

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

K. D. Heineman^{a*}, S. E. Russo^b, I. C. Baillie^{cd}, J. D. Mamit^{de}, P. P-K. Chai^d, L. Chai^d, E. W. Hindley^f,
B.-T. Lau^d, S. Tan^g, and P. S. Ashton^h

^a Program for Ecology, Evolution, and Conservation Biology, University of Illinois-Urbana Champaign, USA

^b School of Biological Sciences, University of Nebraska – Lincoln, USA

^c National Soil Resources Institute, Cranfield University, UK

^d formerly Forest Department, Kuching, Sarawak, Malaysia

^e *Datuk Menteri Yang Berhormat, Federal Parliament of Malaysia, Kuala Lumpur, Malaysia.*

^f 502 591 57th W Avenue, Vancouver, British Columbia, Canada

^gCenter for Tropical Forest Science, Smithsonian Institution, Washington DC, 20013-7012

^hOrganismic and Evolutionary Biology, Harvard University, USA and Royal Botanic Gardens, Kew. UK.

*Corresponding author: kheineman@life.illinois.edu

Keywords carbon storage, Dipterocarpaceae; hollow trees; Sarawak; soil nutrients; heart rot; tropical tree species; wood decay

1 **Abstract**

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

24

1 **1 Introduction**

2 Fungal rot of secondary xylem causes hollows and regions of reduced wood density in tree stems. This
3 type of fungal infection, commonly referred to as stem rot, is important for the structure, dynamics, and
4 functioning of forests, given that it may increase tree mortality (Franklin et al., 1987; Ruxton, 2014),
5 facilitates the creation of cavity habitats for a diversity of wood-inhabiting and decaying species (Cockle
6 et al., 2012; Stockland et al., 2012), and may act as a reservoir of nutrients sequestered in stem rot
7 biomass (Janzen, 1976; Dickinson and Tanner, 1978; Boddy and Watkinson, 1995). Moreover, the effect
8 of stem rot on aboveground biomass is of particular importance for efforts to map carbon storage in
9 tropical regions as part of global conservation and climate change mitigation strategies (Saatchi et al.,
10 2011). However, because stem rot is difficult to detect by non-destructive means, we understand little
11 about what controls its frequency and severity, especially in tropical forests.

12 Most information available on stem rot in tropical forests comes from forestry studies exploring
13 its influence on the volume and quality of timber. Among species commonly logged in Old World
14 dipterocarp forests, stem rot occurs in up to 75% of large *Shorea robusta* (Dipterocarpaceae), reducing
15 stem volumes by 9 – 13% (Bakshi, 1960; Bagchee, 1961). The majority of large mono-dominant *Shorea*
16 *albida* individuals in Sarawak peat swamp forests have been extensively hollowed by fungi and termites
17 (Anderson, 1964). In subalpine silver fir (*Abies densa*; Pinaceae) forests of the Eastern Himalayas, stem
18 rot reduced timber yields to < 33% of those predicted from external stem volumes (Bürgi et al., 1992;
19 Gratzer et al., 1997). The influence of stem rot appears to be less in the Brazilian Amazon, where the
20 average frequency of stem rot was 30% in six commercial timber species in the eastern Amazon
21 (Eleuterio, 2011), and estimation of stem volume hollowed by stem rot in the western Amazon was just
22 0.7% (Nogueira et al., 2006). Together these studies provide evidence that the frequency and severity of
23 stem rot influences AGB estimates. However, there have been few systematic analyses of the
24 interspecific variation in stem rot with respect to tree properties or environmental factors that might
25 mediate susceptibility and engender spatial variation in forest biomass lost to stem rot.

1 Understanding how patterns of stem rot infection vary with tree size is critical to assessing its
2 influence on forest AGB estimation because trees > 70 cm in diameter at breast height (DBH) explain
3 70% of variation in pantropical AGB (Slik et al., 2013). Tree size may be among the best predictors of
4 stem rot in tropical forests because old trees have lived long enough to incur butt, branch, and stem
5 wounds that lead to fungal infection, and trees may become less resistant to infection as they age (Boddy,
6 2001). In temperate forests, where tree age can be estimated precisely, stem rot frequency increases with
7 age in longleaf pine (*Pinus palustris*) (Hooper, 1988), and pedunculate oak (*Quercus robur*) (Ranius et
8 al., 2009). While tree size is an imperfect proxy of tree age (Baker et al., 2005; Brienen and Zuidema
9 2006), stem rot frequency increases with tree diameter in neotropical forests (Nogueira et al., 2006;
10 Eleuterio, 2011). However, variation in the frequency of stem rot in a given size class indicates that there
11 may be interactions between tree size and taxonomic, functional, and environmental factors.

12 Quantifying the strength of taxonomic variation in stem rot frequency in trees and determining
13 functional traits that underlie species differences in stem rot infection should provide insight into patterns
14 of carbon storage in tropical forests, which often show large shifts in species composition over spatial
15 gradients. Cornwell et al. (2009) demonstrated that the inclusion of plant traits improved models of
16 global carbon turnover from coarse woody debris pools, however, the traits that influence wood
17 decomposition in living stems are still poorly understood. Among potentially important species traits,
18 wood properties may explain variation among trees in susceptibility to stem rot. Trees with dense wood
19 may be less likely to experience branch and stem breakage due to wind disturbance (Putz et al., 1983) and
20 are thought to be more resistant to termite and fungal infection than trees with softer wood. However,
21 there is conflicting evidence as to whether wood density and decay resistance are strongly correlated
22 (Yoneda, 1975; Bultman and Southwell, 1976; Weedon et al., 2009; van Geffen et al., 2010; Mori et al.,
23 2013). Dense wood has been found to be associated with pathogen resistance in tropical tree species
24 (Augspurger and Kelly, 1984) and slower fungal growth (Romero and Bolker, 2008), perhaps because
25 denser heart wood may retain more water and thereby inhibit fungal growth (Boddy, 2001) or have low
26 porosity that impedes the growth of fungal hyphae (Bjurman and Viitanen, 1996; Schwarze et al., 2000).

1 Within species, fast-grown trees with lower wood density are associated with faster decay rates by
2 saprophytic fungi (Edman et al., 2006; Ranius et al., 2009), although this pattern does not hold across all
3 fungal taxa (Yu et al., 2003). In an Amazonian forest, little or no covariation was found between species'
4 wood density and frequency of stem rot, but the probability of rot was significantly correlated with other
5 wood traits, such as the lumen diameter and density of vessels (Eleuterio, 2011).

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

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

26

1 **2 Methods**

2 **2.1 Study sites**

3 The data were collected in two locations in Malaysian Borneo: Central Sarawak and Lambir Hills
4 National Park, Sarawak (Fig. 1). The Central Sarawak tree drilling and felling data were collected during
5 a timber inventory of lowland mixed dipterocarp rain forest ($1^{\circ}30'N$ - $2^{\circ}50'N$, $112^{\circ}20'E$ - $113^{\circ}50'E$)
6 (FIDP, 1974a). Annual rainfall averages $3000 - 3500 \text{ mm yr}^{-1}$ in this region with no distinct dry season.
7 The topography consists of long, steep-sided ridges on Tertiary sandstones and narrow valleys in softer
8 shales. The soils are colluvial/residual Acrisols (Udults) and associated Cambisols (Udepts) (FAO,
9 2006). The coarse loams on sandstone ridges tend to be more stable and deeper than the shale-derived
10 fine loams and clays of the lower slopes and valleys. All of the soils are acidic and leached, and
11 exchangeable base saturation is usually $< 10\%$. Reserves of K and Mg are moderate, but those of P and
12 especially Ca are low. Mineral nutrient fertility increases with clay content, and the slope and valley
13 clays are less dystrophic than the coarse loams on the ridges (Baillie et al., 1987). The mixed-dipterocarp
14 forest in this region is among most diverse forests in the Paleotropics, and the distributions of many tree
15 species are associated with soil conditions, producing considerable changes in floristic composition across
16 different soil types (Baillie et al., 1987; Ashton and Hall, 1992; Potts et al., 2002). Average canopy
17 height is 30-50 m with emergent trees reaching 70 m.

18 Tree coring data were collected in 2009 in Lambir Hills National Park (hereafter, Lambir) in
19 northern Sarawak ($4^{\circ}11'N$, $114^{\circ}01'E$). The physical environment is similar to that of the central
20 Sarawak study area, with acid leached Acrisols and associated Cambisols (Baillie et al., 2006; Tan et al.,
21 2009) on a sandstone cuesta (Yamakura et al., 1996), with shale below the scarp and on the lower dip-
22 slope. Sampling was conducted on two of the four soil types present in a 52-ha forest dynamics plot at
23 Lambir (Lee et al., 2002): clay soil, which is more fertile for most nutrients and has greater cation
24 exchange and water-holding capacity, and sandy loam soil, which has lower concentrations for most
25 nutrients, lower cation exchange capacity, and is better drained (Baillie et al., 2006; Tan et al., 2009).
26 The distribution of individual species, and the overall floristic composition, structure, and dynamics of the

1 mixed-dipterocarp forest at Lambir are associated with differences in topography and soils (Lee et al.,
2 2002; Davies et al., 2005; Russo et al., 2005; Russo et al., 2008; Heineman et al., 2011).

3

4 **2.2 Stem rot data**

5 The Central Sarawak felling (1035 trees in 211 species (including morphospecies) in 31 families) and
6 drilling (1780 trees in 206 species in 34 families) data (Table 1, S1) were collected from 422 plots
7 grouped in 69 clusters as part of the Forest Industries Development Project (FIDP) conducted from 1969-
8 1971 (Fig. 1) (FIDP, 1974b). Each cluster consisted of nine plots arrayed in a 3 x 3 grid with 80 m
9 spacing between plots (Fig. S1). Plots were defined using a standard BAF 10 prism, so that all the stems
10 with an angular diameter $>1.74^\circ$ when viewed from the center point were included in the plot. This
11 standard forest inventory method (Avery and Burkhart, 2002) includes larger stems located relatively far
12 away from the center point, whereas small stems are only included if they are close. The plots were
13 therefore irregularly shaped and ranged in size from ca. 200 to $> 2000 \text{ m}^2$ (Fig. S1). On a random subset
14 of 43 of 502 total clusters in the FIDP, all trees that would produce at least one commercial log (i.e. 3.65
15 m long with DBH $\geq 30 \text{ cm}$) were selected for felling, regardless of species. Nearly all stems $\geq 40 \text{ cm}$
16 DBH qualified as containing at least one commercial log. Selected trees were felled at breast height (1.3
17 m) or above the highest buttress head, and stems were cut into 3.65 m logs along the length of the stem
18 until the point of first branching (Fig. S2). Presence or absence of stem rot was recorded based on visual
19 inspection of the log ends, and stem rot was scored as present when the wood contained voids or areas of
20 darkened, soft, or brittle wood (Fig. S2). Logs that were sound at one end but rotten at the other were
21 sawn in half to better quantify rot severity. For each cross-section, the total area and the area occupied by
22 stem rot were measured by grid counts on transparent overlays (Panzer, 1975). The volume of the whole
23 log and volume occupied by stem rot were computed based on tapering cylinders. The percent of stem rot
24 for the tree was estimated as the sum of the rot volumes for each log as a percentage of the total stem
25 volume. Stem rot sampling was augmented with a drilling program because early felling results revealed
26 more frequent and severe stem rot than anticipated. On an additional 26 randomly chosen clusters in

1 which felled logs were not evaluated for stem rot, all trees with at least one commercial log were drilled at
2 two locations on the stem positioned at right angles to each other using a bit 1.5 cm in diameter (Fig. S2).
3 For each hole, the tree was drilled to a depth equal to one half of its DBH or until the presence of stem rot
4 was identified by visual inspection of the drilled debris using the above criteria. The accuracy of finding
5 stem rot by drilling was cross-validated on 419 stems that were drilled prior to felling.

