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

Abbey R. Yatsko[1]*, Baptiste Wijas[1], Jed Calvert[2], Alexander W. Cheesman[3], Keith Cook[2], Paul Eggleton[4], Indigo Gambold[2], Caleb Jones[2], Pedro Russell-Smith[2], Amy E. Zanne[1]

[1]Biology Department, University of Miami, Coral Gables, Florida, USA
[2]ArborMeta, Byron Bay, NSW, Australia
[3]College of Science & Engineering, James Cook University, Cairns, QLD, Australia
[4]Life Sciences Department, The Natural History Museum, London, United Kingdom

*Corresponding author: ayatsko1@gmail.com

Abstract

1. Wood plays a vital role in the terrestrial carbon cycle, serving as a significant carbon store that is then released back to the atmosphere during decomposition. Decomposition has largely been studied in fallen and standing deadwood; however, decomposition can occur within living trees via hollowing by wood-feeding termites and microbial heart rot. Internal stem damage is difficult to measure, leaving many unresolved knowledge gaps, such as 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 39 trees to investigate the relative contributions of microbes and termites to internal stem damage 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 internal stem damage across four tree species.
3. Termite and microbial damage was 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 cross sections, suggesting local competitive exclusion or niche

partitioning. 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 concealed wood decomposition dynamics occurring inside trees, with implications for accurate carbon estimation across savanna ecosystems.

Keywords: Carbon storage, internal stem damage, microbial wood decomposers, tree biomass, wood decomposition, wood-feeding termites

Introduction

Wood serves as both a carbon (C) sink and source in terrestrial ecosystems. Living tree biomass constitutes a large C pool globally, containing an estimated 363±28 Pg C in stems, branches, and roots (Pan et al., 2011). Trees transition into deadwood biomass upon death, 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 decomposed down by biotic agents (e.g., invertebrates or microbes) and abiotic forces (e.g., fire or UV), cycling C back to soils and the atmosphere (Cornwell et al., 2009; Wijas, Allison et al., 2024). With substantial C stocks present in both living and trees, decomposition of this woody biomass is critical for forest C cycling (Zhou et al., 2007).

Our understanding of C cycling in deadwood primarily focuses on fallen and standing deadwood (Harmon et al., 2020; Bradford et al., 2021). However, a third category in living trees, internal tree stem damage (e.g., heart rot, cracks, or hollows), has been acknowledged for some time (Janzen 1976; Highley & Kirk 1979) but remains less understood in how it affects aboveground biomass (AGB) and C cycling. Internal damage has been estimated to impact 3% to 42% of tree AGB (Heineman et al., 2015; Monda et al., 2015; Flores-Moreno et al., 2024), largely affecting tree heartwood (the non-functional wood at the trees center; Hillis 1987). Therefore, internal stem damage remains concealed and often overlooked during biomass assessments (Calvert et al., 2023) and represents wood C loss that takes place during part of the tree life cycle associated with active C sequestration. 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; Ulyshen 2016), while termites are especially important in dry tropical ecosystems, both in living trees which they frequently hollow (Werner & Prior 2007) and in fallen deadwood (Zanne et al., 2022; Wijas, Flores-Moreno et al., 2024). However, microbes and termites differ in wood decomposition strategies, which impacts wood C storage and release. Microbes release 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/mound and chemically digested via microbes and/or endogenous cellulases in their guts (Brune & Dietrich 2015). Some termites live within the deadwood they consume, and, in this 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); this protocol likely overlooks differences in how biotic decomposers colonize and damage trees. Most 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 this is where internal damage is likely concentrated. However, some drywood termites build colonies in dead branches of living trees, which could concentrate damage in the crown (Abe 1987). Microbes on the other hand colonize wood through various means: spores entering wounds in branches or trunks 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, microbial-mediated damage may be less related to position in the tree than termite damage since wounding can occur at different heights, for example from fire scarring at the tree base or branches broken from wind damage in the crown (Perry et al., 1985). This diversity in foraging and dispersal strategies of termites and microbes likely result in varied spatial colonization patterns in living trees, affecting the distribution and extent of internal stem damage.

It is currently unknown if termites and microbes partition internal tree wood resources or simultaneously damage the same space, as measurement methods are unable to differentiate between termite or microbial damage (Flores-Moreno et al., 2024). While it is clear that the assemblage of deadwood decomposer communities is variable through space and time, 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 thus microbial colonization from the soil, with 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, as termites decomposed more wood in contact with the ground. Additionally, it has been shown that the presence of some wood-decay fungi is positively associated with termite foraging (Viana-Junior et al., 2018), but some fungi also deter termite feeding (Kamaluddin et al., 2016). Understanding whether termite and microbial damage co-occurs in living tree wood will illuminate how biotic interactions influence internal biomass decomposition.

Wood decomposition is not solely affected by biotic decomposers; qualities of the decay substrate influence how organisms access and utilize wood resources (Cornwell et al., 2009). Tree traits such as wood specific gravity (defined as wood density relative to water) and tree size have been associated with internal stem damage. 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., 2008). 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). Taken together, determining the interactions among tree species, wood traits, and biotic decomposers is crucial for understanding tree susceptibility to internal stem damage.

In this study, we destructively harvested savanna trees in Queensland, Australia to evaluate the extent of internal stem damage caused by microbes and termites. Table 1 outlines study questions and hypotheses:

Question	**Hypothesis**
Does the amount of termite versus microbial internal damage change at different heights in trees?	Termite damage will be greatest at the tree base (a typical entry point), and microbial damage will have no association with height (entry points occur through trees).
How much tree-level damage is attributed to termites versus microbes?	Termites will cause more internal stem damage since they have a greater role in fallen deadwood decomposition than microbes in savannas.

Does microbial and termite damage co-occur at the cross section and tree-level? To what degree are they spatially separated?	Given limited knowledge of termite and microbe co-occurrence, cross section and tree-level co-occurrence is expected to be equivalent.
How well do tree-level characteristics (species, size, and wood specific gravity) predict microbial or termite damage?	Species will vary in internal stem damage amount; Myrtaceae species will be most damaged by termites. High wood specific gravity will increase termite damage but decrease microbial damage. Larger trees will have more damage from both decomposers.

Table 1. Study questions and hypotheses.

Materials and Methods

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). This site is in the Australian Monsoon Tropics, with a seasonally wet tropical climate and a mean annual rainfall of 2057 mm, ranging from 1110-3299 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*, *C. tessellaris*, *Eucalyptus tetrodonta*, *Lophostemon suaveolens* (all Myrtaceae), and *Parinari nonda* (Chrysobalanaceae). *Planchonia careya* (Lecythidaceae), a sparse subcanopy of *Grevillea parallela* (Proteaceae) and *Acacia flavescens* (Fabaceae) is also present. Tree density at the site averaged 326 trees ha^{-1} with a DBH range of 1.3 to 69.7 cm (mean 17.1 cm, standard deviation (SD) 12.1 cm) (Calvert et al., 2023).

