Title: Higher internal stem damage in dry compared to wet tropics: where are we overestimating forest biomass?

Author list: Habacuc Flores-Moreno[1, *], Abbey R. Yatsko[2], Alexander W. Cheesman[3,4], Steven D. Allison[5,6], Lucas A. Cernusak[3], Rose Cheney[1], Rebecca A. Clement[1], Wendy Cooper[7], Paul Eggleton[8], Rigel Jensen[9], Marc Rosenfield[1], Amy E. Zanne[1,2].

Affiliations:

1. Department of Biological Sciences, George Washington University, Washington, DC, United States
2. Biology Department, University of Miami, Miami, FL, United States
3. College of Science and Engineering, James Cook University, Cairns, QLD, Australia
4. College of Life and Environmental Sciences, University of Exeter, Exeter, United Kingdom
5. Department of Ecology and Evolutionary Biology, University of California, Irvine, Irvine, CA, United States
6. Department of Earth System Science, University of California, Irvine, Irvine, CA, United States
7. Australian Tropical Herbarium, James Cook University, Cairns, WLD, Australia
8. Life Sciences Department, The Natural History Museum, London, United Kingdom
9. Australian Wildlife Conservancy, Malanda, Queensland, 4885, Australia.

[*] **Corresponding Author: habacucfm@gmail.com**

Keywords: internal stem damage, decomposition, carbon storage, plant biomass, precipitation, decay, termites

Summary

- Woody biomass is a large carbon store in terrestrial ecosystems. In calculating biomass, tree stems are assumed to be solid structures; however, decomposer agents such as microbes and insects target heartwood in stems, causing internal wood decay which is poorly quantified.
- We investigated internal stem damage across five sites in tropical Australia along a precipitation gradient. We estimated the amount of internal aboveground biomass damaged in living trees and measured four potential stem damage predictors: density and diameter of the stem, and precipitation and relative damage by termites of downed deadwood at the site.
- Stem damage increased with increasing diameter, wood density, and termite damage in downed deadwood, and decreased with increasing precipitation. A strong interaction occurred between site-level predictors and wood density, likely a result of shifting decomposer communities and their differing responses to changes in tree species and wood traits across sites.
- Aboveground biomass estimates are considerably reduced when stem damage is incorporated, especially in Australian savannas where damage exceeded 30%. Accurate estimates of carbon storage across woody plant communities are critical for understanding the global carbon budget. Future biomass estimates should consider stem damage in concert with effects of changes in decomposer communities and abiotic conditions.

Introduction

Living plant biomass represents 42% of terrestrial carbon (C) storage (Pan et al., 2011). In estimating these stores, trees are typically assumed to be solid structures with biomass often estimated using their height and diameter in relation to regional or global allometric relationships (Zuleta et al., 2023). Yet living tree stems are susceptible to biomass loss via microbial heart rot and insect damage (Romero and Bolker, 2008, Heineman et al., 2015a). External stem damage is easily observable, but internal stem damage (i.e., damage to biomass underneath the bark) while long noted (Janzen, 1976, Brown et al., 1995) is typically unaccounted for in estimates of woody aboveground biomass; it is more difficult to quantify (Heineman et al., 2015b). The assumption that tree stems are internally solid structures with no damage can potentially lead to overestimates of the amount of C that forests hold.

Tropical trees represent ~70% of the global forest C sink (Le Quéré et al., 2016, Mitchard, 2018, Pan et al., 2011). A handful of studies in the tropics demonstrated microbial heart rot and termite hollowing of tree trunks in rainforests (Apolinário and Martius, 2004, Eleuterio et al., 2020, Heineman et al., 2015a), savannas (N'Dri et al., 2011, Werner and Prior, 2007) and peat swamps (Monda et al., 2015). In tropical rainforests, Eleuterio et al. (2020) and Heineman et al. (2015a) provide estimates of the extent of internal stem damage in the Amazon and Borneo, respectively. Additionally, Monda et al. (2015) offered revised allometric models that incorporate stem damage for tropical peat swamp forests in Sarawak; they estimate that stem volume is reduced by 42% from hollowing. Studies in other tropical rainforests, as well as arid and semi-arid forests, have yet to scale up observations of internal stem damage to the ecosystem level. Further, comparative biomass loss from internal stem damage across forest types has not been quantified. Given differences in tree and decomposer species composition and biomass, there is a need to better estimate the extent of internal stem damage and its consequences for aboveground biomass across tropical forests, for example wet to dry, to accurately determine forest biomass and carbon storage in the tropics.

To scale biomass estimates from trees to ecosystems, it is additionally important to understand correlates of internal stem damage. Given that heartwood in living stems is dead, the extent of internal stem damage in living trees may be related to factors that similarly affect rates of deadwood decomposition on the forest floor. Wood decomposition is impacted by wood traits (Kirk and Cowling, 1984, Zanne et al., 2015), moisture availability (Boddy and Rayner, 1983, Chambers et al., 2000), and decomposer activity (Bani et al., 2018, Griffiths et al., 2019). For stem-level wood traits, large diameters may carry more damage because they have more tissue at risk to decay agents. In fact, large trees had more frequent heart rot in tropical rainforests (Eleuterio et al., 2020, Heineman et al., 2015a) and more hollowing by termites in savannas (Werner and Prior, 2007). Trees with high wood density may be slow to decompose (Chambers et al., 2000), mediated by microbial and termite (major biotic decay agents in the tropics, Cornwell et al., 2009) decay capacities. Dense wood can be inaccessible due to its greater structural integrity (Chambers et al., 2000 but see , Harmon et al., 2020, Weedon et al., 2009) and smaller pore spaces, decreasing water permeability and slowing pathogen attack and decomposition (Augspurger and Kelly, 1984, Chave et al., 2009, Mori et al., 2014). Nevertheless, studies in tropical rainforests failed to find links between wood density and internal stem damage (Heineman et al., 2015a).

Across sites, moisture variation directly affects the decay process by determining the composition and activity of the decomposer community in wood (Cheesman et al., 2018, Clement et al., 2021, consortium et al., 2019). For downed deadwood, decomposition by microbes decreases and by termites increases with increasing aridity (Cheesman et al., 2018, Clement et al., 2021, Veldhuis et al., 2017, Zanne et al., 2022). We know less about living tree decomposers, but microbial heart rot (Gilbert et al., 2016, Highley and Kirk, 1979) and termite hollowing have been documented (Eleuterio et al., 2020, N'dri et al., 2014, Werner and Prior, 2007). Based on this past work, we would predict that internal stem damage tips toward microbial decay at wet sites and termite driven decay at dry sites. Precipitation can also indirectly affect decay as it determines the tree species composition and wood construction of those species. Trees are often small in size in dry sites likely in part due to slower growth (Pretzsch et al., 2018) and resource limitations. Additionally, wood density is typically high in dry sites (Chave et al., 2014, Zanne et al., 2015) perhaps mediated through selection for resistance to cavitation (Greenwood et al., 2017) and slow growth. Both maximum plant size and wood density vary across the plant phylogeny, with some clades having particularly dense wood or large stems; these traits will have shaped the biogeographic distribution of tree species. It is therefore likely that clades with more internal stem damage in dry sites are different from those in wet sites, with damage driven by different biotic factors.

Given the interactive ways that wood traits, decay agents and moisture availability change across sites, we examined their effects on internal stem damage individually and in combination. Specifically, we investigated the amount of internal stem damage in living trees across a tropical rainfall gradient in Queensland, Australia. Our sites span a range of biomes (savanna to rainforest) along a precipitation gradient from ~800mm yr^{-1} to ~4,500mm yr^{-1}. We measured four internal stem damage predictors at the stem- and site- level: wood density (stem), stem diameter (stem), precipitation (site), and the relative damage by termites of downed deadwood (site). To understand the within- and across-site patterns in stem damage across the tree-of-life, we compared the distribution of trait values, biomass, and internal stem damage among the different branches of the plant phylogeny present at our sites. To place these findings in a broader context, we used allometric equations to compare aboveground biomass estimates of our sites before and after accounting for internal stem damage, as modeled by our four predictors. Given that internal stem damage may or may not accumulate randomly across the width and height of the tree, we explored the sensitivity of biomass estimates to different assumptions about the extent of internal stem damage. Here we asked the following questions:

1. Do sites differ in internal stem damage and potential predictors? Following, is greater internal stem damage associated with A. lower wood density, B. smaller stem diameters, C. wetter sites, and D. higher termite activity in downed deadwood?
2. With a shift in the dominant decay agent (between microbes and termites), is there a shift in the effect of wood density on internal stem damage?
3. Are there particular plant clades that are more susceptible to internal stem damage and do these susceptible clades differ across the precipitation gradient?
4. Does accounting for internal stem damage strongly alter aboveground biomass estimates, and does the degree of this alteration vary across the precipitation gradient?

Materials and methods

We sampled the woody plants in 50 x 50 m survey plots at five sites along a 100-km rainfall gradient in northeast Queensland, with mean annual rainfall ranging from 812 to 4458 mm. Mean annual rainfall over 30 years was obtained at 90m resolution from the Bureau of Meteorology for each site (Australian Bureau of Meteorology, 2021). Our wettest site is located in the Daintree Rainforest (Rft2; -16.10 S, 145.44 E) part of James Cook University's Daintree Rainforest Observatory next to the Coral Sea. Our driest site, Pennyweight (Sav1; -16.57 S,144.92 E), is a dry savanna 58 km inland from the Coral Sea coast and located on the western side of the Great Dividing Range of northeast Queensland. Three intermediate precipitation sites are found on Mt. Lewis, located to the southeast of site Sav1. Station Creek (Sav2; -16.61 S,145.24 E) averages 1728 mm of rainfall annually and is a wet savanna located at the western slope of Mt. Lewis. A wet sclerophyll forest (Scl1; 2189 mm of rain annually; -16.58 S,145.26 E) and a high elevation rainforest (Rft1; 2630 mm of rain annually; -16.59 S,145.28 E) are located on Mt. Lewis. All sites experience a distinct wet and dry season, with 77% of rainfall occurring between November and April (Cheesman et al., 2018). Sav1, Sav2, Scl1, and Rft1 are located within the Australian Wildlife Conservancy's Brooklyn Sanctuary, Rft2 is located in James Cook University Daintree Research Observatory.

We measured the diameter at breast height (DBH) of all trees $\geq$ 10 cm in each plot at our five sites. Wood density data were extracted from the Tree Functional Attributes and Ecological Database (Harja et al., 2019). Wherever possible we used species-level data. If no species data existed, we used genus- or family-mean values, in that order of preference. Percentage termite damage in downed deadwood was taken from Clement et al. (2021), in which they established 50 m deadwood survey transects within 50 m x 50 m termite survey plots adjacent to the woody plant survey plots studied here. In total, four transects were sampled in each plot, two during the wet season and two during the dry season. Each piece of wood >2 cm diameter intersecting the transect was assessed for termite damage (additional details in Clement et al., 2021).

