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Evaluation of stem rot in 339 Bornean tree species: implications of size, taxonomy, and soil-related variation for aboveground biomass estimates

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Abstract. Fungal decay of heart wood creates hollows and areas of reduced wood density within the stems of living trees known as stem rot. Although stem rot is acknowledged as a source of error in forest aboveground biomass (AGB) estimates, there are few data sets available to evaluate the controls over stem rot infection and severity in tropical forests. Using legacy and recent data from 3180 drilled, felled, and cored stems in mixed dipterocarp forests in Sarawak, Malaysian Borneo, we quantified the frequency and severity of stem rot in a total of 339 tree species, and related variation in stem rot with tree size, wood density, taxonomy, and species' soil association, as well as edaphic conditions. Predicted stem rot frequency for a 50 cm tree was 53 % of felled, 39 % of drilled, and 28 % of cored stems, demonstrating differences among methods in rot detection ability. The percent stem volume infected by rot, or stem rot severity, ranged widely among trees with stem rot infection (0.1–82.8 %) and averaged 9 % across all trees felled. Tree taxonomy explained the greatest proportion of variance in both stem rot frequency and severity among the predictors evaluated in our models. Stem rot frequency, but not severity, increased sharply with tree diameter, ranging from 13 % in trees 10–30 cm DBH to 54 % in stems $\geq$ 50 cm DBH across all data sets. The frequency of stem rot increased significantly in soils with low pH and cation concentrations in topsoil, and stem rot was more common in tree species associated with dystrophic sandy soils than with nutrient-rich clays. When scaled to forest stands, the maximum percent of stem biomass lost to stem rot varied significantly with soil properties, and we estimate that stem rot reduces total forest AGB estimates by up to 7 % relative to what would be predicted assuming all stems are composed strictly of intact wood. This study demonstrates not only that stem rot is likely to be a significant source of error in forest AGB estimation, but also that it strongly covaries with tree size, taxonomy, habitat association, and soil resources, underscoring the need to account for tree community composition and edaphic variation in estimating carbon storage in tropical forests.

1 Introduction

Fungal rot of secondary xylem causes hollows and regions of reduced wood density in tree stems. This type of fungal infection, commonly referred to as stem rot, is important for the structure, dynamics, and functioning of forests, given that it may increase tree mortality (Franklin et al., 1987; Rux-

ton, 2014), facilitate the creation of cavity habitats for a diversity of wood-inhabiting and decaying species (Cockle et al., 2012; Stockland et al., 2012), and may act as a reservoir of nutrients sequestered in stem rot biomass (Janzen, 1976; Dickinson and Tanner, 1978; Boddy and Watkinson, 1995). Moreover, the effect of stem rot on aboveground biomass is of particular importance for efforts to map carbon storage in tropical regions as part of global conservation and climate change mitigation strategies (Saatchi et al., 2011). However, because stem rot is difficult to detect by non-destructive means, we understand little about what controls its frequency and severity, especially in tropical forests.

Most information available on stem rot in tropical forests comes from forestry studies exploring its influence on the volume and quality of timber. Among species commonly logged in Old World dipterocarp forests, stem rot occurs in up to 75 % of large *Shorea robusta* (Dipterocarpaceae), reducing stem volumes by 9–13 % (Bakshi, 1960; Bagchee, 1961). The majority of large mono-dominant *Shorea albida* individuals in Sarawak peat swamp forests have been extensively hollowed by fungi and termites (Anderson, 1964). In subalpine silver fir (*Abies densa*; Pinaceae) forests of the Eastern Himalayas, stem rot reduced timber yields to < 33 % of those predicted from external stem volumes (Bürgi et al., 1992; Gratzer et al., 1997). The influence of stem rot appears to be less in the Brazilian Amazon, where the average frequency of stem rot was 30 % in six commercial timber species in the eastern Amazon (Eleuterio, 2011), and estimation of stem volume hollowed by stem rot in the western Amazon was just 0.7 % (Nogueira et al., 2006). Together these studies provide evidence that the frequency and severity of stem rot influences AGB estimates. However, there have been few systematic analyses of the interspecific variation in stem rot with respect to tree properties or environmental factors that might mediate susceptibility and engender spatial variation in forest biomass lost to stem rot.

Understanding how patterns of stem rot infection vary with tree size is critical to assessing its influence on forest AGB estimation because trees > 70 cm in diameter at breast height (DBH) explain 70 % of variation in pantropical AGB (Slik et al., 2013). Tree size may be among the best predictors of stem rot in tropical forests because old trees have lived long enough to incur butt, branch, and stem wounds that lead to fungal infection, and trees may become less resistant to infection as they age (Boddy, 2001). In temperate forests, where tree age can be estimated precisely, stem rot frequency increases with age in longleaf pine (*Pinus palustris*) (Hooper, 1988), and pedunculate oak (*Quercus robur*) (Ranius et al., 2009). While tree size is an imperfect proxy of tree age (Baker et al., 2005; Brienen and Zuidema 2006), stem rot frequency increases with tree diameter in neotropical forests (Nogueira et al., 2006; Eleuterio, 2011). However, variation in the frequency of stem rot in a given size class indicates that there may be interactions between tree size and taxonomic, functional, and environmental factors.

Quantifying the strength of taxonomic variation in stem rot frequency in trees and determining functional traits that underlie species differences in stem rot infection should provide insight into patterns of carbon storage in tropical forests, which often show large shifts in species composition over spatial gradients. Cornwell et al. (2009) demonstrated that the inclusion of plant traits improved models of global carbon turnover from coarse woody debris pools, however, the traits that influence wood decomposition in living stems are still poorly understood. Among potentially important species traits, wood properties may explain variation among trees in susceptibility to stem rot. Trees with dense wood may be less likely to experience branch and stem breakage due to wind disturbance (Putz et al., 1983) and are thought to be more resistant to termite and fungal infection than trees with softer wood. However, there is conflicting evidence as to whether wood density and decay resistance are strongly correlated (Yoneda, 1975; Bultman and Southwell, 1976; Weedon et al., 2009; van Geffen et al., 2010; Mori et al., 2013). Dense wood has been found to be associated with pathogen resistance in tropical tree species (Augspurger and Kelly, 1984) and slower fungal growth (Romero and Bolker, 2008), perhaps because denser heart wood may retain more water and thereby inhibit fungal growth (Boddy, 2001) or have low porosity that impedes the growth of fungal hyphae (Bjurman and Viitanen, 1996; Schwarze et al., 2000). Within species, fast-grown trees with lower wood density are associated with faster decay rates by saproxylic fungi (Edman et al., 2006; Ranius et al., 2009), although this pattern does not hold across all fungal taxa (Yu et al., 2003). In an Amazonian forest, little or no covariation was found between species' wood density and frequency of stem rot, but the probability of rot was significantly correlated with other wood traits, such as the lumen diameter and density of vessels (Eleuterio, 2011).

The plant traits and environmental constraints associated with variation in the frequency and severity of stem rot may change with the availability of edaphic resources. For instance, low soil fertility and nutrient or water stress may predispose tissues to fungal infection (Boddy and Rayner, 1983; Franklin et al., 1987). There is also a potential indirect effect of age (Ranius et al., 2009), as trees tend to grow slower and live longer on more infertile soils (Russo et al., 2005), and are therefore exposed to chance infection for longer periods. Conversely, trees on more fertile soils not only grow faster, they have less dense and softer wood (Heineman and Russo, unpublished data) and perhaps lower contents of defensive secondary metabolites (Loehle, 1988; Fine et al., 2006). Such wood may be more prone to stem rot (Wagener and Davidson, 1954; Duchesne et al., 1992; Pearce, 1996; Kirker et al., 2013). If stem rot varies along edaphic gradients, then including soil parameters in models estimating forest carbon dynamics (e.g. Yang et al., 2013, 2014) would be important, especially in southeast Asian forests where AGB varies with soil nutrient availability (Lee et al., 2002; Paoli et al., 2008a).

