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Stem Decay in Live Trees: Heartwood Hollows and Termites in Five Timber Species in Eastern Amazonia

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Abstract: *Research Highlights:* Tree size and wood characteristics influenced the susceptibility of five Amazonian timber tree species to heartwood decay and colonization by termites. Termites occurred in the heartwoods of 43% of the trees, with *Coptotermes testaceus* the most abundant species. *Background and Objectives:* Hollows and rotten cores in the stems of living trees have ecological and economic impacts in forests managed for timber. The decision on whether to cut or maintain hollow trees in such forests must account for the susceptibility of different tree species to decay. We investigated tree and wood characteristics of living trees of five commercial timber species in the eastern Amazon that influenced the likelihood of heartwood decay and the occurrence of termite nests inside the rotten cores. *Materials and Methods:* We used Pearson's correlations and one-way analysis of variance (ANOVA) to explore relationships among tree basal area and hollow area. We used principal components analysis (PCA) to analyze the variation of wood anatomical traits, followed by a linear regression to explore the relationships between PCA scores, and heartwood hollow area. We used a logistic model to investigate if the probability the occurrence of colonies of *C. testaceus* inside tree cores varied with tree and species characteristics. *Results:* Heartwood hollow areas increased with stem basal area. Larger hollows were more likely to occur in species with higher vessel and ray densities, and smaller diameter vessels. Termites occurred in the hollows of 43% of the trees sampled, with *C. testaceus* the most common (76%). The probability of encountering termite nests of *C. testaceus* varied among tree species and was positively related to wood density. *Conclusions:* This study shows that given the increased likelihood of stem hollows and rotten cores in large trees, tree selection criteria in managed tropical forests should include maximum cutting sizes that vary with the susceptibility of different tree species to stem decay.

Keywords: heartrot; hollow trees; reduced-impact logging; tropical timber; wood anatomy; *Coptotermes*

1. Introduction

Stem hollows formed by wood decay in living trees are critical for many species, especially cavity-nesting and roosting reptiles, birds, and mammals [1], but are a concern for timber stand managers [2]. Given that in the managed tropical rain forests of eastern Amazonia, trees with hollows can account for up to 30% of trees of commercial species and harvestable size [3], this phenomenon is of both ecological and economic importance. From an economic perspective, forests in which trees with unsound stems are frequent are less valued for their timber [3,4] and estimates of harvestable volumes based on basal areas will be wrong [5,6]. During harvests, hollow trees are often felled in error or in the hopes of finding at least one sound marketable log; their subsequent abandonment in the forest or on log decks often accounts for a substantial proportion of the carbon emissions from logging [2]. The coarse woody debris generated will then increase fuel loads, and consequently enhance forest flammability [7,8]. Even if uncut, high carbon emissions may be expected from forest with abundant hollow trees due to their susceptibility to breakage [9–11] and high mortality rates [12].

Despite the importance of understanding the causes of wood decay in living trees, the few studies on hollow trees in Amazonia focused on their influence on estimates of timber yields and forest biomass [4,5]. Studies conducted in other tropical forests report spatial aggregations of trees with hollow or rotten cores related to patterns of variation in tree characteristics and environmental conditions [6]. Furthermore, clusters of trees with stem or root damage caused by events such as fire or logging [13–15] may favor local pathogenic infections and lead to aggregated distributions of hollow trees. The spread of these infections depends on landscape features, spatial patterns of vegetation, and the existence and abundance of susceptible hosts [16].

The spread of wood decay and development of stem hollows in living trees is slow, but so are the growth rates of many tropical trees, particularly those with medium to high density wood [17]. In a study of eight tree species in old-growth subtropical montane evergreen forest in south-east China, for instance, stem hollows expanded radially at 2.0 mm year^{-1}, marginally less than the rate of radial tree growth, but vertically eight times faster [18]. Decay-causing organisms usually gain access to the heartwood of living trees through sapwood-penetrating wounds [19,20]. Tree defenses, which can change as trees age as well as with species and environmental conditions, mediate the rate of expansion of decay in living trees [12,21–23]. Additionally, wood traits such as high density and vessels with small lumen affect the availability of moisture and oxygen contents and provide mechanical barriers to the spread of decay [18,24]. Much wood decay is caused by fungi, but termites also play a role because, thanks to a symbiotic association with microbes, several species share with some fungi the ability to digest wood in living trees [25]. Evidence for this ability is the presence of active and abandoned termite colonies in hollow cores of living trees [26–28].

