2) dry savanna located at Pennyweight Outstation in Australia Wildlife Conservancy's Brooklyn Sanctuary (−16.5746°N, 144.9163°E). These sites are located on the unceded territory of the Kuku Yalanji, Djabugay and Djungan peoples who are the Traditional Owners of the land. Sites were accessed with permission from James Cook University and the Australian Wildlife Conservancy. Mean temperatures were 24.4°C at the rainforest site and 24.7°C at the savanna site during the study period (https://power.larc.nasa.gov). The rainforest receives over four times as much rainfall as the savanna (rainforest: 4250 mm/yr from 1989 to 2019, weather station 31012; savanna: 960 mm/yr from 1989 to 2020, weather station 31180, https://www.bom.gov.au). Both sites have distinct wet and dry seasons with 80% and 94% of rain during November through April in the rainforest and savanna respectively. A previous survey in the same sites found eight termite species in the rainforest, all wood feeding, and six in the savanna, three of which are wood feeders (Clement et al., 2021). However, compared with the rainforest, termite encounter rates in deadwood are twice as high in the savanna (Cheesman et al., 2017; Clement et al., 2021).

We measured the decay rates of non-native pine blocks and 16 native woody species that vary widely in their traits. Ten woody species were native to the rainforest and six were native to the savanna. No species was native to both sites, and each species was deployed only at its native site. To test site effects such as climate, independent of woody species, we analysed decomposition of *Pinus radiata* (pine) blocks (9 × 9 × 5 cm) in a simultaneous experiment at both sites. Because *Pinus radiata* is a non-native species, there is no concern about decomposer local adaptation influencing its decay rate at either site. Although a reciprocal transplant design with native species could have also addressed this issue, we elected not to transplant native wood across sites to avoid accidentally introducing pests and to keep the experiment size manageable.

Native species were selected based on relative abundance, phylogenetic breadth and availability of stems with 5 to 9 cm diameters. Although our target was 10 species per site, tree diversity in the savanna site is relatively low, and there were only six species present that had multiple individuals with stems sizes ≥5 cm diameter. Myrtaceae dominate the savanna site, so four of the six species were from that family. At the more diverse rainforest site, we selected relatively abundant woody species representing a broader range of families and wood densities. Some palm stems with a diameter up to 10 cm were included because it was difficult to find palms with smaller diameters. At each site, we harvested stems from at least three live individuals per species (except for the palm, for which we could only access one individual) and cut stems to ~10 cm lengths. Any stems with irregularities, including branch nodes or high insect damage, were excluded. All stems and pine blocks were enclosed in 280 μm lumite® mesh (BioQuip) bags that were sealed by sewing shut the ends. Fresh native stems were not dried before deployment in the field. *Pinus radiata* blocks were dried at 120°C to a constant mass and weighed before deployment. We used this high temperature to help volatilize and remove secondary compounds that may deter some species of termites.

Half the stems and pine blocks were randomly assigned to a termite-exclusion (TE) treatment and the other half to a termite-inclusion (TI) treatment. To allow termite access, 10 openings (~5 mm in diameter) were cut into the mesh on the bottom of the TI bags (Figure S1). Within each native species, stems were paired by diameter before assigning treatments at random within each pair, allowing for roughly equivalent diameter distributions between the two treatments. Still, we acknowledge that varying stem diameters may contribute to variance in termite access and wood decay rates, which could impact our statistical power.

At each of the two sites, we established five stations each separated by at least 5 m along a transect line (Figure S1). This separation distance allows for independent termite discovery events within the same site and was used in previous studies (Cheesman et al., 2017; Zanne et al., 2022). To avoid bias in wood discovery by termites, stations were relocated if they were less than 0.5 m from any of the following: coarse woody debris, an existing termite mound, exposed rocks or substantial water flow paths. Intact leaf litter was removed from each station and the surface soil layer was homogenized via scraping. In the savanna site, dead grass within and up to 1 m away from each station was removed at the start of the dry season to minimize wildfire impacts on stems and blocks. Each station contained four TE stems and four TI stems of each species for a total of 80 native stems at each rainforest station and 48 stems at each savanna station. Stations also included six TE and six TI pine blocks. Stems and blocks were placed randomly at least 15 cm apart from each other and secured to the soil using metal lawn staples. For the TI treatment, the side of the mesh bag with holes faced the soil.

Native stems and pine blocks were harvested after 12, 18, 36 and 42 months. For each harvest, one TI and one TE stem or block was retrieved at random for each species from all stations. Harvest dates corresponded with either the end of the wet season (12 and 36 months) or the end of the dry season (18 and 42 months), with exceptions for three species. During the second harvest in the rainforest, we noticed that *Castanospermum australe*, *Normanbya normanbyi* and *Rockinghamia angustifolia* were decaying rapidly; consequently, we moved up the third and fourth harvests to 24 and 30 months (the end of the wet and dry season, respectively) for these three species. Pine blocks were also harvested at 24 and 30 months. In total we deployed 400 native stems (10 species x 2 treatments × 4 harvests × 5

stations) and 60 pine blocks (2 treatments × 6 harvests × 5 stations) in the rainforest as well as 240 native stems (6 species × 2 treatments × 4 harvests × 5 stations) and 60 pine blocks in the savanna. Of the 640 native stems deployed across both sites, 11 stems were either lost to fire ($n = 3$) or removed from the analysis because of handling or recording errors ($n = 8$). Of the 120 pine blocks, we removed four due to fire ($n = 2$) or errors ($n = 2$).