We used legacy and modern data sets to quantify the co-variation of taxonomy, tree size, wood density, and soil resource availability with the frequency and severity of stem rot in two Bornean mixed dipterocarp forests. We quantified the impact of stem rot on forest standing biomass, and evaluated the implications of soil-related variation in stem rot for stand-level variation in biomass. Efforts to quantify stem rot in tropical trees are hampered by the difficulty of evaluating rot without compromising the health of trees in long term monitoring plots. We therefore also compared methods for quantifying stem rot frequency, including the direct assessment of stem rot frequency based on destructive harvesting, with two non-destructive methods (coring and drilling).

2 Methods

2.1 Study sites

The data were collected in two locations in Malaysian Borneo: Central Sarawak and Lambir Hills National Park, Sarawak (Fig. 1). The Central Sarawak tree drilling and felling data were collected during a timber inventory of lowland mixed dipterocarp rain forest ($1°30'$–$2°50'$ N, $112°20'$–$113°50'$ E) (FIDP, 1974a). Annual rainfall averages 3000–3500 mm yr^{-1} in this region with no distinct dry season. The topography consists of long, steep-sided ridges on Tertiary sandstones and narrow valleys in softer shales. The soils are colluvial/residual Acrisols (Udults) and associated Cambisols (Udepts) (FAO, 2006). The coarse loams on sandstone ridges tend to be more stable and deeper than the shale-derived fine loams and clays of the lower slopes and valleys. All of the soils are acidic and leached, and exchangeable base saturation is usually < 10 %. Reserves of K and Mg are moderate, but those of P and especially Ca are low. Mineral nutrient fertility increases with clay content, and the slope and valley clays are less dystrophic than the coarse loams on the ridges (Baillie et al., 1987). The mixed-dipterocarp forest in this region is among the most diverse forests in the Paleotropics, and the distributions of many tree species are associated with soil conditions, producing considerable changes in floristic composition across different soil types (Baillie et al., 1987; Ashton and Hall, 1992; Potts et al., 2002). Average canopy height is 30–50 m with emergent trees reaching 70 m.

Tree coring data were collected in 2009 in Lambir Hills National Park (hereafter, Lambir) in northern Sarawak ($4°11'$ N, $114°01'$ E). The physical environment is similar to that of the central Sarawak study area, with acid leached Acrisols and associated Cambisols (Baillie et al., 2006; Tan et al., 2009) on a sandstone cuesta (Yamakura et al., 1996), with shale below the scarp and on the lower dip-slope. Sampling was conducted on two of the four soil types present in a 52-ha forest dynamics plot at Lambir (Lee et al., 2002): clay soil, which is more fertile for most nutrients and has greater cation exchange and water-holding capacity, and
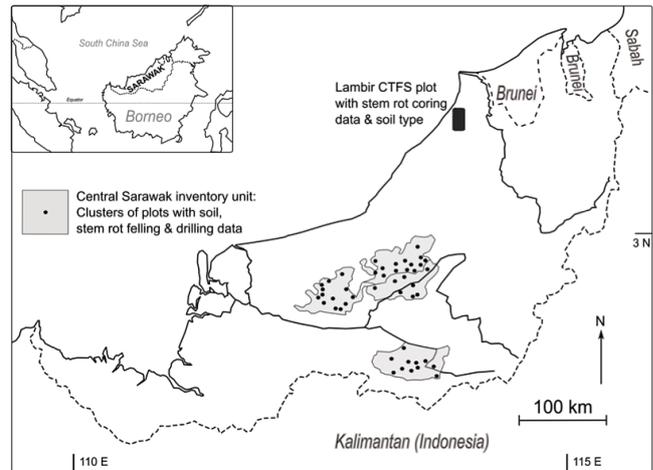

Figure 1. Location of study sites in Sarawak, Malaysian Borneo. Shaded areas are the Central Sarawak inventory units for stem rot felling and drilling data, with clusters of plots indicated by black dots. The black rectangle (not to scale) indicates the location of the Lambir Hills National Park study site for the stem rot coring data.

sandy loam soil, which has lower concentrations for most nutrients, lower cation exchange capacity, and is better drained (Baillie et al., 2006; Tan et al., 2009). The distribution of individual species, and the overall floristic composition, structure, and dynamics of the mixed-dipterocarp forest at Lambir are associated with differences in topography and soils (Lee et al., 2002; Davies et al., 2005; Russo et al., 2005, 2008; Heineman et al., 2011).

2.2 Stem rot data

The Central Sarawak felling (1035 trees in 211 species in 31 families) and drilling (1780 trees in 206 species in 34 families) data (Tables 1, S1 in Supplement) were collected from 422 plots grouped in 69 clusters as part of the Forest Industries Development Project (FIDP) conducted from 1969–1971 (Fig. 1) (FIDP, 1974b). Each cluster consisted of nine plots arrayed in a 3 × 3 grid with 80 m spacing between plots (Fig. S1 in Supplement). Plots were defined using a standard BAF 10 prism, so that all the stems with an angular diameter > 1.74° when viewed from the center point were included in the plot. This standard forest inventory method (Avery and Burkhart, 2002) includes larger stems located relatively far away from the center point, whereas small stems are only included if they are close. The plots were therefore irregularly shaped and ranged in size from ca. 200 to > 2000 m^2 (Fig. S1). On a random subset of 43 of 502 total clusters in the FIDP, all trees that would produce at least one commercial log (i.e. 3.65 m long with DBH $\geq$ 30 cm) were selected for felling, regardless of species. Nearly all stems $\geq$ 40 cm DBH qualified as containing at least one commercial log. Selected trees were felled at breast height (1.3 m) or above the highest buttress head, and stems were cut into 3.65 m logs

Table 1. Total number of trees and species (including morphospecies) evaluated for the presence of stem rot, and the ranges and sample sizes for predictor variables used in mixed-effect models evaluating the association of ecological covariates with frequency and severity of stem rot in the felling, drilling, and coring data sets. See Sect. 2 for details.

	Felling			Drilling			Coring		
	Species	Trees	Range	Species	Trees	Range	Species	Trees	Range
Total Number Sampled	211	1035		206	1780		116	365	
Frequency of Stem rot		53 %			41 %			9 %	
Availability of Model Predictor Variables									
DBH (cm)		1035	27–105		1780	26–161			6–89
Species Covariates									
Wood density (g cm^{-3})	134	834	0.42–1.14	136	1203	0.42–1.14	116	365	0.20–1.02
Species soil association	177	930		167	1330		112	355	
Loam/sandy loam	53	164		48	195		43	131	
Fine loam/loam	43	318		40	545		16	52	
Clay/fine loam	53	283		55	419		29	103	
Generalist	28	165		24	171		24	69	
Edaphic Environment Covariates									
Soil type									
Sandy loam	–	–		–	–		63	201	
Clay/fine loam	–	–		–	–		64	164	
Soil Chemistry (PC Axes)	193	970		152	1058		–	–	
Total Included in Mixed-Effect Models	122	765		102	707		112	355	

along the length of the stem until the point of first branching (Fig. S2). Presence or absence of stem rot was recorded based on visual inspection of the log ends, and stem rot was scored as present when the wood contained voids or areas of darkened, soft, or brittle wood (Fig. S2). Logs that were sound at one end but rotten at the other were sawn in half to better quantify rot severity. For each cross-section, the total area and the area occupied by stem rot were measured by grid counts on transparent overlays (Panzer, 1975). The volume of the whole log and volume occupied by stem rot were computed based on tapering cylinders. The percent of stem rot for the tree was estimated as the sum of the rot volumes for each log as a percentage of the total stem volume. Stem rot sampling was augmented with a drilling program because early felling results revealed more frequent and severe stem rot than anticipated. On an additional 26 randomly chosen clusters in which felled logs were not evaluated for stem rot, all trees with at least one commercial log were drilled at two locations on the stem positioned at right angles to each other using a bit 1.5 cm in diameter (Fig. S2). For each hole, the tree was drilled to a depth equal to one half of its DBH or until the presence of stem rot was identified by visual inspection of the drilled debris using the above criteria. The accuracy of finding stem rot by drilling was cross-validated on 419 stems that were drilled prior to felling.