Some species of termites are known to preferentially feed on wood in advanced stages of decay in which nitrogen contents are elevated and toxic defense substances were rendered ineffective by wood-decay fungi [22,29,30]. Results from bioassays show that some species of subterranean termites, such as *Reticulitermes flavipes*, *Coptotermes formosanus* and *C. gastroi*, distinguish wood extractives from different species and select for particular wood qualities [31–33]. Wood moisture content and temperature may also affect the probability of termite species to colonize and survive inside living trees [34,35].

We investigated the termites that colonized the heartwood of living trees of five commercial timber tree species in the eastern Amazon. We examined how tree dimensions and wood traits influenced the likelihood of heartwood decay. Finally, we collected and identified the termite species occurring in heartwood hollows to assess the relationship between tree characteristics and species-specific termite distributions.

2. Materials and Methods

2.1. The Study Site

Fazenda Rio Capim in Paragominas Municipality, Para, Brazil (2°25′—4°09′ S, 46°25′—48°54′ W) has a tropical moist climate with a well-defined dry season, average annual precipitation of 1766 mm, and an average temperature of 27.2 °C [36]. Soils classified as yellow latosols prevail in the flat to slightly undulating terrain [37,38]. The area is covered by tropical dense moist forest [39], owned by CIKEL Brasil Verde S.A., and managed for timber using reduced-impact logging techniques (RIL). RIL practices consist of carefully planning all aspects of timber extraction to diminish the deleterious impacts of logging on the residual forest [40]; that the concession hosts the training center of Instituto Floresta Tropical makes us confident that RIL practices were indeed utilized in our study area.

Timber extraction is carried out in forest management units (UTs) of approximately 100 ha. One year prior to the harvests, all commercial timber trees ≥45 cm of diameter at breast height (DBH) are identified and mapped, but the minimum cutting DBH was 55 cm. Harvest trees suspected of being hollow or heartrotted are usually tested immediately prior to felling by inserting a chainsaw vertically into the trunk at about 50 cm from the ground. Trees with hollows or rotten cores that exceed 30 cm in diameter (i.e., approximately half of 65 cm bar length) are considered non-marketable and are not supposed to be felled. Although some hollow trees may still be erroneously felled, especially those with large DBHs in which rotten cores are not easily accessed from outside, use of this technique helps minimize stand damage, carbon emissions, and habitat loss.

2.2. Data Collection

In an area of 253 ha, we sampled 30 recently felled trees with hollow stems or rotten cores of *Manilkara elata* (Allemão ex Miq.) Monach, 28 of *M. bidentata* (A. DC.) A. Chev. (both Sapotaceae), 30 of *Pseudopiptadenia psilostachya* (DC.) G.P. Lewis & M.P. Lima (Fabaceae), 8 of *Dinizia excelsa* Ducke (Mimosaceae), and 20 of *Astronium lecointei* Ducke (Anacardiaceae). We selected these species on the basis of their abundance in the study site and because loggers reported that they were prone to heartrots. The selected species vary in wood anatomy and chemical defenses including three with sapwood latex (*Manilkara* spp. and *A. lecointei*). All felled trees of these species were sampled in the same area to minimize environmental heterogeneity that could influence tree susceptibility to decay. Only trees >10 m from the nearest conspecific were sampled to assure independence. Sample sizes were small for *D. excelsa* and *A. lecointei* because they occurred at low densities and were infrequently hollow.

In a selectively logged forest adjacent to the study site [3], forest inventory data indicate that, depending on species, 2.7–21.4% of trees >45 cm DBH were judged non-marketable due to the presence of stem hollows or heartrots (Table 1) [41]. An additional 28.5–36.6% of felled trees presented hollows or rotten cores that were not diagnosed during forest inventories (Table 1).

