

RESEARCH ARTICLE

Why are trees hollow? Termites, microbes and tree internal stem damage in a tropical savanna

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Abstract

1. Wood plays a vital role in the terrestrial carbon cycle, both sequestering and subsequently releasing carbon to the atmosphere via decomposition. Decomposition has largely been studied in fallen and standing deadwood; much less is known about decomposition occurring inside live trees due to hollowing by wood-feeding termites and microbial heart rot. Internal stem damage is difficult to measure, leaving many unresolved knowledge gaps. Little is known regarding the location and total amount of damage done by termites and microbes, as well as whether these decomposers act in concert or separately. Furthermore, tree species, wood density and stem size can influence fallen deadwood decomposition, but their role in living tree internal damage is largely unknown.
2. We destructively harvested 63 trees, finding internal damage in 32. We intensively sampled the internal stem damage in these 32 to investigate the relative contributions of microbes and termites in a tropical savanna in Queensland, Australia. We tested if damage changed at different heights in the tree, quantified tree-level termite and microbial damage and examined if termite and microbial damage co-occurred. We also tested the influence of tree species, wood specific gravity and size on tree-level internal stem damage across four species.
3. Termite and microbial damage were present in 45% and 33% of all trees, respectively. On average, termite damage reduced total tree biomass by 3.3% (maximum 28%, SD = 4.7%) and microbial damage by 1.8% (maximum 26%, SD = 5.3%). The amount of damage from both decomposers decreased with increasing heights up the tree. Termite and microbial damage co-occurrence was greater within trees than within individual cross section samples, suggesting local competitive exclusion or niche partitioning by decomposers. Tree species was a better predictor of damage than either wood specific gravity or tree size.
4. Half of the trees in our study had substantial internal stem damage, highlighting the considerable role that termites and microbes play in decomposing wood within living trees. Our findings unveil the previously concealed wood decomposition

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dynamics occurring inside trees, with implications for accurate carbon estimation across savanna ecosystems.

KEYWORDS

carbon storage, internal stem damage, microbial wood decomposers, live tree biomass, wood decomposition, wood-feeding termites

1 | INTRODUCTION

Wood serves as both a carbon (C) sink and source in terrestrial ecosystems (Pan et al., 2011; Wijas, Allison, et al., 2024). Living tree biomass constitutes a large C sink globally, containing an estimated 363 ± 28 Pg C in stems, branches and roots (Pan et al., 2011). When they die, trees transition into the deadwood biomass pool, which is estimated to store an additional 73 ± 6 Pg C in forest systems (Pan et al., 2011). However, deadwood biomass pools are highly dynamic and are broken down by biotic (e.g. invertebrates or microbes) and abiotic (e.g. fire or UV) drivers, cycling C back into soils and the atmosphere (Cornwell et al., 2009; Wijas, Allison, et al., 2024). With substantial C stocks present in both living and dead trees, decomposition of this woody biomass is critical for C release in ecosystems where trees are present (Wijas, Allison, et al., 2024; Zhou et al., 2007).

Our understanding of C cycling in wood primarily focuses on fallen and standing deadwood (Bradford et al., 2021; Harmon et al., 2020). However, a third category of deadwood found within living trees, internal tree stem damage (e.g. heart rot, cracks or hollows), has been acknowledged for some time (Highley & Kirk, 1979; Janzen, 1976) but is rarely quantified; this knowledge gap means we do not know how much above-ground biomass (AGB) may be missing in living trees (Calvert et al., 2024; Zheng et al., 2016). Furthermore, little is known about how different decomposers break down wood in trees and to what extent they contribute to biomass removal (Flores-Moreno et al., 2024). Internal damage has been estimated to impact 3%–42% of tree AGB (Flores-Moreno et al., 2024; Heineman et al., 2015; Monda et al., 2015; Zheng et al., 2016), largely affecting tree heartwood (the wood at a tree's centre; Hillis, 1987). Therefore, internal stem damage remains concealed and as a result is typically overlooked during biomass assessments (Calvert et al., 2024); it however represents wood C loss that takes place during part of the tree life cycle usually associated with active C sequestration (Flores-Moreno et al., 2024). Wood inside living stems faces little abiotic decomposition (Kataoka et al., 2007; Zhou et al., 2007); therefore, an understanding of internal stem damage rests on measuring the role of biotic decomposers.

Microbes are important biotic wood decomposers in ecosystems around the globe (Cornwell et al., 2009; Law et al., 2023; Ulyshen, 2016), while termites are especially important in dry tropical savanna ecosystems (Wijas, Flores-Moreno, et al., 2024), both in living trees, which they frequently hollow (Werner & Prior, 2007) and in fallen deadwood (Wijas, Flores-Moreno, et al., 2024;

Zanne et al., 2022). Microbes and termites differ in wood decomposition strategies, which impacts wood C storage and release. Microbial decay occurs via releasing extracellular enzymes that degrade cellulose, hemicellulose and, in some cases lignin, in situ (Blanchette, 1991), decreasing wood density throughout the decay process (Harmon et al., 2011). In contrast, termites relocate decomposition away from the original wood source. They consume wood pieces that are moved to the nest or mound and chemically digested via microbes and/or endogenous cellulases in their guts (Brune & Dietrich, 2015). Some termites live within the deadwood they consume, in which case wood decomposition occurs in situ, albeit away from its original placement in the tree (Eggleton & Tayasu, 2001). Termites process labile C compounds, such as cellulose, but cannot digest lignin, which becomes concentrated in their excretions (Myer et al., 2021). These distinct pathways of microbial and termite decomposition therefore impact the quantity of wood consumed, the components decomposed and the location of decomposition.

