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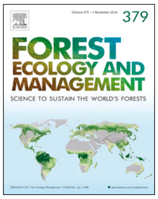

Quantifying the factors affecting wood decomposition across a tropical forest disturbance gradient

Gbadamassi G.O. Dossa[a,b,c,d,*], Ekananda Paudel[e], Douglas Schaefer[a,c], Jiao-Lin Zhang[a,b], Kun-Fang Cao[f], Jian-Chu Xu[c,d], Rhett D. Harrison[g,*]

[a] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China
[b] Center of Plant Ecology, Core Botanical Gardens, Chinese Academy of Sciences, Mengla, Yunnan 666303, China
[c] Key Laboratory for Plant Diversity and Biogeography of East Asia (KLPB), Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650201, China
[d] World Agroforestry Centre, East & Central Asia Regional Office, Kunming 650201, Yunnan, China
[e] Nepal Academy of Science and Technology, Khumaltar, Lalitpur, Nepal
[f] Plant Ecophysiology and Evolution Group, State Key Laboratory for Conservation and Utilization of Subtropical Agro-Bioresources, and College of Forestry, Guangxi University, Nanning, Guangxi 530004, China
[g] World Agroforestry Centre, East & Southern Africa Region, 13 Elm Road, Woodlands, Lusaka, Zambia

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ABSTRACT

Woody debris represents a substantial reservoir of carbon in forests. Disentangling the effects of factors affecting wood decomposition rates is therefore important. We examined the abiotic and biotic factors affecting wood decomposition across a disturbance gradient from mature forest to open land in a tropical montane site in Xishuangbanna, SW China. Wood logs ($n = 280$) of two native species with contrasting wood specific gravity (WSG), *Castanopsis mekongensis* (0.75) and *Litsea cubeba* (0.42), were exposed on the ground for three years. For each log, WSG was monitored at intervals by taking cores from top-half (up) and bottom-half (down) of the log. Mass loss was measured at the end of the experiment.

WSG loss rates were similar across the disturbance gradient and the species effect varied with core position. For *Castanopsis*, which had higher initial WSG and wood N concentration and much thicker bark, up-cores had consistently higher WSG loss over the study period. This species also had substantially higher WSG loss for up-cores, but interspecific difference among down-cores was small.

For mass loss, there was a complex interaction between species, habitat and the presence of termites. *Litsea* with low initial WSG experienced approximately two-fold higher mass loss in the absence of termites, but the difference between species was smaller in the presence of termites. Both species experienced higher mass loss in open habitats than in forests, but the termite effect was smaller in open habitats especially for *Litsea*. There was no interspecific difference in susceptibility to termite infestation, but infestation rates were higher in regenerating forests and open land than in mature forest. WSG loss explained 0% and 19% of mass loss variation in *Listea* and *Castanopsis*, respectively, in absence of termites and 0% for both in the presence of termites.

Afterlife effects of wood functional traits interact with abiotic conditions and decomposition processes (microbial decomposition, macro-organisms (termites), photo-degradation) in a complex manner to determine wood decomposition rates. WSG loss is not a reliable predictor of mass loss. These results have important implications for understanding the carbon cycle in tropical landscapes that are undergoing anthropogenic disturbance.

1. Introduction

Wood decomposition is an important process in forest ecosystems. Woody debris (WD) provides shelter and a nursing medium for plant seedlings and habitat for many arthropods and other organisms (Harmon et al., 1986; Stokland et al., 2012). It comprises a store of nutrients that *via* decomposition are redistributed to the ecosystem. WD also represents a substantial reservoir of carbon in forests (Oettel et al.,

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* Corresponding authors at: CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China (G.G.O. Dossa). World Agroforestry Centre, East & Southern Africa Region, 13 Elm Road, Woodlands, Lusaka, Zambia (R.D. Harrison).

E-mail addresses: dgbadamassi@gmail.com (G.G.O. Dossa), xiedaoan@xtbg.ac.cn (D. Schaefer), zjl@xtbg.org.cn (J.-L. Zhang), kunfangcao@gxu.edu.cn (K.-F. Cao), jxu@mail.kib.ac.cn (J.-C. Xu), r.harrison@cgiar.org (R.D. Harrison).

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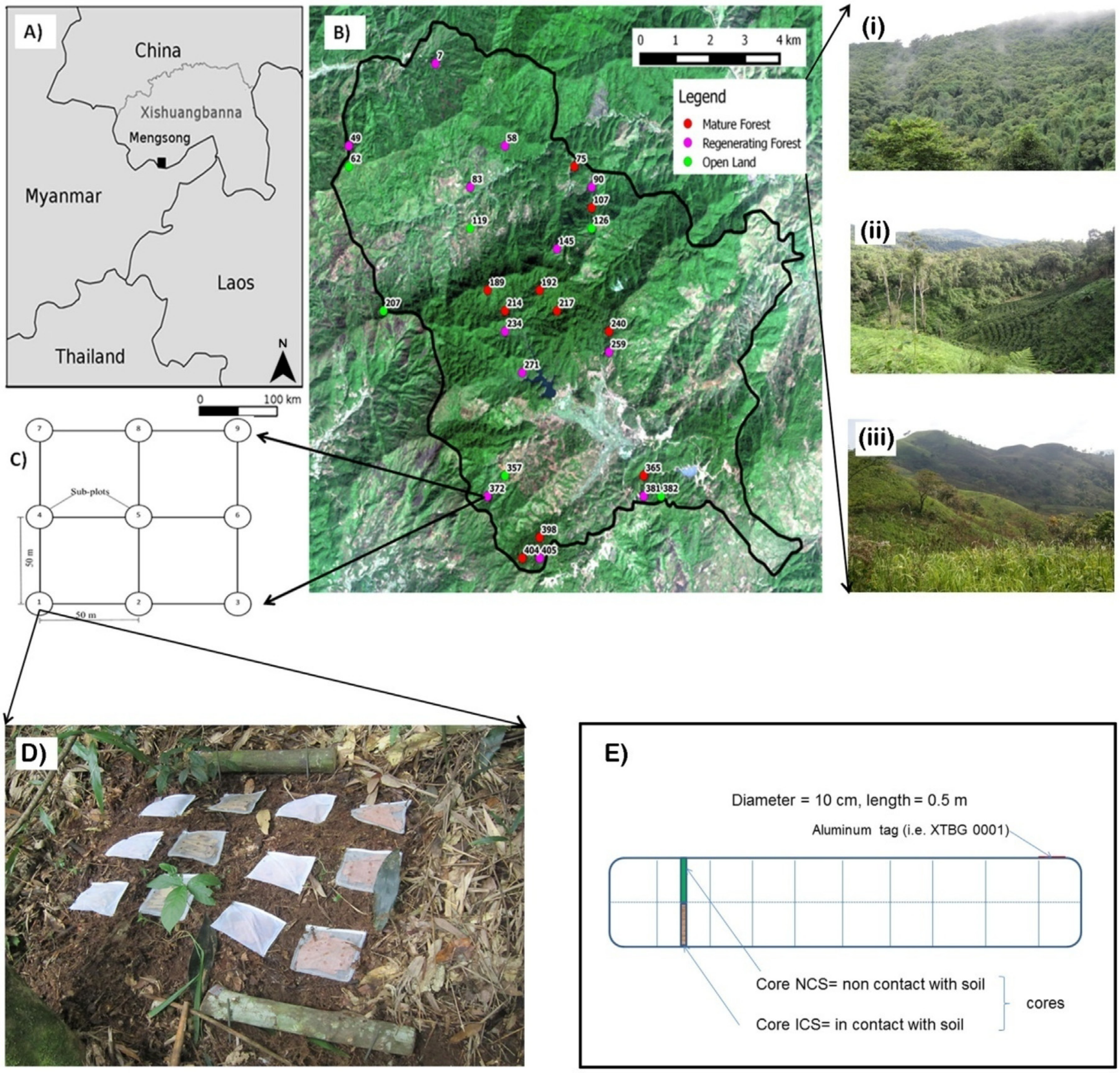

