Rotten to the core? How internal stem damage varies vertically in savanna trees and is influenced by tree species, traits, and external damage pressures

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Abstract

1. Trees are important aboveground carbon sinks in savanna ecosystems, yet consumption of internal wood by decomposers (e.g., termites and microbes) creates uncertainties in tree biomass accounting. It remains unclear whether internal stem damage is constant or variable throughout the tree, making it uncertain if a lower stem sample reflects damage in the entire tree. Furthermore, total damage and damage location are likely influenced by external damage pressures (i.e., termites, microbes, and fire), tree species and tree traits (i.e., diameter at breast height (DBH), wood density), and their interactions.
2. We sampled internal damage in the lower stem of savanna trees in North Queensland, Australia to test for vertical variation in terms of proportional and absolute amount of damage. We compared damage estimates from a single-sample method, assuming constant damage, with a multi-sample method, assuming variable damage, to test how well one sample represents the lower stem. We investigated if tree species accumulated damage differently based on their traits (i.e., DBH and wood density) or susceptibility to external damage pressures (i.e., fire scarring and termite presence). Finally, we tested if external damage pressures differentially affected tree species and if this was mediated by tree traits.
3. The absolute amount, but not proportion, of damage decreased with higher vertical position on the stem. There was no difference in total stem damage between the single-sample and multi-sample methods. Species-specific variation in internal stem damage was influenced by DBH and wood density. Total damage was greatest in large trees, particularly those with external termite presence. Finally, external termite presence, but not fire scarring, differentially affected tree species and was most likely to occur on large, dense trees.
4. *Synthesis*. We demonstrated that a single sample effectively captured total internal damage in the lower stem. Although species differed in total damage, damage accumulation rates with height were consistent, suggesting a general relationship. By integrating the influence of external factors and tree traits, our findings underscore the importance of considering these elements for accurately estimating carbon stored in aboveground tree biomass.

Introduction

Savannas cover 20% of the Earth's terrestrial surface and are ecologically rich ecosystems with unique biogeochemistry (Scholes & Archer 1997), yet are often overlooked for their role in the global carbon cycle (Parr et al., 2014; Dobson et al., 2022). In the savanna, woody plants store carbon both while alive and dead; living trees sequester an estimated 0.39 Pg C every year (Grace et al., 2006), and dead wood

stores a further 9.6 Pg C globally (Wijas, Allison et al., 2024). In terms of savanna carbon storage, woody plant aboveground biomass (AGB) is of particular interest due to its longevity on the landscape. Yet, AGB is eventually cycled back to the atmosphere and soils via the decomposition process (Zhou et al., 2007), of which termites and fire are especially important contributors in savanna ecosystems (Zanne et al., 2022; Murphy et al., 2023).

While many studies focus on carbon storage in living trees (Sullivan et al., 2017) and carbon turnover via decomposition of downed deadwood (Wijas, Flores-Moreno et al., 2024), internal tree stem damage is a component of savanna ecosystem that is largely overlooked in carbon cycling models (Calvert et al., 2024). Internal stem damage occurs when wood within living trees decomposes (Janzen 1976) and has been documented to affect up to a third of savanna tree AGB (Flores-Moreno et al., 2024), resulting in uncertainties in tree AGB estimation (Calvert et al., 2024). Termite decay (Eleuterio et al., 2020; N'Dri et al., 2011; Werner & Prior 2007; Yatsko et al., 2024) and microbial 'heartrot' (Lee et al., 1988; Zeps et al., 2017; Heineman et al., 2015; Eleuterio et al., 2020; Yatsko et al., 2024) contribute to internal stem damage, yet its concealed nature makes measurement challenging. To quantify total damage and determine where it occurs, destructively harvesting trees proves useful (Calvert et al., 2024), however this is often logistically infeasible and cannot be carried out extensively. Nondestructive sampling is more accessible, using increment corers (Heineman et al., 2015), resistograph drills (Flores-Moreno et al., 2024), and sonic tomography (Gilbert et al., 2016) to target sampling in the lower stem or at diameter at breast height (DBH) (Brown et al., 1995; Zeps et al., 2017; Eleuterio et al., 2020; Werner and Prior 2007*;* Flores-Moreno et al., 2023). However, it may be problematic to assume that a single measurement represents damage throughout the entire tree (Flores-Moreno et al., 2023), and capturing vertical variation would require a revised sampling strategy. If the amount of internal damage varies between different parts of the tree, possibly due to different decomposers, it is important to account for these changes when modeling damage.

Towards the goal of understanding vertical variation in internal stem damage, it is important to consider how biotic players (mainly microbes and termites, Yatsko et al., 2024) cause internal stem damage and partition wood resources within trees. From only two studies on internal stem damage vertical variation (Calvert et al., 2024; Yatsko et al., 2024), two non-exclusive hypotheses emerge regarding vertical damage variation, which depend on how damage is quantified. The first internal damage pattern hypothesis is that damage (quantified as an absolute amount of wood) is concentrated at the tree base (see ***H1***, Figure 1a). Here, wood resources are high, since stem diameter is largest, and accessible to ground-colonizing organisms. For instance, termites are usually foraging on the ground and may use the bottom of tree stems as an access point to internal wood or enter through the roots, concentrating damage in the lower stem (Yatsko et al., 2024). Furthermore, the amount of wood consumed by microbes has been positively related to the amount of wood available (Gilbert et al., 2016); decomposers are often targeting tree heartwood (Perry et al., 1985), which is greatest toward the bottom of the tree and can completely disappear in fine branches (Climent et al., 2003).

The second internal damage pattern hypothesis is that damage, as a proportion, remains constant through the lower stem to maintain a strong structure. This hypothesis largely relates to termite-driven internal damage, as some wood-feeding termites live in the same tree that they consume (Werner & Prior 2007), leading to a need to maintain a structurally strong home (see ***H2***, Figure 1b). We expect that termites will

excavate wood in a constant proportion across vertical positions in the lower stem, leaving behind a strong structure to continue to live in. This has been described by termite tree 'piping', where stems are hollowed out like a straw (Werner & Prior 2007), and likely protects termites nesting inside the stem. While extensive hollowing (proportion > 0.6) can increase tree mortality (Werner & Prior 2007), it has been shown that trees with moderate, proportionally constant internal damage can maintain stability (Mattheck et al., 1994), especially if outer wood density is high (Larjavaara & Muller-Landau 2010; Osazuwa-Peters et al., 2014).