Internal stem damage is often quantified from a single measurement near the tree base or at diameter at breast height (DBH) (Eleuterio et al., 2020; Flores-Moreno et al., 2024). This protocol likely overlooks vertical variation in how biotic decomposers colonize and damage trees. The majority of termites (litter, mound and soil-dwelling) occur and forage on the ground, and observations of frequent damage and mound-building at tree bases (Eleuterio et al., 2020) suggest that termite internal damage is greatest at the tree base. However, some drywood termites build colonies in dead branches of living trees (Abe, 1987), which could alternatively concentrate damage in the crown. Microbes, on the other hand, colonize wood through various means and locations: spores entering wounds in crown branches or the main trunk via wind dispersal (Rayner & Boddy, 1988), hyphae entering roots from the soil (Boddy, 1999) or by being latently present in wood as endophytes (Boddy, 1994). As such, microbe-mediated damage may be less related to vertical position in the tree than termite damage since wounding can occur at different heights. Entry points could come from fire scarring at the tree base or broken branches resulting from wind damage in the crown (Perry et al., 1985). This diversity in foraging and dispersal strategies of termites and microbes likely results in varied spatial colonization patterns in living trees, affecting the distribution and extent of internal stem damage.

It is currently unknown whether termites and microbes partition internal tree wood resources or simultaneously damage the same space, as most measurement methods are unable to differentiate between termite or microbial damage (Flores-Moreno et al., 2024).

Studies have shown that the assemblage of deadwood decomposer communities can vary through space and time (Malik, 2023). That said, the interactions between termites and microbes during this process are poorly understood (Ulyshen, 2016). For example, as microbes are reliant on moisture, wood ground contact facilitates moisture transfer and microbial colonization from the soil, resulting in suspended wood being drier, slower to decompose and of different microbial composition compared to fallen deadwood (Barrera-Bello et al., 2023). However, Law et al. (2019) found that termite, but not microbial, deadwood decomposition was vertically stratified, in that termite decomposition was greater for wood in contact with the ground compared to wood that was suspended above the forest floor. There is also reason to believe that wood may undergo simultaneous decay from termite and microbial decomposers; termites could serve as vectors for wood-decay fungi through their foraging (Viana-Junior et al., 2018), which could result in both organisms sharing wood resources for some time. However, other negative interactions such as deterrence have been suggested, where fungi can limit or exclude termite feeding (Kamaluddin et al., 2016), which may result in spatial partitioning of wood resources by the two decomposers. Understanding where in the tree termites and microbes are active decomposers, as well as whether termite and microbial damage co-occur in living wood, will provide new insight into how partitioning and use of wood resources by different decomposers influences internal biomass decomposition.

Wood decomposition is not solely affected by biotic decomposers; wood traits and qualities of the decay substrate influence how organisms access and utilize wood resources (Cornwell et al., 2009; Law et al., 2023). Tree traits such as wood specific gravity (defined as wood density relative to water; Williamson & Wiemann, 2010) and tree size have been associated with internal stem damage (Rayner et al., 2014). In one study, higher wood specific gravity predicted greater internal damage, notably in Myrtaceae savanna trees in sites with high termite activity (Flores-Moreno et al., 2024). Wood specific gravity is often negatively associated with microbial wood decomposition; however, this relationship, though consistent, is typically weak (Weedon et al., 2009). Internal stem damage may also vary based on tree size, as larger trees often have more exposure time to sustain internal damage and offer more biomass for colonization (Werner & Prior, 2007; Zheng et al., 2016). Taken together, determining the interactions among tree species, wood traits and biotic decomposers is crucial for understanding how trees accumulate internal stem damage.

In this study, we destructively harvested savanna trees in north Queensland, Australia, to evaluate the extent of internal stem damage caused by microbes and termites. Our research questions and hypotheses were as follows: (Q1) Does the amount of termite versus microbial internal damage change at different heights in trees? We expected that termite damage would be greatest at the tree base (a typical entry point) and that microbial damage would have no association with height (entry points occur through trees). (Q2) How much tree-level damage is attributed to termites versus microbes? We expected that termites would cause more internal stem damage,

since they have a greater role in fallen deadwood decomposition than microbes in savannas. (Q3) Does microbial and termite damage co-occur at the cross section and at the tree levels? To what degree are microbial and termite damage spatially separated, or adjacent to one another? Given limited knowledge of termite and microbe co-occurrence, cross section and tree-level co-occurrence was expected to be equivalent. (Q4) How well do tree-level characteristics (species, size and wood specific gravity) predict the amount of microbial or termite damage? We expected that species would vary in internal stem damage amount, Myrtaceae species would be most damaged by termites and high wood specific gravity would increase termite damage but decrease microbial damage. Lastly, we expected that large trees would have the most damage from both decomposers.

2 | MATERIALS AND METHODS

2.1 | Study ecosystem

The study was carried out in October 2022 in the Iron Range on Cape York Peninsula, Far North Queensland (−12.7781°N, 143.3199°E, Figure 1). This site is in the Australian Monsoon Tropics, with a seasonally wet tropical climate and mean annual rainfall of 2057 mm, ranging from 1110 to 3299 mm (65-year average, Australian Bureau of Meteorology, 2023). Mean annual temperature of the region averages 26°C with monthly averages ranging between 20.6 and 30.9°C (Australian Bureau of Meteorology, 2023). The study site is a frequently burned savanna with dominant species as follows: *Corymbia clarksoniana*, *Eucalyptus tetrodonta*, *Lophostemon suaveolens* (all Myrtaceae) and *Planchonia careya* (Lecythidaceae). Other species present include *C. tessellaris* (Myrtaceae) *Parinari nonda* (Chrysobalanaceae), *Grevillea parallela* (Proteaceae) and *Acacia flavescens* (Fabaceae). Trees in the study area were identified to the species level by a botanist with local expertise (D. Fell, personal communication). Tree density at the site averaged 326 trees ha⁻¹ with a DBH range of 1.3–69.7 cm (mean 17.1 cm ± 12.1 SD) (Calvert et al., 2024). Access to the site and permission for fieldwork was granted by the private landowner.