Internal stem damage identification

To measure internal stem damage at each of our five sites, we selected trees with varying DBH stratified by species. In total, we sampled 258 unique stems (average 51.6 stems per site) from 87 species. We used an IML-RESI power drill (Residrill; PD-500, IML, Germany) to determine the presence of stem damage in living trees. All trees were drilled at breast height (130 cm) across the longest diameter. Because we were measuring damage based on changes in resistance, damaged wood could not be attributed to microbe versus termite activity. The source of damage was inferred via evidence of termite activity following (Clement et al., 2021).

Internal stem damage was quantified as the percentage change from sound wood (Fig S1). We used a dynamic programming algorithm to detect discontinuities (i.e. change points) in the wood resistance to drilling. This approach assumes that the resistance to drilling fluctuates around some underlying signal (otherwise known as 'sound wood'), "f", associated with properties of the stem. Here, f(t) represents the response at depth z(t), and e_j represents a sequence of residual errors. Then, if $t_1, t_2, \ldots, t_n$ are the sampling radius, we can decompose resistance to drilling y_j as:

(1) $y_j = f(t_j) + e_j; 1 \leq j \leq n$

Assuming the wood properties of the stem do not change within each section means that f is a piecewise constant. We expect that there exist discontinuities $\tau_1,\tau_2,\ldots\tau_{K-1}$ and wood segments values $\mu_1,\mu 2,\ldots,\mu_K$ such that:

(2) $f(t) = \mu_k$ if $\tau_{k-1}<t\leq\tau_k$

where K is the number of wood segments, and where $\tau_0=0$ and $\tau_K=n$.Thus, for any $\tau_{k-1}<j\leq\tau_k$,

(3) $y_j = \mu_k+e_j$

To select the number of segments, we examined the relationship between the residual sum of squares (RSS) from the piecewise function (above) and the number of segments K ($K_{max} = 50$) with the goal of minimizing RSS with respect to the number of segments in the wood. For each stem, we looked for the value of K at which the total RSS of the piecewise regression (above) abruptly changed, that is the inflection or knee point of the curve between RSS and K; this provided an estimate $\hat{K}$ (i.e., optimal number of segments for the piecewise regression). To diagnose whether the segments of wood identified in the previous step were sound or damaged, we ran a lower-tailed z-test (alpha = 0.05). For each stem, we compared the segments derived on the piecewise regression (above) to the mean of sound wood, represented by 10-50% of the stem. Damage may accumulate unevenly across the diameter of the stem; for each stem we split the internal stem damage trace in half prior to detecting discontinuities in the wood resistance to drilling trace as described above.

Analyses

Random vs. nonrandom stem damage

Internal stem damage in trees may accumulate randomly or nonrandomly. Detected internal damage at a given height may be representative of the entire length and diameter of the tree or damage may differ at different heights or parts of the diameter within the tree. We were unable to account for all possible nonrandom patterns, but here we assess one random and three nonrandom assumptions of estimating damage (Table S1). If damage accumulates randomly then a linear transect of the tree stem will be representative of the damage in the tree. On the other hand, damage could accumulate nonrandomly. For example, internal stem damage may be more prevalent near the pith or further out near the sapwood. Damage closer to the pith of the tree will contribute less to the proportion of cross-sectional area damaged than damage closer to the sapwood (due to the nature of radial scaling). Further, damage could change with height in the stem (Li et al., 2016, Roisin et al., 2006) or third, it could affect the amount of biomass in the crown. The consequences of such nonrandom damage could be significant given two of the biggest damage agents, microbes and termites, cause heart rot and stem hollowing in our systems; they are both expected to target the oldest heartwood closest to the pith.

First, to test the sensitivity of our damage estimates to random and nonrandom damage across the radius of the stem, we estimated the proportion of internal stem damage on a linear- and area-basis, with the area-basis allowing us to estimate nonrandom effects of distance from pith. Then we ran a standard major axis analysis to compare the relationship between the linear- and area-based methods to estimate internal stem damage. This analysis revealed a relationship that is not significantly different from isometric (i.e., slope overlaps 1) between these two methods to estimate damage (slope = 0.99 CI 0.92-1.06, $P < 0.0001$, Fig S2), leading us to continue with the linear assumption to estimate how internal stem damage reduces biomass estimates.

Second, the internal stem damage measured at DBH may extend throughout the stem or it may only occur locally. As it extends, the amount of damage may increase, decrease or stay constant across the height of the tree. Third, internal stem damage may lead to crown loss. Consequently, the proportion of internal damage measured at DBH may under or overestimate damage across the tree. To bracket the potential effect of internal stem damage variation on biomass calculations, we compared aboveground (i.e., including canopy) and only stem biomass (i.e., excluding canopy) estimates, as well as aboveground biomass and only stem biomass estimates assuming constant (i.e., excluding the crown), 50% increase and 50% decrease in internal stem damage (see below in section for aboveground biomass calculation; Table S1). We estimated the relationship between stem biomass and AGB using the BAAD dataset (Falster et al., 2015) of individual trees (log-transformed) and applied this regression model to predict stem biomass using our AGB estimates (Table S2).

Stem damage, DBH and wood density across sites

We ran Analysis of Variance (ANOVAs) to test whether stem damage, DBH and wood density varied across our sites, and, for significant ANOVA's, we ran Tukey's HSD tests to determine which sites were significantly different from one another (Q1). To determine if internal stem damage varied with each of the site and species level predictors, we ran bivariate models with each of the individual stem-level (stem diameter, wood density) and site-level (rainfall, percentage of termite damage in downed woody debris) variables as predictors and proportion of internal stem damage as the response variable. Given the expected shift in decomposer activity (between microbes and termites) across sites from rainforest to savanna, we explored how the interaction of wood density and site variables predicted internal stem damage (Q2). For all models, we fit a logistic binomial regression with a weight for the proportion of the stem sampled and random intercept for site. The weight in such models represents the completeness of the internal stem sampled. We used the likelihood ratio to compare the explanatory power of the interaction against the bivariate models.

Stem damage mapped across phylogeny

Additionally, we visualized how species across the phylogeny changed across sites in their susceptibility to internal stem damage (Q3). Finally, we examined the possible impacts of interspecific susceptibility to internal stem damage on species (Q3) and site (Q4) level aboveground biomass estimates. For Q3 and Q4, we first estimated the amount of aboveground biomass contributed by each species at each site in our woody plant survey plots by estimating the aboveground biomass for each individual tree > 10 cm in DBH in our communities following (Chave et al., 2014) and second we added up the individual tree estimates (n = 679) at each site. Briefly, the Chave et al. (2014) pantropical model estimates tree aboveground biomass (AGB) as follows:

$$(4)\ AGB = 0.0673 \cdot (WD \cdot H \cdot D^2)^{0.976}$$

Where WD is wood density in g cm^{-3}, H is height in m, D is diameter in cm and AGB is in Mg (metric tonnes). When height data were not available, we used the Chave et al. (2014) AGB model based on diameter, wood density and environmental stress:

$$(5)\ AGB = \exp\,[-1.803 - 0.976E + 0.976\ln(WD) + 2.673\ln(D) - 0.0299[\ln(D)^2]]$$

In this allometric model of AGB, E is a measurement of environmental stress based on the effect of temperature seasonality, climatic water deficit and precipitation seasonality (Chave et al., 2014). To visualize differences among lineages across the plant phylogeny (Q3), we mapped the average species wood density, as well as species average internal stem damage and total aboveground biomass for species at each site subsetting the Smith and Brown (2018) phylogeny to those species in our study. We use phyndr to maximize the overlap between the phylogenetic tree and the diameter and internal stem damage data (Pennell et al., 2016).

Stem damage and carbon accounting

To understand the consequences of internal stem damage on carbon accounting (Q4), we calculated aboveground biomass with and without damage for every site following the Chave et al. (2014) equation above. First, we used the AGB for every individual tree > 10 cm in DBH in our communities (n = 679). Once we estimated the aboveground biomass at the tree level, we determined area-based estimates at each site by summing all stems and dividing by the plot area. We compared the stem biomass and AGB estimates at the plot level, with and without the damage prediction across our five sites using a paired *t*-test. We use the wood density and precipitation interaction model to predict damage, as few studies quantify termite damaged in downed deadwood (DDW), while precipitation is readily available for most locations. We ran all the analyses above for both linear- and area-based internal stem damage estimates. Area-based estimates allowed us to examine non-random changes in damage with radius, although we only present linear-based estimates in the main text. Area based estimates are presented in Supplementary information (Tables S5 and S6). We performed all analyses using R 4.2.2 (R Core Team, 2022)

Results

Counter to our expectation that stem damage would be greater in forest sites, internal stem damage (proportion of trace with damage) was instead greater in savanna sites ($P < 0.0001$, Fig 1A, Table S3), as precipitation decreased ($P < 0.0001$, $R^2 = 0.20$, n = 226; Fig S3C). Larger stems accumulated more internal damage ($P < 0.0001$, $R^2 = 0.03$, n = 226; Fig S3A), whereas stem diameter distributions showed little variation among sites ($P = 0.18$, Fig 1B, Table S3). Wood density was higher at dry sites ($P < 0.0001$, Fig 1C, Table S3). Denser stems also accumulated more internal damage ($P < 0.0001$, $R^2 = 0.03$, n = 226; Fig 1A, S3). Dry sites were previously shown to have greater termite damage in downed deadwood (Fig 1D, Clement et al 2021); internal stem damage increased at these sites where termite damage in downed deadwood was high ($P <0.0001$, $R^2 = 0.25$, n = 226; Fig S3). The explanatory power of each of the single predictor models of internal stem damage was low to moderate, with stem level predictors explaining 0.8-3% and site level predictors explaining 20-25% of the variation in damage (Table S4).

