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# New Phytologist

## Shifts in internal stem damage along a tropical precipitation gradient and implications for forest biomass estimation

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1 **Title: Shifts in internal stem damage along a tropical precipitation gradient**  
2 **and implications for forest biomass estimation**

3

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29

30

## 31 **Summary**

- 32 • Woody biomass is a large carbon store in terrestrial ecosystems. In calculating  
33 biomass, tree stems are assumed to be solid structures. However, decomposer agents  
34 such as microbes and insects target stem heartwood, causing internal wood decay  
35 which is poorly quantified.
- 36 • We investigated internal stem damage across five sites in tropical Australia along a  
37 precipitation gradient. We estimated the amount of internal aboveground biomass  
38 damaged in living trees and measured four potential stem damage predictors: wood  
39 density, stem diameter, annual precipitation and termite pressure (measured as termite  
40 damage in downed deadwood).
- 41 • Stem damage increased with increasing diameter, wood density, and termite pressure,  
42 and decreased with increasing precipitation. High wood density stems sustained less  
43 damage in wet sites and more damage in dry sites, likely a result of shifting  
44 decomposer communities and their differing responses to changes in tree species and  
45 wood traits across sites.
- 46 • Incorporating stem damage reduced aboveground biomass estimates by >30% in  
47 Australian savannas, compared to only 3% in rainforests. Accurate estimates of  
48 carbon storage across woody plant communities are critical for understanding the  
49 global carbon budget. Future biomass estimates should consider stem damage in  
50 concert with effects of changes in decomposer communities and abiotic conditions.

51

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

54

## 55 **Introduction**

56 Living plant biomass, which includes the dead tissue in heartwood, accounts for 42% of  
57 terrestrial carbon (C) storage (Pan *et al.*, 2011). In estimating these stores, trees are typically  
58 assumed to be solid structures with biomass often estimated using their height and diameter  
59 in relation to regional or global allometric relationships (Zuleta *et al.*, 2023). Yet living tree  
60 stems are susceptible to biomass loss via microbial heart rot and insect damage (Romero &  
61 Bolker, 2008; Heineman *et al.*, 2015). External stem damage is easily observable, but internal  
62 stem damage (i.e., damage to biomass underneath the bark) while long noted (Janzen, 1976;  
63 Brown *et al.*, 1995) is usually at best implicitly accounted for as clustered standard errors in

64 estimates of woody aboveground biomass. It typically cannot be quantified explicitly  
65 (Heineman *et al.*, 2015). The assumption that tree stems are internally solid structures with no  
66 damage can potentially lead to overestimates of the amount of C that forests hold.

67

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

84 To scale biomass estimates from trees to ecosystems, it is additionally important to  
85 understand correlates of internal stem damage. Given that heartwood in living stems is dead,  
86 the extent of internal stem damage in living trees may be related to factors that similarly  
87 affect rates of deadwood decomposition on the forest floor. Wood decomposition is impacted  
88 by wood density, morphology, chemical construction (Kirk & Cowling, 1984; Zanne *et al.*,  
89 2015), as well as moisture availability (Boddy & Rayner, 1983; Chambers *et al.*, 2000), and  
90 decomposer activity (Bani *et al.*, 2018; Griffiths *et al.*, 2019). At the stem-level, large  
91 diameters may carry more damage because they have more tissue at risk to decay agents. In  
92 fact, large trees had more frequent heart rot in tropical rainforests (Heineman *et al.*, 2015;  
93 Eleuterio *et al.*, 2020) and more hollowing by termites in savannas (Werner & Prior, 2007).  
94 Trees with high wood density may be slow to decompose (Chambers *et al.*, 2000), mediated  
95 by microbial and termite (major biotic decay agents in the tropics, Cornwell *et al.*, 2009;  
96 Zanne *et al.*, 2022) decay. Dense wood can be inaccessible due to its greater structural  
97 integrity (Chambers *et al.*, 2000 but see ; Weedon *et al.*, 2009; Harmon *et al.*, 2020) and

98 smaller pore spaces, decreasing water permeability and slowing pathogen attack and  
99 decomposition (Augsburger & Kelly, 1984; Chave *et al.*, 2009; Mori *et al.*, 2014).  
100 Nevertheless, studies in tropical rainforests failed to find links between wood density and  
101 internal stem damage (Heineman *et al.*, 2015), which may be explained by presence of  
102 extractives that confer resistance to decomposers (Bultman & Southwell, 1976).

103         Across sites, moisture variation directly affects the decay process by determining the  
104 composition and activity of the decomposer community in wood (Cheesman *et al.*, 2018;  
105 Steidinger *et al.*, 2019; Clement *et al.*, 2021). For downed deadwood, decomposition by  
106 microbes decreases and by termites increases with increasing aridity (Veldhuis *et al.*, 2017;  
107 Cheesman *et al.*, 2018; Clement *et al.*, 2021; Zanne *et al.*, 2022; but see Law *et al.*, 2023).  
108 We know less about living tree decomposers, but microbial heart rot (Highley & Kirk, 1979;  
109 Gilbert *et al.*, 2016) and termite hollowing have been documented (Werner & Prior, 2007;  
110 N'dri *et al.*, 2014; Eleuterio *et al.*, 2020). Based on this past work, we predict that microbial-  
111 driven internal stem damage is more prevalent at wet sites and termite driven decay at dry  
112 sites. Precipitation can also indirectly affect decay as it determines the tree species  
113 composition and wood construction of those species. Trees are often smaller in dry sites  
114 likely in part due to slower growth (Pretzsch *et al.*, 2018) and resource limitations.  
115 Additionally, wood density is typically high in dry sites (Chave *et al.*, 2014; Zanne *et al.*,  
116 2015), perhaps mediated through selection for resistance to cavitation (Greenwood *et al.*,  
117 2017) and slow growth. Both maximum plant size and wood density vary across the plant  
118 phylogeny, with some clades having particularly dense wood or large stems; these traits will  
119 have shaped the biogeographic distribution of tree species. It is therefore likely that clades  
120 with more internal stem damage in dry sites are different from those in wet sites, with  
121 damage driven by different biotic factors.

122         Given the interactive ways that wood traits, decay agents and moisture availability  
123 change across sites, we examined their effects on internal stem damage individually and in  
124 combination. Specifically, we investigated the amount of internal stem damage in living trees  
125 across a tropical rainfall gradient in Queensland, Australia. Our sites span a range of biomes  
126 (savanna to rainforest) along a precipitation gradient from  $\sim 800\text{mm yr}^{-1}$  to  $\sim 4,500\text{mm yr}^{-1}$ .  
127 We measured four internal stem damage predictors at the stem- and site- level: wood density,  
128 stem diameter, precipitation, and termite pressure (the relative damage by termites of downed  
129 deadwood)). To understand the within- and across-site patterns in stem damage across the  
130 tree-of-life, we visualized the distribution of wood density and diameter at breast height of  
131 individuals, biomass, and internal stem damage among the different clades of the plant

132 phylogeny present at our sites. To place these findings in a broader context, we used  
133 allometric equations to compare aboveground biomass estimates of our sites before and after  
134 accounting for internal stem damage, as modeled by our four predictors. Given that internal  
135 stem damage may or may not accumulate randomly across the width and height of the tree,  
136 we explored the sensitivity of biomass estimates to different assumptions about the extent of  
137 internal stem damage. Here we asked the following questions:

- 138 1. Do sites differ in internal stem damage and potential predictors? Is greater internal  
139 stem damage associated with lower wood density, smaller stem diameters, wetter  
140 sites, and where there is higher termite pressure (measured as amount of termite  
141 damage in downed deadwood), as expected?
- 142 2. With a shift in the expected dominant decay agent (between microbes and termites), is  
143 there a shift in the effect of wood density on internal stem damage?
- 144 3. Are there particular plant clades that are more susceptible to internal stem damage and  
145 do these susceptible clades differ across the precipitation gradient?
- 146 4. Does accounting for internal stem damage strongly alter aboveground biomass  
147 estimates, and does the degree of this alteration vary across the precipitation gradient?

148

## 149 **Materials and methods**

150 We sampled the woody plants in 50 x 50 m survey plots at five sites along a 100-km rainfall  
151 gradient in northeast Queensland, Australia with mean annual rainfall ranging from 812 to  
152 4458 mm (Fig. 1 and Table S1). Mean annual rainfall over 30 years was obtained at 90m  
153 resolution from the Bureau of Meteorology for each site (Australian Bureau of Meteorology,  
154 2021). Our wettest site is located in the Daintree Rainforest (Rft2; -16.10 S, 145.44 E) part of  
155 James Cook University's Daintree Rainforest Observatory next to the Coral Sea. Our driest  
156 site, Pennyweight (Sav1; -16.57 S, 144.92 E), is a dry savanna 58 km inland from the Coral  
157 Sea coast and located on the western side of the Great Dividing Range of northeast  
158 Queensland. Three intermediate precipitation sites are found on Mt. Lewis, located to the  
159 southeast of site Sav1. Station Creek (Sav2; -16.61 S, 145.24 E) averages 1728 mm of rainfall  
160 annually and is a wet savanna located at the western slope of Mt. Lewis. A wet sclerophyll  
161 forest (Sc11; 2189 mm of rain annually; -16.58 S, 145.26 E) and a high elevation rainforest  
162 (Rft1; 2630 mm of rain annually; -16.59 S, 145.28 E) are located on Mt. Lewis. All sites  
163 experience a distinct wet and dry season, with 77% of rainfall occurring between November  
164 and April (Cheesman *et al.*, 2018). Sav1, Sav2, Sc11, and Rft1 are located within the

165 Australian Wildlife Conservancy's Brooklyn Sanctuary, Rft2 is located in James Cook  
166 University's Daintree Rainforest Observatory.