Destructive harvest protocol

Thirty-nine trees were harvested from a pre-planned firebreak clearance on two survey areas (lower plot: 1.84 ha, upper plot: 0.27 ha). From the destructive harvest, we determined tree AGB (see Calvert et al., 2023 for full methods). To assess and quantify internal stem damage, we sampled 4-7 cross sections from trees (4 cm average thickness) along the lower stem from where the tree was felled (C1), at the midpoint in the lower stem (C2, only if damage was present at C1 and C3), and 50 cm below the first branching point (C3). Cross section samples were then taken in the tree crown following decreasing branch sizes (C4-C7, Figure 1a).

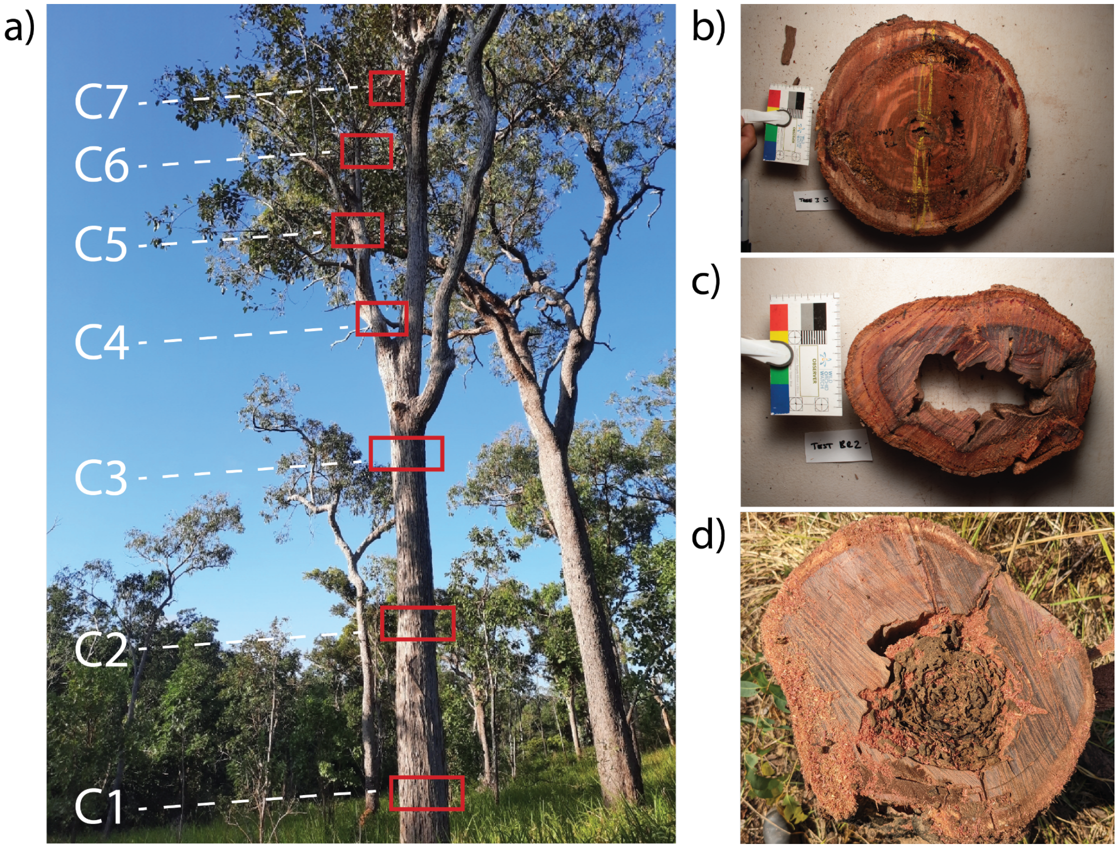


Figure 1. a) Cross section sampling scheme to measure internal stem damage at multiple points up the tree, b) microbial internal stem damage, c) termite damage, and d) stem hollow filled with termite excretion.

Attributing and quantifying internal stem damage at the cross section level

Given differences in how termites and microbes decompose wood, evidence of termite (complete removal) and microbial decomposition (Figure 1b, wood discoloration or spongy texture) was visually estimated. Termite-derived hollows can be filled with termite excretion (Figure 1c-d, Greaves 1962), which we removed to quantify termite damage. Some cross sections had both termite and microbial damage; in this case damage estimates from termites and microbes were separately delineated and quantified.

We quantified the percentage internal stem damage per cross section using an area-based segmentation script in Adobe Illustrator (https://gist.github.com/bryanbuchanan/11387501). The total area of the cross section was divided by the area identified as damaged. It was assumed that damage levels were consistent across both the top and bottom of a given cross section. It is noted that if a cross section had termite damage, it could have been first damaged by microbes, which would be obscured. Therefore, we could only attribute and measure damage at the time of harvest.

Tree-level estimates of damage

To understand how internal stem damage, attributed to both microbes and termites, changed with increasing height in individual trees, we used linear regressions following Calvert et al. (2023) for those trees with >3 cross sections. Cross section diameter (where larger cross sections occur at the tree base; smaller cross sections occur in the crown) was the predictor and percentage internal stem damage (for both termite and microbial damage) was the response. To scale this relationship to estimate tree-level percentage damage, we applied the linear relationship of damage to quantitative structural models derived from terrestrial laser scanning (see full description of methods in Calvert et al., 2023).

Species level wood specific gravity

Cross section samples were kept in airtight bags when transported from the field to the research station. Field mass was determined to the nearest 10 g for large (>500 g) cross sections and to the nearest 0.01g for small (<500 g) cross sections. Field volume was measured using volume displacement via the Archimedes Principle, where displaced water is assumed to have a density of 1.0 g cm^{-3}. Samples were held for less than one 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.

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 50 m 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.

Analyses

Amount of termite versus microbial damage at different tree heights

To test how the amount of damage at the cross section level changed with increasing height in the tree, we used a linear mixed-effect model with percentage damage as a log-transformed response variable, relative height up the tree (as a percentage where 0 is the tree base and 100 is the maximum tree height) and tree species as fixed effects (including an interaction), and tree individual as a random effect. We ran separate models for termite and microbial damage as the response.

Amount of total tree-level internal stem 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. Damage agent (termite or microbial) and tree species were used as predictors, including an interaction. A pairwise post hoc multiple comparisons test was used to compare microbial and termite damage by tree species.

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 presence of termite damage were labeled ‘Y’ and those without termite damage were labeled ‘N’; counts of the two classes were summarized in a contingency table. This was repeated to describe counts of microbial damage. The same process was applied to summarize microbial and termite damage at the tree-level.