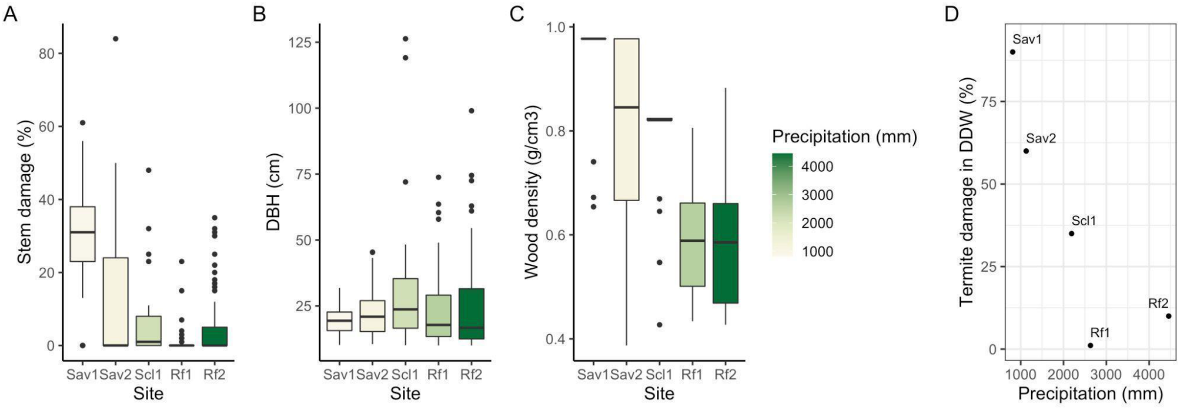

Figure 1. Variation in A. percentage internal stem damage, B. tree diameter at breast height (DBH, in cm), C. wood density (g m^{-3}) across the study sites and D. termite decomposition activity expressed as a percentage of downed deadwood (DDW) across the study sites and precipitation gradient (from Clement et al. 2021 for panel D). Sites are from driest at Sav1 to increasingly wetter moving from Sav2, Scl1, Rf1 to Rf2.

In multivariate models of stem damage, wood density was retained in both site level models, as well as a significant interaction term between wood density and site level predictors (Fig 2, Table S4). Stems with high wood density experienced less internal damage in wet sites and more internal damage in dry sites. Similarly, stems with high wood density experienced more internal stem damage in sites with high termite damage in downed deadwood than those with low termite damage. However, stems with low wood density showed little change in internal stem damage across changes in either precipitation or termite damage in downed deadwood. Although these models with an interaction term between wood density and site level predictors only explained ~3% more variation than the single site-level predictor models, both models had highly significant interaction terms and represented a better explanation of the data (LRT P <0.001) than the single variable models (Fig 2; Table S4).

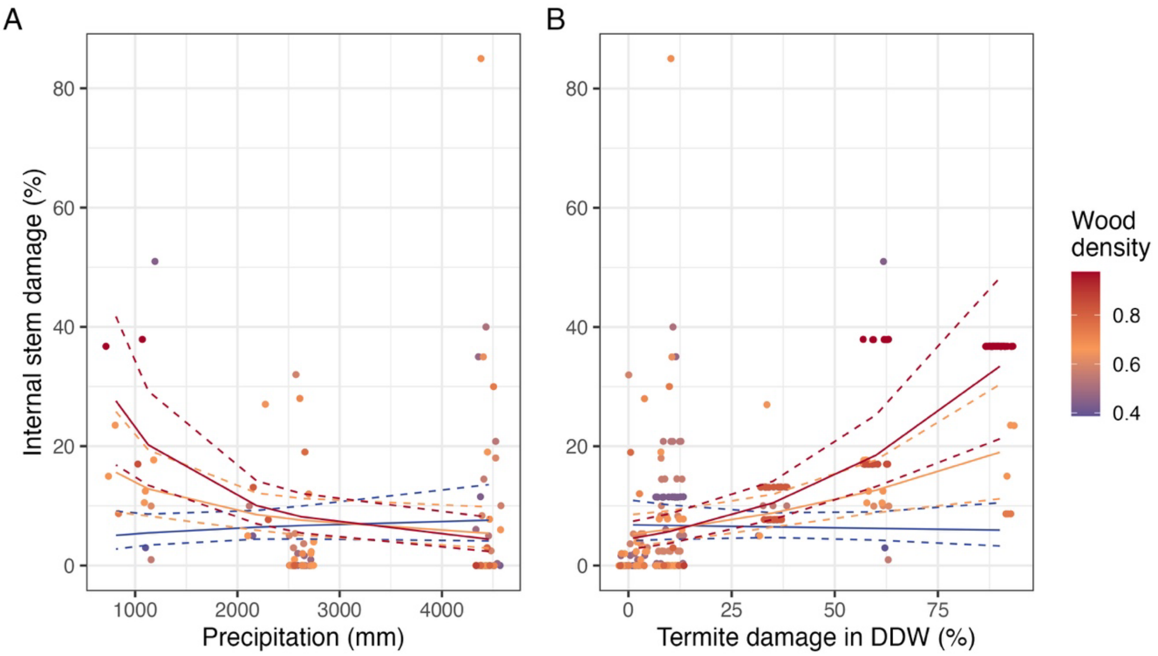

Figure 2. Marginal effects plots of probability of internal stem damage of individual trees (dots) adjusted for low (blue), intermediate (orange) and high (bright red) wood density (g m^{-3}) across A. precipitation (mm) and B. percent termite damage in downed deadwood (DDW). Dashed lines represent a 95% CI.

While across-site differences in internal stem damage appeared at least in part driven by the internal stem damage response of denser wooded species (Fig 2, Table S4), large variation in both internal stem damage and wood density occurred within sites (Fig 1D, Fig 3, Table 1). Aboveground biomass in drier sites was dominated by Myrtaceae which had dense wood and high internal stem damage (Fig 3, Table 1), with internal stem damage also high ($\geq$ 0.1) in members of the Combretaceae, Fabacaeae, Moraceae, Rubiaceae and Santalaceae. Wet sites had species broadly distributed across seed plants with Fabaceae, Lauraceae, Myrtaceae, Proteaceae and Rutaceae contributing considerable aboveground biomass $\geq$ 20 Mg ha^{-1}). Species with the most damage ($\geq$ 0.1) were in the Annonaceae, Cardiopteridaceae, Euphorbiaceae, Fabaceae, Lauraceae, Myrtaceae, Podocarpaceae, Rutaceae and Sapotaceae. Overall, wet site species were more variable in wood density, aboveground biomass, and internal stem damage. The intermediate site aboveground biomass was dominated by Casuarinaceae and Proteaceae ($\geq$0.5), followed by Myrtaceae ($\geq$0.1); interestingly, species in the Lauraceae had the lowest wood density and some of the lowest internal stem damage.

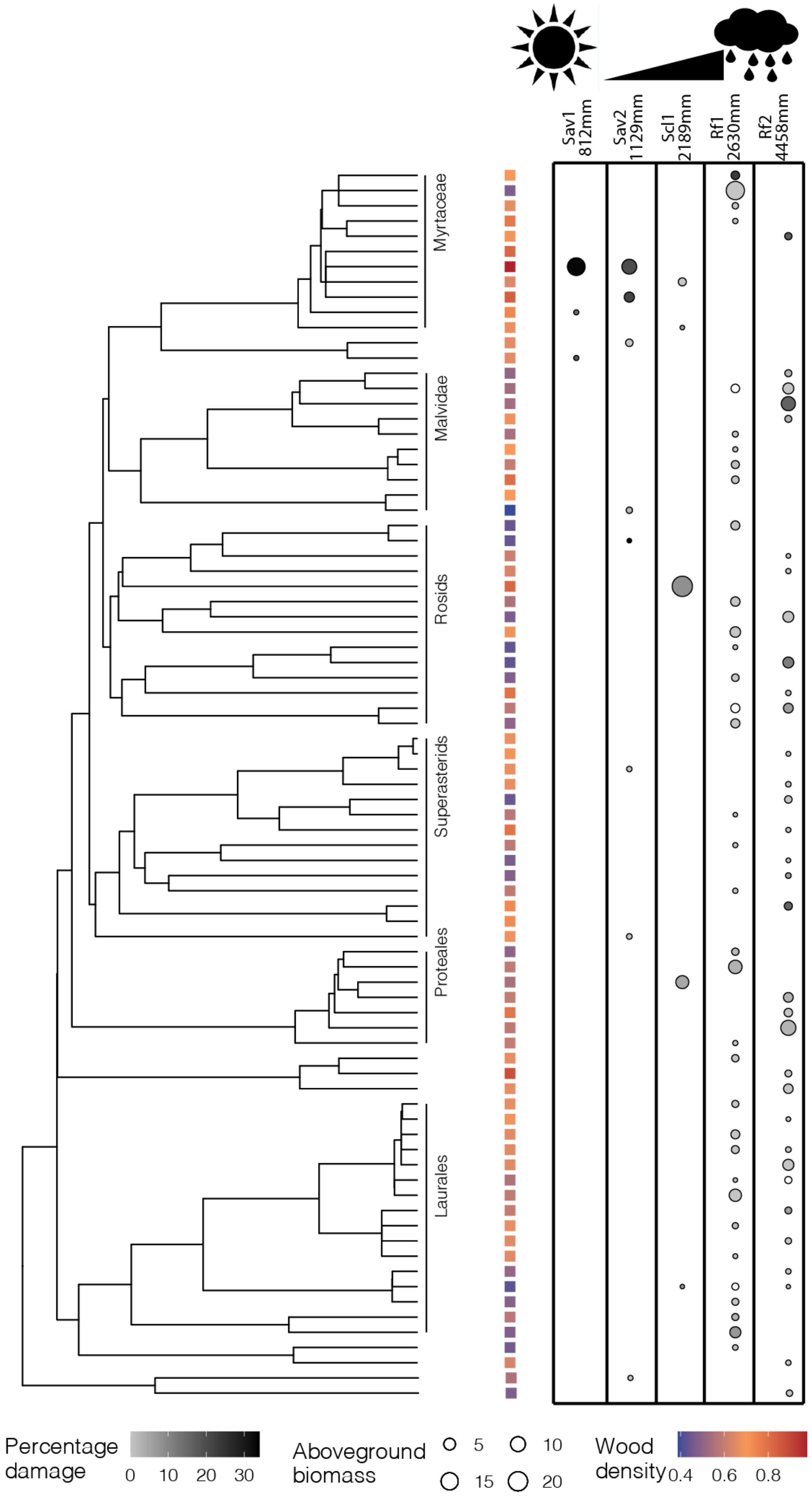
Sav1 812mm
Sav2 1129mm
Scl1 2189mm
Rf1 2630mm
Rf2 4458mm
Myrtaceae
Malvidae
Rosids
Superasterids
Proteales
Laurales
Percentage damage
0
10
20
30
Aboveground biomass
5
10
15
20
Wood density
0.4
0.6
0.8

Figure 4. Phylogeny of sampled tree stems with squares indicating species wood density (g m-^{3}, low in blue, high in red), and circles indicating both average species internal stem damage (in grayscale) and species contributions to 50x50 m plot level aboveground biomass (by size) across a 5-site precipitation gradient (from left to right, wettest to driest).

Table 1. Mean and SD of internal stem damage for species with more than three individuals per site. Species by site are ranked in order of most damaged to least damaged.