167

168

169 We measured the diameter at breast height (DBH) of all trees  $\geq 10$  cm in each plot at our five  
170 sites. Wood density data were extracted from the Tree Functional Attributes and Ecological  
171 Database (Harja *et al.*, 2019). Wherever possible we used species-level data ( $n = 51$ ). If no  
172 species data existed, we used genus- ( $n = 39$ ) or family-mean values ( $n = 13$ ), in that order of  
173 preference. Termite pressure (i.e., percentage termite damage in downed deadwood) was  
174 taken from Clement *et al.* (2021), in which they established 50 m deadwood survey transects  
175 within 50 m x 50 m termite survey plots adjacent to the woody plant survey plots studied  
176 here. In total, four randomly placed transects were sampled in each plot, two during the wet  
177 season and two during the dry season. Each piece of wood  $>2$  cm diameter intersecting the  
178 transect was assessed for termite damage (i.e., piping, runways or termite tunnels) using a  
179 drywall hammer to break wood open in three places to look for termites (additional details in  
180 Clement *et al.*, 2021). Termite damage in downed deadwood was calculated as percentage of  
181 deadwood pieces showing termite damage. Sampling for termite damage took place at wet to  
182 dry and dry to wet seasons, to capture the maximum amount of termite pressure in deadwood  
183 (Clement *et al.*, 2021).

184

#### 185 *Internal stem damage identification*

186 To measure internal stem damage at each of our five sites, we selected trees with varying  
187 DBH stratified by species. In total, we sampled 258 unique stems (average 51.6 stems per  
188 site) from 87 species. We used an IML-RESI power drill, mounted on a tripod to reduce  
189 measurement error (Step 1 in Fig. S1; Residrill; PD-500, IML, Germany), to determine the  
190 presence of stem damage in living trees. Resistance drilling inference is based on the  
191 correlation between drilling resistance and the material composition (Lear *et al.*, 2011). A  
192 slender drill bit ( $\sim 3$ mm in diameter) is rotated into the wood at a constant speed and feed  
193 rate, and the energy needed for the drill to move forward is recorded as a function of its  
194 position. Changes in the resistance (e.g., abrupt loss of resistance) are used to infer changes in  
195 the material, in our case the presence of voids in the wood. Among other applications,  
196 resistance drilling has been used to assess termite damage in wood (Hickman & Forschler,  
197 2012), radial changes in wood density in pedunculate oak stands (Tomczak *et al.*, 2022) and  
198 examine climate-associated variation in wood in *Eucalyptus nitens* plantations (Rocha



199 Sepúlveda, 2023). Trees across all sites were drilled at breast height (at 130 cm above  
 200 ground) across the longest diameter from end to end (Fig. S1). Our goal was to measure a  
 201 trace across the entire longest axis; however, this was not always possible. Given the high  
 202 speeds of drilling, the drill can be damaged if there are problems with the stylus. We  
 203 measured 23.9 - 100% of the stem in the longest direction (median = 97.6, sd = 12.84).  
 204 Because we were measuring damage based on changes in resistance, damaged wood could  
 205 not be attributed to microbe versus termite pressure. The source of damage was inferred via  
 206 evidence of termite pressure measured at the site level and extracted from Clement *et al.*  
 207 (2021; see section above).

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

$$215 \quad (1) \quad y_j = f(t_j) + e_j; 1 \leq j \leq n$$

216 Assuming the wood properties of the stem do not change within each section means  
 217 that  $f$  is a piecewise constant. We expect that there exist discontinuities  $\tau_1, \tau_2, \dots, \tau_{K-1}$  and wood  
 218 segments values  $\mu_1, \mu_2, \dots, \mu_K$  such that:

$$219 \quad (2) \quad f(t) = \mu_k \text{ if } \tau_{k-1} < t \leq \tau_k$$

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

$$221 \quad (3) \quad y_j = \mu_k + e_j.$$

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

232 the stem; for each stem we split the internal stem damage trace in half prior to detecting  
233 discontinuities in the wood resistance to drilling trace as described above.

234

235 *Analyses*

236 *Assumptions on patterns of stem damage accumulation*

237 Internal stem damage in trees may accumulate in different patterns. Detected internal  
238 damage at a given height may represent the amount of damage along the entire height and  
239 diameter of the tree, or damage may differ at different heights or parts of the diameter within  
240 the tree. We were unable to account for all possible patterns of internal stem damage  
241 accumulation, but here we assess four different assumptions for estimating damage (Table  
242 S2). If damage accumulates randomly across the diameter of the tree, then a linear, cross-  
243 sectional transect of the tree stem will be representative of the damage throughout the tree.  
244 On the other hand, damage could accumulate predictably in a few different ways. For  
245 example, internal stem damage may be more prevalent near the pith or further out near the  
246 sapwood, depending on the decay agents. Damage closer to the pith of the tree will contribute  
247 less to the proportion of cross-sectional area damaged than damage closer to the sapwood  
248 (due to the nature of radial scaling). Further, damage could change with height in the stem  
249 depending for instance on where decay agents enter or external damage occurs in the stem  
250 (Roisin *et al.*, 2006; Li *et al.*, 2016). Alternatively, crown damage could differentially affect  
251 the amount of biomass in the crown versus the main stem. The consequences of such  
252 nonrandom damage could be significant given that two of the biggest damage agents,  
253 microbes and termites, cause heart rot and stem hollowing in our systems; they are both  
254 expected to target the oldest heartwood closest to the pith. To determine the pattern of  
255 internal stem damage, we first identified if damage accumulated randomly across the  
256 diameter of the trees, and then tested the effect of vertical change in stem damage  
257 accumulation and its impact on the biomass of the crown using a two-step approach.

258

259 First, to test the sensitivity of our damage estimates to random and nonrandom  
260 damage assumptions across the radius of the stem, we estimated the proportion of internal  
261 stem damage on a linear- and area-basis, with the area-basis allowing us to estimate  
262 nonrandom effects of distance from pith. Then we ran a standard major axis analysis to  
263 compare the relationship between the linear- and area-based methods to estimate internal  
264 stem damage (assumption one versus two). This analysis revealed a relationship that is not  
265 significantly different from isometric (i.e., slope overlaps 1) between these two methods to

266 estimate damage (slope = 0.99 CI 0.92-1.06,  $P < 0.0001$ , Fig. S2), leading us to continue with  
267 the linear assumption to estimate how internal stem damage reduces biomass estimates.

268 Second, the internal stem damage measured at DBH may extend throughout the stem  
269 or it may only occur locally. As it extends, the amount of damage may increase, decrease or  
270 stay constant across the height of the tree (assumption three). Third, internal stem damage  
271 may lead to crown loss (assumption four). Consequently, the proportion of internal damage  
272 measured at DBH may under or overestimate damage across the tree. To bracket the potential  
273 effect of internal stem damage variation on biomass calculations, we compared aboveground  
274 (i.e., including the crown) and only stem biomass (i.e., excluding the crown) estimates, as  
275 well as aboveground biomass and only stem biomass estimates assuming constant (i.e.,  
276 excluding the crown), 50% increase and 50% decrease in internal stem damage (see below in  
277 section for aboveground biomass calculation; Table S2). We estimated the relationship  
278 between stem biomass and AGB using the BAAD dataset (Biomass and Allometry Database,  
279 Falster *et al.*, 2015) of individual trees (log-transformed) and applied this regression model to  
280 predict stem biomass using our AGB estimates (Table S3). We only included records that had  
281 information available for total, stem, and root biomass ( $n = 8642$ ).

