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Fungal succession in decomposing woody debris across a tropical forest disturbance gradient

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ABSTRACT

Fungi decompose woody debris, an important carbon pool in forests. Fungal community structure is expected to vary according to the wood species, habitats and extent of abiotic disturbance, which have consequences for carbon cycling in tropical forests. Here we examined the effects of fungal diversity and composition on woody debris decomposition rates and sought potential mechanisms to explain an observed lack of difference in decomposition rates across a disturbance gradient in a tropical montane rainforest in Xishuangbanna, SW China. We measured wood specific gravity (WSG) loss from 280 logs of *Litsea cubeba* and *Castanopsis mekongensis* over 3 years and monitored fungal communities from 418 samples using next-generation sequencing after 0, 18 and 36 months field exposure. Wood species and termite presence determined changes in fungal diversity through time. Overall there was a peak in fungal diversity at 18 mo, suggesting an initial period of colonization followed by a period of increasingly competitive interactions leading to decreased diversity. *Litsea* logs, which had relatively low initial WSG and thinner bark, harbored higher fungal diversity. Shared fungal OTUs between wood species peaked at 18 mo (~50%). However, fungal diversity was not a significant predictor of WSG loss. An effect of habitat on fungal community composition suggests that functional replacement explains the similar decay rates across the disturbance gradient. In addition, the proportions of saprotroph and white-rot fungi increased through time regardless of wood species. Termite presence reduced WSG loss, but the effect was mediated *via* the abundance of soft rot fungi. Our results suggest that changes in functional traits, rather than fungal species diversity, may better explain variation in WSG loss. Future studies should investigate roles of fungal functional traits and rot types, particularly those of Ascomycete fungi, whose roles in wood decay are still poorly characterized.

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1. Introduction

Saprotrophic fungi are commonly recognized as key biotic agents of wood decomposition. These fungi are functionally classified as brown, soft and white-rot types. Brown and white rot belong primarily to Basidiomycete fungi and play key roles in decay of both lignocelluloses and cellulose, while soft-rot fungi target the decay of cellulose (Stokland et al., 2012). Moreover, studies in temperate forests suggest there is a temporal succession of fungi from sugar-using fungi to wood structural decaying fungi to residual decaying fungi (Stokland et al., 2012). The effects of fungal diversity and functional composition on woody debris decomposition in tropical ecosystems have been understudied (Tomao et al., 2020). Existing studies suggest that wood host species identity has the strongest effect on the composition of fruiting fungal species (Krah et al., 2018; Lee et al., 2020), followed by microclimatic factors (e.g., canopy openness) (Krah et al., 2018), as well as bark presence (Jones et al., 2020), bark coverage (Hagge et al., 2019) and habitat type (terrestrial *vs.* aquatic) (Ferrer et al., 2020). However, critical aspects of fungal community ecology in the decay of woody debris remain to be explored. For example, our understanding of the link between fungal species richness and wood physio-chemical parameters is limited (Lustenhouwer et al., 2020; Purahong et al., 2017). The roles of both the taxonomic and functional composition of the fungal community in determining wood decomposition rates are not well understood (Lustenhouwer et al., 2020).

For microorganisms, such as wood decomposer fungi, both negative and positive diversity-function relationships have been reported in microcosm experiments under controlled laboratory conditions (Fukami et al., 2010; Maynard et al., 2017; Rajala et al., 2015), as well as in several field studies (Ferrer et al., 2020; Jones et al., 2019; Kahl et al., 2017; Krah et al., 2018; Purahong et al., 2017; van Der Wal et al., 2015; Yang et al., 2016). One possible reason for these apparently conflicting relationships arises from changing competitive networks within fungal communities (Maynard et al., 2017). The presence of a stronger competitor underpins negative diversity-function relationships. Finally, a recent study posits that fungal life growth strategies, such as the rate of growth *via* hyphal extension, hyphal density, enzymatic signatures, and the ability to tolerate abiotic stress factors, such as low moisture levels may also constrain the direction of the fungi diversity-decomposition rate relationship. For example fungi with higher hyphal extension rates decay wood faster, with this single predictor explaining 19% of variation in wood decay rates (Lustenhouwer et al., 2020). Understanding how forest disturbance impacts woody debris decomposition is of critical importance (Halme et al., 2013, 2015; Maillard et al., 2020), especially in tropical ecosystems. Tropical biomes are heavily impacted by anthropogenic activities, such as deforestation and degradation, and have high woody plant and fungal diversities, as well as large biomass. Additionally, there are few studies characterizing succession of fungal communities and decay type in woody debris over time, as well as how disturbance alters realized fungal traits, and succession of fungal communities through environmental filtering or *via* dispersal-colonization dynamics. The few studies of woody debris decomposition in the tropics have suggested that white rot dominates the early stages of decay (Schilling et al., 2015), but how fungal communities change in later stages of decay beyond two years and in response to microclimatic variation or forest disturbance are poorly characterized.

In a previous study, Dossa et al. (2020) found that wood decomposition monitored through wood specific gravity loss (which mainly reflects microbial decomposition) did not vary across an anthropogenic forest disturbance gradient. However, there were strong species identity effects in wood decay rates. Hence, the main goal of the current study was to elucidate possible mechanisms driving these observations (Fig. 1). Specifically we aimed to investigate the role of abiotic and biotic factors shaping the diversity and composition of fungal decomposers in decomposing woody debris, and how these characteristics of fungal communities change through time and across a disturbance gradient from open land to mature forest in a tropical montane rain forest in SW China. We addressed the following questions: (i) Does the wood species identity effect on decay rate (measured *via* WSG loss) emerge from differences in fungal community characteristics or in their initial wood properties? (ii) Does the lack of a difference in decay rates observed across the disturbance gradient reflect similarities in fungal diversity and composition? (iii) Do changes in wood decay rates over time reflect changes in fungal diversity and composition? We investigated these underlying hypotheses. (i) The wood species identity effect on wood decay rates emerges indirectly through the effects of woody

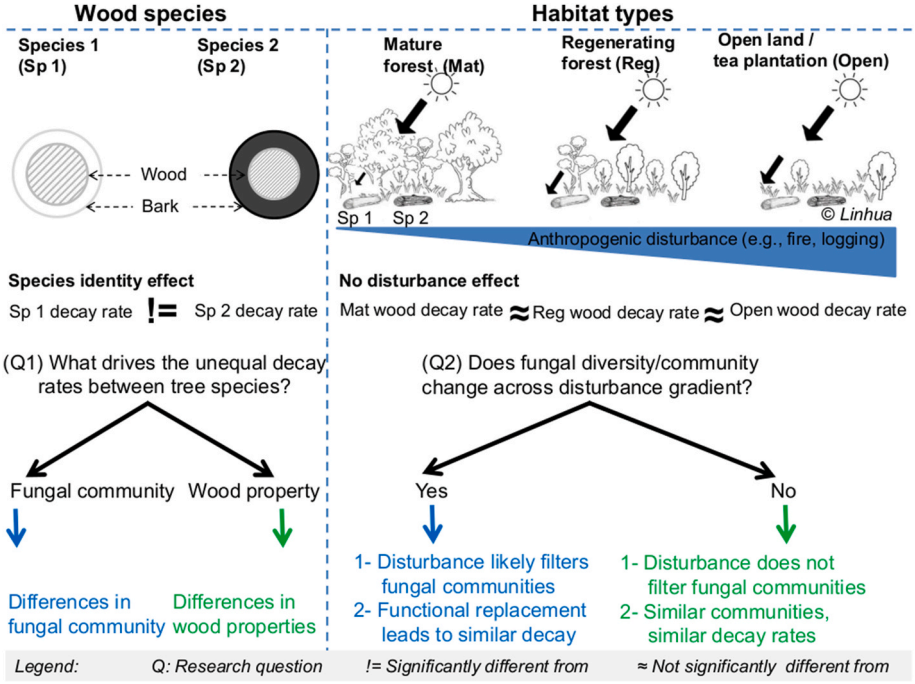

Fig. 1. Conceptual framework for this study illustrating the background of the study, previous results, research questions and hypotheses.

functional traits and chemistry on fungal diversity and communities. (ii) Similarity in wood decomposition rates across the disturbance derives from functional replacement among fungal decomposers and not compositional similarity. (iii) As woody debris has water soluble sugars in the bark and also hosts endophytic fungi, we expect fungal diversity to peak early in the experiment and to decline later as resource decreased, and we expect the peak to occur earlier in the species with lower WSG and a higher proportion of water soluble sugars in the bark.