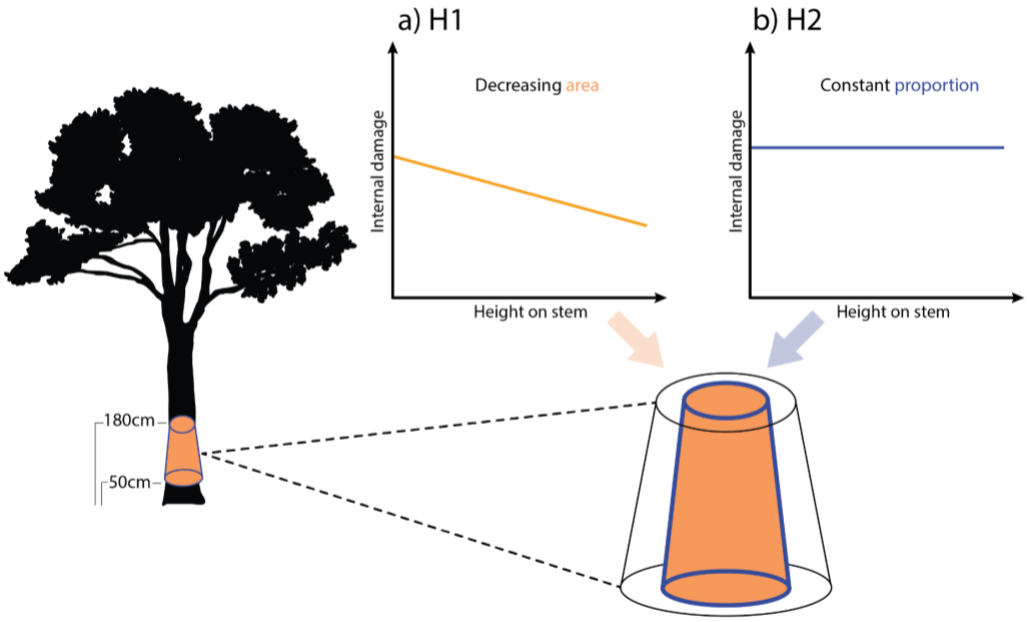

Figure 1: a) Visualization for ***H1*** ('damage at the base'): Internal damage (yellow line) is greatest at the tree base where the diameter is largest. b) Visualization for ***H2*** ('strong home'): Internal damage as a proportion (purple line) remains constant at all heights, but decreases in absolute amount due to stem taper. Both ***H1*** and ***H2*** represent predictions for the lower stem (sampled between 50 and 180 cm, shown on left).

To accurately estimate total internal stem damage and its vertical variation in the tree, it is necessary to consider variation across tree species, and if variation in damage accumulation across species is driven by underlying tree traits. Flores-Moreno et al. (2024) found that species with high wood density accumulated greater internal stem damage across a tropical rainfall gradient. Dense wood is preferred by *Coptotermes acinaciformis* (Oberst et al., 2018), which is known to hollow trees in Australian savannas. Such a preference may lead to tree species with dense wood accumulating more damage. Tree size (here, DBH) is also of importance; some studies found that larger trees had more frequent damage (Nogueira et al., 2006; Heineman et al., 2015), yet others found weak relationships between DBH and total damaged biomass (Flores-Moreno et al., 2024). Ultimately, understanding how internal stem damage varies across different tree species, and identifying tree traits responsible for these differences, remains a key challenge in characterizing internal stem damage.

Beyond tree properties, external damage pressures such as fire and termite activity may also impact damage accumulation by facilitating access to internal wood. Fire is important for woody biomass turnover in savannas (Grace et al., 2006; Wijas, Allison et al., 2024), and external openings from fire

scarring may allow decomposers access to internal wood (N'Dri et al., 2011). The presence or absence of fire scarring could lead to differences in both vertical variation of internal stem damage as well as total damage accumulation. A study in an African savanna concluded that fire was a main 'cavity-opening agent' in tree stems, allowing subsequent termite or microbial entry. Basal fire scarring is even a management strategy that accelerates hollow formation for the benefit of hollow-dwelling fauna (Adkins 2006). External termite presence may also indicate trees undergoing internal damage. Termites build mud tubes, tunnels or 'runways' externally on trees, which indicate infestation (Li et al., 2016), and termite colonies built at the tree base can indicate internal hollowing (Eleuterio et al., 2020). Therefore, the presence of external fire scarring and termite activity on tree stems may be an important predictor of internal stem damage.

In this study, we measured internal damage at multiple vertical positions in the lower 2 m of tree stems in a North Queensland, Australia savanna dominated by Myrtaceae flora. In this system, fire, termites and microbes all contribute to wood decay (Clement et al., 2021; Law et al., 2023; Wijas, Flores-Moreno et al., 2024) and extensive internal stem damage has previously been reported (Flores-Moreno et al., 2023). We address the following questions:

Q1) Does the amount of internal damage change with a) vertical position on the lower stem across species or b) vertical position on the lower stem for trees of different wood density and DBH? We express damage as an absolute amount to test ***H1*** ('damage at the base'), and damage as a proportion to test ***H2*** ('strong home').

Q2) Do estimates of total lower stem damaged biomass change based on vertical variation being accounted for (via a multi-sample method) or not (via a single-sample method)?

Q3) Do species differ in total lower stem damaged biomass, and, if so, is this driven by tree traits and/or external damage pressures?

Q4) Do external damage pressures differentially affect tree species, and are detected differences driven by underlying tree traits?

Materials and Methods

Study site and sampling

Sampling took place at two savanna sites in far north Queensland, Australia, Station Creek (STCK, -16.61 S, 145.24 E) and Pennyweight Station (PNW, -16.57 S, 144.92 E), located on the Australian Wildlife Conservancy (AWC) Brooklyn Sanctuary (Figure 2). PNW is a drier savanna ecosystem (812 mm rainfall annually) compared to STCK (1,728 mm of rainfall annually) (Cheesman et al., 2018). Both sites experience a distinct wet and dry season, with 77% of rainfall occurring between November and April (Cheesman et al., 2018).

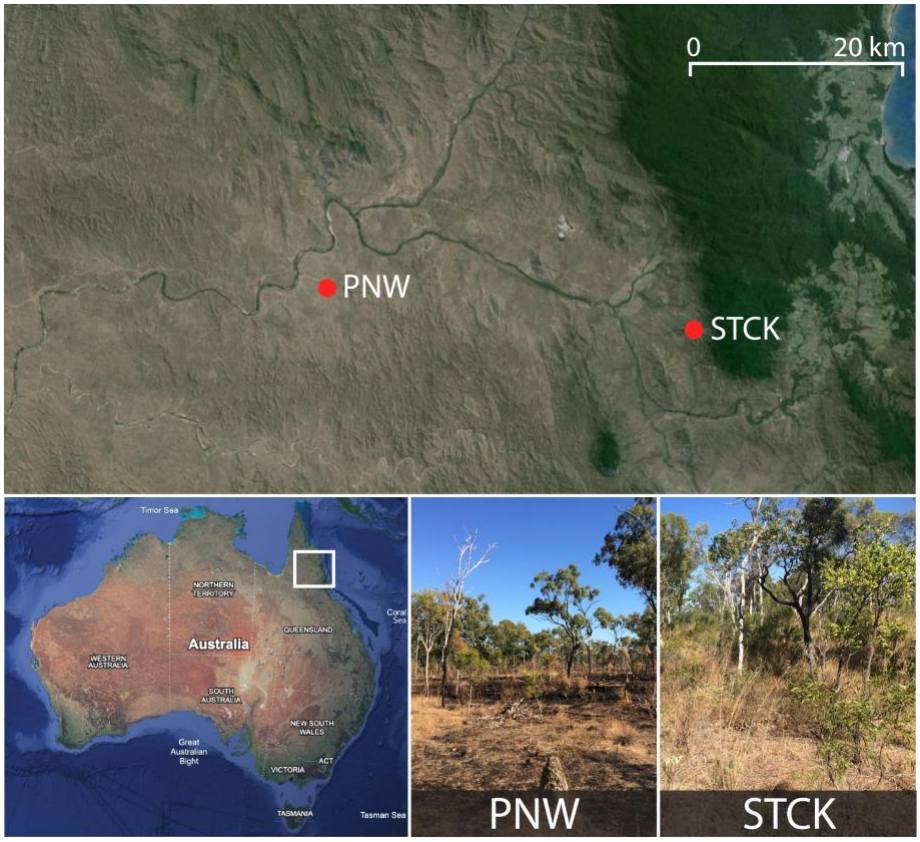

Figure 2. Location of Station Creek (STCK) Pennyweight Station (PNW) in far north Queensland, Australia and characteristic landscapes for each site.

In 2018, 50x50 m plots were established at each site and DBH measurements and species identification were made for all trees in the plot. Wood density values for each species were extracted from the Tree Functional Attributes and Ecological Database (Supplementary Table 2, Harja et al., 2019). PNW is dominated by *Eucalyptus cullenii* and *Melaleuca stenostachya* (Myrtaceae), while STCK is more diverse, but largely dominated by *E. cullenii* and *Corymbia clarksoniana* (Myrtaceae) (Supplementary Table 1).