282

### 283 *Stem damage, DBH and wood density across sites*

284 We ran Analysis of Variance (ANOVAs) to test whether stem damage, DBH and wood  
285 density varied across our sites, and, for significant ANOVA's, we ran Tukey's HSD tests to  
286 determine which sites were significantly different from one another. To determine if internal  
287 stem damage varied with each of the site and species level predictors, we ran bivariate  
288 models with each of the individual stem-level (stem diameter, wood density) and site-level  
289 (rainfall, termite pressure measured as percentage of termite damage in downed woody  
290 debris) variables as predictors and proportion of internal stem damage as the response  
291 variable. Given the expected shift in decomposer activity (between microbes and termites)  
292 across sites from rainforest to savanna, we explored how the interaction of wood density and  
293 site variables predicted internal stem damage. For all models, we fit a logistic binomial  
294 regression with a random intercept for site. It was not possible to measure internal stem  
295 damage across the entire cross section for all stems in our plots, therefore for each stem we  
296 added a weight to the model to account for the proportion of the stem sampled. The weight in  
297 such models represents, for each individual tree, the completeness of the internal stem  
298 sampled. We used the likelihood ratio to compare the explanatory power of the interaction  
299 against the bivariate models.

### 300 *Stem damage mapped across phylogeny*

301         Additionally, we visualized how species across the phylogeny varied across sites in  
 302 their susceptibility to internal stem damage. Given the few species in our study and the  
 303 nonrandom sampling of them across the evolutionary tree, we were unable to run  
 304 comparative analyses. The visualization though, is a first step to consider which clades are  
 305 particularly susceptible (or not) to internal stem damage in different environments. Finally,  
 306 we examined the possible impacts of interspecific susceptibility to internal stem damage on  
 307 species and site level aboveground biomass estimates. We first estimated the amount of  
 308 aboveground biomass contributed by each species at each site in our woody plant survey  
 309 plots by estimating the aboveground biomass for each individual tree > 10 cm in DBH in our  
 310 communities following Chave *et al.* (2014). Second we added up the individual tree estimates  
 311 (n = 679) at each site. Briefly, when height data were available we used the Chave *et al.*  
 312 (2014) pantropical model to estimate tree aboveground biomass (AGB) as follows:

$$313 \quad (4) \text{ AGB} = 0.0673 \cdot (WD \cdot H \cdot D^2)^{0.976}$$

314 Where WD is wood density in g cm<sup>-3</sup>, H is height in m, D is diameter in cm (measured at 130  
 315 cm above ground across all trees and sites) and AGB is in Mg (metric tonnes). When height  
 316 data were not available (in Rf1 and Rf2), we used the Chave *et al.* (2014) AGB model based  
 317 on diameter, wood density and environmental stress:

$$319 \quad (5) \text{ AGB} = \exp [ - 1.803 - 0.976E + 0.976\ln(WD) + 2.673\ln(D) - 0.0299[\ln(D)^2] ]$$

320  
 321 In this allometric model of AGB, E is a measurement of environmental stress based on the  
 322 effect of temperature seasonality, climatic water deficit and precipitation seasonality (Chave  
 323 *et al.*, 2014). To visualize differences among lineages across the plant phylogeny, we mapped  
 324 the average species wood density, as well as species average internal stem damage and total  
 325 aboveground biomass for species at each site subsetting the Smith and Brown (2018)  
 326 phylogeny to those species in our study. We use phyndr to maximize the overlap between the  
 327 phylogenetic tree and the diameter and internal stem damage data (Pennell *et al.*, 2016).

### 329 *Stem damage and C accounting*

330         To understand the consequences of internal stem damage on C accounting, we  
 331 calculated aboveground biomass with and without damage for every site following the Chave  
 332 *et al.* (2014) equation above. First, we used the AGB for every individual tree > 10 cm in

333 DBH in our communities ( $n = 679$ ). Once we estimated the aboveground biomass at the tree  
334 level, we determined area-based estimates at each site by summing all stems and dividing by  
335 the plot area. We compared the stem biomass and AGB estimates at the plot level, with and  
336 without the damage prediction across our five sites using a paired  $t$ -test. We use the wood  
337 density and precipitation interaction model to predict damage, as few studies quantify termite  
338 pressure (i.e., termite damaged in downed deadwood, DDW), while precipitation is readily  
339 available for most locations. We ran all the analyses above for both linear- and area-based  
340 internal stem damage estimates. Area-based estimates allowed us to examine non-random  
341 changes in damage with radius, although we only present linear-based estimates in the main  
342 text. Area based estimates are presented in Supplementary information (Tables S5 and S6).  
343 We performed all analyses using R 4.2.2 (R Core Team, 2022)

344

## 345 **Results**

346 Internal stem damage (proportion of trace with damage) was instead greater in savanna sites  
347 ( $P < 0.0001$ , Fig. 2a, Table S4), as precipitation decreased ( $P = 0.0002$ ,  $R^2 = 0.20$ ,  $n = 226$ ;  
348 Fig. S3c). Larger stems accumulated more internal damage ( $P < 0.0001$ ,  $R^2 = 0.02$ ,  $n = 226$ ;  
349 Fig. S3a), whereas stem diameter distributions showed little variation among sites ( $P = 0.18$ ,  
350 Fig. 2b, Table S4). Wood density was higher at dry sites ( $P < 0.0001$ , Fig. 2c, Table S4).  
351 Denser stems also accumulated more internal damage ( $P < 0.0001$ ,  $R^2 = 0.02$ ,  $n = 226$ ; Fig.  
352 2a, S3). Our dry sites were previously shown to have greater termite pressure damage in  
353 downed deadwood (percentage termite damage in downed deadwood; Fig. 2d, Clement et al  
354 2021); internal stem damage increased at these sites where termite pressure was high ( $P$   
355  $< 0.0001$ ,  $R^2 = 0.25$ ,  $n = 226$ ; Fig. S3). The explanatory power of each of the single predictor  
356 models of internal stem damage was low to moderate, with stem level predictors explaining  
357 2% and site level predictors explaining 20-25% of the variation in damage (Table S4).

358

359

360 In multivariate models of stem damage, wood density was retained in both site level  
361 models, as well as a significant interaction term between wood density and site level  
362 predictors (Fig. 3, Table S6). Stems with high wood density experienced less internal damage  
363 in wet sites and more internal damage in dry sites. Similarly, stems with high wood density  
364 experienced more internal stem damage in sites with high termite pressure than those with  
365 low termite pressure. However, stems with low wood density showed little change in internal  
366 stem damage across changes in either precipitation or termite damage in downed deadwood.

367 Although these models with an interaction term between wood density and site level  
 368 predictors only explained ~3% more variation than the single site-level predictor models,  
 369 both models had highly significant interaction terms and represented a better explanation of  
 370 the data (LRT  $P < 0.001$ ) than the single variable models (Fig. 3; Table S6).

371

372

373

374 While across-site differences in internal stem damage appeared at least in part driven  
 375 by the internal stem damage response of denser wooded species (Fig. 3, Table S5), large  
 376 variation in both internal stem damage and wood density occurred within sites (Fig 2D, Fig.  
 377 4, Table 1). Aboveground biomass in drier sites was dominated by Myrtaceae, which had  
 378 dense wood and high internal stem damage (Fig. 4, Table 1), with internal stem damage also  
 379 high ( $\geq 0.1$ ) in members of the Combretaceae, Fabaceae, Moraceae, Rubiaceae and  
 380 Santalaceae. Wet sites had species broadly distributed across the phylogeny with Fabaceae,  
 381 Lauraceae, Myrtaceae, Proteaceae and Rutaceae contributing considerable aboveground  
 382 biomass ( $\geq 20 \text{ Mg ha}^{-1}$ ). Species with the most damage ( $\geq 0.1$ ) were in the Annonaceae,  
 383 Cardiopteridaceae, Euphorbiaceae, Fabaceae, Lauraceae, Myrtaceae, Podocarpaceae,  
 384 Rutaceae and Sapotaceae. Overall, wet site species were more variable in wood density,  
 385 aboveground biomass, and internal stem damage. The intermediate site aboveground biomass  
 386 was dominated by Casuarinaceae and Proteaceae ( $\geq 0.5$ ), followed by Myrtaceae ( $\geq 0.1$ );  
 387 interestingly, species in the Lauraceae had the lowest wood density and some of the lowest  
 388 internal stem damage.

389

390 To understand consequences of internal stem damage on aboveground biomass  
 391 estimates, we used our internal stem damage prediction model with an interaction for wood  
 392 density and precipitation (see Precipitation model in Table S5). Our modified model  
 393 estimated that across our sites  $60.8 \text{ Mg ha}^{-1}$  may be damaged, or between 2.9-36.2% of  
 394 aboveground biomass per site, with some of this biomass entirely missing. Percentage  
 395 aboveground biomass damage was variable across our sites with the drier savanna sites (with  
 396 the highest termite pressure; Fig. 2D) estimated to have much higher damage than other sites  
 397 (Figure 4A), with  $>30\%$  damaged at our driest and  $<3\%$  damaged at our wettest sites. This  
 398 result is despite the lower total biomass found in savannas than rainforests (Fig. 5b, c). When  
 399 we tested sensitivity of these differences to variation within the tree, our bracketed internal  
 400 stem damage estimate (with a  $\pm 50\%$  increase and decrease in damage across the height of the

401 tree; assumption three) suggests that the damaged biomass across our sites could be as low as  
402 30.4 Mg ha<sup>-1</sup> and as high as 91.2 Mg ha<sup>-1</sup>. Meanwhile, assuming internal stem damage only  
403 impacts stem but not the crown biomass (assumption four), we estimated internal stem  
404 damage to be 38.4 Mg ha<sup>-1</sup> when assuming constant damage across the stem, or as high as  
405 57.6 Mg ha<sup>-1</sup> or as low as 19.2 Mg ha<sup>-1</sup> when assuming a 50% increase or decrease in damage  
406 across the stem height, respectively. All scenarios predicted a significant difference in  
407 aboveground biomass estimates when comparing modified estimates of aboveground biomass  
408 (gray bars and dashed lines) from our internal stem damage model to estimates without  
409 incorporating internal stem damage (white bars) with ( $P = 0.02$ ; Fig. 5b) or without the crown  
410 ( $P = 0.01$ ; Fig. 5c).