Safety was a primary consideration, and felling crews had on-site autonomy to exclude trees with visible rot, asymmetric crowns or other features indicative of increased risk of the stem splitting during felling. Of trees with desired felling di-

mensions, 22 % were not felled due to safety concerns. Half of trees excluded for felling were taxa with extremely hard wood, and the remainder were excluded because of excessive slope, severely asymmetric crown, prominent stem or crown damage, or active bee and hornet nests. The exclusion of very large stems with obvious damage and of species with very hard wood means that the felling data are likely conservative in their representation of rot in the forest as a whole. Safety was less of a concern for drilling.

The stem rot data from Lambir were collected from 365 trees (116 species in 35 families; Tables 1, S1) with a 5 mm increment hand borer (Haglöf Sweden AB, Sweden), bored to half of the DBH at one point on the stem, in contrast to the drilling method which tested for rot at two points on each stem. Trees ≥ 6 cm DBH were identified for coring outside, but within approximately 1 km, of the 52 ha plot boundary. We focused sampling on two soil habitats, sandy loam and clay. Soil type identification was guided by sampling on areas adjacent to known areas of clay and sandy loam soil inside the 52-ha plot, and soil types were verified by visual inspection of soil characteristics and floristic composition. Within each soil type, trees were cored opportunistically based on field identifications by *S*. Tan. Voucher specimens were collected for all trees, and field identifications were validated by *S*. Tan and comparison with herbarium specimens at Lambir Hills National Park. We cored three trees for most species, although intensive intraspecific sampling (> 16 trees) was conducted for five common species (four dipterocarps: *Dryobalanops aromatica*, *Dryobalanops lanceolata*, *Dipterocarpus*

globosus, *Vatica micrantha*, and one euphorb: *Macaranga beccariana*). Secondary xylem from extracted cores was examined for stem rot as above, and presence or absence of stem rot was recorded.

2.3 Tree properties

DBH was recorded for all individuals in the drilling, felling, and coring data sets. Wood density (oven dry mass/fresh volume; $g\,cm^{-3}$) was estimated for each tree in the coring data. Wood cores were broken into segments no greater than 5 cm in length prior to analysis to account for radial variation in wood density. The fresh volume of each segment was estimated by water displacement (Archimedes' principle) for each tree in the coring data set. Mass was recorded for wood segments after drying at 60 °C for 72 h. The density for each core was calculated as the mean of segment densities weighted based on the proportion of the basal area occupied by that annulus.

2.4 Tree species properties

Each tree species in the three data sets was categorized according to its soil association. Generalists were species that are similarly abundant on all soil types. Species with distinct soil associations were categorized as specialists of clay/fine loam, fine loam/loam, loam/sandy loam, in order of decreasing fertility and water retention. Assignments were based on analyses of species' distributions within the 52 ha forest dynamics plot at Lambir (Davies et al., 2005) and across a network of plots in Sarawak (Potts et al., 2002). For species not in these studies, classifications were assigned by P.S. Ashton from his extensive studies of tree species distributions in the region (Ashton, 1964, 1973, 2015). The density of sound wood was assigned to stems in the felling and drilling data sets from timber group values (FIDP, 1974b) and from species average densities in the coring data.

2.5 Soil properties

Edaphic data (Table S2) were collected for each plot in the Central Sarawak data. Soil morphology was described in shallow profile pits at plot centers (Baillie et al., 1987). The profiles and augerings, located 2.5 m from the center, were sampled at 0–10 and 45–55 cm, bulked by depth (topsoil and subsoil, respectively), and the soils analyzed for pH electrometrically, organic carbon by Walkley Black acid dichromate oxidation, and total nitrogen by micro-Kjeldahl distillation. Exchangeable cations were extracted with $1M\,NH_4OOCH_3$. Reserve nutrients and free Fe and Al sesquioxides were extracted with hot concentrated HCl. Extracted cations were assayed by atomic adsorption spectrometry, Fe and Al by titration, and P by molybdenum blue colorimetry. Particle size distribution was analyzed by pipette sampling after oxidation with H_2O_2 and dispersion with sodium hexametaphosphate (Chin, 2002). For the coring data, the soil type of each tree

was assigned categorically as sandy loam or clay (201 and 164 trees, respectively) based on the soil survey of the adjacent 52-ha forest dynamics plot. Soil properties of the two most distinct soil types (clay and sandy loam) are listed for both Lambir and Central Sarawak in Table S3.

For the central Sarawak data, we used principal component analysis (PCA) to create a reduced number of orthogonal axes of soil variation, using the function *prcomp* in the statistical software, R (R Core Development Team, 2011). Prior to PCA, we used multiple imputation to replace sparse missing values in the soil data matrix using the function *aregImpute* in R because PCA cannot be performed on a matrix with missing values, and we sought to maximize sample size for statistical power and reduce bias caused by excluding observations with missing values (Little and Rubin, 1987; Schafer, 1997). We included the first four principle component (PC) axes in analyses, which together explained 58 % of the variance in soil properties (Table S2).

2.6 Linear mixed-effect models

Linear mixed effect models were used to evaluate (1) if the detection of stem rot presence and/or absence differed among data sets, (2) if variance in stem rot frequency and severity is explained by taxonomic levels, and (3) if stem rot frequency and severity varied with species, tree, and edaphic covariates. In models testing variation in the frequency of stem rot, we used generalized linear mixed models (GLMM) with a binomial probability distribution and logit link function using the Laplace method and Cholesky root algorithm for parameter estimation (Bolker et al., 2009). Linear mixed models (LMM) with restricted maximum likelihood parameter estimation were used to evaluate variation in stem rot severity (percent stem volume lost to stem rot), which was log transformed to meet the assumption of normality of residuals. GLMM and LMM models were fit using the package *lme4* (Bates et al., 2014) in R. For each GLMM and LMM, we conducted model selection by testing models with all combinations of fixed effect predictors and interactions to find the model with the lowest Akaike's Information Criterion (AIC) value (Burnham and Anderson, 2002). If multiple models were within 2 AIC of lowest value, we selected the model with the fewest parameters.

2.6.1 Differences in stem rot detection among data sets

Stem rot detection rate of drilling and felling could be compared directly in the validation data set of stems sampled by both methods. To compare the detection rate of coring relative to drilling and felling, we used a GLMM to test the interaction between DBH and data set as fixed effects on the aggregated stem rot frequency data. We included only individuals > 30 cm DBH to account for differences among data sets in size range of trees sampled, and because different numbers of individuals were sampled per species, species identity was

included as a random effect. AIC-based model selection indicated that data set should be retained in the model, and so all other models were fitted separately for each data set.

2.6.2 Variance partitioning among taxonomic levels

To estimate the variance in stem rot frequency and severity explained due to taxonomy, we fit LMM with DBH as a fixed effect and a nested taxonomic random effect (Family/Genus/Species) separately for the drilling, felling, and coring data sets. We used the normal approximation for a binomial error distribution for models of stem rot frequency in order to be able to calculate the variance partitioning coefficient (VPC) for each random effect and the residual variance (Goldstein et al., 2002). VPC for a model with one random effect is calculated as $\sigma_{\mu 0}^2 / (\sigma_{\mu 0}^2 + \sigma_{e0}^2$; Eq. 1), where $\sigma_{\mu 0}^2$ is the variance explained by the random effect, and σ_{e0}^2 is the residual variance.