2. Materials & methods

2.1. Study site

Our study site was located in Mengsong a township within Bulong Nature Reserve (Xishuangbanna, China, UTM/WGS84: 47 Q 656,355 E, 2377646 N, 1100–1900 m above sea level, Fig. S1). The climate in Mengsong is seasonal and monsoonal. Mengsong receives 1600–1800 mm of rainfall annually (Xu et al., 2009) of which 80% occurs within 6 months of the year from May to October. The mountainous vegetation in Mengsong shares many plant families with temperate Asian forests, with Fagaceae and Lauraceae as dominant canopy families (Zhu et al., 2015).

2.2. Plot design to account for disturbance gradient

The current landscape of Mengsong consists of a mosaic that includes open land such as barren fields, grassland and terraced tea fields, as well as regenerating forest and mature forest. Open and regenerating land resulted from logging and slash burn agriculture, which were banned in 1982 (Xu et al., 2009). In total, 28 1-ha plots (10, 12 and 6 plots classified as mature forests, regenerating forests and open land, respectively) were selected and established in 2010 to represent the disturbance gradient seen in the landscape (Paudel et al., 2015). Each plot was then subdivided into 9 subplots on a 3 × 3 grid with 50 m interval among subplots (Fig. S1 Panel C). Only 5 of the 9 subplots per plot were used for the wood exposure experiment (subplots 1, 3, 5, 7, 9; Fig. S1). The biophysical characteristics and microclimatic characteristics of plots are summarized in Table 1 and Table S1, respectively. In brief, in terms of vegetation, mature forest was dominated by (in rank order) *Castanopsis mekongensis*, *Magnolia floribunda*, and *Schima wallichii*; regenerating forest was dominated by *Schima wallichii*, *Castanopsis mekongensis*, and *Betula alnoides*; and open land dominated was by *Imperata cylindrica* or had tea plantations with sparse trees, including *Castanopsis mekongensis*, *Castanopsis calathiformis*, and *Saurautia nepaulensis*.

2.3. Experimental work and wood species selection

We selected two native species contrasting in wood density: 1) *Litsea cubeba* (Lauraceae), which has a relatively low wood specific gravity (0.42), and 2) *Castanopsis mekongensis* (Fagaceae), which has a relatively high wood specific gravity (0.75).

We purchased 29 living individual trees of *Litsea* and 32 of *Castanopsis* from local farmers' firewood plantations and harvested the main stem of healthy trees (i.e. those without termite or other insect infestation, physical damage or lesions to the bark). The harvested stems were ~9 cm in diameter and were cut into logs 0.5 m in length using a handsaw and tagged with unique tag number (later wood log ID). We sterilized the handsaw with ethanol and flamed it between cuts to prevent any microbial cross-contamination among samples. To establish initial wood functional traits, initial wood chemistry, and to examine initial fungal composition, a disk of 10 cm thickness was collected from the bottom of each individual tree and stored at −20 °C.

Logs were randomly deployed across plots and subplots. The logs used for the experiment had a mean diameter of 9.58 ± 1.02 cm and 9.53 ± 1.11 cm (sd), mean initial weight of 1.4 ± 0.36 kg and 2.3 ± 0.53 kg, and mean bark thickness of 2.82 ± 0.82 mm and 6.06 ± 2.83 mm for *Litsea cubeba* and *Castanopsis mekongensis*, respectively. With respect to bark chemistry, *L. cubeba* had lower tannin concentration but higher concentrations of nitrogen (N), phosphorus (P), potassium (K), water soluble sugar, and hemi-cellulose than *C. mekongensis* and similar concentrations of carbon (C), cellulose and lignin. For wood chemistry, *L. cubeba* had higher concentrations of P, cellulose, hemi-celluloses and water soluble sugar, while *C. mekongensis* wood had higher concentrations of C, N, fiber and lignin (Table S2). Detailed chemical analysis protocols of the wood composition were reported elsewhere (Dossa et al., 2016).

At each of the five subplots within the established plots (see above), we set up a small decomposition plot 2 m × 2 m approximately 5 m north of the subplot center and incubated one log of each species. Wood logs were randomly assigned to plots and subplots. In total, 280 logs (28 plots x 5 subplots x 2 species x 1 log) were placed on the forest floor in 2011 and monitored for three years.

2.4. Sample collections

Wood cores were taken with a core borer (Forestry suppliers ®, Jackson, MS, USA). We calculated WSG using the following formula:

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

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).

At the same time, the presence or absence of termites was recorded. Each log was divided longitudinally into 5 cm sections and on each sampling occasion one of these sections was randomly chosen for sampling. A cordless drill (Doug Jones, Doug Jones Jiwei company, Taiwan) was used to collect wood dust next to the core sample, which were placed directly in a tube (Corning tube Corning®) and immediately stored in −20 °C freezer for genomic analysis. One core sample and one wood dust sample were collected from the bottom (surface in contact with the ground) of the selected section, and one from the top of each log. The sampling equipment was cleaned and flamed between samples

Table 1
Habitat biophysical and microclimatic characteristics. Mean (±SD) daily maximum air temperature (Temp.), soil water content (Soil water), relative humidity (RH) and median photosynthetically active radiation (PAR) for 3 mo in the middle of the wet (Jun–Aug) season in 2012 and 2014 and dry (Feb–Apr) season in 2013 and 2014. Data were recorded in the understorey at three sites along a forest-disturbance gradient from mature forest, to regenerating forest and open land. For PAR, readings 1 h either side of the solar noon were used.

Land cover type	Forest age (years)	Basal area (m^2 ha^{-1})	Canopy openness (%)	Season	Temp. (°C)	Soil water (m^3m^{-3})	RH (%)	PAR (μE)
Mature forest	47.1 (6.23)[a]	29.9 (6.38)[a]	4.26 (0.64)[a]	Wet	20.41 (1.36)	0.10 (0.05)	98.78 (1.91)	10.70 (3.78)
Regenerating forest	25.5 (7.72)[b]	19.9 (5.59)[b]	7.11 (3.58)[a]		24.93 (4.35)	0.26 (0.04)	94.46 (5.52)	114.54 (97.15)
Open land	0 (0)[c]	2.35 (2.14)[c]	55.4 (10.3)[b]		27.42 (5.57)	0.22 (0.05)	87.46 (9.61)	753.92 (458.80)
Mature forest	47.1 (6.23)[a]	29.9 (6.38)[a]	4.26 (0.64)[a]	Dry	22.08 (2.38)	0.00 (0.06)	72.12 (17.98)	19.82 (10.67)
Regenerating forest	25.5 (7.72)[b]	19.9 (5.59)[b]	7.11 (3.58)[b]		26.58 (3.46)	0.06 (0.03)	68.80 (15.66)	158.31 (218.80)
Open land	0 (0)[c]	2.35 (2.14)[c]	55.4 (10.3)[c]		31.76 (4.01)	0.05 (0.05)	61.47 (13.70)	1437.57 (330.42)

to avoid cross-contamination, and the holes in the log were plugged with silicone (Tosseal® 381, Tokyo, Japan) to prevent inadvertent introduction of biota. Samples were collected at 3, 6, 12, 18, 24 and 36 mo. However, to reduce costs, only wood dust samples collected at 18 mo and 36 mo, from four subplots (#1,3, 7 and 9 each at the corner of the plot like number four on a dice) and from the bottom of the log were used for genomic analyses. Hence, we planned to do genomic analysis on a total of 448 field samples (28 plots x 4 subplots x 2 species x 2 sample occasions). However, only 384 field samples were conducted due to missing samples (one plot was burnt and some logs stolen). In addition, we analyzed 34 samples from the initial wood discs to obtain time zero samples for all the logs. We chose to use the samples from the bottom of the log to avoid interaction with photo-decomposition.

2.5. Molecular analyses of fungal communities

2.5.1. DNA extraction

Wood dust samples were homogenized to a fine powder with a mortar and a pestle in liquid nitrogen. Subsequently, DNA was extracted from 150 to 250 mg of each homogenized wood dust sample using the ZR Soil Microbe DNA MiniPrep kit (Zymo Research, Irvine, CA, USA) according to the manufacturer's instructions. DNA quality was checked using a NanoDrop ND1000 spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA).