6 Safety was a primary consideration, and felling crews had on-site autonomy to exclude trees with
7 visible rot, asymmetric crowns or other features indicative of increased risk of the stem splitting during
8 felling. Of trees with desired felling dimensions, 22% were not felled due to safety concerns. Half of
9 trees excluded for felling were taxa with extremely hard wood, and the remainder were excluded because
10 of excessive slope, severely asymmetric crown, prominent stem or crown damage, or active bee and
11 hornet nests. The exclusion of very large stems with obvious damage and of species with very hard wood
12 means that the felling data are likely conservative in their representation of rot in the forest as a whole.
13 Safety was less of a concern for drilling.

14 The stem rot data from Lambir were collected from 365 trees (116 species in 35 families; Table 1,
15 S1) with a 5-mm increment hand borer (Haglöf Sweden AB, Sweden), bored to half of the DBH at one
16 point on the stem, in contrast to the drilling method which tested for rot at two points on each stem. Trees
17 ≥ 6 cm DBH were identified for coring outside, but within approximately 1 km, of the 52-ha plot
18 boundary. We focused sampling on two soil habitats, sandy loam and clay. Soil type identification was
19 guided by sampling on areas adjacent to known areas of clay and sandy loam soil inside the 52-ha plot,
20 and soil types were verified by visual inspection of soil characteristics and floristic composition. Within
21 each soil type, trees were cored opportunistically based on field identifications by S. Tan. Voucher
22 specimens were collected for all trees, and field identifications were validated by S. Tan and comparison
23 with herbarium specimens at Lambir Hills National Park. We cored three trees for most species, although
24 intensive intraspecific sampling (> 16 trees) was conducted for five common species (four dipterocarps:
25 *Dryobalanops aromatica*, *Dryobalanops lanceolata*, *Dipterocarpus globosus*, *Vatica micrantha*, and one

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

3

4 **2.3 Tree properties**

5 DBH was recorded for all individuals in the drilling, felling, and coring datasets. Wood density (oven dry
6 mass / fresh volume; g/cm³) was estimated for each tree in the coring data. Wood cores were broken into
7 segments no greater than 5 cm in length prior to analysis to account for radial variation in wood density.
8 The fresh volume of each segment was estimated by water displacement (Archimedes' principle) for each
9 tree in the coring data set. Mass was recorded for wood segments after drying at 60°C for 72 hours. The
10 density for each core was calculated as the mean of segment densities weighted based on the proportion
11 of the basal area occupied by that annulus.

12

13 **2.4 Tree species properties**

14 Each tree species in the three data sets was categorized according to its soil association. Generalists were
15 species that are similarly abundant on all soil types. Species with distinct soil associations were
16 categorized as specialists of clay/fine loam, fine loam/loam, loam/sandy loam, in order of decreasing
17 fertility and water retention. Assignments were based on analyses of species' distributions within the 52-
18 ha forest dynamics plot at Lambir (Davies et al., 2005) and across a network of plots in Sarawak (Potts et
19 al., 2002). For species not in these studies, classifications were assigned by P.S. Ashton from his
20 extensive studies of tree species distributions in the region (Ashton, 1964, 1973, 2015). The density of
21 sound wood was assigned to stems in the felling and drilling datasets from timber group values (FIDP,
22 1974b) and from species average densities in the coring data.

23

24 **2.5 Soil properties**

25 Edaphic data (Table S2) were collected for each plot in the Central Sarawak data. Soil morphology was
26 described in shallow profile pits at plot centers (Baillie et al., 1987). The profiles and augerings, located

1 2.5 m from the centre, were sampled at 0-10 and 45–55 cm, bulked by depth (topsoil and subsoil,
2 respectively), and the soils analysed for pH electrometrically, organic carbon by Walkley Black acid
3 dichromate oxidation, and total nitrogen by micro-Kjeldahl distillation. Exchangeable cations were
4 extracted with 1M NH_4OOC_3 . Reserve nutrients and free Fe and Al sesquioxides were extracted with
5 hot concentrated HCl. Extracted cations were assayed by atomic adsorption spectrometry, Fe and Al by
6 titration, and P by molybdenum blue colorimetry. Particle size distribution was analysed by pipette
7 sampling after oxidation with H_2O_2 and dispersion with sodium hexametaphosphate (Chin, 2002). For the
8 coring data, the soil type of each tree was assigned categorically as sandy loam or clay (201 and 164 trees,
9 respectively) based on the soil survey of the adjacent 52-ha forest dynamics plot. Soil properties of the
10 two most distinct soil types (clay and sandy loam) are listed for both Lambir and Central Sarawak in
11 Table S3.

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

20

21 **2.6 Linear mixed effect models**

22 Linear mixed effect models were used to evaluate: 1) if the detection of stem rot presence/absence
23 differed among datasets, 2) if variance in stem rot frequency and severity is explained by taxonomic
24 levels, and 3) if stem rot frequency and severity varied with species, tree, and edaphic covariates. In
25 models testing variation in the frequency of stem rot, we used generalized linear mixed models (GLMM)
26 with a binomial probability distribution and logit link function using the Laplace method and Cholesky

1 root algorithm for parameter estimation (Bolker et al., 2009). Linear mixed models (LMM) with
2 restricted maximum likelihood parameter estimation were used to evaluate variation in stem rot severity
3 (percent stem volume lost to stem rot), which was log transformed to meet the assumption of normality of
4 residuals. GLMM and LMM models were fit using the package *lme4* (Bates et al., 2014) in R. For each
5 GLMM and LMM, we conducted model selection by testing models with all combinations of fixed effect
6 predictors and interactions to find the model with the lowest Akaike's Information Criterion (AIC) value
7 (Burnham and Anderson, 2002). If multiple models were within 2 AIC of lowest value, we selected the
8 model with the fewest parameters.

9 **2.6.1 Differences in stem rot detection among datasets:** Stem rot detection rate of drilling and felling
10 could be compared directly in the validation dataset of stems sampled by both methods. To compare the
11 detection rate of coring relative to drilling and felling, we used a GLMM to test the interaction between
12 DBH and dataset as fixed effects on the aggregated stem rot frequency data. We included only individuals
13 > 30 cm DBH to account for differences among datasets in size range of trees sampled, and because
14 different numbers of individuals were sampled per species, species identity was included as a random
15 effect. AIC based model selection indicated that dataset should be retained in the model, and so all other
16 models were fit separately for each dataset.

17 **2.6.2 Variance partitioning among taxonomic levels:** To estimate the variance in stem rot frequency
18 and severity explained due to taxonomy, we fit LMM with DBH as a fixed effect and a nested taxonomic
19 random effect (Family/Genus/Species) separately for the drilling, felling, and coring datasets. We used
20 the normal approximation for a binomial error distribution for models of stem rot frequency in order to be
21 able to calculate the variance partitioning coefficient (VPC) for each random effect and the residual
22 variance (Goldstein et al., 2002). VPC for a model with one random effect is calculated as $\sigma_{\mu 0}^2 / (\sigma_{\mu 0}^2 +$
23 σ_{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.

24 **2.6.3 Association of stem rot with ecological covariates:** For each dataset, we fit two models testing
25 the effects of ecological covariates on stem rot frequency and severity. Model 1: Main effects: DBH,
26 wood density, soil PC1, soil PC2, soil PC3, soil PC4; 2-way interaction: wood density x DBH. Model 2:

1 Main effects: DBH, wood density, soil association; 2-way interactions: DBH x wood density, soil
2 association x DBH, soil association x wood density; 3-way interaction: DBH x wood density x soil
3 association. Soil PCs and soil habitat association could not be included in the same model due to
4 collinearity. For the coring data, soil type (clay or sandy loam) replaced the soil PCs. AIC-based model
5 selection was used to identify the best-supported models, and for these, we calculated the change in AIC
6 with single-factor removals to analyze each factor's influence on the response variable. All datasets were
7 filtered to include only observations with species-level covariates (Tables 1, S1). While most trees were
8 identified to species, those not resolved to species were excluded (Table S4). Species identity was
9 included as a random effect in all models.

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

14

15 **2.7 Stand-level estimates of stem biomass lost to rot**

16 Stem rot influences carbon storage and flux in forests, and the ability to predict variation in stem rot due
17 to environmental factors, such as soil resource availability, is important for improving global carbon
18 models. To evaluate how variation in stem rot frequency and severity due to soil properties influenced
19 stand-level carbon stocks, we estimated the maximum percent of stem biomass lost to stem rot at the
20 stand level ($Loss_{max}$) and correlated it with soil habitat variables for each cluster of plots in the felling
21 dataset. $Loss_{max}$ was calculated as:

$$22 Loss_{max} = \frac{\sum_{i=1}^n TSV_i * Wood\ Density_i * Percent\ Rot_i}{\sum_{i=1}^n TSV_i * Wood\ Density_i} \quad (Eq. 2)$$

23 where n is the total number of trees sampled in the felling data for clusters with ≥ 10 felled trees, and TSV
24 is the total stem volume from the base of the tree to the first branch. As described above, the BAF prism
25 plots were variable in size, and so it was impossible to calculate stem biomass lost per unit ground area.

1 However, $Loss_{max}$ is independent of the actual area sampled because it is a percentage that is based on the
2 stem biomass that, given the trees sampled in the plots, would be present if no tree had stem rot. $Loss_{max}$,
3 will not generate the same value as the average percent stem volume lost across trees because $Loss_{max}$ is
4 mass-based, as it accounts for differences among species in wood density, and weights the contribution of
5 individual trees, as it sums across all trees sampled in a cluster. $Loss_{max}$ is the maximum because our
6 calculations assume rotted areas were hollow, as no data were collected on how much wood density was
7 reduced in these areas. Because the severity of rot in coarse roots and tree crowns was not sampled,
8 $Loss_{max}$ represents only the proportion of stem biomass lost to rot. Soil parameters were averages of the
9 plot-level soil measurements in each cluster and varied substantially among clusters (Fig. S3). Pearson
10 correlation tests were used to determine if $Loss_{max}$ correlated with the first four soil PC axes and the six
11 soil chemical variables in the topsoil (pH, total N, reserve P, and exchangeable Ca, K, and Mg) that were
12 used in the PCA. Soil cations (Ca, K, and Mg) were log transformed to meet the assumption of
13 normality.

14

15 **3 Results**

16 **3.1 Frequency of stem rot**

17 There was substantial variation between datasets in the frequency of stem rot (Fig. 2), which occurred in
18 9% of cored, 41% of drilled, and 53% of felled stems. The classification error of the drilling method was
19 18% for the 419 trees scored for rot by first drilling and then felling, where felling observations were
20 taken to be correct. Of the stems misclassified by the drilling method, 58 of the 77 errors (75%) were
21 false negatives, in which drilled stems were scored as having no rot, but rot was later observed when the
22 stem was felled. The average percent rot was substantially less severe in rotted stems misclassified by the
23 drilling method (5%) than in rotted stems trees correctly categorized by drilling (19%), indicating that the
24 drilling method was effective for scoring stems with extensive rot.