2.2 | Laboratory measurements of wood traits and mass loss

To process harvested samples, mesh bags were cut open and any exterior (nontermite produced) soil was brushed off. The fresh weight of the harvested material was recorded in the field before storing in paper bags for transport back to an air-conditioned laboratory for further processing. We found no holes or other evidence that termites escaped from the bags. In the laboratory, any carton or soil translocated by termites was removed. Disassociated bark and all remaining wood materials were weighed separately and included in total mass remaining. Stems and blocks were recorded as discovered (by termites) if we noted the presence of termites, imported soil or carton and/or evidence of termite damage (e.g. internal chambering). As such, evidence of discovery requires termite presence or attack, akin to the definition used by Zanne et al. (2022). It is possible that termites discovered but ignored wood they found unpalatable. Although we would not detect those discoveries, such blocks would not have experienced any termite damage. If termites were present, we collected at least two soldiers and five workers, if available, and stored them at 4°C in tubes of 70% ethanol for later identification.

Holes were drilled into each piece of harvested wood using a sterilized 6 mm drill bit to collect at least 5 g of sawdust for subsequent chemical analyses. The fresh weight of the drilled wood piece was recorded and placed in a preheated drying oven at 105°C for 72 h before reweighing. The dry mass of the harvested wood was calculated by multiplying its fresh mass at harvest by the dry mass fraction of the drilled wood piece. We decided it was not necessary to measure ash-free dry mass because we were able to adequately separate remaining wood from imported soil. To estimate the initial dry weight of each native stem on deployment, four other 'control' stems from the initial harvest of each species were weighed, dried at 105°C to constant mass, and reweighed. The dry weight of deployed stems was estimated by multiplying the fresh weight of the deployed stem by the mean fraction of dry weight calculated from control stems. Finally, to account for differences in the initial weights of stems and blocks, we calculated proportional mass loss for each stem or block using the following equation:

$$\text{Proportional Mass Loss} = \frac{(\text{Initial Dry Weight}) - (\text{Harvest Dry Weight})}{(\text{Initial Dry Weight})}.$$

We measured wood traits on three or four representative initial stems of each native species and on five pine blocks. Native wood density was determined by measuring the volume of water displaced by a stem piece and then weighing the stem after drying at 105°C for 72 h. We obtained pine wood density by dividing the average initial dry weight of all pine blocks without imperfections by the average block volume (405 cm^3). Sawdust samples were collected with a 6 mm drill bit from two initial stems of each native species or from five pine blocks to obtain material for nutrient and chemical analysis at the University of Illinois and Eastern Illinois University. Wood carbon and nitrogen concentrations were determined using elemental analysis by combustion (Costech). Lignin chemistry was determined with thioacidolysis followed by gas chromatography-FID to yield syringyl:guaiacyl ratios (Kalinoski et al., 2017). To measure pH, 500 mg of sawdust was combined with 10 mL 5 mM $CaCl_2$, vortexed and incubated overnight. The suspension was filtered through nylon mesh, and the pH of the filtrate was measured with an electrode (Geffert et al., 2019). Concentrations of P and Ca were determined following combustion of ~500 mg sawdust samples in a muffle furnace, dissolution of the residue in 1 M nitric acid, and analysis via inductively coupled plasma mass spectrometry (PerkinElmer Avio 200).

2.3 | Statistical analysis

2.3.1 | Defining decay agents

We acknowledge that both discovered and undiscovered stems may experience photodegradation and leaching of soluble compounds (Cornwell et al., 2009). Therefore, our definitions of microbial and termite decay may include these abiotic processes. Still, we do not expect much impact from photodegradation or leaching because wood is primarily composed of insoluble compounds, and UV exposure was limited due to canopy cover, the mesh bags we used and the low surface area to volume ratio of the stems. We refer to termite-driven decay as the additional decomposition observed in discovered compared to undiscovered wood. However, we recognize that termite discovery may alter subsequent microbial decay, and our design cannot detect such interactions.

2.3.2 | Testing drivers of termite discovery

To assess the variation in termite-driven decay across wood species, we first coded termite discovery as a binary variable, with wood samples categorized as discovered or undiscovered. To calculate discovery rates, we only used data for termite-inclusion (TI) stems. We tested how the odds of termite discovery depended on site (rainforest or savanna), harvest time (months since deployment) and native wood species using binomial generalized linear models. No interaction terms were included in the models for native wood because no species were shared between sites. We ran a separate model to test site and time effects on pine block discovery. All statistical analyses were carried out using R version 4.2.1 (R Development Core Team, 2022).

2.3.3 | Testing drivers of wood decay rates

To analyse termite contributions to deadwood decay, we fit a beta regression model to mass loss data with a logit link using the R package BETAREG (Cribari-Neto & Zeileis, 2010). The modelled dependent variable was proportional mass loss, and the fixed effects were site, termite discovery, time of harvest and two interaction terms: termite discovery × site and termite discovery × harvest. We included station as a random factor to account for possible autocorrelation among samples harvested from the same station. Separate models were run for the native wood and pine block data (Tables S1 and S2). If a stem was discovered by termites, we treated it as 'discovered' in the analysis, regardless of TI or TE status. In the exclusion treatment, termites managed to discover five stems in the rainforest as well as one stem and one pine block in the savanna.