2.6.3 Association of stem rot with ecological covariates

For each data set, we fit two models testing the effects of ecological covariates on stem rot frequency and severity. Model 1: main effects: DBH, wood density, soil PC1, soil PC2, soil PC3, soil PC4; 2-way interaction: wood density × DBH. Model 2: main effects: DBH, wood density, soil association; 2-way interactions: DBH × wood density, soil association × DBH, soil association × wood density; 3-way interaction: DBH × wood density × soil association. Soil PCs and soil habitat association could not be included in the same model due to collinearity. For the coring data, soil type (clay or sandy loam) replaced the soil PCs. AIC-based model selection was used to identify the best-supported models, and for these, we calculated the change in AIC with single-factor removals to analyze each factor's influence on the response variable. All data sets were filtered to include only observations with species-level covariates (Tables 1, S1). While most trees were identified to species, those not resolved to species were excluded (Table S4). Species identity was included as a random effect in all models.

We examined the variance in stem rot probability and severity explained by random and fixed effects using pseudo-R squared (pR^2) metrics (Nakagawa and Schielzeth, 2013). The marginal pR^2 is the proportion explained by the fixed effects alone, and the conditional pR^2 is the total proportion explained by the model when fixed effects are conditioned on the random effects.

2.7 Stand-level estimates of stem biomass lost to rot

Stem rot influences carbon storage and flux in forests, and the ability to predict variation in stem rot due to environmental factors, such as soil resource availability, is important for improving global carbon models. To evaluate how variation in stem rot frequency and severity due to soil properties influenced stand-level carbon stocks, we estimated the max-

imum percent of stem biomass lost to stem rot at the stand level (Loss$_{max}$) and correlated it with soil habitat variables for each cluster of plots in the felling data set. Loss$_{max}$ was calculated as:

$$\text{Loss}_{max} = \frac{\sum_{i=1}^{n} \text{TSV}_i \times \text{Wood Density}_i \times \text{Percent Rot}_i}{\sum_{i=1}^{n} \text{TSV}_i \times \text{Wood Density}_i}, \quad (1)$$

where n is the total number of trees sampled in the felling data for clusters with ≥ 10 felled trees, and TSV is the total stem volume from the base of the tree to the first branch. As described above, the BAF prism plots were variable in size, and so it was impossible to calculate stem biomass lost per unit ground area. However, Loss$_{max}$ is independent of the actual area sampled because it is a percentage that is based on the stem biomass that, given the trees sampled in the plots, would be present if no tree had stem rot. Loss$_{max}$ will not generate the same value as the average percent stem volume lost across trees because Loss$_{max}$ is mass-based, as it accounts for differences among species in wood density, and weights the contribution of individual trees, as it sums across all trees sampled in a cluster. Loss$_{max}$ is the maximum because our calculations assume rotted areas were hollow, as no data were collected on how much wood density was reduced in these areas. Because the severity of rot in coarse roots and tree crowns was not sampled, Loss$_{max}$ represents only the proportion of stem biomass lost to rot. Soil parameters were averages of the plot-level soil measurements in each cluster and varied substantially among clusters (Fig. S3). Pearson correlation tests were used to determine if Loss$_{max}$ correlated with the first four soil PC axes and the six soil chemical variables in the topsoil (pH, total N, reserve P, and exchangeable Ca, K, and Mg) that were used in the PCA. Soil cations (Ca, K, and Mg) were log transformed to meet the assumption of normality.

3 Results

3.1 Frequency of stem rot

There was substantial variation between data sets in the frequency of stem rot (Fig. 2), which occurred in 9 % of cored, 41 % of drilled, and 53 % of felled stems. The classification error of the drilling method was 18 % for the 419 trees scored for rot by first drilling and then felling, where felling observations were taken to be correct. Of the stems misclassified by the drilling method, 58 of the 77 errors (75 %) were false negatives, in which drilled stems were scored as having no rot, but rot was later observed when the stem was felled. The average percent rot was substantially less severe in rotted stems misclassified by the drilling method (5 %) than in rotted stems trees correctly categorized by drilling (19 %), indicating that the drilling method was effective for scoring stems with extensive rot.
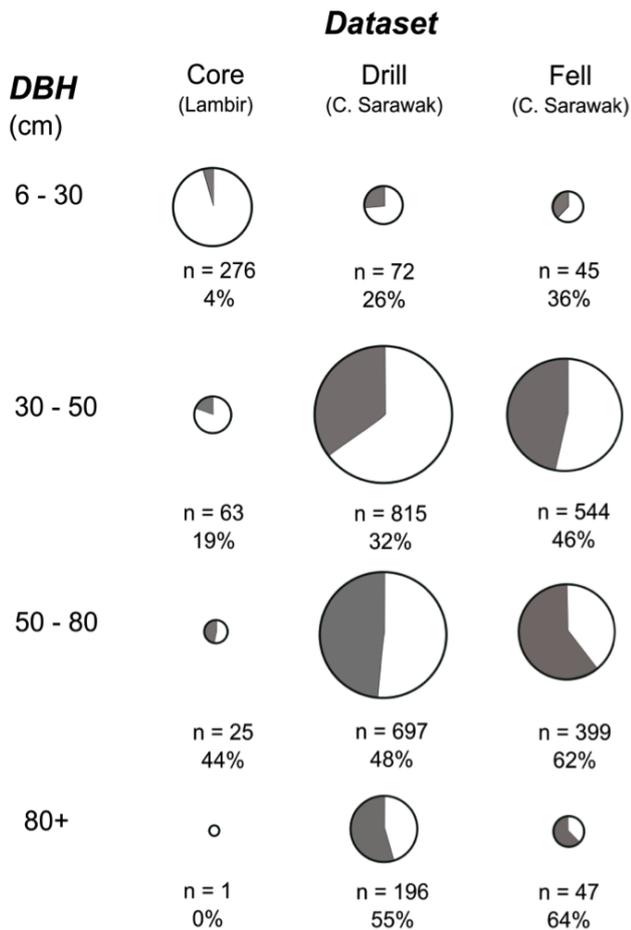
Figure 2. Stem diameter-related variation in the frequency of stem rot found in trees in mixed dipterocarp rain forest of Central Sarawak, Bornean Malaysia. Pie charts show the percentage of trees with stem rot (shaded), with pies sized according to the total number of sampled stems (n), in each diameter at breast height (DBH) size class and three data sets, one from Lambir Hills National Park (Lambir) and two from Central Sarawak (C. Sarawak; see Sect. 2 for details).

The discrepancy in the prevalence of stem rot between the central Sarawak and Lambir data sets may be caused in part by differences in the tree sizes sampled: at Lambir 78 % of the cored trees were < 30 cm DBH, whereas 96 % of trees drilled or felled in Central Sarawak were ≥ 30 cm DBH (Fig. 2; Fig. S4). We investigated these possibilities by sub-setting the data to include the same size range (DBH ≥ 30 cm) across all data sets and testing for differences between data sets in the probability of a tree having stem rot, while accounting for DBH. Based on model selection, the most-supported model after sub-setting retained the effects of DBH (ΔAIC = 86.3) and data set (ΔAIC = 50.9), but not their interaction (ΔAIC = 0.2). Stem rot probability increased with DBH in all data sets (Table S5), and there was no difference in the slope of this relationship across data

sets. Data sets differed in the mean probability of stem rot at a given diameter: for a 50 cm DBH tree, the predicted probability of finding rot was 28 % in the coring data set, compared to 39 % in the drilling and 53 % in the felling data sets.