We selected tree species with high biomass representation to investigate vertical stem damage variation, including three Myrtaceae species. We targeted species with known high levels of high internal stem damage (exceeding 30% of tree biomass damage described by Flores-Moreno et al., 2024) in order to determine vertical patterns of internal damage.

We selected tree species with high plot-level biomass representation and known occurrence of internal stem damage (up to 30%, Flores-Moreno et al., 2024) to examine vertical patterns of stem damage. We selected three Myrtaceae species: *E. cullenii* (occurring at both sites: STCK, 65% of plot-level biomass, PNW, 96% of plot-level biomass), *M. stenostachya* (PNW, 2.3% of plot-level biomass), *C. clarksoniana* (STCK, 20% of plot-level biomass, Supplementary Table 1). We measured vertical variation of internal damage on the lower 2 m of stem for 45 trees (*E. cullenii* n = 21, *C. clarksoniana* n = 14, *M. stenostachya* n = 10), sampling at least 10 individuals per species in four vertical positions (Supplementary Table 2).

Quantifying internal stem damage

We used an IML-RESI power drill to quantify internal damage (residrill; PD-500, IML, Germany, Figure 3a). The residrill measures resistance as the stylus turns, generating a resistograph measurement where high resistance indicates sound wood and low resistance indicates damaged or decaying wood (see Supplementary Figure 1). We drilled along the north-to-south plane at four vertical positions on each tree (targeting sampling at approximately 50 cm, 95 cm, 120 cm, and 180 cm from the tree base, Figure 3a). We recorded the DBH of the tree, the stem diameter at drilling point, as well as the distance from the drilling point to the ground.

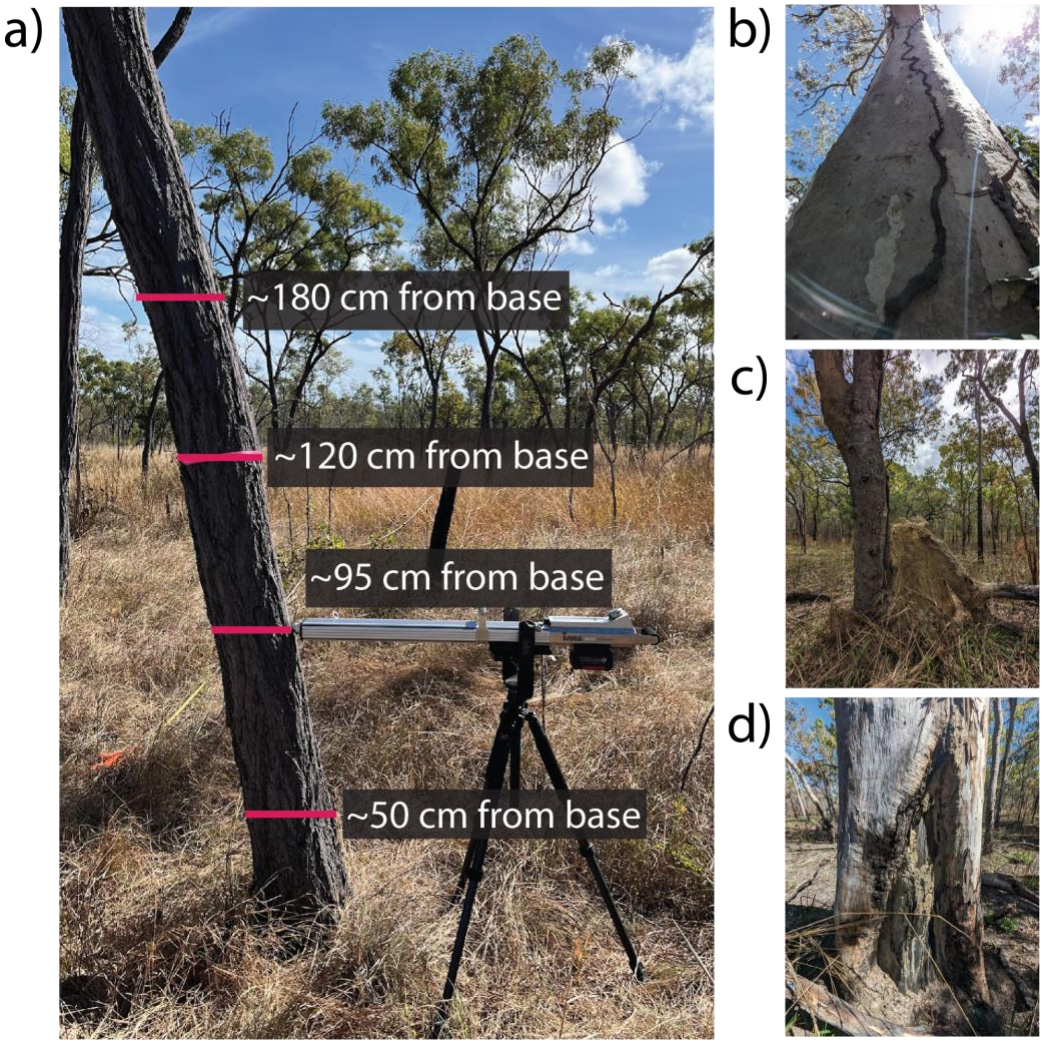

Figure 3. a) Internal stem damage sampling at four positions on the lower stem (approximately 50, 95, 120, and 180 cm above tree base); residrill pictured in the lower right. External termite presence via b) runways on tree bark and c) a mound built at the base of the tree. d) External fire damage via basal scarring.

For each measurement point, we quantified damage as an absolute amount (via area of the sampled cross section, to address ***H1***) and as a proportion (to address ***H2***). To begin, we calculated damage as a proportion from the residrill output data. A sound wood threshold was classified for each residrill sample ('trace', Supplementary Figure 1). Internal stem damage was quantified as the percentage change from the

sound wood threshold (Flores-Moreno et al., 2024). Each trace was segmented using a piecewise function to minimize residual sum of squares (RSS). For each trace, we compared the segments derived on the piecewise regression to the sound wood threshold using a lower-tailed z-test (alpha = 0.05, Flores-Moreno et al., 2024). From this we determined the total proportion of damage on the linear transect captured by the residrill trace (see Flores-Moreno et al., 2024 for data processing details). Proportion damage was estimated on a linear basis on the assumption that damage accumulates randomly. To quantify the absolute amount of internal damage, we calculated the total undamaged area (cm^2) of the cross section of the tree stem at each measurement point using the area of a circle = $\pi(d/2)^2$ (d is stem diameter at the height of measurement). We then multiplied the undamaged area by the damage proportion to derive the total damaged area (cm^2).

Calculating damage in the main stem using a single-sample estimate: constant damage

We modeled the segment of lower stem sampled with the residrill (50-180 cm from the ground) as a truncated cone, or frustum (Figure 1). The frustum tapers linearly from bottom to top, reflecting the tapering shape of tree stems. We calculated the volume of the undamaged frustum (representing a segment of the lower tree stem) using the following equation (Larsen 2017):

$$V = \frac{L}{3}(A_l + \sqrt{A_l A_s} + A_s)$$

Where V is volume of the lower stem, L is the length of the frustum, A_l is the area of the frustum bottom (50 cm from the ground), and A_s is the area of the frustum top (180 cm from the ground).

To calculate damaged volume in the lower stem using a single-sample damage estimate, we multiplied the undamaged frustum volume by the proportion of damage from the residrill measurement ~120 cm from tree base. The 120 cm measurement allowed for comparison with methods from Flores-Moreno et al. (2024), with the caveat that we used the closest measurement to DBH (1.2 m), since our sampling design did not record internal damage exactly at 1.3 m from the ground (true DBH measurement). To convert damaged volume to damaged biomass (in kg) in the lower stem, we multiplied the damaged volume from the single-sample estimate by species-level wood density values (Supplementary Table 2).

