WOOD DECAY IN LIVING TREES IN EASTERN AMAZONIA, BRAZIL

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2011

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To those who shared this road with me

ACKNOWLEDGMENTS

First and foremost, I thank my academic advisor, Francis E. Putz for his support of my pursuit for doctorate degree at the University of Florida (UF). His willingness to share his knowledge about ecology, eagerness to learn about my research progress, and the innumerable discussions we held throughout these last five years have been essential to my development as a researcher. I am also extremely grateful to the other members of my doctoral committee, Wendell Cropper, Jason Smith and Kaoru Kitajima for all their suggestions and guidance through this process. I thank James Kimbrough, also at UF, for all his patience in teaching me the basics of fungi identification.

This research would not have been possible without the support of my Brazilian collaborators at the *Instituto Floresta Tropical* (IFT). I especially thank Johan Zweede and Marco Lentini for believing in my research and for providing incredible logistic support during my field work. I also thank Iran Pires, Paulo Bittencourt, Marlei Nogueira, and Cesar Pinheiro for sharing their amazing field experiences and for facilitating my research in all possible ways. I thank Suelene Couto, Greice Ferreira, and Sonia Machado for their help me dealing with financial issues. I am grateful to the IFT crew, especially my field assistants Arivaldo Souza, Sebastião Santos, Joel Ferreira, Valderez Vieira, Marina Cardoso, and Lorena Cardoso, for turning the sometimes exhausting field work into a joyful experience.

Laboratory experiments were made possible by the logistic support and expertise provided by researchers and staff from the *Coordenação de Pesquisa em Produtos Florestais* (CPPF) at the *Instituto Nacional de Pesquisas da Amazônia* (INPA). I thank Maria Aparecida de Jesus and Rogério Hanada for introducing me to the complex world of fungi and for facilitating my work in many ways, and Jorge Freitas for helping me

understand the basics of wood anatomy research. Laboratory analysis would not have been completed without the help of Francislene Telles. I owe her my deepest gratitude and friendship. I thank Jose Odair Pereira for providing laboratory infrastructure at the *Universidade Federal do Amazonas* (UFAM). I also thank Gabriela Zanette, who is both a collaborator and a friend, for helping me deal with the difficulties that cropped up while carrying out my molecular biology studies.

I thank my friends Marcos Bento, Carla Bantel, Yara Camargo, Pedro Teixeira, Luciana Zago, and Satya Cadenholf in Brazil for all the philosophical discussions about life in general and particularly about life in the Amazon, and for all the happiness they bring to my life. I am grateful to Leonardo Pacheco, Flavio Bocarde and Carlos Anselmo for offering me shelter in Manaus. I also thank Antonio de la Peña, Cynnamon Dobbs, Marco Lentini, Andres Susaeta, Marina Londres, Belen Ragablino, Camila Pizano, Geraldo Silva, Skya Murphy, Christine Lucas, Marlene Soriano, Paula Pinheiro, Daniel Carrillo, Yuan Zhou, and Jordan Mayor at UF for making graduate life fun and unforgettable.

Experiences shared with my office mates Joe Veldman, Paulo Brando, Vincent Medjibe, Allie Shenkin, Claudia Romero, Drew Silver, Xavier Haro, and Yuan Zhou at UF have been essential for improving my critical thinking skills. I thank them for making the office such a friendly environment. Also at UF, I thank the Department of Biology staff, particularly Karen Patterson and Tangelyn Mitchell, for guiding me through UF's bureaucracy, and Ann Wagner for all the help she provided and good laughs we shared when preparing experiments and organizing the laboratory for Introductory Botany and Plant Ecology.

My parents Kathia and Sérgio Eleutério and my brother Sergio consistently provided me with a safe harbor during these ten years that I have been living abroad. Their words of encouragement and their unconditional love have accompanied me everywhere, and supported me through my most difficult moments. I appreciate their trust in me and in my work, even when my study subjects were incomprehensible and required me to walk alone and away from home. I feel extremely lucky to be part of my family and thank them for being always nearby, even when really far away.

My doctorate studies were financed by the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES), the Tropical Conservation and Development Program, and the Department of Biology at the University of Florida. Additional financial support for my research was provided by the International Foundation for Science (IFS) and Ideawild.

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May 2011

Chair: Francis E. Putz
Major: Botany

Tree stem hollows and rotten cores result from the gradual decomposition of the central woody column (heartwood) by a diverse range of organisms, mostly fungi. From both ecological and economic perspectives, the decision whether or not to harvest hollow and heart-rotted trees has substantial consequences. Retaining hollow trees in forests managed for timber, for instance, helps conserve species that use tree hollows as nesting sites. In contrast, felled hollow trees are then abandoned in the forest, which reduces profits to loggers, unnecessarily increases carbon emissions, and increases forest flammability.

Using data from inventoried stands in a naturally regenerated tropical forest managed for timber in the eastern Amazon, I investigated how the characteristics of economically important timber tree species influenced their susceptibility to heartwood decay. Tree species with higher wood specific gravities were more prone to have heartwood cavities made evident by the presence of open holes on the exterior of the trunk. Additionally, the proportion of trees with such stem cavities decreased with tree diameter. In contrast, for trees with no external openings in which hollows and rotten

cores were only detected after felling there was a positive relationship between a tree's size and its likelihood of being hollow.

I evaluated the diversity of wood decay fungi in my study site by comparing the communities of fungi with reproductive bodies emerging from coarse woody debris in an intact and a logged forest stand before logging and through a 10-month period after logging. Although no difference in fungal species richness was observed between sites, changes in the composition of fungal communities through time indicated that rare species were negatively affected by logging while there was no evident effect on fungal species that are mostly tree pathogens.

Finally, I sampled heartwood tissues from recently felled trees of five timber species to explore the diversity of fungi and termites that could actively degrade them, and evaluate tree characteristics that influenced their susceptibility to pathogen invasion. Large trees with smaller heartwood vessel sizes and higher ray and vessel density tended to have larger stem hollows. Fungal specie considered saprophytes and Coptotermes testaceus, a subterranean termite species, were frequently found in stem hollows. The presence of termite nests in heartwood varied among species and increased with wood density, but was not affected by fungal species richness.

CHAPTER 1
DISTRIBUTION OF HEART-ROTTED AND HOLLOW TREES IN A NATURALLY REGENERATED FOREST MANAGED FOR TIMBER IN EASTERN AMAZONIA

Introduction

Hollows and rotten cores in the stems of living trees typically result from gradual colonization and decomposition of heartwood by fungi, coupled with the activity of hole-excavating animals such as termites and woodpeckers (Rayner & Boddy 1988; Hooper *et al.* 1991). Decay organisms gain access to heartwood typically only after a tree suffers a surface wound, but then only if anatomical barriers and chemical defenses produced by bark and sapwood tissues are trespassed (Blanchette 1992; Schwarze *et al.* 2000).

Hollow and hear-trotted trees are common in most forests, including those scheduled for timber harvesting (e.g., Shigo & Hillis 1973; Lindenmayer *et al.* 1997; Grogan & Schulze 2008). Whether to retain or cut trees with unsound stems is a question with both ecological and economic implications. Ecological issues deserving consideration include the fact that hollow, heart-rotted, or even dead-standing trees provide preferred nesting and roosting sites for numerous species of birds, mammals, and invertebrates (Gibbons & Lindenmayer 1996; Ranius 2002; Apolinario & Martius 2004). The densities of such trees therefore influences the population dynamics of numerous species and associated ecosystem processes such as pollination and seed dispersal (Janzen 1976; Daily 1993; Amelung *et al.* 2002; Eltz *et al.* 2003). If defective trees are felled in error or in the hopes of finding at least one sound marketable log, they are typically abandoned in the forest or on log decks, increasing fuel loads and enhancing forest flammability, and unnecessarily increasing carbon emissions (Uhl & Kauffman 1990; Holdsworth & Uhl 1997; Cochrane 2001; Cochrane & Laurance 2002).

From an economic perspective, forests in which trees with unsound stems frequent are less valued for their timber (Holmes *et al.* 2002) and contain less sound wood than expected from their basal areas (Nogueira *et al.* 2006). Moreover, higher carbon emissions, and lower values for carbon sequestration may be expected in such forests (Keller *et al.* 2004; Ferry *et al.* 2010), because these defective trees are susceptible to breakage (Kennard *et al.* 1996; Lindenmayer *et al.* 1997; Mattheck *et al.* 2006) and suffer high mortality rates (Chao *et al.* 2009).

Spatial concentrations of trees with hollows or rotten cores are expected due to synergies between individual tree characteristics and environmental conditions (Holdenrieder *et al.* 2004; Irianto *et al.* 2006). For example, clusters of tress with stem or root damage caused by events such as fire or logging (e.g., Johns *et al.* 1996; Holmes *et al.* 2000; McDonald *et al.* 2000; Holzmueller *et al.* 2008) may favor local pathogenic infections and lead to aggregated distributions of hollow trees. The spread of these infections depend on landscape features, spatial patterns of vegetation, and the existence and abundance of susceptible hosts (Holdenrieder *et al.* 2004).

Trees' anatomical properties and chemical defenses limit the growth of active decomposers (Pearce 1996; Behrendt & Blanchette 1997; Boddy 2000; Abe et al. 2000; Nsolomo & Venn 2000; Deflorio et al. 2008). Thick bark and high wood density confer some protection against damage and the spread of decay fungi (Romero et al. 2009), but all trees are susceptible to decay especially if they are senescent or subjected to physiological stress (Holloway et al. 2007; Chao et al. 2008).

In response to their importance to forest fauna, the incidence of trees with unsound stems, especially cavity trees, in subtropical and temperate forests has been

widely investigated (e.g., Fan *et al.* 2003; Fox *et al.* 2008). Static and dynamic, single or multi-level models using GIS, nearest neighbor imputation models, logistic or negative binomial regressions, and mixed models have been developed to estimate the number of cavities available for fauna in forests managed primarily for timber (Ball *et al.*1999; Fox *et al.* 2008; Eskelson *et al.* 2009). Explanatory variables used in these models usually reflect tree diameters and heights, crown exposure, stem defects, wood density, tree density, and micro-environmental characteristics (e.g., Fan 2003; Temesgen *et al.* 2008; Zheng *et al.* 2009).

Compared to temperate and subtropical forests, knowledge about the occurrence and distribution of heart-rotted and hollow trees in high diversity tropical forests is scarce. In this study, I evaluated the distribution of these trees in a forest managed for timber in the eastern Brazilian Amazon. Additionally, I used individual-level models to estimate the likelihood of a tree having an unsound stem given its dimensions and tree density, and wood density by species. My objective was not to predict the abundance of such trees in the studied forest, but instead to understand individual and species-level characteristics that influence tree susceptibility. I predicted that the likelihood of a tree stem being heart-rotted or hollow increases with its size and the density of trees in its immediate vicinity, and decreases with wood density.

Methods

Study Site

This study was carried out in Fazenda Cauaxi ($3^{o}35'$ - $3^{o}45'$ S, $48^{o}15'$ - $48^{o}25'$ W), a selectively logged naturally regenerated forest in the eastern Brazilian Amazon (Holmes *et al.* 2002; Keller *et al.* 2004). The area is covered by lowland tropical moist forest and is located in the Paragominas municipality, Para, Brazil (IBGE 1988). Oxisols

prevail on the relative flat to slightly rolling terrain dissected by small creeks. The climate is moist tropical with annual rainfall averaging 2200 mm and a pronounced dry season that typically lasts from June to November (Costa & Foley 1998).

In 1995, a non-governmental institution (Instituto Floresta Tropical; IFT) established, in collaboration with the landowner (CIKEL Brasil Verde S.A.), which is currently recognized as the most important training center for reduced-impact logging (RIL) techniques in the Amazon (Putz *et al.* 2008). During selective logging operations, which of the 91 tree species currently recognized as potentially commercial by IFT are harvested is determined by market demand and limited by RIL rules regarding maximum harvestable timber volumes per area. Timber extraction is carried out in forest management areas divided into units (UTs) that average 100 ha and are shaped to suit the terrain. During timber stand inventories conducted 1 yr prior to logging, all commercial or potentially commercial trees ≥ 45 cm diameter at breast height (DBH) were identified, mapped, and classified according to crown and stem characteristics (Fundação Floresta Tropical 2002). DBHs were estimated when stem buttresses extended above 1.3 m. Dead standing trees were not inventoried.

Trees with stem cavities were recorded both in inventories and during logging. During forest inventories, trees having obvious cavities were identified, mapped and subsequently categorized as hollow and non-marketable. Trees were also classified as hollow by harvesting crews immediately before felling if they showed signs of heartwood decay even in the absence of external evidence of internal cavities (e.g., presence of bee hives and/or fungal colonies on the stems). In these cases, foresters usually verified the presence of an internal cavity by testing whether they produce a hollow

sound when knocked. Finally, all trees selected for extraction were tested for the presence of hollows or heartwood decay immediately prior to logging by inserting a chainsaw vertically into the trunk between the buttresses 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) were considered non-marketable and were not felled. In a sample of 3 UTs, approximately 27% of the trees listed for logging by inventory crews were later classified as non-marketable by harvesting crews (data not shown).

To be felled, a tree must meet the following criteria in the sequence shown in Figure 1-1: (1) its DBH is ≥ 45 cm; (2) no obvious cavities or signs of heartwood decay are present; (3) there is a market demand for the wood of that species; (4) the maximum timber volume allowed to be extracted would not be exceeded; and, (5) tests performed just before the tree is felled show no evidence of advanced heartwood decay or hollows. As a consequence of this process, only trees with sound stems that had been selected for harvesting were tested for heartwood decay as a pre-logging procedure (step 5 in Figure 1-1). For this reason, I used two separate models to investigate the probability of a tree having an unsound stem. First, trees with obvious stem cavities detected during inventories (CAV) were evaluated. Then, I used data from the trees with sound stems that had been further investigated for the presence of heart-rots or hollows (ROT) using the chainsaw bar plunge test right before felling to evaluate the probability of those trees to have internal cavities.

Cavity Trees Detected in Forest Inventories (CAVs)

Inventory data from 22 UTs covering approximately 2113 ha were used to investigate the distribution of CAVs. Because the dimensions and shapes of the UTs

varied somewhat with the terrain, only the central 100 ha of each unit and trees >10 m from the edge were considered. The density of trees ≥ 45 cm DBH occurring in an area of 10 m radius around each focal tree was calculated using Proc Variogram (SAS 9.2 Institute Inc. 2009). These criteria resulted in a sample size of 28,115 trees of which 1317 (5%) were classified as hollow during forest inventories. Only the 38 tree species with ≥ 200 individuals in the sampled area were included in this analysis (Table 1-1). These species represent 19 families and 32 genera, with wood densities of 0.26 - 0.99 g/cm^3 (Zanne *et al.* 2009).

I used Moran's Index to investigate the spatial autocorrelations in the distributions of CAVs in each of the twenty-two 100-ha management units. To calculate the index, I used distance intervals up to 50 m to reflect the area of possible influence of a tree on its environment and surrounding trees, and vice-versa. Positive values correspond to spatial aggregation, while negative values correspond to over-dispersion on a -1 to +1 scale. Z-scores reflect autocorrelations with $P<0.05$. The index was calculated in SAS Proc Variogram (SAS 9.2 Institute Inc. 2009).

Logistic tree-level models used to predict the presence or absence of cavities in individual trees were based on its DBH, wood density (WD) by species, and density of trees >45 cm DBH in a 10 m radius area surrounding each focal tree were built in SAS Proc Logistic (SAS 9.2 Institute Inc. 2009). Species-specific WDs were estimated based on the average from values reported in the Global Wood Density Database (Zanne *et al.* 2009; see Chave *et al.* 2009 for a description). Average WD by genus was used for two species due to lack of species-specific data (*Peltogyne lecointei* Ducke and *Protium pernervatum* Cuatrec) and when trees in the same genus were not identified to species

during forest inventories (*Hevea* sp. Aubl., *Pithecellobium* sp. Mart., and *Helicostylis* sp. Trécul), which together corresponded to approximately 12% of the trees studied.

Logistic models with the explanatory variables and their possible interactions were compared using the Akaike's information criterion (AIC; Akaike 1974). Fitting parameters and AIC values are shown for the best-fit model. To investigate the effects of spatial dependence due to sampling trees within plots, I used a generalized linear mixed model (GLMM) with the predictors of the logistic model, and plot as a random factor. This analysis was performed using Proc GLIMMIX (SAS 9.2 Institute Inc. 2009). Fitting parameters are shown for the final model.

Trees with Rotten Cores or Hollows Detected During Exploratory Activities (ROTs)

Post-logging data available for 3 UTs were used to investigate the presence of heartwood hollows or rotten cores in trees selected for harvesting (i.e., trees ≥ 45 cm DBH with straight stems, regular crowns, and no obvious cavities). Only the 6 species with ≥ 30 trees (*Astronium lecointei* Ducke, *Dinizia excelsa* Ducke, *Lecythis paraensis* Huber*, Manilkara bidentata* (A. DC.) A. Chev.*, Manilkara huberi* (Ducke) A. Chev., *Pouteria oppositifolia* (Ducke) Baehni), representing 4 families and 898 individuals in an area of approximately 288 ha were analyzed. Average WD by species varied from 0.32 to 0.79 g/cm^3 (Table 1-1). No spatial autocorrelation analysis was performed because data were available for only a small subset of the trees mapped.

A binary response variable was created to classify trees according to their post-logging categories. Logistic models to predict the presence or absence of heartwood extended hollows or decay on trees selected for harvesting based on DBH, WD, and tree density in a 10 m radius area around each focal tree were built in SAS Proc Logistic

(SAS 9.2 Institute Inc. 2009). Tree densities were calculated for the 700 individuals located ≥ 10 m from the UT borders, and compared among hollow and non-hollow trees identified during logging to evaluate if this variable should be incorporated in the predictive model. Fitting parameters and AIC values are shown for best-fit model.

Results

Descriptive Analysis

Each of the 22 UTs contained a mean of 1300 inventoried trees ≥ 45 cm DBH (range 264 – 2054). *Manilkara huberi* was the most abundant commercial species. The number of cavity trees detected in forest inventories (CAVs) varied considerably among both species and UTs. The proportion of CAVs by unit averaged 5% and ranged 0.1 – 30%, while the proportion of CAVs by species varied from 0.5 to 21% (Figures 1-2 and 1-3). In general, UTs in which tree densities were above average had the highest proportions of CAVs (Figure 1-2). In contrast, this positive relationship between tree abundance and proportion of CAVs was not observed at the species level. *Dinizia excelsa*, for example, a species with an intermediate abundance among the 38 species considered in the analysis, was the most frequently hollow among the 38 studied species (> 20%, Figure 1-3).

Average DBH was higher and more varied for non-CAV than for CAV trees in most species, including those with high percentages of CAVs (e.g., *Dinizia excelsa*, *Manilkara huberi*, *Newtonia psilostachya* (DC.) Brenam and *Tetragastris altissima* (Aublet) Swart; Table 1-2 and Figure 1-4). Trees in this study ranged from 45 – 250 cm DBH, with an average for most species of between 60 and 70 cm (Table 1-2).

The percentage of CAVs by species increased slightly with WD ($R^2 = 0.11$, $p = 0.03$; Figure 1-5). The weakness of this relationship was in part due a few species with

low cavity incidence and low WD, and to *Dinizia excels*a, a species with high WD but also the highest cavity incidence. Most trees grew in areas with low densities of trees ≥ 45 cm DBH (i.e., only 1-2 trees ≥ 45 cm DBH in an area of 10 m radius surrounding each focal tree). Even in UTs with above average tree densities, most inventoried trees were not locally crowded by other large trees (Table 1-3).

The proportion of defective trees increased substantially after trees were tested using the chainsaw bar plunge test right before logging. In other words, the foresters that conducted the inventories were not consistently able to predict the presence of heart-rots and hollows in the stems of trees large enough to be harvested. The underestimations varied from approximately 17% for *Pouteria oppositifolia* to 36% for *Astronium lecointei* (Table 1-4). Average DBHs among ROT trees were higher than for non-ROT trees for the 6 species analyzed (Table 1-4 and Figure 1-6).

Spatial Autocorrelation Among CAVs

Weak significant positive spatial autocorrelations in the locations of inventoried trees with cavities were observed in only 5 of the 22 UTs studied. The UT designed C2, which had the lowest total number of trees from all sampled units, showed the highest spatial autocorrelation among the units studied ($I = 0.24$; $p < 0.0001$; Table 1-6).

Predictive Model for CAV Occurrence

The best-fit logistic model to predict the occurrence of CAVs in forest inventories included the variables DBH, WD, and their interaction (1-1):

$$\text{logit}[\pi(\text{CAV})] = \log\left(\frac{\pi(\text{CAV})}{1-\pi\,(\text{CAV})}\right) = \alpha + \beta_1\text{DBH} + \beta_2\text{WD} + \beta_3(\text{DBH} * \text{WD}) \qquad (1\text{-}1)$$

Where π(CAV) is the probability of an individual tree being hollow, α is the intercept, and β_1, β_2, and β_3 are the variable coefficients. All variables were significantly

different from 0 (Table 1.7). The model AIC was 10389.9, and the predicted probabilities were 62.7% concordant with observed values. The likelihood of a tree being classified as CAV decreased with DBH, but increased with WD (Figure 1-5).