25 The discrepancy in the prevalence of stem rot between the central Sarawak and Lambir datasets
26 may be caused in part by differences in the tree sizes sampled: at Lambir 78% of the cored trees were <

1 30 cm DBH, whereas 96% of trees drilled or felled in Central Sarawak were \geq 30 cm DBH (Fig. 2; Fig.
2 S4). We investigated these possibilities by sub-setting the data to include the same size range (DBH \geq 30
3 cm) across all datasets and testing for differences between datasets in the probability of a tree having stem
4 rot, while accounting for DBH. Based on model selection, the most-supported model after sub-setting
5 retained the effects of DBH ($\Delta AIC = 86.3$) and dataset ($\Delta AIC = 50.9$), but not their interaction ($\Delta AIC =$
6 0.2). Stem rot probability increased with DBH in all datasets (Table S5), and there was no difference in
7 the slope of this relationship across data sets. Datasets differed in the mean probability of stem rot at a
8 given diameter: for a 50 cm DBH tree, the predicted probability of finding rot was 28% in the coring
9 dataset, compared to 39% in the drilling and 53% in the felling datasets.

10 Variance partitioning analysis using nested taxonomic random effects revealed that family
11 identity explained a negligible proportion of variance in stem rot frequency, whereas the genus-level
12 effect was retained in all three datasets (Table S6). Among the three most well sampled genera (all
13 Dipterocarpaceae) in the felling dataset, stem rot occurred significantly more frequently in *Dryobalanops*
14 (66% of stems) and *Shorea* (62% of stems) than in *Dipterocarpus* (23% of stems; Fig. 3a). The species-
15 level effect was retained in the drilling and felling, but not coring datasets (Table S6). The variance
16 partitioning coefficients (VPC) for genus (0.09) and species (0.08) were similar in the felling dataset,
17 whereas species (0.11) explained a greater proportion of variance than genus (0.03) in the drilling dataset.
18 The combined taxonomic VPC was 0.17 for the felling, 0.14 for drilling, and 0.09 for coring datasets.

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

25 Stem rot significantly increased in probability with tree diameter in all data sets (Tables 2, S5;
26 Fig. 2, S5). Indeed, DBH was the only significant predictor in the coring dataset. Across all datasets, the

1 frequency of rot increased drastically with larger DBH: stem rot was present in 13% of stems 10-30 cm
2 DBH, 37% of stems 30-50 cm DBH, and 54% of stems \geq 50 cm DBH.

3 Stem rot frequency varied significantly with edaphic variables, represented by soil PCs. In the
4 drilling and felling data, the probability of stem rot increased significantly with soil PC3 (Tables 2, S5;
5 Fig. S6a, c), which had a strong negative association with reserve and exchangeable Ca in the topsoil
6 (Table S2). In the drilling dataset, the probability of stem rot also decreased with increasing values of soil
7 PC2, which were associated with high pH and high exchangeable Mg in both topsoil and subsoil (Tables
8 2, S5; Fig. S6b). Overall, these results suggest that stem rot in Central Sarawak was found more
9 frequently on lower fertility soils with reduced cation availability.

10 The effect of DBH on the incidence of stem rot varied significantly among species with different
11 soil associations, for the felling, but not the drilling or coring data (Tables 2, S5). For species associated
12 with high fertility clay and fine loam soil, the probability of rot did not increase with DBH, whereas the
13 probability of rot significantly increased with DBH in all other soil association groups (Fig. S7). Thus,
14 for large diameter trees, stem rot frequency was lower in stems of species associated with more fertile,
15 finer textured soil, than for species in the other three soil association groups.

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

21

22 **3.2 Severity of stem rot**

23 For the 53% of felled trees showing stem rot, the percent of stem volume lost (stem rot severity) averaged
24 16%, but ranged widely, from 0.1% - 82%. Similar to stem rot frequency, stem rot severity in felled
25 stems did not differ among tree families, and genus had a higher VPC (0.10) than did species (0.04)
26 (Table S6). Stem rot severity did not vary significantly with DBH, nor any soil PC, as none of these

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

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

11

12 **3.3 Stem biomass lost to rot**

13 Our estimate of the maximum percent of stand-level stem biomass lost to rot, $Loss_{max}$, was 10% on
14 average and ranged substantially among spatial clusters of trees (0.03 - 20.9%). Yamakura et al. (1986)
15 estimated that 70% of aboveground biomass (AGB) in Bornean mixed-dipterocarp forests is located in the
16 boles of trees > 30 cm DBH, where stem biomass was estimated by multiplying stem volume by wood
17 density. Although we did not quantify biomass remaining in rotted regions of stems as necromass or
18 fungal biomass, our estimate of 10% $Loss_{max}$ indicates that biomass measurements that do not correct for
19 stem rot could overestimate average total AGB in Bornean mixed-dipterocarp by up to 7% or 37 Mg/ha.

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

1

2 **4 Discussion**

3 Understanding the prevalence and ecology of stem rot in tropical forests is limited by the scarcity of data
4 on stem rot and its potential explanatory correlates. Our analysis of extensive legacy and recently
5 collected data from a total of 339 tree species of mixed-dipterocarp forests is the first to highlight the
6 importance of edaphic properties, along with tree size, taxonomy, and functional traits, in explaining the
7 frequency and severity of stem rot among trees. Together, these factors generated spatial variation among
8 forest stands in the maximum percent of AGB lost to stem rot, and this variation was correlated with soil
9 properties. Our finding that 7% of forest AGB is in some stage of wood decay in these Bornean forests
10 not only justifies greater consideration of stem rot and its soil-related variation in the estimation of carbon
11 storage by tropical forests, but also underscores the need for standardized methods of stem rot detection to
12 be applied across tropical forest regions.

13

14 **4.1 Methodological variation in stem rot detection**

15 Our results affirm the few existing previous findings that stem rot infection is frequent and often severe in
16 dipterocarp forests (Bakshi, 1960; Bagchee, 1961). Stem rot occurred in 41% of drilled, 53% of felled
17 stems, and encompassed 9% of stem volume on average in our study of central Sarawak. These estimates
18 exceed observations from neotropical forests, where 30-38% of trees among Amazonian species were
19 found to have hollow stems (Apolinário and Martius, 2004; Eleuterio, 2011), and volume losses to stem
20 rot ranged 0.7%-4% (Brown et al., 1995; Clark and Clark, 2000; Nogueira et al., 2006). There may be
21 several reasons for these discrepancies, many related to methodological differences. First, most studies
22 from neotropical forests measured the hollow fraction of stems, whereas our study quantified the volume
23 of wood in any stage of decay visible in the field. Therefore, our methods would inherently generate
24 larger estimates of volume and biomass loss. Second, approaches that quantify stem rot in decomposing
25 stems, such as stumps cut along access roads (Brown et al., 1995) or in naturally fallen logs in coarse
26 woody debris censuses (Clark and Clark, 2000), may confound rotting that occurs *post mortem* with stem

1 rot originating while the tree was alive, or, conversely, may be biased toward logs resistant to
2 decomposition. Such studies are thus unlikely to provide accurate estimates of wood decay in the living
3 trees that comprise standing forest AGB. Third, since stem rot frequency increased dramatically with tree
4 size, studies that under-sample large trees may underestimate stem rot in forest stands. Noguiera et al.
5 (2006), measured the hollow area in cross-sectional discs of freshly felled stems, but included five
6 individuals ≥ 80 cm DBH, compared to the 244 trees ≥ 80 cm drilled or felled in this study. While there
7 is no measure of stem rot severity in the literature equivalent to ours, which was based on harvested
8 stems, our measure of stem rot frequency via drilling was similar to Eleuterio (2011), which evaluated
9 wood decay in the debris created by plunging a chainsaw into stems of trees to be logged in the eastern
10 Brazilian Amazon. This study found wood decay in only 30% of stems ≥ 45 cm DBH for the six most
11 common timber species. Another study in the Brazilian Amazon found stem hollows in 38% of felled
12 trees > 50 cm, representing 16 species (Apolinário and Martius, 2004). These frequencies are lower than
13 the 48% for drilled stems ≥ 45 cm DBH and 62% of felled stems > 50 cm with any wood decay in our
14 study, providing evidence that stem rot may be more prevalent in Sarawak than other tropical forests.
15 Owing to the large range of tree sizes and taxonomic groups examined, our study likely presents robust
16 and well-constrained estimates of stem rot frequency and severity for Bornean mixed dipterocarp forests.
17 Aside from methodological differences, climate, rainfall seasonality, geology, and biogeographic and
18 phylogenetic history are also likely important, but existing data are insufficient to make inferences about
19 their potential roles in explaining any regional variation in stem rot.

20 While logging concessions may be opportunistically exploited for detailed evaluation of stem rot,
21 accurate non-destructive measures are still needed to estimate stem rot where destructive harvest is
22 impossible. Drilling proved to be an accurate means of scoring trees for stem rot, correctly characterizing
23 stem rot presence/absence in 80% of trees. The majority of misclassifications likely occurred because
24 drilling tested for areas of wood decay only at breast height, missing rot occurring higher or lower in the
25 stem. However, classification error diminished to 8% for stems that had lost more than 10% of their
26 volume to rot, indicating that drilling at breast height is a reliable means of identifying trees containing

1 large sections of rot. Moreover, the drilling data sampled larger trees than did the felling data. Hence,
2 results of felling and drilling analyses require subtly different interpretations, with the felling dataset
3 exploring the correlates of stem rot infection overall, and the drilling dataset exploring the correlates of
4 severe stem rot infection. There was no way to validate the accuracy of the coring method; however, the
5 probability of detecting rot was lower at a given stem diameter in the coring dataset relative to the drilling
6 dataset. Assuming that the true dependence of stem rot frequency on DBH was the same in Lambir and
7 the Central Sarawak sites, then we suspect the drilling method may have been more effective at detecting
8 rot because it was conducted in two perpendicular directions at breast height, whereas trees in the coring
9 dataset were bored only once. Inclusion of all three datasets not only allowed assessment of non-
10 destructive methodologies for estimation of stem rot, but also improved inferences about correlates of
11 stem rot by increasing size range to span the smaller and larger trees included in the coring and drilling
12 datasets, respectively. Sonic tomography has been applied non-destructively to evaluate both the
13 frequency and severity of hollows in tree stems (Nicolotti et al., 2003; Deflorio et al., 2008; Wunder et al.,
14 2013). In the absence of access to this costly equipment, drilling may be a viable, less expensive
15 alternative for assessing the presence of stem rot in remote tropical forests.