Calculating damage in the main stem using a multi-sample estimate: variable damage

To calculate damaged volume in the lower stem using a multi-sample damage estimate, we defined a tapering relationship for how damage changed between the bottom and top of the lower stem. We modified the frustum equation from Larsen (2017) so that A_l and A_s represented the area of damage from the lowest (50 cm) and highest measurements (180 cm) on the stem. We multiplied the damaged volume by species-level wood density values to convert to biomass (kg).

Assessing external damage pressures: termite presence and fire scarring

Trees were inspected for external termite presence, defined as termite runways on the stem (Figure 3b) or mounds built at the tree base (Figure 3c). Additionally, we recorded the presence or absence of moderate to severe fire scarring, identified as damage to basal bark or charred surfaces covering at least 25% of the lower stem (Figure 3d).

Analyses

Internal stem damage variation with vertical position across tree species

We tested how damage, both as an absolute amount (***H1***) and as a proportion (***H2***), changed with vertical position and if this varied by tree species. To determine the relationship between proportion damage, vertical position on the lower stem, and tree species, we used a beta regression model with a logit link from the package glmmTMB (Brooks et al., 2017). Proportional stem damage was the response variable and vertical position (i.e., residrill height from the ground, cm) and tree species were fixed effects, with tree individual and site as random effects. A Tukey's Honest Significant Difference (HSD) pairwise post-hoc multiple comparisons test was used to determine which species significantly differed.

To determine the relationship between absolute amount of damage, vertical position on the lower stem, and species, we used a linear mixed effect model from the package lmer (Bates et al., 2015). In the model, area of stem damage (cm^2) was the log-transformed response (to meet the normality assumption) while vertical position (cm) and tree species were fixed effects, and tree individual and site as random effects. A Tukey's HSD pairwise post-hoc multiple comparisons test was used to determine which species significantly differed.

Internal stem damage variation with vertical position across tree traits (DBH and wood density)

We tested if tree traits underlie species-level differences in vertical variation of both proportion and absolute amount of internal stem damage. We use a beta regression model with a logit link where proportion stem damage was the response variable, vertical position on the lower stem, DBH, and species-level wood density were fixed effects, and tree individual and site as random effects. To test the effect of tree traits on the absolute amount of damage, we used a linear mixed effect model where damaged area was the log-transformed response variable (for normality) and vertical position, tree DBH, and species-level wood density were fixed effects, with tree individual and site as random effects.

Damaged biomass in the lower stem: comparing single-sample versus multi-sample methods

We used a non-parametric paired Wilcoxon signed rank exact test (due to a non-normal distribution) to determine if a single-sample estimate of total damaged biomass in the lower stem differed from a multi-sample estimate.

Differences in total damaged biomass by species, tree traits and presence of external damage pressures

We first tested species-level differences in total damaged biomass in the lower stem (in kg) using a linear mixed effects model with total damaged biomass as a response variable (log-transformed), species as a fixed effect, and site as a random effect. A Tukey's HSD pairwise post-hoc multiple comparisons test was used to determine which species were significantly different. To test if underlying tree traits explained species-level differences, we ran a linear mixed effect model with total damaged biomass as a response variable (log-transformed), tree DBH and species-level wood density as fixed effects, and site as a random effect. We also ran an ANOVA to test for species-level differences in DBH, followed by a Tukey HSD pairwise post-hoc test. Lastly, we tested if external damage pressures contributed to greater damaged biomass using a linear mixed effect model where damaged biomass was the response (log-transformed), external termite presence or fire scarring were fixed effects, and site as a random effect. We also tested for an interaction between external termite presence or fire scarring.

External damage pressure effects across tree species and traits

We used a Fisher's exact test to determine if the presence or absence of external termite and fire scarring differed across species. We prepared the data as counts of presence or absence of external termite and external fire damage into separate contingency tables. Following a significant test result we used a pairwise Fisher test as a post-hoc comparison with a False Discovery Rate (FDR) test to correct p-values for multiple comparisons. Then, we tested the role of tree traits (DBH and species-level wood density) in influencing external damage pressures (presence/absence) using a binomial model with a logit link. When DBH and wood density were included as predictors in a combined model, collinearity was high. For this reason, we ran separate binomial models testing each tree trait (DBH, wood density) against external termite presence and fire scarring. All analyses were performed in R 4.4.1 (R Core Team, 2024).

Results

Internal stem damage variation with vertical position across tree species

The absolute amount of internal stem damage varied by species ($p < 0.001$, Figure 4a) and decreased with higher vertical position on the stem ($p = 0.01$, Figure 4c). Proportional damage varied by species ($p = 0.001$, Figure 4b) but did not change with vertical position on the main stem ($p = 0.09$, Figure 4d, Supplementary Table 3).

Internal stem damage variation with vertical position across tree traits (DBH and wood density)

Damaged area increased for trees with larger DBH ($p < 0.001$) and decreased at higher vertical positions on the lower stem ($p = 0.02$, Figure 4e). Wood density did not affect the amount of damaged area ($p = 0.70$). Proportion damage did not significantly change across tree DBH, wood density, or vertical position on the lower stem (Figure 4f, Supplementary Table 4).

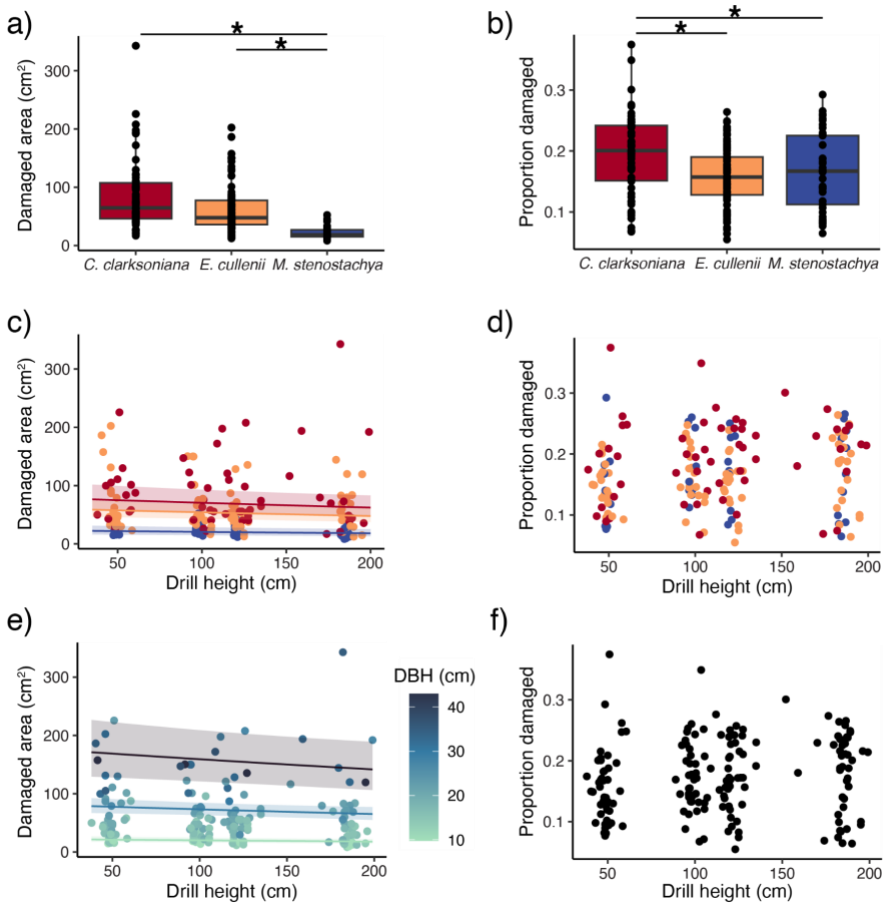

Figure 4. Species-level differences in a) absolute amount and b) proportion stem damage. Species-level differences for c) absolute amount of damage and d) proportion damage for vertical positions (cm from ground). Colors in c) and d) represent tree species indicated in a) and b). Tree traits that significantly affect e) absolute amount of damage and f) proportion damage at different vertical stem positions. Colors in e) indicate three selected DBH values capturing small, medium, and large trees respective to our dataset (purple = 34 cm, blue = 25 cm, green = 10 cm). Shading represents 95% confidence intervals.