Beta regression is recommended for analysing continuous proportion data because it can incorporate heteroscedasticity and produces less biased parameter estimates compared with linear models on transformed data, particularly as values approach asymptotic values of 0 or 1 (Douma & Weedon, 2019). We used maximum likelihood estimation to fit the model to the data. For stems that gained mass ($n = 17$, maximum gain = 15%), proportional mass loss was set to 0. Thus, as some proportions were equal to 0 or 1, we scaled the data by applying the following transformation: $(y^*(n - 1) + 0.5)/n$, where y is proportional mass loss, and n is the sample size (Smithson & Verkuilen, 2006). We subsequently ran ANOVAs to test the significance of fixed effects using the R package CAR (Fox & Weisberg, 2019). Post hoc comparisons of means were run using the 'emmeans' function from the R package EMMEANS (Lenth, 2021) with proportional averaging and Tukey HSD or Sidak corrections for multiple comparisons.

2.3.4 | Testing decay relationships with wood traits

To test the effects of wood species and site on microbial decay rates, we calculated *k*-values using only undiscovered stems or blocks (due to low termite discovery rates, we could not calculate *k*-values for discovered stems). The *k*-values were obtained by fitting a negative exponential model to proportional mass loss for the set of samples harvested over time for each combination of species and treatment at each station using the *nls* function in R. We then fit log-transformed *k*-values to linear models with site or wood species as fixed effects. We ran separate native species models for the rainforest and savanna because there were no overlapping species across sites. We also fit a separate linear model to the pine data with site as a fixed effect. After verifying normality, we used ANOVA to test for significant effects.

We used principal component analysis and linear regression to test for relationships between native wood traits and decay parameters. For each wood species, we calculated an average termite discovery rate by dividing the number of discovered stems or blocks by the total number of stems or blocks. We also computed an index of relative termite decay as $100^*(D1 - D0)/D1$ where $D1$ is the marginal mean mass loss for discovered wood and D0 is the marginal mean mass loss for undiscovered wood of each species. A principal component analysis was performed on mean trait values for each native wood species that were zero-centred and scaled to unit variance. The first two principal components were used as predictors in linear regressions with log-transformed *k*-values (microbial decay), average termite discovery rates and relative termite decay. Wood traits are reported for pine but were not included in these trait analyses because pine is non-native.

3 | RESULTS

3.1 | Wood discovery by termites depends on native wood species but not site

We assessed termite discovery of deadwood as the first step in quantifying termite contributions to wood decay. Discovery of native stems was low in both the rainforest and savanna, with only 17.3% (34 of 196) of termite-inclusion stems discovered in the rainforest and 22.0% (26 of 118) discovered in savanna. Discovery rates were higher for pine blocks, reaching 27.6% (8 of 29) in the rainforest and 62.1% (18 of 29) in the savanna. Termite discovery of native stems did not differ significantly between sites, but there were significant differences among wood species (LR $\chi^2 = 29.7$, $p = 0.013$; Figure 1a) and with time since deployment (LR $\chi^2 = 14.2$, $p < 0.001$; Figure 1b). Model coefficients were significant for *Eucalyptus cullenii* ($p = 0.036$) and marginally significant for *Rockinghamia angustifolia* ($p = 0.076$) indicating that these species experienced greater odds of attack by termites. Note that *Rockinghamia* was one of the three rainforest species harvested early due to rapid decay rates. For the pine blocks, discovery was higher in the savanna (LR $\chi^2 = 10.4$, $p = 0.001$) and varied significantly with time (LR $\chi^2 = 20.7$, $p < 0.001$; Figure S2).

3.2 | Termites increase wood decay rates only in rainforest

After determining which stems were discovered by termites, we tested our first hypothesis by quantifying the termite impact on wood decay at each site. The effect of termite discovery on native wood mass loss depended on site as indicated by a significant interaction between termite discovery and site ($\chi^2 = 22.6$, $p < 0.001$, Table S1). In contrast with our hypothesis, post-hoc contrasts showed that termites significantly increased native mass loss in the rainforest ($p < 0.001$) but not in the savanna ($p = 0.93$; Figure 2). In the rainforest, mean native mass loss for discovered stems was 73.2 ± 3.1% compared with 47.0 ± 2.4% for undiscovered stems and 49.9 ± 2.4% for all stems. In the savanna, mean native mass loss was 15.4 ± 2.7% for discovered stems, 14.8 ± 1.6% for undiscovered stems and 14.8 ± 1.6% for all stems. These values are marginal