By incorporating a random plot effect to account for variation derived from sampling trees by UTs, the following GLMM was generated (1-2):

$$\text{logit}[\pi(\text{CAV})] = \log\left(\frac{\pi(\text{CAV})}{1-\pi\,(\text{CAV})}\right) = X\beta + Z\gamma + \varepsilon \qquad (1\text{-}2)$$

where Xβ refers to the estimate (β) of the fixed factors (X) for the logistic model, Zγ refers to the estimate (γ) of the random plot effect, and ε is the error. WD and the interaction between DBH and WD were significant predictors of the incidence of CAVs Figure 1-7). The residual variance of 0.88 showed that the model fits the observed data reasonably well.

ROT Occurrence Predictive Model

Logistic regressions were used to test the relevance of DBH, WD, and tree density as explanatory variables for predicting the occurrence of ROTs by species and UT. Initial analyses were performed with the 700 trees located ≥ 10 m from the UT borders. Because tree density did not improve the model's capacity to explain the observed proportions of heart-rotted and hollow trees, this variable was discarded from further analyses and trees located close to the margins of UTs were then added to the total sample size to assure that at least 30 individuals per species were evaluated.

In contrast to the results from the analysis, DBH was the only variable among those tested that predicted the occurrence of heart-rotted and hollow trees among commercial trees designated for harvesting. In this case, larger trees were more likely to

have hollow stems or rotten cores (Table 1-4 and Figure 1-6). The following equation (1-3) represented the best-fit model with an AIC of 985.5:

$$\text{logit}[\pi(\text{HO})] = \log\left(\frac{\pi(\text{HO})}{1-\pi(\text{HO})}\right) = \alpha + \beta\text{DBH} \quad (1\text{-}3)$$

where π(HO) is the probability of an individual tree to being hollow, α is the intercept, and β represent is the parameter estimate. Parameter estimates (Table 1-9) showed a positive relationship between the likelihood of being hollow and tree DBH (Figure 1-8). Predicted probabilities were 71% concordant with the observed responses. No differences were observed among species or UTs.

Discussion

Tree census data have been used to evaluate the abundance and distribution of cavity trees in temperate and subtropical forests (e.g., Ball *et al. 1*999; Fan 2003; Fan *et al.* 2003; Zheng *et al.* 2009). Understanding spatial patterns of distribution based on tree-level data becomes challenging in tropical forests where most tree species occur at low densities (Chave 2008). In this study, I performed separate analyses using forest inventory and pre-logging data to provide complementary information about individual-based variables that explain the occurrence of heart-rots and hollows in the stems of abundant commercial timber tree species in eastern Brazilian Amazon.

Wood density was the most important variable for predicting the occurrence of cavity trees (CAVs) recorded in forest inventories. Unexpectedly, tree species with higher WD were more likely to have externally evident stem cavities. In contrast, the proportion of trees with stem cavities decreased with DBH. Because cavity trees may be prone to mechanical failure (Lindenmayer *et al.* 1997; Mattheck *et al.* 2006), they may fall over or break before becoming very large (Chao *et al.*2009). A similar argument can

be made to explain the higher incidence of stem cavities among species with higher WDs: higher WD may confer higher resistance to biotic and abiotic forces that cause stem breakage, thus heart-rotted and hollow trees with high density wood may survive for long periods (Anten & Schieving 2010).

Positive spatial autocorrelations in the distribution of CAVs were only observed in 2 UTs and those relationships were weak. The aggregation of heart-rotted and hollow trees in UT C2 is possibly an artifact of low overall tree density. Spatial aggregation among cavity trees would be expected as a result of microenvironmental factors that may enhance a tree being damaged by falling trees and branches or in areas with seasonally flooded soils (Chao *et al.* 2009; Ferry *et al.* 2010). It may also result from local concentrations of tree pathogens and stem-damaging animals such as woodpeckers (Castello *et al.* 1995; McCallum & Dobson 2002; Holdenrieder *et al.* 2004; Condeso & Meentemeyer 2007). In addition, areas with high densities of trees would facilitate colonization by poorly dispersed pathogens and promote the spread of infections through root connections (Boddy 1993; Sivasithamparam 1998; Van der Putten *et al.* 2001; Freckleton & Lewis 2006). This facilitation was unlikely in the study area where densities of trees ≥ 45 cm DBH were low. The lack of positive autocorrelation may be indicative of a low frequency of events that promote heartwood infections in this site in the eastern Amazon.

Using data from the exploratory efforts of harvesting crews, DBH was the only variable that explained the incidence of hollows or heartwood decay. Other studies have shown this positive relationship between a tree's size and its likelihood of being hollow (Nogueira *et al.* 2006; Gibbons *et al.* 2008). Based on the complimentary results of the

analyses of inventory and post-logging data, I conclude that trees with rots and hollows that extend out through the sapwood and bark, and were thus detected during inventories, were more susceptible to failure and therefore survive for a shorter period in the forest in comparison to trees in which the defect was restricted to the heartwood. A possible explanation for these results resides in the time lag since the tree stem was damaged, on wound dimensions, and on debilitating conditions that restrained wound closure and compartmentalization (Cherubini *et al.* 2002; Dujesiefken *et al.* 2005; Davison & Tay 2008; Deflorio *et al.* 2008). Trees with evident external cavities, for example, may have been wounded in their early in life or may have suffered more extensive damage. Alternatively, a tree can fail to close a wound if stressed (Burrill *et al.* 1999). Large trees experience energy constraints on growth while successfully defending against pathogens, which can affect their abilities to compartmentalize decay (Schwarze *et al.* 2000; Thomas 2004).

Some constraints may arise from having sampled only of trees ≥ 45 cm DBH, identifying cavities during ground surveys, or estimating the extension of hollow or rotten cores by inserting a chainsaw into the base of stems selected for felling. Studies aiming to quantify the density of cavity trees in temperate forests have shown that the number of trees with stem cavities may be high among smaller trees but that there is also a positive relationship among cavity and tree dimensions (Fox *et al.* 2008). Consequently, although I may have underestimated the number of cavity trees by inaccurate ground observations and not sampling small trees, my study provides valuable data for quantifying the density of trees with the wide cavities and external apertures that are most commonly utilized by hole nesting and roosting mammals and

birds (Boyle *et al.* 2008; Eltz *et al.* 2003; Gibbons & Lindenmayer, 1996). Paradoxically, I may have overlooked the presence of hollows or rotten cores in the largest trees selected for logging because the chainsaw used to test them would only reach outer heartwood layers. Forest managers in the study site try to avoid this possibility by not selecting the largest trees for harvesting, which means they are not tested for hollowness, and are maintained in the forest as seed sources. Results from analyses based on post-logging data may then be biased towards intermediate size trees, while trees with low and extremely high DBHs are underrepresented because they, respectively, return low timber volumes or are likely to be defective.

Identifying variables that explain a tree's susceptibility to heart-rots is problematic because it is the result of interactions between biotic and abiotic factors. The complexity of interactions among these different factors can only be assessed through long-term controlled studies in which trees are damaged and long-term responses are monitored (Romero *et al.* 2009). Even in this case, responses would be subjected to random environmental variation and catastrophic events that (Canham *et al.* 2010).

Few researches have tried to untangle the complexity of tropical tree susceptibility to damage and their responses after damage (Boyle *et al.* 2008). This study assesses some of this complexity by looking at the distributions and wood properties of trees in which decay is mostly confined in dead heartwood tissues, and tree in which decay has extend outwards reaching sapwood and bark at the base of trees, and possibly affecting their susceptibility to failure.

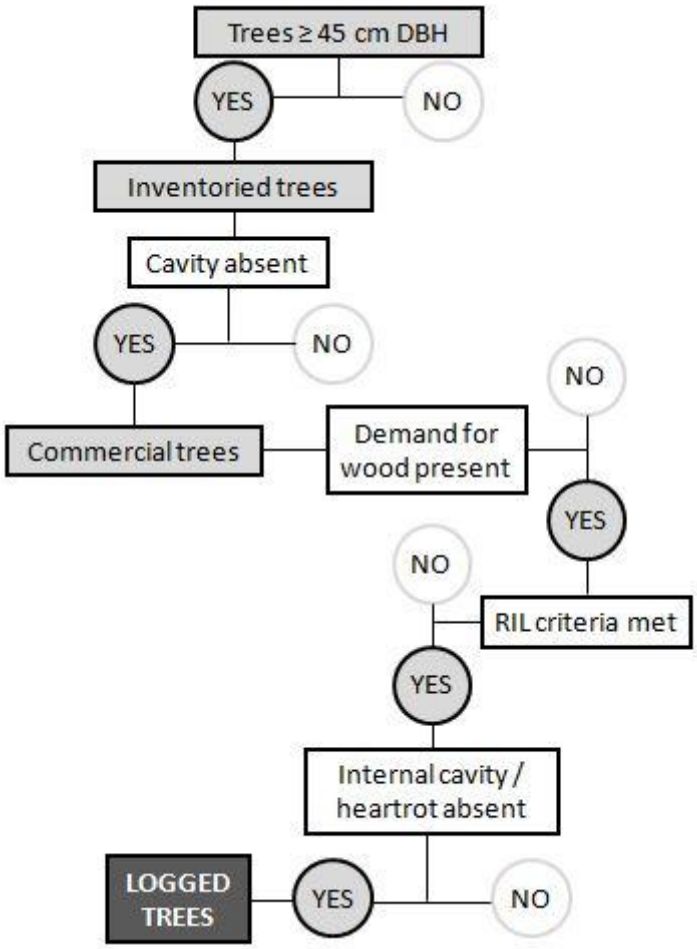

Figure 1-1. Steps performed to select commercial trees for logging in Fazenda Cauaxi. In light and dark grey are the steps for which inventory and pre-logging data were available.

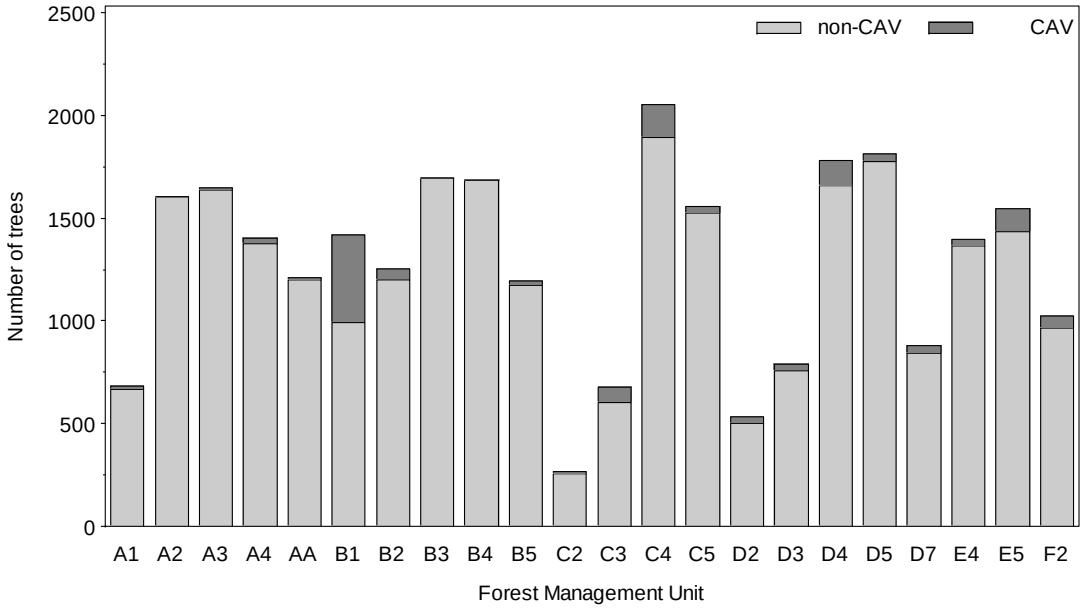

Figure 1-2. Number of trees ≥ 45 cm DBH of the 38 most abundant timber tree species encountered in each of the 22 forest management units (approximately 100 ha each) showing the proportion of cavity trees identified by the presence of external openings during forest inventories (CAVs) in each unit.

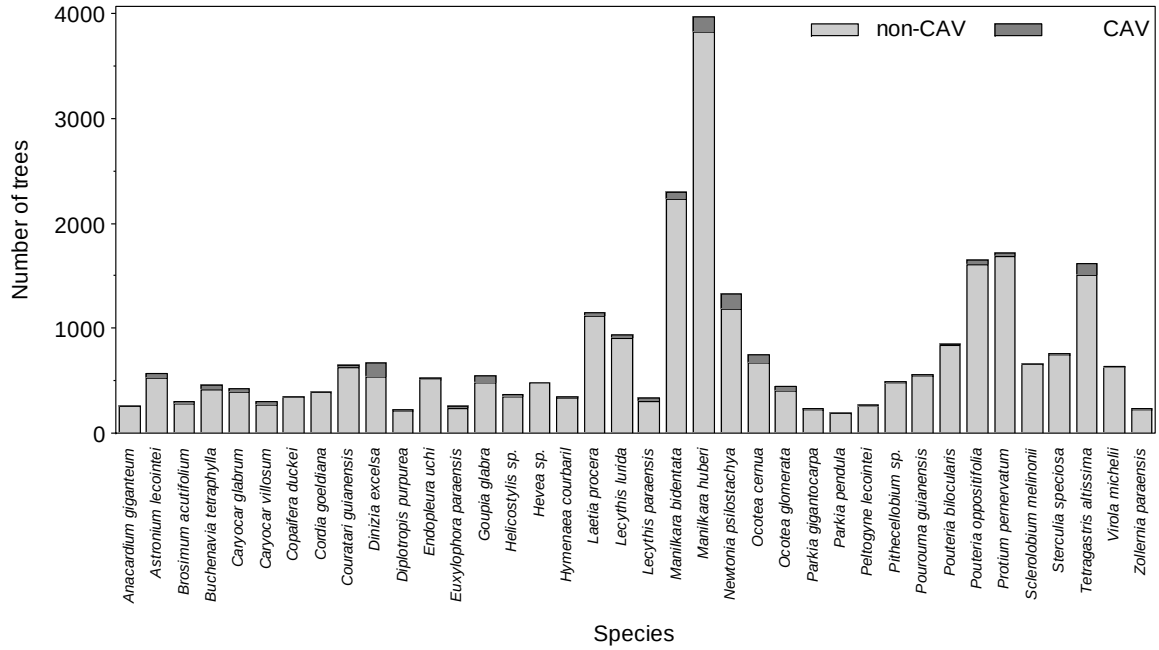

Figure 1-3. Number of trees of each of the 38 most abundant timber tree species with ≥200 individuals, showing the proportion of cavity trees classified as hollow in forest inventories (CAVs).

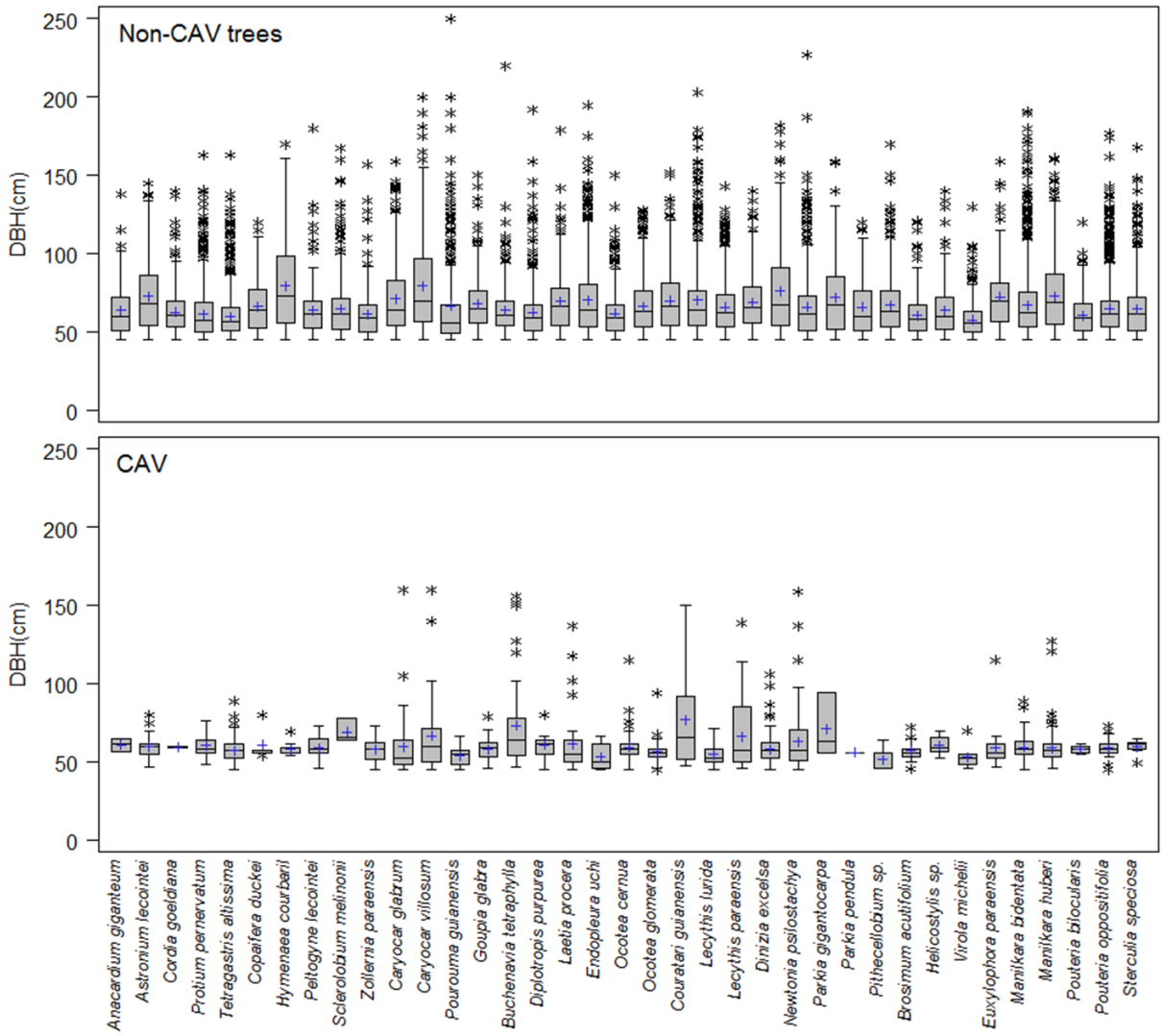

Figure 1-4. Variation in the distribution of trees ≥ 45 cm diameter at breast height (DBH) inventoried in all forest management units, and classified as non-cavity and cavity trees by inventory crews (CAVs) according to DBH by species.

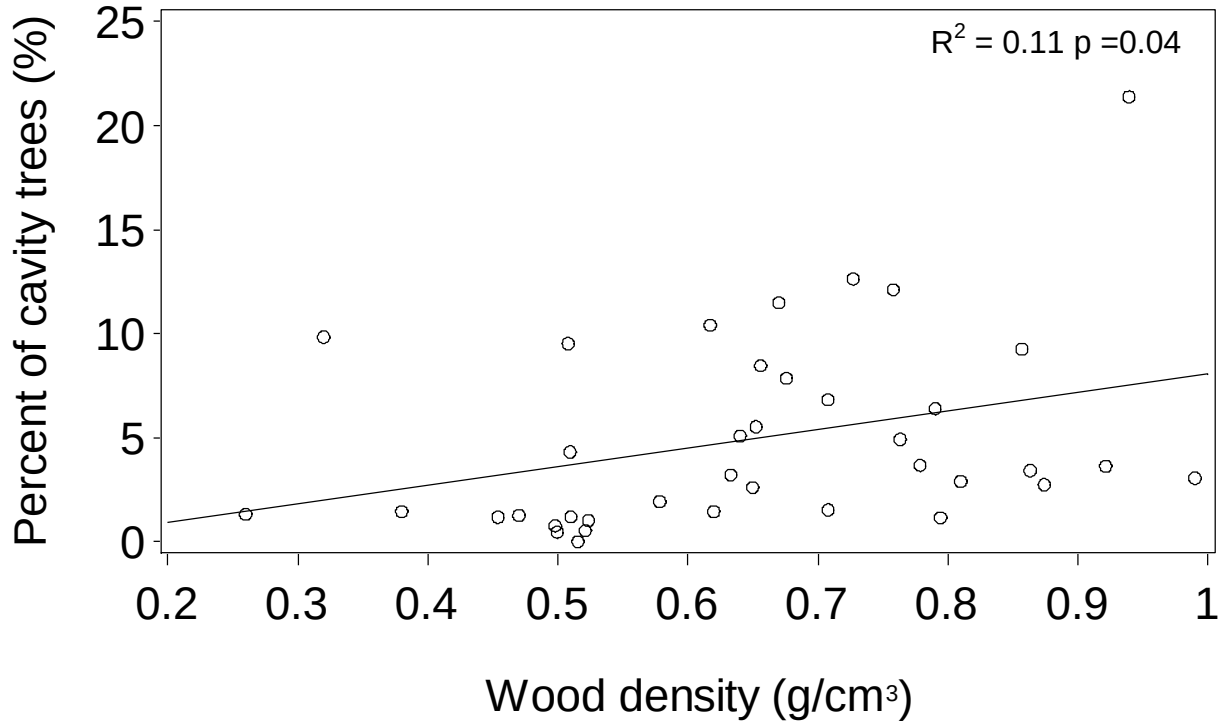

Figure 1-5. Percentage of cavity trees identified during forest inventories (CAVs, N = 1317) by species according to their wood density (g/cm^3).