Damaged biomass in the lower stem: comparing single-sample versus multi-sample methods

There was no difference in the amount of damaged biomass when assuming constant damage (single-sample) or variable damage (multi-sample) ($p = 0.75$, Supplementary Figure 2).

Differences in total damaged biomass by species, tree traits and presence of external damage pressures

Total lower stem internal damage varied by species ($p < 0.001$). *E. cullenii* trees had significantly higher damage than *M. stenostachya* trees ($p < 0.0001$, Figure 5a). Larger ($p < 0.001$) and densely-wooded ($p = 0.01$) trees had more total damaged biomass (Figure 5b). Species significantly differed in DBH (Supplementary Table 5); *E. cullenii* and *C. clarksoniana* trees were larger than *M. stenostachya* (Supplementary Figure 3). Total damaged biomass was higher for trees with external termite presence ($p < 0.001$, Figure 5c), but not fire scaring ($p = 0.30$, Figure 5d).

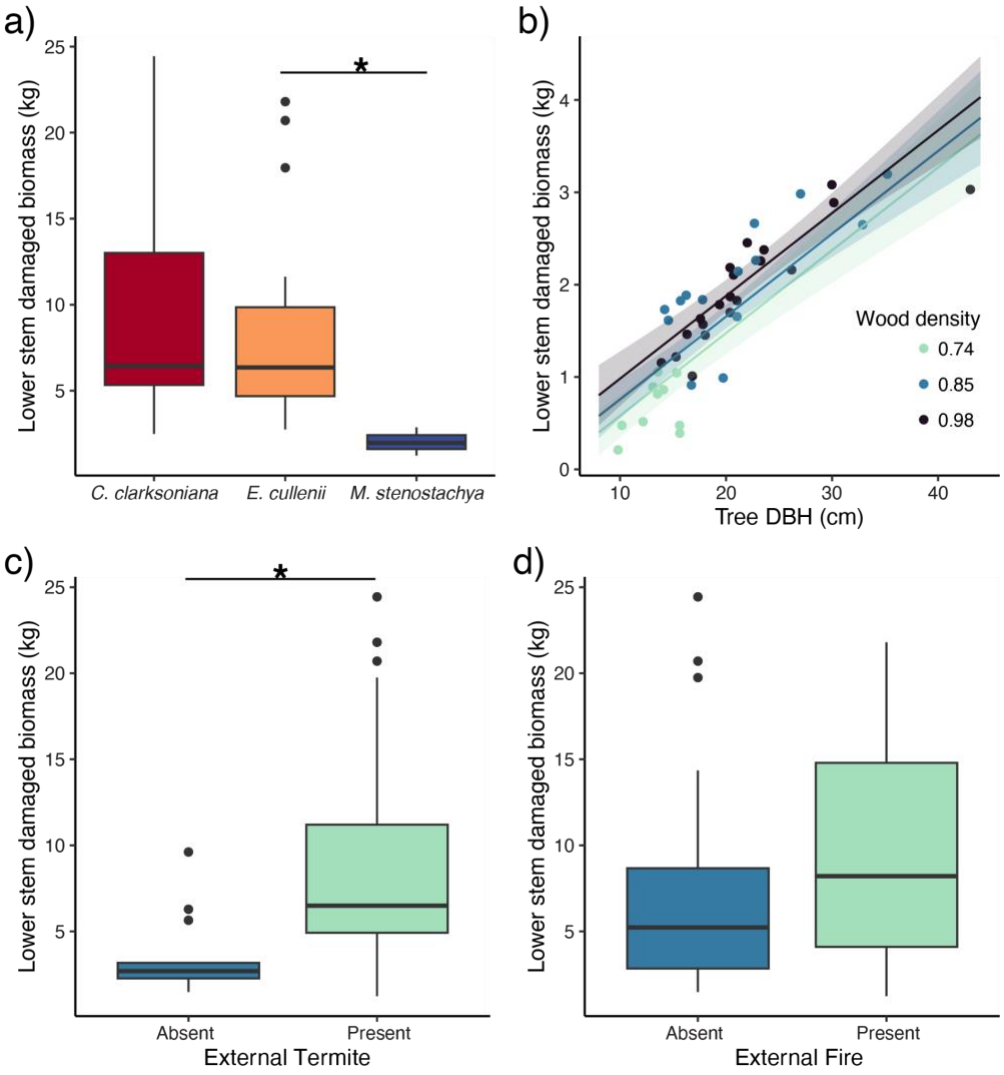

Figure 5. Total damaged biomass (kg) in the lower stem for a) different species, b) DBH and wood densities, c) external termite presence/absence, and d) external fire scarring presence/absence.

External damage pressure effects across tree species and traits

Species differed in how external termite presence predicted internal damage ($p = 0.003$), with significant differences between *E. cullenii* and *M. stenostachya* trees ($p = 0.01$, Figure 6a). There was no significant difference between species in how the presence of external fire scarring predicted damage ($p = 0.65$, Figure 6b). External termite presence increased with tree DBH ($p = 0.001$, Figure 6c) and wood density ($p < 0.001$, Figure 6d), but external fire scarring on the stem was not predicted by tree DBH ($p = 0.79$) or wood density ($p = 0.83$).

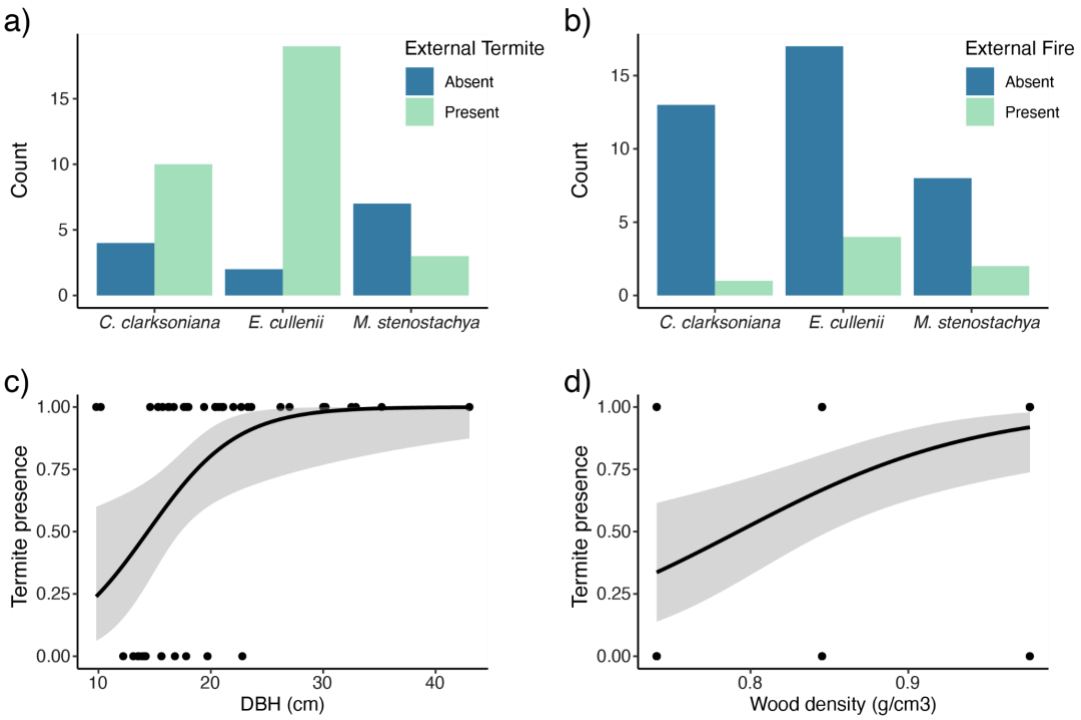

Figure 6. a) External termite presence/absence and b) external fire scarring presence/absence for the three study species. Relationship between trees with external termite presence and c) tree DBH and d) wood density. Shaded areas represent 95% confidence intervals.