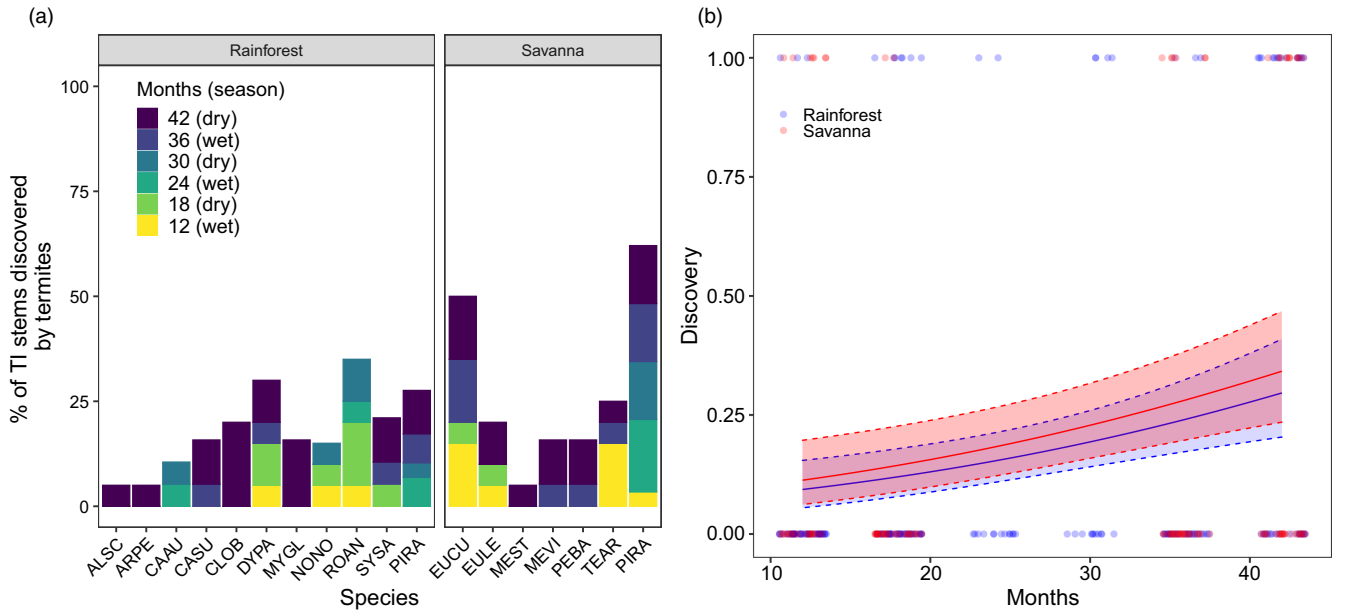

FIGURE 1 Discovery of wood by termites. (a) Percentage of termite-inclusion (TI) stems or blocks that were discovered by termites for each wood species and time point; number of TI stems recovered for each native species across all harvests ranged from 18 to 20. See Table 1 for species abbreviations. (b) Significant positive relationship between the number of months since deployment and the likelihood that a stem was discovered by termites (1 = stem discovery and 0 = undiscovered by termites). Dashed lines represent 95% confidence intervals around binomial regression predictions (solid lines). The difference between sites is not significant.

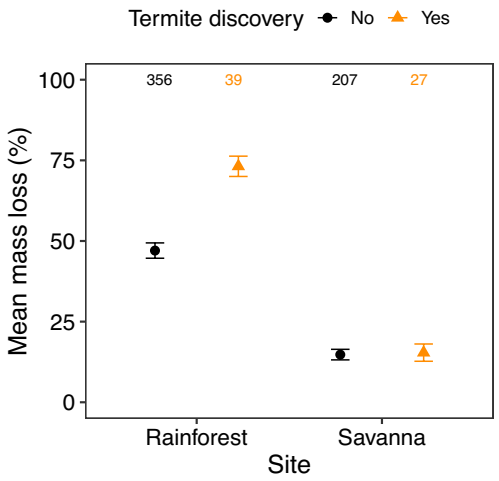

FIGURE 2 Decay of native stems. Percentage of mass lost across all harvests (marginal mean estimates from beta regression with standard error bars) for stems undiscovered by termites (primarily microbial decay) and stems discovered by termites (microbial and termite decay) in the rainforest and savanna. Undiscovered stems include all termite-exclusion stems and termite-inclusion stems that showed no evidence of termite discovery. Numbers at the top of the panel show sample sizes for each group.

means averaged across time points and wood species. There was an interaction between termite discovery and harvest time, but post-hoc tests did not indicate a clear directional change in discovery impact on native mass loss over time. Termites increased native mass loss at harvests after 12, 30, 36 and 42 months but not after 18 or 24 months.

Consistent with our third hypothesis, mean mass loss of pine blocks was much greater in the rainforest (40.0 ± 5.2%) than in the savanna (12.7 ± 2.6%). The main effects of termite discovery, site, and time of harvest were all highly significant determinants of pine mass loss, but there were no significant interactions (Table S2). Termites increased mean pine mass loss from 31.8 ± 4.6% to 68.6 ± 7.9% in the rainforest and from 10.0 ± 2.3% to 25.4 ± 5.0% in the savanna (Figure S3).

3.3 | Microbial decay rates vary significantly among wood species

To address our second hypothesis regarding wood traits, we assessed variation in microbial and termite-driven decay across wood species. When only undiscovered stems were considered, reflecting primarily microbial decay, mass loss rates varied significantly among native species at both sites (ANOVA; $p < 0.001$ for species effect at both sites; Figure 3). Mean decay rates were $0.36 \pm 0.02\,\text{year}^{-1}$ in the rainforest and four times lower ($p < 0.001$) in the savanna at $0.09 \pm 0.01\,\text{year}^{-1}$. Decay rates in the rainforest ranged from $0.15 \pm 0.02\,\text{year}^{-1}$ for *Alstonia scholaris* to $0.57 \pm 0.02\,\text{year}^{-1}$ for *Normanbya normanbyi* and in the savanna from $0.03 \pm 0.01\,\text{year}^{-1}$ for *Melaleuca stenostachya* to $0.20 \pm 0.02\,\text{year}^{-1}$ for *Petalostigma banksii* (Table 1). Pine decay rates were $0.21 \pm 0.04\,\text{year}^{-1}$ in the rainforest and a factor of five lower in the savanna at $0.041 \pm 0.004\,\text{year}^{-1}$ (ANOVA; $p < 0.001$).