Fig. 1. Illustration of the study site and methods. A-C. Study site location: A-Mengsong, Xishuangbanna, southern Yunnan, China. B- Distribution of the network of 28 1-ha plots. Colored dots represent plots with different disturbance gradient categories (Green = Open land, Pink = Regenerating forest, Red = Mature forest) and i-iii. Within Mengsong landscape (i) mature forest behind with regenerating forest in the foreground; (ii) mature forest in background with tea plantation in the foreground; (iii) *Imperata cylindrica* grasslands; C- Subdivision of a sample plot with 3 × 3 array of subplots at 50 m spacing, only five (#1, 3, 5, 7, 9) subplots as in the shape of number 5 on a die). D- Wood logs incubated on the forest floor. The log placed above is *Litsea cubeba* and the one below is *Castanopsis mekongensis*. Note that because wood logs were on steep slope, these were supported by nails inserted into the ground down slope of each log. The litter bags were part of another experiment. E- Wood log representation with virtual 10 sections of 5 cm length. At harvest time, a corer was used to obtain cores from a randomly selected section. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2020). Thus the rate at which the sequestrated carbon is released to the atmosphere through wood decomposition is an important topic for research, although the time-frame of observations may vary from seconds to a century or more (Yoon et al., 2014). Some studies have examined the effects of substrate quality on wood decomposition, while others have examined substrate structural characteristics, such as size and toughness (i.e., wood density) (Zanne et al., 2015). Deforestation and forest degradation have had a substantial impact on tropical biodiversity, and hence on biodiversity dependent ecosystem functions such as organic matter decomposition (Eichenberg et al., 2017; Haddad et al., 2015; Handa et al., 2014; Pereira et al., 2010; Pietsch et al., 2018). Among the few studies, which have examined the effects of disturbance, most are based on studies of decomposition following natural disturbance such as hurricanes (Koster et al., 2009), although Forrester and colleagues created artificial canopy gaps and followed the decomposition course of tree stumps (Forrester et al., 2012). Studies examining the effects of anthropogenic disturbance on wood decomposition are lacking (Pietsch et al., 2018). Moreover, although studies have established certain relationships between rates of wood decomposition and wood traits (see Weedon et al., 2009; Cornwell et al., 2009; Pietsch et al., 2014; Hu et al., 2018; Parisi et al., 2018) understanding of the factors controlling wood decomposition and their interactions is still poor (Cornelissen et al., 2012; Mackensen and Bauhus, 2003; Oberle et al., 2019). More empirical studies on biotic and abiotic determinants of wood decomposition rates are needed to clarify the mechanisms involved, especially in the tropics (Harmon et al., 2020; Seibold et al., 2015). Doing so will shed light on the decomposition process and contribute to reducing uncertainties in global carbon models (Harmon et al., 2020; van Geffen et al., 2010).

To enhance our understanding of the factors determining the decomposition of WD, we examined the decomposition of freshly cut logs of two native species with contrasting wood specific gravities (WSG) in a tropical montane rain forest landscape in Xishuangbanna, SW China. Leveraging an existing network of permanent vegetation plots that were established across the disturbance gradient from mature forest to open land, we incubated 280 logs on the ground over a 3 yr period. We measured the WSG loss at intervals and total mass loss at the end of the experiment. Through this experiment we aimed to test the following hypotheses: i) wood decomposition rates decrease from open land > regenerating forest > mature forest due the changes in light availability (as a consequence of decomposition by photo-degradation) (Austin et al., 2016; Austin and Ballaré, 2010; Wu et al., 2019), (ii) the lower half of a woody log, which is in direct contact with soil decomposes faster than the upper half, (iii) short-term measurements of WSG loss are a good predictor of long-term mass loss, and (iv) tree functional traits, especially WSG and bark thickness, have important afterlife effects; specifically, we predicted that the species with lower WSG and thinner bark would decompose faster.

2. Materials and methods

2.1. Study site

This experiment was carried out in Mengsong (21° 28–34 N; 100° 26–31 E), a village within Xishuangbanna prefecture, Yunnan province, SW China. The field site is situated on the border with Myanmar. Since the early 1990s, the entire prefecture had been through a substantial land use change involving conversion of natural forest and swidden cultivation areas to cash crop monoculture plantations, either tea at higher elevations or rubber and banana at lower elevations (Zhang et al., 2019). Today, remnant forests are mostly located within protected areas including the newly established Bulong nature reserve within our study area (Zhu et al., 2015). Mengsong has a monsoonal climate and the six months wet season occurs between May and October of each year (Xu et al., 2009). Mean annual precipitation is between 1600 and 1800 mm and the average temperature is around 18 °C. The vegetation is characterized as tropical Asian rainforest with a dominance of Lauraceae and Fagaceae trees in the canopy (Zhu et al., 2015). Our experiment made use of an existing network of 28 vegetation plots (1 ha), which were established across a disturbance gradient in this landscape from old growth forest to open land, consisting of fire-maintained grasslands and tea fields. The plots were established using a stratified random approach during 2010 and 2011 resulting 10 mature forest plots, 12 regenerating forest plots and six open land plots (Fig. 1B). Each plot was further divided into 9 subplots arranged on a 3 × 3 grid with 50 m spacing (Fig. 1C).