Discussion

In this study, we examined vertical variation of internal stem damage and tested how species, tree traits, and external damage pressures contributed to internal stem damage. The absolute amount of internal stem damage decreased with higher vertical position on the stem, supporting ***H1***, the 'damage at the base' hypothesis. The amount of damage varied by species, which was likely due to the underlying influence of stem size. Proportion damage remained constant in the lower stem and no differences were found between single and multiple point estimates of total damage, supporting ***H2***, the 'strong home' hypothesis. Total damage in the lower stem varied by species likely due to differences in tree DBH and wood density; external termite presence was also associated with increased total damaged biomass. Furthermore, external termite presence varied by tree species and occurred more frequently in large, dense trees. Below we discuss the implications of our findings on modeling internal stem damage and propose that understanding the specific role of termites can help address uncertainties in tree carbon estimates beyond savanna ecosystems.

Amount of internal damage decreased with increasing vertical position on the lower stem

The decline in the absolute amount of damage with height supports the 'damage at the base' hypothesis (***H1***) and indicates a biophysical constraint where damage accumulation was dictated by the amount of wood at any given point on the stem. Due to tree taper, stem size decreases from the base to crown branches (McTague & Weiskittel 2021). Therefore, more wood is available for consumption at the lowest point of measurement (50 cm from the ground) compared to the highest point (180 cm) from the ground. Our models showed that larger trees had greater internal damage, further supporting that there is a

biophysical constraint on damage accumulation, since these trees hold more biomass. The presence of damage pressures (termites and fire scarring) often coincides with where wood resources are highest: at the tree base (Li et al., 2016; N'Dri et al., 2011). Therefore the tree base serves as an access point for decomposers (Adkins 2006) and area where damage is concentrated.

Our results also support the 'strong home' hypothesis (***H2***), as proportional internal stem damage did not change through the lower stem. This supports the key assumption used in Flores-Moreno et al. (2024) for estimating internal stem damage: a single proportion was used to represent damage incurred by the whole tree, which was then applied to scale internally damaged biomass to the plot-level. Tree hollowing from termites (Werner & Prior 2007) is likely responsible for the constant damage proportion, as termites are the main wood decomposer at the study sites (Clement et al., 2021; Flores-Moreno et al., 2024). Tree hollowing termites often reside in the cavities they create (Greaves 1962). It may be strategic for termites to remove wood in a constant proportion, as the tree structure can still maintain stability if hollowing does not exceed 70% of the trunk radius (Mattheck et al., 2006).

However, it remains critical to quantify vertical variation in internal stem damage in other locations with and without strong termite decomposition pressures, such as other savannas as well as non-savanna ecosystems. In contrast to our findings, in a higher rainfall savanna ecosystem in Australia, Calvert et al. (2024) showed a decreasing pattern in internal damage. This ecosystem had strong internal decomposition pressures from both termites and microbes (Yatsko et al., 2024), and damage was modeled using samples from the main stem and crown branches. While the present study does not show the same decreasing trend, variation in both the strength of termite decomposition pressure and environmental conditions (i.e., rainfall) could explain the differences. Rainfall may be important for predicting the relative strength of termites versus microbes as internal decomposers, which could alter patterns of damage through the tree. Flores-Moreno et al. (2024) showed that rainforest trees had less internal stem damage than savanna trees but could not identify how each process was influenced by different decomposers. Yet, it is known in downed deadwood that microbial decay played a greater role in tropical wet rainforest wood decomposition compared to savanna sites (Wijas, Flores-Moreno et al., 2024). Therefore, if microbial decay dominates internal stem damage, vertical variation may present differently than what was observed here for savanna trees, making the 'strong home' hypothesis less applicable. Since many accounts of microbial heartrot in both temperate and tropical trees have been noted (Frank et al., 2018; Lee et al., 1988; Heineman et al., 2015), efforts to sample stem damage vertical variation in such environments are required to determine if the patterns in this study can be generalized.

Damage across species, tree traits, and wood characteristics

We detected differences in species-level damage accumulation, with *C. clarksoniana* trees being most damaged and *M. stenostachya* least. Cross-species differences were most strongly driven by stem size, wood density, and external termite presence, however the broad shift in damage across species occurred at the overall amount of damage (i.e., intercept) but not in the accumulation of damage across the stem (i.e., slope). From this, we draw two main conclusions: 1) wood characteristics at the species-level are important controls on how much wood is consumed (i.e., explaining species differences in intercepts), and 2) across species, there may be a general relationship between internal damage accumulation and height (i.e., consistency of slopes across species). A closer evaluation of other physical and chemical wood properties that may improve palatability for decomposers is a necessary next step. For example, termites

consider factors other than wood density and resource size in foraging decisions, such as the early wood content (lighter colored, less dense wood), moisture levels, and even how well the substrate serves as a communication medium (Oberst et al., 2018). Such factors could be quantified using termite choice experiments to test for species-level differences in wood palatability. Following the second conclusion, we propose that if patterns of internal damage are generalizable across species or environments, they could be easily integrated into biomass models by assuming a constant slope. This would be an important next step toward incorporating internal stem damage into AGB accounting, which has yet to be accomplished (Flores-Moreno et al., 2024; Calvert et al., 2024). Yet it remains essential to test whether the patterns we find here extend to other ecosystem types and species to best inform AGB models more broadly.

Interestingly, both this study and Calvert et al. (2024) found 20% internal stem damage in *Corymbia clarksoniana* trees at two different savanna sites 600 km apart, despite variations in annual rainfall. This consistency suggests a potential pattern, but more sampling across different locations is essential to confirm whether this trend holds. To our knowledge, no studies have compared internal stem damage within species across sites, but such data will be invaluable in documenting the robustness of patterns on species-specific internal stem damage. Expanding data collection efforts to measure internal stem damage at the species-level across geographic and size ranges could directly feed into novel AGB models built to incorporate the effect of internal stem damage. A comprehensive database of species-level damage and vertical variation would greatly improve our understanding of missing biomass across ecosystems.

A home for termites inside of trees: contributing factors and global extent

The role of wood density and stem size in predicting internal damage goes hand in hand with ***H1*** and ***H2***, where termites are targeting trees that can provide large, strong homes. For example, *C. clarksoniana* trees had the greatest amount of internal damage in the lower stem, which is reflected in their high density wood (0.85 g/cm^3) and generally larger stem size. Dense wood and large stem size provides strength to the tree structure (Larjavaara & Muller-Landau 2010), and since damage has not passed a critical breakage threshold of 70% (Mattheck et al., 2006), the tree remains structurally uncompromised and forms a well-protected hollow. Here, we tested a limited range of wood densities (0.7-0.9 g/cm^3) and DBH values (10-43 cm), yet the general patterns remain congruent with Flores-Moreno et al. (2024), who showed moderate strength of wood density and DBH as predictors of internal damage across a broader range of values (wood density: 0.4-0.9 g/cm^3, DBH: 10-125 cm).