Variance partitioning analysis using nested taxonomic random effects revealed that family identity explained a negligible proportion of variance in stem rot frequency, whereas the genus-level effect was retained in all three data sets (Table S6). Among the three most well-sampled genera (all Dipterocarpaceae) in the felling data set, stem rot occurred significantly more frequently in *Dryobalanops* (66 % of stems) and *Shorea* (62 % of stems) than in *Dipterocarpus* (23 % of stems; Fig. 3a). The species-level effect was retained in the drilling and felling, but not coring data sets (Table S6). The variance partitioning coefficients (VPC) for genus (0.09) and species (0.08) were similar in the felling data set, whereas species (0.11) explained a greater proportion of variance than genus (0.03) in the drilling data set. The combined taxonomic VPC was 0.17 for the felling, 0.14 for drilling, and 0.09 for coring data sets.

In the GLMMs fit for each data set, the following predictor variables were not retained in the final models either as main effects or interactions, and so had little effect on variation in stem rot frequency (Table S7): felling Model 1 – species wood density and soil PC1, PC2, and PC4; Felling Model 2 – species wood density; Drilling Model 1 – species wood density, soil PC1 and PC4; Drilling Model 2 – species wood density, soil association; Coring Model 1 – tree wood density, soil type; Coring Model 2 – tree wood density, soil association.

Stem rot significantly increased in probability with tree diameter in all data sets (Tables 2, S5; Figs. 2, S5). Indeed, DBH was the only significant predictor in the coring data set. Across all data sets, the frequency of rot increased drastically with larger DBH: stem rot was present in 13 % of stems 10–30 cm DBH, 37 % of stems 30–50 cm DBH, and 54 % of stems ≥ 50 cm DBH.

Stem rot frequency varied significantly with edaphic variables, represented by soil PCs. In the drilling and felling data, the probability of stem rot increased significantly with soil PC3 (Tables 2, S5; Fig. S6a, c), which had a strong negative association with reserve and exchangeable Ca in the topsoil (Table S2). In the drilling data set, the probability of stem rot also decreased with increasing values of soil PC2, which were associated with high pH and high exchangeable Mg in both topsoil and subsoil (Tables 2, S5; Fig. S6b). Overall, these results suggest that stem rot in Central Sarawak was found more frequently on lower fertility soils with reduced cation availability.

The effect of DBH on the incidence of stem rot varied significantly among species with different soil associations, for the felling, but not the drilling or coring data (Tables 2, S5). For species associated with high-fertility clay and fine loam soil, the probability of rot did not increase with DBH, whereas the probability of rot significantly increased with

Table 2. Changes in model fit based on Akaike's Information Criterion (AIC) with removal of single factors from the most-supported generalized linear mixed-model testing associations of the probability of stem rot in trees of mixed dipterocarp rain forest in Sarawak, Borneo, in the drilling, felling, and coring data sets. The ΔAIC shows the increase in AIC when each predictor is removed from the final model. For all models species identity was specified as a random effect. The fixed effects shown are those retained in the best-supported model after model selection based on AIC; see Sect. 2 for details. The following predictor variables were not retained in the final models either as main effects or interactions and so had little effect on variation in stem rot frequency: Felling Model 1 – species wood density and soil PC1, PC2, and PC4; Felling Model 2 – species wood density; Drilling Model 1 – species wood density, soil PC1 and PC4; Drilling Model 2 – species wood density, soil association; Coring Model 1 – tree wood density, soil type; Coring Model 2 – tree wood density, soil association. Abbreviations are as follows: DBH, diameter at breast height; PC, principle component; and Soil Assoc., species soil association. When all predictors are removed, the model is an intercept-only model.

Data set	Model	Final Model	Predictor Removed	AIC	ΔAIC
Felling	Model 1	DBH, Soil PC3	–	970	–
			remove DBH	1009	39
			remove Soil PC3	972	2
			remove all	1009	39
Felling	Model 2	DBH × Soil Assoc.	–	962	–
			remove interaction term.	9670	8
			remove DBH	1006	44
			remove Soil Assoc.	972	10
			remove all	1009	47
Drilling	Model 1	DBH, Soil PC2, Soil PC3	–	863	–
			remove DBH	901	38
			remove Soil PC2	876	13
			remove Soil PC3	865	2
			remove all	908	45
Drilling	Model 2	DBH	–	877	–
			remove all	910	33
Coring	Model 1 & 2	DBH	–	180	–
			remove all	216	36

DBH in all other soil association groups (Fig. S7). Thus, for large diameter trees, stem rot frequency was lower in stems of species associated with more fertile, finer textured soil, than for species in the other three soil association groups.

Overall, the variation in the probability of stem rot explained by the fixed effects in our models differed among the data sets, ranging from the lowest marginal pR^2 values of 5 % in the drilling data to the highest of 21 % in the coring data (Table S8). The variance explained by the species random effects was higher, 17–45 % (conditional pR^2; Table S8), indicating that species differed in stem rot probability even after accounting for variation due to the fixed effect predictors.

3.2　Severity of stem rot

For the 53 % of felled trees showing stem rot, the percent of stem volume lost (stem rot severity) averaged 16 %, but ranged widely, from 0.1–82 %. Similar to stem rot frequency, stem rot severity in felled stems did not differ among tree families, and genus had a higher VPC (0.10) than did species (0.04) (Table S6). Stem rot severity did not vary significantly with DBH, nor any soil PC, as none of these predictors was

retained in the final model (Tables 3, S7). In Model 2, there was a significant interaction between wood density and soil habitat association (Table 3), whereby stem rot severity declined with increasing wood density in species associated with low-fertility soils but increased with wood density for generalist species (Table S5).

Alone, the fixed effects explained a very small proportion of variance in stem rot severity (range of marginal $pR^2 = 0.02$–0.07; Table S8). A larger proportion of variance was explained when fixed effects were conditioned on the random effect of species identity (range of conditional $pR^2 = 0.17$–0.18; Table S8), suggesting that stem rot severity differed among species due largely to characteristics not measured in this study, and the majority of overall variation in stem rot severity remained unexplained by the tree and environmental properties measured.

3.3　Stem biomass lost to rot

Our estimate of the maximum percent of stand-level stem biomass lost to rot, Loss$_{max}$, was 10 % on average and ranged substantially among spatial clusters of trees (0.03–20.9 %).

Table 3. Changes in model fit based on Akaike's Information Criterion (AIC) with removal of single factors from the most-supported linear mixed-model testing associations of the stem rot severity (percent stem volume lost to rot) in trees of mixed dipterocarp rain forest, Central Sarawak, Borneo, in the felling data set. The Δ AIC shows the increase in AIC when each predictor is removed from the final model. Species identity was specified as a random effect. The fixed effects shown are those retained in the best-supported model after model selection based on AIC; see Sect. 2 for details. The following predictor variables were not retained in the final models either as main effects or interactions and so had little effect on variation in stem rot severity: Model 1, DBH, species wood density and soil PC1, PC2, PC3, and PC4; Model 2, DBH. Abbreviations are as follows: WD, wood density and Soil Assoc., species soil association. When all predictors are removed, the model is an intercept-only model.

Data set	Model	Final Model	Predictor Removed	AIC	ΔAIC
Stem rot severity	Model 1	Intercept only	–	1635	–
	Model 2	WD × Soil Assoc.	–	1624	–
			remove interaction term	1638	14
			remove WD	1638	14
			remove Soil Assoc.	1636	12
			remove all	1635	11

Yamakura et al. (1986) estimated that 70 % of aboveground biomass (AGB) in Bornean mixed-dipterocarp forests is located in the boles of trees > 30 cm DBH, where stem biomass was estimated by multiplying stem volume by wood density. Although we did not quantify biomass remaining in rotted regions of stems as necromass or fungal biomass, our estimate of 10 % $Loss_{max}$ indicates that biomass measurements that do not correct for stem rot could overestimate average total AGB in Bornean mixed-dipterocarp forests by up to 7 % or 37 Mg ha^{-1}.