2.2. Log preparation and installation

We selected the species to provide a wide WSG spectrum (WSG being one of the most important functional traits among woody plants). Thus, prior to species selection, we conducted a survey on the uses of common species found in the landscape. We later selected two native tree species (*Litsea cubeba* and *Castanopis mekongensis*) to the landscape with contrasting wood specific gravities (WSG). *Litsea cubeba* (Lauraceae, hereafter *Litsea*) is a fast growing pioneer species with low WSG (0.42), thin bark, and used for aromatic purposes while *Castanopsis mekongensis* (Fagaceae, hereafter *Castanopsis*) is a slow growing species with relatively high WSG (0.75), thick bark, and used for roofing trusses as well as fire wood purposes. In term of resistance to decay these two species were rated as fastest and slowest to decay. Trees were purchased from local farmers' fuel wood lots. Logs with scars, deformations or branch knots were discarded. The logs used for the experiment had a mean diameter of 9.53 ± 1.11 cm (sd), mean initial weight of 2.3 ± 0.53 kg, length of 50.3 ± 0.66 cm, and mean bark thickness of 6.06 ± 2.83 mm for *Castanopsis* and 9.58 ± 1.02 cm, 1.4 ± 0.36 kg, 50.5 ± 0.68 cm, and 2.82 ± 0.82 mm for *Litsea,* respectively. Logs were deployed in the 28 plots. For this experiment only five out of nine subplots per plot were used (as in the shape of #5 on a die, Fig. 1). Logs were assigned randomly to plots and subplots. In total 280 logs (28 plots × 5 subplots per plot × 2 species × 1 log per species) were incubated on the ground for 3 years from October 2011 to November 2014. We set up a 2 m × 2 m experimental area ~5 m north of the subplot centre where we placed two logs (1 log per species) (Fig. 1D). Logs on steep slopes were supported with iron nails hammered into the ground (not through the log) to prevent any movement of the log. We tracked the change in wood specific gravity (WSG) of cores taken from the incubated logs at intervals. We also considered mass loss by measuring changes in log dry mass from the beginning to the end of the monitoring period.

2.3. Data collection

Disks cut from each individual stem when the logs were harvested were stored at – 20 °C for wood chemical analyses and for establishing initial water content and WSG. Wood cores were harvested from logs after 6, 12, 18, 24 and 36 months exposure in the field. On each occasion, a 5 mm diameter (Forestry Supplier ®) increment borer was used to collect a wood core from a randomly chosen section of each log (see Fig. 1E). Prior to core collection, we examined visually for the presence of termites on the logs. To examine our hypothesis concerning the position on the log, we collected two cores: the upper side (no contact with soil, "up") and lower side (in contact with soil, "down" Fig. 1E). After harvesting, we immediately put cores into a straw for protection, which was then placed in a ziplock plastic bag and returned to the laboratory. The hole created in the log was filled up with inert silicon (Tosseal® 381, Tokyo, Japan) to reduce the risk of introducing a fungal infection or providing access to insects. The increment borer was sterilized with ethanol and flamed between uses to prevent any fungal cross contamination. The collected cores were weighed using an electronic balance to 0.001 g before and after drying in oven at 105 °C. The oven dry volume was measured using the water displacement method (Williamson and Wiemann, 2010). WSG was calculated using the following equation (1):

$$WSG = \frac{Ovendrymassofwoodcore}{Ovendryvolumeofwoodcore} * \rho_{water} \tag{1}$$

where: WSG is the wood specific gravity (unit less), Oven dry mass (g), oven dry volume (cm^{-3}) and ρ_{water} is density of water (1.00 g cm^{-3}) (Williamson and Wiemann, 2010).

After 36 months incubation, logs were retrieved from the forest floor (including pieces that had broken off) and the total dry weight of the remaining log was measured. This was done by drying the logs at 105 °C until constant mass. To obtain the initial dry mass of each log, measurement of initial moisture content obtained from the off-cut disks was combined with volume using Newton's formula (Harmon and Sexton, 1996), calculated by measuring the diameters at both ends and middle and the total length of the log.

2.4. Chemical analysis

The initial concentrations of carbon (C), nitrogen (N), phosphorus (P), potassium (K), cellulose, hemicellulose, lignin and water soluble sugar were analyzed for each harvested tree stem and for bark and wood separately. In addition, fiber content and tannin content were measured for wood and bark, respectively. All the chemical analyses were performed following standard methods at the biogeochemistry central laboratory of Xishuangbanna Tropical Botanical Garden (XTBG). Briefly, C and N were determined by Vario Max CN element analyzer (Elementa Analsensysteme, Germany). Prior to P, and K concentrations determination samples were dissolved in HCl and digested with HNO3-HClO4, then passed to an inductively coupled plasma atomic emission spectrometer (iCAP 6300, IRIS Advantage, E R, Thermo Fisher Scientific, USA). Water-soluble sugars were analysed with Analyzer 3 (SEAL Analytical GmbH, Germany). We employed UV–visible spectrometer (UV 2450, SHIMADZU, Japan) to measure tannin content. Finally, NDF, ADF, ADL, fiber contents were determined using Fibertec™ 2010 (FOSS Analytical AB, Sweden). ADL, NDF and ADF were later converted to lignin, hemicellulose and cellulose (Chen et al., 2012). Details on each chemical analysis protocol can be found elsewhere (Dossa et al., 2016).

2.5. Microclimate monitoring

Bradford et al. emphasized that the long held assumption of the predictive power of climate over wood decomposition failed at the regional scale (Bradford et al., 2014). This suggests that climatic effects on wood decomposition are stronger at local and micro scales. Therefore, we installed Hobo Onset microclimate station loggers (Version 5.0.0, Onset Computer Corporation, Cape Cod, MA, USA) at a representative plot for each forest degradation category across the forest disturbance gradient. These loggers were set to measure continuously at 2 min intervals the following variables: (i) ambient air temperature and relative humidity (Smart sensor S-THB-M00x), (ii) surface soil moisture (0–5 cm, Smart sensor S-SMx-M005-EC-5), and (iii) photosynthetic active radiation (PAR) (Smart sensor S-LIA-M003). Due to failures caused by low batteries and destruction of wires by rodents, some data were not available. Therefore, we compared climatic variables across the forest disturbance gradient for 3 months in the middle of the wet season and 3 months in the middle of the dry season.

2.6. Data analysis

All analyses were performed in R version 3.5.2 (R Foundation for Statistical Computing, 2018) and the "nlme" package (Pinheiro et al., 2013), using the modeling function *lme (linear mixed effect models)*. To correct for heteroscedasticity, we fitted an exponential function (varExp (form = ~fitted(.)) to model the error term for the WSG loss model and for the mass loss model we used either (varExp(form = ~fitted(.)) or (varIdent(form = ~1|Forest type). We examined model fit by plotting model diagnostics. We used Akaike information criteria (AIC) to select optimal models, and the function *anova* to examine effect of each independent variable. All independent variables along with their significant two-way interactions were included in the model. Three-way interactions were incorporated from the beginning of the analysis but these terms were not significant terms, thus were removed subsequently.