Effect of tree traits on tree internal stem damage

To test if tree size and wood specific gravity predicted percentage internal stem damage by each of the damage agents, 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.

Damaged biomass at the plot level

We calculated damaged tree biomass (kg) from each decomposer (termite/microbe) per hectare (ha) using species-level AGB from the two firebreak plots combined (2.1 ha total). We calculated total and percentage AGB for each species on this plot using biomass data from Calvert et al. (2023). We converted AGB to the hectare level and multiplied by species-level microbial and termite damage to determine damaged biomass in kg ha^{-1}. All analyses were performed in R 4.3.1 (R Core Team, 2023).

Results

Amount of termite versus microbial damage through tree height

Termite damage decreased with increasing height in the tree (χ^2=83.4, df=1, p<0.001, Figure 2a, Supplementary Table 2) and varied by tree species (χ^2=14.1, df=6, p=0.028); a significant interaction was found between species and height in the tree (χ^2=21.1, df=6, p=0.002). *C. clarksoniana* trees had the highest intercepts (greatest damage at the tree base) and steepest negative slopes (decreasing damage with height), followed by *E. tetrodonta* and *L. suaveolens*, while *P. careya* trees had the lowest intercepts and a shallow slope (Figure 2a). Microbial damage also decreased with increasing height in the tree (χ^2=4.2, df=1, p=0.041, Figure 2b, Supplementary Table 2) but did not vary across species (χ^2=1.6, df=6, p=0.949); for microbial damage there was no significant interaction between species and height in the tree.

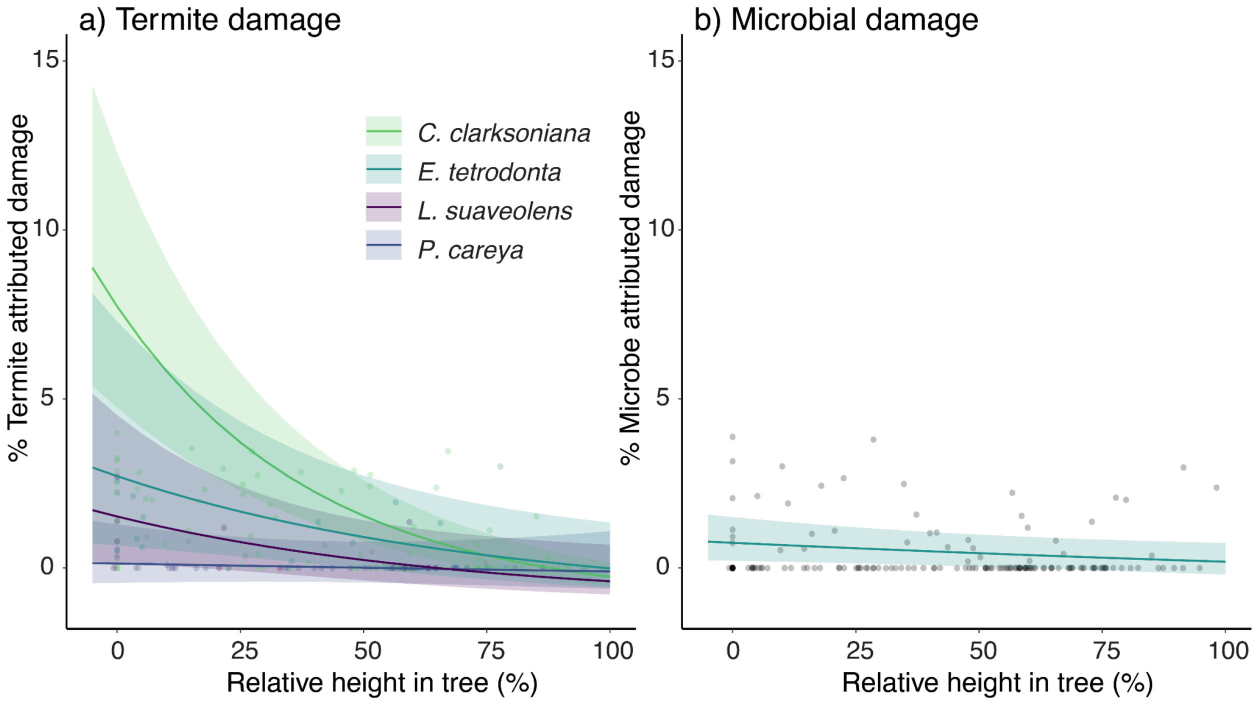


Figure 2. Changes in cross section damage across relative tree height (% of total height) for a) termite and b) microbial internal damage. Shaded areas represent 95% confidence intervals.

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, Supplementary Table 3). 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 3).

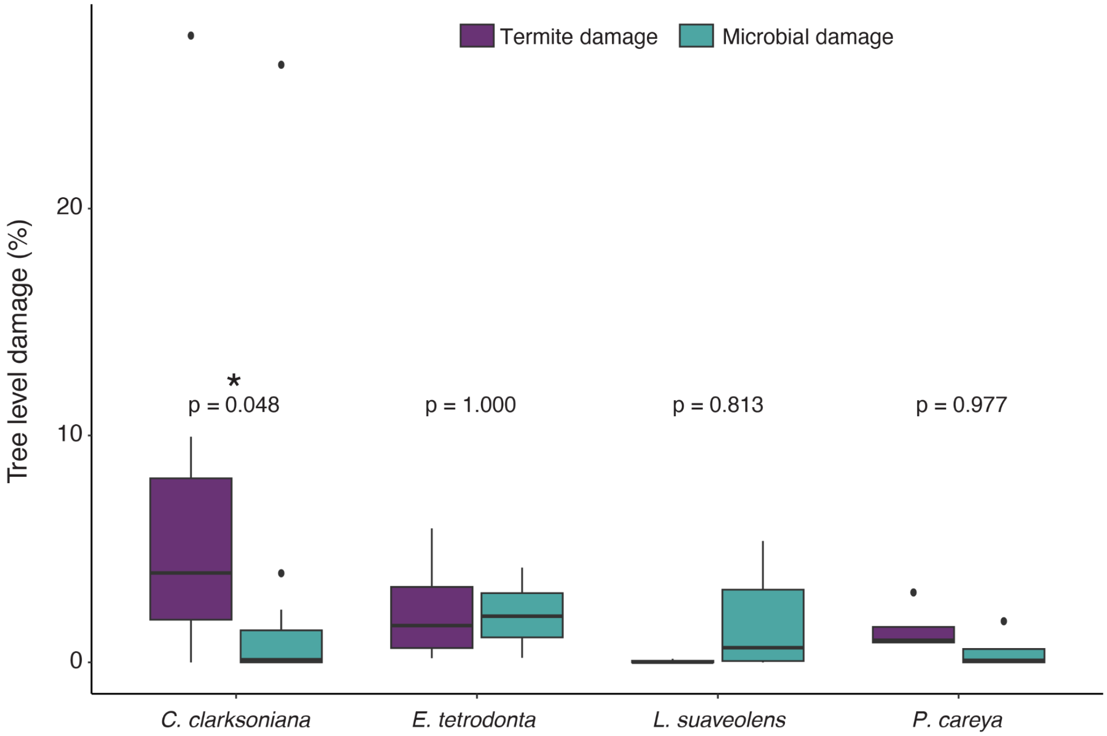


Figure 3. Differences in microbial and termite damage across species. Sample sizes by species group are as follows: *C. clarksoniana* (n=15), *E. tetradonta* (n=4), *L. suaveolens* (n=6), *P. careya* (n=4).