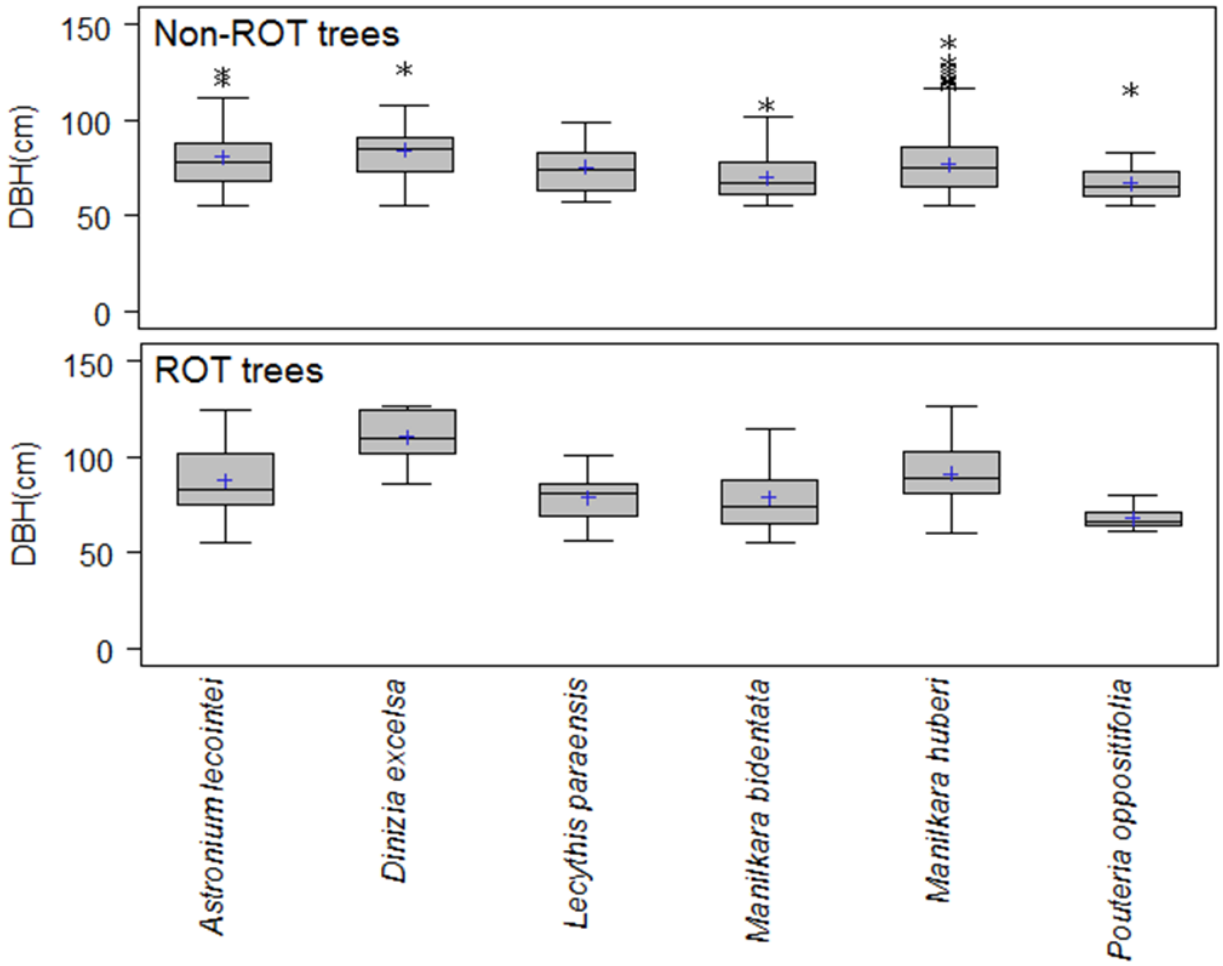

Figure 1-6. DBH variation between trees tested for hollowness immediately before logging, classified according to the presence (ROT) or absence (non-ROT) of heart-rots and hollows. Only trees ≥ 45 cm DBH of the 6 commercial tree species with ≥ 30 individuals selected for harvesting in three forest management units (UTs) are considered.

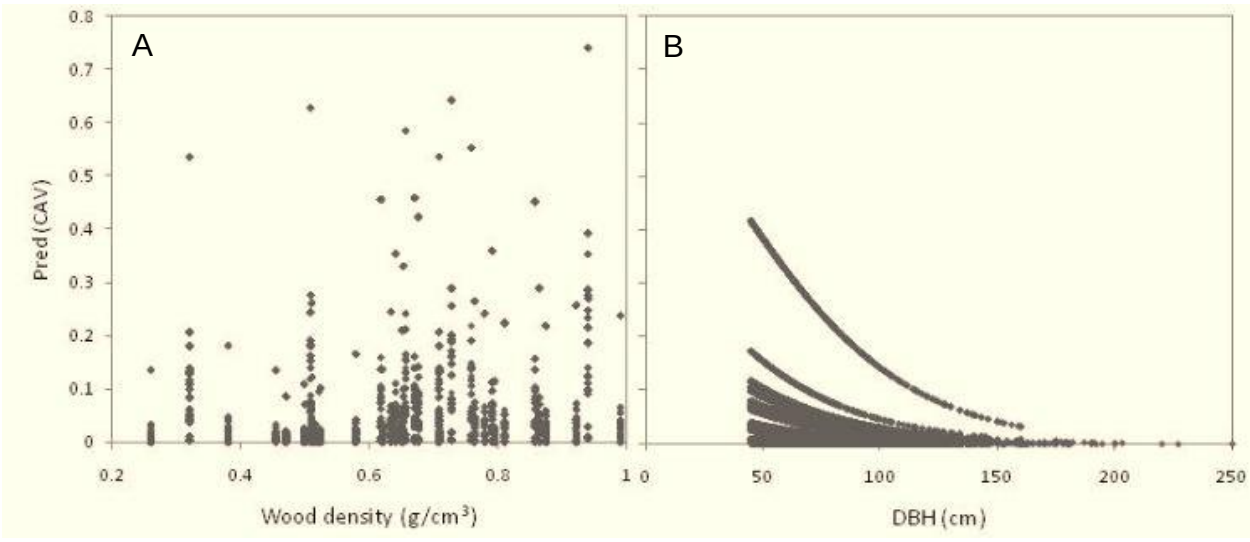

Figure 1-7. Probability of the incidence of trees with cavities identified during forest inventories (CAVs) by A) WD and B) DBH.

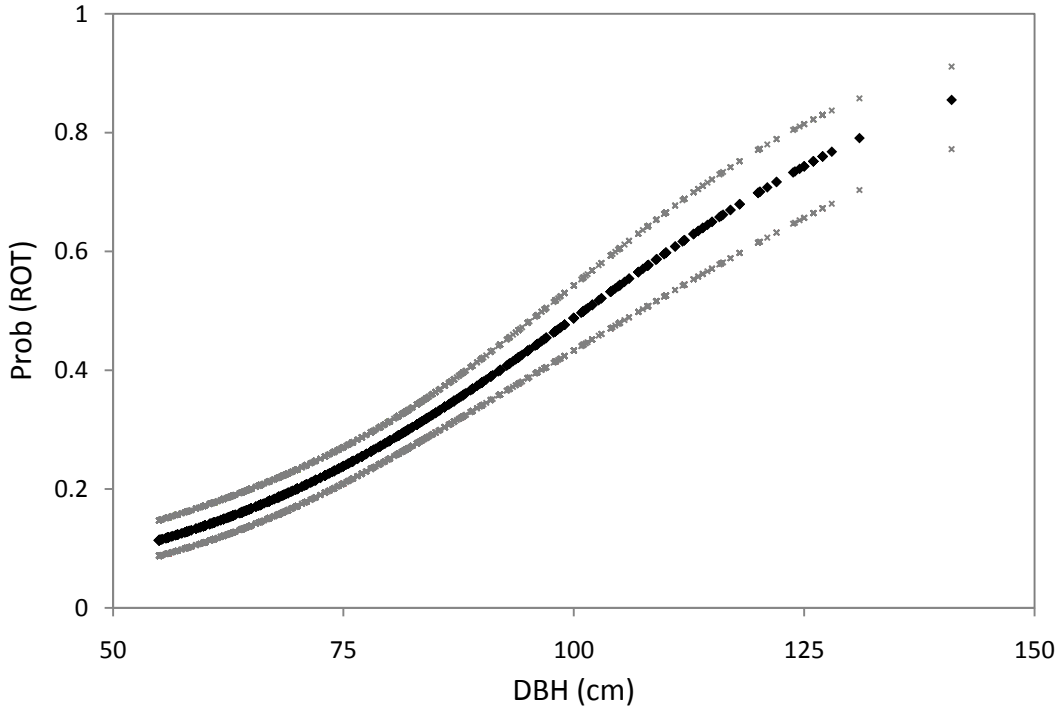

Figure 1-8. Probability ± 95% confidence intervals of the incidence of trees with heart-rots and hollows among supposedly sound trees selected for harvesting and diagnosed during logging activities (ROTs) as a function of tree DBH.

Table 1-1. Tree species with ≥ 200 individuals ≥ 45 cm DBH in the sampled area of approximately 2113 ha in Fazenda Cauaxi.

Family	Genus	Species	Number of trees	Wood density (g/cm^3)*
Anacardiaceae	*Anacardium*	*giganteum*	255	0.45
	Astronium	*lecointei*	563	0.79
Boraginaceae	*Cordia*	*goeldiana*	394	0.64
Burseraceae	*Protium*	*pernervatum*	1717	0.62
	Tetragastris	*altissima*	1612	0.68
Caesalpinaceae	*Copaifera*	*duckei*	345	0.76
	Hymenaea	*courbaril*	345	0.62
	Peltogybe	*lecointei*	264	0.50
	Sclerolobium	*melinonii*	656	0.51
	Zollernia	*paraensis*	229	0.94
Caryocaraceae	*Caryocar*	*glabrum*	420	0.78
		villosum	297	0.79
Cecropiaceae	*Pourouma*	*guianensis*	553	0.66
Celastraceae	*Goupia*	*glabra*	546	0.73
Combretaceae	*Buchenavia*	*tetraphylla*	461	0.65
Euphorbiaceae	*Hevea*	sp.	478	0.52
Fabaceae	*Diplotropis*	*purpurea*	218	0.81
Flacortiaceae	*Laetia*	*procera*	1151	0.63
Humiriaceae	*Endopleura*	*uchi*	520	0.86
Lauraceae	*Ocotea*	*cernua*	742	0.86
		glomerata	441	0.87
Lecythidaceae	*Couratari*	*guianensis*	649	0.92
	Lecythis	*lurida*	935	0.67
		paraensis	335	0.32
Mimosaceae	*Dinizia*	*excelsa*	673	0.51
	Newtonia	*psilostachya*	1332	0.26
	Parkia	*gigantocarpa*	229	0.52
		pendula	191	0.76
	Pithecellobium	sp.	487	0.52
Moraceae	*Brosimum*	*acutifolium*	295	0.38
	Helicostylis	sp.	362	0.71
Myristidaceae	*Virola*	*michelii*	637	0.65
Rutaceae	*Euxylophora*	*paraensis*	260	0.58
Sapotaceae	*Manilkara*	*bidentata*	2298	0.50
		huberi	3967	0.51
	Pouteria	*bilocularis*	851	0.71
		oppositifolia	1649	0.47
Sterculiaceae	*Sterculia*	*speciosa*	758	0.99

* Data extracted from Zanne *et al.* (2009).

Table 1-2. DBH means and standard deviations for all trees sampled in forest inventories, and divided into non-cavity and cavity trees (CAVs).

Species	Total			Non-cavity trees			Cavity trees (CAV)		
	N	Mean	SD	N	Mean	SD	N	Mean	SD
Anacardium giganteum	255	63.6	15.9	252	63.7	16.0	3	60.9	3.9
Astronium lecointei	563	71.7	21.5	527	72.6	21.9	36	59.6	7.6
Brosimum acutifolium	295	60.4	13.0	280	60.6	13.3	15	57.1	6.6
Buchenavia tetraphylla	461	64.7	17.8	413	63.7	15.8	48	73.2	28.9
Caryocar glabrum	420	70.4	23.4	387	71.3	23.3	33	59.8	21.9
Caryocar villosum	297	78.1	30.3	261	79.6	30.7	36	66.6	25.2
Copaifera duckei	345	65.9	15.8	340	66.0	15.9	5	60.8	10.8
Cordia goeldiana	394	62.6	14.4	391	62.6	14.4	3	59.3	0.6
Couratari guianensis	649	70.7	25.0	621	70.5	24.7	28	76.7	31.8
Dinizia excelsa	673	72.1	25.6	529	75.9	27.3	144	58.2	8.9
Diplotropis purpurea	218	69.1	19.9	210	69.4	20.1	8	60.8	10.6
Endopleura uchi	520	61.6	14.6	514	61.7	14.6	6	53.2	8.7
Euxylophora paraensis	260	71.1	19.4	238	72.3	19.5	22	58.6	13.7
Goupia glabra	546	66.7	16.4	477	67.9	17.0	69	58.3	6.7
Helicostylis sp.	362	63.8	15.3	342	64.0	15.7	20	60.4	4.9
Hevea sp.	478	62.5	17.5	478	62.5	17.5	0	-	-
Hymenaea courbaril	345	78.9	27.7	335	79.5	27.9	10	58.0	4.5
Laetia procera	1151	70.1	22.6	1114	70.4	22.6	37	61.6	20.1
Lecythis lurida	935	65.4	16.1	903	65.7	16.2	32	54.6	6.7
Lecythis paraensis	335	68.4	17.9	304	68.6	17.4	31	66.5	22.9
Manilkara bidentata	2298	66.9	20.2	2235	67.2	20.4	63	59.2	8.0
Manilkara huberi	3967	72.3	20.3	3823	72.8	20.4	144	58.9	10.6
Newtonia psilostachya	1332	65.6	19.3	1179	65.9	19.6	153	63.0	17.4
Ocotea cernua	742	65.7	16.6	669	66.4	17.1	73	59.2	9.3
Ocotea glomerata	441	68.6	19.0	399	69.8	19.4	42	56.5	7.7
Parkia gigantocarpa	229	72.0	23.7	226	72.0	23.8	3	71.0	20.2
Parkia pendula	191	65.8	18.0	190	65.9	18.0	1	56.0	-
Peltogyne lecointei	264	63.3	16.3	251	63.6	16.7	13	58.8	7.3
Pithecellobium sp.	487	66.9	18.5	482	67.0	18.5	5	51.5	8.3
Pourouma guianensis	553	66.5	29.2	545	66.6	29.4	8	54.0	6.9
Pouteria bilocularis	851	60.4	11.4	838	60.4	11.5	13	57.9	2.1
Pouteria oppositifolia	1649	64.8	16.2	1606	64.9	16.4	43	58.9	5.0
Protium pernervatum	1717	61.1	14.5	1684	61.1	14.6	33	60.5	6.6
Sclerolobium melinonii	656	64.5	16.8	653	64.4	16.8	3	69.2	7.7
Sterculia speciosa	758	64.2	17.2	749	64.3	17.3	9	59.6	4.6
Tetragastris altissima	1612	59.7	12.9	1502	59.9	13.2	110	57.5	7.3
Virola michelii	637	57.6	10.5	629	57.7	10.5	8	53.3	7.5
Zollernia paraensis	229	61.1	15.2	222	61.2	15.4	7	57.8	8.7

Table 1-3. Percent frequencies of tree densities (≥ 45 cm DBH) within 10 m radius around cavity (CAV) and non-cavity trees by forest management unit (UT). All trees identified and mapped in forest inventories are considered.

UT	Densities of trees ≥ 45 cm DBH in an area of 10 m radius									
	Non-cavity trees					Cavity trees (CAV)				
	Total	0 (%)	1 (%)	2 (%)	≥ 3 (%)	Total	0 (%)	1 (%)	2 (%)	≥ 3 (%)
A1	683	87	12	1	0	15	93	7	0	0
A2	2396	50	50	0	0	2	100	0	0	0
A3	1647	73	22	4	1	9	89	11	0	0
A4	1405	76	20	3	1	28	75	25	0	0
AA	1208	80	17	3	0	6	100	0	0	0
B1	1420	80	17	3	0	427	81	15	4	0
B2	1253	80	18	2	0	55	84	16	0	0
B3	1696	74	21	5	1	2	100	0	0	0
B4	1685	72	21	5	2	1	100	0	0	0
B5	1192	79	17	3	1	20	80	15	5	0
C2	264	93	6	0	0	7	100	0	0	0
C3	678	85	14	1	0	79	86	14	0	0
C4	2054	71	23	5	1	158	76	20	3	2
C5	1558	73	22	4	1	35	69	26	6	0
D2	531	89	10	1	0	29	97	3	0	0
D3	788	83	15	2	0	32	78	22	0	0
D4	1784	73	22	4	1	124	63	30	6	1
D5	1816	72	23	5	1	7	86	14	0	0
D7	881	83	15	3	0	40	90	8	3	0
E4	1396	77	18	4	1	30	83	17	0	0
E5	1546	77	19	4	0	114	82	17	2	0
F2	1025	81	16	2	0	63	89	11	0	0

Table 1-4. DBH means and standard deviations (SD) for trees ≥ 45 cm DBH of the 6 tree species with >30 individuals selected for harvesting in 3 forest management units (UTs), and classified according to the presence (ROT) or absence (non-ROT) of extensive rotten cores or hollows.

Species	Total			Non-ROT trees			ROT trees			
	N	Mean	SD	N	Mean	SD	N	N(%)	Mean	SD
A. lecointei	69	83.3	18.5	44	80.5	17.7	25	36.2	88.1	19.3
D. excelsa	31	93.5	20.2	20	84.3	16.6	11	35.5	110.4	14.7
L. paraensis	34	76.1	12.7	27	75.4	12.4	7	20.6	78.9	14.2
M. bidentata	165	72.6	13.9	118	70.2	11.6	47	28.5	78.5	17.3
M. huberi	528	70.2	7.6	368	77.1	16.0	160	30.3	91.3	15.8
P. oppositifolia	71	67.1	9.2	59	67.0	9.7	12	16.9	67.8	6.2

Table 1-5. Percent frequencies of tree densities (≥ 45 cm DBH) by species within 10 m radius around trees selected for harvesting, distinguished between ROT and non-ROT trees.

Species	Densities of trees ≥ 45 cm DBH in an area of 10 m radius									
	Non-ROT trees					ROT trees				
	Total	0 (%)	1 (%)	2 (%)	≥3 (%)	Total	0 (%)	1 (%)	2 (%)	≥3 (%)
A. lecointei	35	66	26	6	3	19	79	21	0	0
D. excelsa	14	64	21	14	0	10	78	22	0	0
L. paraensis	17	88	6	6	0	4	75	25	0	0
M. bidentata	90	71	22	7	0	31	70	27	3	0
M. huberi	289	71	23	5	1	132	72	21	6	1
P. oppositifolia	51	76	24	0	0	8	63	25	0	13

Table 1-6. Analysis of the spatial correlations in the distributions of cavity trees (CAVs) among all trees ≥ 45 cm DBH inventoried in each 100 ha forest management unit (plots) according to the Moran's Index, considering lag distances of 50 m. Values marked with an asterisk refer to significant correlations.

Plot	N	Moran's Index	P > |Z|
A1	683	-0.0081	0.7562
A2	1605	-0.0009	0.9750
A3	1647	-0.0056	0.5954
A4	1405	0.0037	0.6880
AA	1208	-0.0066	0.6484
B1	1420	0.0130	0.2134
B2	1253	0.0010	0.8850
B3	1696	-0.0007	0.9884
B4	1685	-0.0006	0.9960
B5	1192	-0.0036	0.8294
C2	264	0.2440	<0.0001*
C3	678	0.0313	0.1200
C4	2054	0.0174	0.0199*
C5	1558	-0.0021	0.8809
D2	531	0.0982	0.0002*
D3	788	0.058	0.0016*
D4	1784	0.0115	0.1666
D5	1816	0.0007	0.8888
D7	881	0.0139	0.3536
E4	1396	0.0123	0.2493
E5	1546	-0.0051	0.6651
F2	1025	0.0324	0.0254*

Table 1-7. Parameter estimates for the logistic model of incidence of trees with stem cavities identified in ground surveys during forest inventories (CAVs).

Parameter	Estimate	Error	Chi-square	P
Intercept	-5.12	0.49	109.37	< 0.0001
DBH	0.02	0.01	7.77	0.0053
WD	5.13	0.68	57.11	< 0.0001
DBH*WD	-0.06	0.01	36.12	< 0.0001

Table 1-8. Parameter estimates for the general linear mixed model of incidence of cavity trees detected in forest inventories (CAVs).