2.5.2. DNA metabarcoding and next generation sequencing

The DNA extracted from each sample was quantified using the Qubitfluorometer (Thermo-Fischer) and approximately 10–25 ng of DNA for each sample were submitted to the University of Minnesota Genomics Center (UMGC) for amplification, sequencing and library analyses. Additional samples to assess quality and accuracy of the amplification and sequencing steps included a mock fungal community which contained equal quantities of 37 known fungal taxa (See supplementary material Table S3 for the list of species in the mock community) and technical replicates consisting of replicate libraries of the same DNA sample. A two-step dual-indexed amplification method (Gohl et al., 2016) was used for amplifying the fungal internal transcribed spacer 1 (ITS1) barcode region. The universal fungal primers employed in this study were ITS1F (CTTGGTCATTTAGAGGAAG*TAA) and ITS2R (GCTGCGTTCTTCATCGA*TGC) (Hu et al., 2018). All the samples were amplified individually and the amplified PCR products were barcoded prior to pooling. Pooled samples were sequenced across two 300 base pair (bp) pair-end IlluminaMiseq lanes to obtain sufficient coverage for each sample. Sequences from all Miseq lanes were aggregated together for downstream quality control.

2.6. Data analysis

2.6.1. Bioinformatics

MOTHUR (Schloss et al., 2009) was used to pair the sequences and make contigs, excluding sequences with less than 100 bp overlap. The remaining sequences that had less than 2 bp mismatch to the fungal ITS1 region primer were retained for further filtering. The remaining sequences were filtered to remove those that had more than one ambiguous base, more than eight homopolymers, or were shorter than 150 bp or longer than 420 bp. The sequences that passed filtering in MOTHUR were transferred into the QIIME platform (Caporaso et al., 2010). Chimeras were removed based on both the *de novo* and reference-based chimera check algorithms of the USEARCH61 pipeline (Edgar et al., 2011). Representative OTUs were picked *de novo* at 97% similarity using USEARCH (Edgar and Flyvbjerg, 2015). The taxonomy of OTUs was assigned using a 97% similarity blast threshold. The UNITE database dynamic version November 20, 2016 (Koljalg et al., 2014) was used for the taxonomy assignment. The OTU table was transferred into R for subsequent statistical analyses.

FUNGuild was used to map OTUs to trophic modes and ecological guilds (Nguyen et al., 2016). Our analyses first looked at dynamics of major trophic modes of fungi (e.g., pathotrophs, saprotrophs and symbiotrophs). Second, we explored taxonomic diversity of saprotrophs, as those fungi actively degrade wood constituents. Lastly, we focused on three functional traits/guilds relevant to wood decay, namely white, soft and brown rot fungi which denote decay rot types.

2.6.2. Availability of DNA sequences data and materials

All sequences were submitted to the NCBI database under the project bioproject accession https://www.ncbi.nlm.nih.gov/bioproject/PRJNA503471. Raw data file along with r script are available at https://github.com/dossag/Mengsong-fungal-succession-on-woody-debris_SBB.

2.7. Statistical analyses

2.7.1. Wood specific gravity (WSG) dynamics

We checked for homogeneity in variance of WSG loss among different forest types using Bartlett test (Bartlett's K-squared = 0.6646, df = 2, P-value = 0.7173) (Bartlett, 1937). WSG loss was reported in a previous study examining the habitat, species and abiotic effects on wood decomposition (Dossa et al., 2020). Here our objective was to investigate dynamics of fungal community characteristics along the course of wood decay and their effects on WSG loss. Specifically, we aimed to elucidate the drivers of the wood species identity we detected in wood decay rates, and explain observed lack of habitat effects.

2.7.2. Fungal taxonomic diversity (Alpha diversity) and community structure (Beta-diversity)

We used Chao 1 as an estimator of alpha diversity. The Chao 1 estimator was computed as follows: $N + S^2/(2\,D)$ where N is the number of OTUs, S is the number of singleton OTUs and D is the number of doublet OTUs, (i.e. OTUs with abundance 2) (Chao, 1984). We estimated alpha diversity per sample and modeled it as a function of exposure time, habitat, species, and termite status, including interactions, as fixed factors and plot|subplot/wood log ID as the random factor (See Table S4 on statistical approaches in the data analysis) with linear mixed effect *lme* from "nlme" package (Pinheiro et al., 2013). We simplified the maximal model to an optimal model by subtracting variables one at a time starting from the higher level interactions, respecting the principle of marginality and using the likelihood ratio test. We also used variance partitioning through linear modeling to assess how much of the variation in WSG was explained by alpha diversity.

We also examined the dynamics of both saprotrophs and fungal rot types (brown, soft and white rot) through time and across disturbance gradients. These models were incorporated later into a structural equation model (SEM) and with the current limitations of the SEM package used (see below), we opted to use *lme* on log transformed (Ives, 2015) data of rot type abundance and saprotrophs abundance, as this permitted normalization of the data, and a random factor plot|subplot/wood log ID.

To assess community structure and turn over (beta diversity) we generated a dissimilarity distance matrix based on Bray-Curtis distance using the function *vegdist* method "bray" from the package "vegan" (Oksanen et al., 2018). We conducted a non-metric multidimensional scaling (NMDS) based on this dissimilarity matrix using the function *metaMDS* from the "vegan" package. We then assessed effects of the factors wood species, forest disturbance, termites, and time on the dissimilarity between fungal communities at 18 and 36 mo by performing a constrained permutational multivariate anova (PerMANOVA) (Anderson and Walsh, 2013) with the function *adonis* from the "vegan" package. We used the argument strata = Wood log ID to account for the random factor. Our PerMANOVA analysis was followed by betadisper analysis with setting the argument bias.adjust = TRUE (Stier et al., 2013).

Finally, we used structural equation modeling (SEM) to investigate both the direct and indirect effects of species, time, habitat type, and termites on WSG loss *via* fungal alpha diversity, saprotroph abundance and brown, soft, and white rot fungi abundances (Figure S2 illustrates the initial SEM analysis model). We employed the package "piecewiseSEM" (Lefcheck, 2016) to conduct SEM using the function *psem*. First, we simplified the model by log transforming the abundance data for the rot type and saprotrophs and used *lme* (see above). Second, "piecewiseSEM" does not currently produce standardized estimates for categorical variables, however, it uses a wrapper function through the package "emmeans" (Lenth et al., 2020) to compute marginal means at each level of the categorical variable using the function *emmeans*. This *emmeans* function also does pairwise comparison of the marginal means. We included time in the modeling as an ordered categorical factor. We examined the direct effects of main factors (time, woody species, termites, and habitat type) on the total response variable (WSG loss). Then, as we hypothesized that the fungal diversity and abundance of rot type fungi would change over time, we tested indirect effects of the main factors on WSG loss mediated *via* partial responses (fungal diversity, saprotroph abundance and rot type abundance). From the initial model, we used the function *dSep* to check whether any relationships were left out from our initial model. If so, we checked whether those potential links have biological meaning before considering including them in the model. Last, we reduced the initial model to the best fit model using the likelihood ratio test with *anova* function. All analyses were performed in R version 4.0.02 (R Foundation for Statistical Computing, 2020).

3. Results

3.1. Dynamics of WSG loss

We previously examined abiotic factors affecting wood decomposition in this landscape (Dossa et al., 2020). After 36 months exposure, the WSG loss varied from 29.5 to 48.5% (Fig. 2). The effect of habitat on WSG loss was not significant (Table S5 and S6), while wood species identity had a significant interaction with exposure time (Table S5-6), indicating a different temporal pattern of WSG loss in the two species (Dossa et al., 2020).