Damage rank	Site	Species	Family	Mean damage	SD damage
1	Sav2	*Eucalyptus cullenii*	Myrtaceae	37.9	20.05
2	Sav1	*Eucalyptus cullenii*	Myrtaceae	36.78	25.32
3	Rf2	*Flindersia bourjotiana*	Rutaceae	20.8	19.52
4	Sav2	*Larsenaikia ochreata*	Rubiaceae	17.67	15.37
5	Sav2	*Corymbia clarksoniana*	Myrtaceae	17	22.16
6	Rf2	*Brombya platynema*	Rutaceae	14.5	10.85
7	Scl1	*Eucalyptus resinifera* subsp. *resinifera*	Myrtaceae	13.15	11.22
8	Rf2	*Macaranga subdentata*	Euphorbiaceae	11.5	15.15
9	Scl1	*Banksia aquilonia*	Proteaceae	10	12.49
10	Sav2	*Acacia disparrima* subsp. *calidestris*	Fabaceae	10	17.32
11	Sav1	*Melaleuca stenostachya*	Myrtaceae	8.67	10.26
12	Rf2	*Austromuellera trinervia*	Proteaceae	8.33	7.37

13	Rf2	*Medicosma fareana*	Rutaceae	7.8	13.01
14	Scl1	*Allocasuarina torulosa*	Casuarinaceae	7.69	8.6
15	Rf1	*Castanospora alphandii*	Sapindaceae	5.33	5.51
16	Rf1	*Daphnandra repandula*	Atherospermataceae	3.67	4.04
17	Rf2	*Carnarvonia araliifolia*	Proteaceae	1.67	4.08
18	Rf1	*Syzygium trachyphloium*	Myrtaceae	1.67	2.89
19	Rf2	*Ormosia ormondii*	Fabaceae	0.33	0.58
20	Rf2	*Licuala ramsayi*	Arecaceae	0	0

To understand consequences of internal stem damage on aboveground biomass estimates, we used our internal stem damage prediction model with an interaction for wood density and precipitation (see Precipitation model in Table S4). Our modified model estimated that across our sites 608 Mg ha^{-1} of cumulative biomass may be damaged, or between 2.9-36.2% of aboveground biomass per site, with some of this biomass entirely missing. Percentage above ground biomass damage was variable across our sites with the drier savanna sites (with the highest termite activity; Fig 1D) estimated to have much higher damage than other sites (Figure 4A), with >30% damaged at our driest and <30% damaged at our wettest sites. This result is despite the lower total biomass found in savannas than rainforests (Fig 4 B and C). When we tested sensitivity of these differences to variation within the tree, our bracketed internal stem damage estimate (with a ±50% increase and decrease in damage across the height of the tree) suggests that the damaged biomass across our sites could be as low as 38 Mg and as high as 114 Mg. Meanwhile, in our sensitivity analyses in which we assume internal stem damage only impacts stem but not canopy biomass, we estimated internal stem damage to be ~ 48 Mg when assuming constant damage across the stem, or as high as 72 Mg or as low as 24 Mg when assuming a 50% increase or decrease in damage across the stem height, respectively. All scenarios predicted a significant difference in aboveground biomass estimates when comparing modified estimates of aboveground biomass (red, orange and blue bars) from our internal stem damage model to estimates without incorporating internal stem damage (light green bars) with (P = 0.02; Fig 4B) or without the canopy (P = 0.01; Fig 4C).

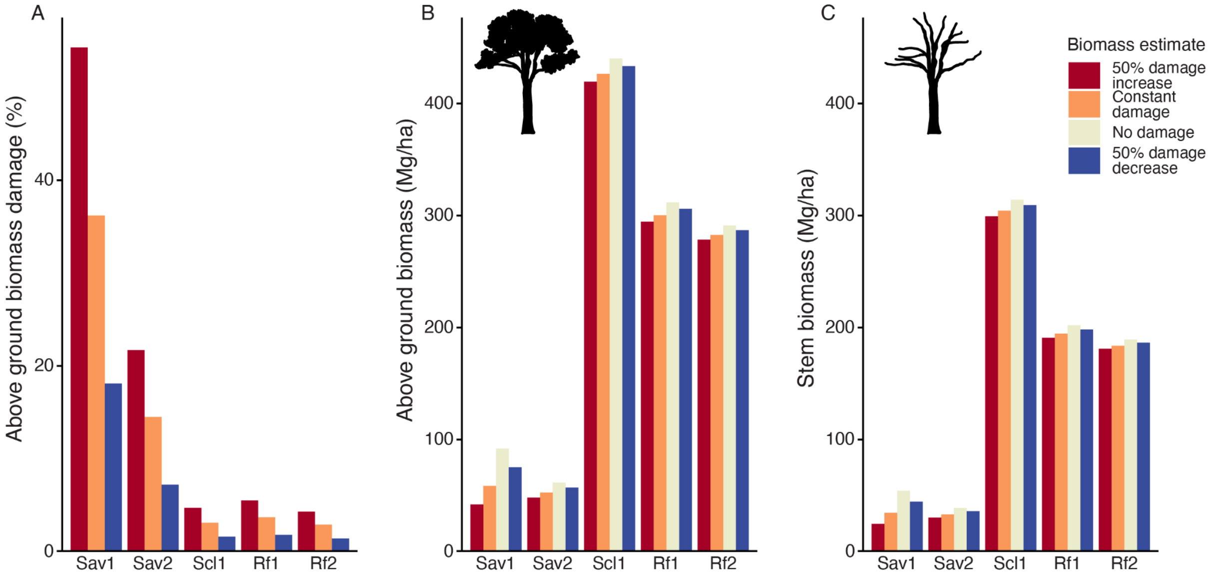

Figure 5. Aboveground biomass estimates per site (Mg ha^{-1}). Panel A shows percentage above ground biomass damage assuming: constant damage (orange), 50% increase in internal stem damage (red), or 50% decrease in internal stem damage (blue). Aboveground biomass estimates (Panel B) and only stem biomass estimates (Panel C) using traditional allometric equations to estimate biomass for each site (i.e. no damage, light green), constant damage (orange), 50% increase in internal stem damage (red), or 50% decrease in internal stem damage (blue).

Discussion

Here we show that internal stem damage can significantly reduce the carbon stores of living trees across ecosystems over a 5-fold change in precipitation. This finding has implications for the mapping and accounting of living tree biomass across our study sites and in tropical and subtropical ecosystems in general. The relationship that we detected between internal stem damage and wood density does not fit expectations based on microbial decomposition studies of coarse woody debris. Internal stem damage did not decrease with increasing wood density, as would be expected if wood density always has a defensive effect against predators and pathogens. In fact, the shape of the relationship between internal stem damage and wood density varied across our sites. Higher wood density was associated with higher internal stem damage in arid and semiarid ecosystems, where termites are abundant, and lower internal stem damage in wet ecosystems where fungal damage is more prevalent. Deadwood in arid and semiarid ecosystems may therefore be more dynamic experiencing shorter residence times than expected, with decomposition beginning even before trees die. Our observations suggest internal stem damage is likely defined by the composition and activity of the decomposer community. Understanding the evolution and interactions of trees and their decomposers will be important in estimating internal stem damage and ultimately key in measuring the residence time of wood in ecosystems.

The role of wood density in internal stem damage

The interaction between wood density and decomposer activity (measured as damage in downed deadwood) or, to a lesser extent, precipitation, revealed a complex relationship between wood density and internal stem damage. Dense wood confers mechanical strength (Chave et al., 2014, Van Gelder et al., 2006), is more common in arid sites (Chave et al., 2009), and is generally thought to protect against herbivores, pests and pathogens (Larjavaara and Muller-Landau, 2010, Scheffer and Morrell, 1998). Local studies however have reported weak or inconsistent relationships between wood density and pathogen protection (Augspurger and Kelly, 1984, Eleuterio et al., 2020, Heineman et al., 2015a). Our sites encompassed a large range in precipitation, plant composition and decomposer communities. Across them, we found an overall weak negative relationship between wood density and internal stem damage.

Resistance to biotic decay agents is dependent on the wood substrate availability, including accessibility of the substrate and a range of wood traits, as any given wood trait may not deter all potential biotic decay agents (Scheffer and Morrell, 1998); what repels a fungal pathogen or saprobe may not repel a termite, and vice versa. For example, high wood density has been shown to be related to higher fungal resistance and both high and low termite resistance (Bultman and Southwell, 1976; see above, Oberst et al., 2018). Aromatic phenolics such as stilbenes have been shown to have antifungal properties (Simonetti et al., 2020, Hart, 1981), while compounds such as obtusoquinanone, guaiacol, and lapachol have been shown to repel termites (Bultman and Southwell, 1976). Our data demonstrate the impact that the decomposer community composition has on the relationship between plant traits and internal stem damage (in particular the differences between termite- and microbial-driven decomposition) and suggest that internal stem damage in drier tropical sites is likely driven by termites. This finding is yet to be tested in other systems; however, there is evidence that hollowing may be important in dry tropical sites in other continents (Jones and Eggleton, 2010, N'Dri et al., 2011), as well as broadly across other ecosystems (Eleuterio et al., 2020, Monda et al., 2015). Relative to the rainforest, termites in the savanna sites were higher in abundance, species richness, and activity in downed deadwood compared to fungi (Clement et al., 2021). Importantly, here we show that: 1) wood decomposition starts earlier than expected, while trees are still alive and standing already accessible to biotic decay agents and 2) different decomposers respond to wood density in different ways, and these individualistic responses cannot be extrapolated from previous microbial-focused wood decomposition work.

Internal stem damage selective filters

The variation we observed in internal stem damage reflects changes in the abiotic and biotic filters faced by the relevant players. Differences in wood density and other traits of plants across our communities are mediated at least in part through variation in abiotic conditions (Chave et al., 2009, Reich, 2014). Dry sites had lower biomass, had higher and less variable wood density and were largely composed of Myrtaceae species, especially *Eucalyptus*. Wet sites had more total living tree biomass, as well as tree species distributed broadly across seed plants, with variable wood density. The climate sensitivities of pests, pathogens and decomposers will also mediate variation in internal stem damage. Microbial decay of downed deadwood increases with increasing humidity and temperature, while termite wood decay is highly sensitive to temperature but not humidity (Zanne et al., 2022). As decay occurs in the dead heartwood in living trees, there is potential for selection of different wood densities (Cornelissen et al., 2022) by the co-occurring decay agents. Particularly key are the interactions between the abiotic and biotic components, including how variation in plant traits in turn also mediates the decomposer community and therefore decay (Weedon et al., 2009, Cornwell et al., 2009, Harmon et al., 2020, Hu et al., 2018). From the evidence here, it is clear that while abiotic factors directly or indirectly mediate the decomposer community and hence internal stem damage. However, the wood trait preferences of termite- vs microbial-dominated systems lead to variation in which plant lineages sustain the greatest internal stem damage across our communities.