411

412

### 413 **Discussion**

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

431

### 432 **The role of wood density in internal stem damage**

433 The interaction between wood density and decomposer activity (measured as damage in  
434 downed deadwood) or, to a lesser extent, precipitation, revealed a complex relationship

435 between wood density and internal stem damage. Dense wood confers mechanical strength  
436 (Van Gelder *et al.*, 2006; Chave *et al.*, 2014), is more common in arid sites (Chave *et al.*,  
437 2009), and is generally thought to protect against herbivores, pests and pathogens (Scheffer &  
438 Morrell, 1998; Larjavaara & Muller-Landau, 2010). Local studies however reported weak or  
439 inconsistent relationships between wood density and pathogen protection (Augspurger &  
440 Kelly, 1984; Heineman *et al.*, 2015; Eleuterio *et al.*, 2020). Our sites encompassed a large  
441 range in precipitation, plant composition and decomposer communities. Across them, we  
442 found an overall weak negative relationship between wood density and internal stem damage.

443

444 Resistance to biotic decay agents is dependent on the wood substrate availability, including  
445 accessibility of the substrate and range of wood traits, as any given wood trait may not deter  
446 all potential biotic decay agents (Scheffer & Morrell, 1998); what repels a fungal pathogen or  
447 saprobe may not repel a termite, and vice versa. For example, high wood density has been  
448 related to higher fungal resistance and both high and low termite resistance (Bultman &  
449 Southwell, 1976; see above; Oberst *et al.*, 2018). Aromatic phenolics such as stilbenes have  
450 antifungal properties (Hart, 1981; Simonetti *et al.*, 2020), while compounds such as  
451 obtusoquinanone, guaiacol, and lapachol can repel termites (Bultman & Southwell, 1976).  
452 Further, silica organic extractives are often associated with lower susceptibility of wood to  
453 decomposition (Schultz & Nicholas, 2000; Andrews *et al.*, 2023), while prismatic crystals  
454 may contribute to mechanical support and protection against animals (Schneider, 1901). Our  
455 data demonstrate the impact that the decomposer community composition has on the  
456 relationship between plant traits (here wood density) and internal stem damage (in particular  
457 the differences between termite- and microbial-driven decomposition) and suggest that  
458 internal stem damage in drier tropical sites is likely driven by termites. This finding is yet to  
459 be tested in other systems; however, there is evidence that hollowing may be important in dry  
460 tropical sites in other continents (Jones & Eggleton, 2011; N'Dri *et al.*, 2011), as well as  
461 broadly across other ecosystems (Monda *et al.*, 2015; Eleuterio *et al.*, 2020). Relative to the  
462 rainforest, termites in the savanna sites were higher in abundance, species richness, and had  
463 higher pressure in downed deadwood compared to fungi in our system (Clement *et al.*, 2021).  
464 Importantly, here we show that: 1) wood decomposition starts earlier than expected, while  
465 trees are still alive and standing, meaning they are already accessible to biotic decay agents  
466 and 2) different decomposers respond to wood density in different ways, and these  
467 individualistic responses cannot be extrapolated from previous microbial-focused wood  
468 decomposition work.



469

470 **Internal stem damage selective filters**

471 The variation we observed in internal stem damage reflects changes in the abiotic and biotic  
472 filters faced by the relevant players. Differences in wood density and other traits of plants  
473 across our communities are mediated at least in part through variation in abiotic conditions  
474 (Chave *et al.*, 2009; Reich, 2014). Dry sites had lower biomass, had higher and less variable  
475 wood density and were largely composed of Myrtaceae species, especially *Eucalyptus*. Wet  
476 sites had more total living tree biomass, as well as tree species distributed broadly across the  
477 plant phylogeny, with variable wood density. The climate sensitivities of pests, pathogens  
478 and decomposers will also mediate variation in internal stem damage. Microbial decay of  
479 downed deadwood increases with increasing humidity and temperature (Cornwell *et al.*,  
480 2009), while termite wood decay is highly sensitive to temperature but not humidity (Zanne  
481 *et al.*, 2022). As decay occurs in the dead heartwood in living trees, there is potential for  
482 selection of different wood densities (Cornelissen *et al.*, 2022) by the co-occurring decay  
483 agents. Particularly key are the interactions between the abiotic and biotic components,  
484 including how variation in plant traits, such as wood density but also secondary chemistry  
485 and wood morphology in turn also mediate the decomposer community and therefore decay  
486 (Cornwell *et al.*, 2009; Weedon *et al.*, 2009; Hu *et al.*, 2018; Harmon *et al.*, 2020). From the  
487 evidence here, abiotic factors directly or indirectly affect the decomposer community and  
488 hence internal stem damage. However, the wood trait preferences, such as high and low wood  
489 density, of termite- vs microbial-dominated systems lead to variation in which plant lineages  
490 sustain the greatest internal stem damage across our communities.

491

492 In line with evidence from microbial-driven decay in coarse woody debris, we found that in  
493 rainforest, where microbial decomposition is prevalent, plant species with lower wood  
494 density sustained higher internal stem damage. Anecdotally, plant species with darker colored  
495 brown and red heartwoods (e.g., *Ormosia ormondii*) also sustained less internal stem damage  
496 than lighter colored species with yellow or white heartwood (e.g., Euphorbiaceae and  
497 Rutaceae; Table 2 and Figure 4). Darker colored woods were associated with higher  
498 resistance to microbial decay as compared with lighter colored heartwoods (Gierlinger *et al.*,  
499 2004; Chave *et al.*, 2009), perhaps because of higher deposition of extractives during  
500 heartwood formation (Kramer, 2012). Many wood rotting fungi show host preferences; for  
501 instance, white rot fungi are often angiosperm specialists, while brown rot fungi are often  
502 gymnosperm specialists (Krah *et al.*, 2018), with individual fungal species even showing

503 preferences for specific tree species (Baxter, 1925; Ador *et al.*, 2023). The observed higher  
 504 variation in internal stem damage across plant families in our wet sites most likely reflects  
 505 filtering of microbial decomposers (the most active decomposers in these sites) by the  
 506 differences in wood density and chemistry among plant clades.

507

508 In our savanna sites, Myrtaceae species with denser wood had the most internal stem damage.  
 509 An important termite in these dry sites is *Coptotermes acinaciformis*, which builds  
 510 aboveground mounds or subterranean nests at the base of living savanna trees, especially  
 511 *Eucalyptus* species, and hollows out the inside of these trees (Werner & Prior, 2007). The  
 512 high wood density of *Eucalyptus* trees reduces wood water (Meinzer *et al.*, 2003; Sperry *et al.*,  
 513 2005) and their high stilbene content inhibits delignification of wood (Hart, 1981; Pietsch  
 514 *et al.*, 2014), which may reduce fungal decomposition. Given the extensive excavation and  
 515 nest site construction in savanna trees by *C. acinaciformis*, it makes sense that these termites  
 516 target Myrtaceae species with their dense wood which can maintain strong structures despite  
 517 hollowing. Similar patterns have been observed in timber species in the Amazon, where  
 518 termites preferentially damage species with high wood density (Eleuterio *et al.*, 2020). In  
 519 downed deadwood, results are conflicting across studies with termites preferring low density  
 520 wood (Liu *et al.*, 2015; Guo *et al.*, 2021; Tuo *et al.*, 2021), no relationship between termite  
 521 preference and wood traits (Law *et al.*, 2023), and certain termites species preferring decayed  
 522 wood (Cornelius *et al.*, 2002). It seems likely that termite preference for high or low wood  
 523 density species will depend on their ability to access the wood, whether they are solely  
 524 sampling the wood for food or also living within the wood, as well as the co-occurring  
 525 saprotrophic microbial community competing for wood as a resource. For example, variation  
 526 in termite mandible hardness, elasticity, and structure (Cribb *et al.*, 2007) allows for  
 527 differentiation in wood preference among termite species. Similarly, negative (Kirker *et al.*,  
 528 2012) and positive interactions (Hyodo *et al.*, 2003) between termites and their saprotrophic  
 529 microbial competitors should play a key role in termites' wood preference and consumption.