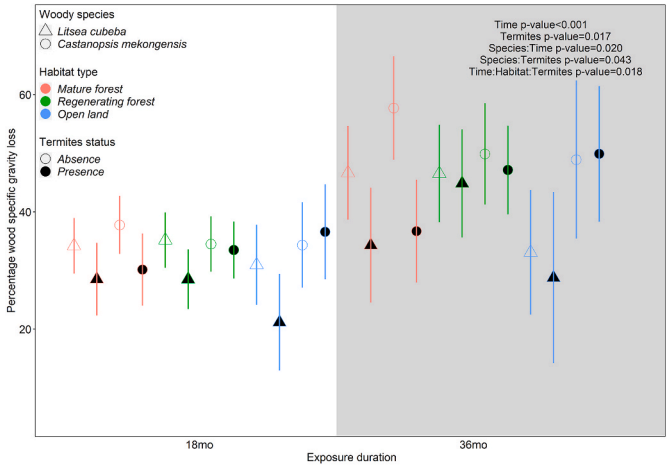

Fig. 2. Percentage wood specific gravity (WSG) loss from logs installed across 28 plots in the Mengsong landscape (Xishuangbanna, SW China) after 18 mo and 36 mo exposure (Dossa et al., 2020). The experiment used two species, *Litsea cubeba* and *Castanopsis mekongensis*. Points represent predicted mean values (±95% confidence interval) for two species (*Litsea cubeba*, triangles and *Castanopsis mekongensis*, circles) with respect to habitat type (mature forest (red), regenerating forest (green), and open-land (blue)), and termite status (no termites (empty) and termites present (filled)). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.2. Taxonomic and functional classification of fungal community

In total, after quality control steps, we obtained 9773 operational taxonomic units (OTUs), a percentage of which were identified to Phylum (91%), to Class (78%), to Order (73%), to Family (51%), to Genus (44%), to trophic mode (45%), and to rot type (6%) (See Table S7 for unidentified OTU percentages based on abundance and presence/absence across all samples). Ascomycota was the dominant phylum followed by Basidiomycota across all samples (Fig. 3, S3), with fewer Basidiomycota in L. *cubeba* than in *C. mekongensis*. Ascomycota abundance was high initially and at 36 mo but lower at 18 mo in both species and across habitats. Sordariomycetes, Agaricomycetes, Leotiomycetes, and Dothideomycetes were the most abundant fungal classes regardless of wood species, habitat type and exposure time. Other moderately abundant (>5% of total reads) classes included Eurotiomycetes, Saccharomycetes, and Tremellomycetes (Fig. S4).

The relative abundance of fungal orders varied with species, habitat and exposure time (Fig. S4). Those with greater than 5% abundance included two basidiomycete orders, Agaricales and Polyporales, and various ascomycete orders, dominated by (in order of overall rank abundance) Helotiales, Xylariales, Hypocreales, Pleosporales, Chaetothyriales, Coniochaetales, Saccharomycetales, and Capnodiales (Fig. S4).

At the family level, Sclerotiniaceae (Helotiales), which was dominated by the genus *Botrytis*, and Trichocomaceae (Eurotiales), were most abundant in the initial (0 mo) fungal community in *L. cubeba* while Sclerotiniaceae and Dermateaceae (genus *Pezicula*) (Helotiales) were most abundant at 0 mo in *C. mekongensis*. At detection >7% abundance, across habitat types at 18 mo, Herpotrichiellaceae (Chaetothyriales) was the most abundant family in *L. cubeba*, while Xylariaceae (Xylariales) was most abundant in *C. mekongensis* and was comprised of multiple genera, while fungi of the genus *Nemania* were most abundant in mature forest. At 36 mo, in *L. cubeba* Dermateaceae was the most abundant family, while in *C. mekongensis* it was Hyaloscyphaceae and Strophariaceae. Genera with >5% abundance included the Ascomycetes (in order of overall rank abundance) *Penicillium* (Hepotrichiellaceae), *Trichoderma* (Nectriaceae), *Hyaloscypha* and *Mollisia* (Dermataceae; Helotiales), *Exophiala* (Herpotrichiellaceae), *Nemania* (Xylariaceae), *Coniocheata* (Coniochaetaceae), and *Candida* (Saccharomycetales), as well as the basidiomycete genera *Phlebia* (Meruliaceae; Polyporales), and *Hypholoma* (Strophariaceae; Agaricales) (Fig. S4).

At 36 mo the average proportions of pathotrophs, saprotrophs, and symbiotrophs across all habitat types were 7.7%, 70.3% and 22.1%, respectively for *L. cubeba*, and 9.2%, 84.5%, and 6.3%, respectively, for *C mekongensis* (Figs. 3 and 4, Table S8-10; Fig. S4). Regardless of wood species, saprotroph abundance increased with time except in open land. Saprotroph abundance also increased with the abundance of both soft rot and white rot fungi (Fig. 4, Table S9-10). Symbiotrophs increased in abundance over time, also regardless of wood species and habitat type, but at a higher rate in *L. cubeba* than *C. mekongensis*. For pathotrophs, these increased with time regardless of wood species and habitat except for *L. cubeba* in open land and regenerating forest.

Both L. *cubeba* and *C. mekongensis* harbored a relatively small proportion (<1%) of brown rot initially. As decomposition proceeded, the abundance of white rot fungi increased, and white rot fungi were more abundant in mature forest followed by regenerating forest than in open land, and were less abundant in the presence of termites (Figs. 3–4, Table S11-12). In our model of white rot fungal abundanceregardless of habitat type, at 36 mo, there was less white rot fungi in *L. cubeba* than in *C. mekongensis* logs. With regard to soft rot fungi, their abundance decreased with time except in open land for both wood species and mature forest only for *L. cubeba*. Termite infestation led to a higher abundance of soft rot fungi (Fig. 3, Table S13-14). For brown rot, *L. cubeba* showed significantly lower abundance than *C. mekongensis*, while brown rot was more abundant in open land than in mature forest. Brown rot abundance was also higher in woody debris infested by

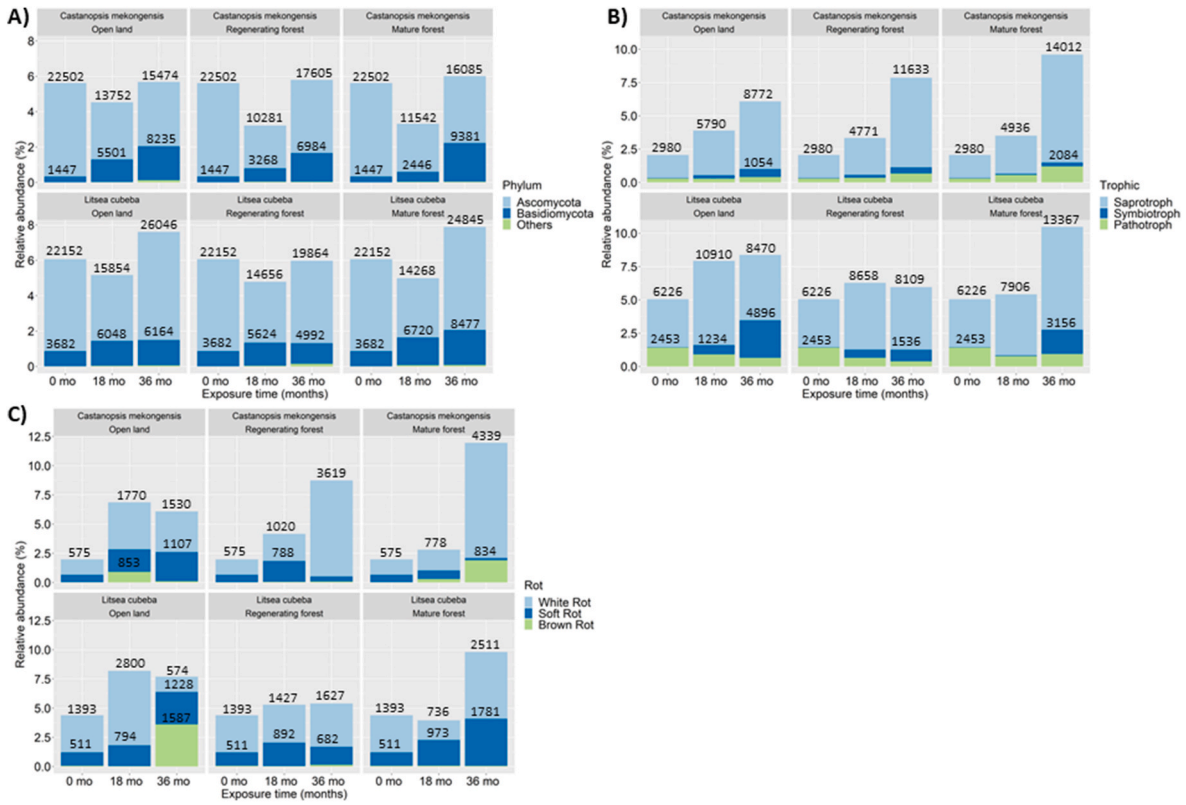

Fig. 3. A) Average relative abundance of operation taxonomic units (OTUs) assigned to higher taxonomic units (Ascomycota, Basidiomycota, Other), B) Average relative abundance of OTUs assigned by FUNGuild to different tropic modes (Pathotroph, Saprotroph, Symbiotroph) and C) Average relative abundance of OTUs assigned by FUNGuild to different rot types (white-rot, brown-rot, and soft-rot fungi). In order to have comparable values, the relative abundance was calculated across all our samples regardless of habitats, exposure time and species. Thus within each panel (A–C) the total percentage sums to 100. Numbers above the bars represent the sum of abundances of OTUs belonging to a particular group. Note some bars are not high enough to write their corresponding numbers thus we have put these in table S7 in the supplementary materials). For statistical analysis for differences among groups refer to Fig. 4 and tables S8-15. Note that panels A, B and C are not independent (i.e. data may derive from the same OTUs categorized into different taxa/functional guilds).