Microbial and termite damage co-occurrence

We found that 27% (n=17) of trees had both termite and microbial internal stem damage present (in at least one cross section), compared with just 7.5% of all cross sections examined. Cross sections had significantly less co-occurrence of microbial and termite damage compared to whole trees ($\chi^2_{(1,200)}$=25.3, p<0.001, Figure 4).

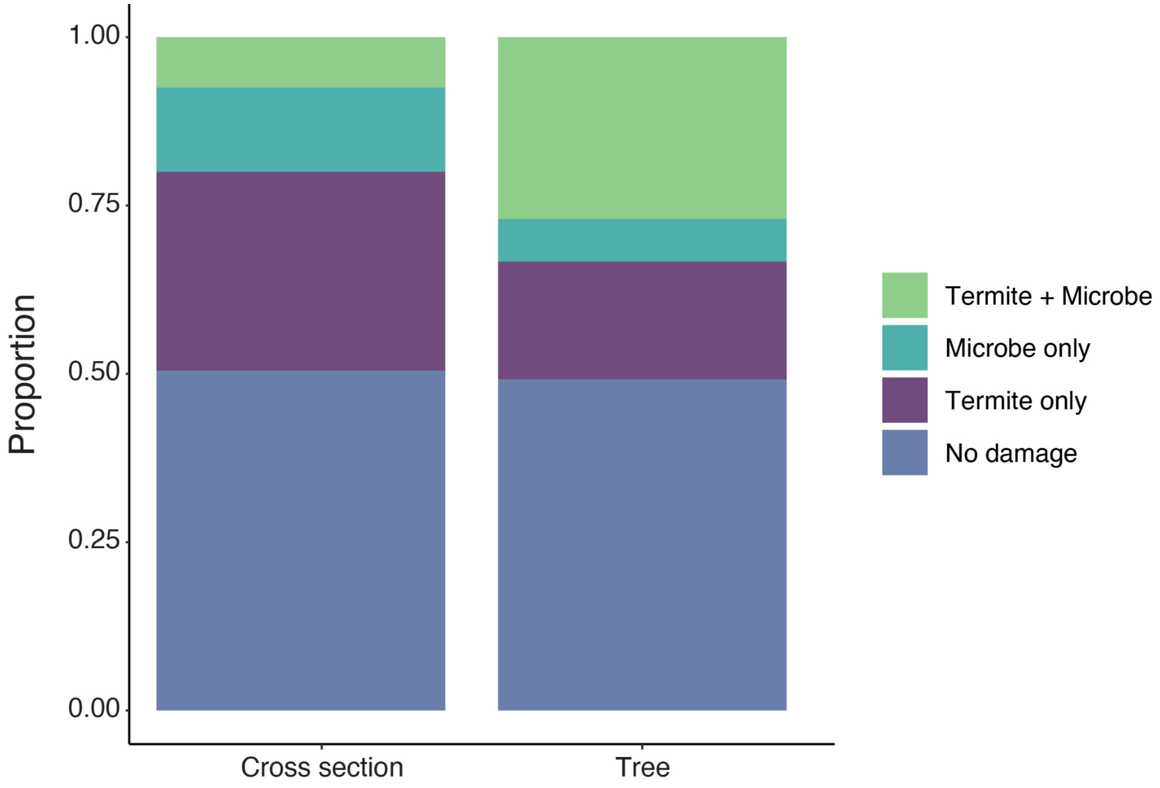


Figure 4. Proportion of cross sections (n=200 total) and trees (n=63 total) with microbial only, termite only, termite and microbial, and no damage.

Effect of tree traits on tree internal stem damage

Wood specific gravity was a marginally significant (positive) predictor of termite damage ($F_{(1,29)}=3.97$, $p=0.056$, Supplementary Table 4), but had no influence on microbial damage ($F_{(1,29)}=1.39$, $p=0.249$). Tree size was not a significant predictor of either termite or microbial damage (Supplementary Table 4).

Damaged total measured biomass

Termites damaged an estimated 200 kg ha^{-1}, while microbes damaged an estimated 147 kg ha^{-1} (Supplementary Table 6). Termite damage was present in most *C. clarksoniana* trees (93%), all *E. tetrodonta* trees and all *P. careya* trees (Supplementary Table 1). Microbial damage was present in all *E. tetrodonta* trees and most *L. suaveolens* trees (83%). *E. tetrodonta* and *C. clarksoniana* trees constituted the majority of biomass in the plot.

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 (Supplementary Figure 1, Supplementary Table 5).

Discussion

Termites and microbes were important internal stem damage agents in our study system, with an estimated 200 kg ha^{-1} of internal tree wood removed by termites and 147 kg ha^{-1} damaged by microbes; together this represents ~5% of estimated AGB. 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 base in this ecosystem. Interestingly, the co-occurrence of termite and microbial damage was greater at the tree than at the cross section level, suggesting that termites and microbes capitalize on wood resources within the same tree, but largely remain spatially separated. Despite expectations from other systems, wood density and tree size were not strong predictors of internal stem damage; 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 wood decomposition occurring not just outside, but also inside living trees.

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 toward the crown. The basal concentration of termite damage is congruent with frequent patterns of ground colonization (Law et al., 2019) and association 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 windstorms, lightning, large herbivores, etc.) is a prevalent source of external stem damage (Zuleta et al., 2021). Such differences in external damage may result in varied patterns of internal stem damage accumulation, with more microbial damage likely occurring in the crown due to increased entry points.

Internal stem damage remains an important and unaddressed source of error in tree AGB models, with implications for improving AGB estimation methodology (Monda et al., 2015; Flores-Moreno et al., 2024). For example, Calvert et al. (2023), on which this study builds, demonstrated that increased internal stem damage resulted in overestimated AGB but did not assign such damage to different decay agents. 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 representativeness of our models.