In our models, the response variable was percent WSG loss (log transformed) or decay rate constant (*k*) (log transformed) calculated on a mass loss basis. Fixed effects included species (*Castanopsis/Litsea*), wood core position (up/down) (WSG loss only), forest disturbance category (mature forest, regenerating forest, open land) and all two-way interactions. For the WSG loss model, which was a repeated measure design, number of days of incubation was modeled as second-order polynomial and we included a random effect for subplot nested within plot. The function *confint* was employed to compute the 95% confidence interval of each estimated parameter within the model. For mass loss model, we used plot as a random factor. In addition, for the mass loss model, we included the presence or absence of termites. To calculate the decay rate constant (*k*), we assumed decomposition followed a negative exponential trajectory (Cornwell and Weedon, 2014) using the following equation (Oberle et al., 2018):

$$M_t = M_o * e^{-\left(\frac{k*t}{365.25}\right)} \quad (2)$$

where M_t represents dry mass at harvest time *t, t* is the number of days of incubation, $M_o$in the dry mass at initial time (zero day of incubation), 365.25 is the converter constant of days to year, and *k* is the decay rate constant (per year). We calculated decay rate constant as it enables comparison with studies that employ different observation periods. However, we also present the model based on percent mass loss at 36 mo in the supplementary materials (Table S2). Last, we examined whether the susceptibility to termite attack differed between the two species and also among habitats through a survival analysis (logs infested *vs.* non infested), for which we used the *survreg* function in the "survival" package (Lumley, 2019).

Within the forest disturbance categories, many factors might either individually or in concert affect wood decomposition. Hence, in order to disentangle some of these factors, we investigated the amount of variation in the decomposition rates that is explained by some factors separately, including vegetation (plant diversity consisted of trees, herbs and lianas), edaphic parameters (sand, silt and clay content, total C, N, K, P, Mn, Ca and Fe, C:N ratio, pH (H_2O) and topography (slope and elevation). To reduce the number of variables we employed non metric multidimensional scaling (NMDS) and principal component analysis for species composition among plots and soil/topographic parameters, respectively. For the NMDS, we used Jaccard's distance computed within the vegan package. For the principal component analysis (PCA), we used the function *prcomp*. Prior to carrying out the PCA, we standardized all parameters by setting the mean to zero and standard deviation to one with the function *scale*. We calculated the r^2 through the likelihood ratio function *r.squaredLR* and compared them among the best selected models. We also used the likelihood ratio test while simplifying the model.

3. Results

In total 280 logs were deployed in the field. However, the results reported here are based on 247 logs. Data from 33 logs were lost due to fire (one plot was entirely burnt) or loss (people collecting them as fire wood).

We expected lowest daily maximum temperature in mature forest and highest in open land. The surface soil moisture, patterns were season specific. Within the wet season, highest and lowest values were recorded in regenerating and mature forest, respectively. As time since rain events increased, the soil surface moisture decreased to baseline values in both open land and mature forest (Fig. S2). Regardless of season, photosynthetically active radiation (PAR) was highest in open land and lowest in mature forest (Fi. S3). Finally, mean relative humidity was highest in the mature forest and lowest in the open land (Table 1, Fig. S4). The micro-climate monitoring results were as expected and we do not consider them further here, but present a summary in the online Supplementary Materials (Table S1, Figs. S1-S4). Our results from our HOBO loggers were compared to a permanent climate station located at the site (Fig. S1). For instance, the daily maximum temperature at the climate station during dry season

Table 1
Initial chemical concentrations of *Litsea cubeba* and *Castanopsis mekongensis*. Wood and bark were analysed separately. Values represent means.

Chemistry	Wood		Bark	
	Litsea Cubeba	*Castanopsis mekongensis*	*Litsea cubeba*	*Castanopsis mekongensis*
Carbon (%)	46.9	47.3	49.9	47.4
Nitrogen (%)	1.887	2.91	10.165	5.76
Phosphorus (%)	0.187	0.063	0.585	0.28
Potassium (%)	1.627	1.163	2.87	2.02
Lignin	10.527	24.183	27.55	25.46
Cellulose (%)	59.722	53.243	47.69	44.27
Hemicellulose (%)	25.077	15.477	16.425	9.58
Sugar (%)	0.667	0.337	0.78	0.32
Fiber content (%)	72.463	76.12	NA	NA
Tannin (%)	NA	NA	0.33	1.28
C/N	24.85	16.25	4.91	8.23
Lignin/N	5.579	8.31	2.71	4.42
Lignin/C	0.22	0.51	0.55	0.54

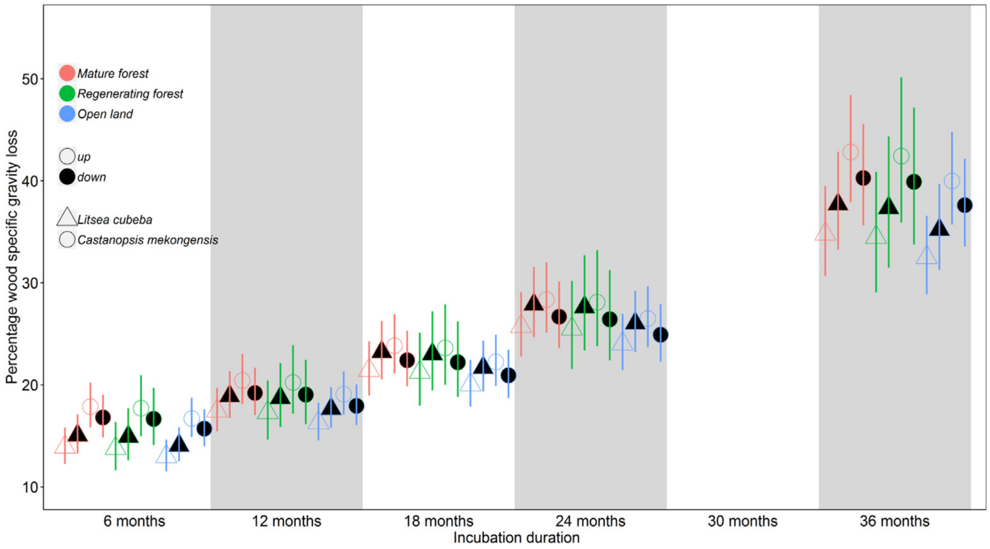

Fig. 2. Percent wood specific gravity (WSG) loss from logs installed across 28 plots in the Mengsong landscape after 6 mo, 12 mo, 18 mo, 24 mo and 36 mo incubation. The experiment used two species, *Litsea cubeba* and *Castanopsis mekongensis*. We considered the relative position of harvested core (filled symbols represent the core which was in direct contact with soil (down) and empty symbols represent the core which was from the side facing upwards (up)). Points represent predicted mean values from the optimal model (± 95 % confidence interval) for two species (*Litsea cubeba* and *Castanopsis mekongensis*) with respect to disturbance gradient categories (mature forest, regenerating forest and open-land). We did not collect cores at 30 mo.

followed a pattern close to that observed in the regenerating forest, whereas during the wet season it resembled those recorded in open land (Fig. S1).