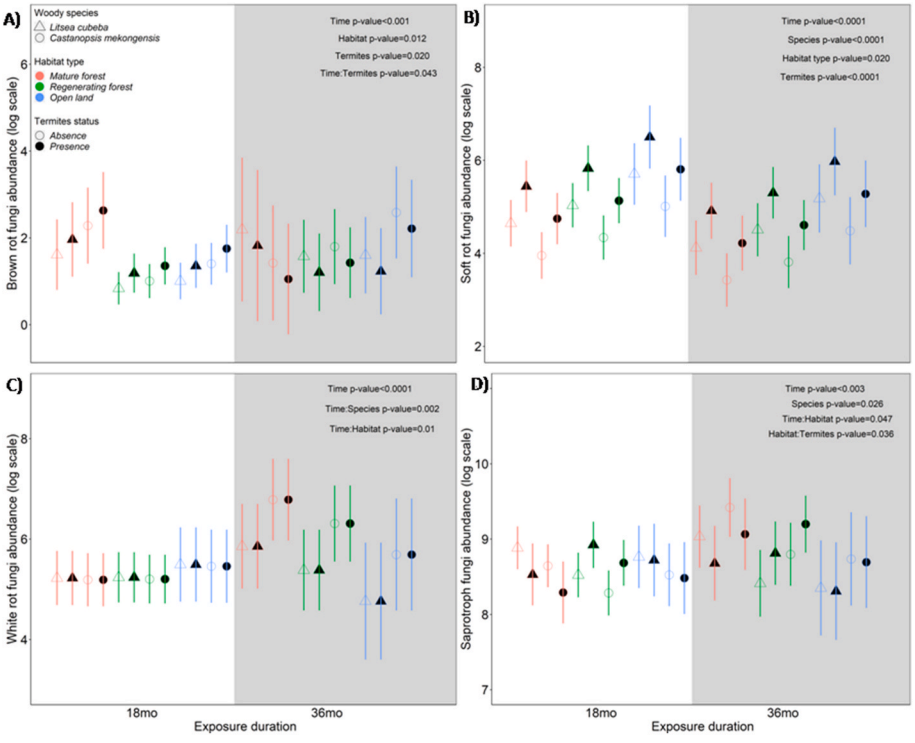

Fig. 4. Change in abundance of fungi classified to rot types and saprotroph from OTUs assigned to different rot types (white-rot, brown-rot, and soft-rot fungi) and saprotrophic trophic mode found from logs installed across 28 plots in the Mengsong landscape (Xishuangbanna, SW China) after 18 mo and 36 mo exposure. A) Brown rot fungi abundance, B) Soft rot fungi, C) White rot fungi, and D) Saprotroph fungi. Points represent predicted mean values (±95% confidence interval) for two wood species (*Litsea cubeba* and *Castanopsis mekongensis*) with respect to habitat (mature forest (red), regenerating forest (green), and open-land (blue)), and termite status (no termites (empty) and termites present (filled)). Note that for 0 mo error bars represent standard error of the mean (from pooled logs) while for the remainder error bars are ± 95% from the best predicted model. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

termites. There was a larger total abundance of fungi from all rot types in *C. mekongensis* than in *L. cubeba*, except in open land, where the total proportion of rot types did not differ substantially between species.

3.3. Fungal alpha diversity in decomposing logs

L. cubeba harbored more fungal OTUs than *C. mekongensis* (Fig. 5) Table 2 and S17. In both species, fungal diversity peaked at 18 mo exposure. The best model for alpha diversity explained 67.2% of the total variance including both fixed and random factors, while fixed factors explained 39.3% of the variance. Exposure time and wood species had significant main effects on fungal diversity (Table 2, Table S17) and we found significant three-way interactions among wood species, time and termite status, and among wood species, habitat, and termite status. However, fungal diversity explained only ~2% of the variation in WSG loss, although this was still marginally significant. (Table 2, S5-6).

3.4. Fungal community structure

NMDS plots of fungal communities at the Class level showed substantial overlap among species, but variation among samples increased through time from 18 to 36 mo ($F_{1, 382} = 5.883$, $P = 0.016$, Fig. 6), and varied among habitat type ($F_{2, 381} = 5.561$ $P = 0.004$, Fig. 5 and S5-6). Nevertheless, a multivariate analysis of factors influencing differences in fungal communities (Oksanen et al., 2018) found that time, wood species identity, habitat type and the interaction between time and presence of termites, had significant effects on community composition (Table 3). However, the model explained only ~11% of variance in fungal species composition. A Venn diagram depicting the number of unique or shared OTUs over time shows that regardless of wood species, there was a peak in the number of unique OTUs at 18 mo, which declined afterwards. The percentage of unique OTUs at 18 mo was 1.16 times higher for *C. mekongensis* than for *L. cubeba* (Fig. 7), but the absolute number of

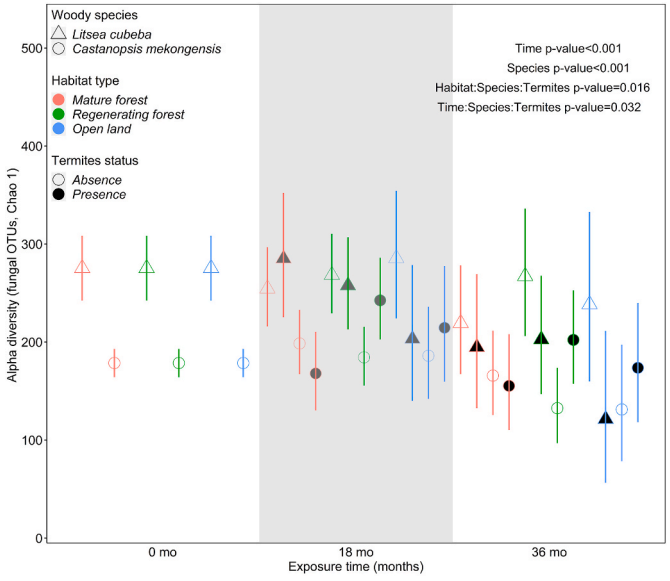

Fig. 5. Change in fungal alpha diversity (Chao 1) across time and habitat types for two wood species during 36 months exposure in a tropical montane forest, Mengsong, Xishuangbanna, SW, China. Points represent predicted mean values (±95% confidence interval) for two wood species (*Litsea cubeba* and *Castanopsis mekongensis*) with respect to habitat (mature forest (red), regenerating forest (green), and open-land (blue)), and termite status (no termites (empty) and termites present (filled)). Note that for 0 mo error bars represent standard error of the mean (from pooled logs) while for the remainder error bars are ± 95% from the best predicted model. The initial time (0 mo) has no termite infestation. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Model results for fungal alpha diversity (Chao 1, square root transformed) as function of time, species, habitat type, termite presence, abundance of different rot types with significant two and three way interactions on logs of *Litsea cubeba* and *Castanopsis mekongensis* during 36 month of wood decomposition in tropical montane forest, Mengsong, Xishuangbanna, SW, China. Forest has three levels (baseline regenerating forest, mature forest, and open land) and species has two levels (*Castanopsis mekongensis*, *Litsea cubeba*). DF = degree of freedom (see Table S9 for forest based line open land).