2.2 | Destructive harvest protocol

Sixty-three trees were harvested from a pre-planned firebreak clearance in two survey areas (lower plot: 1.84 ha, upper plot: 0.27 ha, Figure 1). A permit was not required for clearing the firebreak. As trees were felled ~1 m from the base, they were assessed at the cut point for internal stem damage; those displaying no signs of internal stem damage were not further sampled due to the intensity of labour involved in sampling. For trees showing signs of internal stem damage at the felling point, we sampled four to seven cross sections per tree (cross sections had a 4-cm average thickness) along the lower stem from where the tree was felled (C1), at the midpoint in

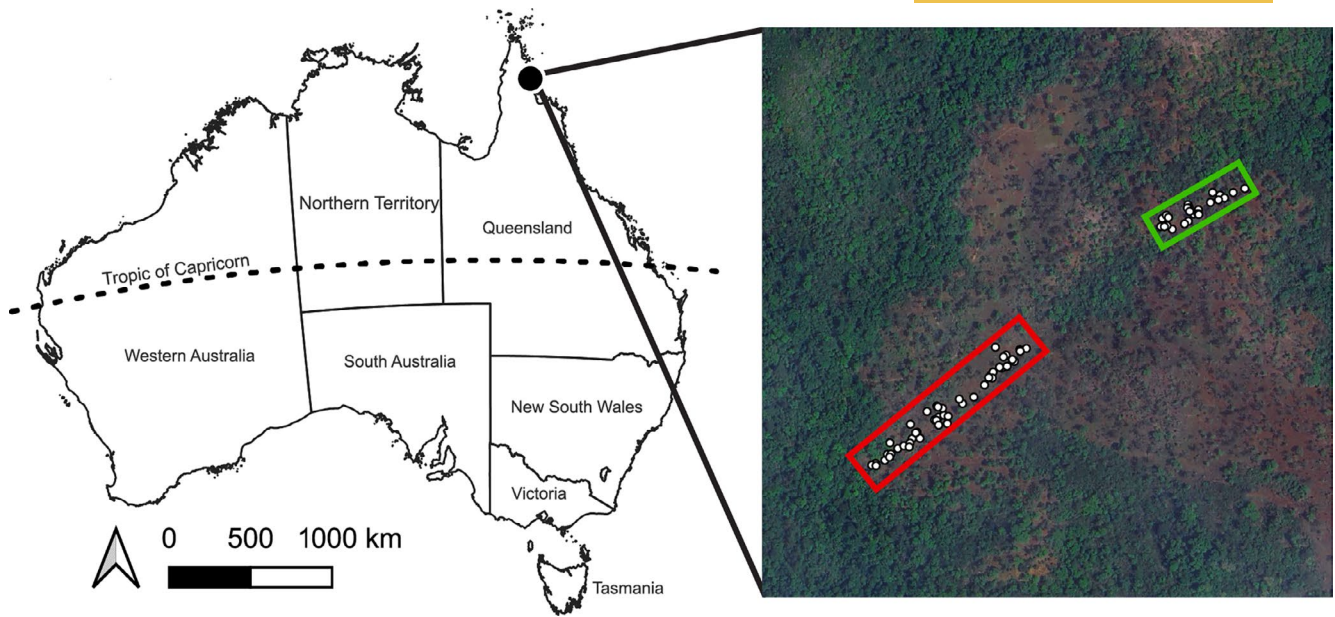
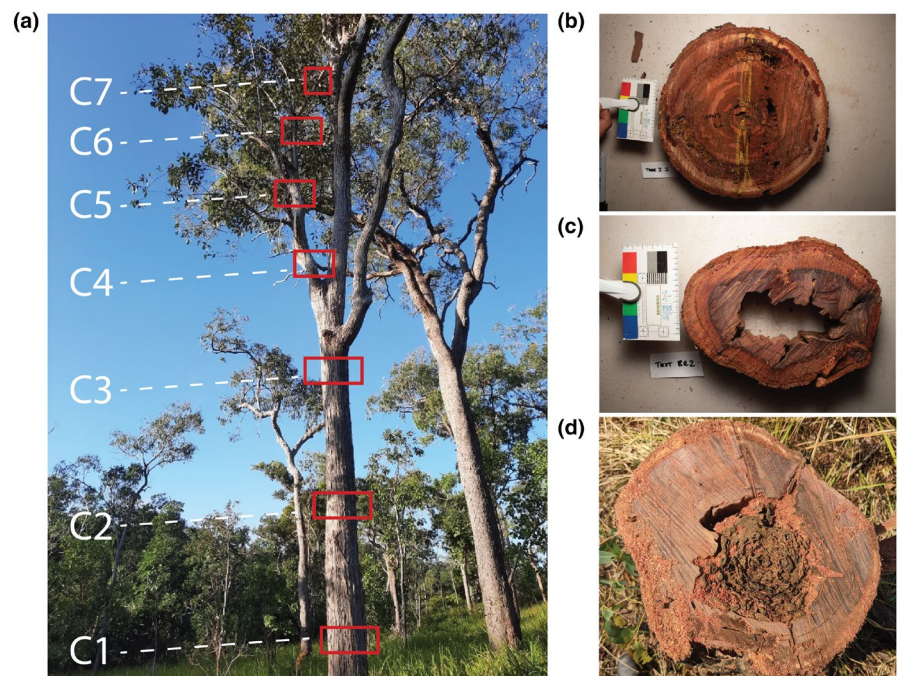


FIGURE 1 Location of the study site in the Iron Range on Cape York Peninsula, Far North Queensland and the two pre-planned firebreak clearance areas, including the lower plot (outlined in red, 1.84 ha) and upper plot (outlined in green, 0.27 ha) from which trees ($n=63$) were destructively harvested.

FIGURE 2 (a) Cross section sampling scheme to measure internal stem damage at multiple points through the entire height of the tree, (b) microbial internal stem damage via heart rot, (c) termite internal stem damage via hollowing and (d) stem hollow filled with termite excretion.



the lower stem (C2, only if damage was present at C1 and C3) and 50cm below the first branching point (C3). Cross section samples were then taken in the tree crown following decreasing branch sizes (C4–C7, Figure 2a). To test our assumption that trees without signs of damage at the felling point did not have damage occurring in other tree parts, for seven trees that were undamaged at the felling point we carried out the full cross-sectional sampling (collecting C1–C7); we observed no damage in other parts of the tree, confirming our assumption. From the 63 total harvested trees, 32 trees had internal stem damage along the main stem and 31 trees were undamaged

(see Table S1). This sampling procedure required roughly 12 person hours per sampled tree.