530

### 531 **Implications and future directions**

532 At the ecosystem scale, the rate and amount of internal stem damage is important in  
 533 determining the residence time of C in living biomass, with up to ~30% of biomass already  
 534 damaged or even missing before the stem dies. Globally, living trees in tropical savannas are  
 535 estimated to contain ~66 Gt C (Watson *et al.*, 2000; Giri *et al.*, 2005). Savannas, dominated  
 536 by *Eucalyptus* species, represent 77% of Australia's native forested area, totaling ~134

537 million ha (National Forest Inventory Steering Committee, 2019), and they are predicted to  
538 contain between 6 to 34 Mg ha<sup>-1</sup> of C in biomass of living trees (Chen *et al.*, 2003; Cook *et al.*,  
539 *et al.*, 2015). Given that most termites physically remove wood to be digested in their guts  
540 within their mounds or nests whereas microbes decay wood *in situ*, termite-driven damage  
541 represents a complete removal of C from where the wood has been produced. Across  
542 Australia, internal hollowing may be a common phenomenon as *C. acinaciformis* is widely  
543 distributed (not including Tasmania; Lee *et al.*, 2017; Wijas *et al.*, 2022; GBIF Secretariat,  
544 2023). Such widespread internal stem damage may significantly decrease the stocks of C in  
545 live trees, well before trees senesce. The effects of these early stages of wood loss, if  
546 pervasive, could speed up the rates of C loss from wood.

547  
548 A central question derived from our analysis is to what extent internal stem damage, and in  
549 particular termite-driven internal stem damage, is pervasive at a pantropical/global scale. The  
550 processes generating internal stem damage remain largely unknown at these scales. Thus far,  
551 the pursuit of this question at local and regional scales (including our study across  
552 ecosystems) suggests that the process by which wood is lost in living stems is highly variable  
553 but stem hollowing by termites is not solely an Australian phenomenon, with evidence from  
554 sites in the African and New World tropics (Apolinário & Martius, 2004; N'Dri *et al.*, 2011;  
555 Eleuterio *et al.*, 2020). Building on existing evidence for both the distribution of wooded  
556 vegetation and termites that hollow trees, an approach to better understand the prevalence of  
557 internal stem damage around the globe would be to quantify the prevalence of internal stem  
558 damage in systems where both conditions are met. Woody vegetation across the Americas,  
559 Australasia, Africa, and even southern Europe – where single and intermediate dry wood  
560 feeding termites (species that completely or partially feed on their nesting substrate *sensu*  
561 Abe, 1987) are distributed – may experience at least some degree of internal stem damage  
562 (Eggleton & Tayasu, 2001). Beyond a pantropical to global focus on the presence of internal  
563 stem damage, there is substantial scope for further empirical studies measuring the internal  
564 stem damage variation within trees (e.g., at different heights, into the crown, belowground) or  
565 quantifying the relationship between additional wood traits and termite preferences.

566  
567 Residence time of C remains a main source of uncertainty in global vegetation models  
568 (Friend *et al.*, 2014). Much recent focus has been on forest where large trees reside (e.g,  
569 tropical forest), but savanna systems comprise a large portion of the globe, may lose wood  
570 more rapidly than rainforest, and have been understudied as compared to rainforest (Austin &

571 Vivanco, 2006; Dahlin *et al.*, 2017; Vourlitis *et al.*, 2022). How much the pattern of large  
572 internal stem damage in savannas carries over into other continents remains an open  
573 question with global consequences. Recent advances in technologies such as remote sensing  
574 can now be blended with on-the-ground measurements (such as ours) to better understand the  
575 residence of C in woody plants. Long term monitoring of forest plot data are providing better  
576 estimates of AGB losses that now includes estimation of external damage (e.g., branch loss)  
577 and whole plant mortality (Zuleta *et al.*, 2023). Some allometric models, when based on  
578 harvested trees, implicitly incorporate internal stem damage into their estimates, while other  
579 methods, such as Terrestrial Laser Scanning (TLS) do not. TLS is an emerging remote  
580 sensing tool that rapidly provides highly accurate estimates of tree volumes; these are  
581 translated into AGB estimates; however where internal tree damage is large (>10%) this  
582 method can overestimate AGB (Calvert *et al.*, 2023). We suggest that combining empirical  
583 approaches outlined in this study with long term monitoring and non-invasive technologies  
584 (e.g., sonic tomograph and ground penetrating radar) will facilitate parameterization of  
585 mechanistic allometric assessments and connections to better models of C residence times.  
586 Currently, the lack of internal stem damage measures prohibits their incorporation into  
587 emerging technology estimates of forest C and biomass (but see Calvert *et al.*, 2023). A  
588 starting place would be to test the predictions on this study in other regions where tree-  
589 hollowing termites are present. Similarly, there is substantial scope to understand the effect  
590 that climatic controls of biogeochemical cycles (Delgado-Baquerizo *et al.*, 2018) may have  
591 on internal stem damage through changes in soil, wood, and decomposer communities.

592

### 593 **Conclusions**

594 We have shown that internal wood loss starts well before a tree dies which may have direct  
595 impacts on the contribution of wood degradation to C loss. Describing the variability in  
596 internal stem damage across communities, including the interaction between plants and their  
597 decomposers (microbes, termites or otherwise), requires more attention particularly in  
598 tropical communities. The proportion of C potentially lost through internal stem damage may  
599 be high, especially in arid and semi-arid systems where wood is currently assumed to be  
600 immobilized until tree senescence. The accurate measurement of forest biomass, including  
601 internal stem damage, will have implications in our understanding of the fates of C and may  
602 therefore have implications for the modelling of wood and its contribution to biogeochemical  
603 cycles in global vegetation models. Understanding the prevalence of internal stem damage  
604 across woody ecosystems with high wood feeding termite diversity and pressure may also

605 shed light on the variable relationship between wood density and mortality (Kraft *et al.*,  
606 2010) or the observed weak relationship between tree aboveground living and deadwood  
607 biomass (Palace *et al.*, 2012). Our study and others (Cornwell *et al.*, 2009; Liu *et al.*, 2015;  
608 Hu *et al.*, 2018; Guo *et al.*, 2023) suggest that, while environmental selection may determine  
609 wood density and other traits that affect when and how fast woody tissue cycles, there may be  
610 other biotic factors (such as the decomposer community) that modify the effect of wood traits  
611 on wood cycling, sometimes in unexpected ways, as shown here. As C disappears from the  
612 living tree pool, this will have direct implications for global C modeling, the extent of which  
613 remains unseen. Further, insect-driven decomposition impacts the fate of the wood in  
614 different ways to predictions based on microbial-driven decomposition (Griffiths *et al.*, 2021;  
615 Zanne *et al.*, 2022). It is therefore critical to explore the mechanisms and implications of  
616 internal stem damage in ecosystems across the globe.

617

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630

### 631 **Competing interests**

632 The authors declared no competing interests.

633

### 634 **Author contributions**

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

638

639

640 **Data availability**

641 The data that support the findings of this study are openly available in

642 <https://github.com/Zanne-Lab/stem-damage-wd>, a doi will be minted upon acceptance.

643

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## Tables

**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	<i>Eucalyptus cullenii</i>	Myrtaceae	37.9	20.05
2	Sav1	<i>Eucalyptus cullenii</i>	Myrtaceae	36.78	25.32
3	Rf2	<i>Flindersia bourjotiana</i>	Rutaceae	20.8	19.52
4	Sav2	<i>Larsenaikia ochreatea</i>	Rubiaceae	17.67	15.37
5	Sav2	<i>Corymbia clarksoniana</i>	Myrtaceae	17	22.16
6	Rf2	<i>Brombya platynema</i>	Rutaceae	14.5	10.85
7	Sc11	<i>Eucalyptus resinifera</i> subsp. <i>resinifera</i>	Myrtaceae	13.15	11.22
8	Rf2	<i>Macaranga subdentata</i>	Euphorbiaceae	11.5	15.15
9	Sc11	<i>Banksia aquilonia</i>	Proteaceae	10	12.49
10	Sav2	<i>Acacia disparrima</i> subsp. <i>calidestris</i>	Fabaceae	10	17.32
11	Sav1	<i>Melaleuca stenostachya</i>	Myrtaceae	8.67	10.26
12	Rf2	<i>Austromuelleria trinervia</i>	Proteaceae	8.33	7.37
13	Rf2	<i>Medicosma fareana</i>	Rutaceae	7.8	13.01

14	Sc11	<i>Allocasuarina torulosa</i>	Casuarinaceae	7.69	8.6
15	Rf1	<i>Castanospora alphandii</i>	Sapindaceae	5.33	5.51
16	Rf1	<i>Daphnandra repandula</i>	Atherospermataceae	3.67	4.04
17	Rf2	<i>Carnarvonnia araliifolia</i>	Proteaceae	1.67	4.08
18	Rf1	<i>Syzygium trachyphloium</i>	Myrtaceae	1.67	2.89
19	Rf2	<i>Ormosia ormondii</i>	Fabaceae	0.33	0.58
20	Rf2	<i>Licuala ramsayi</i>	Areaceae	0	0