16

17 **4.2 Controls over stem rot in individual stems**

18 Identifying the environmental and tree-related correlates of stem rot provides insight into potential
19 mechanisms governing stem rot and its implications for forest ecosystem processes. Tree size was the
20 only factor significantly associated with stem rot frequency in all three datasets, consistent with previous
21 observations of substantial increases in stem rot frequency with diameter in tropical forests (Nogueira et
22 al., 2006; Eleuterio, 2011). To the extent that diameter correlates with tree age, these results suggest that
23 trees experience accumulating risks of becoming infected with stem rot with time. Future studies should
24 ensure that large trees are not under-sampled, especially considering that large, dominant canopy trees
25 predominantly structure carbon dynamics in tropical forests (Slik et al., 2013; Bastin et al., 2015). Given
26 that tree size was not a significant predictor of the percent stem volume lost to rot in infected trees, the

1 advancement of stem rot infection may depend less on tree age than on the identity of the fungi involved
2 and the physical and chemical properties of the heart wood (Wagener and Davidson, 1954; Pearce, 1996;
3 Schilling et al., 2015).

4 Species wood density was not a significant predictor of stem rot frequency, consistent with
5 findings from an Amazonian forest (Eleuterio, 2011). This result is somewhat surprising, as high wood
6 density has been associated with pathogen protection in tropical tree species (Augspurger and Kelly,
7 1984). However, any pathogen protection conferred by higher wood density may not result in lower
8 incidence of stem rot, because of the inverse relationship between wood density and mortality rates (King
9 et al., 2006): at the same size, trees with high wood density are expected to be older than trees with low
10 wood density and so may have longer exposure time to incur stem rot infection.

11 Stem rot frequency was higher in trees on lower fertility soils, and to a lesser extent, soils with
12 lower pH, in Central Sarawak, but did not differ between edaphic habitats in the smaller trees cored at
13 Lambir. Our results cannot identify how soil properties affect stem rot, but soil PC axes included in final
14 models were correlated with soil Ca and Mg which have also been found to associate strongly with
15 Bornean tree species distributions (Baillie et al., 1987) and explained significant variation in fine root
16 growth at Lambir (Kochsiek et al., 2013). In the Lambir coring dataset, the smaller sample size of larger
17 trees may have prevented us from detecting differences in stem rot frequency among soil types. The
18 association of stem rot with lower fertility soils in Central Sarawak is in some ways counter-intuitive, as
19 forests on high fertility sites generally have more frequent canopy disturbance (Coomes and Grubb,
20 2000), potentially causing more wounds and opportunities for infection. In addition to the longer
21 exposure times presumably experienced by tree species characteristic of more dystrophic and drought-
22 prone soils (Russo et al., 2005), trees under nutrient stress may be more prone to infection, if resources to
23 produce secondary compounds are limited (Bryant et al., 1983). Soil chemistry may also influence the
24 composition of the soil microbial community, from which wood decay fungi often originate (Boddy,
25 2001). At Lambir, the community composition of soil bacteria (Russo et al., 2012) and root-associated
26 mycorrhizal fungi (Peay et al., 2009) differ between clay and sandy loam soil types, which vary in many

1 properties including texture, nutrient supply, and pH (Table S3), indicating that the taxa and functional
2 groups present to colonize wood may differ among edaphic habitats. Furthermore, the relative availability
3 of nutrients in soil versus wood may influence the infection and growth of wood decay of nutrient-limited
4 fungi in trees, however, this interaction is likely to be complex (Merrill and Cowling, 1966; Donnelly and
5 Boddy, 1998).

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

21

22 **4.3 Taxonomic variation in stem rot**

23 While tree size and edaphic factors were significantly associated with stem rot infection, these factors
24 alone explained a relatively small fraction of the variance in the frequency of stem rot, and even less for
25 stem rot severity. The explanatory power of models improved dramatically when fixed effects were
26 conditioned on the species random effect, meaning that the occurrence of stem rot had a strong taxonomic

1 component due to species properties other than wood density and soil association. Perhaps surprisingly,
2 stem rot frequency varied among genera but not among families, suggesting that dipterocarp taxa do not
3 differ systematically in susceptibility to rot from non-dipterocarp taxa in MDF forests, despite showing
4 broad differences in other traits such as mycorrhizal association (Wang and Qiu, 2006).

5 Among species traits not evaluated in this study, wood anatomical properties and wood chemical
6 content with respect to nutrient stoichiometry and secondary defense may be particularly important to
7 understanding taxonomic variation in stem rot. Lumen diameter and vessel density are significantly
8 correlated stem rot frequency in Amazonian tree species (Eleuterio, 2011) and have been hypothesized to
9 influence the growth of fungal hyphae (Schwarze et al., 2000). Chemical properties of wood may also
10 influence rates of fungal colonization in stems, as tree species wood N and P concentrations correlate with
11 wood decomposition rates in angiosperms (Weedon et al., 2009), and wood decomposition rates decline
12 with initial wood pH among Costa Rican tree species (Schilling et al., 2015). Furthermore, secondary
13 defensive chemistry has been shown to vary among species and generate differences in the microbial
14 colonization of woody debris (Cornwell et al., 2009). Most dipterocarps are known for copious resin
15 production (Appanah and Turnbull, 1998) and are likely to differ widely in the composition and
16 mycostatic effectiveness of these compounds (Bisset et al., 1966; Bisset et al., 1971; Norhayati et al.,
17 2013).

18 In addition to constitutive chemical defences, some of the taxonomic variation in the
19 susceptibility to stem rot may be due to differences in induced defenses against fungal or insect pathogens
20 (Pearce, 1996; Kovalchuk et al., 2013). When wounding allows exposure to pathogens, anatomical
21 modification of xylem in the living sapwood, including compartmentalization, limits the spread of
22 infection (Shigo, 1984; Pearce, 1996), and the extent and effectiveness of this response likely differs
23 among species (Guariguata and Gilbert, 1996; Romero and Bolker, 2008). During formation, heart wood
24 is suffused with secondary metabolites considered inimical to fungal growth (Yamada, 2001; Taylor et
25 al., 2002; Kirker et al., 2013), and interspecific variation in this process may also affect susceptibility to
26 fungal rot. Even after accounting for species identity, most variation in stem rot frequency and severity

1 remained unexplained. Stem rot infection may be highly stochastic because it appears to require both
2 wounding and subsequent colonization by fungal spores or their insect vectors, which have varying
3 dispersal capacities (Peay and Bruns, 2014) and host requirements (Gilbert, 2002).

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

19
20 **4.4 Implications of Tree-level Variation in Stem Rot for Forest Biomass**
21 When tree-level stem rot was scaled to the stand-level, we found large spatial variation in the potential
22 ecosystem stem biomass lost to rot in central Sarawak. Stems of trees > 30 cm DBH account for ~70% of
23 the standing AGB in mature mixed-dipterocarp forests (Yamakura et al., 1986), and trees > 70 cm DBH
24 make up 40% of the AGB in southeast Asian forests (Slik et al., 2013). In light of these regional studies,
25 our results suggest that correcting for biomass lost to stem rot reduces total forest AGB estimates by up to
26 7% relative to what would be predicted assuming all stems are composed strictly of intact wood, with the

1 true stem rot correction depending on the relative densities of decayed versus sound wood. While
2 estimates of biomass loss due to stem rot in living trees are rare, studies of standing dead trees and woody
3 debris found that biomass loss over time is approximately exponential (Harmon et al., 1986; Freschet et
4 al., 2012), indicating that the biomass density of rotted stem fractions should be much less than the
5 density of intact wood. Moreover, Bornean dipterocarp forests are taller, with more large-diameter trees,
6 and thus have higher AGB than many other tropical forests (Yamakura et al., 1986; Slik et al., 2013;
7 Banin et al., 2014). These differences may be reduced by potentially greater incidence of stem rot in
8 mixed-dipterocarp forests, since, as noted above, considerably lower estimates of biomass lost to stem rot
9 have been reported in neotropical forests.

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

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

25

26 **5 Conclusions**

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

10

11 **Acknowledgements**

12 We thank Sarawak Conservator of Forests for permission to use Central Sarawak inventory and soils data
13 and photographs for research, and the Sarawak Forest Department and the Protected Areas and
14 Biodiversity Conservation unit of Sarawak Forestry Corporation for permission to conduct research in
15 Lambir Hills National Park. We are grateful to many colleagues in the FIDP inventory, which was a
16 substantial team effort involving scores of people working for several field seasons in difficult conditions.
17 We thank two anonymous reviewers, James Dalling, and Amy Zanne for providing comments that
18 improved this manuscript. Data collection at Lambir was funded by the Center for Tropical Forest
19 Science, NSF DUE-0531920, the University of Nebraska – Lincoln (UNL) UCARE undergraduate
20 research program, and the UNL School of Biological Sciences.

21

22 **Literature Cited**

23 Anderson, J. A. R.: The structure and development of the peat swamps of Sarawak, *Journal of Tropical*
24 *Geography*, 18, 7-16, 1964.
25 Apolinário, F. E., and Martius, C.: Ecological role of termites (Insecta, Isoptera) in tree trunks in central
26 Amazonian rain forests, *For. Ecol. Manage.*, 194, 23-28, 2004.

1 Appanah, S., and Turnbull, J. M.: A Review of Dipterocarps: Taxonomy, ecology and silviculture, Center
2 for International Forestry Research, Bogor, Indonesia, 220 pp., 1998.

3 Ashton, P. S.: Ecological studies in the mixed dipterocarp forests of Brunei state, Oxford Forestry
4 Memoirs, 25, 1-75, 1964.

5 Ashton, P. S.: Report on research undertaken during the years 1963-1967 on the ecology of Mixed
6 Dipterocarp Forest in Sarawak, University of Aberdeen and Ministry of Overseas Development,
7 London, 1973.

8 Ashton, P. S., and Hall, P.: Comparisons of structure among mixed dipterocarp forests of north-western
9 Borneo, J. Ecol., 80, 459-481, 1992.

10 Ashton, P. S.: On the Forests of Tropical Asia: Lest the Memory Fade, The University of Chicago Press,
11 Chicago, 670 pp., 2015.

12 Augspurger, C. K., and Kelly, C. K.: Pathogen mortality of tropical tree seedlings: experimental studies
13 of the effects of dispersal distance, seedling density, and light conditions, Oecologia, 61, 211-217,
14 1984.

15 Avery, T. E., and Burkhardt, H. E.: Forest measurements, McGraw-Hill, 2002.

16 Bagchee, K.: Fungal diseases of sal (Shores robusta Gaertn.) IV *Fomes caraphylli* (Rac.) Bres. A
17 destructive heartrot of sal, Indian Forest Records, Mycology, 2, 25-59, 1961.

18 Baillie, I. C., Ashton, P. S., Court, M. N., Anderson, J. A. R., Fitzpatrick, E. A., and Tinsley, J.: Site
19 characteristics and the distribution of tree species in mixed dipterocarp forest on Tertiary
20 sediments in Central Sarawak, Malaysia, J. Trop. Ecol., 3, 201-220, 1987.

21 Baillie, I. C., Ashton, P. S., Chin, S. P., Davies, S. J., Palmiotto, P. A., Russo, S. E., and Tan, S.: Spatial
22 associations of humus, nutrients, and soils in mixed dipterocarp forest at Lambir, Sarawak,
23 Malaysian Borneo, J. Trop. Ecol., 22, 543-553, 2006.

24 Baker, P. J., Bunyavejchewin, S., Oliver, C. D., and Ashton, P. S.: Disturbance history and historical
25 stand dynamics of a seasonal tropical forest in Western Thailand, Ecol. Monogr., 75, 317-343,
26 2005.