Table 1. Numbers of trees with stem hollows (cavities, hollow or rotten cores) detected during forest inventories, and the additional number of felled trees with hollows not detected by inventory crews. In parenthesis are the percentages of the total number of trees inventoried or felled for each species.

Tree Species	Number of Trees Inventoried	Number of Hollow Trees (%)	Number of Trees Felled	Number of Felled Hollow Trees (%)
Astronium lecointei	563	36 (6.4)	69	25 (36.2)
Dinizia excelsa	673	144 (21.4)	31	11 (35.5)
Pseudopiptadenia psilostachya	1332	153 (11.5)	27	7 (25.9)
Manilkara elata	3967	63 (2.7)	528	160 (30.3)
Manilkara bidentata	2298	144 (3.6)	165	47 (28.5)

In August and September 2008, 1–5 days after felling and before the logs were yarded from the forest, trunk diameters, and horizontal extents of heartwood hollows were measured for each felled tree 50 cm from the ground. Hollow areas were calculated from two diameter measures using the formula for an ellipse; heartwood that was degraded but not hollow was not included in this analysis.

To measure anatomical traits and wood density, two samples of 200–300 cm^3 of sound heartwood 5–10 cm from the sapwood were collected from opposite sides of the hollows. From these wood sections, five 2 × 2 × 2 cm samples were extracted and used to measure wood density (WD) by water displacement ($N = 3$ samples/tree). Wood samples were oven-dried at 101–105 °C for 72 h or until constant weight, measured at 0.01 g precision. Histological analysis of wood anatomy was performed on transverse sections ($N = 5$ sections/species; $N = 10$ trees/species for all tree species but *D. excelsa*, with $N = 8$ trees) after at least 24 h in a 1:1 solution of glycerin and distilled water 24 h ($N = 5$/species). Wood was sectioned using a sliding microtome and permanent slides were prepared to measure maximum vessel lumen diameter (N = 5–10 vessels/section), vessel density (number of vessels/mm^2) within fields of 2 mm^2, ray width at its non-dilated extent, and distance between adjacent rays measured along 2 mm transects.

Termites forming colonies inside heartwood hollows of the 116 selected trees were collected 1–5 days after logging and identified to species [42,43]. Termite samples were stored at Instituto Nacional de Pesquisas da Amazônia (INPA).

2.3. Data Analysis

Pearson's correlations were used to explore relationships among tree basal area and hollow area. To meet normality assumptions, square-root transformations were applied to hollow area data. For the four tree species with $N \geq 20$ trees sampled, interspecific variation in hollow and tree basal areas were compared using one-way analysis of variance (ANOVA) followed by Tukey HSD post-hoc comparisons.

Relationships among wood anatomical traits were explored using principal components analysis (PCA) with varimax rotation. Only principal components (PCs) with eigenvalues ≥ 1 and variables loading ≥ $|0.35|$ were reported. Linear regression was used to explore the relationships between PCA scores, and heartwood hollow area. Among species differences in traits were investigated using ANOVA followed by Tukey HSD post-hoc comparisons.

A logistic model of tree characteristics was created to investigate the occurrence of colonies of the most abundant termite species (*Coptotermes testaceus* L.) in the sampled trunks. Tree characteristics used were species, wood density, and interactions among these variables, with data transformed as needed to meet normality assumptions. The best-fit model was selected based on log-likelihood comparisons of models produced by backward elimination of non-significant variables. Log-likelihood differences were tested using chi-squared tests at $\alpha = 0.05$. All analyses were performed with SAS Software 9.2 [44].

3. Results

Basal areas of sampled trees varied among species ($F_{3,105} = 27.51$, $p < 10^{-4}$), while heartwood hollow areas were similar among the four species with ≥ 20 individuals sampled ($F_{3,105} = 2$, $p = 0.12$). *Manilkara elata* trees were larger than *M. bidentata*. *Dinizia excelsa* was not included in the analyses due to its small sample size, but generally had larger hollows (up to 60% of the stem cross section with an average of approximately 31%) than the other four tree species (10–23%; Figure 1). For the four tree species with $N \geq 20$ individuals sampled, heartwood hollow area increased with overall stem basal area ($r = 0.46$, $p < 10^{-3}$; Figure S1).