In line with evidence from microbial-driven decay in coarse woody debris, we found that in rainforest, where microbial decomposition is prevalent, plant species with lower wood density sustained higher internal stem damage. Anecdotally, plant species with darker colored brown and red heartwoods (e.g. *Ormosia ormondii*) also sustained less internal stem damage than lighter colored species with yellow or white heartwood (e.g. Euphorbiaceae and Rutaceae; Table 2 and Figure 4). Darker colored woods have been associated with higher resistance to microbial decay as compared to lighter colored heartwoods (Chave et al., 2009, Gierlinger et al., 2004), perhaps as a result of higher deposition of extractives during heartwood formation (Kramer, 2012). Many wood rotting fungi show host preferences; for instance, white rot fungi are often angiosperm specialists, while brown rot fungi are often gymnosperm specialists (Krah et al., 2018), with individual fungal species even showing preferences for specific tree species (Ador et al., 2023, Baxter, 1925). The observed higher variation in internal stem damage across plant families in our wet sites most likely reflects filtering of microbial decomposers (the most active decomposers in these sites) as a result of the differences in wood density and chemistry among plant clades.

In our savanna sites, Myrtaceae species with denser wood had the most internal stem damage. An important termite in these dry sites is *Coptotermes acinaciformis*, which builds aboveground mounds or subterranean nests at the base of living savanna trees, especially *Eucalyptus* species, and hollows out the inside of these trees (Werner and Prior, 2007). The high wood density of *Eucalyptus* trees reduces wood water (Sperry et al., 2005, Meinzer et al., 2003) and their high stilbene content inhibits delignification of wood (Hart, 1981, Pietsch et al., 2014), which may reduce fungal decomposition. Given the extensive excavation and nest site construction in savanna trees by *C. acinaciformis*, it makes sense that these termites target Myrtaceae species with their dense wood which can maintain strong structures despite hollowing. Similar patterns have been observed in timber species in the Amazon, where termites preferentially damage species with high wood density (Eleuterio et al., 2020). Nevertheless, there is also evidence for the opposite pattern, albeit in downed deadwood, that termite prefer low density wood(Guo et al., 2021, Liu et al., 2015, Tuo et al., 2021), and certain termites species show preference for decayed wood (Cornelius et al., 2002). It seems likely that termite preference for high or low wood density species will depend on their ability to access the wood, whether they are solely sampling the wood for food or also living within the wood, as well as co-occurring saprotrophic microbial community competing for wood as a resource. For example, variation in termite mandible hardness, elasticity, and structure (Cribb et al., 2007) allows for differentiation in wood preference among termite species. Similarly, negative (Kirker et al., 2012) and positive interactions (Hyodo et al., 2003) between termites and their saprotrophic microbial competitors will play a key role in termites' wood preference and consumption.

Implications and future directions

At the ecosystem scale, the rate and amount of internal stem damage is important in determining the residence time of carbon in living biomass, with up to ~30% of biomass already damaged or even missing before the stem dies. Globally, living trees in tropical savannas are estimated to contain ~66 Gt C (Giri et al., 2005, Watson et al., 2000). Savannas, dominated by *Eucalyptus* species, represent 77% of Australia's native forested area, totaling ~134 million ha (Committee, 2019), and they are predicted to contain between 6 to 34 Mg ha^{-1} of carbon in biomass of living trees (Chen et al., 2003, Cook et al., 2015). Given that most termites physically remove wood to be digested in their guts within their mounds or nests whereas microbes decay wood *in situ*, termite-driven damage represents a complete removal of carbon from where the wood has been produced. Across Australia, internal hollowing may be a common phenomenon as *C. acinaciformis* is widely distributed (not including Tasmania; GBIF Secretariat, 2023, Lee et al., 2017, Wijas et al., 2022). Such widespread internal stem damage may significantly decrease the stocks of carbon in live trees, well before trees senesce. The effects of these early stages of wood loss, if pervasive, could speed up the rates of carbon loss from wood.

A central question derived from our analysis is to what extent is internal stem damage, and in particular termite-driven internal stem damage, pervasive at a pantropical/global scale. The processes generating internal stem damage remain largely unknown at these scales. Thus far, the pursuit of this question at local and regional scales (including our study across ecosystems) suggests that the process by which wood is lost in living stems is highly variable but stem hollowing by termites is not solely an Australian phenomenon. Such has been found in sites in the African and New World tropics (Apolinário and Martius, 2004, Eleuterio et al., 2020, N'Dri et al., 2011). Building on existing evidence for both the distribution of wooded vegetation and termites that hollow trees, an approach to better understand the prevalence of internal stem damage around the globe would be to quantify the prevalence of internal stem damage in systems where both conditions are met. Woody vegetation across the Americas, Australasia, Africa, and even southern Europe –where single and intermediate dry wood feeding termites (species that completely or partially feed on their nesting substrate *sensu* Abe, 1987) are distributed -- may experience at least some degree of internal stem damage (Eggleton and Tayasu, 2001). Beyond a pantropical to global focus on the presence of internal stem damage, there is substantial scope for further empirical studies measuring the internal stem damage variation within trees (e.g., at different heights, into the canopy, belowground) or quantifying the relationship between additional wood traits and termite preferences.

Conclusions

We have shown wood loss starts well before a tree dies. Describing the variability in internal stem damage across communities, including the interaction between plants and their decomposers (microbes, termites or otherwise), requires more attention particularly in tropical communities. The proportion of carbon potentially lost through internal stem damage may be high, especially in arid and semi-arid systems where wood is currently assumed to be immobilized until tree senescence. Understanding the prevalence of internal stem damage across woody ecosystems with high wood feeding termite diversity and activity may also shed light on the variable relationship between wood density and mortality (Kraft et al., 2010) or the observed weak relationship between tree aboveground living tree and deadwood biomass (Palace et al., 2012). Our study and those of others (Cornwell et al., 2009, Guo et al., 2023, Hu et al., 2018, Liu et al., 2015) suggest that, while environmental selection may determine wood density and other traits that affect when and how fast woody tissue cycles, there may be other biotic factors (such as the decomposer community) that modify the effect of wood traits on wood cycling, sometimes in unexpected ways, as shown here. As carbon disappears from the living tree pool, this will have direct implications for global carbon modeling, the extent of which remains unseen. Further, insect-driven decomposition impacts the fate of the wood in different ways to predictions based on microbial-driven decomposition (Zanne et al., 2022, Griffiths et al., 2021). It is critical to explore the mechanisms and implications of internal stem damage in ecosystems across the globe.

Acknowledgements

We acknowledge the KukuYalanji people on whose land we have carried out our research and pay our respects to their elders past and present. This research was funded by the US National Science Foundation, Ecosystem Studies Cluster, under awards DEB-1655759 and

DEB-2149151 to A.E.Z. and DEB-1655340 to S.D.A., as well as UK NERC grant NE/K01613X/1 to P.E. We thank the Australian Wildlife Conservancy and Daintree Rainforest Observatory of James Cook University for access to field sites. We also thank Ana Palma, Paula Gavarró, Gabby Hoban, Jessica Braden, Amy Smart, Xine Li, Baoli Fan, Xennephone Hadeen, Iftakharul Alam and Donna Davis for help with field work; Michelle Schiffer and the Cornwell and Wright laboratories for help with logistics; and Rhiannon Dalrymple for comments and suggestions which improved the quality of the manuscript.

Competing interests

The authors declared no competing interests

Author contributions

HFM, AEZ, AWC design the study and methodology. HFM, AWC, WC, RJ, MR, RC, AEZ, LC did the investigation. HFM, AY and AEZ wrote the original draft. HFM and RC analyzed the data. All authors reviewed and edited the original draft.

References

ABE, T. 1987. Evolution of life types in termites. *Evolution and coadaptation in biotic communities*.

ADOR, M. A. H., AHMED, R., KHATUN, R., RAHMAN, M. A. & HAQUE, M. M. U. 2023. Identification, diversity and host specificity of the wood-decay fungi in major sawmill depots of north-eastern Bangladesh. *Forest Pathology,* 53.

APOLINÁRIO, F. E. & MARTIUS, C. 2004. Ecological role of termites (Insecta, Isoptera) in tree trunks in central Amazonian rain forests. *Forest Ecology and Management,* 194**,** 23-28.

AUGSPURGER, C. K. & KELLY, C. K. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia,* 61**,** 211-217.

AUSTRALIAN BUREAU OF METEOROLOGY 2021. High resolution mean monthly and mean annual rainfall data (base climatological data sets). *In:* METEOROLOGY, A. B. O. (ed.) 1 ed.

BANI, A., PIOLI, S., VENTURA, M., PANZACCHI, P., BORRUSO, L., TOGNETTI, R., TONON, G. & BRUSETTI, L. 2018. The role of microbial community in the decomposition of leaf litter and deadwood. *Applied Soil Ecology,* 126**,** 75-84.

BAXTER, D. V. 1925. THE BIOLOGY AND PATHOLOGY OF SOME OF THE HARDWOOD HEART-ROTTING FUNGI: PART I. *American Journal of Botany,* 12**,** 522-552.

BODDY, L. & RAYNER, A. D. M. 1983. ORIGINS OF DECAY IN LIVING DECIDUOUS TREES: THE ROLE OF MOISTURE CONTENT AND A RE-APPRAISAL OF THE EXPANDED CONCEPT OF TREE DECAY. *New Phytologist,* 94**,** 623-641.

BROWN, I. F., MARTINELLI, L. A., THOMAS, W. W., MOREIRA, M. Z., FERREIRA, C. A. C. & VICTORIA, R. A. 1995. Uncertainty in the biomass of Amazonian forests: an example from Rondonia, Brazil. *Forest Ecology and Management,* 75**,** 175-189.

BULTMAN, J. D. & SOUTHWELL, C. R. 1976. Natural Resistance of Tropical American Woods to Terrestrial Wood-Destroying Organisms. *Biotropica,* 8**,** 71.

CHAMBERS, J. Q., HIGUCHI, N., SCHIMEL, J. P., FERREIRA, L. V. & MELACK, J. M. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia,* 122**,** 380-388.

CHAVE, J., COOMES, D., JANSEN, S., LEWIS, S. L., SWENSON, N. G. & ZANNE, A. E. 2009. Towards a worldwide wood economics spectrum. *Ecology letters,* 12**,** 351-366.

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. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global change biology,* 20**,** 3177-3190.

CHEESMAN, A. W., CERNUSAK, L. A. & ZANNE, A. E. 2018. Relative roles of termites and saprotrophic microbes as drivers of wood decay: a wood block test. *Austral Ecology,* 43**,** 257-267.

CHEN, X., HUTLEY, L. B. & EAMUS, D. 2003. Carbon balance of a tropical savanna of northern Australia. *Oecologia,* 137**,** 405-416.

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. *Frontiers in ecology and evolution,* 9**,** 657444.

COMMITTEE, N. F. I. S. 2019. Australia's state of the forests report 2018.