1 Bakshi, B. K.: Heart rot of Sal in India, *Phytopathological News*, 6, 45-46, 1960.

2 Banin, L., Lewis, S. L., Lopez-Gonzalez, G., Baker, T. R., Quesada, C. A., Chao, K.-J., Burslem, D. F. R.

3 P., Nilus, R., Abu Salim, K., Keeling, H. C., Tan, S., Davies, S. J., Monteagudo Mendoza, A.,

4 Vásquez, R., Lloyd, J., Neill, D. A., Pitman, N., and Phillips, O. L.: Tropical forest wood

5 production: a cross-continental comparison, *J. Ecol.*, 102, 1025-1037, 2014.

6 Bastin, J. F., Barbier, N., Réjou-Méchain, M., Fayolle, A., Gourlet-Fleury, S., Maniatis, D., de

7 Haulleville, T., Baya, F., Beeckman, H., Beina, D., Couteron, P., Chuyong, G., Dauby, G.,

8 Doucet, J. L., Droissart, V., Dufrêne, M., Ewango, C., Gillet, J. F., Gonmadje, C. H., Hart, T.,

9 Kavali, T., Kenfack, D., Libalah, M., Malhi, Y., Makana, J. R., Pélissier, R., Ploton, P., Serckx,

10 A., Sonké, B., Stevart, T., Thomas, D. W., De Cannière, C., and Bogaert, J.: Seeing Central

11 African forests through their largest trees, *Scientific Reports*, 5, 13156, 2015.

12 Bates, D., Maechler, M., Bolker, B., and Walker, S.: *lme4*: Linear mixed-effects models using Eigen and

13 S4. R package version 1.1-7. <URL:<http://CRAN.R-project.org/package=lme4>>, 2014.

14 Bisset, N. G., Diaz, M. A., Ehret, C., Ourisson, G., Palmade, M., Patil, F., Pesnelle, P., and Streith, J.:

15 Etudes chimio-taxonomiques dans la famille des diptérocarpacées-II. : Constituants du genre

16 Diptérocarpus gaertn. F. Essai de classification chimio-taxonomique, *Phytochemistry*, 5, 865-880,

17 1966.

18 Bisset, N. G., Chavanel, V., Lantz, J.-P., and Wolff, R. E.: Constituants sesquiterpéniques et

19 triterpéniques des résines du genre *Shorea*, *Phytochemistry*, 10, 2451-2463, 1971.

20 Bjurman, J., and Viitanen, H.: Effect of wet storage on subsequent colonisation and decay by *Coniophora*

21 *puteana* at different moisture contents, *Material Und Organismen*, 30, 259-277, 1996.

22 Boddy, L., and Rayner, A. D. M.: Origins of decay in living deciduous trees; the role of moisture content

23 and a re-appraisal of the expanded concept of decay, *New Phytol.*, 94, 623-641, 1983.

24 Boddy, L., and Watkinson, S. C.: Wood decomposition, higher fungi, and their role in nutrient

25 redistribution, *Can J Botany*, 73, 1377-1383, 1995.

1 Boddy, L.: Fungal community ecology and wood decomposition processes in Angiosperms: From
2 standing tree to complete decay of coarse woody debris, Ecological Bulletins, 43-56, 2001.

3 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., and White,
4 J.-S. S.: Generalized linear mixed models: a practical guide for ecology and evolution, Trends
5 Ecol. Evol., 24, 127-135, 2009.

6 Brienen, R. J. W., and Zuidema, P. A.: Lifetime growth patterns and ages of Bolivian rain forest trees
7 obtained by tree ring analysis, J. Ecol., 94, 481–493, 2006.

8 Brown, I. F., Martinelli, L. A., Thomas, W. W., Moreira, M. Z., Cid Ferreira, C. A., and Victoria, R. A.:
9 Uncertainty in the biomass of Amazonian forests: An example from Rondônia, Brazil, For. Ecol.
10 Manage., 75, 175-189, 1995.

11 Bryant, J. P., Chapin, F. S., III, and Klein, D. R.: Carbon/nutrient balance of boreal plants in relation to
12 vertebrate herbivory, Oikos, 40, 357-368, 1983.

13 Bultman, J. D., and Southwell, C. R.: Natural resistance of tropical American woods to terrestrial wood-
14 destroying organisms, Biotropica, 8, 71-95, 1976.

15 Bürgi, A., Rinchen, G. F., and Dorji, T.: Structure, productivity, regeneration and possible
16 utilisation of the Fir (*Abies densa* Griff.) forests in central Chumi Valley, Central Bhutan, 1992.

17 Burnham, K. P. and Anderson, D. R.: Model Selection and Multimodel Inference: a Practical
18 Information-Theoretic Approach, Springer Science & Business Media, New York, 2002.

19 Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., Folster, H., Fromard, F.,
20 Higuchi, N., Kira, T., Lescure, J. P., Nelson, B. W., Ogawa, H., Puig, H., Riera, B., and
21 Yamakura, T.: Tree allometry and improved estimation of carbon stocks and balance in tropical
22 forests, Oecologia, 145, 87-99, 2005.

23 Chin, S. P.: Soil test methods, Agriculture Research Centre, Department of Agriculture, Semongok,
24 Kuching, Malaysia, 73, 2002.

1 Clark, D. B., and Clark, D. A.: Landscape-scale variation in forest structure and biomass in a tropical rain
2 forest, *For. Ecol. Manage.*, 137, 185-198, 2000.

3 Cockle, K. L., Martin, K., and Robledo, G.: Linking fungi, trees, and hole-using birds in a neotropical
4 tree-cavity network: Pathways of cavity production and implications for conservation, *For. Ecol.*
5 *Manage.*, 264, 210-219, 2012.

6 Comita, L. S., Muller-Landau, H. C., Aguilar, S., and Hubbell, S. P.: Asymmetric Density Dependence
7 Shapes Species Abundances in a Tropical Tree Community, *Science*, 329, 330-332, 2010.

8 Coomes, D. A., and Grubb, P. J.: Impacts of root competition in forests and woodlands: A theoretical
9 framework and review of experiments, *Ecol. Monogr.*, 70, 171-207, 2000.

10 Cornwell, W. K., Cornelissen, J. H. C., Allison, S. D., Bauhus, J., Eggleton, P., Preston, C. M., Scarff, F.,
11 Weedon, J. T., Wirth, C., and Zanne, A. E.: Plant traits and wood fates across the globe: rotted,
12 burned, or consumed?, *Global Change Biol.*, 15, 2431-2449, 2009.

13 Davies, S. J., Tan, S., LaFrankie, J. V., and Potts, M. D.: Soil-related floristic variation in the
14 hyperdiverse dipterocarp forest in Lambir Hills, Sarawak, in: *Pollination Ecology and Rain Forest*
15 *Diversity*, Sarawak Studies, edited by: Roubik, D. W., Sakai, S., and Hamid, A., *Ecological*
16 *Studies*, Springer-Verlag, New York, New York, 22-34, 2005.

17 Deflorio, G., Fink, S., and Schwarze, F. M. R.: Detection of incipient decay in tree stems with sonic
18 tomography after wounding and fungal inoculation, *Wood Sci Technol*, 42, 117-132, 2008.

19 Dickinson, T. A., and Tanner, E. V. J.: Exploitation of hollow trunks by tropical trees, *Biotropica*, 10,
20 231-233, 1978.

21 Donnelly, D. P., and Boddy, L.: Developmental and morphological responses of mycelial systems of
22 *Stropharia caerulea* and *Phanerochaete velutina* to soil nutrient enrichment, *New Phytol.*, 138,
23 519-531, 1998.

24 Duchesne, L. C., Hubbes, M., and Jeng, R. S.: Biochemistry and molecular biology of defense reactions
25 in the xylem of Angiosperm trees, in: *Defense Mechanisms of Woody Plants against Fungi*,
26 edited by: Blanchette, R. A., and Biggs, A. R., Springer, 133-146, 1992.

1 Edman, M., Möller, R., and Ericson, L.: Effects of enhanced tree growth rate on the decay capacities of
2 three saprotrophic wood-fungi, *For. Ecol. Manage.*, 232, 12-18, 2006.

3 Eleuterio, A. A.: Wood Decay in Living Trees in Eastern Amazonia, Brazil, Ph.D., University of Florida,
4 102 pp., 2011.

5 FAO: World reference base for soil resources, World Soil Resources Report 103, Food & Agriculture
6 Organisation of United Nations, Rome, 2006.

7 FIDP: An Inventory of the Mixed Dipterocarp Forest of Sarawak 1969 -1972, FIDP Technical Report 2,
8 Forest Industries Development Project, Kuala Lumpur, 1974a.

9 FIDP: A description of methodology and techniques used in the inventory of selected areas of Mixed
10 Dipterocarp Forest in Sarawak, Working Paper 24, Forest Industries Development Project, Kuala
11 Lumpur, 1974b.

12 Fine, P. V. A., Miller, Z. J., Mesones, I., Irazuzta, S., Appel, H. M., Stevens, M. H. H., Saksjarvi, I.,
13 Schultz, J. C., and Coley, P. D.: The growth-defense trade-off and habitat specialization by plants
14 in Amazonian forests, *Ecology*, 87, 150-162, 2006.

15 Franklin, J. F., Shugart, H. H., and Harmon, M. E.: Tree death as an ecological process, *Bioscience*, 37,
16 550-556, 1987.

17 Freschet, G. T., Weedon, J. T., Aerts, R., van Hal, J. R., and Cornelissen, J. H. C.: Interspecific
18 differences in wood decay rates: insights from a new short-term method to study long-term wood
19 decomposition, *J. Ecol.*, 100, 161-170, 2012.

20 Gale, N., and Hall, P.: Factors Determining the Modes of Tree Death in Three Bornean Rain Forests,
21 *Journal of Vegetation Science*, 12, 337-346, 2001.

22 Gilbert, G. S.: Evolutionary ecology of plant diseases in natural ecosystems, *Annu. Rev. Phytopathol.*, 40,
23 13-43, 2002.

24 Goldstein, H., Browne, W., and Rasbash, J.: Partitioning variation in multilevel models, in:
25 *Understanding Statistics: Statistical Issues in Psychology, Education, and the Social Sciences*,
26 223-231, 2002.

1 Gratzer, G., Rai, P. B., and Glatzel, G.: Ecology of *Abies densa* Forests of the IFMP--Ura, Bhutan:
2 Research Report in the Framework of IFMP, Integrated Forest Management Project, 1997.

3 Guariguata, M. R., and Gilbert, G. S.: Interspecific variation in rates of trunk wound closure in a
4 Panamanian lowland forest, *Biotropica*, 28, 23-29, 1996.

5 Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H.,
6 Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K. J., and Cummins, K.
7 W.: Ecology of coarse woody debris in temperate ecosystems, *Adv. Ecol. Res.*, 15, 133–302,
8 1986.

9 Heineman, K. D., Jensen, E., Shapland, A., Bogenrief, B., Tan, S., Rebarber, R., and Russo, S. E.: The
10 effects of belowground resources on aboveground allometric growth in Bornean tree species, *For.*
11 *Ecol. Manage.*, 261, 1820-1832, 2011.

12 Hooper, R. G.: Longleaf pines used for cavities by red-cockaded woodpeckers, *The Journal of Wildlife*
13 *Management*, 52, 392-398, 1988.