Parameter	Estimate	Error	t-value	P
Intercept	-4.98	0.62	-8.01	< 0.0001
DBH	0.01	0.01	1.16	0.2470
WD	4.18	0.73	5.66	< 0.0001
DBH*WD	-0.05	0.01	-4.43	< 0.0001
Random plot effect	2.17	0.73		
Residual variance	0.88	0.01		

Table 1-9. Parameter estimates for the logistic model of incidence of trees classified as having extensive rotten cores or hollows among trees selected for logging (ROTs).

Parameter	Estimate	Error	Chi-square	P
Intercept	-4.50	0.39	131.05	< 0.0001
DBH	0.04	0.01	91.26	< 0.0001

CHAPTER 2
SHORT-TERM IMPACTS OF SELECTIVE LOGGING ON THE DIVERSITY OF DECAY FUNGI IN EASTERN AMAZONIA

Coarse woody debris (CWD; i.e., standing dead trees, fallen stems, and fallen branches ≥ 10 cm diameter) are typically more abundant after than before selective logging of naturally regenerated forests (Keller *et al.* 2004; Feldpausch *et al.* 2005; Palace *et al.* 2008). Selective timber harvesting, no matter how careful, kills some trees and damages others that subsequently suffer high mortality rates (Edman *et al.* 2007; Thorpe *et al.* 2008). CWD resulting from timber harvesting provides abundant habitats and resources for a diverse range of saprophytic organisms (Harmon *et al.* 1986). Among saprophytes, polypore fungi (basidiomycetes) are often the major determinants of the rates of wood degradation and nutrient turnover in forest ecosystems (Rayner & Boddy 1988; Schwarze *et al.* 2000).

Wood characteristics such as size, proportions of heartwood and sapwood, anatomical characteristics, and the presence of resins and extractives all influence decomposition rates and define the microhabitats available for fungal colonization (Harmon *et al.* 1986). Throughout the process of decomposition, changes in wood properties, temperature, moisture, and nutrient and oxygen availability create heterogeneous environments that affect the dynamics of communities of decay fungi (Rayner & Boddy 1988). Among the environmentally sensitive species are fungi that produce soft and ephemeral sporocarps and typically colonize small and fast-decomposing woody debris (Heilmann-Clausen & Christensen 2004; Bässler *et al.* 2010).

The decomposition process and the decomposer community also depend on the distribution and abundance of colonizable wood (Vasiliauskas *et al.* 2002; Siitonen *et al.*

2005). In a European beech forest, for example, Odor *et al.* (2006) showed that fungal species richness increased with the amount of CWD. In addition, the light intensity to which woody material is exposed alters microenvironmental characteristics and increases mortality rates of fungal species that produce thin and fragile, and therefore drought-susceptible, fruiting bodies (Boddy 2001).

Fungal communities establishing in woody substrates produced by logging may also vary with species' abundances prior to logging and with species-specific abilities to adapt to post-logging microenvironmental conditions (Edman *et al.* 2004; Heilmann-Clausen & Christensen 2005; Junninen *et al.* 2008). For instance, by altering microenvironmental conditions and generating an aggregated distribution of logs in early stages of decay, timber extraction activities may induce sexual reproduction of fungi present as mycelia prior to logging (Heilmann-Clausen & Christensen 2003; Stokland & Kauserud 2004; Junninen *et al.* 2008).

An increasing number of studies in temperate forests have examined the impacts of forest management activities and natural disturbances on the diversity of wood decay fungi, focusing on the conservation of rare species or on the spread of pathogens (Burrill *et al.* 1999; Heilmann-Clausen & Christensen 2003; Stokland & Kauserud 2004; Berglund *et al.* 2005; Jonsson *et al.* 2006; Josefsson *et al.* 2010; Olsson & Jonsson 2010). Results suggest that to preserve rare fungi that have preferences for certain host tree species or wood qualities, forest management strategies directed to maintaining a constant stock of CWD are required (Allen *et al.* 2000; Takahashi & Kagaya 2005; Anderson *et al.* 2010).

The few studies conducted on the diversity of wood decay fungi in natural tropical forests failed to reveal host specificity for most of the surveyed tree-fungus interactions (Lindblad 2000; Gilbert 2002; Gilbert *et al.* 2002; Urcelay & Robledo 2004; Beadle *et al.* 2007; but see Ferrer & Gilbert 2003). A better understanding of the dynamics of wood decay fungal communities in tropical forests managed for timber is essential to assess the impacts of timber harvesting on the maintenance of fungal diversity. In addition, because patterns of resource use and decay rates differ across fungal taxa, changes in fungal diversity that result from logging may also affect nutrient cycling (McGuire *et al.* 2010).

This study evaluates how low-intensity, selective, reduced-impact logging (RIL) affects the diversity of wood decay fungi in a *terra-firme* forest in the eastern Amazon Basin of Brazil. Selective logging effects on critical forest communities in the tropics, such as decay fungi, have been poorly researched. By monitoring the occurrence of fruiting bodies, I compared the diversity of fungi in a naturally regenerated forest area managed for timber using RIL techniques and an adjacent unlogged area. Prior to logging, pieces of CWD in each site were marked and then sampled for fungal basidiocarps once prior to logging and then twice at 5 month intervals for 10 months after logging to examine how post-logging conditions affected the composition and diversity of decay fungi. I predicted that the diversity of decay fungi is lower in logged then unlogged sites due to differences in species responses to post-logging microenvironmental conditions.

Methods

Study Site

This study was carried out in Fazenda Cauaxi (3°35' - 3°45' S, 48°15' - 48°25' W), a selectively logged naturally regenerated forest in the eastern Brazilian Amazon (Holmes *et al.* 2002; Keller *et al.* 2004). The area is covered by lowland tropical moist forest and is located in the Paragominas municipality, Para, Brazil (IBGE 1988). Oxisols prevail on the relative flat to slightly rolling terrain dissected by small creeks. The climate is moist tropical with annual rainfall averaging 2200 mm and a pronounced dry season that typically lasts from June to November (Costa & Foley 1998).

In 1995, a non-governmental institution named Instituto Floresta Tropical (IFT) established, in collaboration with the landowner (CIKEL Brasil Verde S.A.), what is currently recognized as the most important training center for reduced-impact logging (RIL) operations in the Amazon. Timber extraction is carried out in forest management areas divided into units (UTs) that average 100 ha. Each UT is divided into 50 x 50 m grids delimited by transects laid perpendicular to the main access road (Fundação Floresta Tropical 2002). Logging intensity is typically 20 – 25 m^3/ha (Holmes *et al.* 2002).

In comparison to conventional selective logging, RIL practices have fewer negative environmental impacts (e.g., diminish tree damage and the production of CWD) on the residual forest (Holmes *et al.* 2002; Putz *et al.* 2008), but alteration of forest structure nevertheless exceeds what is typically caused by treefalls. For example, in the forest in which I worked Schulze and Zweede (2006) estimated that canopy gaps in logged stands were larger than in unlogged adjacent forests, 277 ± 13.1 in the former versus 174 ± 17.6 m^2 (mean ± SE) in the latter. Likewise, Keller *et al.* (2004) verified that the

mean volumes of CWD stands in Fazenda Cauaxi subjected to RIL practices at an intensity of 3.3 trees harvested per ha (74.7 (0.6 SE) Mg ha^{-1}) were higher than in unlogged areas (55.2 (4.7 SE) Mg ha^{-1}).

Data Collection

Using transect-based surveys I compared the diversity of polypore fungi of an area of intact forest and a nearby forest management unit (UT) logged in August 2008. Only species in the Polyporaceae, Hymenochaetaceae, and Ganodermaceae were sampled. Three permanent 10 x 700 m transects (2.1 ha per area) oriented perpendicular to the main access road, > 20 m from the UT borders, and spaced at 200 – 300 m intervals were established in each forest area. All fallen CWD ≥ 2 m long and ≥ 10 cm thick at the center, and standing dead trees ≥ 10 cm DBH were marked and inspected prior to logging in August 2008 and then re-inspected twice after logging (January and June 2009) for the presence of basidiocarps. CWD that resulted from logging was not included in the study. In the case of standing dead trees, only basidiocarps growing within 3 m of the forest floor were sampled.

A total of 441 fallen logs and standing dead trees (225 and 216 samples in the control and logged areas, respectively) were marked and carefully inspected for the presence of sporocarps to assure that even hard-to-detect species were recorded (Lõhmus 2009). Hence, fungal incidence was estimated based on the number of samples of CWD on which the species was recorded. The number of basidiocarps per sample unit was not quantified because multiple fruiting bodies might have been produced by the same individual. By only recording fruiting bodies, I omitted species present only as mycelia, and therefore underestimated fungal diversity. That limitation notwithstanding, this survey strategy is accepted for sampling fungi over wide areas

(Lindblad 2001; Gilbert *et al.* 2002; Edman *et al.* 2004; Heilmann-Clausen & Christensen 2005; Olsson & Jonsson 2010).

CWD was classified into diameter ranges measured at the center of the log or at DBH height of standing trees: 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, and >71 cm and assigned to one of four decay classes based on Harmon *et al.* (1986): 1) recently fallen trunks or branches, or standing dead trees in initial stages of decomposition with > 80% of the bark still intact; 2) trees or logs with 50 – 80% of bark remaining and with most of the sapwood intact or only slightly degraded; 3) trees or logs in intermediate to late stages of decay with < 50% of bark present but only < 50% of the sapwood heavily decomposed; and, 4) trees or logs in advanced stages of decay with > 50% of the remaining sapwood heavily decomposed or non-recognizable, and softened or intensely decayed heartwood tissues.

All fruiting bodies were identified to species in the field or collected for laboratory identification based on microscopic features. Nomenclature follows Gilbertson & Ryvarden (1986; 1987), Ryvarden & Johansen (2000), and Ryvarden (2004). Vouchers of all specimens collected were deposited at the Herbarium of the National Institute for Research in the Amazon (INPA), Manaus, Brazil.

Data Analysis

I performed t-tests to evaluate intrinsic differences in CWD structure (diameter classes and decay categories) and in the number of fungal species between the control and logged areas prior to logging (i.e., during the first survey conducted in August 2008). To investigate changes in fungal species richness by log between sites and census periods, I used repeated-measures ANOVA. Due to the inequality of variances revealed with a Manchy's test, Wilks' lambda multivariate results were reported. Data

were log-transformed (or log(x+1))-transformed in the case of species counts) to meet normality assumptions.

I used sample-based (or Coleman) rarefaction curves to compare fungal species richness between the control and logged areas, compiled from presence / absence data collected in the three censuses (Gotelli & Colwell 2001). Rarefaction curves were constructed in EstimateS version 8.2 based on 100 randomizations of species accumulation curves (Colwell 2000). To correct for the between site difference in the number of pieces of CWD sampled, 216 randomly selected samples were considered for the control area. Non-parametric indexes Chao 2 and ICE were used to estimate total species richness, and Simpson's index in its reciprocal form (1/D) was used to estimate species diversity by site (Colwell 2000; Magurran 2004; Gotelli & Colwell 2001).

To investigate differences in species composition in the control and logged areas over time, I performed nonmetric multidimensional scaling ordination using PRIMER version 6 (Clark & Gorley 2006). Data from the three transects per area were combined for this analysis. To avoid unwarranted effects of extremely rare species on the calculation of similarities among sites, only species recorded more than once were considered to investigate species composition, which represented 42% of the species and 24% of the specimens recorded. Count data were log transformed ($\log_{10}(x + 1)$) and Sorensen's distance measures were used to determine similarities based on presence/absence data. To perform the ordination, 100 runs with real data were used and the adequacy of the results was analyzed based on the stress value of the final interaction.

The effects of the site (logged or control), type of substrate (CWD on the forest floor or dead standing trees), decay stage, and tree or log diameter class on the total fungal species richness by sampled piece of CWD were analyzed using negative binomial regression models. The dispersion parameter was significantly different from 0, justifying the use of a negative binomial model. Model selection was based on the backward elimination of non-significant variables included in the full model with all variables and possible interactions; models were compared using chi-squared tests of log likelihood differences, and considered different when $p < 0.05$. All statistical analyzes were performed with SAS Software 9.2 (2009).

Results

A total of 187 specimens of 55 species were recorded in this study, 97% of which were identified to species. Most species (73%) were in the Polyporaceae, with 40 species in 25 genera; other taxa encountered included five species of *Phellinus* (Hymenochaetaceae), and 3 species of *Ganoderma* (Ganodermaceae). In the control site, 87 specimens representing 37 fungal species were collected from 167 fallen logs and 56 standing dead trees, while 100 specimens representing 36 species were collected in 169 fallen logs and 47 standing dead trees at the logged site. *Phellinus gilvus* (Sch.) Pat., *P. rhytiphloeus* (Mont.)Ryv., *Rigidoporus microporus* (Fr.) Overeem, and *Trametes modesta* (Fr.) Ryv. were the most abundant species in both sites (Table 2-1).

Average diameter and decay class of CWD samples marked prior to logging and re-sampled twice after logging differed between the logged and control sites. Most CWD (≥ 75%) in both sites was on the ground, with 56 (25%) and 47 (22%) standing dead trees >10 cm DBH per hectare in the unlogged and logged sites respectively (Table 2-

2). Fallen CWD and standing dead trees in the logged site were larger in diameter and less decayed than logs in the control area (Figure 2-1; Table 2-2).

Although the mean number of fungal species per sample of CWD was lower in the control than in the logged site before logging ($t_{439} = 0.03$, $p = 0.003$; Figure 2-2), this difference disappeared after logging. Considering the three census periods from August 2008 to June 2009, the number of fungal species found by sample of CWD was similar between sites ($F_{1,439} = 0.91$, $p = 0.34$) and among census periods ($F_{2,438} = 1.78$, $p < 0.17$; Figure 2-2). The interaction between site and census period ($F_{1,439} = 4.44$, $p = 0.01$) indicates that fungal species richness by sample of CWD varied differently between sites through time. While in the control area no differences over time were detected, in the other site the number of species recorded by sample was substantially higher before than after logging (Figure 2-2).

Rarefaction curves for the logged and control areas did not asymptote over the 2.1 ha area sampled through the 10-month sampling period, indicating that the number of samples of CWD inspected and duration of the study were insufficient to capture each site's fungal species richness. Curves representing species accumulation in the two sites overlapped until approximately half of the 216 samples of CWD analyzed by site were recorded, denoting similar species richness between sites (Figure 2-3). Chao 2 and ICE estimates of species richness were 39.0 and 43.9 for the logged site and 38.4 and 43.3 for the control site, respectively. Species diversity expressed as the reciprocal of Simpson's diversity index (1/D) was high for both sites: 19.01 and 18.15 for the control and logged areas, respectively.

Species composition varied substantially between the logged and the unlogged areas and among census periods (Figure 2-4). Only 8 of the 55 sampled species were collected more than 5 times, but 2 species (*Phellinus gilvus* and *Trametes modesta*) were sampled in all sites and all censuses. Approximately 33% of the species were shared between the logged and control areas, and 42% of all species were recorded only once (Table 2-1).

The negative binomial model used to predict fungal species abundance by CWD sample included diameter class, substrate type, and decay stage (-2 Log Likelihood = 724.68; Table 2-3). Site and all two-way interactions evaluated with the full model were not significant, and were therefore dropped from the best-fit model by backwards elimination. Estimates of species richness showed that the most species were found on fallen CWD and standing dead trees in intermediate stages of decay (classes 2 and 3, Figure 2-5A). Additionally, species richness was highest for samples of CWD > 70 cm of diameter (Figure 2-5B). Finally, more fruiting bodies were recorded on fallen CWD than on standing dead trees (Figure 2-5C).

Discussion

Despite the higher fungal species richness by sample prior to logging, higher average diameter, and lower average decay stage of the sampled pieces of CWD in the logged area than in the control area, the mean number of fungal species per fallen log or standing dead tree was similar in the two areas when data from all censuses were combined. These results contrast with previous studies that showed a direct relationship between the size of pieces of CWD and fungal species richness, and an inverse relationship between wood decay stage and the number of fungi recorded from CWD

(Allen *et al.* 2000; Heilmann-Clausen & Christensen 2004; Rolstad *et al.* 2004; Odor *et al.* 2006).

Based on the interaction between site and time, I conclude that the number of fungi recorded by sample of CWD varied differently through time in the control and logged areas. The faster decline in species richness through time in the logged area may have resulted from delayed responses of the fungi to the microenvironmental conditions created by logging (Vasiliauskas *et al.* 2002). A high percentage of occasional species with low specificity for qualities of woody substrates, as observed in previous studies conducted in tropical forests, also contributes to this variation (Lindblad 2001; Ferrer & Gilbert 2003).

Large differences in fungal species composition between logged and unlogged areas and substantial temporal fluxes in species composition indicate that less common species may exhibit a seasonal fruiting pattern, being represented only as mycelia during the rest of the year. Seasonal changes in wood moisture contents and temperature are known to affect species survival and reproduction (Rayner & Boddy 1988; Barker 2008). Seasonal microenvironmental variation intensified by the increased post-logging canopy opening in the logged forest may have contributed to the rapid post-logging decrease in species richness by sample in the logged stand. In contrast to previous studies that showed a positive relationship between CWD abundance and fungal species richness, I did not observe this response (Norden & Paltto 2001; Keller *et al.* 2004; Heilmann-Clausen & Christensen 2005; Jonsson *et al.* 2006).

A different sampling methodology would be required to address questions related to effects of spatial heterogeneity of woody substrates within and between the logged

and control forests (e.g., Josefsson *et al.* 2010). A longer time sequence would have been needed to incorporate delayed responses of late successional fungal species to logging-induced environmental changes and to understand how logging affects the composition of fungal communities through time (Vasiliauskas *et al.* 2002; Olsson & Jonsson 2010).

CWD decay stage, diameter class, and substrate were the only variables among the ones tested that affected total species richness. As observed in less diverse European forests, more fruiting bodies were recorded on CWD samples in intermediate than initial or late stages of decay (Heilmann-Clausen & Christensen 2004; Jonsson *et al.* 2008; Josefsson *et al.* 2010). Wood in initial stages of decomposition was probably not an appropriate substrate for colonization by polypores due to the continued presence of high concentrations of phenolic compounds. At the other end of the wood decay spectrum, anaerobic conditions generated by moisture saturation of heavily decayed woody substrates and changes in the concentration of lignin and cellulose inhibit the growth of many species of wood decay fungi (Harmon *et al.* 1986; Rayner & Boddy 1988; Schwarze *et al.* 2000).

As reported in studies in temperate forests, species richness by sample of CWD was affected by the dimensions of the wood: the most species were recorded in woody materials > 70 cm diameter (Heilmann-Clausen & Christensen 2004; Heilmann-Clausen & Christensen 2005). This pattern may be a result of a larger surface area available for the establishment of decay fungi, a larger volume of decayable wood, and a slower degradation of woody materials with high proportions of heartwood with high concentrations of constitutive defense compounds (Harmon *et al.* 1986; Rayner &

Boddy 1988). Fallen logs were apparently a better substrate for fungi than standing dead trees, which may have been a consequence of the reduced surface available for fungal colonization due to drier conditions inhibiting fungal growth on portions of trees that were not in close proximity to the ground (Harmon *et al.* 1986).

Contrary to what was expected, no significant differences in fungal species richness were observed between the logged and control areas. Changes in the composition of fungal communities through time indicated that the growth and reproduction of species that produce drought-susceptible fruiting bodies (e.g., *Polyporus* spp. and *Gloeoporus thelephoroides*) may have been negatively affected by post-logging microenvironmental conditions such as higher daily fluctuations in temperature and moisture, and exposure to direct sunlight (Edman & Jonsson 2001; Junninen *et al.* 2008). On the other hand, reproduction species considered to be tree pathogens (*Phellinus gilvus*, *P. rhytiphloeus, Rigidoporus biokoensis* and *R. microporus)* was apparently not affected by logging activities.

Few studies have examined the responses of fungal communities to logging in tropical forests (Drechsler-Santos *et al.* 2010). My results showed no short-term impacts of selective logging on the diversity of wood decay fungi. Further research will be needed to elucidate the longer-term impacts on species diversity, and how tropical fungal communities respond to post-logging microenvironmental conditions over larger spatial scales. The relationships between fungal species richness and the explanatory variables I tested indicate that positive long-term impacts are expected as consequence of an increase in the size and number of fallen logs in intermediate stages of decomposition.