Studies in north Australian savannas have shown that dense-wooded Myrtaceae trees (including *Corymbia* and *Eucalyptus*) are often hollowed by *Coptotermes* termites (Greaves 1962, Perry et al., 1985, Werner & Prior 2007). These trees dominate the species diversity in Australian savannas (Crisp & Cook 2013) and quantifying the extent of internal damage in these trees across the continent will improve AGB estimation at landscape scales (Calvert et al., 2024). While tree hollowing has been most extensively described in Australian savannas, it remains an open question if these patterns hold in other Australian ecosystems or other parts of the globe where wood nesting termites are present. Termite-derived internal stem damage has been reported in other ecosystems, such as *Coptotermes* species in the Brazilian Amazon described to colonize heartwood of living trees (Eleuterio et al., 2020). In southeastern Florida, USA, an invasive pest species, *C. gestroi*, threatens the urban tree canopy by causing extensive damage in numerous tree species (Chouvenc & Foley 2018). Also, *C. formosanus* in Louisiana, USA infest and

internally damage multiple species of urban trees (Osbrink et al., 1999). *C. gestroi and C. formosanus* are highly invasive species with global distributions (GBIF 2024), providing a strong case for future efforts to quantify internal stem damage extent more thoroughly outside of Australian savannas.

Linking external damage to internal damage

While internal damage is concealed within trees and therefore challenging to detect without invasive measurements, we find that external termite presence can indicate what is happening inside trees. One caveat is that it is not entirely possible to confirm termites as the direct cause without examining the interior wood (Yatsko et al., 2024). Yet, links between external and internal damage have also been demonstrated by Flores-Moreno et al. (2024), where authors found a strong positive relationship between the activity of termites in surrounding deadwood and internal stem damage, especially for densely-wooded savanna trees. Other studies in northern Australia related increased termite activity with greater numbers of tree hollows (Woinarski & Westaway 2008; Woolley et al., 2018) and indicated termites, particularly those of the genus *Coptotermes*, as agents of internal damage (Greaves 1962; Werner & Prior 2007; Yatsko et al., 2024). However, it is not enough to rely only on termite presence; knowing which species are present is critical. For example, *Nasutitermes graveolus*, an arboreal-nesting species common to our study area creates external runways on tree stems but is not known to forage in crown or stem wood. Rather, *N. graveolus* uses the runways for protection as they transit to reach deadwood on the ground (Hill 1942). In contrast, *C. acinaciformis* often build mounds at the tree base and then feed on internal tree wood (Yatsko et al., 2024). Most termites that we found associated with sampled stems were *C. acinaciformis*. *N. graveolus* was present to a lesser extent, and a *Microcerotermes* species was also found, which has not been widely associated with internal wood decomposition. Overall, external termite presence can indicate greater internal tree hollowing, but it is necessary to consider which species are present.

We did not observe increased internal damage for trees with basal fire scarring as expected; internal stem damage can be facilitated by fire, which creates conditions for further biotic colonization (N'Dri et al., 2011). In our system, external fire damage may not indicate greater internal stem damage due to fire severity. N'Dri et al. (2011) found more frequent basal openings in trees exposed to higher severity fires, yet the region of our study site is managed with low-severity fires through early dry-season burning. Therefore, lower fire intensity may not result in suitable basal scarring that promotes biotic invasion. Furthermore, external fire damage did not vary across tree species or sizes, suggesting that its influence is not mediated by selection of tree traits, at least for the species considered here.

Incorporating internal stem damage into estimates of tree carbon

Accurate estimation of carbon sequestered in trees is necessary for validating nature-based climate change solutions and forest carbon markets (Chave et al., 2014). In this study among a few others (Flores-Moreno et al., 2024, Calvert et al., 2024), we demonstrate that internal stem damage removes tree AGB in the lower stem, with consequences for reducing aboveground carbon storage. It is necessary for future studies to broaden internal damage sampling to other forest types and locations, especially to capture damage in the main stem where a large proportion of total tree biomass is held (Ribeiro et al., 2015). Additionally, little is known about crown branch damage due to sampling difficulty; it will be important to characterize the amount of damage and the role of microbes and termites in these structures. Consideration should also be paid to large, dense trees that contain high biomass on the landscape for long time periods (Stephenson

et al., 2014; Lutz et al., 2018). Indeed, Calvert et al. (2024) showed how unaccounted for damage in such trees can result in consequential biomass overestimation, demonstrating that even with the use of high-accuracy biomass estimation (e.g., terrestrial laser scanning), internal damage cannot be captured, inevitably resulting in biomass overestimates.

Current internal stem damage sampling efforts remain quite sparse and efforts to extend measurements to new species and ecosystems will determine the generalizability of the patterns observed in the present study. The following practices will help to overcome current limitations in incorporating internal stem damage into AGB estimation for the world's forests: Where termites are prominent wood decomposers, it should be a priority to survey trees for external termite presence, as this can indicate where hollowing may take place. Widespread characterization of internal damage (i.e., using a resistograph at DBH) in other termite-dominated systems will help to determine the extent of this phenomenon. Focused sampling on large, dense trees is key as these are large carbon reservoirs. Lastly, future research should test if tree hollowing is a *Coptotermes* genus-wide behavior, and target internal damage sampling in regions where *Coptotermes* occurs, either naturally or as an invasive species. Prioritizing these efforts and increasing the global coverage of internal stem damage sampling will provide clearer insights into its ecological impact and help refine forest biomass and carbon accounting.

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Author contribution

Abbey R. Yatsko, Habacuc Flores-Moreno, and Amy E. Zanne conceived the ideas and designed methodology; Abbey R. Yatsko and Michaela Fitzgerald collected the data; Abbey R. Yatsko and Habacuc Flores-Moreno analyzed the data; Abbey R. Yatsko led the writing of the manuscript. All authors contributed to manuscript editing and review and gave final approval for publication.

Data availability statement

We intend to archive the data for this study at Zenodo through the Zanne Lab, University of Miami. Specific DOIs will be provided once data is uploaded.

Statement on inclusion

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

Conflicts of interest

The authors declare no conflicts of interest.

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Supplementary Materials

Supplementary Table 1. Species composition and site descriptions for Pennyweight (PNW) and Station Creek (STCK) biomass plots.

Site	Annual Rainfall (mm)	Species	Family	Stem Abundance (%)	Biomass (Mg)	Biomass (%)
PNW	812	*Eucalyptus cullenii*	Myrtaceae	86	2.24	96.4
		Melaleuca stenostachya	Myrtaceae	8	0.05	2.3
		Terminalia aridicola subsp. *chillagoensis*	Combretaceae	4	0.02	0.7
		Gardenia vilhelmii	Rubiaceae	2	0.01	0.5
STCK	1728	*Eucalyptus cullenii*	Myrtaceae	30	10.0	65.3
		Corymbia clarksoniana	Myrtaceae	28	3.11	20.2
		Acacia disparrima subsp. *calidestris*	Fabaceae	12	0.40	2.6
		Larsenaikia ochreata	Rubiaceae	12	0.14	0.9
		Terminalia subacroptera	Combretaceae	8	0.95	6.2
		Santalum acuminatum	Santalaceae	4	0.19	1.2
		Ficus opposita	Moraceae	2	0.03	0.2
		Callitris intratropica	Cupressaceae	2	0.10	0.6
		Brachychiton diversifolius subsp. *orientalis*	Sterculiaceae	2	0.42	2.7

Supplementary Table 2. Sample size of species measured for changes in internal damage at PNW and STCK sites.

Species	Site	Sampled stems	Wood density (g/cm^3)
E. cullenii	PNW	15	0.9770
E. cullenii	STCK	6	0.9770
C. clarksoniana	STCK	14	0.8453
M. stenostachya	PNW	10	0.7405

Supplementary Table 3. Model summaries for the effect of vertical position and tree species on proportion and absolute amount damaged (corresponds with Figure 4a-d).