3.1. Initial wood chemistry and wood functional traits

The logs used for the experiment had a mean bark thickness of 6.06 ± 2.83 mm for *Castanopsis* and 2.82 ± 0.82 mm for *Litsea*. Regardless of species, N, P, and K had higher concentrations in bark than in wood. However, bark C and lignin concentrations were higher than in wood only for *Litsea*. With regard to bark, all chemicals showed a higher concentration in *Litsea* than in *Castanopsis* except tannin. For wood, *Litsea* had higher concentrations of P, K, cellulose, hemicelluloses and water soluble sugar, while *Castanopsis* wood had higher concentrations of C, N, fiber content (FC) and lignin (Table 1).

3.2. Wood specific gravity loss

After 36 months of exposure, the WSG loss varied from 29.47 to 48.46 % (Fig. 2). There was no significant effect of land cover type on WSG loss ($F_{2,\ 24}$ = 0.436, P = 0.652, Table 2, Table S3). In addition, although we expected cores in direct contact with soil (down) to show higher decomposition rates, we found that the pattern was species dependent. In *Litsea* down cores decomposed faster, whereas the opposite was true for *Castanopsis* ($F_{1,\ 2765}$ = 4.617, P = 0.032, Fig. 2, Table 2). Also, contrary to expectations, species had no significant main effect on WSG loss ($F_{1,\ 2765}$ = 1.911, P = 0.167, Table 2), although the interaction between incubation time (days) and species was significant ($F_{1,\ 2765}$ = 5.386, P = 0.005, Table 2). For up cores, *Castanopsis* showed a consistently higher rate of WSG loss than *Litsea* throughout the 36 mo incubation period (Fig. 2). However, for down cores the pattern was not consistent (Fig. 2).

3.3. Effects of plants species composition, soil chemistry and topography on WSG loss

To attempt to tease apart the factors determining WD decomposition rates, we replaced forest disturbance category with plant species composition in the model. NMDS1 was closely related to disturbance gradient as well as a basal area gradient, and NMDS2 reflected compositional differences (i.e., in forest this represented the difference between broadleaf evergreen sites and rainforest, while for open land it reflected the difference between grassland and terraced tea sites (Paudel et al., 2015)). The new model did not differ much from the original using the disturbance categories (Table S4-5), but explained slightly more variance in the dataset (adjusted r^2 = 38 % *vs.* 36 % using disturbance categories). The main effects of both NMDS axes were not significant (e.g., NMDS2: $F_{1,\ 24}$ = 2.143, P = 0.156), but their interactions with incubation time were significant (Table S4-5).

When we also substituted disturbance categories with the first two principle component axes for the soil/topography parameters (Paudel et al., 2015), the model explained a similar amount of the variance (adjusted r^2 = 37 %) but neither axes had a significant effect, either as main effects (e.g., PC2: $F_{1,\ 105}$ = 2.974, P = 0.088, Table S6-7) or as

Table 2

Model results for wood specific gravity (WSG) loss. Percent loss (log transformed) was modeled over 36 months as function of number of days (2nd order polynomial), core position, wood species, termite presence and their interactive effects (for the full model ANOVA results see Table S3 in supplementary materials). There were two species: *Castanopsis mekongensis* and *Litsea cubeba*; three disturbance gradient categories: mature, regenerating and open land; and two core positions (up and down), and termite presence/absence. The simplified model is presented and model fit was examined by plotting model diagnostics. DF denotes degree of freedom.

Variables	Estimate	Standard error	DF	t-value	p-value
(Intercept)	3.130	0.060	2765	51.992	0.000
Polynomial (Number of incubation days, 1st degree)	17.582	0.770	2765	22.835	0.000
Polynomial (Number of incubation days, 2nd degree)	1.824	0.763	2765	2.390	0.017
Litsea cubeba	−0.044	0.032	2765	−1.383	0.167
Regenerating forest	−0.068	0.078	24	−0.881	0.387
Open land	−0.009	0.100	24	−0.093	0.927
Position (up)	0.061	0.029	2765	2.149	0.032
Polynomial (Number of incubation days, first degree):*Litsea cubeba*	1.356	1.169	2765	1.160	0.246
Polynomial (Number of incubation days, 2nd degree):*Litsea cubeba*	−3.735	1.138	2765	−3.282	0.001
Litsea cubeba:Position	−0.142	0.043	2765	−3.321	0.001

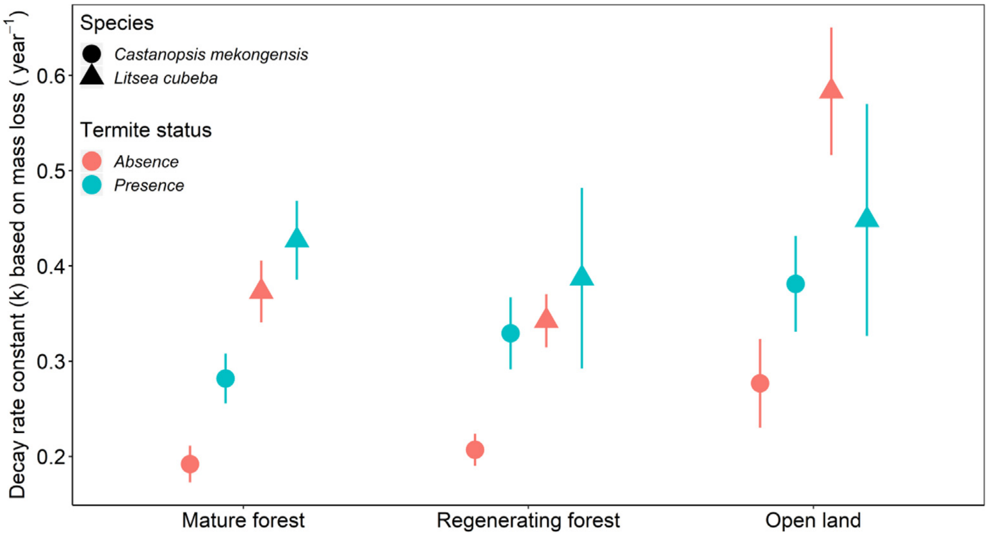

Fig. 3. Decay rate constant (k) for logs installed across 28 plots in the Mengsong landscape as measured after 36 mo incubation. The k values were calculated on a mass loss basis. Points represent mean k value for logs for two species (triangle symbols for *Litsea cubeba* and circle symbols for *Castanopsis mekongensis*) with respect to termite infestation status at end of the experiment (blue = presence; red = absence) within different disturbance gradient categories (mature forest, regenerating forest and open-land). Error bars represent the standard error around the mean within each land cover type. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

two way-interactions (e.g., PC2: $F_{2,\ 2739} = 2.01$, $P = 0.134$, Table S6-7).