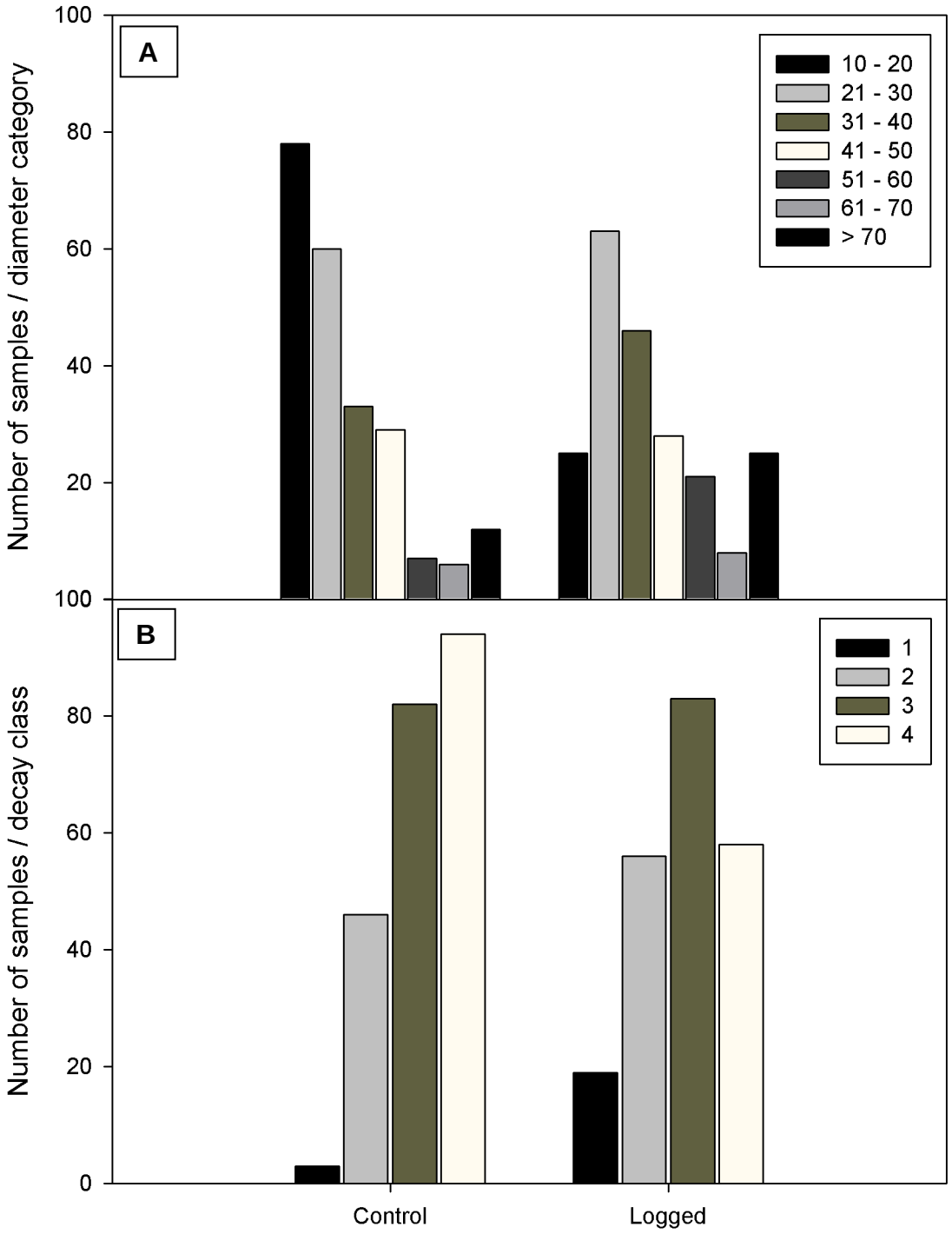

Figure 2-1. Distribution of sampled coarse woody debris (CWD) by A) diameter range measured in cm, and B) decay categories (1 – 4 from light to intensely decayed wood) in the control (N = 225) and logged sites (N = 216).

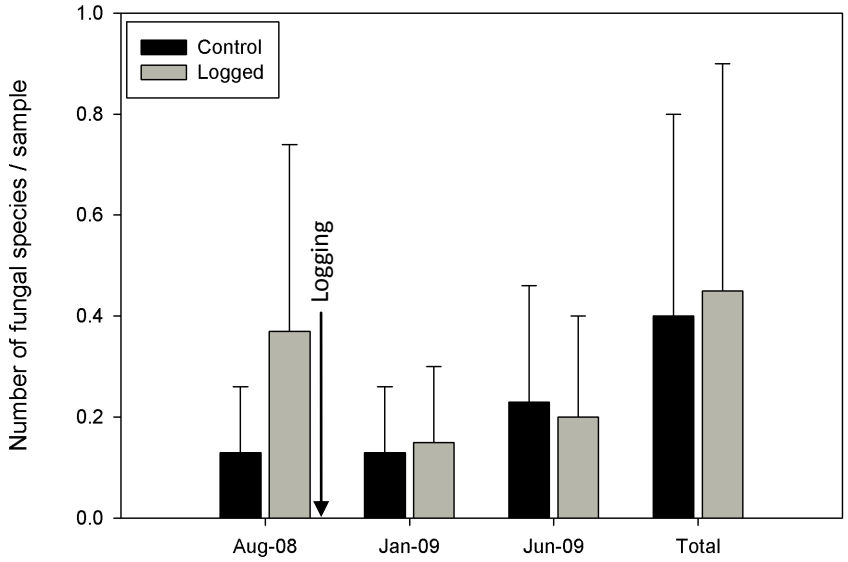

Figure 2-2. Mean (± SE) number of fungal species by sample of CWD in each census period and for all periods together (sample sizes: N = 225 in the control, and N = 216 in the logged site.

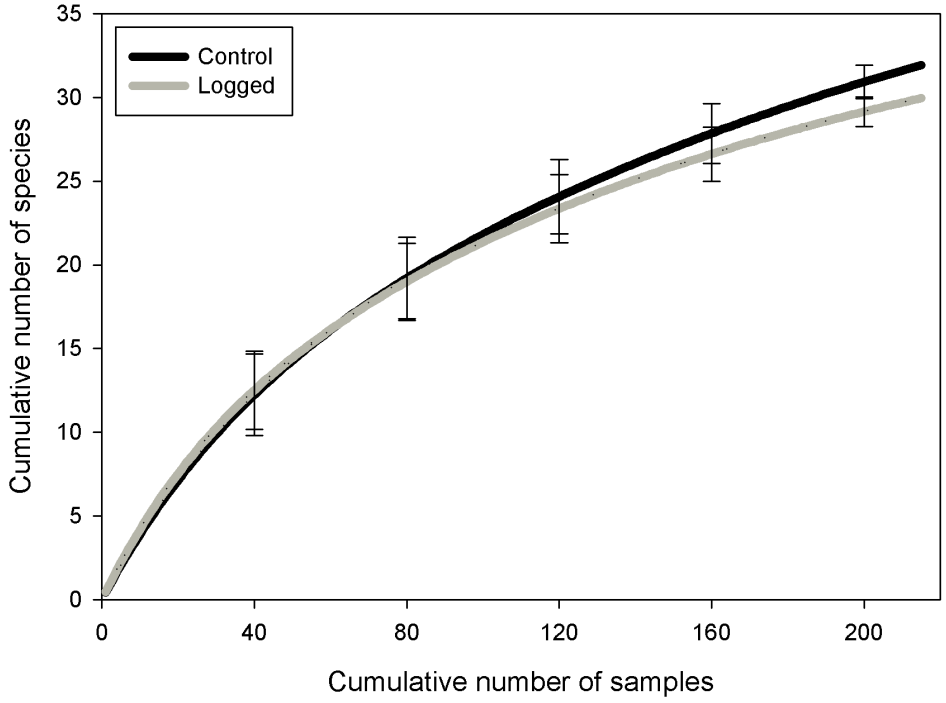

Figure 2-3. Coleman rarefaction curves of fungal species richness by sample in the control and logged sites for all census periods compiled (N = 216 per site). Error bars were estimated based on 95% confidence intervals for the mean.

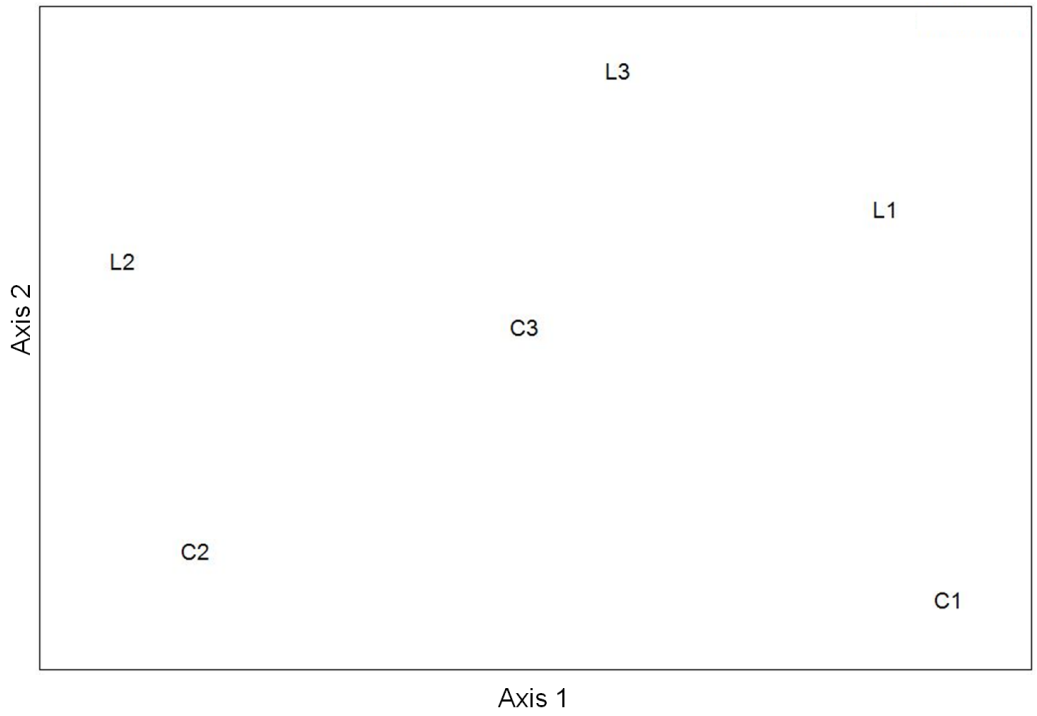

Figure 2-4. Two-dimensional solution of the nonmetric multidimensional scaling (NMS) ordination comparing species composition in each census period (numbered 1 – 3) and site (L = logged, N = 216; C = control, N = 225). Species that occurred in only one sample were not considered in this analysis.

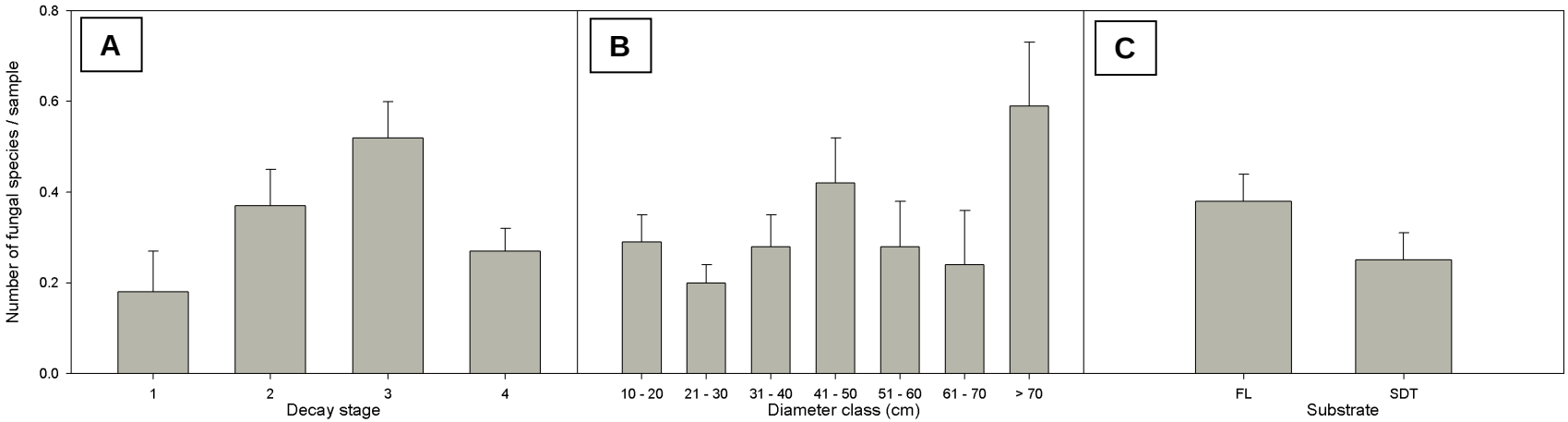

Figure 2-5. Model predictions of fungal species richness by sample of CWD (N = 441) for the significant variables A) decay stage, B) diameter class, and C) substrate (i.e., CWD sampled; FL = fallen logs, and SDT = standing dead trees).

Table 2-1. Fungal species richness by sample for each site and census period. Taxa that produce drought-susceptible fruiting bodies are marked with asterisks.

	Control				Logged			
Species	Aug-08	Jan-09	Jun-09	Total	Aug-08	Jan-09	Jun-09	Total
Abundisporus subflexibilis (Berk. & W. Curtis) Parmasto	-	-	-	-	4	-	2	6
Antrodiella resurpina (Berk. & Curt.)*	2	-	-	2	-	-	1	1
Ceriporia ferruginicincta (Murr.) Ryv.*	-	-	1	1	-	-	1	1
Ceriporia microspora (Lindblad & Ryvarden)*	-	-	1	1	-	-	-	-
Ceriporia spissa (Schw .: Fr.) Rajch.*	-	-	-	-	1	-	-	1
Coriolopsis cfr floccosa (Junhgh.) Ryvarden*	-	-	-	-	1	-	-	1
Dichomitus setulosus (Hrennings) Masuka & Ryvarden*	-	-	-	-	1	-	-	1
Earliella scabrosa (Pers.) Gilbn. & Ryv.	-	-	-	-	1	-	2	3
Flavodon flavus (Kl.) Ryv.	-	-	1	1	-	-	2	2
Fomes fasciatus Cooke	-	-	-	-	1	-	-	1
Ganoderma amazonense Weir.	-	-	1	1	-	-	-	-
Ganoderma australe (Fr.) Pat	-	-	1	1	2	1	2	5
Ganoderma oerstedtii (Fr.) Murrill	-	-	1	1	-	-	-	-
Gloeoporus thelephoroides (Hook.) Cunn.*	-	-	-	-	2	-	-	2
Hexagonia papyraceae Berk.	2	-	-	2	-	-	-	-
Megasporoporia setulosa (Henn.) Rajch.	-	-	-	-	1	-	-	1
Nigrofomes melanodermus (Mont.) Murrill	-	-	1	1	2	-	3	5
Oxyporus obducens (Pers.) Donk	-	2	-	2	-	-	-	-
Perennioporia latissima (Bres.) Ryvarden	-	-	1	1	-	-	-	-
Perenniporia inflexibilis (Berk.) Ryvarden	-	-	-	-	-	1	-	1
Perenniporia medulla painis (Pers.) Donk.	-	-	-	-	1	-	-	1
Phellinus calcitratus (Berk. & Curt.) Ryvarden	-	-	1	1	-	-	-	-
Phellinus ferrugineo-velutinus (Henn.) Ryv.	1	-	1	2	-	-	-	-
Phellinus gilvus (Schw.) Pat.	3	3	3	9	4	1	3	8
Phellinus homrichae M.A. Souza nov. sp.	-	-	-	-	-	1	1	2
Phellinus noxius (Corner) G. Cunningh.	-	-	1	1	-	-	-	-
Phellinus punctatus (Fr.) Pilat	1	0	1	2	1	-	1	2
Phellinus rhytiphloeus (Mont.) Ryvarden	1	1	8	10	3	-	3	6
Phellinus spp.	1	-	-	1	2	-	-	2

Table 2-1. Continued.

Species	Control				Logged			
	Aug-08	Jan-09	Jun-09	Total	Aug-08	Jan-09	Jun-09	Total
Polyporus dictyopus Mont.*	-	1	-	1	-	-	1	1
Polyporus guianensis Mont*.	-	1	-	1	-	1	-	1
Polyporus leuprieurii Mont.*	-	1	1	2	-	1	-	1
Polyporus tricholoma Mont.*	-	-	-	-	1	-	-	1
Polyporus varius Fr.*	-	-	-	-	-	2	-	2
Porogramme albocinata (Cooke & Massee) Lowe*	-	1	-	1	-	-	-	-
Pycnoporus sanguineus (Fr.) Murr.*	-	-	1	1	-	-	-	-
Rigidoporus biokoensis (Lloyd) Ryv.	-	6	1	7	-	4	-	4
Rigidoporus concrescens (Mont.) Rajchenb	-	1	-	1	-	-	-	-
Rigidoporus lineatus (Pers.) Ryv.	-	2	-	2	-	3	-	3
Rigidoporus microporus (Fr.) Overeem	-	5	3	8	-	7	2	9
Rigidoporus ulmarius (Fr.) Imazeki	-	-	-	-	-	-	1	1
Trametes cingulata Berk.	-	-	1	1	-	-	-	-
Trametes elegans (Spreng . : Fr.) Fr.	-	1	2	3	-	-	-	-
Trametes lactinea Berk.	2	-	-	2	-	-	-	-
Trametes marianna (Pers.) Ryv.	-	-	-	-	-	1	-	1
Trametes modesta (Fr.) Ryv.	2	1	5	8	6	2	7	15
Trametes ochroflava Cooke	1	1	-	2	-	-	-	-
Trametes versicolor (Fr.) Pilat	1	-	-	1	2	-	-	2
Trechispora regularis (Murr.) Liberta*	-	-	-	-	-	1	-	1
Morphospecies 1	-	-	-	-	2	-	-	2
Morphospecies 2	1	-	-	1	-	-	-	-
Morphospecies 3	-	-	-	-	-	-	2	2
Morphospecies 4	-	-	1	1	-	-	-	-
Morphospecies 5	-	-	1	1	-	-	-	-
Number of CWD sampled	225	225	225	225	216	216	216	216
Number of species	12	15	24	37	21	14	15	36
Numbers of specimens recorded	17	27	42	87	40	27	33	100

Table 2-2. Distribution of coarse woody debris (CWD) sampled in the control and logged sites according to the type of substrate, diameter class, and decay stage. Values refer to total number of samples by site and substrate, and mean diameter or decay class ± SE.

CWD	Control	Logged	t	d.f.	P
N	225	216			
Logs	169	169			
Dead standing trees	56	47			
Diameter class	2.52 ± 0.11	3.38 ± 0.12	5.11	439	0.001
Decay stage	3.19 ± 0.05	2.83 ± 0.06	4.29	439	< 0.001

Table 2-3. Variables and estimates for the best-fit negative binomial regression model to predict fungal species richness by sample.

Parameter	Estimate	d.f.	LEM	SEM
Intercept	-0.46	1		
Decay stage				
1	-0.41	430	0.18	0.09
2	0.34	430	0.37	0.08
3	0.66	430	0.52	0.08
4	0		0.27	0.05
Diameter class				
10 – 20	-0.73	430	0.29	0.06
21 – 30	-1.07	430	0.20	0.04
31 – 40	-0.77	430	0.28	0.07
41 – 50	-0.34	430	0.42	0.10
51 – 60	-0.74	430	0.28	0.10
61 – 70	-0.89	430	0.24	0.12
> 70	0		0.59	0.14
Substrate				
FL	-0.41		0.25	0.06
SDT	0		0.38	0.06
Scale	0.28			
Pearson χ^2 / d.f.	1.08			

d.f., degrees of freedom; LME, least square means; SEM, standard error of the mean; FL, fallen logs; SDT, standing dead trees.

CHAPTER 3
HEARTWOOD DECAY IN LIVING TREES IN EASTERN AMAZON

Heartwood in living trees is enclosed in layers of sapwood and bark that generally provide effective barriers against pathogens (Pearce 1996). Heartwood decay (heart-rots and stem hollows) thus usually follows stem or root damage that allows pathogens direct access to xylem tissues (Shigo & Hillis 1973; Rayner and Boddy 1988). After bark is breached, sapwood tissues may respond by developing additional chemical and anatomical barriers to compartmentalize potential pathogens (Shigo 1984; Blanchette 1992). Decay-causing organisms successfully gain access to heartwood when this compartmentalization process in the sapwood fails or through deep wounds (Shigo 1989). In this study conducted in a tropical rainforest in Amazonian Brazil, I explore some of the characteristics of trees with hollow stems that are related to their susceptibility to heartwood decay.

High concentrations of phenolic extractives in heartwood make it a harsh environment for most potential decomposers (Rayner and Boddy 1988). Additionally, wood anatomical traits such as high density, narrow vessels, and narrow parenchyma rays provide mechanical barriers to decay spread (Romero *et al.* 2009). Expansion of decay organisms such as fungi and termites through tree stems varies with the efficacy of inducible and constitutive tree defenses (Pearce 1991; 1996; Behrendt & Blanchette 1997; Abe *et al.* 2000; Boddy 2000; Nsolomo & Venn 2000). Such defenses, in turn, vary with tree age, species, and environmental conditions experienced by a tree (Griffith & Boddy, 1990; 1991; Chao *et al.* 2008; 2009).

Some wood decay fungi are tolerant of constitutive heartwood defenses and capable of breaking down cellulose and lignin. Nevertheless, decay is a successional

process that requires an initial breakdown of phenolic compounds by endophytic fungi, bacteria, and other microbes (Blanchette & Shaw 1978; Carroll 1988; Osono *et al.* 2009; McGuire *et al.* 2010). As these organisms slowly colonize and modify the chemical composition of wood tissues, they create microenvironmental conditions appropriate for the spread of decay fungi, mostly basidiomycetes, which produce chitinolytic enzymes used to digest plant cell walls (Rayner and Boddy 1988; Blanchette 1992).