## Figure legends

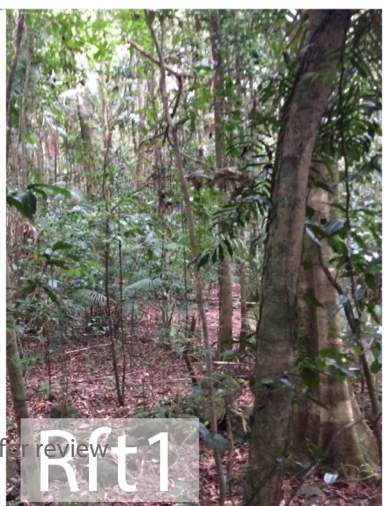
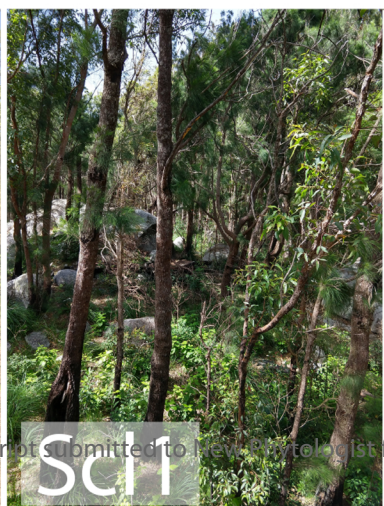
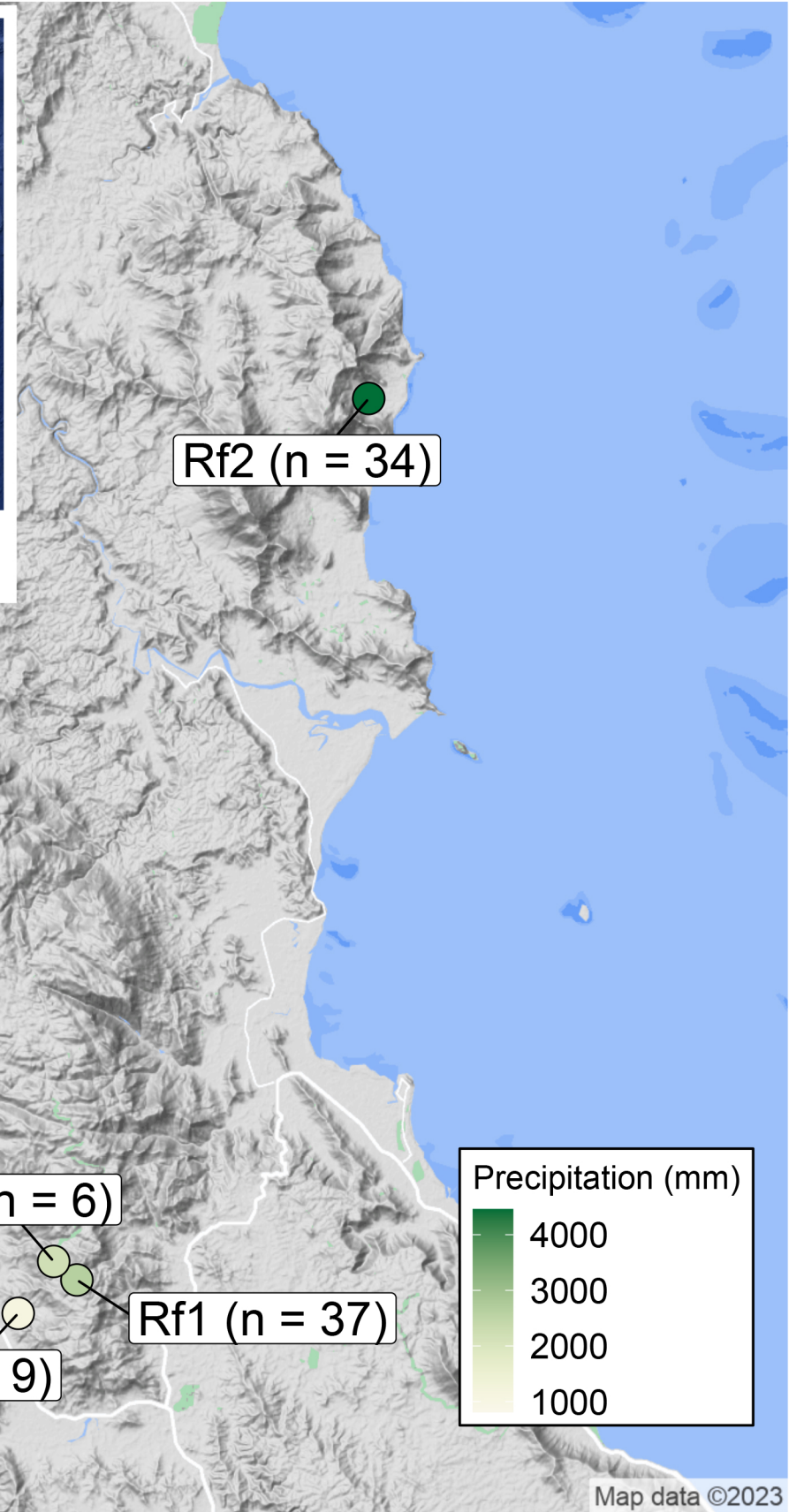
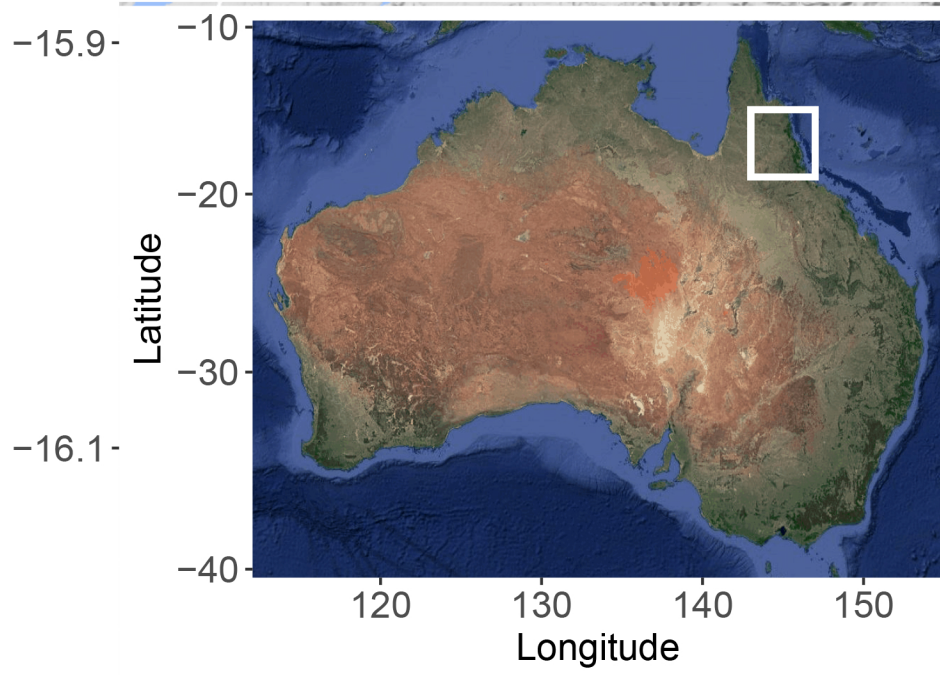
**Figure 1.** Locations of the five sites in the study area in Far North Queensland, Australia and number of species. From driest to wettest: Sav1 (Pennyweight savanna), Sav2 (Station Creek savanna), Scl1 (Mt. Lewis sclerophyll), Rft1 (Mt. Lewis rainforest), and Rft2 (Daintree rainforest). Species number appear inside parenthesis.

**Figure 2.** Variation in A. percentage internal stem damage, B. tree diameter at breast height (DBH, in cm), C. wood density ( $\text{g m}^{-3}$ ) across the study sites and D. termite pressure expressed as percentage of termite damage in 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.