14 Janzen, D. H.: Why tropical trees have rotten cores, *Biotropica*, 8, 110, 1976.

15 King, D. A., Davies, S. J., Tan, S., and Noor, N. S. M.: The role of wood density and stem support costs
16 in the growth and mortality of tropical trees, *J. Ecol.*, 94, 670-680, 2006.

17 Kirker, G. T., Blodgett, A. B., Arango, R. A., Lebow, P. K., and Clausen, C. A.: The role of extractives in
18 naturally durable wood species, *Int. Biodeterior. Biodegrad.*, 82, 53-58, 2013.

19 Kochsiek, A., Tan, S., and Russo, S. E.: Fine root dynamics in relation to nutrients in oligotrophic
20 Bornean rain forest soils, *Plant Ecol.*, 214, 869-882, 2013.

21 Kovalchuk, A., Keriö, S., Oghenekaro, A. O., Jaber, E., Raffaello, T., and Asiegbu, F. O.: Antimicrobial
22 defenses and resistance in forest trees: Challenges and perspectives in a genomic era, *Annu. Rev.*
23 *Phytopathol.*, 51, 221-244, 2013.

24 Lee, H. S., Davies, S. J., LaFrankie, J. V., Tan, S., Yamakura, T., Itoh, A., Ohkubo, T., and Ashton, P. S.:
25 Floristic and structural diversity of mixed dipterocarp forests in Lambir Hills National Park,
26 Sarawak, Malaysia, *J. Trop. For. Sci.*, 14, 379-400, 2002.

1 Little, R. J. A., and Rubin, D. B.: Statistical Analysis with Missing Data, J. Wiley & Sons, New York,
2 1987.

3 Loehle, C.: Tree life history strategies: the role of defenses, *Can. J. Forest Res.*, 18, 209-222, 1988.

4 Mangan, S. A., Schnitzer, S. A., Herre, E. A., Mack, K. M. L., Valencia, M. C., Sanchez, E. I., and Bever,
5 J. D.: Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest,
6 *Nature*, 466, 752-755, 2010.

7 Mattheck, C., Bethge, K., and Tesari, I.: Shear effects on failure of hollow trees, *Trees*, 20, 329-333,
8 2006.

9 Merrill, W., and Cowling, E. B.: Role of nitrogen in wood deterioration: amounts and distribution of
10 nitrogen in tree stems, *Can. J. Botany*, 44, 1555-1580, 1966.

11 Mori, S., Itoh, A., Nanami, S., Tan, S., Chong, L., and Yamakura, T.: Effect of wood density and water
12 permeability on wood decomposition rates of 32 Bornean rainforest trees, *J. of Plant Ecol.*, 7356-
13 7363, 2013.

14 Nakagawa, S., and Schielzeth, H.: A general and simple method for obtaining R2 from generalized linear
15 mixed-effects models, *Methods in Ecology and Evolution*, 4, 133-142, 2013.

16 Nicolotti, G., Socco, L., Martinis, R., Godio, A., and Sambuelli, L.: Application and comparison of three
17 tomographic techniques for detection of decay in trees, *Journal of Arboriculture*, 29, 66-78, 2003.

18 Nogueira, E. M., Nelson, B. W., and Fearnside, P. M.: Volume and biomass of trees in central Amazonia:
19 influence of irregularly shaped and hollow trunks, *For. Ecol. Manage.*, 227, 14-21, 2006.

20 Norhayati, M., Nazlima, N., Nor-Azah, A., Laily, D., Zuraiati, Z., Wan-Ahmad, J., and Noramly, M.:
21 Chemical composition, antioxidant and antibacterial properties of the essential oils of *Shorea*
22 *acuminata* (Dipterocarpaceae), *J. Essent. Oil-Bear. Plants*, 14, 708-716, 2013.

23 Ohkubo, T.: Spatial and topographic patterns of canopy gap formation in a mixed dipterocarp forest in
24 Sarawak, Malaysia., *Tropics*, 16, 152-153, 2007.

25 Panzer, K. F.: Quantification of decay and related volume loss in tropical forest inventories, *Mitt.*
26 *Bundesforsch*, 109, 117-128, 1975.

1 Paoli, G., Curran, L., and Slik, J.: Soil nutrients affect spatial patterns of aboveground biomass and
2 emergent tree density in southwestern Borneo, *Oecologia*, 155, 287-299, 2008a.

3 Paoli, G. D., Curran, L. M., and Slik, J. W. F.: Soil nutrients affect spatial patterns of aboveground
4 biomass and emergent tree density in southwestern Borneo, *Oecologia*, 155, 287-299, 2008b.

5 Pearce, R. B.: Tansley Review No. 87. Antimicrobial defences in the wood of living trees, *New Phytol.*,
6 132, 203-233, 1996.

7 Peay, K. G., Kennedy, P. G., Davies, S. J., Tan, S., and Bruns, T. D.: Potential link between plant and
8 fungal distributions in a dipterocarp rainforest: community and phylogenetic structure of tropical
9 ectomycorrhizal fungi across a plant and soil ecotone, *New Phytol.*, 185, 529-542, 2009.

10 Peay, K. G., and Bruns, T. D.: Spore dispersal of basidiomycete fungi at the landscape scale is driven by
11 stochastic and deterministic processes and generates variability in plant-fungal interactions, *New
12 Phytol.*, 204, 180-191, 2014.

13 Potts, M. D., Ashton, P. S., Kaufman, L. S., and Plotkin, J. B.: Habitat patterns in tropical rain forests: A
14 comparison of 105 plots in northwest Borneo, *Ecology*, 83, 2782-2797, 2002.

15 Putz, F. E., Coley, P. D., Lu, K., Montalvo, A., and Aiello, A.: Uprooting and snapping of trees -
16 structural determinants and ecological consequences, *Can. J. Forest Res.*, 13, 1011-1020, 1983.

17 R Core Team: R: a language and environment for statistical computing, Vienna, Austria, available at:
18 <http://www.R-project.org/> (last access: 1 April 2015), 2014.

19 Ranius, T., Niklasson, M., and Berg, N.: Development of tree hollows in pedunculate oak (*Quercus
20 robur*), *For. Ecol. Manage.*, 257, 303-310, 2009.

21 Romero, C., and Bolker, B. M.: Effects of stem anatomical and structural traits on responses to stem
22 damage: an experimental study in the Bolivian Amazon, *Can. J. Forest Res.*, 38, 611-618, 2008.

23 Russo, S. E., Davies, S. J., King, D. A., and Tan, S.: Soil-related performance variation and distributions
24 of tree species in a Bornean rain forest, *J. Ecol.*, 93, 879-889, 2005.

25 Russo, S. E., Brown, P., Tan, S., and Davies, S. J.: Interspecific demographic trade-offs and soil-related
26 habitat associations of tree species along resource gradients, *J. Ecol.*, 96, 192–203, 2008.

1 Russo, S. E., Legge, R., Weber, K. A., Brodie, E. L., Goldfarb, K. C., Benson, A. K., and Tan, S.:
2 Bacterial community structure of contrasting soils underlying Bornean rain forests: Inferences
3 from microarray and next-generation sequencing methods, *Soil Biol. Biochem.*, 55, 48-59, 2012.

4 Ruxton, G. D.: Why are so many trees hollow?, *Biol. Lett.*, 10, 2014.

5 Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T. A., Salas, W., Zutta, B. R.,
6 Buermann, W., Lewis, S. L., Hagen, S., Petrova, S., White, L., Silman, M., and Morel, A.:
7 Benchmark map of forest carbon stocks in tropical regions across three continents, *P. Natl. Acad.*
8 *Sci. USA*, 108, 9899-9904, 2011.

9 Schafer, J. L.: *Analysis of Incomplete Multivariate Data*, Chapman & Hall, London, 1997.

10 Schilling, J. S., Ayres, A., Kaffenberger, J. T., and Powers, J. S.: Initial white rot type dominance of wood
11 decomposition and its functional consequences in a regenerating tropical dry forest, *Soil Biol.*
12 *Biochem.*, 88, 58-68, 2015.

13 Schwarze, F. W. M. R., Engels, J., and Mattheck, C.: *Fungal Strategies of Wood Decay in Trees*,
14 Springer, 2000.

15 Shigo, A. L.: Compartmentalization: A conceptual framework for understanding how trees grow and
16 defend themselves, *Annu. Rev. Phytopathol.*, 22, 189-214, 1984.

17 Slik, J. W. F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F.,
18 Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E., Ferreira, L.,
19 Forshed, O., Fredriksson, G., Gillet, J.-F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y.,
20 Mansor, A., Martin, E., Miyamoto, K., Araujo-Murakami, A., Nagamasu, H., Nilus, R.,
21 Nurtjahya, E., Oliveira, Á., Onrizal, O., Parada-Gutierrez, A., Permana, A., Poorter, L., Poulsen,
22 J., Ramirez-Angulo, H., Reitsma, J., Rovero, F., Rozak, A., Sheil, D., Silva-Espejo, J., Silveira,
23 M., Spironelo, W., ter Steege, H., Stevart, T., Navarro-Aguilar, G. E., Sunderland, T., Suzuki, E.,
24 Tang, J., Theilade, I., van der Heijden, G., van Valkenburg, J., Van Do, T., Vilanova, E., Vos, V.,
25 Wich, S., Wöll, H., Yoneda, T., Zang, R., Zhang, M.-G., and Zweifel, N.: Large trees drive forest

1 aboveground biomass variation in moist lowland forests across the tropics, *Global Ecol.*
2 *Biogeogr.*, 22, 1261-1271, 2013.

3 Stockland, J. N., Siiiton, J., and Jonsson, B. G.: *Biodiversity in Dead Wood*, Cambridge University
4 Press, Cambridge, 509 pp., 2012.

5 Tan, S., Yamakura, T., Tani, M., Palmiotto, P., Mamit, J. D., Pin, C. S., Davies, S., Ashton, P., and
6 Baillie, I.: Review of soils on the 52-ha long term ecological research plot in mixed dipterocarp
7 forest at Lambir, Sarawak, Malaysian Borneo, *Tropics*, 18, 61-86, 2009.

8 Taylor, A. M., Gartner, B. L., and Morrell, J. J.: Heartwood formation and natural durability - a review,
9 *Wood and Fiber Science*, 34, 587-611, 2002.

10 van Geffen, K. G., Poorter, L., Sass-Klaassen, U., van Logtestijn, R. S. P., and Cornelissen, J. H. C.: The
11 trait contribution to wood decomposition rates of 15 Neotropical tree species, *Ecology*, 91, 3686-
12 3697, 2010.

13 Wagener, W. W., and Davidson, R. W.: Heart rots in living trees, *Bot. Rev.*, 20, 61-134, 1954.

14 Wang, B., and Qiu, Y. L.: Phylogenetic distribution and evolution of mycorrhizas in land plants,
15 *Mycorrhiza*, 16, 299-363, 2006.

16 Weedon, J. T., William, K. C., Johannes, H. C. C., Amy, E. Z., Christian, W., and David, A. C.: Global
17 meta-analysis of wood decomposition rates: a role for trait variation among tree species?, *Ecol.*
18 *Lett.*, 12, 45-56, 2009.

19 Whitmore, T. C.: *Tropical Rain Forests of the Far East*, Clarendon Press, Oxford, 1984.

20 Wunder, J., Manusch, C., Queloz, V., Brang, P., Ringwald, V., and Bugmann, H.: Does increment coring
21 enhance tree decay? New insights from tomography assessments, *Can. J. Forest Res.*, 43, 711-
22 718, 2013.