Identifying fungal species that decompose heartwood is challenging due to the frequent lack of fruiting bodies, which are the clearest indicators of their presence and identity (e.g., Edman & Jonsson 2001; Ferrer & Gilbert 2003; Josefsson *et al.* 2010). Molecular approaches to assessing fungal diversity, such as sequencing of internal transcribed spacer (ITS) of the ribosomal DNA, have been used in temperate forests to identify mycorrhizal species as well as decay fungi in living trees (Lim *et al.* 2005; Guglielmo *et al.* 2007; Guglielmo *et al.* 2010). In these studies, species-specific primers were developed to allow the amplification of ITS sequences from each taxon (Vainio & Hantula 2000; Lynch & Thorn 2006). Despite the existence of this and other methods for assessing the diversity of fungal species in the absence of fruiting bodies, much remains unknown about wood decay fungi in tropical forests (Liew *et al.* 1998; Vandenkoornhuyse *et al.* 2002).

Thanks to a symbiotic association with microbes, several species of termites share with decay-fungi the ability to digest wood in living trees (Roisin *et al.* 2006). Active and abandoned termite colonies are commonly found in hollow cores of living trees (Apolinario & Martius 2004; Werner & Prior 2007). Some species can only feed on wood in advanced stages of decomposition in which nitrogen contents are elevated and toxic defense substances have already been rendered ineffective by wood-decay fungi (Abe

et al. 2000; Cornelius *et al.* 2002). On the other hand, some chemical compounds produced by wood degrading fungi repel termites (Esenther *et al.* 1961; Amburgey & Beal 1977; Amburgey 1979; Yanagawa *et al.* 2010).

Tree species or even trees of the same species growing under contrasting environmental conditions vary in their resistance to the growth of decomposers (Pearce 1996; Amusant *et al.* 2004). Such variation could result in host-pathogen specificity, but the few studies conducted in tropical forests classified most decay fungi as generalists (Lindblad 2000; Gilbert 2002; Gilbert *et al.* 2002; Urcelay & Robledo 2004; Berglund *et al.* 2005; Beadle *et al.* 2007). Similarly, several species of tropical wood-feeding termites do not show host specificity (e.g., Apolinario & Martius 2004; Zanetti *et al.* 2005), with the exception of a few species of subterranean termites in genera such as *Coptotermes, Reticulitermes,* and *Zootermopsis;* in bioessays these species were able to differentiate between wood extractives from different species and select for particular wood qualities (Morales-Ramos & Rojas 2003; Ohmura *et al.* 2006; Judd & Corbin 2009; Wong & Lee 2010).

I investigated how tree dimensions, wood anatomical traits, and microenvironmental characteristics influenced tree susceptibility to heartwood decay of five economically important timber tree species in a tropical forest in the eastern Amazon Basin in Brazil. I predicted that heartwood hollow dimensions are directly related to vessel and ray density and terrain slope, and inversely related to wood density. To assess the diversity of fungal species colonizing heartwood tissues, fungal colonies that could potentially cause wood decay were isolated from heartwood tissue of the selected species and identified using molecular biology techniques. I predicted that fungal species colonizing heartwood tissues differ among trees thanks to wood

anatomical characteristics. Additionally, I predicted that fungal species richness is directly related to heartwood hollow size. Termites collected from heartwood hollows were identified to assess relationships between tree characteristics, fungal species richness, and termite distribution. I predicted that termite colonies are more likely to be found in trees with larger stem hollows and lower wood density, and that the presence of termites is affected by the number of fungal species isolated from heartwood.

Methods

The Study Site

Fazenda Rio Capim is in the Paragominas municipality of Para, Brazil (2º25' - 4º09'S, 46º25' - 48º 54'W). The climate is tropical moist with a well defined dry season, average annual precipitation of 1766 mm, and an average temperature of 27.2^{o}C (Watrin & Rocha 1992). The natural vegetation is tropical moist forest (IBGE 1991). The area is managed for timber using reduced-impact logging techniques (RIL) by CIKEL Brasil Verde S.A. RIL practices consist of carefully planning all aspects of timber extraction to diminish the deleterious impacts of logging on the residual forest by minimizing the infrastructure necessary for timber extraction, protecting riparian zones, establishing protected areas, and reducing of the amount of coarse woody material left on the forest floor(Putz *et al.* 2008).

Timber extraction was carried out in forest management units (UTs) of approximately 100 ha in which all commercial timber trees ≥ 45 cm of diameter at breast height (DBH) were identified and mapped one year prior to logging (Fundação Floresta Tropical 2002). Immediately before logging, all trees marked for extraction were tested for the presence of hollows or heartwood decay by inserting a chainsaw into the trunk

between the buttresses at about 50 cm from the ground. As a general rule, felling only happened if a tree's hollow or rotten core did not exceed 30 cm in diameter.

Heartwood Hollow Dimensions

In an area of 253 ha, I sampled 30 recently felled trees with hollow stems or rotten cores of *Manilkara huberi* (Ducke) A. Chev., 30 of *M. bidentata* (A.DC.) A. Chev. sp. *surinamensis* (Miq.) Penn. (both Sapotaceae), 30 of *Pseudopiptadenia psilostachya* (DC.) G.P. Lewis & M.P. Lima, eight of *Dinizia excelsa* Ducke (both Mimosaceae), and 20 of *Astronium lecointei* Ducke (Anacardiaceae). These species were selected on the basis of their abundance in the study site and because loggers reported that they are prone to having hollow trunks. The selected species vary in wood anatomical traits such as density and chemical defenses including the presence of sapwood latex (*Manilkara* spp. and *A. lecointei*). Only trees > 10 m from their nearest conspecific were sampled. Sampling was restricted to one area of 253 ha to minimize environmental heterogeneity that could influence tree susceptibility to decay. Sample sizes were smaller for *D. excelsa* and *A. lecointei* than for the other species because they occurred at lower densities and were less frequently hollow.

In August and September 2008 soon (1-5 days) after logging, trunk diameters, terrain slopes, 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 area that was degraded but not hollow was disregarded in this analysis. Two wood samples of 6000-7000 cm^3 representing the length of each tree radius were taken from opposite sides of the trunk to quantify anatomical traits and wood density.

Three 2 x 2 x 2 cm samples were extracted from the heartwood in these sections at a distance < 10 cm from the sapwood. Wood density (WD) was determine by water displacement (N = 3 samples/tree; N = 30 trees/species for *M. huberi*, *M. bidentata*, and *P. psilostachya,* N = 20 trees for *A. lecointei,* and N = 8 trees for *D. excelsa*). Pearson's correlations were used to explore relationships among tree basal area, hollow area, slope, and wood density. Variables fungal species richness by tree and terrain slope were log(x + 1)-transformed, and square-root transformation was applied to hollow area data to meet normality assumptions. For the four tree species with N ≥ 20 trees sampled, variation in hollow and tree basal areas were explored using one-way analysis of variance (ANOVA) followed by Tukey HSD post-hoc comparisons. All statistical analyzes were performed with SAS Software 9.2 (2009).

Heartwood Anatomy

Histological analysis of wood anatomy was performed on wood transverse sections (N = 5 sections/species; N = 10 trees/species for all tree species but *D. excelsa,* with N = 8 trees) that were previously soaked in a 1:1 solution of glycerin and distilled water for at least 24 h (N = 5 samples/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/section, ray width at its non-dilated extent, and distance between adjacent rays measured along 2 mm transects/section. For this analysis, I only used wood density values that corresponded to the trees sampled for wood anatomy.

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 the dimension of heartwood hollows. Pearson's correlations were used to explore relationships among tree basal area and wood anatomical traits. Among species differences in traits were investigated using one-way analysis of variance (ANOVA) followed by Tukey HSD post-hoc comparisons. All statistical analyzes were performed with SAS Software 9.2 (2009).

Fungal Diversity

Three wood samples of approximately 1 cm^3 were collected from heartwood directly adjacent to hollows in each tree at a distance of 50 cm from the ground (N = 30 trees/species for *M. huberi*, *M. bidentata*, and *P. psilostachya,* N = 20 trees for *A. leointei* and N = 8 trees for *D. excelsa*). Samples were stored in sterilized plastic vials for approximately 5–10 days before laboratory analyses began. Wood sections < 0.5 cm long x 0.5 cm wide were extracted from the inner portions of the wood samples, sterilized in sodium hypochlorite for 90 s, rinsed in distilled autoclaved water, placed on 3 x 3 cm sterilized filter paper to dry, and stored in sterilized Petri dishes with no medium. Five sections per tree were placed on malt-agar plates, and stored in a dark chamber at 37^oC until fungal colonies started to develop. Morphologically distinct colonies were then isolated on separated malt-agar plates and kept in a dark chamber for continued mycelial growth and subsequent extraction. Isolates were stored in the Fungal Collection at the National Institute of Research in the Amazon (INPA), Manaus, Brazil.

Five or more agar plugs were extracted from each isolate, transferred to 150 ml Erlenmeyer flasks containing 50 ml of potato-dextrose broth (PDB), and kept under 90 rpm agitation at room temperature for 5–10 days. Mycelia were then dried under sterilized conditions and ground in an autoclaved mortar using liquid nitrogen. Frozen

ground mycelia were transferred to 2 ml microcentrifuge tubes (approximately 750 µl of mycelia/tube, 1–4 tubes/isolate) containing 700 µl extraction buffer (200 mM of Tris–HCl 1 M (pH 8.0), 20 mM of EDTA (pH 8.0) 0.5 M, 0.8 % of SDS 10 %, and 200 mM of NaCl 5 M), and then incubated for 50 min at 65^{o}C. After incubation, 700 µl phenol was added to the microcentrifuge tubes, which were then centrifuged for 10 min at 12,000 rpm. Approximately 600 µl of the supernatant was transferred to a 1.5 ml tube followed by the addition of 600 µl of a phenol:chloroform (1:1) solution. Tubes were again centrifuged for 10 min at 12,000 rpm. Supernatant was collected and transferred to 1.5 ml tubes with 600 µl of a chloroform:alcohol isoamilic 24:1 solution, which was then centrifuged at 12,000 rpm for 10 min. Finally, 600 µl of the supernatant was transferred to a new 1.5 ml microcentrifuge tube, to which was added 45 µl NaOH 3 M and 800 µl ice-cold absolute ethanol. Samples were kept at -18^{o}C overnight and then centrifuged at 12,000 rpm for 15 min. Supernatant was discarded, DNA dried at room temperature, and subsequently re-suspended in 100 µl TE buffer (Tris – HCl (pH 8.0) 1 M, EDTA (pH 8.0) 0.5 M). RNAse mix (100 µg of RNAse A and 10 U of RNAse T1) was added to the final solution after which tubes were incubated at 37^{o}C bath for 30 min to allow RNA digestion.

Internal transcribed spacer (ITS) sequences of ribosomal DNA of each fungal isolate were amplified in a thermal cycler using primers ITS-1 and ITS-4. Polymerase chain reactions (PCRs) contained 25 mM deoxynucleoside triphosphates, 0.1 mM of ITS-1, 0.1 mM of ITS-4, 1x PCR buffer with 1.5 mM $MgCl_2$, 1 µl of DNA, and 1 U of *Taq* polymerase (Qiagen). The reaction consisted of an initial denaturation step at 96^{o}C for 4 min, followed by 35 cycles of denaturation at 95^{o}C for 1 min, annealing at 55-57^{o}C for 45 s, and extension at 72^{o}C for 35 s, and followed by a final 10 min extension period at

72^{o}C. PCR products were quantified by electrophoresis in 1.3 % agarose gels. Amplified sequences were purified using the Illutra GFX^{TM} PCR DNA Purification Kit (GE Healthcare) following manufacturer's instructions. Either primer ITS-1 or ITS-4 was used for DNA sequencing of each isolate. Fungal taxa were determined based on a search of the GenBank database using the Basic Local Alignment Search Tool (BLAST; http://www.ncbi.nlm.nih.gov/BLAST/). Only taxa with E-values = 0 and maximum identity > 90% were reported.

Sample-based (or Coleman) rarefaction curves were used to compare fungal species richness considering all morphologically distinct colonies among the four tree species with N ≥ 20 trees sampled (Gotelli & Colwell 2001). Rarefaction curves were constructed in EstimateS version 8.2 based on 100 randomizations of species accumulation curves (Colwell 2000). Non-parametric indexes Chao 2 and ICE were used to estimate total species richness, and Simpson's index of diversity (1 – D; D = Simpson's index) was used to estimate fungal diversity by species (Colwell 2000; Magurran 2004; Gotelli & Colwell 2001). Pearson's correlations were used to explore relationships between fungal species richness and tree basal area, hollow area, wood density, and slope of the terrain.

A nonmetric multidimensional scaling ordination using PRIMER version 6 was performed to explore differences in fungal species composition among tree species (Clark & Gorley 2006). For this analysis, only fungal species recorded more than once were considered. Count data were log transformed ($\log_{10}(x + 1)$) and Sorensen's distance measures were used to investigate similarities based on presence/absence. Ordinations were performed with 100 runs with real data.

Termite Assemblages

Termites forming colonies inside heartwood hollows of the selected trees were collected 1-5 days after logging and identified to species. Samples were stored in the invertebrate collection at INPA. A logistic model was created to predict the occurrence of colonies of *Coptotermes testaceus* (L.), the most abundant termite species sampled, as a function of tree species, wood density, slope, fungal species abundance, and relevant interactions. Data were 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-square tests at $p < 0.05$. All analyses Pere performed with SAS Software 9.2 (2009).

Results

Heartwood Hollow Dimensions

Although the basal areas of sampled trees varied among species ($F_{3,105} = 27.51$, $p < 0.0001$), for the four tree species with $N \geq 20$ individuals, heartwood hollow areas were similar among species ($F_{3,105} = 2$, $p = 0.12$). *Manilkara huberi* trees were larger than *M. bidentata*. *Dinizia excelsa* was not included in the analyses due to small sample size, but generally had larger hollows (approximately 33% of the stem cross section) than the other four tree species (10–23%; Figure 3-1). For the four tree species with $N \geq 20$ individuals, heartwood hollow size increased with stem basal area ($r = 0.46$, $p < 0.001$; Figure 3-2). No relationships were observed between heartwood hollow area and wood density or terrain slope.

Heartwood Anatomy

The five tree species differed only moderately in the measured heartwood anatomical features (Table 3-1). *D. excelsa* and *A. lecointei* had the largest vessel lumen diameters (162.4 and 151.8 µm respectively) and, accordingly, lower vessel densities (5.0 and 7.9 vessels/mm^2 respectively; Figure 3-6; Figure 3-7). *M. bidentata* had the lowest average vessel lumen diameter (111.4 µm) and the highest vessel density (15.6 vessels/mm^2; Figure 3-4). Average ray density varied from 5.86 in *D. excelsa* to 10.5 rays/mm^2 in *M. bidentata*. The average distance between rays was 20.7-23.4 µm for all species but *P. psilostachya*, in which rays were approximately 11.7 µm apart (Figure 3-5). Wood density varied from 0.83 g/cm^3 in *P. psilostachya* and *A. lecointei* to 0.94 g/cm^3 in *D. excelsa*.

In the PCA of wood characteristics, *Manilkara* spp. (Figure 3-3; Figure 3-4) and *A. lecointei* (Figure 3-7) formed a diffuse cluster due to intermediate ray and vessel densities, and vessel lumen diameters. The first two principal components (PCs) explained 63.8 and 25.67%, respectively, of the variation in heartwood anatomical traits (Figure 3-8). The first principal component (PC1) was negatively associated with ray and vessel densities, and positively associated with maximum vessel lumen diameter. The second principal component (PC2) was positively associated with both distance between rays and wood density (Figure 3-8). PC1 scores were negatively related to hollow area (Table 3-2) indicating that larger heartwood hollows were more likely in trees with higher vessel and ray densities, and smaller diameter vessels. Hollow size was positively related to tree size (Table 3-2). Additionally, analysis of the residuals suggested that the model results were strongly influenced by the presence of *D. excelsa,* a species with large vessels, and low ray and vessel densities. Tree basal area

was positively associated with vessel lumen maximum diameter ($r = 0.44$; $p < 0.01$) and distance between rays ($r = 0.44$; $p < 0.01$), and negatively related to vessel density ($r = -0.31$; $p < 0.05$) for all species combined.

Fungal Diversity

A total of 102 morphologically distinct fungal colonies were isolated from 198 samples obtained from heartwood tissue of the five tree species studied. Approximately 72% of them occurred just once. Fungal diversity by tree species was low, with Simpson's diversity indexes varying from 0.9 for *D. excelsa* to 0.99 for *P. psilostachya* (Table 3-3). *M. bidentata* showed substantially higher species richness based on estimates provided by the indexes Chao 2 and ICE than the other three species with N ≥ 20 individuals sampled (Table 3-3). Sample sizes of 20–30 trees/species were apparently insufficient to estimate fungal species richness by species, as shown by the non-asymptotic species accumulation curves (Figure 3-9). Fewer fungal species were isolated from heartwood of *A. lecointei,* but fewer trees of that species were sampled. Surprisingly*, M. bidentata* showed substantially higher species richness that the congeneric *M. huberi,* followed by *P. psilostachya* with intermediate species richness (Figure 3-9). No relationships were found between fungal species richness and tree or site characteristics. Fungal species composition varied substantially among tree species. Fungal species isolated from *M. huberi* were similar to those from *A. lecointei*, whereas the fungal communities in heartwood of *M. bidentata* and *P. psilostachya* were more alike (Figure 3-10).

Due to no matches in GenBank and poor sequence quality, only 41 (40%) of the 102 morphologically distinct fungal colonies could be classified at least to genus using molecular techniques. From these, 35% were in the genus *Trichoderma* or the

teleomorph *Hypocrea*, and 27% were *Penicillium* and *Eupenicillium*. Species of mold in the genera *Aspergillus* and *Nigrospora* were also isolated. Only four basidiomycetes were successfully identified to genus (*Phanaerochaete* and *Phlebia;* Table 3-4).

Termite Assemblages

Termites were found in 50 (43%) of the 116 trees sampled. Approximately 76% of the termites were represented by the species *Coptotermes testaceus* (Table 3-5)*.*This species most commonly formed colonies in heartwood hollows of *M. huberi* (Figure 3-11). 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 ≥ 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 3-6). The probabilities of encountering *C. testaceus* colonies were respectively highest and lowest for the two congeneric species, *M. huberi* and *M. bidentata* (Figure 3-12).

Discussion

Despite differences in wood density, latex production, and microenvironmental conditions experienced in Amazonian Brazil by trees in *Manilkara* spp., *Astronium lecointei,* and *Pseudopiptadenia psilostachya*, heartwood decay measured as hollow cross-sectioned area only varied with tree basal area. Differences in wood density among species, for instance, often help explain species susceptibility to pathogen invasion (Larjavaara & Muller-Landau 2010), but in this study apparently did not affect hollow size. Lack of relationships among hollow size, wood density, terrain slope and fungal species richness by tree were probably a result of low variation among trees and across species.

During their ontogeny, trees become commonly damaged and suffer environmental stresses that weaken their defenses and increase their vulnerability to attacks by pathogens and herbivores (Thomas 2004). Wood decay in living trees is a slow process in which a variety of organisms, many of which are thought to be saprophytes, benefit from periods of weakened defense during which they can successfully trespass induced defenses produced by living sapwood tissues to colonize and break down constitutive phenolic compounds in heartwood tissues (Rayner & Boddy 1988; Schwarze *et al.* 2000). 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 induced defense (Cherubini *et al.* 2002; King *et al.* 2006).

Heartwood anatomical traits in the five tree species analyzed possibly influenced the rate of heartwood colonization and wood degradation by fungi and termites. Stem hollows were smaller in trees with higher densities of vessels and rays, and larger diameter vessels. These results partially contradict previous studies that showed that small vessel size and low vessel and ray densities slow wood degradation by imposing resistance to the growth of decay organisms through two of the most commonly used routes of wood colonization, vessels and parenchymatous tissues (Kuroda 2001; Angyalossy-Alfonso & Miller 2002; Romero & Bolker 2008). The unpredicted relationships between anatomical traits and hollow area observed for the five tree species analyzed can be partially explained by ontogenetic changes in wood anatomy. I observed positive relationships between tree basal area, average vessel lumen diameter, and ray density, and a negative relationship with vessel density. Previous research also showed increased wood density and vessel diameter, and decreased ray

width and ray and vessel densities in wood samples taken from conspecific trees of increasing basal areas (Niklas 1997; Noshiro & Suzuki 2010; Salguero-Gómez & Casper 2011).

Fungal diversity in the heartwood samples of the four species with N ≥ 20 trees was low but not fully accounted for due to the low sample sizes of trees and the high proportion of rare fungal species. Nevertheless, other assessments of fungal species richness based on the presence of fruiting bodies on coarse woody debris in tropical forests also reported low diversity (Lodge 1997; Lindblad; 2000; 2001; Gilbert *et al.* 2002). The number of fungal species isolated from heartwood using culture-based methods was also low, but varied substantially among tree species and was not related to tree or hollow sizes. Likewise, fungal communities greatly varied among tree species, supporting the idea that species composition changes but fungal species richness does not increase as decay progresses (Toofanee & Dulymamode 2002; Osono *et al.* 2009).