A significant proportion of this variation was explained by soil variables. $Loss_{max}$ was significantly correlated with two soil principal component axes, soil PC2 ($r = -0.40$, $P = 0.016$) and soil PC3 ($r = 0.38$, $p = 0.022$), although the correlation with soil PC3 was strongly influenced by one cluster and was no longer significant without it ($r = 0.21$, $p = 0.113$). $Loss_{max}$ was also marginally associated with soil PC4 ($r = -0.31$, $p = 0.060$; Fig. 4). The estimated amount of stem biomass lost to rot declined with topsoil exchangeable Ca ($r = -0.59$, $p < 0.001$) and Mg ($r = -0.50$, $p = 0.002$), but there was no relationship between $Loss_{max}$ with topsoil measures of soil pH, reserve P, or exchangeable K (Fig. 5).

4 Discussion

Understanding the prevalence and ecology of stem rot in tropical forests is limited by the scarcity of data on stem rot and its potential explanatory correlates. Our analysis of extensive legacy and recently collected data from a total of 339 tree species of mixed-dipterocarp forests is the first to highlight the importance of edaphic properties, along with tree size, taxonomy, and functional traits, in explaining the frequency and severity of stem rot among trees. Together, these factors generated spatial variation among forest stands in the maximum percent of AGB lost to stem rot, and this variation

was correlated with soil properties. Our finding that 7 % of forest AGB is in some stage of wood decay in these Bornean forests not only justifies greater consideration of stem rot and its soil-related variation in the estimation of carbon storage by tropical forests, but also underscores the need for standardized methods of stem rot detection to be applied across tropical forest regions.

4.1 Methodological variation in stem rot detection

Our results affirm the few existing previous findings that stem rot infection is frequent and often severe in dipterocarp forests (Bakshi, 1960; Bagchee, 1961). Stem rot occurred in 41 % of drilled, 53 % of felled stems, and encompassed 9 % of stem volume on average in our study of central Sarawak. These estimates exceed observations from neotropical forests, where 30–38 % of trees among Amazonian species were found to have hollow stems (Apolinário and Martius, 2004; Eleuterio, 2011), and volume losses to stem rot ranged 0.7–4 % (Brown et al., 1995; Clark and Clark, 2000; Nogueira et al., 2006). There may be several reasons for these discrepancies, many related to methodological differences. First, most studies from neotropical forests measured the hollow fraction of stems, whereas our study quantified the volume of wood in any stage of decay visible in the field. Therefore, our methods would inherently generate larger estimates of volume and biomass loss. Second, approaches that quantify stem rot in decomposing stems, such as stumps cut along access roads (Brown et al., 1995) or in naturally fallen logs in coarse woody debris censuses (Clark and Clark, 2000), may confound rotting that occurs *post mortem* with stem rot originating while the tree was alive, or, conversely, may be biased toward logs resistant to decomposition. Such studies are thus unlikely to provide accurate estimates of wood decay in the living trees that comprise standing forest AGB. Third, since stem rot frequency increased dramatically with tree size, studies that under-sample large
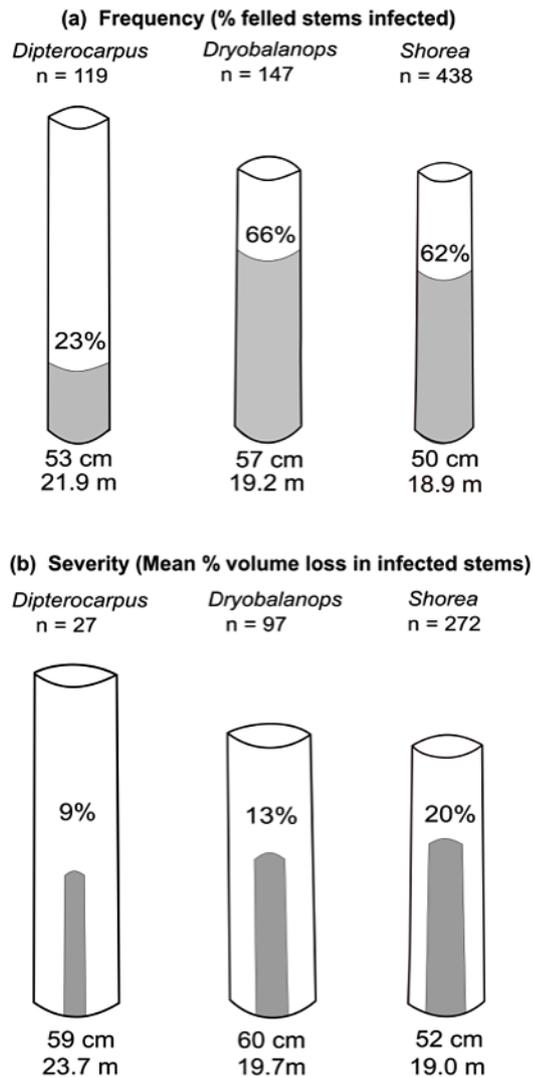
Figure 3. Variation in the frequency and severity of stem rot among three important dipterocarp genera (representing a subset of the 65 genera from the felling data) in the rain forest of Central Sarawak, Borneo, Malaysia. The number of trees (*n*) sampled for each genus is listed. For each genus, *Dipterocarpus*, *Dryobalanops*, and *Shorea*, 17, 4, and 61 species were sampled, respectively. Mean diameter at breast height (DBH; cm) is on the first row beneath each cylinder, and mean stem length (m) is below that, with cylinders sized according to mean diameter and stem length. The shaded portions represent in **(a)** the frequency of stem rot (the percent of felled trees with stem rot) and in **(b)** the severity of stem rot (the mean percent volume lost to stem rot), with actual percentages above the shading.

trees may underestimate stem rot in forest stands. Noguiera et al. (2006) measured the hollow area in cross-sectional discs of freshly felled stems, but included five individuals ≥ 80 cm DBH, compared to the 244 trees ≥ 80 cm drilled or felled in this study. While there is no measure of stem rot severity in the literature equivalent to ours, which was based on har-
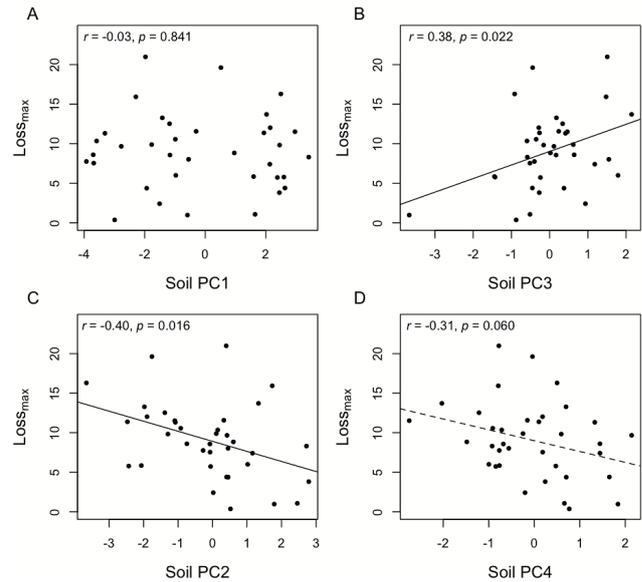

Figure 4. The relationship between the stand-level percent stem biomass lost to stem rot ($Loss_{max}$) among trees sampled in a cluster and mean values of the first four soil principle component (PC) axes for 36 tree clusters containing at least 10 trees ≥ 30 cm DBH. The Pearson correlation coefficient (*r*) and associated probability of each relationship is in its respective panel.

vested stems, our measure of stem rot frequency via drilling was similar to Eleuterio (2011), which evaluated wood decay in the debris created by plunging a chainsaw into stems of trees to be logged in the eastern Brazilian Amazon. This study found wood decay in only 30 % of stems ≥ 45 cm DBH for the six most common timber species. Another study in the Brazilian Amazon found stem hollows in 38 % of felled trees > 50 cm, representing 16 species (Apolinário and Martius, 2004). These frequencies are lower than the 48 % for drilled stems ≥ 45 cm DBH and 62 % of felled stems > 50 cm with any wood decay in our study, providing evidence that stem rot may be more prevalent in Sarawak than other tropical forests. Owing to the large range of tree sizes and taxonomic groups examined, our study likely presents robust and well-constrained estimates of stem rot frequency and severity for Bornean mixed dipterocarp forests. Aside from methodological differences, climate, rainfall seasonality, geology, and biogeographic and phylogenetic history are also likely important, but existing data are insufficient to make inferences about their potential roles in explaining any regional variation in stem rot.