From these scaled estimates, we show that 350 kg ha^{-1} of internal wood is under some state of decomposition from both termites and microbes in living trees. This is approximately half of the amount of deadwood estimated to be on the ground (800 kg ha^{-1}) in northern Australian savanna ecosystems (Cook et al., 2020), which termites and microbes will decompose through time. It is clear from our estimates that internal stem decomposition can therefore play a significant role in AGB estimates and C turnover in the savanna landscape. Fallen deadwood is often incorporated into models of terrestrial C cycling (Cook et al., 2020); it is evident that C cycling models should consider internal stem damage as well.

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. This result suggests that while termites and microbes can colonize the same tree, they use separate spaces. 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 decreases 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 *Cordycepioideus*), 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 are, we could not 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. Biotic interactions may facilitate damage progression, for instance, if mechanical or chemical changes to the wood from microbial decomposition create favorable 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, testing the succession of decomposer communities and interactions between termites and microbes remains a challenge for future study, as current non-invasive measurements cannot distinguish between microbial and termite internal damage.

Termites as important internal stem damage agents

While microbial heart rot has long been documented around the globe (Heineman et al., 2015; Frank et al., 2018), termites as agents of internal stem damage have received less attention. In our study system, termite damage was found in approximately half of trees and removed up to 28% of tree biomass. Interestingly, *C. clarksoniana* trees were much more preferred by termites compared to microbes, and most (>90%) *C. clarksoniana* and *E. tetrodonta* 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 to 0.9 g cm^{-3}) found a positive relationship with internal stem damage (Flores-Moreno et al., 2024). The four species we measured had lower variation in wood specific gravity (range: 0.5 to 0.7 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 tree 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, which build arboreal mounds in the crown (Beasley-Hall et al., 2019), although they are not likely 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.

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 progresses (Harmon et al., 2011). In contrast, termite damage completely removes wood from a given site, reducing the volume but not wood specific gravity 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 carton nest material (Figure 1d), 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. Therefore, the on-site C consequences of internal damage are likely to shift depending on whether microbes or termites dominate.

Conclusions

From nature-based climate change solutions to a push for natural capital accounting (Pan et al., 2011), there is a pressing need to accurately measure and model C storage and cycling in wooded landscapes. 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 are among the first to quantify how termites and microbes alter live tree AGB, highlighting the importance of incorporating this process into C cycling models. Indeed, termites release CH_4, in addition to CO_2, while decomposing organic matter (Chiri et al., 2020). CH_4 has a greater climate warming potential compared to CO_2, meaning shifts between microbial- and termite-mediated wood decay may have different feedbacks in the Earth system. Investigation of such questions is an important next step given that global climate models predict increased termite-driven wood decomposition in savanna ecosystems under hotter, drier conditions (Zanne et al., 2022).

References

Abe T. 1987. Evolution of life types in termites. In: Kawano S, Connell J, Hidaka T, editors. Evolution and coadaptation in biotic communities. Tokyo: University of Tokyo Press. p. 125–148.

Adkins, M.F. (2006). A burning issue: Using fire to accelerate tree hollow formation in Eucalyptus species. *Australian Forestry*, *69*(2), 107–113. https://doi.org/10.1080/00049158.2006.10676236

Australian Bureau of Meteorology. (2023). Queensland Observations [dataset]. http://www.bom.gov.au/qld/observations/index.shtml?ref=hdr

Barrera-Bello, Á.M., Lucas, J. M., & Gora, EM. (2023). Suspended Sections Within Downed Deadwood Are Drier, Have Altered Decomposer Communities, and Slower Decomposition. *Ecosystems*. https://doi.org/10.1007/s10021-023-00874-w

Beasley-Hall, P.G., Chui, J., Arab, D. A., & Lo, N. (2019). Evidence for a complex evolutionary history of mound building in the Australian nasute termites (Nasutitermitinae). *Biol. J. Linn. Soc. 126*(2), 304–314. https://doi.org/10.1093/biolinnean/bly187

Blanchette, R.A. (1991). Delignification by Wood-Decay Fungi. *Annu. Rev. Phytopathol.*, *29*, 381–398. https://doi.org/10.1146/annurev.py.29.090191.002121

Boddy, L. (1994). Latent Decay Fungi: The Hidden Foe? *Arboricultural Journal*, *18*(2), 113–135. https://doi.org/10.1080/03071375.1994.9747007

Boddy, L. (1999). Saprotrophic Cord-Forming Fungi: Meeting the Challenge of Heterogeneous Environments. *Mycologia*, *91*(1), 13–32. https://doi.org/10.2307/3761190

Boué, S.M., & Raina, A.K. (2003). Effects of Plant Flavonoids on Fecundity, Survival, and Feeding of the Formosan Subterranean Termite. *J. Chem. Ecol. 29*(11), 2575–2584. https://doi.org/10.1023/A:1026318203775

Bradford, M.A., Maynard, D.S., Crowther, T.W., Frankson, P.T., Mohan, J.E., Steinrueck, C., Veen, G.F., King, J.R. and Warren R.J. II. (2021). Belowground community turnover accelerates the decomposition of standing dead wood. *Ecology 102*(11):e03484. https://doi.org/10.1002/ecy.3484

Brune, A., & Dietrich, C. (2015). The Gut Microbiota of Termites: Digesting the Diversity in the Light of Ecology and Evolution. *Annu. Rev. Microbiol. 69*(1), 145–166. https://doi.org/10.1146/annurev-micro-092412-155715

Calvert, J., Yatsko, A.R., Bresgi, J., Cheeseman, A., Cook, K., Crowe, J., Gambold, I., Jones, C., O'Connor, L., Peter, T., Russell-Smith, P., Taylor, E., Trigger, B., Wijas, B., & Zanne, A.E. (2023). Comparing the effects of internal stem damage on aboveground biomass estimates from terrestrial laser scanning and allometric scaling models. *EcoEvoRxiv*. https://doi.org/10.32942/X2M89C

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., … Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Change Biol., 20*(10), 3177–3190. https://doi.org/10.1111/gcb.12629

Chiri E., Greening C., Lappan R., Waite, D.W., Jirapanjawat, T., Dong X., Arndt S.K., Nauer P.A. (2020). Termite mounds contain soil-derived methanotroph communities kinetically adapted to elevated methane concentrations. *ISME J. 14*:2715–2731. https://doi.org/10.1038/s41396-020-0722-3

Clement, R.A., Flores-Moreno, H., Cernusak, L.A., Cheesman, A.W., Yatsko, A.R., Allison, S.D., Eggleton, P., Zanne, A.E. (2021). Assessing the Australian Termite Diversity Anomaly: How Habitat and Rainfall Affect Termite Assemblages. *Front. Ecol. Evol. 9:657444.* https://doi.org/10.3389/fevo.2021.657444