Variable	Estimate	Standard error	DF	t-value	p-value
(Intercept)	13.72038	0.62212	148	22.054	<0.0001
Time.L	−1.29832	0.60961	148	−2.130	0.035
Regenerating forest	−0.45942	0.79189	24	−0.580	0.567
Open land	−0.42855	1.03162	24	−0.415	0.682
Litsea cubeba	1.69168	0.71587	101	2.363	0.020
Termite status (Presence)	−1.15593	0.92027	148	−1.256	0.211
White rot abundance	−0.00016	0.00004	148	−3.900	0.000
Saprotroph abundance	0.00009	0.00003	148	3.325	0.001
Time.L:Regenerating forest	−0.86175	0.72217	148	−1.193	0.235
Time.L:Open land	−1.07287	0.97173	148	−1.104	0.271
Time.L:*Litsea cubeba*	0.14425	0.89235	148	0.162	0.872
Regenerating forest: *Litsea cubeba*	1.13358	0.99616	101	1.138	0.258
Open land:*Litsea cubeba*	1.25500	1.33095	101	0.943	0.348
Time.L:Termite status (Presence)	0.78325	0.69763	148	1.123	0.263
Regenerating forest: Termite status (Presence)	3.07536	1.22421	148	2.512	0.013
Open land:Termite status (Presence)	2.07355	1.53148	148	1.354	0.178
Litsea cubeba:Termite status (Presence)	1.78536	1.31520	148	1.357	0.177
Time.L:Regenerating forest:*Litsea cubeba*	2.13397	1.12103	148	1.904	0.059
Time.L:Open land:*Litsea cubeba*	0.86935	1.47829	148	0.588	0.557
Time.L:*Litsea cubeba*: Termite status (Presence)	−2.82866	1.09160	148	−2.591	0.011
Regenerating forest: *Litsea cubeba*:Termite status (Presence)	−4.50865	1.73793	148	−2.594	0.010
Open land:*Litsea cubeba*: Termite status (Presence)	−5.10235	2.31792	101	−2.201	0.030

unique OTUs was higher in *L. cubeba*. The shared OTUs between the two woody species peaked at ~50% after 18 mo of exposure (Fig. 7).

3.5. Structural equation modeling

Our SEM revealed a best model that included few direct effects (Fig. 8). The final results showed a good fit (Fisher's C = 38.81, P-value = 0.34, degrees of freedom = 36, AIC = 144.81 Fig. 8). The SEM confirmed many results of the linear mixed effect modeling. As expected, time had a direct effect on WSG loss. Time also had an effect on saprotroph and soft rot abundances. Saprotroph abundance overall had a positive effect on WSG loss, while soft rot abundance negatively affected WSG loss. Taken together, time, saprotroph abundance, and soft rot abundance explained about 32% of the variance found in WSG loss (Table S18). The SEM confirmed that there was no direct effect of habitat type on WSG loss. However, the SEM expanded our understanding by revealing that habitat, time, termite presence, and wood species all had indirect effects on WSG loss *via* soft rot abundance. .

4. Discussion

Current understanding of fungal ecology in wood decomposition

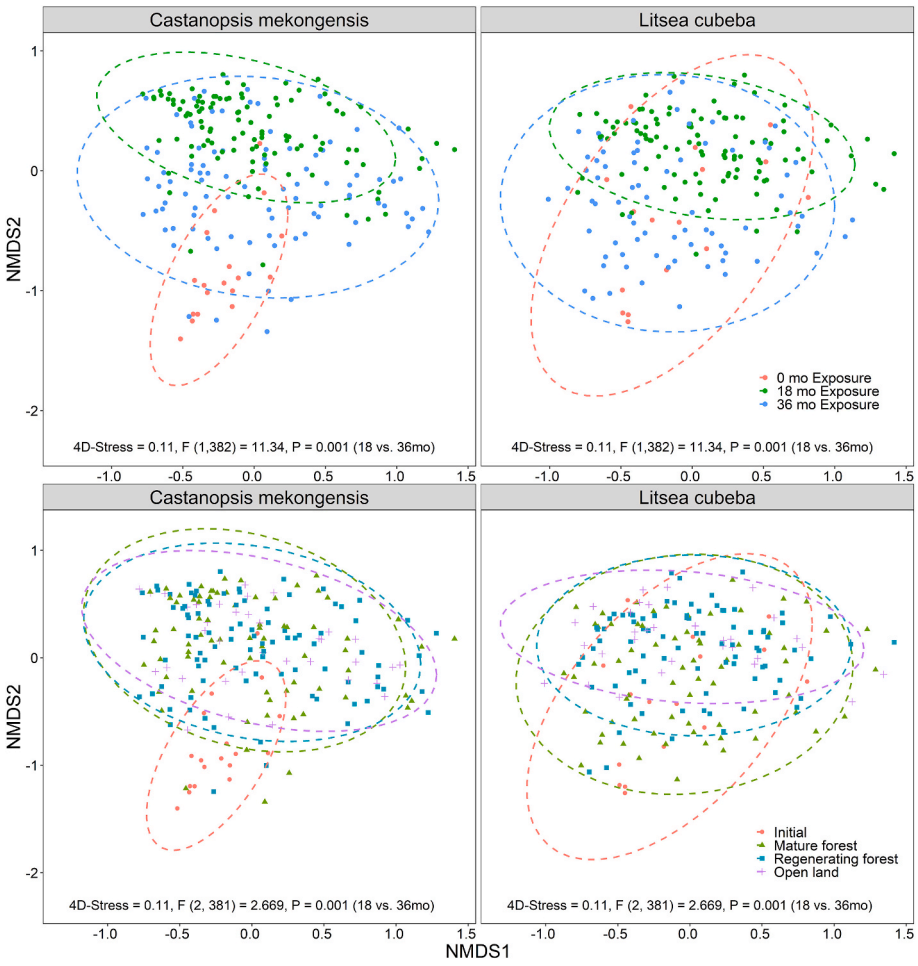

Fig. 6. Change in fungal composition (based on classes) through time based on Bray-Curtis dissimilarity over 36 month of wood decomposition in tropical montane forest, Mengsong, Xishuangbanna, SW, China (each point representing a sample; 95% confidence intervals around centroids are shown (ellipses)). The upper two panels show ellipses (colored dashed lines) for exposure time. The lower two panels show ellipses for habitat types. "Initial" in the lower two panels represent the communities at 0 mo before exposure. The statistics presented are the distance based redundancy analysis (db-RDA). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Analysis of factors affecting Bray-Curtis dissimilarity between fungal communities using permutational multivariate analysis PerMANOVA with repeated measurement implemented in adonis for fungal communities found in log of *Litsea cubeba* and *Castanopsis mekongensis* during 36 month of wood decomposition in tropical montane forest, Mengsong, Xishuangbanna, SW, China. DF = Degree of freedom. The initial maximum model included all main factors and all two and three possible interactions and then was simplified to the best model.

Variable	DF	Sums of squares	Mean of sum of squares	F. Model	R^2	Pr (>F)
Time	1	4.690	4.695	11.342	0.027	0.001
Habitat type	2	2.210	1.105	2.669	0.013	0.001
Species	1	4.110	4.113	9.938	0.024	0.001
Termite status	1	1.030	1.033	2.496	0.006	0.422
Time:Habitat type	2	1.110	0.555	1.341	0.007	0.001
Time:Species	1	1.740	1.739	4.202	0.010	0.001
Habitat type: Species	2	1.130	0.565	1.366	0.007	0.009
Time:Termite status	1	0.520	0.524	1.266	0.003	0.017
Habitat type: Termite status	2	1.100	0.550	1.328	0.006	0.011
Species: Termite status	1	0.690	0.693	1.674	0.004	0.001
Residuals	369	152.740	0.414		0.893	
Total	383	171.080			1.000	

relies heavily on patterns found in temperate and boreal ecosystems. Here we explored whether fungal communities in decomposing logs could explain our previously observed wood species identity effects, and lack of habitat effects, on WSG loss over three years in a tropical montane forest in SW China. We investigated successional changes in fungal diversity and composition in decomposing logs of two tree species across a disturbance gradient and their effects on WSG loss. We found that fungal species diversity consistently peaked at 18 mo regardless of wood species and habitat. Fungal species diversity was also significantly influenced by wood species identity, and the peakin fungal species diversity at 18 mo coincided with a peak in the number of unique OTUs in each wood species. Fungal community composition varied significantly with time, wood species, habitat type and termite presence. White rot fungi abundance increased with time, except in open land where they peaked at 18 mo. The abundance of soft rot fungi peaked at 18 mo in regenerating forest for *L. cubeba* and regenerating and mature forest for *C. mekongensis*. The termite effect on WSG loss was mediated by their effect on soft rot fungi. Fungal diversity only explained ~2% of the variance in WSG loss, but abundance of soft rot fungi and saprotrophs explained a larger amount (11%) of the variation in WSG loss.