While logging concessions may be opportunistically exploited for detailed evaluation of stem rot, accurate non-destructive measures are still needed to estimate stem rot where destructive harvest is impossible. Drilling proved to be an accurate means of scoring trees for stem rot, correctly characterizing stem rot presence/absence in 80 % of trees. The majority of misclassifications likely occurred because
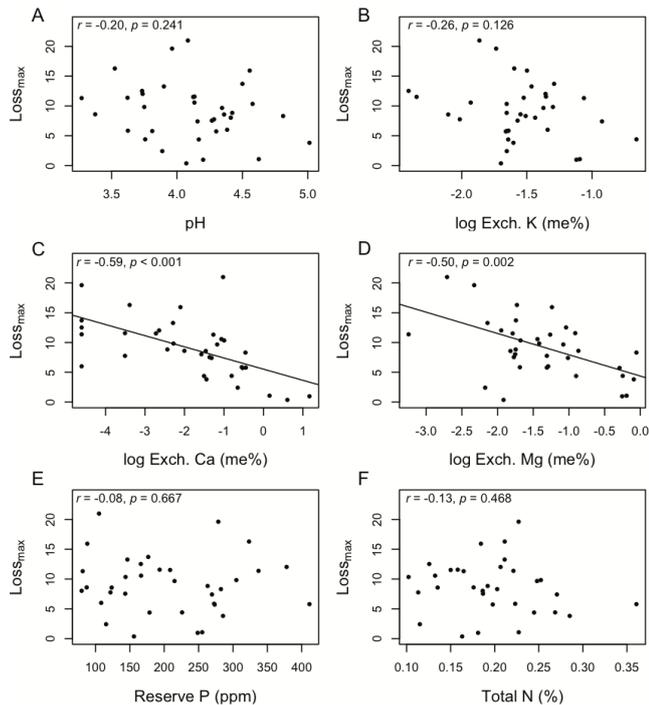
Figure 5. The relationship between the stand-level percent stem biomass lost to stem rot ($Loss_{max}$) among trees sampled in a cluster and mean soil chemical properties for 36 tree clusters containing at least 10 trees ≥ 30 cm DBH. The Pearson correlation coefficient (r) and associated probability of each relationship is in its respective panel. Soil concentrations are expressed in units of milliequivalents per 100 g of soil (me %), parts per million (ppm), or percent dry weight (%).

drilling tested for areas of wood decay only at breast height, missing rot occurring higher or lower in the stem. However, classification error diminished to 8 % for stems that had lost more than 10 % of their volume to rot, indicating that drilling at breast height is a reliable means of identifying trees containing large sections of rot. Moreover, the drilling data sampled larger trees than the felling data. Hence, results of felling and drilling analyses require subtly different interpretations, with the felling data set exploring the correlates of stem rot infection overall, and the drilling data set exploring the correlates of severe stem rot infection. There was no way to validate the accuracy of the coring method; however, the probability of detecting rot was lower at a given stem diameter in the coring data set relative to the drilling data set. Assuming that the true dependence of stem rot frequency on DBH was the same in Lambir and the Central Sarawak sites, then we suspect the drilling method may have been more effective at detecting rot because it was conducted in two perpendicular directions at breast height, whereas trees in the coring data set were bored only once. Inclusion of all three data sets not only allowed assessment of non-destructive methodologies for estimation of stem rot, but also improved inferences

about correlates of stem rot by increasing size range to span the smaller and larger trees included in the coring and drilling data sets, respectively. Sonic tomography has been applied non-destructively to evaluate both the frequency and severity of hollows in tree stems (Nicolotti et al., 2003; Deflorio et al., 2008; Wunder et al., 2013). In the absence of access to this costly equipment, drilling may be a viable, less expensive alternative for assessing the presence of stem rot in remote tropical forests.

4.2 Controls over stem rot in individual stems

Identifying the environmental and tree-related correlates of stem rot provides insight into potential mechanisms governing stem rot and its implications for forest ecosystem processes. Tree size was the only factor significantly associated with stem rot frequency in all three data sets, consistent with previous observations of substantial increases in stem rot frequency with diameter in tropical forests (Nogueira et al., 2006; Eleuterio, 2011). To the extent that diameter correlates with tree age, these results suggest that trees experience accumulating risks of becoming infected with stem rot with time. Future studies should ensure that large trees are not under-sampled, especially considering that large, dominant canopy trees predominantly structure carbon dynamics in tropical forests (Slik et al., 2013; Bastin et al., 2015). Given that tree size was not a significant predictor of the percent stem volume lost to rot in infected trees, the advancement of stem rot infection may depend less on tree age than on the identity of the fungi involved and the physical and chemical properties of the heart wood (Wagener and Davidson, 1954; Pearce, 1996; Schilling et al., 2015).

Species wood density was not a significant predictor of stem rot frequency, consistent with findings from an Amazonian forest (Eleuterio, 2011). This result is somewhat surprising, as high wood density has been associated with pathogen protection in tropical tree species (Augspurger and Kelly, 1984). However, any pathogen protection conferred by higher wood density may not result in lower incidence of stem rot, because of the inverse relationship between wood density and mortality rates (King et al., 2006): at the same size, trees with high wood density are expected to be older than trees with low wood density and so may have longer exposure time to incur stem rot infection.

Stem rot frequency was higher in trees on lower fertility soils, and to a lesser extent, soils with lower pH, in Central Sarawak, but did not differ between edaphic habitats in the smaller trees cored at Lambir. Our results cannot identify how soil properties affect stem rot, but soil PC axes included in final models were correlated with soil Ca and Mg which have also been found to associate strongly with Bornean tree species distributions (Baillie et al., 1987) and explained significant variation in fine root growth at Lambir (Kochsiek et al., 2013). In the Lambir coring data set, the smaller sample size of larger trees may have prevented us

from detecting differences in stem rot frequency among soil types. The association of stem rot with lower fertility soils in Central Sarawak is in some ways counter-intuitive, as forests on high-fertility sites generally have more frequent canopy disturbance (Coomes and Grubb, 2000), potentially causing more wounds and opportunities for infection. In addition to the longer exposure times presumably experienced by tree species characteristic of more dystrophic and drought-prone soils (Russo et al., 2005), trees under nutrient stress may be more prone to infection, if resources to produce secondary compounds are limited (Bryant et al., 1983). Soil chemistry may also influence the composition of the soil microbial community, from which wood decay fungi often originate (Boddy, 2001). At Lambir, the community composition of soil bacteria (Russo et al., 2012) and root-associated mycorrhizal fungi (Peay et al., 2009) differ between clay and sandy loam soil types, which vary in many properties including texture, nutrient supply, and pH (Table S3), indicating that the taxa and functional groups present to colonize wood may differ among edaphic habitats. Furthermore, the relative availability of nutrients in soil vs. wood may influence the infection and growth of wood decay of nutrient-limited fungi in trees, however, this interaction is likely to be complex (Merrill and Cowling, 1966; Donnelly and Boddy, 1998).