Cook, G.D., Liedloff, A.C., Meyer, C.P., Richards, A.E., & Bray, S.G. (2020). Standing dead trees contribute significantly to carbon budgets in Australian savannas. *Int. J. Wildland Fire, 29*(3), 215-228. https://doi.org/10.1071/WF19092

Cornwell, W.K., Cornelissen, J.H.C., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C.M., Scarff, F., Weedon, J.T., Wirth, C., & Zanne, A.E. (2009). Plant traits and wood fates across the globe: Rotted, burned, or consumed? *Glob. Change Biol.*, *15*, 2431–2449. https://doi.org/10.1111/j.1365-2486.2009.01916.x

Eggleton, P., & Tayasu, I. (2001). Feeding groups, lifetypes and the global ecology of termites. *Ecological Research*, *16*(5), 941–960. https://doi.org/10.1046/j.1440-1703.2001.00444.x

Eleuterio, A.A., de Jesus, M.A., & Putz, F.E. (2020). Stem decay in live trees: Heartwood hollows and termites in five timber species in eastern Amazonia. *Forests*, *11*(10), 1–12. https://doi.org/10.3390/f11101087

Flores-Moreno, H., Yatsko, A.R., Cheeseman, A.W., Allison, S.D., Cernusak, L.A., Cheney, R., Clement, R., Cooper, W., Eggleton, P., Jensen, R., Rosenfield, M., & Zanne, A.E. (2024). Shifts in internal stem damage along a tropical precipitation gradient and implications for forest biomass estimation. *New Phytol., 241*: 1047-1061. https://doi.org/10.1111/nph.19417

Frank, J., Castle, M.E., Westfall, J.A., Weiskittel, A.R., Macfarlane, D.W., Baral, S.K., Radtke, P.J., & Pelletier, G. (2018). Variation in occurrence and extent of internal stem decay in standing trees across the eastern US and Canada: Evaluation of alternative modelling approaches and influential factors. *Forestry*, *91*(3), 382–399. https://doi.org/10.1093/forestry/cpx054

Gilbert, G.S., Ballesteros, J.O., Barrios-Rodriguez, C.A., Bonadies, E.F., Cedeño-Sánchez, M.L., Fossatti-Caballero, N.J., Trejos-Rodríguez, M.M., Pérez-Suñiga, J.M., Holub-Young, K.S., Henn, L.A.W., Thompson, J.B., García-López, C.G., Romo, A.C., Johnston, D.C., Barrick, P.P., Jordan, F.A., Hershcovich, S., Russo, N., Sánchez, J.D., … Hubbell, S.P. (2016). Use of sonic tomography to detect and quantify wood decay in living trees. *Appl. Plant Sci.*, *4*(12), 1600060–1600060. https://doi.org/10.3732/apps.1600060

Greaves, T. (1962). Studies of foraging galleries and the invasion of living trees by Coptotermes acinaciformis and C. Brunneus (Isoptera). *Aust. J. Zool.*, *10*(4), 630–651. https://doi.org/10.1071/ZO9620630

Harmon, M.E., Fasth, B.G., Yatskov, M., Kastendick, D., Rock, J., & Woodall, C.W. (2020). Release of coarse woody detritus-related carbon: A synthesis across forest biomes. *Carbon Balance Manag.*, *15*(1), 1. https://doi.org/10.1186/s13021-019-0136-6

Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., & Yatkov, M. (2011). Differences between standing and downed dead tree wood density reduction factors: A comparison across decay classes and tree species. USDA, Forest Service. https://doi.org/10.2737/NRS-RP-15

Heineman, K.D., Russo, S.E., Baillie, I.C., Mamit, J.D., Chai, P.P.K., Chai, L., Hindley, E.W., Lau, B.T., Tan, S., & Ashton, P.S. (2015). Evaluation of stem rot in 339 Bornean tree species: Implications of size, taxonomy, and soil-related variation for aboveground biomass estimates. *Biogeosciences*, *12*(19), 5735–5751. https://doi.org/10.5194/bg-12-5735-2015

Highley, T. L. (1979). Mechanisms of Wood Decay and the Unique Features of Heartrots. *Symposium on Wood Decay*, *69*(10), 1151–1157. https://doi.org/10.1094/Phyto-69-1151

Hill, G. F. (1942). Termites (Isoptera) from the Australian region. https://www.cabdirect.org/cabdirect/abstract/19420602503

Hillis, W. E. (1987). Function, Formation and Control of Heartwood and Extractives. In W. E. Hillis (Ed.), *Heartwood and Tree Exudates* (pp. 180–208). Springer. https://doi.org/10.1007/978-3-642-72534-0_7

Jacobsen, R.M., Kauserud, H., Sverdrup-Thygeson, A., Bjorbækmo, M.M., & Birkemoe, T. (2017). Wood-inhabiting insects can function as targeted vectors for decomposer fungi. *Fungal Ecology*, *29*, 76–84. https://doi.org/10.1016/j.funeco.2017.06.006

Janzen, D.H. (1976). Why Tropical Trees Have Rotten Cores. *Biotropica*, *8*(2), 110–110.

Kamaluddin, N.N., Nakagawa-Izumi, A., Nishizawa, S., Fukunaga, A., Doi, S., Yoshimura, T., & Horisawa, S. (2016). Evidence of Subterranean Termite Feeding Deterrent Produced by Brown Rot Fungus Fibroporia radiculosa (Peck) Parmasto 1968 (Polyporales, Fomitopsidaceae). *Insects*, *7*(3), 41. https://doi.org/10.3390/insects7030041

Kataoka, Y., Kiguchi, M., Williams, R.S., & Evans, P.D. (2007). Violet light causes photodegradation of wood beyond the zone affected by ultraviolet radiation. *Holzforschung*, *61*(1), 23–27. https://doi.org/10.1515/HF.2007.005

Law, S., Eggleton, P., Griffiths, H., Ashton, L., & Parr, C. (2019). Suspended Dead Wood Decomposes Slowly in the Tropics, with Microbial Decay Greater than Termite Decay. *Ecosystems*, *22*(6), 1176–1188. https://doi.org/10.1007/s10021-018-0331-4

Law, S., Flores-Moreno, H., Cheesman, A.W., Clement, R., Rosenfield, M., Yatsko, A.R., Cernusak, L.A., Dalling, J.W., Canam, T., Iqsaysa, I.A., Duan, E.S., Allison, S.D., Eggleton, P., & Zanne, A.E. (2023). Wood traits explain microbial but not termite-driven decay in Australian tropical rainforest and savanna. *J. Ecol.,* 111, 982–993. https://doi.org/10.1111/1365-2745.14090

Li, H., & Greening, C. (2022). Termite-engineered microbial communities of termite nest structures: A new dimension to the extended phenotype. *FEMS Microbiol. Rev.*, *46*(6), fuac034. https://doi.org/10.1093/femsre/fuac034