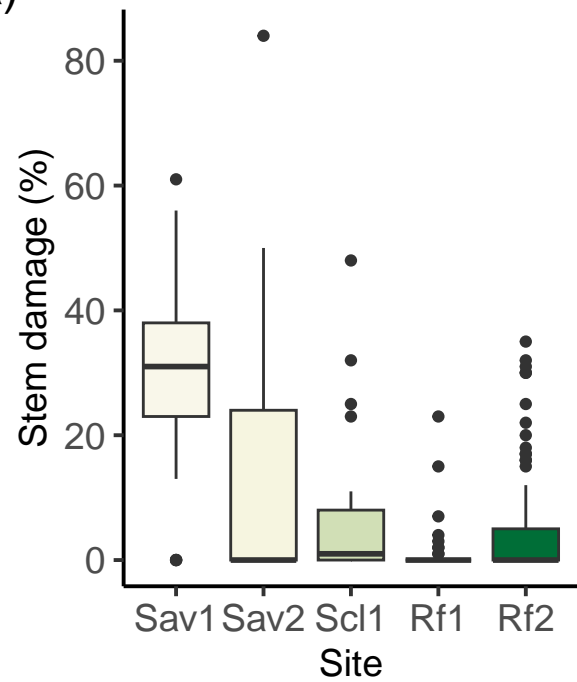
**Figure 3.** Marginal effects plots of probability of internal stem damage of individual trees (dots) adjusted for low (blue), intermediate (orange) and high (bright red) wood density ( $\text{g m}^{-3}$ ) across A. precipitation (mm) and B. termite pressure (percentage termite damage in downed deadwood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

**Figure 4.** Phylogeny of sampled tree stems with squares indicating species wood density ( $\text{g m}^{-3}$ , 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).

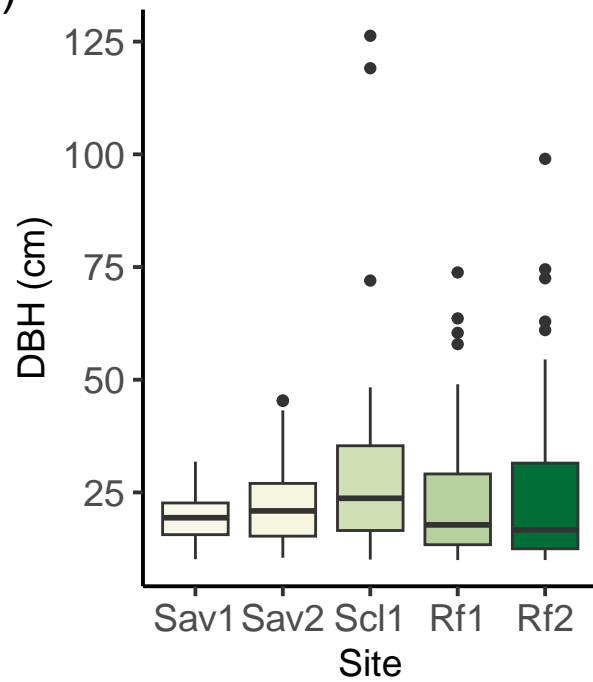
**Figure 5.** Aboveground biomass estimates per site ( $\text{Mg ha}^{-1}$ ). Panel A shows percentage aboveground biomass damage assuming constant damage (gray) and  $\pm 50\%$  change in internal stem damage (dashed lines). Aboveground biomass estimates (Panel B) and only stem biomass estimates (Panel C) using traditional allometric equations to estimate biomass for each site (i.e., no damage, white), constant damage (gray),  $\pm 50\%$  change in internal stem damage (dashed lines).



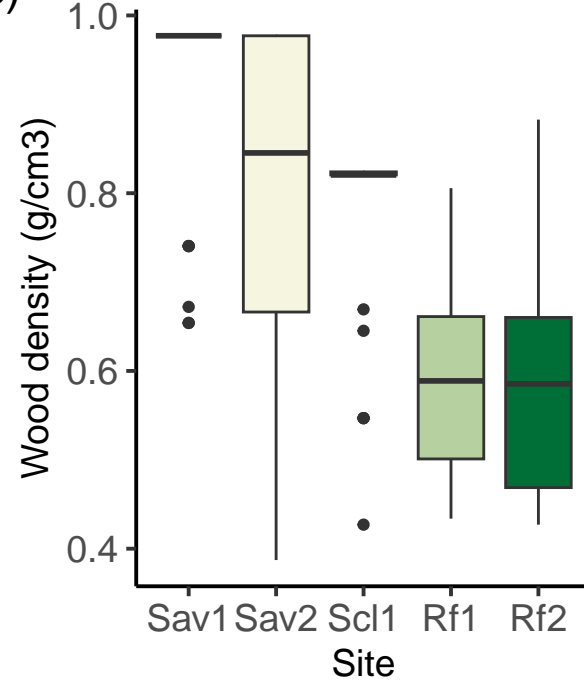
(a)



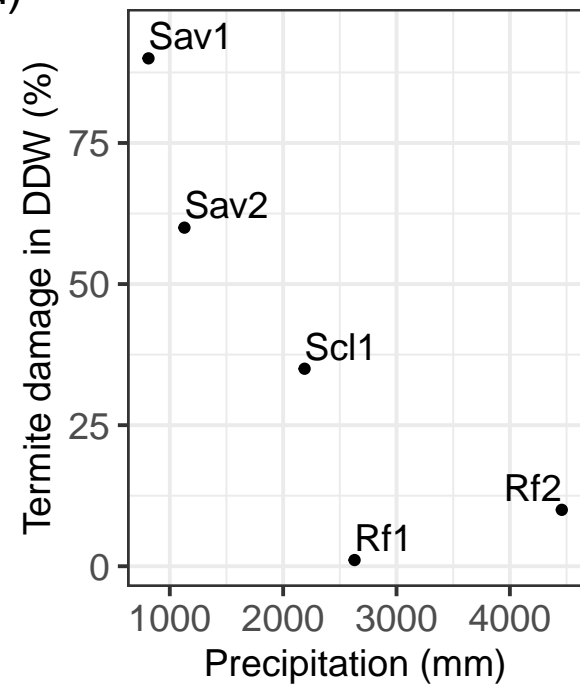
(b)



(c)



(d)



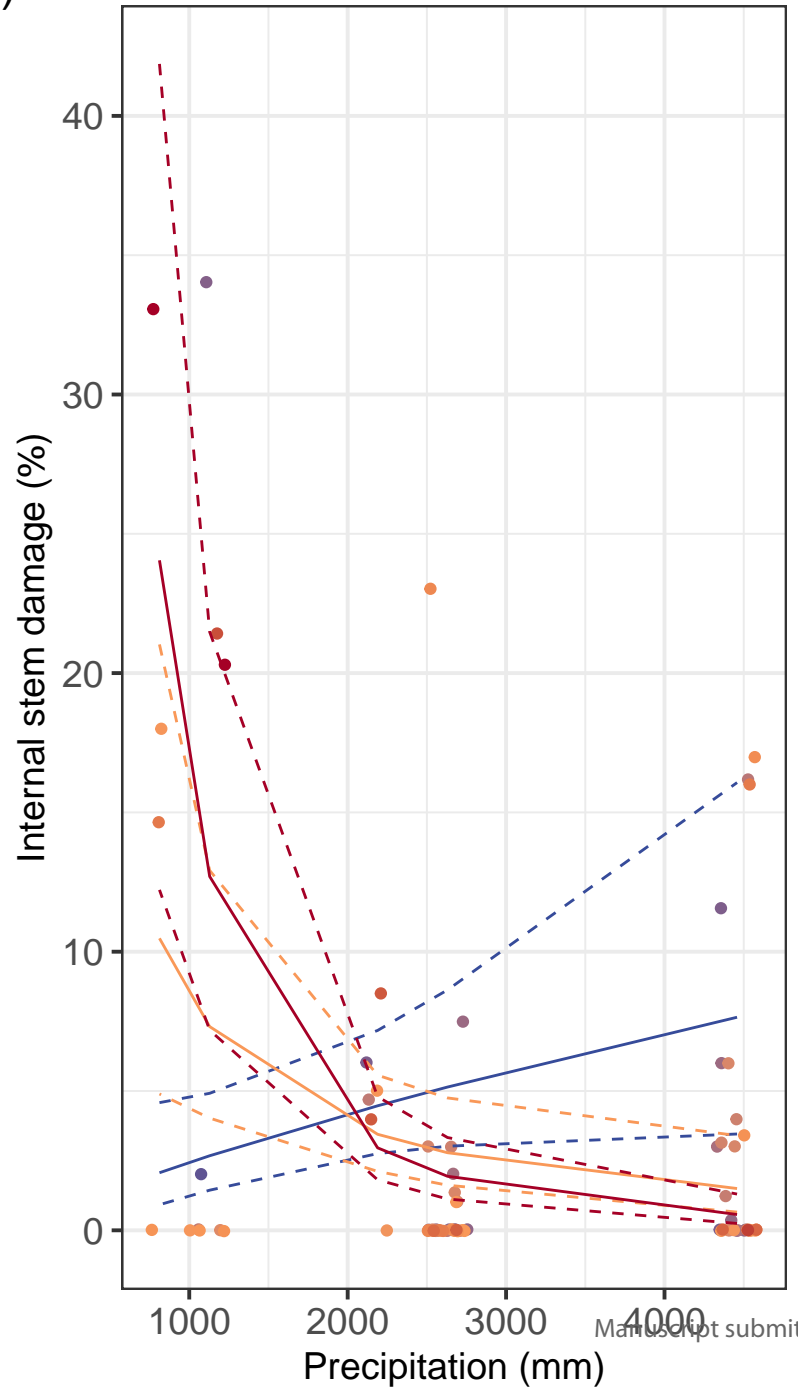
Precipitation (mm)