As reported in other studies, few fungal species were isolated from more than one tree species (e.g., Suryanarayanan *et al.* 2000). Unfortunately, due to methodological limitations, conclusions regarding host specificity would be highly speculative at this point. Slow growing fungi, for instance, could be underrepresented and a small percentage of fungal species grow well in cultures, many of which only grow on specific media (Lim *et al.* 2005; Hyde & Soytong 2008). Results based on DNA fingerprinting methods and similarities between operational taxonomic units would possibly provide more reliable conclusions (Schloss & Handelsman 2005; Seena *et al.* 2008; McGuire *et al.* 2010).

That only 40% of the morphologically distinct fungal isolates matched known sequences in GenBank suggests the existence of new fungal taxa (Vandenkoornhuyse

et al. 2002). Frequently sampled genera such as *Aspergillus, Penicillium,* and *Trichoderma* are usually considered saprophytes that play important roles in initial stages of wood degradation (Rayner & Boddy 1988). *Trichoderma* species, for example, may act as antagonists to pathogens such as *Heterobasidium annosum*, and produce anti-fungal compounds that have been investigated for biological control purposes (Nicolotti 1996; Humphris *et al.* 2001). Only few species of decay fungi were isolated. Basidiomycetes in the genera identified (*Phanaerochaete* and *Phlebia*) have been found mostly in temperate forests but are also known from the tropics (Croan *et al.* 1999; Olsson & Jonsson 2010).

Termites were present in heartwood of almost half of the trees analyzed, with *Coptotermes testaceus* the most common species. *Coptotermes testaceus* was previously reported to be associated with heartwood hollows in Amazonian forest trees (Constantino 1991; 1999), but at lower frequencies (Apolinario & Martius, 2004). Maintaining hollow trees in these forests managed for timber extraction is therefore crucial to conserve *C. testaceus*, as well as the species that benefit from the cavities they excavate (Gibbons & Lindenmayer 1996; Apolinario & Martius 2004; Werner & Prior 2007; Fox *et al.* 2008; Zheng *et al.* 2009).

Subterranean termites in the genus *Coptotermes* build their nests in the soil and infest sound wood in direct contact with the ground (Verma *et al.* 2009). In my study area, *C. testaceus* nests were more frequent in *M. huberi* 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, presumable on the basis of wood extractives, as

observed in bioassays with *Zootermopsis nevadensis* (Ohmura *et al.* 2006). The other species that also produced latex, *A. lecointei,* was generally not inhabited by termites.

Nutritional qualities of wood may influence tree selection by termites (Morales-Ramos & Rojas, 2001; 2003). Higher cellulose content in heartwood was possibly related to *C. testaceus* preference for trees with higher wood density (Judd & Corbin, 2009). Finally, despite previously reports of positive and negative associations between fungi and termites (Ohkuma *et al.* 2001; Aanen *et al.* 2002; Roose-Amsaleg *et al.* 2004), no association was found between the presence of termite nests and the abundance of fungal species in heartwood tissues.

Conclusion

Heartwood decay increased with tree size for the studied commercial tree species in eastern Amazonia. Heartwood anatomical traits such as vessel lumen diameter and vessel and ray density explained much of the among-species variation in hollow size. Further studies on heartwood decay and wood properties would benefit from bigger samples sizes and from the selection of tree species that differ more in wood traits. Most fungal species isolated from heartwood samples were represented by saprophytes that usually participate in initial stages of decomposition. Fungal diversity estimates would be more reliable if based on DNA-fingerprinting or similar molecular techniques, instead of producing pure cultures to identify isolates. Termite colonies were found in a high proportion of hollow trees. The most frequent species, *Coptotermes testaceus,* was most common in trees with high density wood. Strategies to conserve this termite species and the ecosystem processes it provides, such as provision of habitat for cavity nesting species, should regulate the harvest of hollow trees with the characteristics selected by the *C. testaceus*.

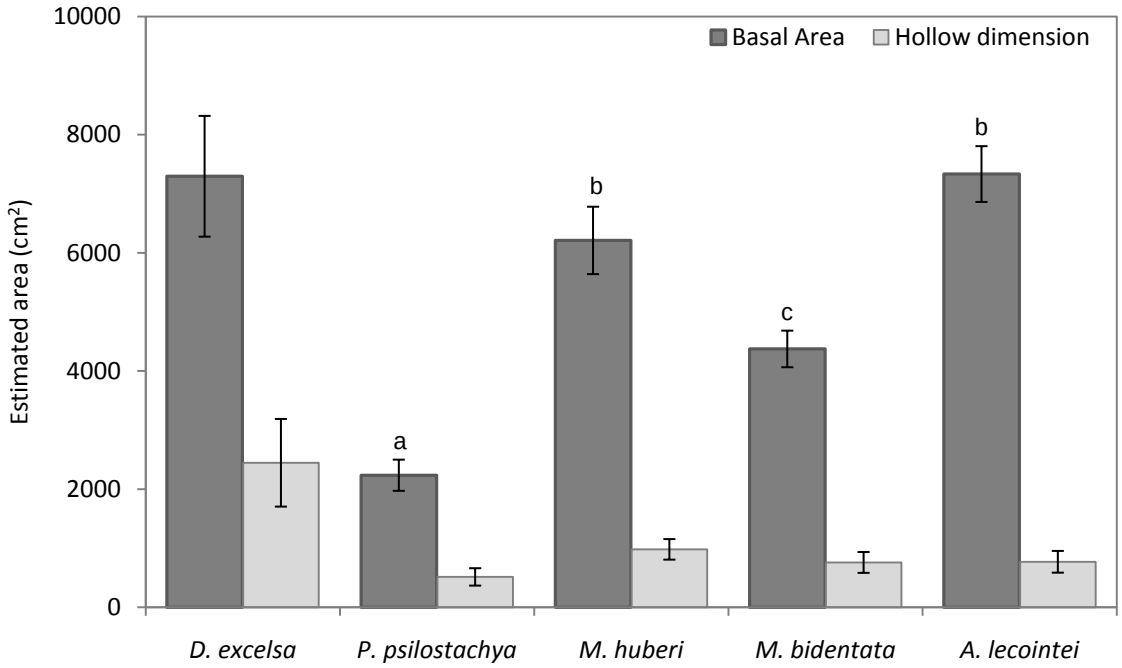

Figure 3-1. Tree stem basal area and area of stem hollows by tree species; both measured at 50 cm from the ground (N = 8 for *D. excelsa*, N = 30 for *P. psilostachya* and *M. huberi*, N = 28 for *M. bidentata*, and N = 20 for *A. lecointei*). Letters indicate differences at $p < 0.05$. Statistical comparisons included all species but *D. excelsa*.

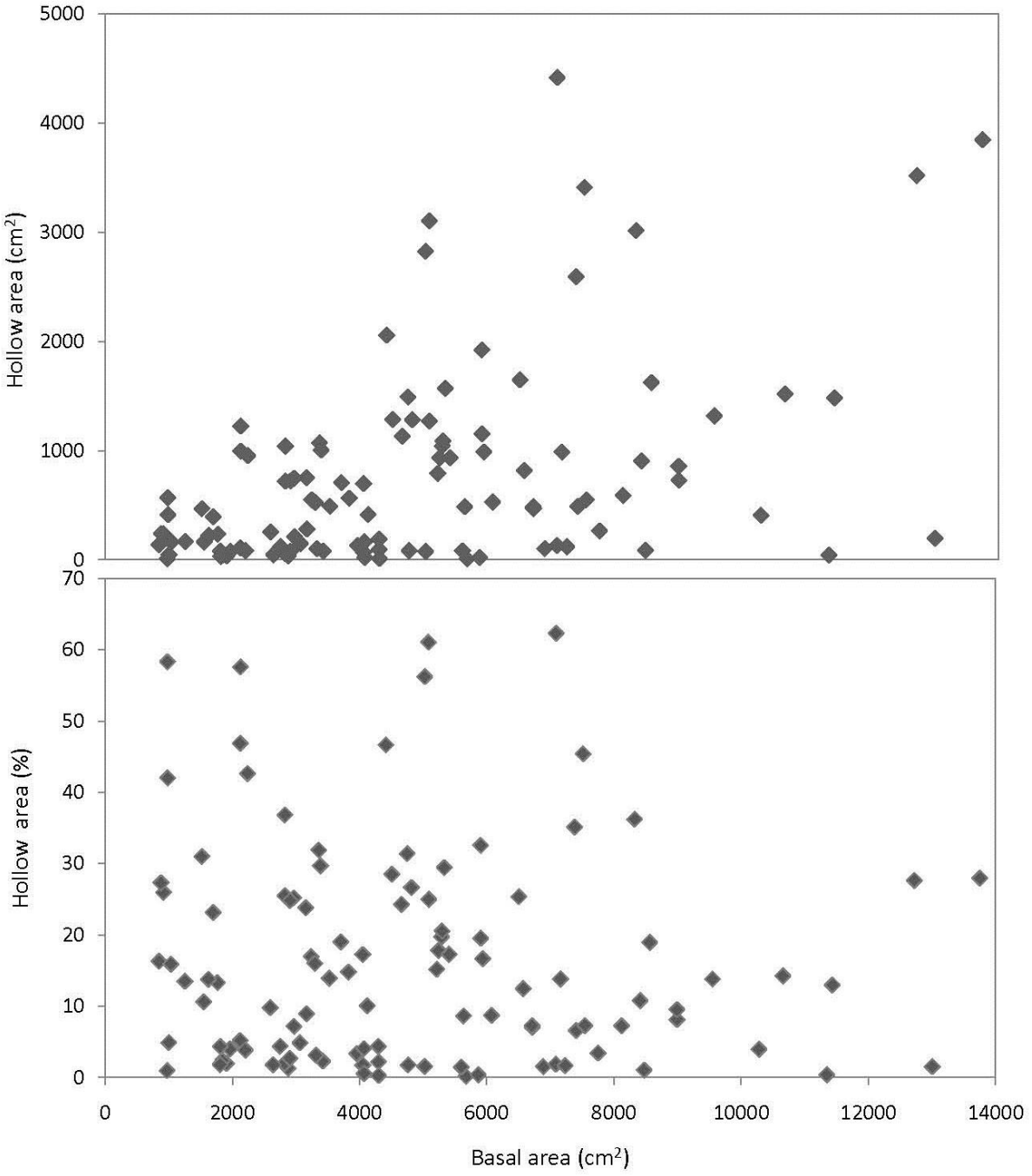

Figure 3-2. Variation in A) stem hollow area and B) percent hollow area by tree basal area for the four tree species with N ≥ 20 individuals sampled (P. psilostachya, M. huberi (N = 30), M. bidentata (N = 28), and A. lecointei (N = 20)).

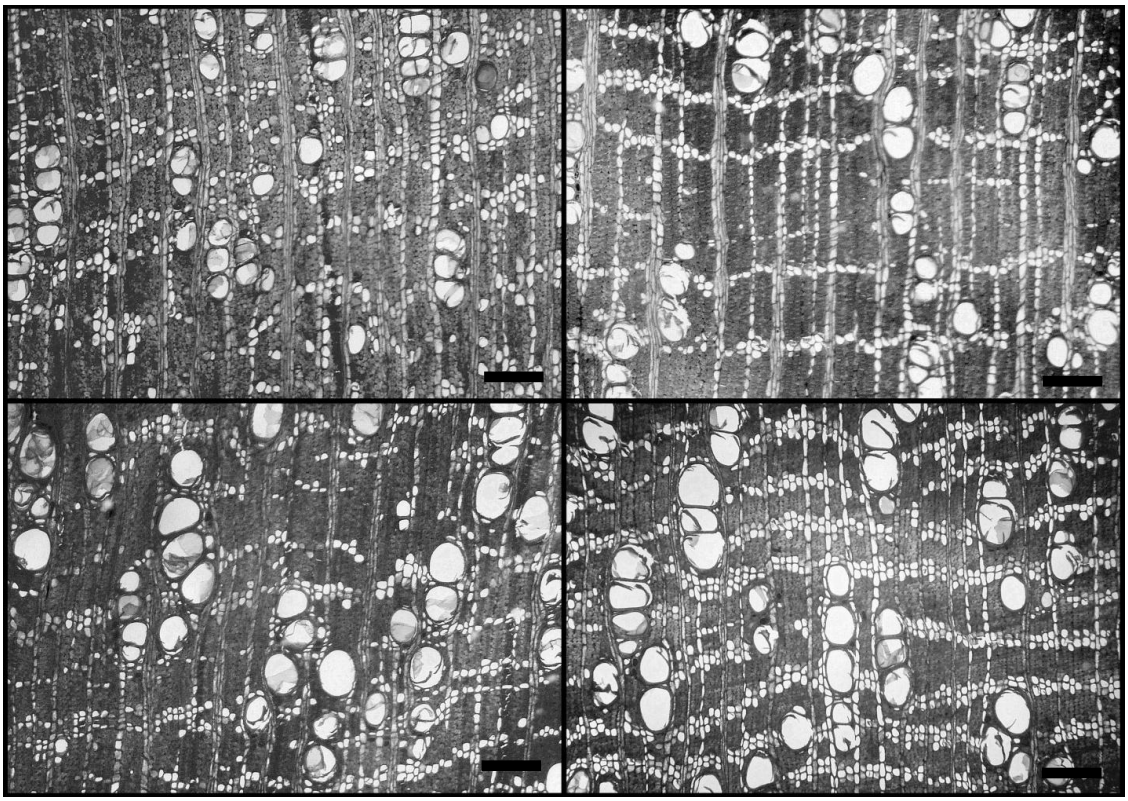

Figure 3-3. Heartwood anatomy of *Manilkara huberi.* Scale bar = 200 µm.

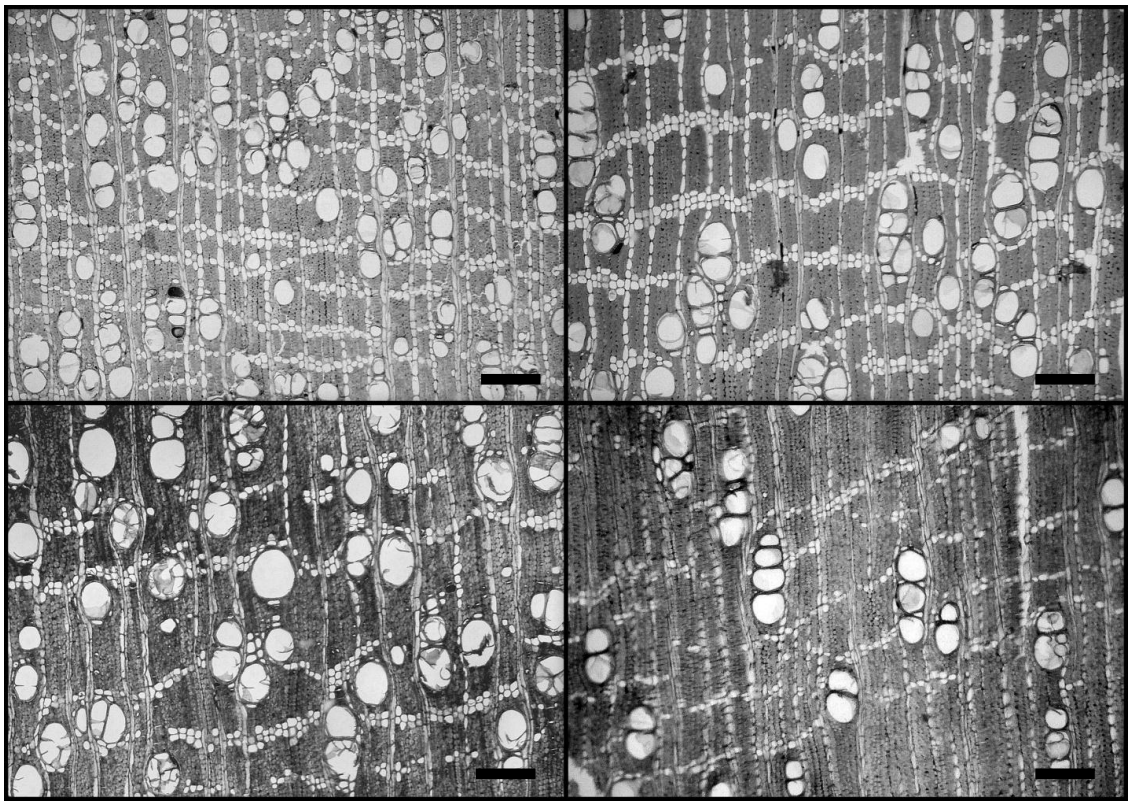

Figure 3-4. Heartwood anatomy of *Manilkara bidentata*. Scale bar = 200 µm.

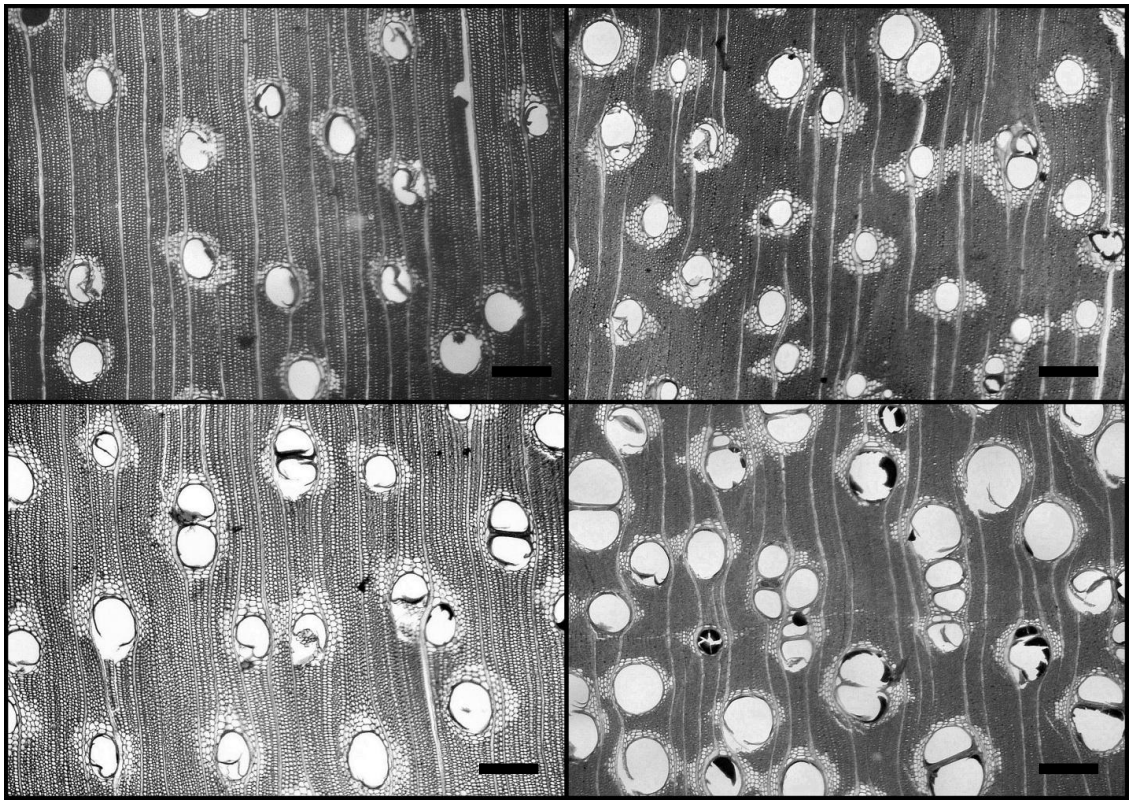

Figure 3-5. Heartwood anatomy of *Pseudopiptadenia psilostachya*. Scale bar = 200 µm.

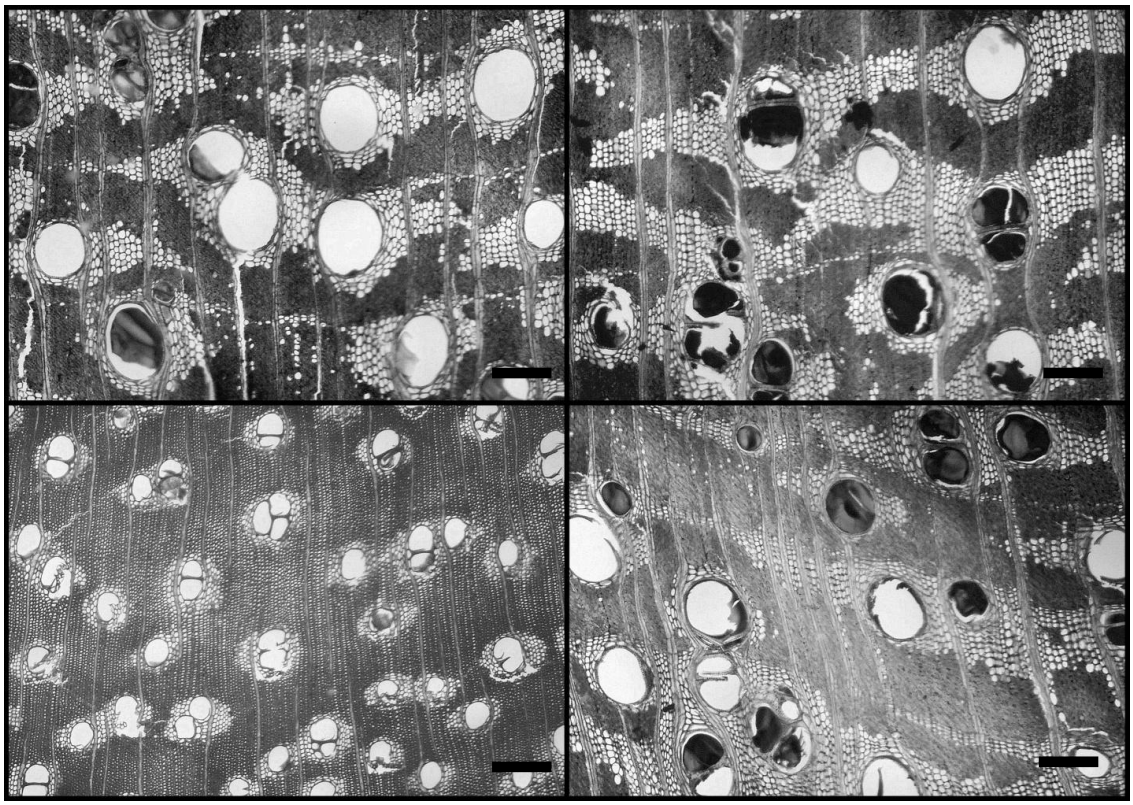

Figure 3-6. Heartwood anatomy of *Dinizia excelsa.* Scale bar = 200 µm.