In total, we obtained 200 tree cross sections from extensively sampling 39 trees (32 damaged trees plus 7 undamaged trees that were still fully sampled). The 32 trees with damage at ≥ 3 cross sections were used in our analyses. Sample sizes were not evenly distributed across species since some species, for example, *C. clarksoniana*, are more abundant in the region, making up a larger proportion of the trees in the study area. Frequently damaged and abundant species included *C. clarksoniana* ($n=15/16$ damaged), *L.*

suaveolens ($n=6/11$ damaged), *E. tetradonta* ($n=4/4$ damaged) and *P. careya* ($n=4/20$ damaged) (Table S1). Infrequently damaged species that were also less abundant in the study area had low sample size ($n=1$) were as follows: *C. tessellaris*, *D. tetraphylla* and *P. nonda* (see Figure S2 for a visual depiction of the characteristic morphologies of damaged tree species).

2.3 | Attributing and quantifying internal stem damage at the cross section level

Given differences in how termites and microbes decompose wood, evidence of termite and microbial decomposition was visually estimated (Tuo et al., 2021) and quantified digitally as percentage internal stem damage per cross section. With no precedent for quantifying internal wood decomposition occurring from different biotic decomposers in the above-ground wood of standing trees, we developed a method using characteristic signs of microbial and termite damage that are known from downed deadwood and heart rot studies. Termite-attributed damage often involves the complete removal of wood (Ulyshen, 2016), which is a noted behaviour in live trees that takes the form of 'piping' (Werner & Prior, 2007, Figure 2c); the hollowed area may be filled with termite excretion (Figure 2d, Greaves, 1962). As encountered, we removed termite excretions to quantify termite damage to the wood. Microbe-attributed damage appears as discoloured or disintegrating wood, or wood with a spongy texture (Cornwell et al., 2009; Highley & Kirk, 1979; Figure 2b). Some cross sections had both termite and microbial damage; in this case, damage estimates from termites and microbes were separately delineated and quantified. For cross sections with co-occurrence, the majority of samples ($n=12/15$) had microbial and termite damage occurring in separate, discrete locations; a small number of samples ($n=3/15$) displayed adjacent microbial and termite damage. These areas of adjacent co-occurrence could be locations of active succession where termite damage followed microbial damage or they could indicate locations where both are simultaneously active. It is unknown if termite damage commonly follows microbial damage (Wijas, Allison, et al., 2024), and if this is the case, prior microbial damage would be obscured. Therefore, we could only attribute and measure damage at the time of harvest; however, adjacent decay was rare (1.5% of all cross sections) in our study suggesting biotic succession from microbes to termites is rare.

The evening after trees were harvested, cross section samples were photographed with an object of known size for scale to later digitally quantify damaged area from termites and microbes. For each cross section, the total area was first calculated in Adobe Illustrator using an area-based segmentation script (<https://gist.github.com/bryanbuchanan/11387501>). Then, total area with termite-attributed damage and total area with microbial-attributed damage were calculated. Percentage internal stem damage by

termites was calculated by dividing area of termite-attributed damage by total area for each cross section sample, multiplied by 100. Percentage internal stem damage by microbes was calculated by dividing area of microbial attributed damage by total area of the cross section, multiplied by 100. It was assumed that damage levels were consistent across both the top and bottom of a given cross section.

2.4 | Species-level wood specific gravity

Cross section samples were kept in airtight bags to minimize moisture loss when transported from the field to the research station. Field mass was determined to the nearest 10g for large (>500g) cross sections and to the nearest 0.01g for small (<500g) cross sections. Field volume was measured using volume displacement via the Archimedes' principle, where displaced water is assumed to have a density of 1.0gcm^{-3} . Samples were held for less than 1 week at the research station before being dried at 105°C to constant mass. Dry mass was used to calculate cross section wood specific gravity in g cm^{-3} (dry mass divided by field volume). Field-measured wood specific gravity was determined as average values across the undamaged cross sections for each species.

2.5 | Termite sampling, identification and deadwood occupancy transects

Termites associated with living trees were sampled from mounds at the tree base, external termite runways and in cross section samples. We also carried out two 50m deadwood occupancy transects adjacent to the upper and lower plots following the protocol described in Clement et al. (2021). Deadwood pieces >2cm intersecting the transect were thoroughly searched for termites. Collected termite specimens were stored in 95% ethanol for later visual identification to the species-level based on soldier morphologies. When visual identification was not possible, we followed the protocol in Clement et al. (2021) for species identification using DNA barcoding.

2.6 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Cross section samples	Microbial and termite damage	200
Whole tree	Microbial and termite damage, tree species	32, 4

2.7 | Analyses

2.7.1 | Amount of termite versus microbial damage at different tree heights

To understand how internal stem damage, attributed to both microbes and termites, changed with increasing height in individual trees, we used a beta regression model with a logit link from the package `glmmTMB` (Brooks et al., 2017). In the model, internal stem damage (as a proportion) was the response variable; we transformed it using $(y \times (n-1) + 0.5) / n$ (where n is the sample size) following Smithson and Verkuilen (2006) to address zeros in the dataframe. Predictor variables included cross section height and tree species, and tree individual was included as a random effect. Cross section height in the tree was evaluated in terms of both relative height (as a percentage, where 0% is the base of the tree and 100% is the maximum height) and absolute height (m). We ran separate models for termite and microbial damage as the response. We did a supplementary test to determine how damage changed in trees with only microbial damage ($n=4$ trees, $n=16$ cross sections); since microbial decomposition could potentially be obscured by termite decay occurring in the same place, we wanted to isolate microbial decomposition and test its spatial distribution. In this beta regression model, proportion of internal stem damage was the response variable and relative height was the predictor, and tree individual was included as a random effect.