The five tree species sampled differed only moderately in heartwood anatomy (Table 2). *Dinizia excelsa* and *A. lecointei* had the largest vessel lumen diameters (162.4 and 151.8 µm, respectively) and low vessel densities (5.0 and 7.9 vessels/mm^2, respectively; Figures S5 and S6). *M. bidentata* had the lowest average vessel lumen diameter (111.4 µm) and the highest vessel density (15.6 vessels/mm^2; Figure S3). Average ray density ranged from 5.86 in *D. excelsa* to 10.5 rays/mm^2 in *M. bidentata*. Average distance between rays was 20.7–23.4 µm for all species except *P. psilostachya*, in which rays were approximately 11.7 µm apart (Figure S4). All species produce high density wood, with a range of from 0.83 g/cm^3 in *P. psilostachya* and *A. lecointei* to 0.94 g/cm^3 in *D. excelsa*.

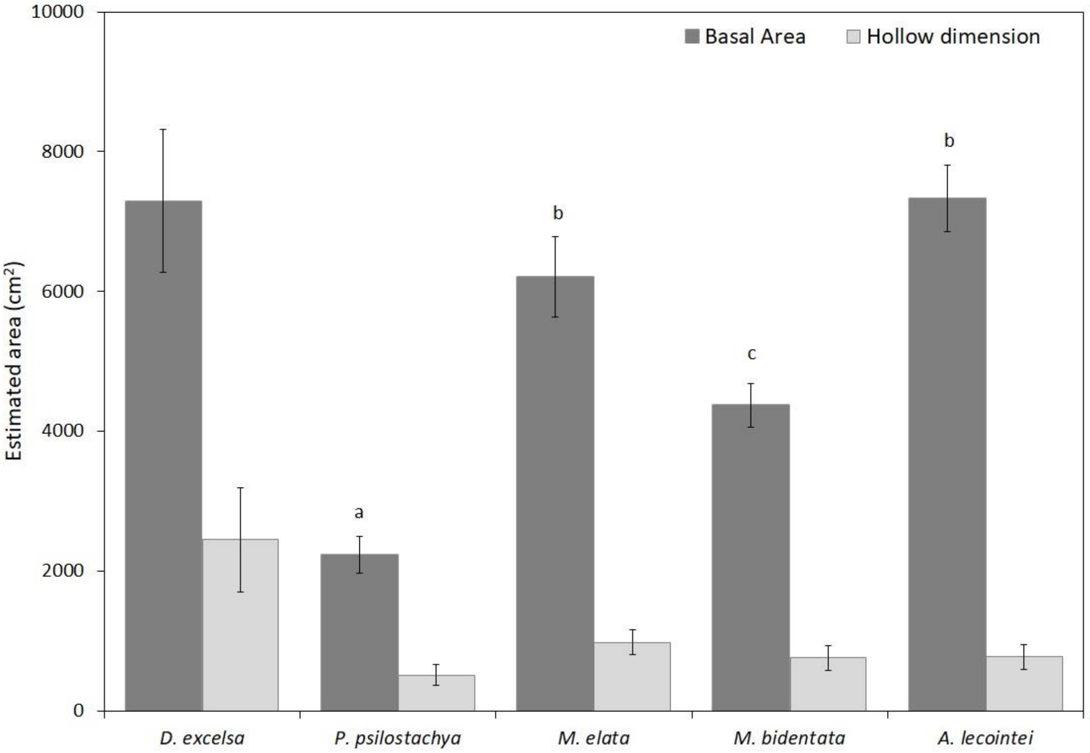

Figure 1. Tree stem basal area and area of stem hollows by tree species measured at 50 cm from the ground ($N = 8$ for *D. excelsa*, $N = 30$ for *P. psilostachya* and *M. elata*, $N = 28$ for *M. bidentata*, and $N = 20$ for *A. lecointei*). Letters indicate differences at $p < 0.05$. Statistical comparisons included all species but *D. excelsa*.

Table 2. Heartwood anatomical traits (mean ± SD) for the five tree species studied. Letters indicate differences at $p < 0.05$.