3.4. Mass loss

At the end of the experiment, total mass loss was on average 66.54 % (16.66–93.99 %) for *Litsea* and 52.35 % (4.91–91.46 %) for *Castanopsis*. We observed higher total mass loss (~2 fold) and higher variation in mass loss in *Litsea* (decay rates $k = 0.34$–$0.58\ \text{yr}^{-1}$ for logs without termites and 0.38–0.45 yr^{-1} for logs with termites) than in *Castanopsis* (decay rates $k = 0.19$–$0.34\ \text{yr}^{-1}$ for logs without termites and 0.28–0.39 yr^{-1} for logs with termites). While there was no significant difference between mature and regenerating forest, we found mass loss in open land was substantially faster (~1.4 fold) (Fig. 3, Table 3, Table S2, Table S8). In overall, we found a weak effect of disturbance on mass loss. As expected, the presence of termites increased mass loss overall, but the effect size was species and habitat dependent (Fig. 3, Table 3, Fig. S5, Table S2, Table S8). The termite effect was greater in *Castanopsis* and in forested habitats than in *Litsea* and open habitats, respectively. The model explained 26 % of the variation found in the decay rate constant, but only 23 % if the presence of termites was not included (For model based on percent mass loss see supplementary material S9). In addition, for *Litsea*, WSG loss was not a significant predictor of decay rate (k). While, for *Castanopsis*, WSG loss was a highly significant predictor of k in the absence of termites (19 % variance explained) but not in the presence of termites (Fig. 4, Table 4, Table S10).

Table 3
Model of decay rate constant (k) (log transformed) of logs calculated on mass loss basis after 36 months incubation as function of disturbance gradient categories, wood tree species and termite presence. We used a linear mixed effects model with plot as random factor. There were two species: *Castanopsis mekongensis* (baseline level) and *Litsea cubeba*, three disturbance gradient categories (mature forest (baseline level), regenerating forest and open-land), and termite presence (absence (as baseline level) and presence)). To control for the problem of heteroscedascity we allowed the variance to differ among plots (function *varIdent(form = ~1|Plot)*). The simplified model is presented and model fit was examined by plotting model diagnostics. See also Table S8 in the supplementary materials.

Variable	Estimate	Standard error	DF	t-value	p-value
(Intercept)	−1.633	0.109	184.000	−14.963	0.000
Litsea cubeba	0.642	0.083	184.000	7.699	0.000
Termite status (Presence)	0.201	0.096	184.000	2.079	0.039
Regenerating forest	−0.036	0.139	24.000	−0.262	0.796
Open land	0.338	0.167	24.000	2.027	0.054
Litsea cubeba: Termite status (Presence)	−0.233	0.135	184.000	−1.722	0.087

When we substituted the disturbance categories with vegetation data or soil/topographic data in the model, only the NMDS1 for the vegetation data explained a significant component of the variation (Tables S11 and S12). The model using NMDS axes showed a substantial improvement and explained 39 % of the variation in k values. When presence of termites was included in the model, the explained variation did not change (Tables S10, S11).

The survival analysis indicated that the species were equally susceptible to termite infestation. In addition, logs in open land and regenerating forest were more susceptible to termite infestation than logs in mature forest (Table 5, Fig. 5).

4. Discussion

Fragmentation and forest degradation lead to an erosion of biodiversity (Haddad et al., 2015). Since, biodiversity itself is interlinked with ecosystems processes, there is a potential impact of biodiversity loss on ecosystem functioning. However, the effect of forest disturbance on ecosystem functioning is poorly understood. In this study, we examined factors affecting wood decomposition across a tropical forest disturbance gradient using logs of two native species with contrasting WSG. WSG loss is expected to reflect mostly microbial decomposition, whereas mass loss will also include the effects of macro-organisms and photo-degradation. We found that species and disturbance gradient categories had significant effects (weak effect for disturbance gradient) on wood decomposition rates when measured on a mass loss basis, but not on a WSG loss basis. Moreover, WSG loss was an unreliable predictor of mass loss, which has important bearing on the interpretation of studies that focus on the short-term monitoring of WSG loss.

4.1. Wood quality and core position effects

The contrast between the species used in this experiment in terms of initial WSG, bark thickness, lignin content and C:N ratio was marked. However, we did not detect any significant main effect of species on WSG loss, although there was a significant interaction with incubation time and core position. For up cores, contrary to expectation *Castanopsis* showed consistently higher WSG loss. This may reflect higher initial wood nitrogen concentration (Hu et al., 2018; Weedon et al., 2009), combined with a thicker bark (2 times thicker than that of *Litsea*) that

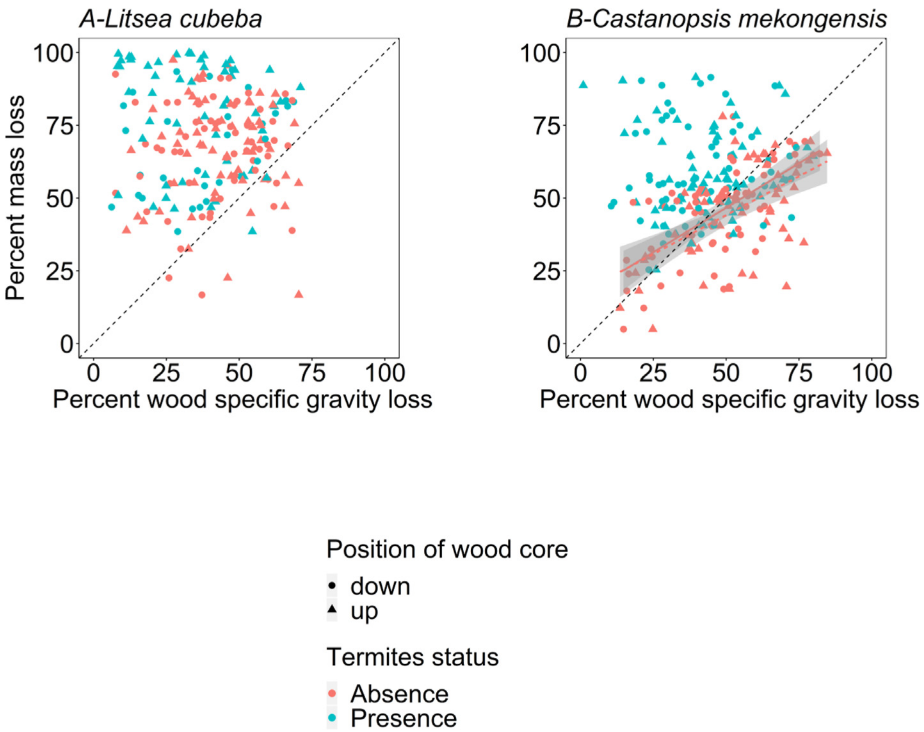

Fig. 4. Correlation between wood specific gravity loss and absolute mass loss for logs installed across 28 plots in the Mengsong landscape after 36 mo incubation; A) *Litsea cubeba* and B) *Castanopsis mekongensis* (termite infestation: red = absence, green = presence; core position: triangle = up, circle = down). Points represent percent mass loss and percent wood specific gravity loss of individual tree logs. Lines (dashed for up cores and continuous for down cores) represent significant linear regression with 95% standard error interval enveloping the mean. The black dash line represents the 1:1 line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Model of decay rate constant (*k*) of logs calculated on mass loss basis after 36 months incubation as function of wood specific gravity loss, position of core, and presence of termites. Modeling was done separately on wood tree species. We used linear mixed effects model with above factors as fixed factors and plot as random factor. There were two species: *Castanopsis mekongensis* and *Litsea cubeba*, two core positions (down (as baseline level) and up), and presence of termites (absence (as baseline level) and presence)). When a transformation was done to *k* before modeling, this is specified next to variable intercept. We modeled the error term with appropriate function to account for heteroscedascity. Model fit was examined by plotting model diagnostics. See also Table S10 in the supplementary materials for model based on mass loss.