2.7.2 | Amount of total tree-level internal stem damage

We estimated tree-level percentage internal damage by applying a relationship between internal stem damage and stem diameter to quantitative structural models (QSMs) derived from terrestrial laser scanning (see eq. 1, Calvert et al., 2024). Each tree was represented by a QSM that consisted of numerous cylinders. For each cylinder, damaged biomass was estimated using a regression predicting internal stem damage from diameter (which corresponds to height in the tree, where bigger cylinders were at the tree base, and smaller cylinders represented fine branches). Then, the damaged biomass from each cylinder comprising the tree QSM was summed and divided by total tree biomass to derive tree-level percentage internal damage.

To test if termite or microbial damage was greater at the tree level, we used linear models with tree-level percentage damage as a log-transformed response variable. Decomposer (termite or microbial) and tree species were used as predictors, including an interaction. A Tukey's honest significant difference (HSD) pairwise post hoc multiple comparisons test was used to compare microbial and termite damage by tree species.

2.7.3 | Microbial and termite damage co-occurrence

Tree-level microbial and termite damage co-occurrence represented our baseline expectation in testing if co-occurrence within cross

sections was equivalent. We used a chi-squared test to determine if damage co-occurrence in cross sections (observed) differed from what we measured at the tree level (expected). Cross sections with the presence of termite damage were labelled 'Y' and those without termite damage were labelled 'N'; counts of the two classes were summarized in a contingency table. This was repeated to describe counts of microbial damage occurrence. The same process was applied to summarize microbial and termite damage at the tree level. We did not do significance testing for adjacent co-occurrence as the number of adjacent co-occurrences was so low ($n=3$ out of the 200 cross sections, 1.5%).

2.7.4 | Effect of tree traits on tree internal stem damage

To test if tree size (DBH in cm) and wood specific gravity predicted percentage internal stem damage by each of the decomposers (termite and microbe), we used a linear model with percent damage (separate models for termite and microbial damage) as a log-transformed response variable and wood specific gravity and tree DBH as predictors.

2.7.5 | Damaged biomass at the plot level

The total AGB of trees (plot-level biomass, in kg) on the two firebreak plots (2.1 ha combined) was determined by manually weighing harvested trees in the field (see Calvert et al., 2024 for full methods). All of the trees were identified to species in field surveys prior to felling, and from this, we derived species-level biomass per hectare (kg ha^{-1}), as well as plot biomass (%) (see Table S6). We estimated the amount of damage (attributed to both termites and microbes) at the hectare level for the four internally damaged species with replication ≥ 4 (*C. clarksoniana*, *L. suaveolens*, *E. tetradonta*, *P. careya*). For each species, we calculated average tree-level termite and microbe damage (%). Then, to determine termite and microbe damaged biomass per hectare (kg ha^{-1}), we multiplied biomass per hectare by percentage of damaged biomass (in kg ha^{-1} for both termite and microbial damage, see Table S6).

All analyses were performed in R 4.3.1 (R Core Team, 2023).

3 | RESULTS

3.1 | Amount of termite versus microbial damage with tree height

Termite damage decreased with increasing relative height in the tree ($\chi^2 = 73.9$, $df = 1$, $p < 0.001$; Figure 3a; Table S2) and varied by tree species ($\chi^2 = 16.6$, $df = 6$, $p = 0.01$). *Corymbia clarksoniana* trees had the highest intercepts (greatest damage at the tree base), followed by *E. tetradonta* and *L. suaveolens*, while *P. careya* trees had the lowest intercepts (Figure 3a). Microbial damage also decreased with increasing relative height, albeit more weakly ($\chi^2 = 6.4$, $df = 1$, $p = 0.01$; Figure 3b; Table S2) but did not vary across species ($\chi^2 = 1.1$, $df = 6$,

$p=0.98$). For the small subset of trees with only microbial damage, damage also decreased with increasing relative height ($\chi^2=6.7$, $df=1$, $p=0.03$; Table S8). In terms of absolute height, the same relationships were found; termite damage decreased with height for different species; and microbial damage decreased with height but did not differ among species (see Table S7). We focused our discussion of these findings on relative height, as this allowed for comparison of different positions in the tree for different sized trees.

3.2 | Amount of internal stem damage at the tree level

At the tree level, there was a significant interaction between damage type (microbial or termite) and tree species ($F_{(3,50)}=3.13$, $p=0.034$; Table S3). A pairwise post hoc test showed that termite damage was greater than microbial damage only in *C. clarksoniana* trees ($t_{(50)}=3.17$, $p=0.049$; Figure 4).

3.3 | Microbial and termite damage co-occurrence

We found that 27% ($n=17$) of trees had both termite and microbial internal stem damage occurring in at least one sampled cross section. Within individual cross sections, we found that just 7.5% of all samples had evidence of co-occurring termite and microbial damage. Cross sections had significantly less co-occurrence of microbial and termite damage compared to whole trees ($\chi^2_{(1200)}=25.3$, $p<0.001$, Figure 5). Only 1.5% ($n=3$) of cross sections had adjacent microbial and termite damage, suggesting a rare presence of simultaneous or successional damage by microbes and termites.

3.4 | Effect of tree traits on tree internal stem damage

Wood specific gravity was a marginally significant positive predictor of termite damage ($F_{(1,29)}=3.97$, $p=0.056$; Table S4), but had no influence

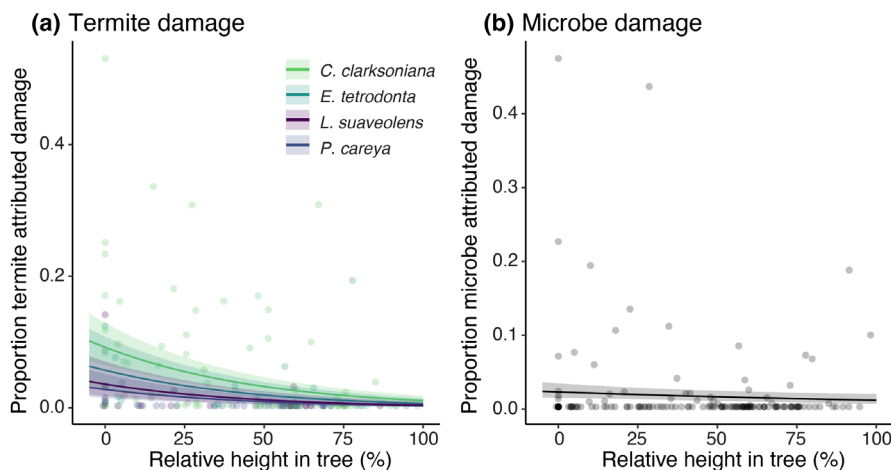


FIGURE 3 Changes in cross section damage (as a proportion) across relative height in the tree (%) for (a) termite and (b) microbial internal damage. Shaded areas represent 95% confidence intervals. Species are indicated by coloured lines for panel (a) but not for panel (b), as species was a significant predictor in the termite, but not the microbial internal stem damage model.