	N	Number of Vessels/mm^2	Maximum Vessel Lumen Diameter (µm)	Number of Rays/mm^2	Inter-Ray Distance (µm)	Wood Density (g/cm^3)
D. excelsa	8	5.01 ± 2.20 ^{a}	162.37 ± 27.19 ^{a}	5.86 ± 0.71 ^{a}	23.45 ± 4.18 ^{a}	0.94 ± 0.01 ^{a}
P. psilostachya	10	11.62 ± 2.84 ^{b,c}	127.68 ± 10.94 ^{b}	8.98 ± 1.29 ^{b}	11.73 ± 1.65 ^{b}	0.83 ± 0.06 ^{b,d}
M. elata	10	10.27 ± 2.27 ^{b,d}	123.60 ± 17.77 ^{b}	9.39 ± 1.23 ^{b}	23.46 ± 3.63 ^{a}	0.91 ± 0.02 ^{a,c}
M. bidentata	10	15.58 ± 5.94 ^{b}	111.36 ± 10.94 ^{b}	10.50 ± 1.25 ^{b}	20.68 ± 3.37 ^{a}	0.89 ± 0.05 ^{a}
A. lecointei	10	7.90 ± 1.33 ^{a}	151.82 ± 13.45 ^{a}	8.69 ± 1.74 ^{b}	22.82 ± 3.92 ^{a}	0.83 ± 0.07 ^{b}

In the PCA of wood characteristics, *Manilkara* spp. (Figures S2 and S3) and *A. lecointei* (Figure S5) formed a diffuse cluster due to intermediate ray and vessel densities, and vessel lumen diameters. The first two principal components (PCs) explained 63.80 and 25.67% of the variation in heartwood anatomical traits, respectively (Figure 2). PC1 was negatively associated with ray and vessel densities, and positively associated with maximum vessel lumen diameter. PC2 was positively associated with both distance between rays and wood density (Figure 2).

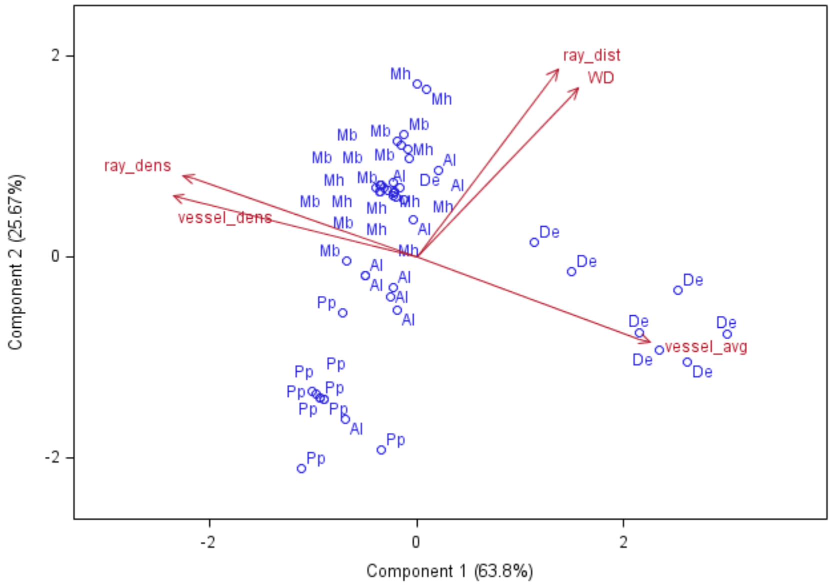

Figure 2. Principal components analysis of wood anatomical characteristics for *D. excelsa* (De; $N = 8$), *P. psilostachya*, *M. elata*, *M. bidentata*, and *A. lecointei* (respectively Pp, Mh, Mb, and Al; $N = 10$). Variables considered were number of vessels/mm^2 (vessel_dens), number of rays/mm^2 (ray_dens), average distance between rays (ray_dist), average vessel maximum lumen diameter (vessel_avg), and wood density (WD). Values in parenthesis correspond to the variance (%) explained by each principal component.

PC1 scores were negatively related to hollow area (Table 3), which suggests that larger heartwood hollows were more likely in trees with higher vessel and ray densities, and smaller diameter vessels. Hollow size was also positively related to tree size (Table 3). Additionally, analysis of the residuals suggested that the model results were strongly influenced by the presence of *D. excelsa*, a species with large vessels, low ray and vessel densities, and large hollows.