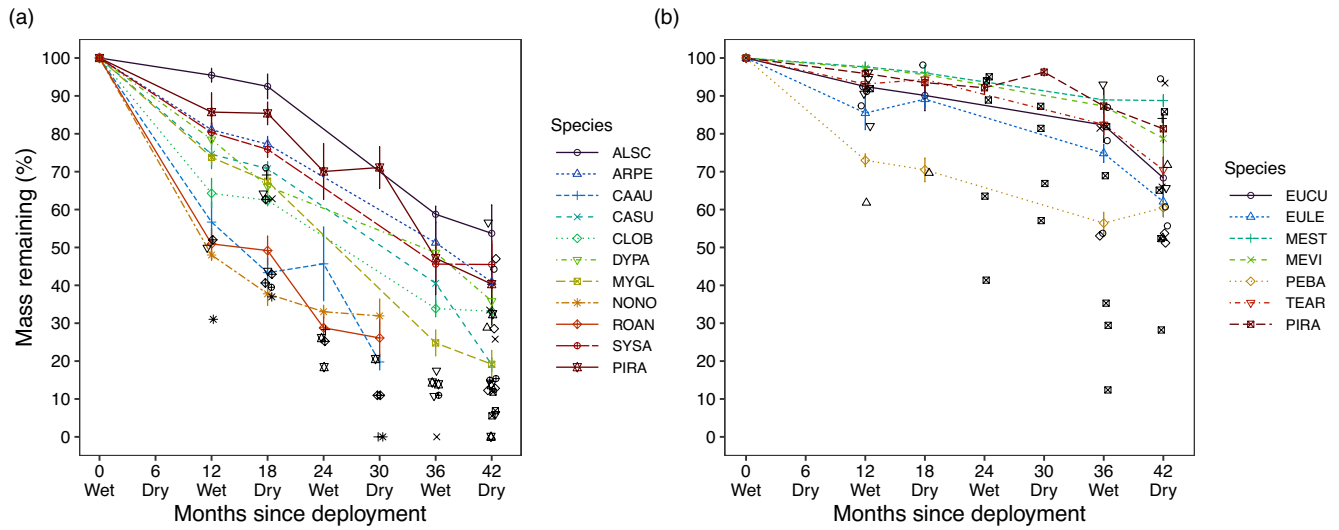

FIGURE 3 Percentage mass remaining (mean with standard error bars) of undiscovered stems or blocks (primarily microbial decay) for each harvest (months since deployment) in the rainforest (a) and savanna (b). Stems or blocks discovered by termites are shown with individual black symbols that are not included in the means. See Table 1 for species abbreviations.

TABLE 1 Details of species deployed in each site, microbial decay rates and wood traits measured including wood density, % carbon, % nitrogen, % calcium, syringyl:guaiacyl ratios and pH.

Wood species	Code	Native site	$k \pm$ SE (year^{-1})	Density (g cm^{-3})	% C	% N	% P	% Ca	S:G	pH
Alstonia scholaris	ALSC	Rainforest	0.15 ± 0.02	0.28	50.0	0.39	0.0130	0.219	0.57	5.93
Argyrodendron peralatum	ARPE	Rainforest	0.22 ± 0.02	0.65	51.4	0.31	0.0073	0.350	2.80	5.26
Castanospermum australe	CAAU	Rainforest	0.52 ± 0.03	0.54	48.6	0.37	0.0188	0.049	2.26	4.43
Cardwelia sublimis	CASU	Rainforest	0.32 ± 0.02	0.48	50.0	0.39	0.0192	0.216	2.82	4.98
Cleistanthus oblongifoloius	CLOB	Rainforest	0.35 ± 0.01	0.59	49.0	0.47	0.0233	0.157	1.31	4.66
Dysoxylum papuanum	DYPA	Rainforest	0.26 ± 0.02	0.57	49.0	0.41	0.0225	0.278	2.15	5.41
Myristica globosa	MYGL	Rainforest	0.37 ± 0.02	0.43	49.5	0.49	0.0306	0.149	1.82	5.61
Normanbya normanbyi	NONO	Rainforest	0.57 ± 0.02	0.61	46.9	0.25	0.0135	0.078	3.02	4.25
Rockinghamia angustifolia	ROAN	Rainforest	0.56 ± 0.02	0.55	48.2	0.62	0.0292	0.243	2.40	5.04
Syzygium sayeri	SYSA	Rainforest	0.23 ± 0.02	0.57	49.7	0.34	0.0244	0.078	1.61	4.15
Eucalyptus cullenii	EUCU	Savanna	0.09 ± 0.01	0.85	51.3	0.25	0.0014	0.625	2.20	4.04
Eucalyptus chlorophylla	EULE	Savanna	0.11 ± 0.01	0.73	48.2	0.24	0.0027	0.224	1.94	4.13
Melaleuca stenostachya	MEST	Savanna	0.03 ± 0.01	0.67	51.9	0.49	0.0031	0.248	1.30	5.59
Melaleuca viridiflora	MEVI	Savanna	0.05 ± 0.01	0.62	52.4	0.35	0.0035	0.079	0.46	4.67
Petalostigma banksii	PEBA	Savanna	0.20 ± 0.02	0.68	50.0	0.62	0.0088	0.163	1.26	5.05
Terminalia aridicola	TEAR	Savanna	0.08 ± 0.01	0.74	49.4	0.40	0.0040	0.599	1.03	4.11
Pinus radiata	PIRA	—	0.041 ± 0.004	0.43	49.2	0.14	0.0009	0.044	0.02	4.32
			0.21 ± 0.043							

3.4 | Wood traits explain microbial but not termite-driven decay rates

We next asked if variation in wood traits could explain observed differences in microbial and termite-driven decay. Native species varied along two principal components that together explained 65% of the variation in their wood traits (Figure 4). PC1 separated species primarily based on wood density and nutrients, especially % P. PC2 separated species primarily based on % C and S:G ratio. Species traits differed among the savanna and rainforest sites (Figure 4a). Savanna species tended to have higher PC1 and PC2 scores associated with higher % C or higher wood density.