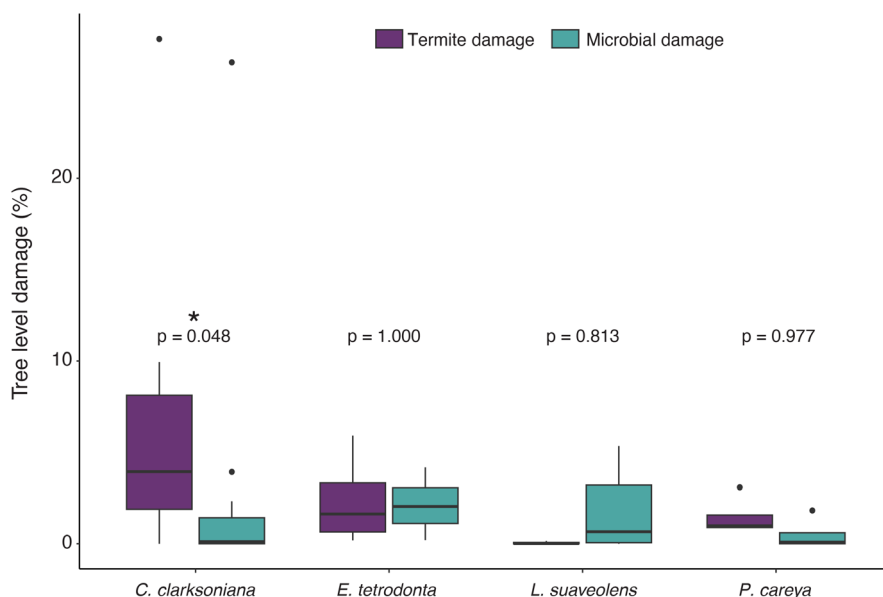


FIGURE 4 Differences in microbial and termite damage across species. Sample sizes by species group were as follows: *C. clarksoniana* ($n=15$), *E. tetradonta* ($n=4$), *L. suaveolens* ($n=6$), *P. careya* ($n=4$).

on microbial damage ($F_{(1,29)}=1.39$, $p=0.249$). Tree size was not a significant predictor of either termite or microbial damage (Table S4).

3.5 | Damaged total measured biomass

Termites damaged an estimated 200kg ha^{-1} , while microbes damaged an estimated 147kg ha^{-1} (Table S6) of tree biomass. Termite damage was present in most *C. clarksoniana* trees (93%), all *E. tetradonta* trees and all *P. careya* trees (Table S1). Microbial damage was present in all *E. tetradonta* trees and most *L. suaveolens* trees (83%). *E. tetradonta* and *C. clarksoniana* trees constituted the majority of biomass in the plot.

3.6 | Termites associated with living trees and fallen deadwood

Living trees and deadwood were occupied by different termite species. In living trees, *Nasutitermes graveolus* and *Coptotermes acinaciformis* were most abundant, while in deadwood, termites in the genera *Microcerotermes* and *Schedorhinotermes* dominated (Figure S1; Table S5).

4 | DISCUSSION

Termites and microbes were important internal stem decomposers in our study system, with an estimated 200kg ha^{-1} of internal tree wood removed by termites and 147kg ha^{-1} damaged by microbes; together, this represented ~5% of estimated living tree AGB in the study area. Individual stems could be up to ~30% damaged, from both termites and microbes. Additionally, termite and microbial damage decreased with height, suggesting a general phenomenon of damage proceeding from the ground up and being concentrated at the tree base in this savanna ecosystem. Interestingly, the co-occurrence of termite and microbial damage was greater at the tree than at the individual cross

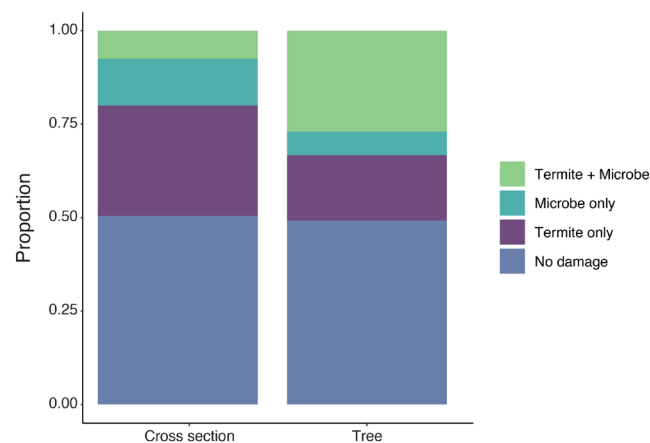


FIGURE 5 Proportion of cross sections ($n=200$ total) and trees ($n=63$ total) with microbial only, termite only, termite and microbial and no damage.

section level and almost never were found to decay adjacent to one another. This suggests that termites and microbes capitalized on wood resources within the same tree, but remained spatially separated at the stage of the decay process at which we carried out our sampling. Despite expectations from other systems, wood density and tree size were not strong predictors of internal stem damage, yet the model may have had relatively low power to detect this effect due to a smaller sample size. However, species still differed in amount of damage; specifically, termite damage was greater than microbial damage for *C. clarksoniana* trees. Below we discuss the importance of accounting for the amount of wood decomposition occurring inside living trees by termite and microbial decomposers.