CONSORTIUM, G., STEIDINGER, B. S., CROWTHER, T. W., LIANG, J., VAN NULAND, M. E., WERNER, G. D. A., REICH, P. B., NABUURS, G. J., DE-MIGUEL, S., ZHOU, M., PICARD, N., HERAULT, B., ZHAO, X., ZHANG, C., ROUTH, D. & PEAY, K. G. 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature,* 569**,** 404-408.

COOK, G. D., LIEDLOFF, A. C., CUFF, N. J., BROCKLEHURST, P. S. & WILLIAMS, R. J. 2015. Stocks and dynamics of carbon in trees across a rainfall gradient in a tropical savanna: Carbon Dynamics along a Rainfall Gradient. *Austral Ecology,* 40**,** 845-856.

CORNELISSEN, J. H. C., CORNWELL, W. K., FRESCHET, G. T., WEEDON, J. T., BERG, M. P. & ZANNE, A. E. 2022. Coevolutionary legacies for plant decomposition. *Trends in Ecology & Evolution*.

CORNELIUS, M. L., DAIGLE, D. J., CONNICK, W. J., PARKER, A. & WUNCH, K. 2002. Responses of <I>Coptotermes formosanus</I> and <I>Reticulitermes flavipes</I> (Isoptera: Rhinotermitidae) to Three Types of Wood Rot Fungi Cultured on Different Substrates. *Journal of Economic Entomology,* 95**,** 121-128.

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? *Global Change Biology,* 15**,** 2431-2449.

CRIBB, B. W., STEWART, A., HUANG, H., TRUSS, R., NOLLER, B., RASCH, R. & ZALUCKI, M. P. 2007. Insect mandibles—comparative mechanical properties and links with metal incorporation. *Naturwissenschaften,* 95**,** 17-23.

EGGLETON, P. & TAYASU, I. 2001. Feeding groups, lifetypes and the global ecology of termites. *Ecological research,* 16**,** 941-960.

ELEUTERIO, A. A., JESUS, M. A. D. & PUTZ, F. E. 2020. Stem Decay in Live Trees: Heartwood Hollows and Termites in Five Timber Species in Eastern Amazonia. *Forests,* 11**,** 1087.

FALSTER, D. S., DUURSMA, R. A., ISHIHARA, M. I., BARNECHE, D. R., FITZJOHN, R. G., VÅRHAMMAR, A., AIBA, M., ANDO, M., ANTEN, N., ASPINWALL, M. J., BALTZER, J. L., BARALOTO, C., BATTAGLIA, M., BATTLES, J. J., BOND-LAMBERTY, B., VAN BREUGEL, M., CAMAC, J., CLAVEAU, Y., COLL, L., DANNOURA, M., DELAGRANGE, S., DOMEC, J.-C., FATEMI, F., FENG, W., GARGAGLIONE, V., GOTO, Y., HAGIHARA, A., HALL, J. S., HAMILTON, S., HARJA, D., HIURA, T., HOLDAWAY, R., HUTLEY, L. S., ICHIE, T., JOKELA, E. J., KANTOLA, A., KELLY, J. W. G., KENZO, T., KING, D., KLOEPPEL, B. D., KOHYAMA, T., KOMIYAMA, A., LACLAU, J.-P., LUSK, C. H., MAGUIRE, D. A., LE MAIRE, G., MÄKELÄ, A., MARKESTEIJN, L., MARSHALL, J., MCCULLOH, K., MIYATA, I., MOKANY, K., MORI, S., MYSTER, R. W., NAGANO, M., NAIDU, S. L., NOUVELLON, Y., O'GRADY, A. P., O'HARA, K. L., OHTSUKA, T., OSADA, N., OSUNKOYA, O. O., PERI, P. L., PETRITAN, A. M., POORTER, L., PORTSMUTH, A., POTVIN, C., RANSIJN, J., REID, D., RIBEIRO, S. C., ROBERTS, S. D., RODRÍGUEZ, R., SALDAÑA-ACOSTA, A., SANTA-REGINA, I., SASA, K., SELAYA, N. G., SILLETT, S. C., STERCK, F., TAKAGI, K., TANGE, T., TANOUCHI, H., TISSUE, D., UMEHARA, T., UTSUGI, H., VADEBONCOEUR, M. A., VALLADARES, F., VANNINEN, P., WANG, J. R., WENK, E., WILLIAMS, R., DE AQUINO XIMENES, F., YAMABA, A., YAMADA, T., YAMAKURA, T., YANAI, R. D. & YORK, R. A. 2015. BAAD: a Biomass And Allometry Database for woody plants: <i>Ecological Archives</i> E096-128. *Ecology,* 96**,** 1445-1445.

GBIF SECRETARIAT. 2023. *GBIF Backbone Taxonomy* [Online]. Available: https://www.gbif.org/species/4802734 [Accessed 16 of July 2023].

GIERLINGER, N., JACQUES, D., GRABNER, M., WIMMER, R., SCHWANNINGER, M., ROZENBERG, P. & P□QUES, L. E. 2004. Colour of larch heartwood and relationships to extractives and brown-rot decay resistance. *Trees - Structure and Function,* 18**,** 102-108.

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., FÁBREGA, J. P., LUMPKIN, R., MCWILLIAMS, H. A., CHESTER, K. N., BURGOS, A. C., WONG, E. B., DIAB, J. H., RENTERIA, S. A., HARROWER, J. T., HOOTON, D. A., GLENN, T. C., FAIRCLOTH, B. C. & HUBBELL, S. P. 2016. Use of sonic tomography to detect and quantify wood decay in living trees. *Applications in Plant Sciences,* 4**,** 1600060.

GIRI, C., ZHU, Z. & REED, B. 2005. A comparative analysis of the Global Land Cover 2000 and MODIS land cover data sets. *Remote Sensing of Environment,* 94**,** 123-132.

GREENWOOD, S., RUIZ-BENITO, P., MARTÍNEZ-VILALTA, J., LLORET, F., KITZBERGER, T., ALLEN, C. D., FENSHAM, R., LAUGHLIN, D. C., KATTGE, J. & BÖNISCH, G. 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology letters,* 20**,** 539-553.

GRIFFITHS, H. M., ASHTON, L. A., EVANS, T. A., PARR, C. L. & EGGLETON, P. 2019. Termites can decompose more than half of deadwood in tropical rainforest. *Current Biology,* 29**,** R118-R119.

GRIFFITHS, H. M., ASHTON, L. A., PARR, C. L. & EGGLETON, P. 2021. The impact of invertebrate decomposers on plants and soil. *New Phytologist,* 231**,** 2142-2149.

GUO, C., TUO, B., CI, H., SAI, B. L., ZHANG, Y., YAN, E. R. & CORNELISSEN, J. H. C. 2023. How detritivores, plant traits and time modulate coupling of leaf versus woody litter decomposition rates across species. *Journal of Ecology,* 111**,** 227-239.

GUO, C., TUO, B., CI, H., YAN, E. R. & CORNELISSEN, J. H. C. 2021. Dynamic feedbacks among tree functional traits, termite populations and deadwood turnover. *Journal of Ecology,* 109**,** 1578-1590.

HARJA, D., RAHAYU, S. & PAMBUDI, S. 2019. Tree functional attributes and ecological database.

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 and management,* 15**,** 1-21.

HART, J. H. 1981. Role of phytostilbenes in decay and disease resistance. *Annual review of Phytopathology,* 19**,** 437-458.

HEINEMAN, K. D., RUSSO, S. E., BAILLIE, I. C., MAMIT, J. D., CHAI, P.-K., CHAI, L., HINDLEY, E. W., LAU, B. T., TAN, S. & ASHTON, P. S. 2015a. Evaluation of stem rot in 339 Bornean tree species: implications of size, taxonomy, and soil-related variation for aboveground biomass estimates. *Biogeosciences,* 12**,** 5735-5751.

HEINEMAN, K. D., RUSSO, S. E., BAILLIE, I. C., MAMIT, J. D., CHAI, P. P., CHAI, L., HINDLEY, E. W., LAU, B. T., TAN, S. & ASHTON, P. S. 2015b. Influence of tree size, taxonomy, and edaphic conditions on heart rot in mixed-dipterocarp Bornean rainforests: implications for aboveground biomass estimates. *Biogeosciences Discussions,* 12**,** 6821-6861.

HIGHLEY, T. L. & KIRK, T. K. 1979. Mechanisms of wood decay and the unique features of heartrots. *Phytopathology,* 69.

HU, Z., MICHALETZ, S. T., JOHNSON, D. J., MCDOWELL, N. G., HUANG, Z., ZHOU, X. & XU, C. 2018. Traits drive global wood decomposition rates more than climate. *Global Change Biology,* 24**,** 5259-5269.

HYODO, F., TAYASU, I., INOUE, T., AZUMA, J. I., KUDO, T. & ABE, T. 2003. Differential role of symbiotic fungi in lignin degradation and food provision for fungus-growing termites (Macrotermitinae: Isoptera): <i>Role of the symbiotic fungi in fungus-growing termites</i>. *Functional Ecology,* 17**,** 186-193.

JANZEN, D. H. 1976. Why tropical trees have rotten cores.

JONES, D. T. & EGGLETON, P. 2010. Global Biogeography of Termites: A Compilation of Sources. *In:* BIGNELL, D. E., ROISIN, Y. & LO, N. (eds.) *Biology of Termites: a Modern Synthesis.* Dordrecht: Springer Netherlands.

KIRK, T. K. & COWLING, E. B. 1984. Biological decomposition of solid wood. *The chemistry of solid wood,* 207**,** 455-487.

KIRKER, G. T., WAGNER, T. L. & DIEHL, S. V. 2012. Relationship between wood-inhabiting fungi and Reticulitermes spp. in four forest habitats of northeastern Mississippi. *International Biodeterioration & Biodegradation,* 72**,** 18-25.

KRAFT, N. J., METZ, M. R., CONDIT, R. S. & CHAVE, J. 2010. The relationship between wood density and mortality in a global tropical forest data set. *New Phytologist,* 188**,** 1124-1136.

KRAH, F.-S., BÄSSLER, C., HEIBL, C., SOGHIGIAN, J., SCHAEFER, H. & HIBBETT, D. S. 2018. Evolutionary dynamics of host specialization in wood-decay fungi. *BMC Evolutionary Biology,* 18**,** 119.

KRAMER, P. 2012. *Physiology of woody plants*, Elsevier.

LARJAVAARA, M. & MULLER-LANDAU, H. C. 2010. Rethinking the value of high wood density. *Functional Ecology***,** 701-705.

LE QUÉRÉ, C., ANDREW, R. M., CANADELL, J. G., SITCH, S., KORSBAKKEN, J. I., PETERS, G. P., MANNING, A. C., BODEN, T. A., TANS, P. P. & HOUGHTON, R. A. 2016. Global carbon budget 2016. *Earth System Science Data,* 8.