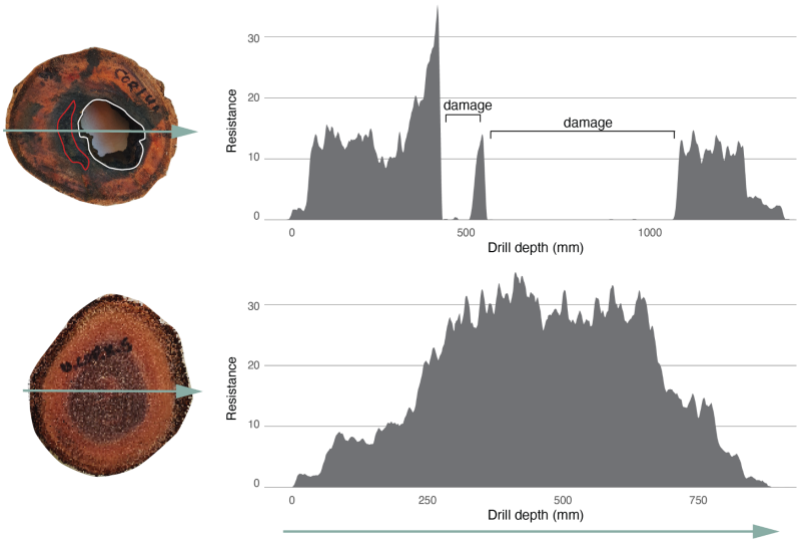
Response	Predictor	χ^2	df	p
Proportion damage	Drill height (cm)	2.80	1	0.09
	Species	13.44	2	**0.001**
Absolute amount damaged	Drill height (cm)	6.11	1	**0.01**
	Species	35.05	2	< **0.001**

Supplementary Table 4. Model summaries for the effect of vertical position and tree traits (DBH and wood density) on proportion and absolute amount damaged (corresponds with Figure 4e-f).

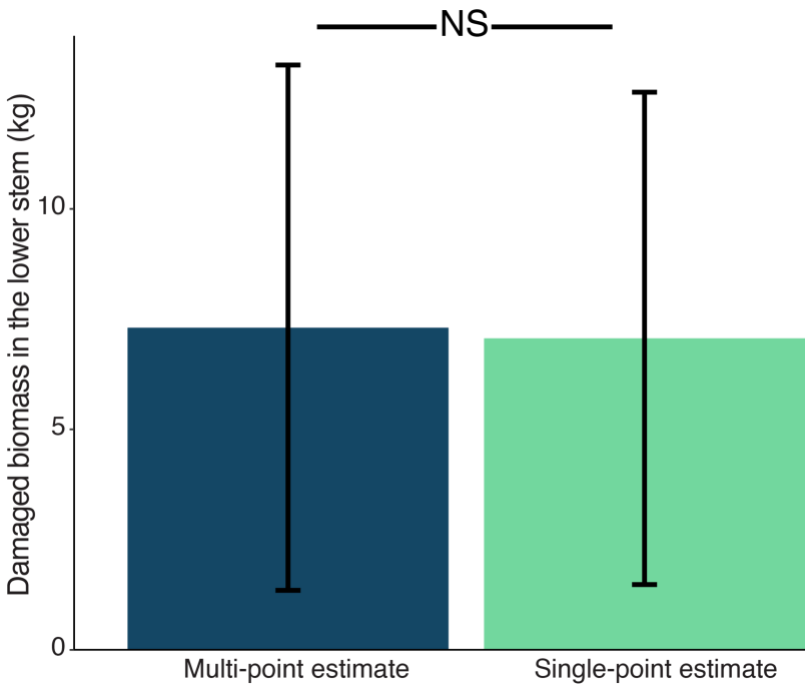
Response	Predictor	χ^2	df	p
Proportion damage	Drill height (cm)	2.61	1	0.11
	DBH (cm)	0.09	1	0.76
	Wood density (g cm^{-3})	0.63	1	0.43
Absolute amount damaged	Drill height (cm)	5.48	1	**0.02**
	DBH (cm)	96.45	1	< **0.001**
	Wood density (g cm^{-3})	0.15	1	0.70

Supplementary Table 5. ANOVA table for species-level differences in DBH.

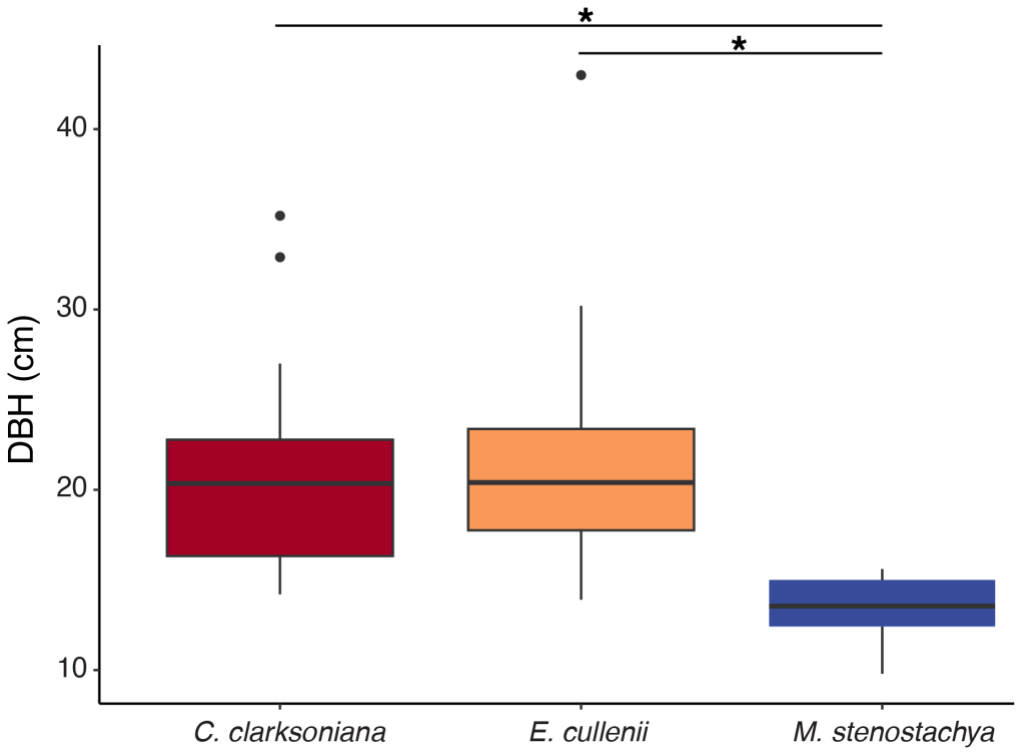
Response	df	SS	MS	F-value	p
Species	2	533	226.5	7.7	**0.001**
Residuals	41	1425	34.76		



Supplementary Figure 1. Residrill trace paired with a cross section photo of the stem segment that the trace was taken from (Yatsko et al., 2024). Drill depth is represented on the X axis, with the measurement beginning at X = 0 and ending at the diameter of the tree. The Y axis represents resistance, where high values indicate sound wood and low values indicate damaged wood. The top trace shows a damaged cross section (microbial damage is outlined in red and termite damage is outlined in white); on the residrill trace, decreases in resistance indicate segments with internal damage. The bottom trace depicts a sound cross section, where resistance does not drop off as the drill passes through the tree stem.



Supplementary Figure 2. Comparison of damaged biomass in the lower stem estimated from a multi-sample method (blue) and a single-sample method (green). Error bars indicate ± standard deviation.



Supplementary Figure 3. Species-level differences in diameter at breast height (DBH).