4.1 | Termite and microbial damage scaling: Implications for AGB storage and turnover

Termite and microbial internal stem damage was highest at the tree base and decreased towards the crown, both for relative and absolute height in the tree. The basal concentration of termite damage is congruent with frequent patterns of ground colonization (Law et al., 2019) and termites frequently found associated with tree bases (Eleuterio et al., 2020). Microbial damage did not occur equally across tree heights as expected. Our findings for microbial damage may reflect the nature of savannas as fire-prone ecosystems, where fire-induced basal scarring is a primary contributor to access points for both termites and microbes (Adkins, 2006; N'Dri et al., 2011). It remains to be seen if the patterns observed here in a savanna system are similar to those in other wooded ecosystems. For instance, in some tropical forests, crown loss (from wind storms, lightning or large herbivores) is a prevalent source of external stem damage (Zuleta et al., 2022) that could allow for different entry points for internal decomposers. In savanna systems with megaherbivores (such as Africa and India), crown damage may also emerge as an important (but untested) predictor of vertical variation in internal stem damage (Calenge et al., 2002). Such differences in external damage may result in varied patterns of internal stem damage accumulation, with more microbial or termite damage occurring in the crown due to increased entry points.

Internal stem damage remains an important and unaddressed source of error in tree AGB models, and its inclusion has the potential of improving AGB estimations (Flores-Moreno et al., 2024; Monda et al., 2015). For example, Calvert et al. (2024), on which this study builds, demonstrated that increased internal stem damage resulted in overestimated AGB, but did not assign such damage to different decomposers. In the current study, we described separate scaling relationships for microbial and termite damage; for termite damage, we further capture some of the nuances in how this varies across tree species. These scaling relationships can serve as a starting point for incorporating error from internal stem damage into AGB models, although testing internal stem damage changes through tree height in different ecosystems and tree species will help to determine the generalizability of our findings.

From scaled estimates, we show that 350kg ha^{-1} of internal wood was in some state of decomposition from both termites and microbes within living trees. The amount of deadwood estimated to be on the ground in a similar northern Australian savanna ecosystem is 800kg ha^{-1} (Cook et al., 2020), which termites, microbes and abiotic factors will decompose through time. Therefore, in addition to the 800kg ha^{-1} of wood decomposing on the ground, 350kg ha^{-1} of wood inside trees is decomposing, but unaccounted for in C models. Furthermore, this 350kg ha^{-1} of internal wood would be improperly allocated as a C sink in tree AGB, as it is inside living trees and therefore associated with C sequestration (Pan et al., 2011). In reality, this C is actively being transformed and released into the atmosphere through decomposition and is currently a source of error in AGB and C turnover estimates in the savanna landscape. Fallen and standing deadwood is already incorporated into models of terrestrial C cycling (Cook et al., 2020); C cycling models should include parameters that incorporate internal stem damage which will require an increase in sampling efforts, since internal stem damage is largely under-quantified across global tropical ecosystems (Calvert et al., 2024; Flores-Moreno et al., 2024).

4.2 | Spatial co-occurrence of termite and microbial damage

Termite and microbial damage co-occurrence was greater at the tree level than for individual cross sections and was almost never adjacent. These results suggest that while termites and microbes can colonize the same tree, they likely use separate spaces, at least when considering a single point in the decay process as captured by our sampling methods. Such partitioning of wood resources may stem from differences in colonization patterns, negative biotic interactions at local scales (i.e. cross sections) through direct or indirect competition (Bradford et al., 2021) and/or environmental filtering (Li & Greening, 2022). Given that damage from both agents decreased with height in trees, it seems unlikely that colonization differences drive the observed patterns. Termites have been shown to filter microbial communities that occur in their mounds (Li & Greening, 2022), and this may also occur in internal tree wood if termites deter other competing wood decay fungi (Martin & Bulmer, 2018). Furthermore, some soft rot fungal genera (e.g. *Termitaria*, *Laboulbenia*, *Antennopsis* and *Cordycepioides*) are parasitic on termites and could reduce or prevent termite activity (Wong & Cheok, 2001). Further research on how biotic interactions between termites and wood-decay microbes shape internal stem damage is needed to resolve how facilitation and competition interact to shape observed damage patterns.

Given how destructive our methods were, it was not possible to follow biotic decay through time to track colonization, spread and interactions of microbes and termites within stems. How such damage progresses remains an open but challenging question; repeated measurements of the same tree stem with minimally invasive methods of estimating damage such as sonic tomography (Gilbert et al., 2016) could give insight, but would remain unable to attribute damage to microbes or termites. Biotic interactions may facilitate damage progression, for

instance, if mechanical or chemical changes to the wood from microbial decomposition create favourable conditions for termite entry (Ulyshen, 2016). Termites could also be vectors of wood-decomposing microbes that later establish in the wood; such vectoring has been described for wood-inhabiting beetles (Jacobsen et al., 2017). However, to track both the co-occurrence of decomposers within living trees as well as the amount of damage that they are causing in internal wood through time, a non-invasive survey method that differentiates between these biotic decayers would need to be developed. Some studies have attempted to physically and chemically remove termites from litter and wood decomposition processes (Cheesman et al., 2018; Teo et al., 2020), but it is complicated to fully exclude microbes from the decomposition process (in agricultural soils: Beare et al., 1992), especially in live trees. In the future, with further technological developments, the development of fine-resolution, non-invasive internal damage surveying methods that can detect termite presence or microbial decomposition would be a step towards parsing the role of termite and microbial decomposers in internal stem damage.