4.1. Initial wood quality and WSG loss

With strong differences in wood quality and density, we expected pronounced differences in the decomposition rates between species. Indeed, our earlier results revealed that the species differed in their temporal pattern of WSG loss (Dossa et al., 2020). *C. mekongensis* logs had much higher initial WSG, slower initial loss of WSG and consistently lower fungal diversity. We observed that the bark of *L. cubeba* is thinner

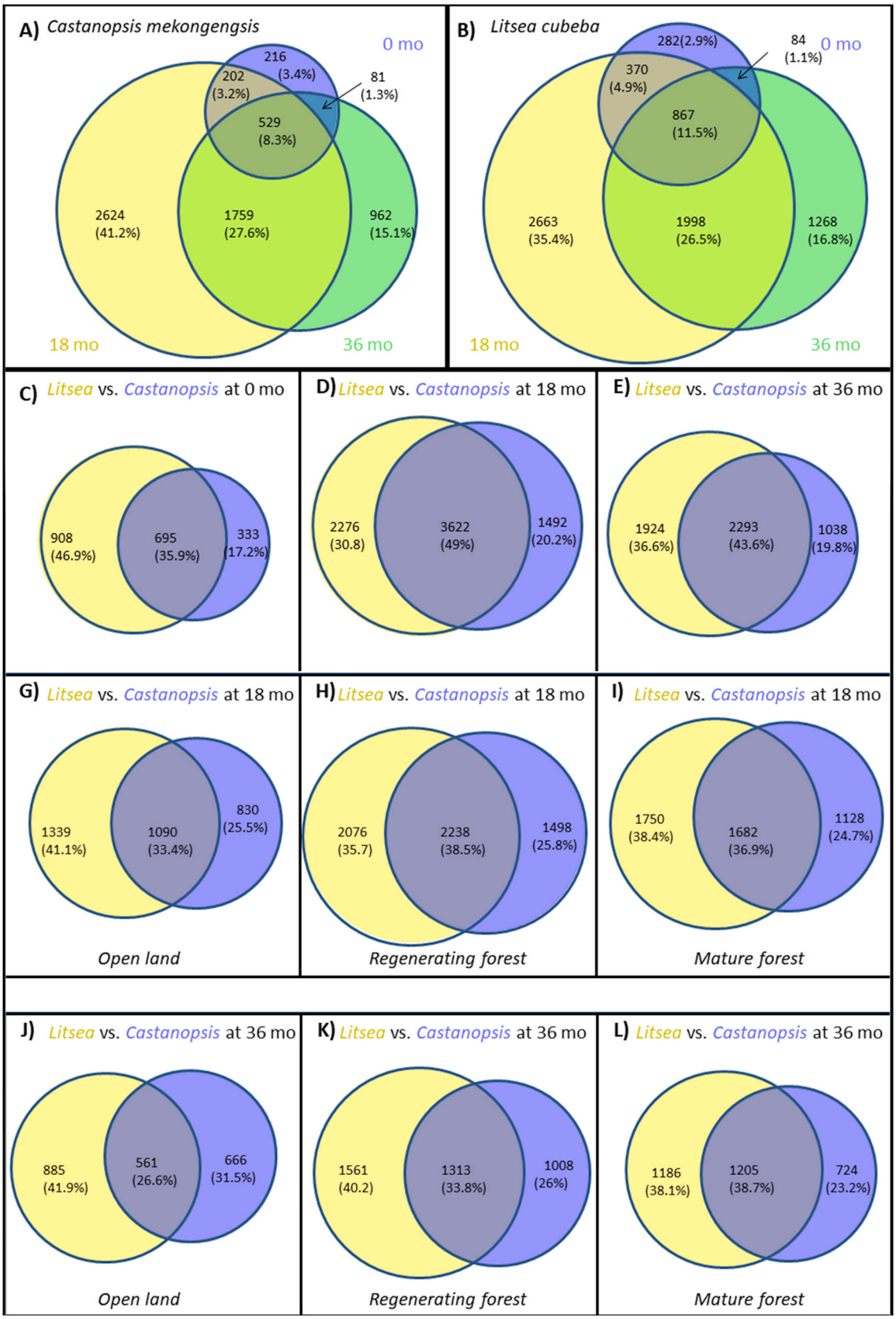

Fig. 7. Venn diagram displaying the temporal dynamics of unique and shared fungal species (OTUs) harbored by logs of A) *Castanopsis mekongensis*, B) *Litsea cubeba*, C) both species at initial time 0 mo, D) both species at 18 mo, E) both species at 36 mo exposure, G-H-I) Litsea cubeba vs. Castanopsis mekongensis at 18 mo in open land, regenerating forest and mature forest, J, K, L) Litsea cubeba vs. Castanopsis mekongensis at 36 mo in open land, regenerating forest and mature forest in tropical montane forest, Mengsong, Xishuangbanna, SW, China.

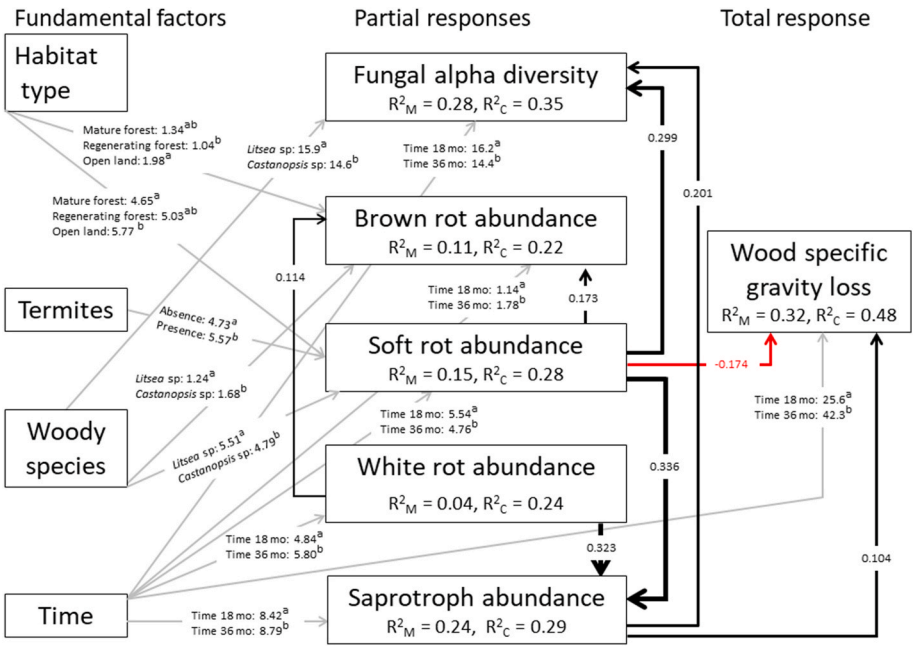

Fig. 8. Structural equation modeling summarizing the direct and indirect effects of time, fungal alpha diversity, woody species, brown-, soft-, and white–rot abundances, saprotroph abundance, termites infestation status and habitat type on wood specific gravity (WSG) loss for logs of *Litsea cubeba* and *Castanopsis mekongensis* exposed for 36 months in tropical montane forest, Mengsong, Xishuangbanna, SW, China. Thickness of the path equates to the strength of path coefficient. Black and red arrows indicate positive and negative paths, respectively. Whereas grey arrows emerge from categorical variables. For clarity we did not include non-significant path standardized coefficients in the diagram (but see Table S15 for full SEM results). Fisher's C = 38.811 with P-value = 0.344 and on 36 degrees of freedom with an AIC = 144.81. For simplicity only main effects of variables were tested. Values emerging from numerical variables represent standardized path coefficients, whereas those from categorical variables represent marginal means. These are accompanied by letters that indicate the marginal means pairwise comparison (different letter indicate a significant effect between the levels). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

and contains more labile sugars and hemicelluloses that are easily accessible to microorganisms, which may explain the more rapid initial WSG loss (Fig. 2) and higher fungal alpha-diversity observed in this species (Dossa et al., 2018). In L. *cubeba* there was rapid growth of fungi which are known to utilize labile carbohydrates (Fig. 2) (Stokland et al., 2012). Consequently, we assumed that bark chemical content affects WSG loss through fungal colonization. However, whether this is a general effect of bark chemistry on fungal diversity in decomposing woody debris will require investigation of more wood species (Lee et al., 2019). The abundance of Basidiomycota and white rot fungi were ~1.3 and ~2 times higher, respectively, in *C. mekongensis* than in *L. cubeba.* This might reflect the higher initial wood density and lignin content of *C. mekongensis*. In *C. mekongensis*, but WSG loss increased over time presumably reflecting the breakdown of recalcitrant substrates and an increasingly amenable environment for fungi that decompose less recalcitrant substrates.