23 Yamada, T.: Defense mechanisms in the sapwood of living trees against microbial infection, *J. Forest*
24 *Res.*, 6, 127-137, 2001.

25 Yamakura, T., Haghara, A., Sukardjo, S., and Ogawa, H.: Aboveground biomass of tropical rain forest
26 stands in Indonesian Borneo, *Vegetatio*, 68, 71-82, 1986.

1 Yamakura, T., Kanzaki, M., Itoh, A., Ohkubo, T., Ogino, K., Chai O.K., E., Lee, H. S., and Ashton, P. S.:
2 Forest structure of a tropical rain forest at Lambir, Sarawak with special reference to the
3 dependency of its physiognomic dimensions of topography, *Tropics*, 6, 1-18, 1996.
4 Yang, X., Post, W. M., Thornton, P. E., and Jain, A.: The distribution of soil phosphorus for global
5 biogeochemical modeling, *Biogeosciences*, 10, 2525-2537, 2013.
6 Yang, X., Thornton, P. E., Ricciuto, D. M., and Post, W. M.: The role of phosphorus dynamics in tropical
7 forests – a modeling study using CLM-CNP, *Biogeosciences*, 11, 1667-1681, 2014.
8 Yoneda, T.: Studies on the rate of decay of wood litter on the forest floor I. Some physical properties of
9 decaying wood, *Jap. J. Ecol.*, 25, 40–46, 1975.
10 Yu, Q., Yang, D.-Q., Zhang, S. Y., Beaulieu, J., and Duchesne, I.: Genetic variation in decay resistance
11 and its correlation to wood density and growth in white spruce, *Can. J. Forest Res.*, 33, 2177-
12 2183, 2003.
13
14
15

Table 1. Total number of trees and species evaluated for the presence of stem rot, and the ranges and sample sizes for predictor variables used in mixed-effect models predicting the frequency and severity of stem rot in the felling, drilling, and coring datasets. See the Methods section for details.

	Felling			Drilling			Coring				
	Species	Trees	Range	Species	Trees	Range	Species	Trees	Range		
Total Number Sampled	211	1035				206	1780				
Frequency of Stem rot	53%			41%			9%				
<i>Availability of Model Predictor Variables</i>											
DBH (cm)	1035		27.1 – 105.8		1780		26.2 – 161.5		6.0 – 89.0		
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 Models	122	765			102	707			112 355		

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 datasets. The Δ AIC 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 Methods section 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.

Dataset	Model	Final Model	Predictor Removed	AIC	Δ AIC
Felling	Model 1	DBH, Soil PC3	--	970	--
			remove DBH	1009	39
			remove Soil PC3	972	2
			remove all	1009	39
Felling	Model 2	DBH x 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

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 dataset. 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 Methods section 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.

Dataset	Model	Final Model	Predictor Removed	AIC	Δ AIC
Stem rot severity	Model 1	Intercept only	--	1635	--
		WD*Soil Assoc.	--	1624	--
			remove interaction term	1638	14
			remove WD	1638	14
			remove Soil Assoc.	1636	12
			remove all	1635	11

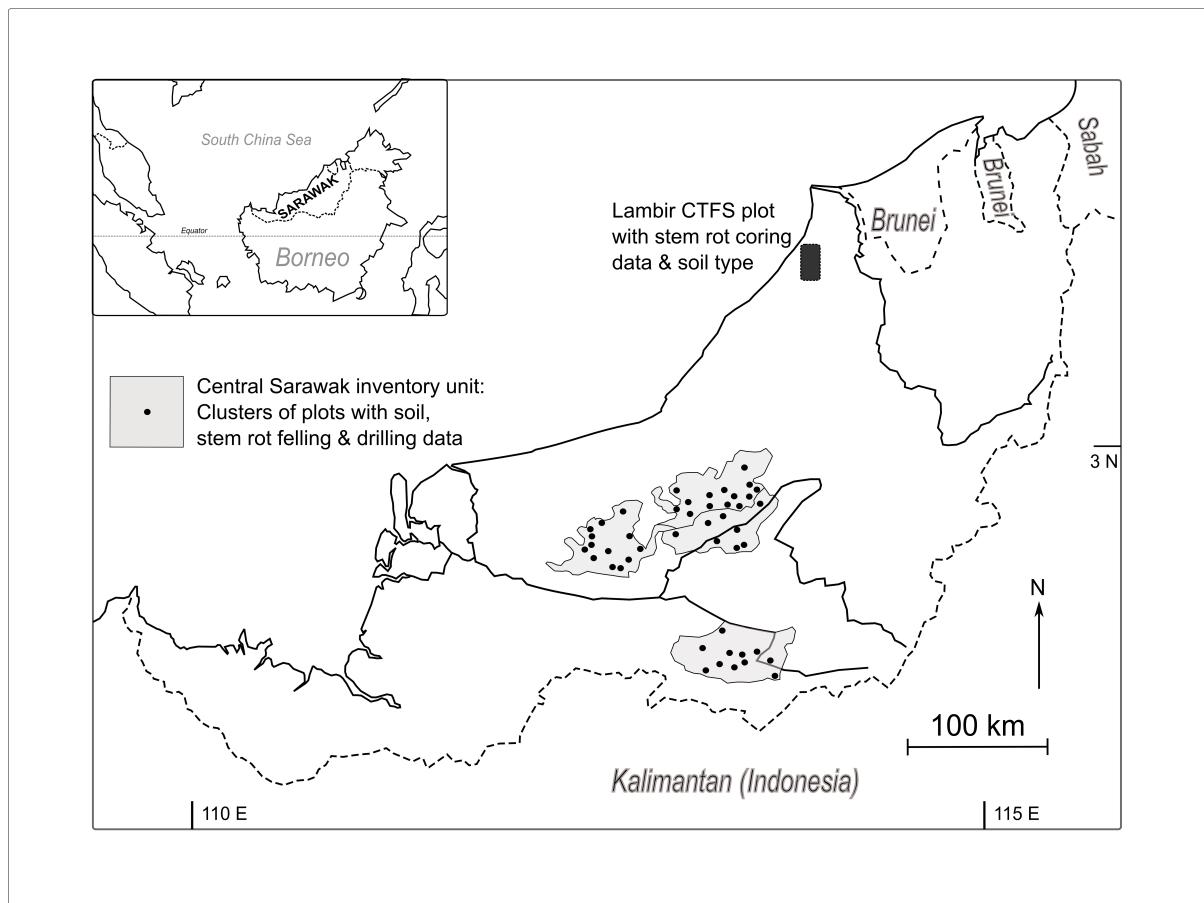


Figure 1. Location of study sites in Sarawak, Malaysian Borneo. Shaded areas are the Central Sarawak inventory units for stem rot felling and drilling data, with clusters of plots indicated by black dots. The black rectangle (not to scale) indicates the location of the Lambir Hills National Park study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

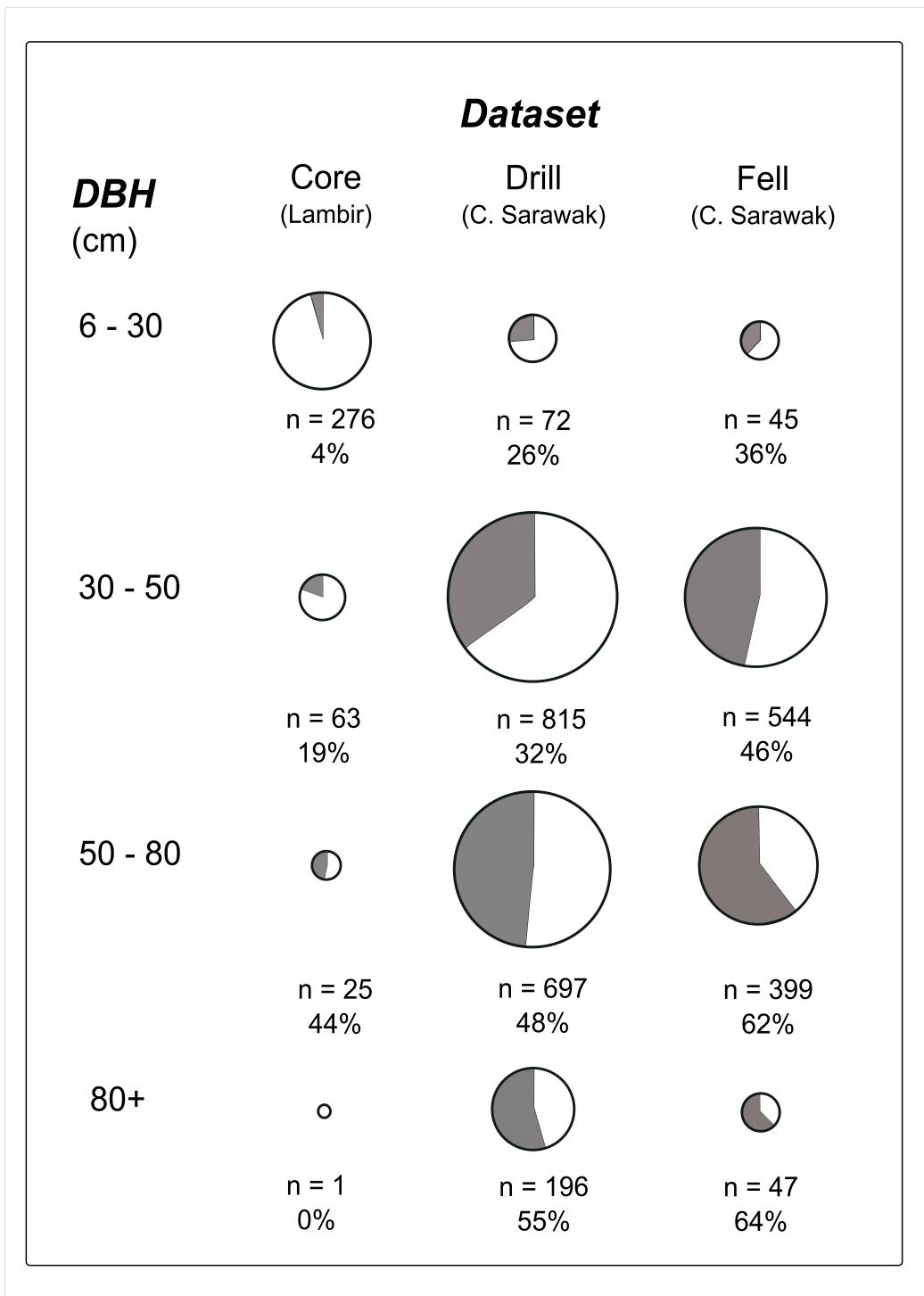


Figure 2. Stem diameter-related variation in the frequency of stem rot found in trees in mixed dipterocarp rain forest of Central Sarawak, Bornean Malaysia. Pie charts show the percentage of trees with stem rot (shaded), with pies sized according to the total number of sampled stems (n), in each diameter at breast height (DBH) size class and three datasets, one from Lambir Hills National Park (Lambir) and two from Central Sarawak (C. Sarawak; see the *Methods* section for details).