4.3 | Termites as important internal stem decomposers

While microbial heart rot has been documented around the globe (Frank et al., 2018; Heineman et al., 2015), termites as agents of internal stem damage have received less attention. In our savanna study system, termite damage was found in approximately half of trees and removed up to 28% of tree biomass. Understanding the extent to which internal stem damage from termites occurs in other savanna ecosystems is an important next step given that models predict increased termite-driven wood decomposition in savanna ecosystems around the globe under hotter, drier conditions (Zanne et al., 2022). In our savanna system, we found that *C. clarksoniana* trees had greater termite damage compared to microbial damage, and most (>90%) *C. clarksoniana* and *E. tetradonta* trees (both in the Myrtaceae) had evidence of termite damage. Why termites target such tree species is unclear; we predicted that wood specific gravity and large stem size could play a role, but did not find evidence to support this. However, other studies including more tree species ($n=87$) and a wider range of wood specific gravities (range: $0.4\text{--}0.9\text{g cm}^{-3}$) found a positive relationship with internal stem damage (Flores-Moreno et al., 2024). The four species we measured had low variation in wood specific gravity (range: $0.5\text{--}0.7\text{g cm}^{-3}$) and may not differ enough to detect relationships between internal stem damage and these tree traits. Additionally, other tree traits such as secondary chemistry could influence termite preferences. Myrtaceae trees have many polyphenolic compounds, including flavonoids (Saber et al., 2023), some of which are attractive to (Boué & Raina, 2003) and even preferred by (Ohmura et al., 2000) *Coptotermes formosanus* termites. However, little is known about how termites interact with polyphenols specific to Myrtaceae; future work could test for termite preferences in secondary compounds unique to these trees.

In documenting termite damage, we could not definitively ascribe which termite species were responsible; however, we found different termite species associated with live standing trees and fallen deadwood. These associations give initial expectations as to which termites may be causing damage in live trees and fallen deadwood pools. *Coptotermes acinaciformis* only occurred in association with living trees and are suggested as a primary agent of internal stem damage in Australian eucalypt forests (Werner & Prior, 2007), as well as *Coptotermes testaceus* in Brazil (Eleuterio et al., 2020). *Nasutitermes graveolus* was also found in association with living trees; this species builds arboreal mounds in the crown (Beasley-Hall et al., 2019), although they are not known to forage in the canopy and rather descend to forage on the ground (Hill, 1942). *Microcerotermes* and *Schedorhinotermes*, two wood-feeding genera (Clement et al., 2021), were most frequently encountered on deadwood transects. Wood-feeding termites likely distinguish between living and fallen deadwood resources, with distinct species (*C. acinaciformis* and *N. graveolus*) colonizing live tree wood resources for use as both food and habitat.

4.4 | Internal tree stem damage and wood C cycling

Through visual assessment of cross sections, it was evident that microbes damaged wood in situ (i.e. via excretion of extracellular enzymes), keeping wood volume largely intact while reducing density as decomposition progressed (Harmon et al., 2011). In contrast, termite damage completely removed wood from a given site, reducing the volume but not the density of the remaining wood. Furthermore, termites translocate the consumed wood in their guts to their nests and mounds (Ulyshen, 2016), meaning that internal wood decomposition is taking place ex situ, even if translocation is to another part of the same tree. Importantly, the void resulting from termite hollowing does not always remain empty, as it can be refilled with termite excretions (Figure 2d), which is often enriched in lignin (Rückamp et al., 2011). This carton material could potentially contribute to C storage, albeit in a different form than the original wood C, within the tree; however, little is known about the decomposability of this material. The on-site C consequences of internal damage are therefore likely to shift depending on whether microbes or termites dominate.

5 | CONCLUSIONS

Prior work on wood decomposition and biomass storage has overlooked internal wood decomposition in living trees, leaving a knowledge gap in our understanding of when and how C cycles out of wood. We have quantified how termites and microbes alter live tree AGB, highlighting the importance of incorporating this process into C cycling models. Internal stem damage occurred in half of the trees in our study, and for both termite and microbe attributed internal stem damage, biomass removal was greatest at the tree base. Further efforts to describe patterns of internal stem damage across other ecosystems are necessary to broaden our understanding of microbial and termite-mediated wood decay inside trees.

AUTHOR CONTRIBUTIONS

Conceptualization: Abbey R. Yatsko, Jed Calvert, Alexander W. Cheesman, Keith Cook, Baptiste Wijas, Amy E. Zanne. Data collection: Abbey R. Yatsko, Jed Calvert, Alexander W. Cheesman, Keith Cook, Paul Eggleton, Indigo Gambold, Caleb Jones, Pedro Russell-Smith, Baptiste Wijas. Data analysis: Abbey R. Yatsko, Baptiste Wijas. Writing: Abbey R. Yatsko. Editing and review: all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code have been uploaded to Zenodo <https://zenodo.org/records/14238876> (Yatsko, 2024).

STATEMENT ON INCLUSION

This study is a collaboration between researchers from the United States and Australia, and all members were involved in the conceptualization and data collection process. We cite regionally relevant literature when available in our manuscript.

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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: Summary of species investigated and wood specific gravity. Counts of damaged/undamaged individuals are reported for each species, and counts for damaged trees with microbial/termite internal stem damage are also summarized.

Table S2: Beta regression model output summarized in an analysis of deviance table testing how internal stem damage changed across relative height in the tree for different species.

Table S3: Linear model output summarized in an analysis of variance table testing the amount of overall tree-level damage for different damage type (termite and microbial) and tree species.

Table S4: Linear model output summarized in an analysis of variance table testing wood density (wd) and tree size (dbh) as predictors of

the amount of internal stem damage (for both termites and microbes).

Table S5: List of species and total counts of occurrences with termites found in/associated with living trees and fallen deadwood.

Table S6: Plot-level damaged tree AGB from both termites and microbes for four damaged species in the study. Other species (including those with damage but low replication as well as undamaged species) included *Acacia polystachya*, *Corymbia tessellaris*, *Deplanchea tetraphylla*, *Grevillea parallela*, *Parinari nonda* and *Timonius timon*.

Table S7: Beta regression model output summarized in an analysis of deviance table testing how internal stem damage changed across absolute height in the tree for different species.

Table S8: Beta regression model output summarized in an analysis of deviance table testing how internal stem damage changed across relative height in trees damaged only by microbes.

Figure S1: Termite species observed in fallen deadwood and living trees.

Figure S2: Tree morphologies of damaged tree species in the study.

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