Principal component scores based on traits explained significant variation in microbial decay rates but not termite discovery or relative termite decay. Together, negative relationships with PC1 and PC2 explained 85% of the variance in average decay rates across species, with 50% of the variance attributed to PC2 and 35% to PC1 ($p < 0.001$, multiple linear regression, Table S3). The factor loadings indicate that higher rates of wood decay correlate with higher S:G and % P but lower % C and wood density (Figure 4b). In contrast, linear regressions showed no significant relationships between trait-based PCA scores and average termite discovery rate or relative decay of discovered stems across wood species (Table S3). Along those same lines, the two species with the highest rates of termite discovery, *Eucalyptus cullenii* and *Rockinghamia angustifolia*, had divergent scores along PC1 (Figures 2a and 4a). Although we did not include pine blocks in the principal component analysis because pine is a non-native species, we found that pine wood had low nutrient concentrations and decay rates relative to most native species (Table 1). Pine S:G ratios were also very low as expected because *P. radiata* is a gymnosperm.

4 | DISCUSSION

To our knowledge, this study is the first to assess the relative contributions of microbes and termites to decomposition of woody species from the Australian tropics. As expected based on rainfall differences, we found that wood undiscovered by termites decayed four times faster in the rainforest than in the much drier savanna. Surprisingly, in contrast to our first hypothesis, termite-driven decay of native wood was greater in the rainforest. Both termite discovery and microbial decay rates varied significantly among wood species, and microbial decay rates were well-explained by the suite of traits that we measured, consistent with our second hypothesis. However, species with the greatest rates of microbial decay were not necessarily more appealing to termites, and wood traits did not explain rates of termite discovery or termite impact on decay rates.

4.1 | Patterns in termite-driven wood decay

Overall, native wood in savanna and rainforest showed remarkably little termite-driven decay. At both sites, termite discovery rates were relatively low—22% or less on average during a 3.5-year period.

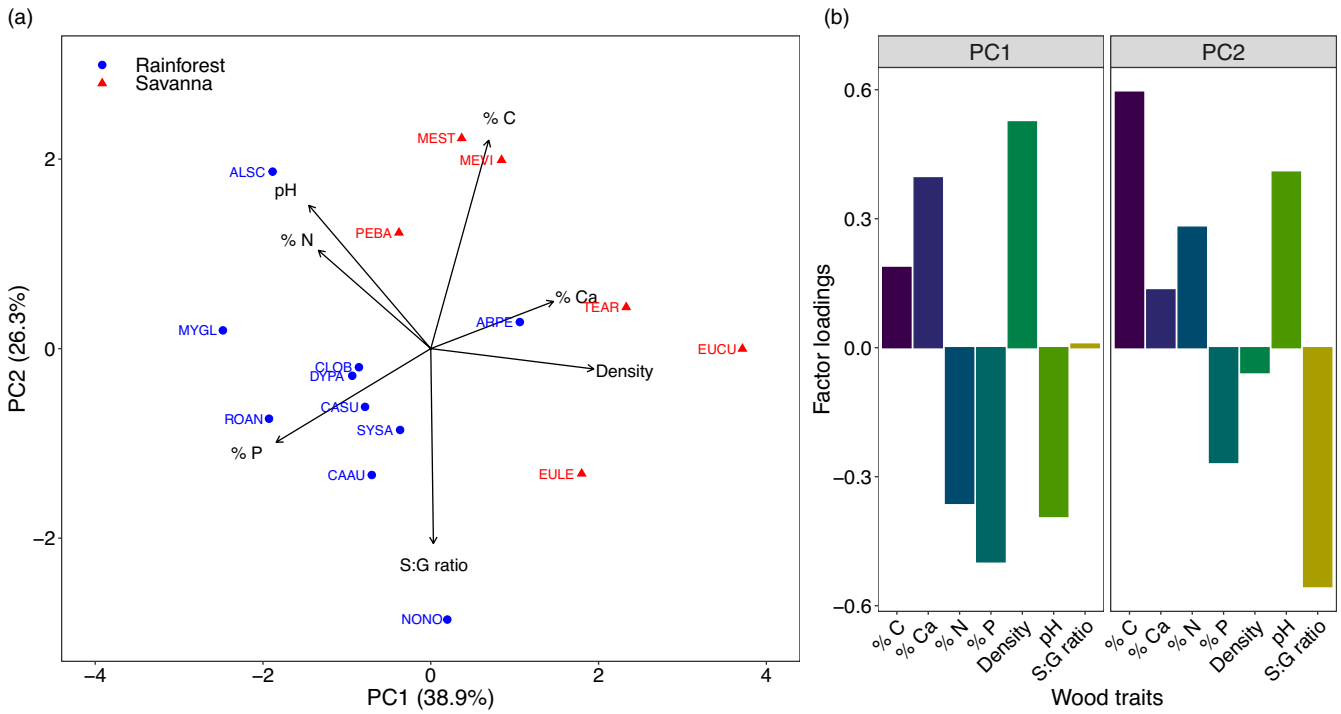

FIGURE 4 Principal component ordination of native woody species (a) and wood trait factor loadings on the first and second principal components (b). See Table 1 for species codes.