Table 3. Regression with the two most important principal components (PC) for heartwood anatomical traits on hollow area.

	d.f.	**Estimate**	**SE**	***t*-Value**	**$p > \|t\|$**
Intercept	1	253.63	392.74	0.64	0.52
Tree Basal Area	1	0.14	0.07	2.10	0.04
PC1	1	−391.46	174.18	−2.25	0.03
PC2	1	206.55	165.46	1.25	0.22

Termites colonies occupied the stem hollows of 50 (43%) of the 116 trees sampled. Approximately 76% of the termite colonies encountered were of *Coptotermes testaceus* (Table S1). This species most commonly formed colonies in heartwood hollows of *M. elata* (Figure 3). The logistic model used to predict the presence of *C. testaceus* showed that the probabilities of encountering termite colonies varied among the four tree species sampled with $N \geq 20$ trees ($F_{3,104} = 3.03$; $p = 0.03$) and was positively related to wood density ($F_{1,104} = 5.42$; $p = 0.02$; Table 4). The likelihoods of encountering *C. testaceus* colonies were respectively highest and lowest for the two congeneric species, *M. elata* and *M. bidentata* (Figure 3).

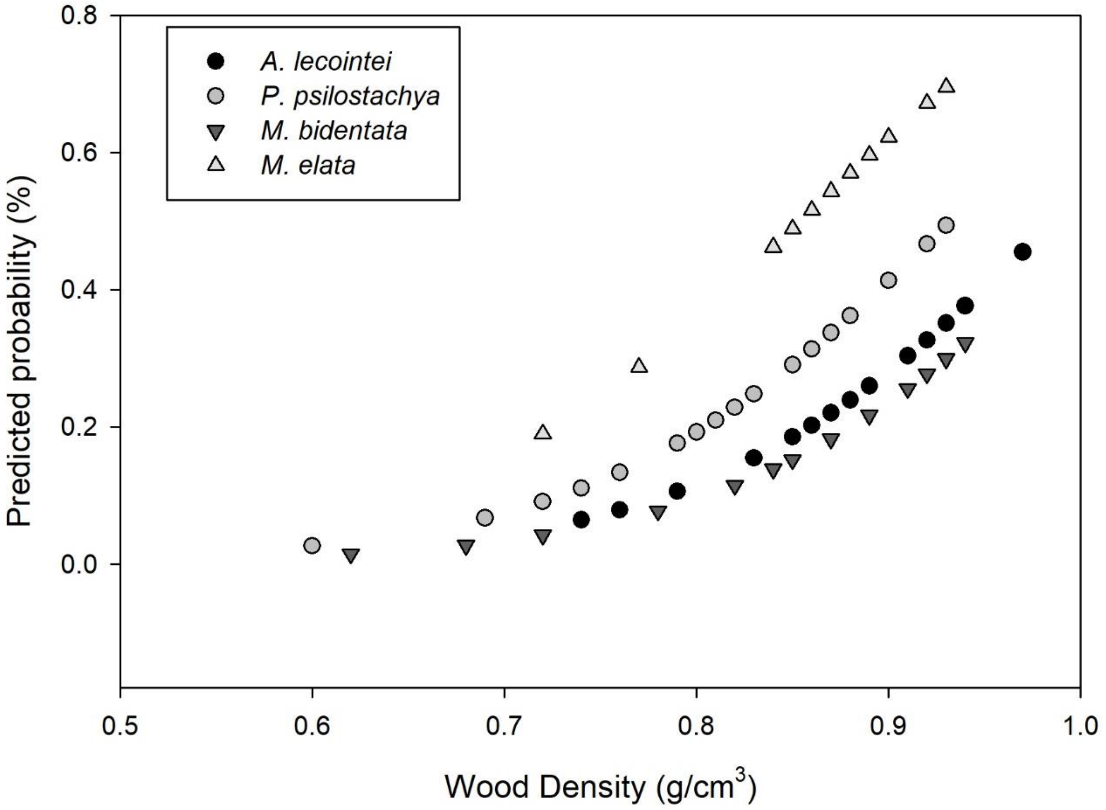

Figure 3. The probability of a tree hosting a *Coptotermes testaceus* colony as a function of wood density. Samples sizes were as follows: *P. psilostachya* and *M. elata* (*N* = 30), *M. bidentata* (*N* = 28), and *A. lecointei* (*N* = 20).