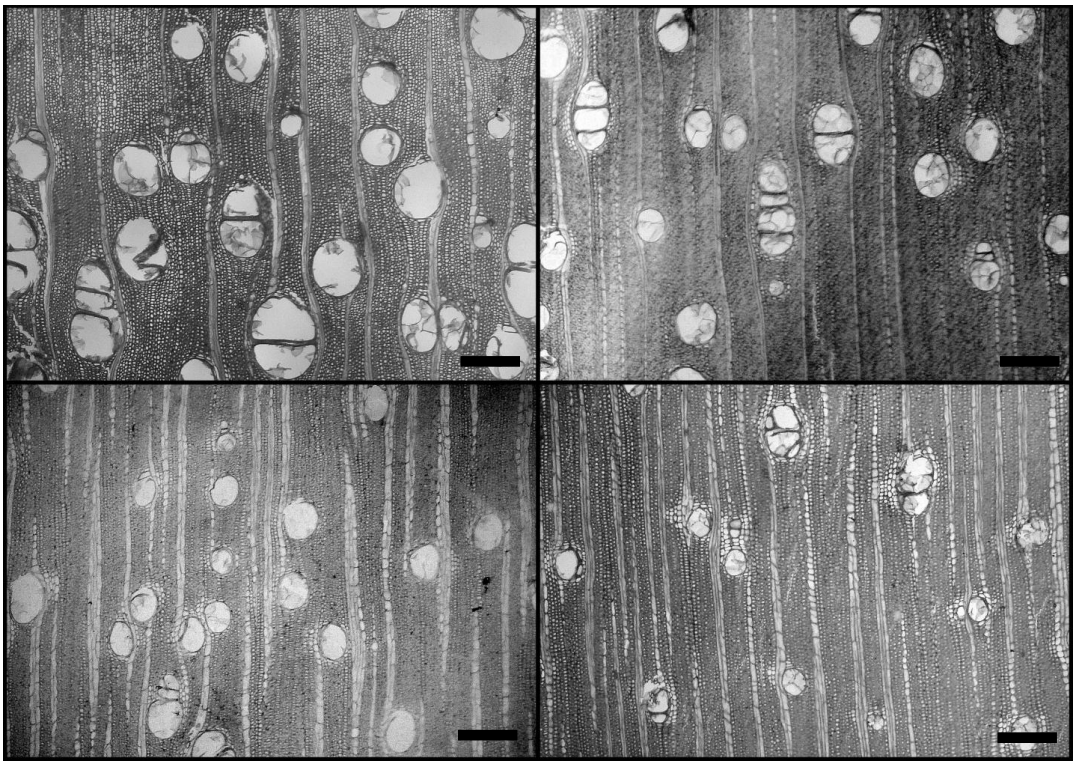

Figure 3-7. Heartwood anatomy of *Astronium lecointei.* Scale bar = 200 µm.

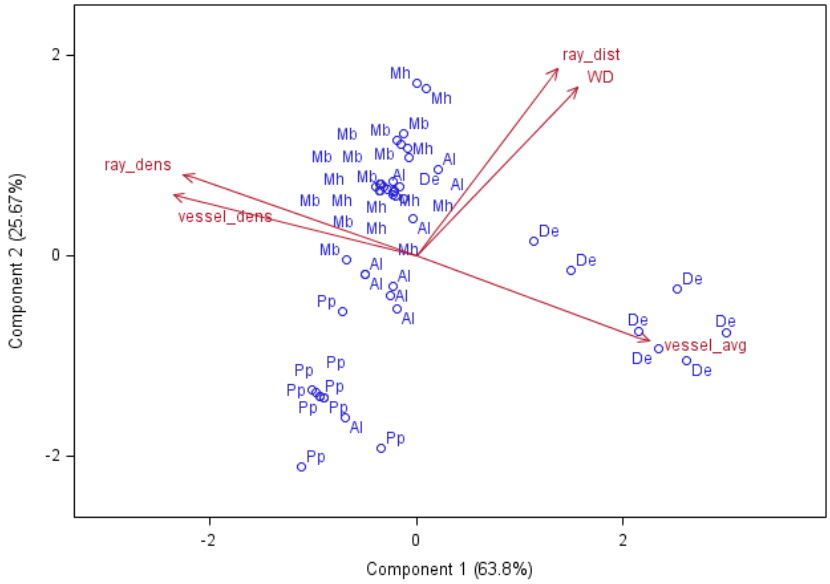

Figure 3-8. Principal components analyses of wood anatomical characteristics for *D. excelsa*, *P. psilostachya* (respectively De and Pp; N = 9), *M. huberi, M. bidentata* (Mb), and *A. lecointei* (respectively Mh, Mb, and Al; N = 10). Variables considered were number of vessels/mm^2 (vessel_dens), number 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.

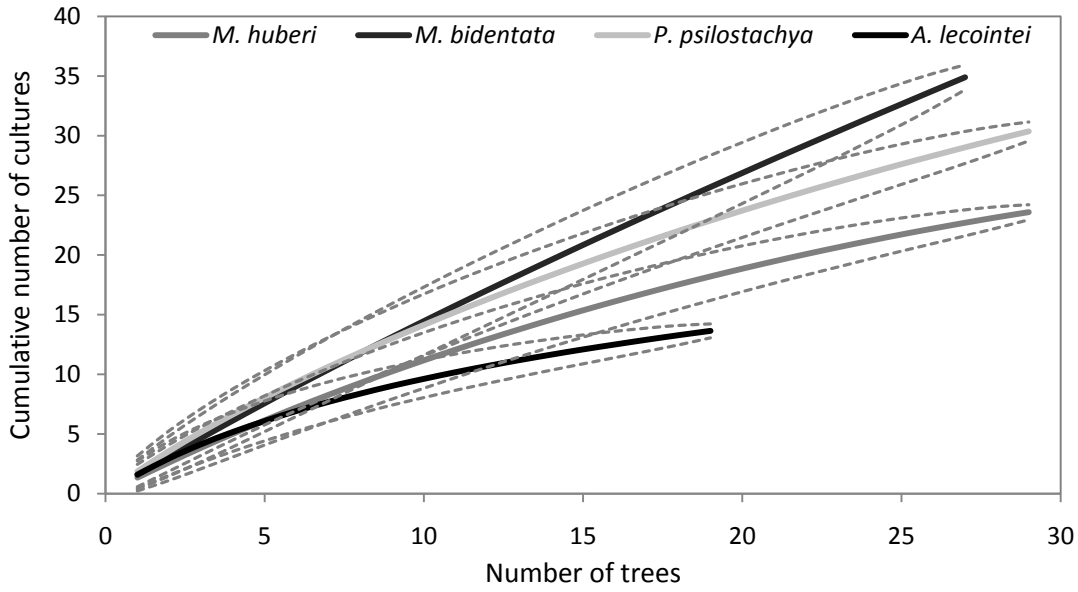

Figure 3-9. Coleman rarefaction curves of fungal species richness by heartwood sample for the four tree species with N ≥ 20 individuals sampled (N = 30 for P. psilostachya and M. huberi, N = 28 for M. bidentata, and N = 20 for A. lecointei). Error bars were estimated based on 95% confidence intervals of the mean.

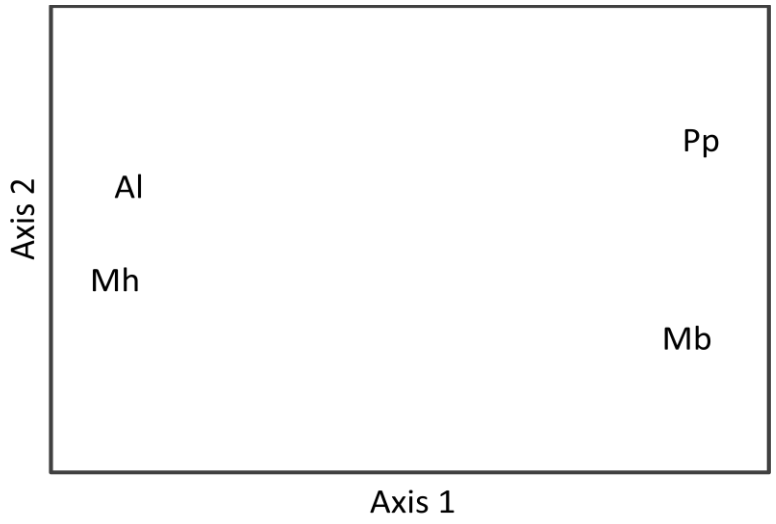

Figure 3-10. Two-dimensional solution of the nonmetric multidimensional scaling (NMS) ordination comparing fungal species composition isolated from heartwood samples from the four tree species with N ≥ 20 individuals (N = 30 for *P. psilostachya* (Pp) and *M. huberi* (Mh), N = 28 for *M. bidentata* (Mb), and N = 20 for *A. lecointei* (Al)). Fungal species that occurred in only one sample were not included in this analysis.

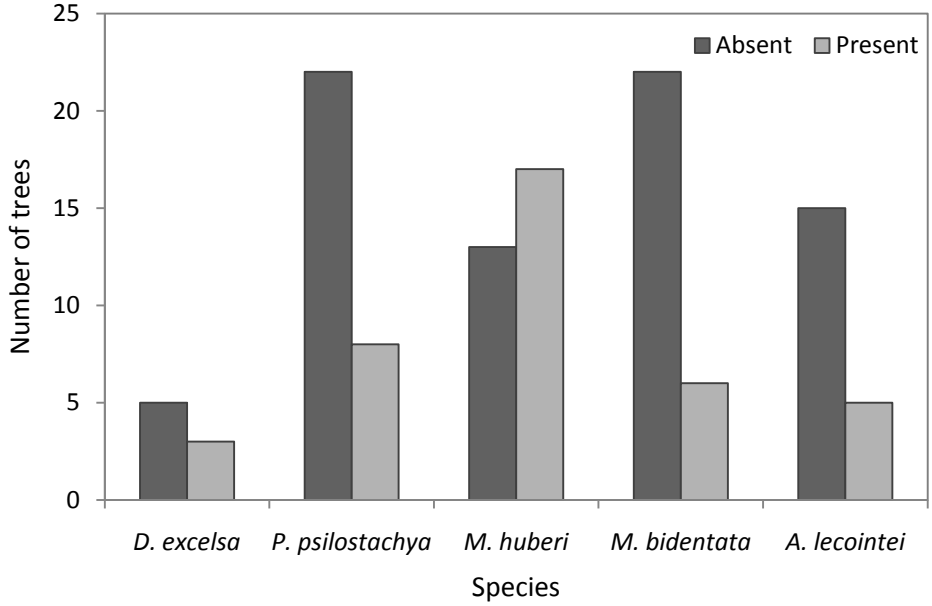

Figure 3-11. Presence and absence of termite colonies in the rotten heartwood per tree species: *D. excelsa* (N = 8), *P. psilostachya*, *M. huberi* (N = 30)*, M. bidentata* (N = 28), and *A. lecointei* (N = 20 trees).

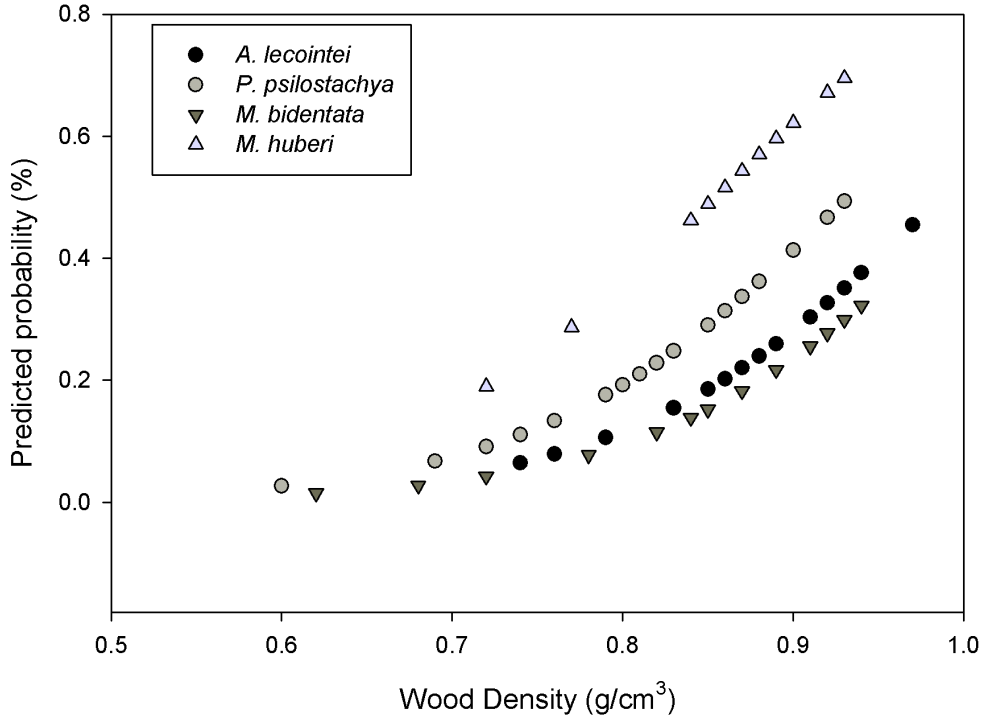

Figure 3-12. The probability of a tree hosting a *Coptotermes testaceus* colony as a function of wood density. Samples sizes were as follows: *P. psilostachya* and *M. huberi* (N = 30)*, M. bidentata* (N = 28), and *A. lecointei* (N = 20).

Table 3-1. Heartwood anatomical traits (mean ± SD) for the five tree species studied.

	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,c}	11.73 ± 1.65^{b}	0.83 ± 0.06^{b,d}
M. huberi	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,d}	22.82 ± 3.92^{a}	0.83 ± 0.07^{b}

Table 3-2. 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

Table 3-3. Fungal species isolated from cultures of wood samples of the five tree species studied, and corresponding species richness estimators Chao 2 and ICE, and Simpson's diversity index (1 - D).

	Number of trees sampled	Number of fungal specimens	Number of fungal species isolated	Chao 2	ICE	Simpson's Diversity Index (1 - D)
D. excelsa	8	15	11	-	-	0.90
P. psilostachya	30	58	38	46.14	52.66	0.95
M. huberi	30	48	38	48.02	54.83	0.99
M. bidentata	30	45	36	196.17	211.67	0.98
A. lecointei	20	32	19	24.31	27.06	0.91

Table 3-4. Fungal species isolated from cultures of heartwood samples of the 5 tree species studied, and identified through DNA purification and amplification of ITS sequences using primers ITS-1 and ITS-4. Only taxa with E-values = 0 and maximum identity > 90% are reported.

Primer	Query length	Coverage (%)	E-value	Maximum identity (%)	Species match	De	Pp	Mh	Mb	Al
ITS4	636	84	0	96	*Aspergillus japonicus*	-	1	-	-	-
ITS1	408	100	0	98	*Aspergillus nomius*	-	2	-	-	-
ITS1	386	100	0	99	*Aspergillus nomius*	-	3	2	-	1
ITS1	400	100	0	97	*Chloridium virescens*	-	1	-	-	-
ITS1	477	100	0	97	*Eupenicillium shearii*	-	-	1	2	-
ITS4	610	87	0	98	*Eupenicillium shearii*	-	1	-	-	-
ITS4	773	64	0	96	*Fusarium* sp.	-	1	-	-	-
ITS1	508	95	0	96	*Hypocrea koningii*	-	2	-	-	-
ITS4	729	79	0	96	*Hypocrea virens*	1	-	-	-	-
ITS4	575	98	0	98	*Hypocrea virens*	-	-	-	1	-
ITS4	748	98	0	98	*Hypocrea virens*	-	-	-	1	-
ITS1	393	99	0	99	*Monascus fuliginosus*	-	-	-	1	-
ITS4	518	94	0	97	*Nigrospora sphaerica*	-	1	-	-	-
ITS4	732	72	0	99	*Penicilium*	-	1	-	1	-
ITS1	470	92	0	98	*Penicillium aculeatum*	-	-	-	1	-
ITS1	423	100	0	99	*Penicillium citrinum*	-	-	1	-	3
ITS1	379	100	0	99	*Penicillium citrinum*	-	-	-	1	-
ITS4	510	97	0	97	*Penicillium glabrum*	-	-	-	1	-
ITS1	389	100	0	100	*Penicillium*	-	1	-	-	1
ITS4	660	82	0	96	*Penicillium paxilli*	-	1	-	2	-
ITS1	444	94	0	98	*Penicillium*	-	2	-	1	-
ITS1	384	100	0	100	*Penicillium*	-	-	-	1	-
ITS1	440	99	0	95	*Penicillium* sp.	-	1	-	-	-
ITS4	742	76	0	93	*Penicillium* sp.	-	-	-	1	-
ITS1	466	100	0	98	*Penicillium toxicarium*	-	-	1	-	-
ITS4	1015	56	0	99	*Phanerochaete*	-	-	-	1	-
ITS1	401	100	0	98	*Phanerochaete*	-	-	1	-	-
ITS4	641	87	0	92	*Phlebia brevispora*	-	1	-	-	-
ITS1	506	99	0	93	*Phlebia brevispora*	-	1	-	-	-
ITS4	518	98	0	98	*Pleurostoma ootheca*	-	-	-	-	1
ITS1	382	100	0	98	*Trichoderma*	-	-	-	1	-
ITS1	363	100	0	99	*Trichoderma*	-	-	1	-	-
ITS1	453	99	0	98	*Trichoderma*	-	-	1	-	-
ITS4	876	60	0	92	*Trichoderma* sp.	-	-	-	1	-
ITS4	678	84	0	92	*Trichoderma* sp.	-	1	1	-	1
ITS4	712	80	0	93	*Trichoderma spirale*	-	-	-	1	-
ITS4	670	83	0	96	*Trichoderma spirale*	-	1	-	1	-
ITS1	497	97	0	97	*Trichoderma spirale*	-	-	-	1	-
ITS4	806	68	0	98	*Trichoderma spirale*	1	-	-	-	-
ITS4	807	48	0	98	*Trichoderma spirale*	-	1	-	-	-
ITS4	636	83	0	95	*Trichoderma viride*	-	1	1	1	1

De, *Dinizia excelsa;* Pp, *Pseudopiptadenia psilostachya;* Mh, *Manilkara huberi*; Mb, *Manilkara bidentata*; Al, *Astronium lecointei*

Table 3-5. Termite species sampled in heartwood hollows of the five studied tree species.

	D. excelsa	*P. psilostachya*	*M. huberi*	*M. bidentata*	*A. lecointei*	Total
Anoplotermes sp.	1	1	-	-	-	2
Armitermes c.f. *holmgreni*	-	1	-	-	-	1
Armitermes sp.	-	-	-	1	-	1
Convexitermes manni	-	-	-	-	1	1
Coptotermes testaceus	3	8	17	6	5	39
Heterotermes sp.	-	1	-	-	-	1
Nasutitermes guayanae	-	-	1	-	-	1
N. surinamensis	-	-	1	-	-	1
Ruptitermes sp.	1	-	-	-	-	1
Termitinae	-	-	1	-	1	2
Number of trees sampled	8	30	30	28	20	116
Number of trees with termites	5	11	20	7	6	50

Table 3-6. 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. huberi* (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. huberi	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				

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BIOGRAPHICAL SKETCH

Ana Eleutério grew up in Sao Paulo, Brazil. She received her bachelor's degree in biological sciences in 2001 from the University of Sao Paulo. Since then, she conducted plant ecology research in many very different tropical and temperate forests. In 2004, Ana Eleutério received her master's degree in environmental sciences from the *Universidad Nacional Autonoma de Mexico*. During the 3 years she lived in Mexico, she had the opportunity to interact with a variety of different research teams and to develop her own interdisciplinary study on the management of endangered species of tree ferns. She started her doctorate studies in the Department of Biology (then the Department of Botany) at the University of Florida in August 2005. Her current research focuses on issues related to forest health in natural tropical forests managed for timber. For her research, she received financial support from the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES) – Fulbright Commission, the International Foundation for Science (IFS), and IdeaWild. After graduating, Ana plans to return to her home country and secure a research position at a Brazilian university that will enable her to continue investigating the ecology of tropical plants in managed forests.