LEE, T. R., EVANS, T. A., CAMERON, S. L., HOCHULI, D. F., HO, S. Y. & LO, N. 2017. Ecological diversification of the Australian Coptotermes termites and the evolution of mound building. *Journal of Biogeography,* 44**,** 1405-1417.

LI, H.-F., YEH, H.-T., CHIU, C.-I., KUO, C.-Y. & TSAI, M.-J. 2016. Vertical Distribution of Termites on Trees in Two Forest Landscapes in Taiwan. *Environmental Entomology,* 45**,** 577-581.

LIU, G., CORNWELL, W. K., CAO, K., HU, Y., VAN LOGTESTIJN, R. S. P., YANG, S., XIE, X., ZHANG, Y., YE, D., PAN, X., YE, X., HUANG, Z., DONG, M. & CORNELISSEN, J. H. C. 2015. Termites amplify the effects of wood traits on decomposition rates among multiple bamboo and dicot woody species. *Journal of Ecology,* 103**,** 1214-1223.

MEINZER, F. C., JAMES, S. A., GOLDSTEIN, G. & WOODRUFF, D. 2003. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant, Cell & Environment,* 26**,** 1147-1155.

MITCHARD, E. T. A. 2018. The tropical forest carbon cycle and climate change. *Nature,* 559**,** 527-534.

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**,** 11-22.

MORI, S., ITOH, A., NANAMI, S., TAN, S., CHONG, L. & YAMAKURA, T. 2014. Effect of wood density and water permeability on wood decomposition rates of 32 Bornean rainforest trees. *Journal of Plant Ecology,* 7**,** 356-363.

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. *Journal of Tropical Ecology,* 27**,** 269-278.

N’DRI, A. B., GIGNOUX, J., BAROT, S., KONATÉ, S., DEMBÉLÉ, A. & WERNER, P. A. 2014. The dynamics of hollowing in annually burnt savanna trees and its effect on adult tree mortality. *Plant Ecology,* 215**,** 27-37.

OBERST, S., LAI, J. C. S. & EVANS, T. A. 2018. Key physical wood properties in termite foraging decisions. *Journal of The Royal Society Interface,* 15**,** 20180505.

PALACE, M., KELLER, M., HURTT, G. & FROLKING, S. 2012. A review of above ground necromass in tropical forests. *Tropical forests***,** 215-252.

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. 2011. A large and persistent carbon sink in the world’s forests. *Science,* 333**,** 988-993.

PENNELL, M. W., FITZJOHN, R. G. & CORNWELL, W. K. 2016. A simple approach for maximizing the overlap of phylogenetic and comparative data. *Methods in Ecology and Evolution,* 7**,** 751-758.

PIETSCH, K. A., OGLE, K., CORNELISSEN, J. H. C., CORNWELL, W. K., BÖNISCH, G., CRAINE, J. M., JACKSON, B. G., KATTGE, J., PELTZER, D. A. &

PENUELAS, J. 2014. *Global relationship of wood and leaf litter decomposability: the role of functional traits within and across plant organs*, Wiley Online Library.

PRETZSCH, H., SCHÜTZE, G. & BIBER, P. 2018. Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. *Forest Ecosystems,* 5**,** 1-19.

R CORE TEAM 2022. R: A Language and Environment for Statistical Computing. 4.2.2 ed. Vienna, Austria: R Foundation for Statistical Computing.

REICH, P. B. 2014. The world-wide 'fast–slow'plant economics spectrum: a traits manifesto. *Journal of ecology,* 102**,** 275-301.

ROISIN, Y., DEJEAN, A., CORBARA, B., ORIVEL, J., SAMANIEGO, M. & LEPONCE, M. 2006. Vertical stratification of the termite assemblage in a neotropical rainforest. *Oecologia,* 149**,** 301-311.

ROMERO, C. & BOLKER, B. M. 2008. Effects of stem anatomical and structural traits on responses to stem damage: an experimental study in the Bolivian Amazon. *Canadian Journal of Forest Research,* 38**,** 611-618.

SCHEFFER, T. C. & MORRELL, J. J. 1998. Natural durability of wood: A worldwide checklist of species.

SIMONETTI, G., BRASILI, E. & PASQUA, G. 2020. Antifungal Activity of Phenolic and Polyphenolic Compounds from Different Matrices of Vitis vinifera L. against Human Pathogens. *Molecules,* 25**,** 3748.

SMITH, S. A. & BROWN, J. W. 2018. Constructing a broadly inclusive seed plant phylogeny. *American journal of botany,* 105**,** 302-314.

SPERRY, J. S., HACKE, U. G. & WHEELER, J. K. 2005. Comparative analysis of end wall resistivity in xylem conduits. *Plant, Cell & Environment,* 28**,** 456-465.

TUO, B., YAN, E. R., GUO, C., CI, H., BERG, M. P. & CORNELISSEN, J. H. C. 2021. Influences of the bark economics spectrum and positive termite feedback on bark and xylem decomposition. *Ecology,* 102.

VAN GELDER, H. A., POORTER, L. & STERCK, F. J. 2006. Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist,* 171**,** 367-378.

VELDHUIS, M. P., LASO, F. J., OLFF, H. & BERG, M. P. 2017. Termites promote resistance of decomposition to spatiotemporal variability in rainfall. *Ecology,* 98**,** 467-477.

WATSON, R. T., NOBLE, I. R., BOLIN, B., RAVINDRANATH, N. H., VERARDO, D. J. & DOKKEN, D. J. 2000. *Land use, land-use change and forestry: a special report of the Intergovernmental Panel on Climate Change*, Cambridge University Press.

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**,** 45-56.

WERNER, P. A. & PRIOR, L. D. 2007. Tree-piping termites and growth and survival of host trees in savanna woodland of north Australia. *Journal of Tropical Ecology,* 23**,** 611-622.

WIJAS, B. J., LIM, S. & CORNWELL, W. K. 2022. Continental-scale shifts in termite diversity and nesting and feeding strategies. *Ecography,* 2022.

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.-I. & PARR, C. L. 2022. Termite sensitivity to temperature affects global wood decay rates. *Science,* 377**,** 1440-1444.

ZANNE, A. E., OBERLE, B., DUNHAM, K. M., MILO, A. M., WALTON, M. L. & YOUNG, D. F. 2015. A deteriorating state of affairs: How endogenous and exogenous factors determine plant decay rates. *Journal of Ecology,* 103**,** 1421-1431.

ZULETA, D., ARELLANO, G., MCMAHON, S. M., AGUILAR, S., BUNYAVEJCHEWIN, S., CASTAÑO, N., CHANG-YANG, C. H., DUQUE, A., MITRE, D., NASARDIN, M., PÉREZ, R., SUN, I. F., YAO, T. L., VALENCIA, R., KRISHNA MOORTHY, S. M., VERBEECK, H. & DAVIES, S. J. 2023. Damage to living trees contributes to almost half of the biomass losses in tropical forests. *Global Change Biology,* 29**,** 3409-3420.

Supporting Information

Article title: Higher internal stem damage in dry compared to wet tropics: where are we overestimating forest biomass?
Authors: Habacuc Flores-Moreno, Abbey R. Yatsko, Alexander W. Cheesman, Steven D. Allison, Lucas A. Cernusak, Rebecca Clement1, Wendy Cooper, Paul Eggleton, Rigel Jensen, Marc Rosenfield, Amy E. Zanne.
Article acceptance date: Click here to enter a date.

The following Supporting Information is available for this article:

Fig S1 Depiction of internal stem damage measurement, identification, and quantification
Fig S2 Standard major analysis of the area vs. linear biomass scaling estimate of internal stem damage
Fig S3 Percentage internal stem damage correlation with site and stem level variables.
Table S1 Approaches taken to bracket the effect of several random and nonrandom damage accumulation patterns
Table S2 Regression models predicting stem biomass based on aboveground biomass.
Table S3 One-way ANOVAs comparing sites difference in termite damage in downed deadwood, DBH and wood density.
Table S4 Regression coefficients for percentage internal stem damage as a function of the interaction between wood density and site level variables (precipitation and termite damage in downed deadwood).
Table S5 Regression coefficients for area-based percentage internal stem damage correlation with site and stem level variables.
Table S6 Regression coefficients for area-based percentage internal stem damage as a function of the interaction between wood density and site level variables (precipitation and downed deadwood termite damage).

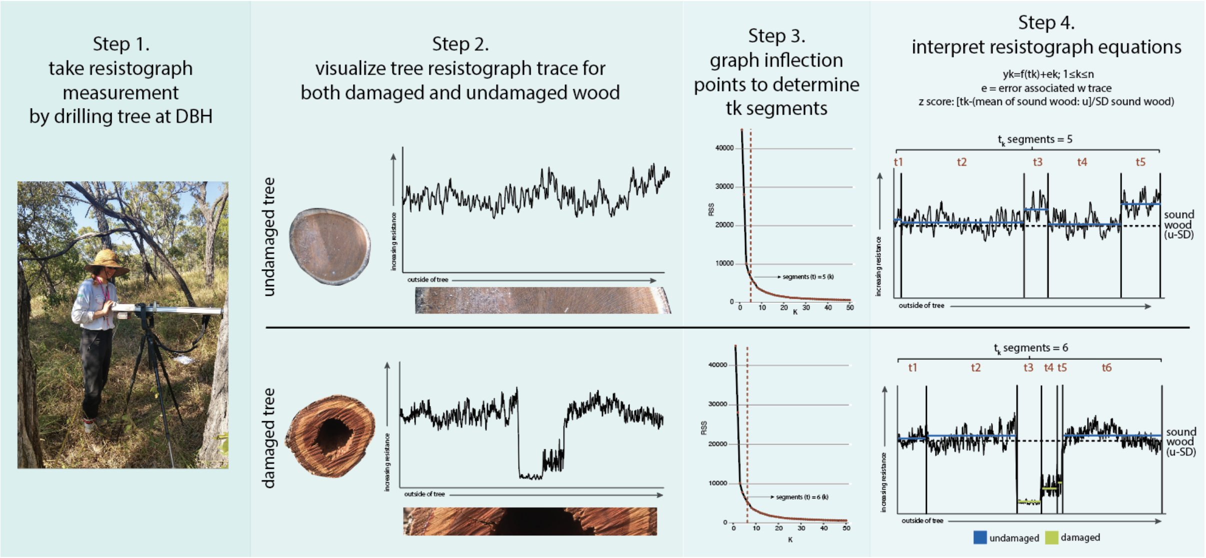

Fig S1 Depiction of internal stem damage measurement, identification, and quantification.. The top row illustrates analysis of an undamaged tree stem, and the bottom row compares measurement of a damaged stem. Step 1 field measurement of damage, Step 2 visualization of damage, Step 3 analyses of resistograph trace and step 4 segment identification and damage calculation.