Species	Model r^2	Termites status	Variable	Estimate	Standard error	DF	t-value	p-value
Litsea cubeba	0.0035	without	(Intercept, cubic transformation)	0.7102	0.0366	107	19.3884	0.0000
			Percent wood specific gravity (WSG) loss	0.0003	0.0007	107	0.3649	0.7159
			Position core (Up)	0.0084	0.0192	107	0.4353	0.6642
	0.0065	with	(Intercept, log transformation)	−0.905	0.176	59	−5.155	0.000
			Percent WSG loss	0.003	0.003	59	1.098	0.277
			Position core (Up)	0.079	0.073	59	1.081	0.284
Castanopsis mekongensis	0.1881	without	(Intercept, no transformation)	0.112	0.022	100	5.061	0.000
			Percent WSG loss	0.002	0.000	100	6.643	0.000
			Position core (Up)	−0.008	0.009	100	−0.870	0.387
	0.0060	with	(Intercept, log transformation)	−1.478	0.119	102.000	−12.456	0.000
			Percent WSG loss	0.003	0.002	102.000	1.797	0.075
			Position core (Up)	−0.007	0.048	102.000	−0.155	0.878

Table 5
Survival regression analysis results on the probability of termite infestation of logs installed across 28 plots in the Mengsong landscape after 6 mo, 12 mo, 18 mo, 24 mo and 36 mo incubation. The experiment used two species, *Litsea cubeba* and *Castanopsis mekongensis* and three disturbance gradient categories (mature forest, regenerating forest and open-land). *Castanopsis mekongensis* is used as the baseline level for tree species while mature forest is used as baseline level for habitat. Scale (log transformed) is a parametric value for the logistic distribution used for the survival regression analysis.

Variable	Estimate	Standard error	z-value	p-value
(Intercept)	36.175	1.004	36.020	< 0.001
Litsea cubeba	0.333	1.001	0.330	0.739
Regenerating forest	−3.590	1.121	−3.200	0.001
Open land	−4.049	1.441	−2.810	0.005
Log (scale)	1.874	0.038	48.900	< 0.001

had higher tannin concentration (Dong et al., 2016; Dossa et al., 2018). Higher N concentration may stimulate microbial colonisation and initial decomposition, while thicker bark may serve to maintain a moist environment suitable for microbial growth) (Schilling et al., 2015). Also contrary to expectation, the up cores in *Castanopsis* had consistently higher WSG loss than down cores. This might reflect some warming by direct sunlight of the top of the log, again creating favourable conditions for microbial growth (Austin et al., 2016; Austin and Ballaré, 2010; Fasth et al., 2011; Wu et al., 2019). In contrast, the down cores of *Litsea* had consistently higher WSG loss than the up cores as has been reported elsewhere (Fasth et al., 2011; Garrett et al., 2010; Gora et al., 2019; Meier et al., 2010; Přívětivý et al., 2016). Previous authors have suggested that the soil maintains high moisture content and provides easy access for soil micro- and meso-fauna into decomposing logs (Gora and Lucas, 2019). The contrasting pattern between our two species may reflect the effects of bark thickness, whereby the thin barked species tends to dry out above, slowing down microbial decomposition, while

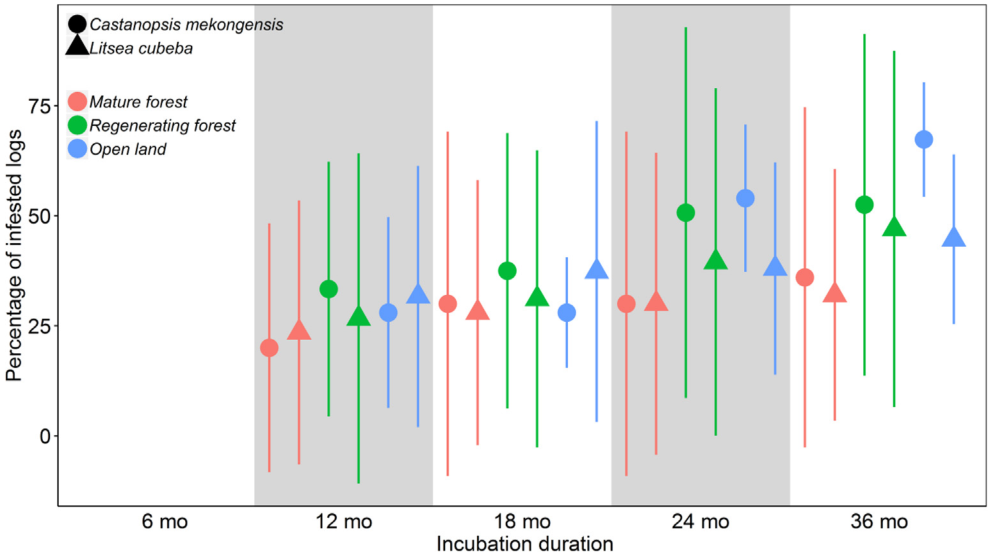

Fig. 5. Percent logs infested by termites observed at each sampling period for logs installed across 28 plots in the Mengsong landscape. Points represent mean percentage of infested logs for two species (triangle symbols for *Litsea cubeba* and circle symbols for *Castanopsis mekongensis*) with respect to disturbance gradient categories (red for mature forest, green for regenerating forest and blue for open-land). Error bars represent the standard deviation around the mean within each disturbance gradient category. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the upper side of the thick barked species retains more moisture and is warmed by direct sun, which accelerates microbial decomposition. However, the contrasting patterns in our two species also caution against post-hoc explanations and suggest we need data from a wider range of species, ideally collected under similar conditions, to understand the effects of bark and wood traits on rates of microbial decomposition.

In contrast to the WSG, the results for mass loss as measured at the end of the experiment were as predicted. Namely, *Litsea,* the species with lower initial WSG and thinner bark, experienced much higher total mass loss than *Castanopsis* over the 36 mo incubation period (Fig. 3). The decay rate constant *k* varied from 0.19 to 0.58 yr^{-1}, which is in similar range to other reports for tropical sites (Harmon et al., 2020; Song et al., 2017; Lalnunzira and Tripathi, 2018), although the rate of decay for *Castanopsis* was slightly lower than previous reports (Chambers et al., 2000; Lalnunzira and Tripathi, 2018).