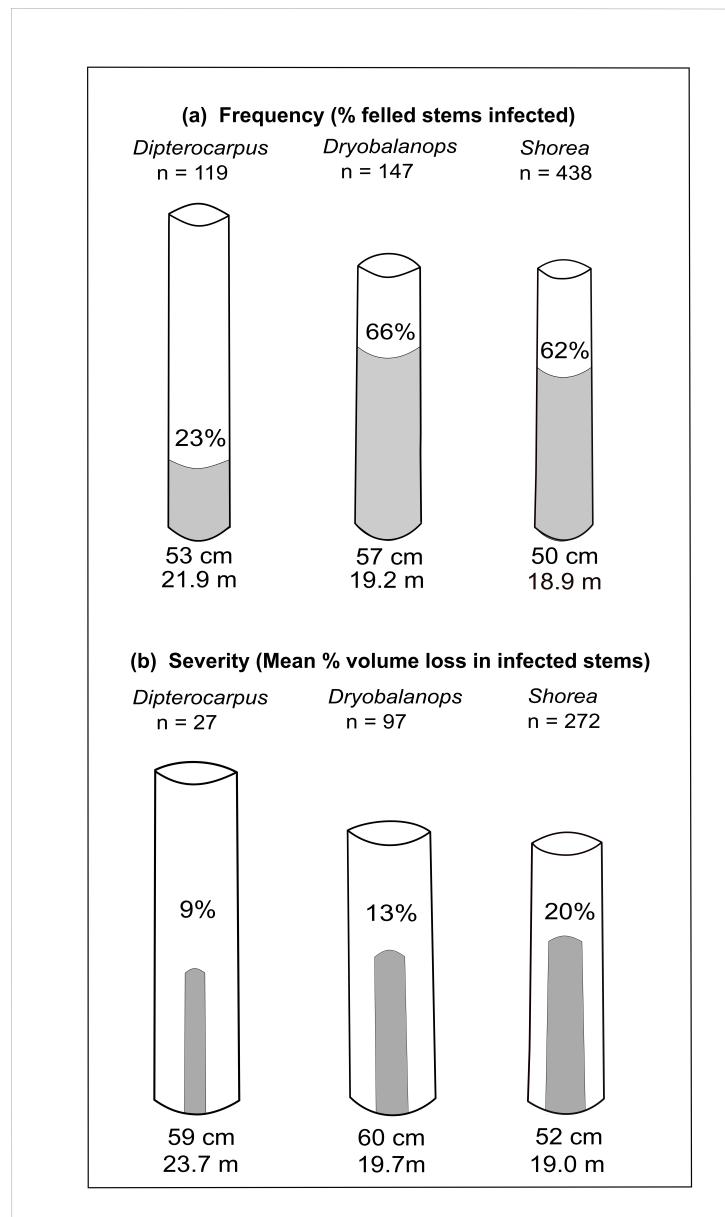


Figure 3. Variation in the frequency and severity of stem rot among three important dipterocarp genera (representing a subset of the 65 genera from the felling data) in the rain forest of Central Sarawak, Borneo, Malaysia. The number of trees (n) sampled for each genus is listed. For each genus, *Dipterocarpus*, *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.

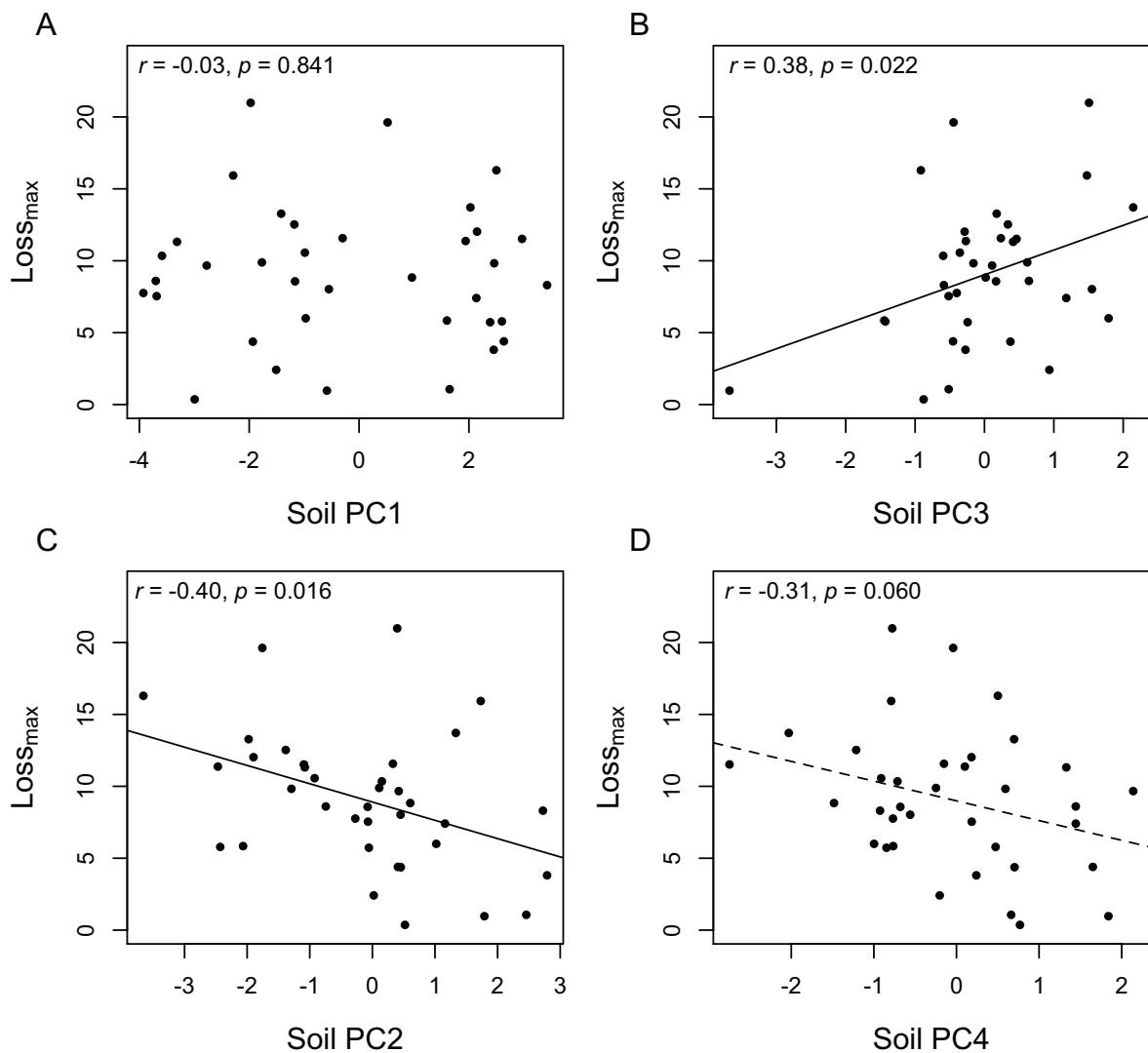


Figure 4. The relationship between the stand-level percent stem biomass lost to stem rot (Loss_{max}) among trees sampled in a cluster and mean values of the first four soil principle component (PC) axes for 36 tree clusters containing at least 10 trees ≥ 30 cm DBH. The Pearson correlation coefficient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

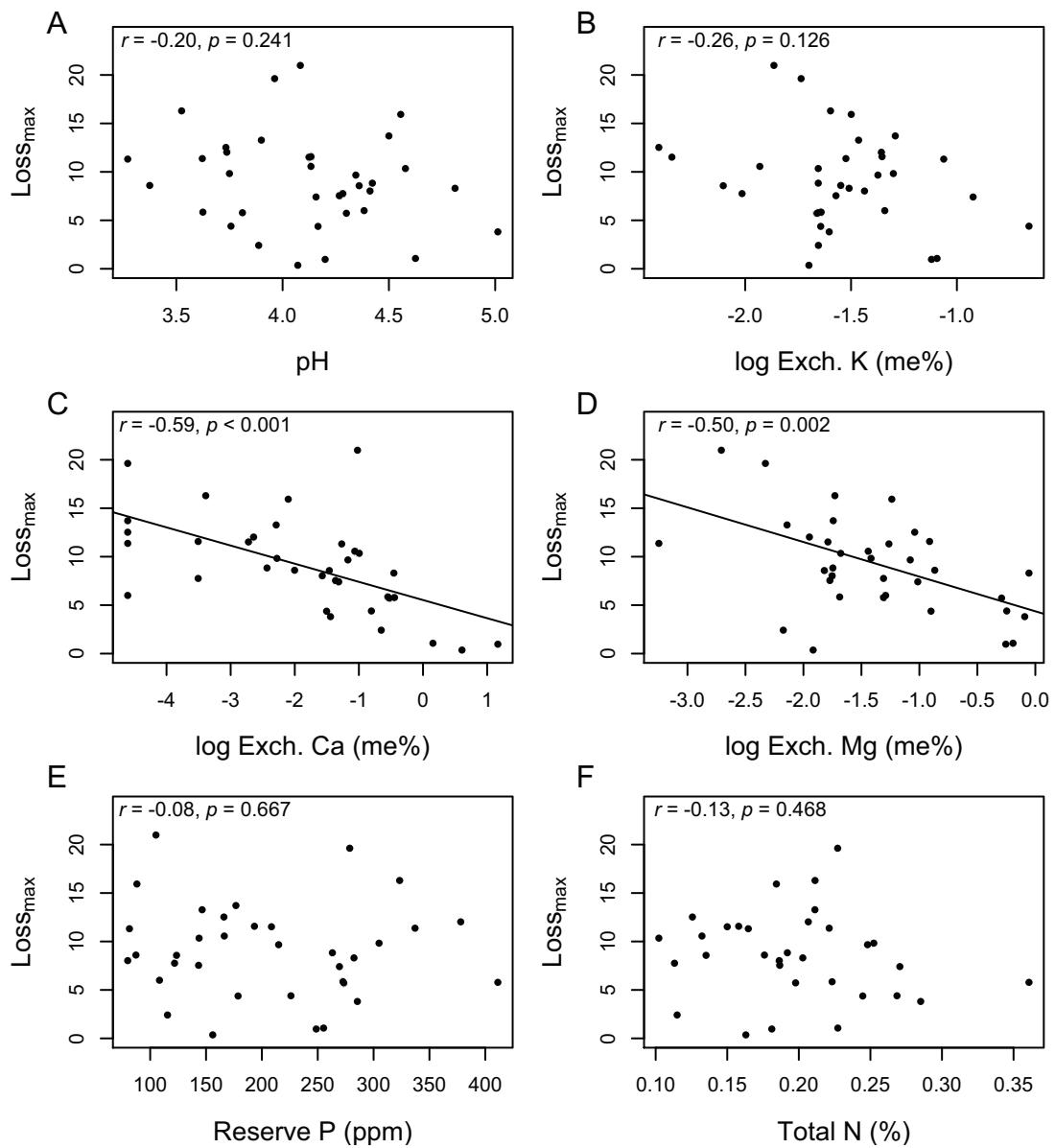


Figure 5. The relationship between the stand-level percent stem biomass lost to stem rot (Loss_{max}) among trees sampled in a cluster and mean soil chemical properties for 36 tree clusters containing at least 10 trees ≥ 30 cm DBH. The Pearson correlation coefficient (r) and associated probability of 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 (%).