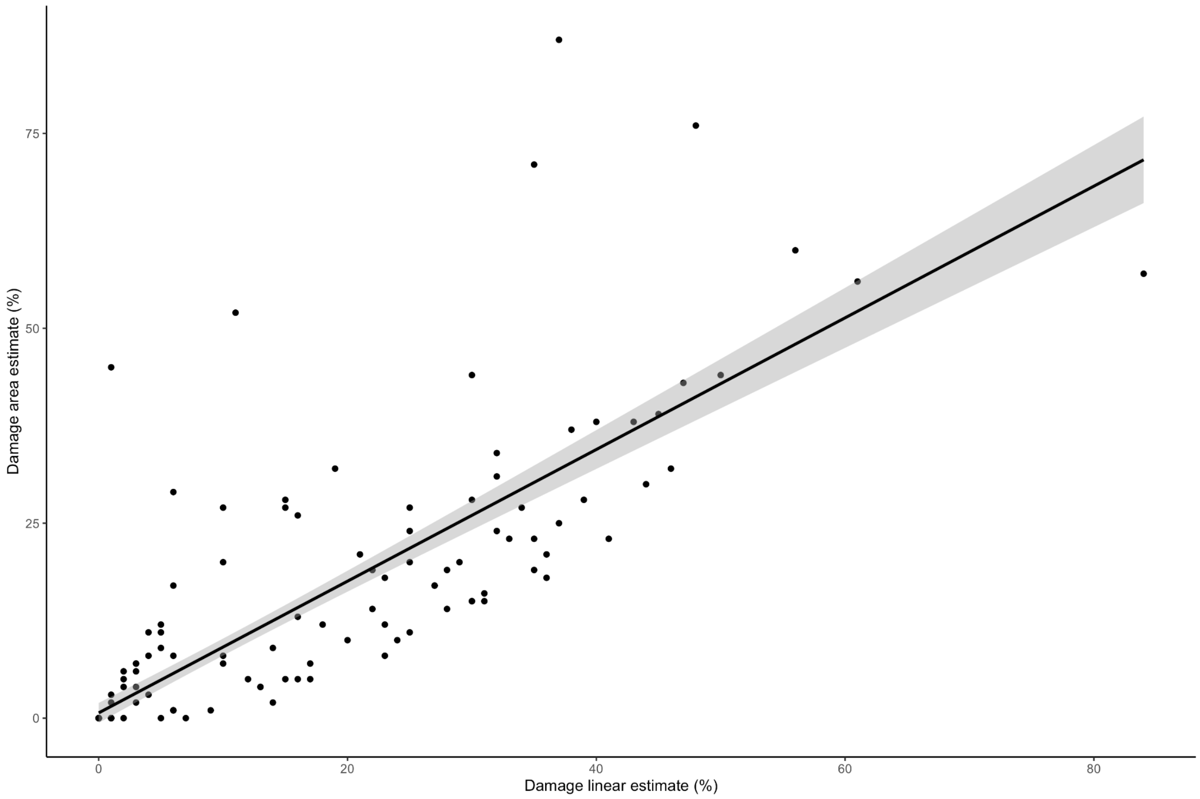

Fig S2 Standard major analysis of the area vs. linear biomass scaling estimate of internal stem damage. Points represent individual stems. As the slope does not differ from 1, the regression indicates a near isometric relationship between the two methods (slope = 0.99 CI 0.92-1.06, $P < 0.0001$; $R^2 = 0.70$) and the shaded region represents a 95% CI .

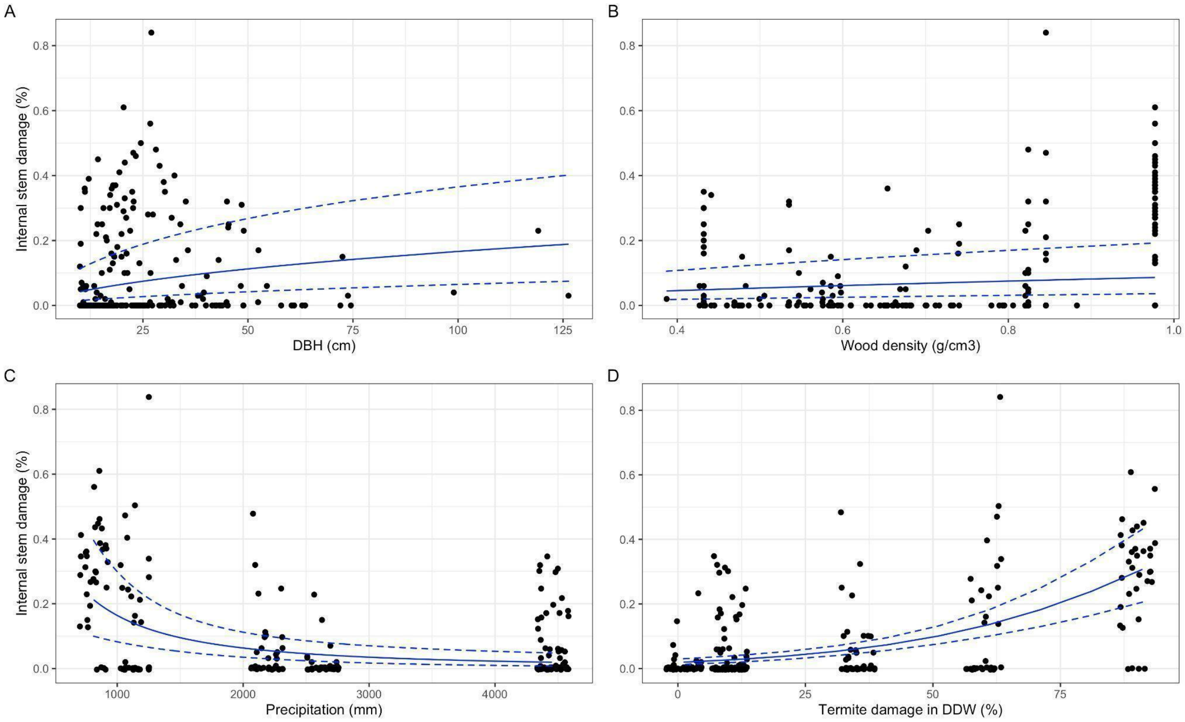

Fig S3 Percentage internal stem damage correlation with site and stem level variables.

Percentage internal stem damage correlation with A. stem diameter at breast height (DBH, in cm), B. wood density (g m^{-3}), C. site precipitation (mm) and D. percentage termite damage in downed deadwood (DDW). Dashed lines represent a 95% CI.

Table S1 Approaches taken to bracket the effect of several random and nonrandom damage accumulation patterns

Type of damage	**Damage accumulation pattern**	**Scale**	**Approach**
radial	random or nonrandom	cross-sectional area	linear and area-basis damage estimation
Vertical	nonrandom	stem-level	+/- 50% change in damage
Tree level	nonrandom	tree-level	Aboveground vs no-canopy

			aboveground biomass calculation

Table S2 Regression models predicting stem biomass based on aboveground biomass (log-transformed).

Parameter	Coefficient	SE	95% CI	t(8640)	p
Intercept	-0.43	0.01	[-0.45, -0.40]	-35.49	<0.001
Slope	1.07	1.78E-03	[1.07, 1.07]	602.66	<0.001

Table S3 One-way ANOVAs comparing sites difference in termite damage in downed deadwood), DBH and wood density.

Model	Parameter	Sum of Squares	df	Mean square	F	p
Damage	site	21222.77	4	5305.69	19.81	5.81E-14
	residuals	59449.66	222	267.79		
DBH	site	1.85	4	0.46	1.59	0.18
	residuals	64.48	222	0.29		
Wood density	site	8.03	4	2.01	60.16	2.35E-34
	residuals	7.41	222	0.03		

Table S4 Regression coefficients for percentage internal stem damage as a function of the interaction between wood density and site level variables (precipitation and deadwood termite damage in downed deadwood).

Model	Parameter	Log-odds	SE	95% CI	Z	R^2	p
Precipitation	Model					0.23	
	Intercept	-3.53	0.29	(-4.10, -2.95)	-12.08		0.003

	Precipitation	-1.81	0.60	(-2.99, -0.64)	-3.02		<0.001
	Wood density	-0.63	0.01	(-0.65, -0.61)	-53.02		<0.001
	Precipitation* wood density	-3.25	0.02	(-3.29, -3.20)	-146.50		<0.001
Termite damage in DDW	Model					0.25	<0.001
	Intercept	-3.46	0.34	(-4.14, -2.79)	-10.06		<0.001
	Termite damage in DDW	1.42	0.63	(0.17, 2.66)	2.23		0.026
	Wood density	-0.58	0.01	(-0.60, -0.56)	-52.48		<0.001
	Termite damage in DDW*wood density	3.00	0.02	(2.96, 3.05)	136.35		<0.001

Table S5 Regression coefficients for area-based percentage internal stem damage correlation with site and stem level variables.

Model	Parameter	Log-Odds	SE	95% CI	z	p	R^2
DBH	(Intercept)	-4.13	0.48	[-5.07, -3.18]	-8.58	<0.001	0.015
	dbh cm [log10]	1.11	0.01	[1.08, 1.13]	82.75	<0.001	
Wood density	(Intercept)	-2.49	0.44	[-3.36, -1.63]	-5.65	<0.001	0.003
	wood density [log10]	1.06	0.04	[0.99, 1.13]	29.73	<0.001	

Precipitation	(Intercept)	7.69	2.76	[2.27, 13.11]	2.78	0.005	0.17
	prec 90m [log10]	-3.16	0.84	[-4.81, -1.50]	-3.74	<0.001	
termite damage in down deadwood	(Intercept)	-3.86	0.24	[-4.33, -3.38]	-15.97	<0.001	0.21
	termite damage in down deadwood	0.03	4.73E-03	[0.02, 0.04]	6.52	<0.001	

Table S6 Regression coefficients for area-based percentage internal stem damage as a function of the interaction between wood density and site level variables (precipitation and termite damage in downed deadwood).

Model	Parameter	Log-Odds	SE	95% CI	z	p	R^2
Precipitation x wood density	(Intercept)	-3.53	0.29	[-4.10, -2.95]	-12.08	<0.001	0.23
	Precipitation	-1.81	0.6	[-2.99, -0.64]	-3.02	0.003	
	Wood density	-0.63	0.01	[-0.65, -0.61]	-53.02	<0.001	
	Precipitation * wood density	-3.25	0.02	[-3.29, -3.20]	-146.5	<0.001	
termite damage in downed deadwood x wood density	(Intercept)	-3.46	0.34	[-4.14, -2.79]	-10.06	<0.001	0.25
	termite damage in downed deadwood	1.42	0.63	[0.17, 2.66]	2.23	0.026	
	Wood density	-0.58	0.01	[-0.60, -0.56]	-52.48	<0.001	

	Termite damage in downed deadwood * wod density	3	0.02	[2.96, 3.05]	136.35	<0.001	