Martin, J.S., & Bulmer, M.S. (2018). A Lab-Based Study of Temperate Forest Termite Impacts on Two Common Wood-Rot Fungi. *Environmental Entomology*, *47*(6), 1388–1393. https://doi.org/10.1093/ee/nvy122

Mattheck, C., Bethge, K., & West, P.W. (1994). Breakage of hollow tree stems. *Trees*, *9*(1). https://doi.org/10.1007/BF00197869

Monda, Y., Kiyono, Y., Melling, L., Damian, C., & Chaddy, A. (2015). Allometric equations considering the influence of hollow trees: A case study for tropical peat swamp forest in Sarawak. *Tropics*, *24*(1), 11–22. https://doi.org/10.3759/tropics.24.11

Myer, A., Myer, M.H., Trettin, C.C., & Forschler, B.T. (2021). The fate of carbon utilized by the subterranean termite *Reticulitermes flavipes*. *Ecosphere*, *12*(12), e03872. https://doi.org/10.1002/ecs2.3872

N'Dri, A.B., Gignoux, J., Konaté, S., Dembélé, A., & Aïdara, D. (2011). Origin of trunk damage in West African savanna trees: The interaction of fire and termites. *J. Trop. Ecol.*, *27*(3), 269–278. https://doi.org/10.1017/S026646741000074X

Ohmura, W., Doi, S., Aoyama, M., & Ohara, S. (2000). Antifeedant activity of flavonoids and related compounds against the subterranean termite Coptotermes formosanus Shiraki. *J. Wood Sci.*, *46*(2), 149–153. https://doi.org/10.1007/BF00777362

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science, 333*(6045), 988–993. https://doi.org/10.1126/science.1201609

Perry, D.H., Lenz, M., & Watson, J.A.L. (1985). Relationships between fire, fungal rots and termite damage in Australian forest trees. *Australian Forestry*, *48*(1), 46–53. https://doi.org/10.1080/00049158.1985.10674422

R: A language and environment for statistical computing. (2023). R Foundation for Statistical Computing. R Core Team. https://www.R-project.org/

Rayner, A.D.M., & Boddy, L. (1988). Fungal decomposition of wood. Its biology and ecology. https://www.cabdirect.org/cabdirect/abstract/19911369864

Rayner, L., Ellis, M., & Taylor, J.E. (2014). Hollow occurrence and abundance varies with tree characteristics and among species in temperate woodland Eucalyptus. *Austral Ecology*, *39*(2), 145–157. https://doi.org/10.1111/aec.12052

Rückamp, D., Martius, C., Bragança, M.A.L., & Amelung, W. (2011). Lignin patterns in soil and termite nests of the Brazilian Cerrado. *Appl. Soil Ecol.*, *48*(1), 45–52. https://doi.org/10.1016/j.apsoil.2011.02.003

Saber, F.R., Munekata, P.E.S., Rizwan, K., El-Nashar, H.A.S., Fahmy, N.M., Aly, S.H., El-Shazly, M., Bouyahya, A., & Lorenzo, J.M. (2023). Family Myrtaceae: The treasure hidden in the complex/diverse composition. *Crit. Rev. Food Sci. Nutr.* https://www.tandfonline.com/doi/full/10.1080/10408398.2023.2173720

Ulyshen, M.D. (2016). Wood decomposition as influenced by invertebrates. *Biological Reviews*, *91*(1), 70–85. https://doi.org/10.1111/brv.12158

Viana-Junior, A., Côrtes, M., Cornelissen, T., & Neves, F. (2018). Interactions between wood-inhabiting fungi and termites: A meta-analytical review. *Arthropod-Plant Interactions*, *12*. https://doi.org/10.1007/s11829-017-9570-0

Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C., & Coomes, D.A. (2009). Global meta-analysis of wood decomposition rates: A role for trait variation among tree species? *Ecology Letters*, *12*(1), 45–56. https://doi.org/10.1111/j.1461-0248.2008.01259.x

Werner, P.A., & Prior, L.D. (2007). Tree-piping termites and growth and survival of host trees in savanna woodland of north Australia. *J. Trop. Ecol.*, *23*(6), 611–622. https://doi.org/10.1017/S0266467407004476

Wijas, B., Allison, S., Austin, A., Cornwell, W., Cornelissen, J.H., Eggleton, P., Fraver, S., Ooi, M., Powell, J., Woodall, C., & Zanne, A.E. (2024). The role of deadwood in the carbon cycle: Implications for models, forest management, and future climates. *EcoEvoRxiv*. https://doi.org/10.32942/X2690K

Wijas, B.J., Flores-Moreno, H., Allison, S.D., Rodriguez, L.C., Cheesman, A.W., Cernusak, L.A., Clement, R., Cornwell, W.K., Duan, E.S., Eggleton, P., Rosenfield, M.V., Yatsko, A.R., &

Zanne, A.E. (2024). Drivers of wood decay in tropical ecosystems: Termites versus microbes along spatial, temporal and experimental precipitation gradients. *Functional Ecology*, 1365-2435.14494. https://doi.org/10.1111/1365-2435.14494

Wong, A.H.H., & Cheok, K.S. (2001). Observations of Termite-Fungus Interactions of Potential Significance to Wood Biodeterioration and Protection. Timber Technology Centre. http://myagric.upm.edu.my/id/eprint/11429

Zanne, A.E., Flores-Moreno, H., Powell, J.R., Cornwell, W.K., Dalling, J.W., Austin, A.T., Classen, A.T., Eggleton, P., Okada, K., Parr, C.L., Adair, E.C., Adu-Bredu, S., Alam, A., Alvarez-Garzón, C., Apgaua, D., Aragón, R., Ardon, M., Arndt, S.K., Ashton, L.A., … Curran, T.J. (2022). Termite sensitivity to temperature affects global wood decay rates. *Science 377*, 1440–1444. https://doi.org/10.1126/science.abo3856

Zhou, L., Dai, L., Gu, H., & Zhong, L. (2007). Review on the decomposition and influence factors of coarse woody debris in forest ecosystem. *J. For. Res.*, *18*(1), 48–54. https://doi.org/10.1007/s11676-007-0009-9

Zuleta, D., Arellano, G., Muller-Landau, H.C., McMahon, S.M., Aguilar, S., Bunyavejchewin, S., Cárdenas, D., Chang-Yang, C.H., Duque, A., Mitre, D., Nasardin, M., Pérez, R., Sun, I.F., Yao, T.L., & Davies, S.J. (2022). Individual tree damage dominates mortality risk factors across six tropical forests. *New Phytol.*, *233*(2), 705–721. https://doi.org/10.1111/nph.17832

Supporting Information

Supplementary Table 1. Summary of damaged trees in the study (with sample size n > 3).