1000 2000 3000 4000

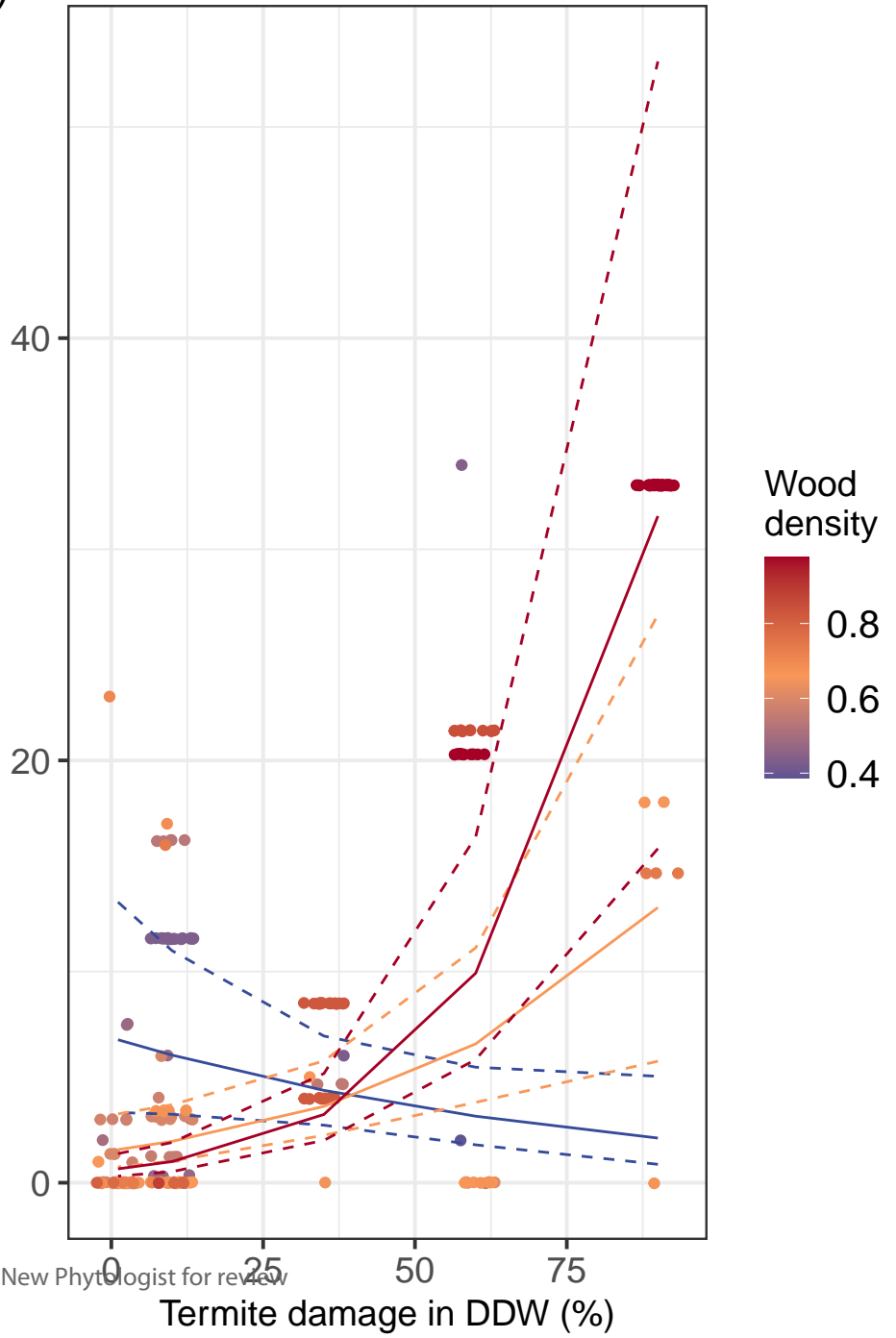
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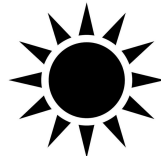


(a)

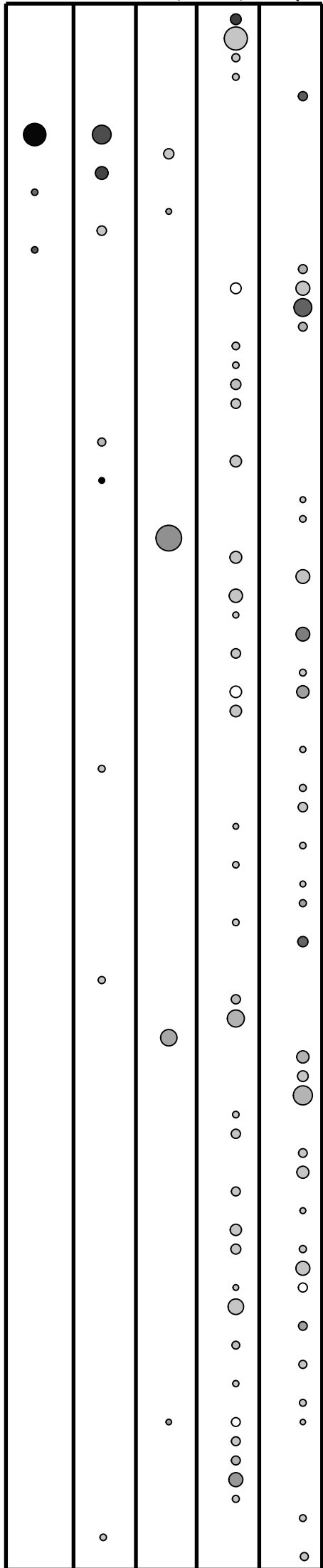
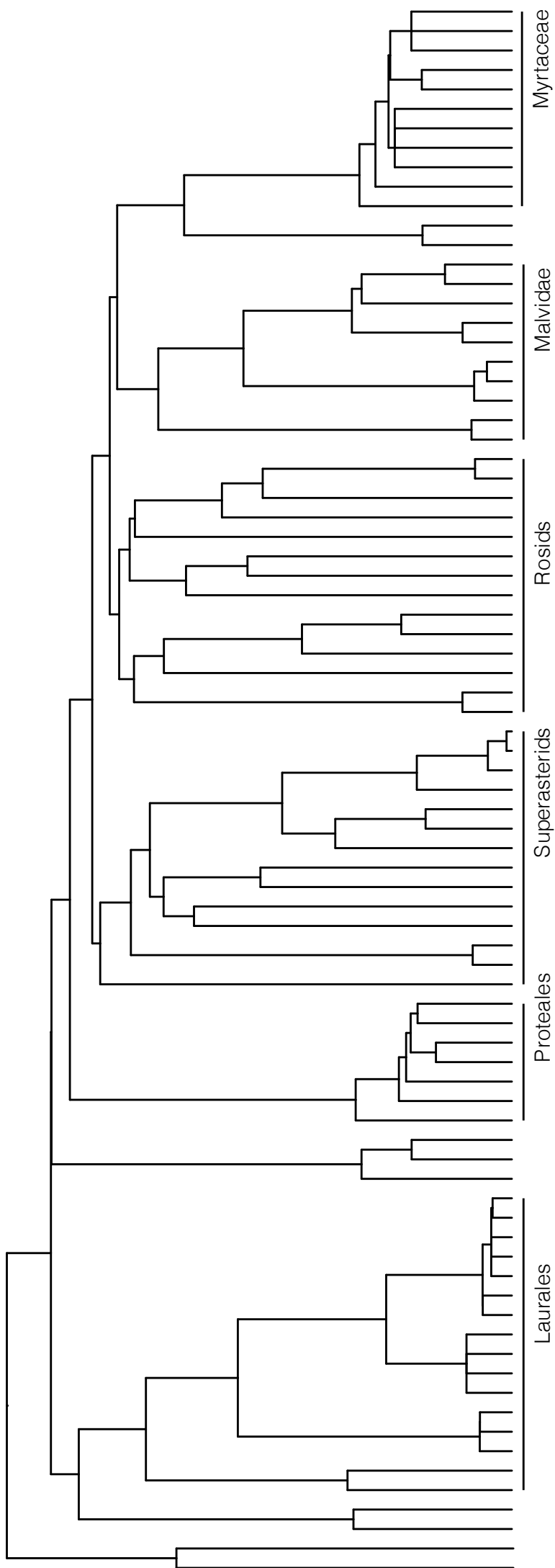


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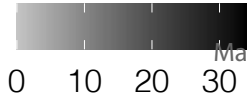




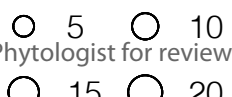
Sav1 812mm  
 Sav2 1129mm  
 Scl1 2189mm  
 Rf1 2630mm  
 Rf2 4458mm



Percentage damage



Aboveground biomass



Wood density