Table 4. Logistic regression estimates for the presence of *Coptotermes testaceus* colonies in heartwood hollows of the four tree species with *N* ≥ 20 individuals sampled: *P. psilostachya* and *M. elata* (*N* = 30), *M. bidentata* (*N* = 28), and *A. lecointei* (*N* = 20).

	Estimate	**SE**	**d.f.**	***t*-value**	***p* > |t|**
Intercept	−10.1030	3.9592	104	−2.55	0.0122
Species					
P. psilostachya	0	-	-	-	-
M. elata	0.8493	0.5918	104	−1.19	0.2365
M. bidentata	−0.8247	0.6927	104	1.44	0.1542
A. lecointei	−0.5888	0.7160	104	−0.82	0.4128
WD	10.8358	4.6548	104	2.33	0.0219
−2 Log Likelihood	120.97				
Pearson χ^2/d.f.	0.98				

4. Discussion

Heartwood hollow areas increased with stem basal area but were similar among the four species with ≥20 individuals sampled. Larger hollow areas were more likely to occur in species with higher vessel and ray densities, and smaller diameter vessels. Termites occurred in the stem hollows of 43% of the trees sampled; approximately 76% of the infested trees hosted *Coptotermes testaceus*. The probability of encountering termite nests of *C. testaceus* varied according to the tree species, was positively related to wood density, and was highest and lowest in *Manilkara elata* and *M. bidentata*, respectively. Large and old trees perform diverse roles in forest ecosystems, such as assisting the distribution of water and nutrients in the soil and providing wildlife habitat [1]. In forests managed for timber, such trees are often harvested. The results of this study suggest that tree selection criteria should consider tree species' susceptibility to development of stem hollows. The fact that heartwood hollow area increased with tree stem basal area may indicate that a maximum DBH (besides the minimum DBH already applied) should be considered when selecting trees for logging. Setting a DBH range may assist in diminishing the loss of tree cavities that are so important for biodiversity [45] and reduce economic losses due to wasteful felling [4].

During their ontogeny, trees are often damaged and suffer environmental stresses that weaken their defenses and increase their vulnerability to attacks by pathogens and herbivores [46]. Rotten tree cores may confer benefits to the living tree, such as soil fertilization [47]. Heartwood decay may also represent a low cost to the tree compared to the costs of wood protection [48]. Wood decay in living trees is a slow process in which a variety of organisms [49], many of which are thought to be saprophytes, benefit from periods of weakened defense during which they can successfully avoid the induced defenses produced by living sapwood tissues and colonize and break down constitutive phenolic compounds in heartwood tissues [21,50]. Decay organisms more often succeed in colonizing the heartwood of larger trees at least partially because such trees must invest substantial energy in maintaining their biomass, thereby having fewer resources to invest in inducible and constitutive defenses [51,52]. That the larger trees are also often older, and therefore were exposed to damage and decay organisms more years, also needs to be considered.

Heartwood anatomical traits in the five tree species analyzed were correlated with the incidence of heartwood decay. Stem hollows were larger in trees with high densities of vessels and rays, and large diameter vessels. These results partially support previous studies that showed that small vessels and low vessel and ray densities slow wood degradation apparently by slowing the growth of decay organisms through two of the most commonly used routes of wood colonization, vessels and parenchymatous tissues [53–55]. The observed relationships between anatomical traits and hollow areas might be partially explained by ontogenetic changes in wood anatomy insofar as previous research demonstrated that with tree size, wood density and vessel diameter increase while ray width and ray and vessel densities decrease [56–58].