In the savanna site, even when termites discovered native wood, mass loss remained similar to undiscovered wood. Termite impacts on mass loss were greater in the rainforest, but too few stems were discovered to have much effect on overall wood decay rates. Our results contrast with previous findings in southeast and east Asian rainforests (Griffiths et al., 2019; Wu, Ulyshen, et al., 2021) as well as South African savanna where termites were responsible for up to 65% of wood block decay (Walker et al., 2022).

The patterns we observed with native wood decay also contrast with our pine block results. Termites discovered pine blocks at much higher rates than native stems, especially in the savanna site, despite having lower nutrient concentrations than most native stems. Once discovered, the termite impact on mass loss was greater for pine blocks than for native wood. Termites more than doubled the mass loss of discovered pine blocks in both the rainforest and savanna, in line with a previous study (Cheesman et al., 2017). This finding may reflect a general termite preference for gymnosperm over angiosperm wood that does not apply to microbial decomposers (Guo et al., 2023).

Our results suggest that long-term associations between wood traits and decomposers may shape decay patterns, such that inferences based on non-native substrates like pine blocks may not apply to local wood species. The presence of bark and endogenous factors within the wood can influence the colonization of deadwood by saprotrophic microbes and macroinvertebrates, resulting in different decomposition patterns for native compared to non-native wood (Dossa et al., 2018; Ulyshen, 2016; Ulyshen et al., 2016). Therefore, studies like ours that include a broad range of native wood stems may give a more complete picture of ecosystem-scale wood dynamics compared to studies focused on pine blocks or a single woody species (Cheesman et al., 2017; Griffiths et al., 2021; Hu et al., 2017; Law et al., 2019; Stoklosa et al., 2016; Wu, Ulyshen, et al., 2021). Still, including the pine blocks in our experiment provided useful data on site-driven differences in decay rates while ruling out the possibility that we pseudoreplicated our savanna stations in an area with unusually low termite abundance.

4.2 | Drivers of termite-driven decay in savanna versus rainforest

We were surprised to find only minor termite impacts on native wood decay in our savanna site, given the relatively high termite abundance, diversity and impact on pine block decomposition there. In Australia, termite abundance and richness are greater in dry savannas compared with wet rainforests, in contrast with Africa or Central and South America (Eggleton, 2000, Dahlsjö et al., 2014, Clement et al., 2021). Clement et al. (2021) found that termite occupancy of deadwood was 21% in the savanna but only 3% in our rainforest site.

In the savanna, termite-driven decay may happen before stems fall to the ground. The dominant wood-feeding *Coptotermes* termites specialize on the heartwood of living trees rather than foraging for fallen deadwood (Cheesman et al., 2017). *Eucalyptus* species, such as *E. cullenii*, dominate the savanna tree biomass, and most of their living stems are hollow (Flores-Moreno et al. *unpublished*), most likely due to *Coptotermes* activity. This hollowing is so common that the Traditional Owners of the land have used such stems to make didgeridoos. Thus, wood-feeding termites in the savanna may have a substantial impact on wood turnover, but more so in standing live rather than fallen stems.

Other factors may have also contributed to our study's unique patterns of termite discovery and wood decay. In the savanna, moisture limitation may have inhibited termite-driven decay more than we expected initially. Previous studies indicate that termite foraging increases when moisture is higher (Davies et al., 2015; Dawes-Gromadzki & Spain, 2003) and humidity is more stable (Wu, Ulyshen, et al., 2021). Also, Australia lacks wood-feeding, fungus-farming termites belonging to the subfamily Macrotermitinae (Clement et al., 2021; Davies et al., 2003). Fungus-farming termites are thought to contribute substantially to deadwood decay; thus, their absence may mean termites play a smaller decomposer role in Australia compared with Africa or Southeast Asia where fungus-farming termites are abundant (Davies et al., 2003).

Termite discovery increased over time at both rainforest and savanna sites as indicated by the increasing slope of the curves in Figure 1b and Figure S2. It is possible that the nutritional composition and quality of deadwood changes as decomposition progresses, influencing the likelihood of termite discovery (Guo et al., 2021). For example, greater microbial decay observed in the rainforest may have aided termite-driven decay by making the deadwood softer and more palatable to termites (Liu et al., 2015; Waller et al., 1987). Termites may attack certain wood substrates only later in decay because of changes in the nutritional composition of the wood (Guo et al., 2021) or because white and brown rot fungi become more prevalent in the substrate (Rajala et al., 2012). Termite attack rates could also be higher during the wet season, although the seasonality of termite activity at our sites is not clear (Cheesman et al., 2017; Clement et al., 2021), and our study did not assess seasonal changes in decay. We note that the damage caused by termites did not change systematically with time, as might be expected if discovered stems harvested later had more time to be eaten. It may be that once a stem is discovered, termites attack it quickly and then move on.

4.3 | Impacts of wood species and traits on decay agents

We found that termite-driven decay depended on wood species. *E. cullenii*, the same species that has many hollow stems, was also discovered more frequently by termites foraging on the ground. These results lend support to other field studies suggesting that termites preferentially attack some species of wood over others (Guo et al., 2021).