Species	**Wood specific gravity (g cm^{-3})**	**n**		
		Total	*With termite damage*	*With microbial damage*
Corymbia clarksoniana	0.668	15	14	9
Eucalyptus tetrodonta	0.699	4	4	4
Lophostemon suaveolens	0.569	6	3	5
Planchonia careya	0.513	4	4	2

Supplementary Table 2. Linear mixed-effect model output summarized in an analysis of deviance table testing how internal stem damage changed across heights in the tree for different species.

Response		χ^2	**df**	**p**
log(percent termite damage)	height	83.4	1	< 0.001***
	species	14.2	6	0.028*
	height*species	21.1	6	0.002**
log(percent microbe damage)	height	4.2	1	0.041*
	species	1.7	6	0.949

Supplementary Table 3. 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.

Response		**Sum sq**	**df**	**F-value**	**p**
log(percent damage)	species	4.4	3	2.30	0.089
	damage type	2.4	1	3.81	0.057
	species*damage type	6.0	3	3.13	0.034*
	residuals	31.8	50		

Supplementary Table 4. 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).

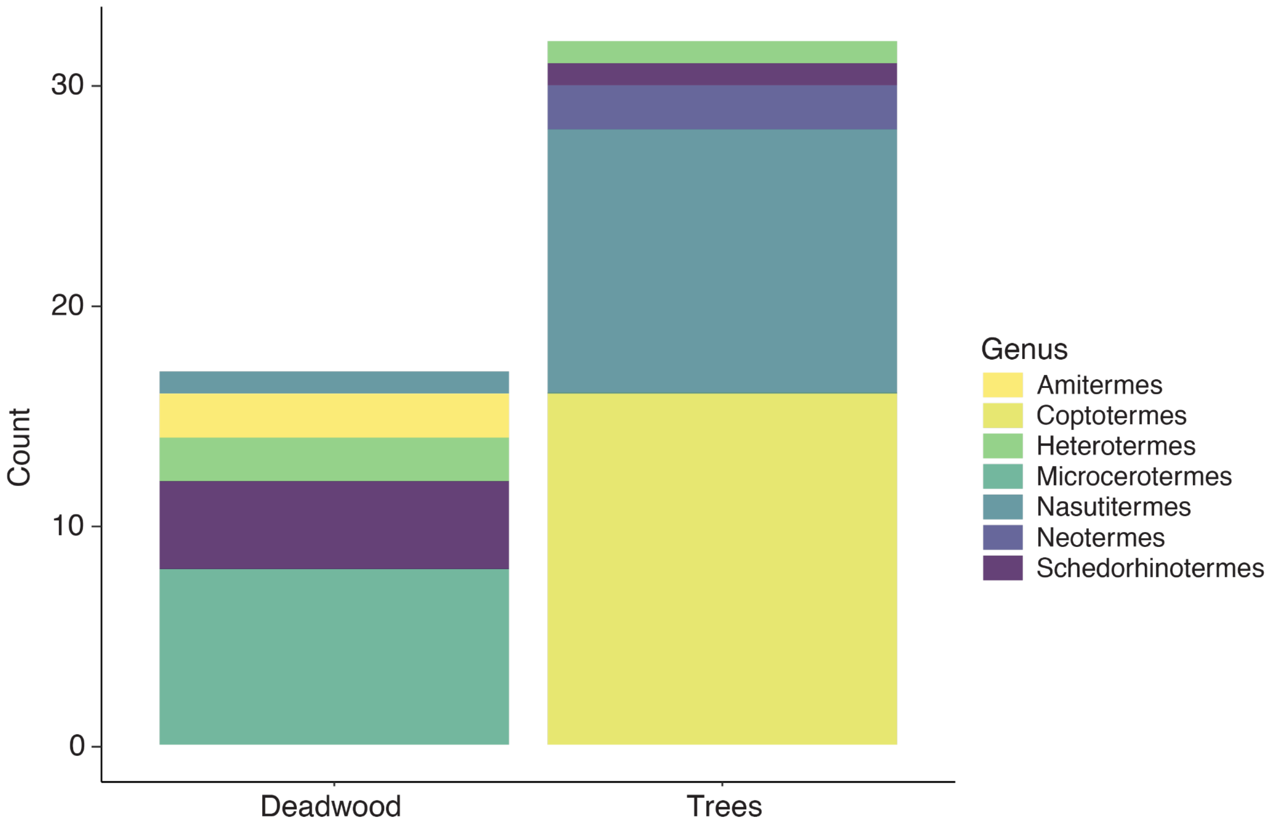
Response		**Sum sq**	**df**	**F-value**	**p**
log(percent termite damage)	wd	2.993	1	3.971	0.056
	dbh	0.394	1	0.523	0.475
	residuals	21.854	29		
log(percent microbe damage)	wd	0.868	1	1.386	0.249
	dbh	0.388	1	0.619	0.438
	residuals	18.168	29		

Supplementary Table 5. List of species and total counts of occurrences with termites found in/associated with living trees and fallen deadwood.

Species	**Deadwood count**	**Living tree count**
Amitermes sp. A	2	-
Coptotermes acinaciformis	-	13
Coptotermes sp. A	-	3
Heterotermes vagus	1	-
Heterotermes sp. A	1	-
Heterotermes sp. B	-	1
Microcerotermes sp. A	2	-
Microcerotermes sp. B	2	-
Microcerotermes sp. C	1	-
Microcerotermes sp. D	3	-
Nasutitermes graveolus	1	9
Nasutitermes sp. A	-	3
Neotermes sp. A	-	2
Schedorhinotermes breinli	3	-
Schedorhinotermes sp. A	1	1

Supplementary Table 6. Plot-level damaged tree AGB from both termites and microbes for four damaged species in the study. Undamaged species included *Acacia polystachya*, *Corymbia tessellaris*, *Deplanchea tetraphylla*, *Grevillea parallela*, *Parinari nonda*, and *Timonius timon.*

Species	**Biomass per hectare (kg ha^{-1})**	**Plot biomass (%)**	**%Tree-level termite damage (SD)**	**Termite damaged biomass (kg ha^{-1})**	**%Tree-level microbial damage (SD)**	**Microbial damaged biomass (kg ha^{-1})**
C. clarksoniana	2,158	24.6	5.68 (± 6.95)	122.6	2.42 (± 6.71)	52.2
E. tetrodonta	2,818	32.1	2.34 (± 2.57)	65.9	2.11 (± 1.71)	59.5
L. suaveolens	1,889	21.5	0.04 (± 0.06)	7.6	1.76 (± 2.3)	33.2
P. careya	258	2.9	1.47 (± 1.08)	3.8	0.50 (± 0.88)	2.3
Other species (undamaged)	1,658	18.9	N/A	N/A	N/A	N/A



Supplementary Figure 1. Termite species observed in fallen deadwood and living trees.