Variation among soil habitats in stem rot may also be driven by the change in species composition of the tree community combined with differences among taxa in susceptibility to stem rot. Yet, the effect of tree species' soil habitat association on stem rot frequency and severity was less consistent among data sets than the effects of soil properties. In the felling data set, stem rot frequency increased more slowly with DBH in species adapted to high-fertility soil than in species from other association groups: at 80 cm in diameter, tree species associated with sandy loam/loam soil were 8.6 times more likely to have stem rot than species associated with clay/fine loam and 4.1 times more likely to have stem rot than species associated with loam/fine loam. These results are consistent with the notion that trees specializing on more fertile soils may be younger at the same size compared to species adapted to resource-depleted soils, as their growth and mortality rates are higher (Russo et al., 2005). This pattern may not have been detected by drilling, which was less effective than felling at detecting minor stem rot infections. The significant interaction between soil association and wood density explaining the severity of stem rot remained difficult to parse, aside from the indication that the relationship of stem rot with species traits could be highly multi-dimensional and driven by a complex combination of interacting factors.

4.3 Taxonomic variation in stem rot

While tree size and edaphic factors were significantly associated with stem rot infection, these factors alone explained a relatively small fraction of the variance in the frequency of stem rot, and even less for stem rot severity. The explanatory power of models improved dramatically when fixed effects were conditioned on the species random effect, meaning that the occurrence of stem rot had a strong taxonomic component due to species properties other than wood density and soil association. Perhaps surprisingly, stem rot frequency varied among genera but not among families, suggesting that dipterocarp taxa do not differ systematically in susceptibility to rot from non-dipterocarp taxa in MDF forests, despite showing broad differences in other traits such as mycorrhizal association (Wang and Qiu, 2006).

Among species traits not evaluated in this study, wood anatomical properties and wood chemical content with respect to nutrient stoichiometry and secondary defense may be particularly important in understanding taxonomic variation in stem rot. Lumen diameter and vessel density are significantly correlated stem rot frequency in Amazonian tree species (Eleuterio, 2011) and have been hypothesized to influence the growth of fungal hyphae (Schwarze et al., 2000). Chemical properties of wood may also influence rates of fungal colonization in stems, as tree species wood N and P concentrations correlate with wood decomposition rates in angiosperms (Weedon et al., 2009), and wood decomposition rates decline with initial wood pH among Costa Rican tree species (Schilling et al., 2015). Furthermore, secondary defensive chemistry has been shown to vary among species and generate differences in the microbial colonization of woody debris (Cornwell et al., 2009). Most dipterocarps are known for copious resin production (Appanah and Turnbull, 1998) and are likely to differ widely in the composition and mycostatic effectiveness of these compounds (Bisset et al., 1966, 1971; Norhayati et al., 2013).

In addition to constitutive chemical defences, some of the taxonomic variation in the susceptibility to stem rot may be due to differences in induced defenses against fungal or insect pathogens (Pearce, 1996; Kovalchuk et al., 2013). When wounding allows exposure to pathogens, anatomical modification of xylem in the living sapwood, including compartmentalization, limits the spread of infection (Shigo, 1984; Pearce, 1996), and the extent and effectiveness of this response likely differs among species (Guariguata and Gilbert, 1996; Romero and Bolker, 2008). During formation, heart wood is suffused with secondary metabolites considered inimical to fungal growth (Yamada, 2001; Taylor et al., 2002; Kirker et al., 2013), and interspecific variation in this process may also affect susceptibility to fungal rot. Even after accounting for species identity, most variation in stem rot frequency and severity remained unexplained. Stem rot infection may be highly stochastic because it appears to require both wounding and subsequent colonization by fungal spores or their insect vectors, which have varying dispersal capacities (Peay and Bruns, 2014) and host requirements (Gilbert, 2002).

Density-dependent population mortality caused by the differential susceptibility of tree species to pathogens has been

hypothesized to explain the relative abundance of tree species in forest communities (Comita et al., 2010; Mangan et al., 2010). Given that stem rot affects dead tissue, it is unclear whether this hypothesis also applies to wood decay fungi. Stem rot, often when combined with other stressors, has been implicated in tree death, as it is thought to make trees more vulnerable to sources of mortality (Franklin et al., 1987). The high stem rot frequency and severity among these Bornean species is surprising in this light, and their great longevity (Whitmore, 1984) suggests a large capacity to tolerate stem rot. Stem rot may structurally weaken trees and predispose them to buckling from wind-throw or other disturbances, which often vary in frequency in relation to soil properties and topography (Gale and Hall, 2001; Ohkubo, 2007). The severity of stem rot required for biomechanical failure may be high: only when the radius of the hollow region is ca. 70 % of the total stem radius, which would constitute a loss of stem volume due to stem rot of 49 %, is structural failure viewed to become considerably more likely (Mattheck et al., 2006; Ruxton, 2014). Among Bornean trees with any stem rot in the felling data, 6 % had stem rot of this severity or greater. Whether stem rot contributes to tree death and if so, how, are topics that merit more investigation in tropical forests.

4.4 Implications of tree-level variation in stem rot for forest biomass

When tree-level stem rot was scaled to the stand-level, we found large spatial variation in the potential ecosystem stem biomass lost to rot in central Sarawak. Stems of trees > 30 cm DBH account for ∼ 70 % of the standing AGB in mature mixed-dipterocarp forests (Yamakura et al., 1986), and trees > 70 cm DBH make up 40 % of the AGB in southeast Asian forests (Slik et al., 2013). In light of these regional studies, our results suggest that correcting for biomass lost to stem rot reduces total forest AGB estimates by up to 7 % relative to what would be predicted assuming all stems are composed strictly of intact wood, with the true stem rot correction depending on the relative densities of decayed vs. sound wood. While estimates of biomass loss due to stem rot in living trees are rare, studies of standing dead trees and woody debris found that biomass loss over time is approximately exponential (Harmon et al., 1986; Freschet et al., 2012), indicating that the biomass density of rotted stem fractions should be much less than the density of intact wood. Moreover, Bornean dipterocarp forests are taller, with more large-diameter trees, and thus have higher AGB than many other tropical forests (Yamakura et al., 1986; Slik et al., 2013; Banin et al., 2014). These differences may be reduced by potentially greater incidence of stem rot in mixed-dipterocarp forests, since, as noted above, considerably lower estimates of biomass lost to stem rot have been reported in neotropical forests.

The effect of stem rot on standing biomass showed strong spatial variation, and was significantly greater for stands growing on less fertile soil. An analysis in a lowland Bornean rainforest found that AGB positively correlated with surface soil nutrient concentrations, including P, K, and Mg, due to the increased stem density of trees > 120 cm DBH on high-fertility soils (Paoli et al., 2008b). Our results suggest that the discrepancy in AGB between low- and high-fertility soils may in fact be even larger because large stems on low-fertility sites are more likely to contain extensive rot.

It is difficult to determine if current methods of biomass estimation adequately account for stem rot in tropical trees. In principle, stem rot may be implicitly incorporated into allometric equations used to estimate AGB from forest inventories (e.g., Chave et al., 2005), which are empirically derived from destructive harvest data sets likely to include trees with stem rot. In practice, however, large trees are often severely under-represented in such allometric data sets. Moreover, the strong variability in biomass loss among species and edaphic habitats in this study indicate that site-specific corrections for stem rot may be needed. Thus, greater consideration of soil conditions and broader-scale quantification of stem rot using standardized methods are critical to improving the estimation of carbon storage in tropical forests.

5 Conclusions

Stem rot is a poorly quantified source of error in aboveground biomass estimation throughout the tropics. Our study of stem rot frequency and severity in mixed-dipterocarp forests in Sarawak Borneo indicates that spatial variation among forest stands in biomass losses to stem rot coincidences with variation in soil-related factors, which may influence patterns of tropical forest carbon storage across edaphically heterogeneous landscapes. Moreover, the considerable taxonomic variation in heart rot susceptibility observed here could potentially underlie differences in the ecosystem consequences of stem rot among tropical regions with contrasting biogeographic histories. Consequently, using standardized, nondestructive methods to quantify stem rot across tropical regions and environmental gradients would help better constrain estimates of carbon dynamics in tropical forests.

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