In contrast to other studies (Liu et al., 2015), we found no relationship between wood traits and termite discovery or decay. Given

that termite communities in Australia are unique and less diverse compared with other tropical regions (Clement et al., 2021), they may show different preferences for wood traits. It is also possible that we did not detect a relationship between termite decay and wood traits due to the low discovery of stems by termites. Furthermore, termite communities are completely distinct between Australian savanna and rainforest, potentially leading to different preferences for wood traits across our sites. Due to the dominance of Eucalypts in Australian savanna (Franklin, 2022) our range of species was small, and it is possible that secondary chemical compounds in Myrtaceae deterred termite attack.

In our study, wood traits played a stronger role in constraining microbial compared to termite-driven decay. Microbial decay varied significantly with both wood species and site. Conditions for fungal growth are likely more favourable in the rainforest which receives four times more rainfall than the savanna (A'Bear et al., 2014; Brischke & Alfredsen, 2020; Meentemeyer, 1978; Whitford et al., 1981). In addition, the wood species in the rainforest had trait values distinct from those in the savanna. On average, the rainforest species had higher % P, lower wood density and higher S:G lignin ratios, all of which may contribute to faster rates of decomposition. However, microbial decay rates for pine blocks were five times greater in the rainforest than the savanna, implying that much of the difference in microbial decay between sites was likely due to climate, particularly soil moisture. By including pine blocks with standardized wood physical and chemical properties in our design, we were able to identify strong site effects on decomposition independent of wood species. Within sites, though, wood traits explained significant variation in rates of microbial decay.

5 | CONCLUSIONS

Our study provides valuable insight into the mechanisms driving decay of woody species in the tropics. At the ecosystem scale, rates of carbon cycling through deadwood depend on termite communities, including their wood-feeding preferences, along with woody species composition. We found that rates of termite discovery and microbial decay varied widely across wood species, meaning that decay rates from a single species, especially non-native *P. radiata*, may not be representative at the ecosystem level (Cheesman et al., 2017). Termite discovery of native wood stems was not only much lower relative to *P. radiata* but also highly variable. Moreover, once wood was discovered, termite-driven decay differed significantly between sites. Despite low abundances compared to the savanna, termites at our rainforest site had a relatively larger impact on the wood decay rates of multiple native species.

Our study also suggests that predictive models should incorporate site-specific mechanisms and variation in wood traits when estimating ecosystem-scale patterns in wood decay. A major goal of decomposition studies is to use estimated rates of decay to predict the fate of carbon stored at ecosystem to global scales. Yet, existing Earth system models exclude decomposer soil fauna (Filser et al., 2016) and represent wood as a homogenous carbon pool (Koch et al., 2021; Thornton & Rosenbloom, 2005). To predict the fate of carbon from deadwood more accurately, these models could incorporate decomposition relationships with wood traits along with regional data on termite communities and contributions to wood decay, as we report here.

AUTHOR CONTRIBUTIONS

Stephanie Law and Steven D. Allison drafted the manuscript. Stephanie Law, Steven D. Allison and Habacuc Flores-Moreno analysed the data. Habacuc Flores-Moreno, Marc Rosenfield, Rebecca Clement and Amy E. Zanne set up the experiment. Abbey Yatsko, Habacuc Flores-Moreno, Rebecca Clement, Marc Rosenfield, Alexander W. Cheesman, Lucas A. Cernusak, James W. Dalling, Thomas Canam, Isra Abo Iqsaysa, Elizabeth S. Duan 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

The authors have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and code associated with this study are publicly available at Zenodo https://doi.org/10.5281/zenodo.7672145 (Law et al., 2023).

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SUPPORTING INFORMATION

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

Figure S1. (A) Study sites: dry savanna at Pennyweight Outstation (left) and moist tropical rainforest at Daintree Rainforest Observatory (right); (B) bags for termite exclusion (TE) and termite inclusion (TI, with holes); (C) schematic of station transects for both sites, with images of sample stations from the savanna (left) and rainforest (right).

Figure S2. Discovery of pine blocks by termites. Significant positive relationship between the number of months since deployment and the likelihood that a stem was discovered by termites (1 = stem discovery and 0 = undiscovered by termites). Solid lines represent binomial regression predictions for each site (rainforest in blue; savanna in red), and dashed lines represent 95% confidence intervals around predictions. The difference between sites is significant ($p = 0.001$).

Figure S3. Decay of pine blocks. Percentage of mass lost across all harvests (marginal mean estimates from beta regression with standard error bars) for stems undiscovered by termites (only microbial decay) and stems discovered by termites (microbial and termite decay) in the rainforest and savanna. Undiscovered blocks include all termite-exclusion blocks and termite-inclusion blocks that showed no evidence of termite decay. Numbers at the top of the panel show sample sizes for each group.

Table S1. ANOVA (type II) outputs for the beta regression model conducted on percent mass loss of native stems with station included as a random factor. Harvest is treated as a categorical variable based on AIC comparison with harvest as a continuous variable.

Table S2. ANOVA (type II) outputs for the beta regression model conducted on percent mass loss of pine blocks with station included as a random factor. Harvest is treated as a continuous variable because models with harvest as a categorical variable did not converge.

Table S3. Multiple regression model outputs for dependent variables as a function of principal component 1 (PC1) and principal component 2 (PC2) scores derived from native woody species traits. *** denotes $p < 0.001$.

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