Termites were present in heartwood of almost half of the trees sampled, with *Coptotermes testaceus* the most common species. This species was previously reported to be associated with heartwood hollows in Amazonian forest trees [42,43], but at low frequencies [26]. Species of *Reticulitermes*, another member of the Rhinotermitidae, and other species of *Coptotermes* are reportedly common colonizers of the heartwoods of urban trees and trees in forests subjected to prescribed burns [59,60]. The Formosan subterranean termite, *C. formosanus*, which is considered an urban pest, for instance, was present in 37 and 52% of forest fragments near two urban areas in Southeastern USA [28]. *Coptotermes testaceus* is also a minor pest of eucalyptus, cassava and rubber tree crops in several South American countries including Brazil [61]. Although we did not aim to assess the pest status of *C. testaceus*, this species displays the three characteristics that authors of reference [62] name as shared by invasive termite species: it eats wood, nests in wood, and produces reproductive propagules. The fact that this species was so abundant in commercial trees in our study site reinforces the importance of avoiding its introduction elsewhere in the world.

Given that *C. testaceus* reduces timber yields but helps maintain forest biodiversity by contributing to the formation of hollow cores and tree cavities, more attention should be paid to its impacts on tropical forests. Cavities in living and dead-standing trees, like those opened by termites, provide nesting and roosting sites for numerous species of birds, reptiles, mammals, and invertebrates [1,63–66]. In contrast, it should be noted that in a forest in northern Australia, termites blocked almost half the tree hollows identified during ground surveys, thereby reducing the availability of cavities for several threatened mammal species [67].

Subterranean termites in the genus *Coptotermes* build their nests in the soil and infest sound wood in direct contact with the ground [68]. In our study area, *C. testaceus* nests were more frequent in *M. elata* heartwood than in *M. bidentata*, a congeneric species with which it shares anatomical features and the production of latex by the sapwood. This finding suggests that this termite species differentiates among tree species, presumably on the basis of wood extractives, as observed in bioassays with *Zootermopsis nevadensis* [69]. The other species that also produced latex, *A. lecointei*, was generally not inhabited by termites. Nutritional qualities of wood may also influence tree selection by termites [33,70]. Higher cellulose content in heartwood was possibly related to *C. testaceus* preference for trees with higher wood density [34].

5. Conclusions

Heartwood decay increased with tree size for the studied commercial timber species in eastern Amazonia. Heartwood anatomical traits of vessel lumen diameter and vessel and ray densities explained much of the among-species variation in hollow size. Further studies on heartwood decay and wood properties will benefit from larger samples sizes and from the selection of tree species with a wider variation in wood traits. Our results indicate that tree species characteristics affect their susceptibility to wood-decay organisms and that hollow dimensions increase with tree size, which indicates that older and larger trees are particularly susceptible. For this reason, we recommend that, to diminish the loss of cavity trees and associated biodiversity impacts, avoidable stand damage, and carbon emissions, there should be an upper size limit on trees allowed to be felled. For the sake of efficiency, the retained large trees might be categorized as seed trees during forest inventories, which would reduce the time spent testing them for hollow or rotten cores. More studies are required to set species-specific limits that reflect their size-specific susceptibility to decay. Given that *Coptotermes testaceus* presents invasive abilities and is considered a pest of urban forests and diverse crops in its native range, special attention should be paid to the handling of wood in which there is evidence for the presence of this species. Finally, more research is needed on the factors that control the distribution and abundance of the cavity-excavating organisms that are so important to forest ecology and the profitability of forest management.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/11/10/1087/s1, Figure S1. Variation in A) stem hollow area and B) percent hollow area by tree basal area for the four tree species with $N \geq 20$ individuals sampled (*P. psilostachya*, *M. elata* ($N = 30$), *M. bidentata* ($N = 28$), and *A. lecointei* ($N = 20$)), Figure S2: Wood anatomy of *Manilkara elata* (Sapotaceae). Scale bar = 200 µm, Figure S3: Wood anatomy of *Manilkara bidentata* (Sapotaceae). Scale bar = 200 µm, Figure S4: Wood anatomy of *Pseudopiptadenia psilostachya* (Fabaceae). Scale bar = 200 µm, Figure S4: Wood anatomy of *Astronium lecointei* (Anacardiaceae). Scale bar = 200 µm, Figure S5: Wood anatomy of *Dinizia excelsa* (Mimosaceae). Scale bar = 200 µm, Table S1: Termite species sampled in heartwood hollows of the five studied tree species.

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