Our modeling showed that the presence of termites was an important determinant of total mass loss and increased the variance explained by the model based on decay rates from 23 % to 26 %. This is in accordance with previous studies of wood decomposition (Cheesman et al., 2018; Griffiths et al., 2019; Ulyshen et al., 2016), including in Xishuangbanna (Liu et al., 2015). In fact, a decomposition experiment in Malaysia suggested that termites can consumed more than 50% of the mass of decomposing wood (Griffiths et al., 2019). Together, these studies suggest a strong effect of termites in wood decomposition.

Contrary to expectations, we found that the species were equally susceptible to termite infestation and we found that the effect of termite attack on mass loss was bigger in *Castanopsis*, the species with higher initial WSG. This could be explained by the fact that *Castanopsis* logs were a preferred food source. Recent studies on termite food preferences suggest that termites prefer dense wood with high moisture content (Oberst et al., 2018). In addition, the effect of termites declined from mature forest, to regenerating forest, to open land. This might reflect changing microsite conditions in the logs, with logs in more open habitats having a lower moisture content (Oberst et al., 2019, 2018), or changes in the abundance and species composition of termites. Importantly, these interactions with wood species and habitat, indicate that the presence of termites alone is not a reliable predictor of their effects on wood decomposition. We also found that logs in open land and regenerating forest were more susceptible to termite attack than those in mature forest. Whether this reflects an increase in the abundance or composition of termites, and an associated shift in feeding preferences, requires further investigation. Clearly, given the importance of termites in wood decomposition in the tropics, it would be worthwhile combining studies of termite feeding ecology with measurements of wood decomposition rates.

4.2. *Effects of forest degradation*

Contrary to our expectations, we did not find any significant effect of disturbance category on WSG loss. However, considering mass loss we found a significant effect (weak effect, Figs. 3, S5, Tables 3, S8) in the anticipated direction, with open land promoting higher mass loss than mature forest.

Our results for WSG loss may reflect the opposite consequences of increased canopy openness for moisture and temperature, which both facilitate microbial decomposition (Law et al., 2019). Nonetheless, our mass loss results corroborate earlier work by Koster and colleagues who found that wood decomposed faster under a fully damaged canopy than under a partially damaged canopy (Koster et al., 2009), which most likely reflects increased photo-degradation.

4.3. *Plant community and soil chemistry/topographic effects*

Using information on plant composition in place of disturbance category marginally improved the variance explained by both the WSG and mass loss models. The first NMDS axes essentially reflected the disturbance gradient, but the second axes reflected variance in tree species composition superimposed on this pattern (Paudel et al., 2015). Hence, the improvement in both models suggests that tree species composition had a small effect independent of disturbance.

When we replaced forest disturbance category with the first two PCA axes of soil/topography parameters, the models had a similar r^2 to the original models. This may reflect the non-random distribution of land use within the landscape which is often strongly associated with edaphic factors. An earlier study at the same site on leaf litter decomposition found that soil/topographic parameters were poor predictors of leaf litter decomposition rates (Paudel et al., 2015).

4.4. *Reconciling WSG loss and mass loss results*

Using various approaches (e.g., Jurgensen et al. (2006) for boreal forests, Curling et al. (2002) in vitro treatment exposure to brown rot fungi degradation, and Fraver et al. (2018) field exposure with wood stakes) previous authors have suggested that strength loss (bending strength or radial compression strength) could be a reliable proxy for wood decomposition (mass loss) (Curling et al., 2002; Fraver et al., 2018; Jurgensen et al., 2006), although there is a time lag between strength loss detection and mass loss detection, which may reflect a non-linear relationship between strength loss and cell wall chemical degradation (Curling et al., 2002). The advantage of monitoring WSG loss (~strength loss) is that short-term and repeated measurements can be made, which given the long-term nature of WD decomposition might greatly speed up our understanding. To our knowledge, this is first attempt to elucidate the relationship between WSG loss and mass loss in the tropics. Unfortunately, our results suggest that WSG loss is not a reliable predictor of mass loss (Harmon et al., 2008). Regardless of species, in the presence of termites, WSG loss was not a significant predictor of *k*. However, WSG loss explained from 0 (in the species with low initial WSG) to 18.81 % (in the species with high initial WSG) of the variance in *k* in the absence of termites. Inclusion of more species studied across more environments is needed to enhance our understanding of the relationship between WSG and mass loss, and how these interact with wood functional traits. However, in the short term, our results caution against using WSG loss, or similar metrics, as a proxy for mass loss.

5. Conclusion

In the tropics, forest degradation and land use change represent significant anthropogenic factors that affect biodiversity, which in turn affects ecosystem functioning. We conducted an experiment to examine the biotic and abiotic factors determining wood decomposition rates across a forest disturbance gradient. We measured WSG loss at intervals and mass loss at the end of the experiment. There was no significant effect of forest disturbance on WSG loss. In addition, the effect of contact with the ground was significant but the direction differed between the two study species. When considering mass loss, we found logs of the species with low initial WSG and logs placed in open land decomposed faster, as expected. The presence of termites was an important predictor of mass loss, but the effect size was strongly species and habitat dependent. Our results suggest that wood functional traits, in particular WSG and probably bark thickness, have important afterlife effects. However, these effects may have substantially different consequences for microbial decomposition, as compared to photo-degradation or decomposition by macro-organisms, such as termites.

6. Data availability

Data used for in this manuscript is available from Harvard Dataverse (accession # https://doi.org/10.7910/DVN/PZBWEP).

7. Authors' contribution

G.G.O.D, E.P., D.S., K.F.C., and R.D.H. conceived the ideas and designed methodology; G.G.O.D. and E.P. collected the data; G.G.O.D., E.P., and R.D.H. analyzed the data; G.G.O.D., R.D.H., and D.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CRediT authorship contribution statement

Gbadamassi G.O. Dossa: Conceptualization, Investigation, Methodology, Validation, Formal analysis, Resources, Visualization, Writing - original draft, Writing - review & editing. **Ekananda Paudel:** Conceptualization, Investigation, Methodology, Validation, Formal analysis, Resources, Visualization, Writing - review & editing. **Douglas Schaefer:** Conceptualization, Writing - original draft, Writing - review & editing. **Jiao-Lin Zhang:** Writing - review & editing. **Kun-Fang Cao:** Conceptualization, Supervision, Funding acquisition, Writing - review & editing. **Jian-Chu Xu:** Supervision, Funding acquisition, Writing - review & editing. **Rhett D. Harrison:** Conceptualization, Methodology, Validation, Formal analysis, Resources, Visualization, Writing - original draft, Supervision, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118166.

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