Rates of fungal decomposition were expected to be higher in forest habitats, where ambient moisture is higher. However, our earlier results indicated there was no habitat effect on WSG loss, even though we observed 3 fold difference in the proportions of white rot fungi in mature forest and open land. This would suggest that similarities in WSG loss among habitats may arise from functional redundancy at the landscape scale (Lee et al., 2020).

4.2. Taxonomic and functional classification of fungal community

Over three years monitoring, we expected Ascomycota and Basidiomycota to dominate decomposing fungal communities, which was confirmed with Ascomycetes more abundant than Basidiomycetes. We also observed an increase in the proportion of saprotrophs with time in both species. Similar findings were recently reported in Panama based on aboveground decay (Ferrer et al., 2020; Gora and Lucas, 2019; Jones et al., 2019). Basidiomycota contain the majority of known white rot fungi which are able to degrade both lignin and cellulose, as well as brown rot fungi which modify lignin and degrade cellulose (Stokland et al., 2012). Ascomycota include many soft-rot fungi and play underappreciated roles in early wood decay, utilizing sugars and lignocellulose compounds (Blanchette et al., 2004; van der Wal et al., 2012).

We predicted that white rot fungi would dominate early fungal communities in woody debris and increase with time (Schilling et al., 2015). This expectation was confirmed in regenerating and mature forests but not in open land. The proportion of brown rot and soft rot fungi also increased in *C. mekongensis* in later stages of decay in forest habitats, but not in open land. Presumably, early degradation of lignin by white rot fungi exposed cellulose and sugars for degradation by these other fungi. We acknowledge the lack of fungal DNA sequences for tropical fungi and the lack of knowledge of trophic modes and functions of many fungi. A more complete assignment to functional guilds and rot types could lead to different patterns to those described here. Moreover, future potential assignment of OTUs based on a "grey rot scale" as proposed recently will also help to fill gap in our understanding (Schilling et al., 2020).

On specific fungal taxa that may play roles in woody debris decay, fungal communities were dominated by Sordariomycetes and Dothideomycetes, both large and diverse classes of Ascomycetes found in many different habitats (Ferrer et al., 2020), as well as the Basidiomycetes class Agaricomycetes, which contains a majority of both white rot and brown rot fungi that preferentially degrade lignin and cellulose (Naranjo-Ortiz and Gabald, 2019). In a previous study of early decomposition (11 mo) of five tropical wood species in Panama, abundance of Agaricomycetes increased with time, which was not observed here, but similar to our study, Sordariomycetes decreased over time (Jones et al., 2019). Among Xylariales (Sordariomycetes), many species are endophytes of woody plants, including tropical trees (Bills et al., 2012) and many cause white rot (Stokland et al., 2012). Leotiomycetes, especially members of the family Sclerotiniaceae (Helotiales), genera *Botrytis* and *Pezicula,* were abundant at the initial sampling in our study and decreased through time. These fungi are also endophytes of diverse angiosperms (Mckinnon et al., 2017; Reay et al., 2010). These patterns suggest that these Sordariomycetes and Leotiomycetes taxa may represent endophytic taxa that may not persist in later fungal communities in woody debris. This is in contrast to other studies that have shown a strong priority effect for endophytic taxa or initial hyphal inoculum in dead wood in microcosm studies (Song et al., 2017). It is possible that competitive interactions among later colonizers lead to decrease of initially abundant taxa during succession in wood decay communities (Maynard et al., 2017). It is also possible that some taxa, initially present in low abundance, may increase in abundance in woody debris and contribute substantially to decay over time (Song et al., 2017). In *C. mekongensis*, for example, while Leotiomycetes as a whole increased

over time, specific families (e.g. Sclerotiniaceae (Helotiales)) which were most abundant in initial sampling, decreased over time. The Ascomycetes family Coniochaetaceae (Coniochaetales) which were found in high abundance in the decaying wood of 13 temperate European tree species, were also detected in our study. The abundance of these fungi has been found to correlate with abundance of laccases and different (hemi)cellulolytic enzymes, supporting a role in wood decay (Leonhardt et al., 2019). Ecological and functional traits of these orders of Ascomycetes fungi have not been well characterized, but our study and others suggests they warrant further attention for their role in wood decay in tropical systems (Lustenhouwer et al., 2020).

4.3. Fungal alpha diversity

We predicted that fungal diversity would peak during the course of decomposition and we observed a peak of diversity at 18 mo. In addition to time, we found that wood species identity, and termite infestation were the main determinants of fungal alpha diversity. L. cubeba had higher wood C:N ratio and consistently higher fungal diversity through time. Our result corroborates recent findings in a subtropical forest in China, where Kahl and colleagues monitored the decomposition of *Pinus* sp. and *Schima* sp. over 2 years found that *Pinus* sp., which had higher C:N ratio harbored higher fungal diversity than *Schima* sp. (Kahl et al., 2017; Purahong et al., 2017). A previous study in Australia also reported high fungal diversity on woody debris with low density and thin bark (Lee et al., 2019).

Previous studies have reported both negative (Purahong et al., 2017) and positive relationships (Mäkipää et al., 2017; Rajala et al., 2015; van Der Wal et al., 2015) between fungal alpha diversity and exposure time, but they focused on early stages of decay (less than 2 years). Comparing these studies to ours, one should also consider the different decomposition rates in temperate *vs.* tropical environments. In early wood decomposition (18 mo in tropical ecosystems and up to 36 mo elsewhere), fungal diversity increases through time. However, after 18 mo, we observed a decrease in fungal diversity. This suggests dynamic shifts in diversity, composition, and interactions among fungi through time, depending on various factors including wood properties. The first phase may reflect colonization, when woody debris is still relatively rich in easily decomposable components, with weak competitive interactions (van Der Wal et al., 2015) and with fungi having fast hyphal extension rates (Lustenhouwer et al., 2020). In contrast, the next phase may reflect exhaustion of easily decomposable components and increasingly competitive fungal interactions. Indeed, the sharp increase in numbers of unique species (Fig. 6) up to 18 mo may be explained by colonization of newly available resources. Increasing competition through time for remaining resources may have led to a decline of fungal richness from 18 mo to 36 mo. Moreover, the increase in the abundance of white rot fungi up to 36 mo may indicate use of recalcitrant lignin, thereby exposing cellulose and hemicellulose which become available to brown and soft rot fungi (Schilling et al., 2015).

4.4. Fungal community structure

Fungal composition should change through time because both available carbon substrates (van Der Wal et al., 2015) as well as competitive interactions between fungi (Hiscox and Boddy, 2017; Maynard et al., 2017) change throughout wood decay. We found that fungal community composition at 0, 18 and 36 mo overlapped considerably, suggesting priority effects were important (Hiscox et al., 2015; Song et al., 2017). According to our PerMANOVA analysis exposure time, woody debris species, termite presence, and habitat significantly affected fungal community composition (Fig. 6, Table 3). Earlier studies from temperate forest also reported an effect of woody debris species (Lee et al., 2020).

Microclimates of different habitats may not only affect which species of fungi colonize woody debris, but also may dictate the outcome of fungal interactions. Our model explained ~11% of the variance in fungal composition. Much of the variance in composition may be stochastic, such as dispersal-colonization, which is supported by variance in composition increasing through time (Fig. 4). Recent findings from temperate forests on 21 wood species showed that wood species identity *via* its construction and initial chemical content is a more important determinant of fungal community composition than habitat (Lee et al., 2020). They found that wood characteristics explain as much as 11% of variation among fungal communities after 12 months exposure but this decreased to 4% after 5 years. Concerning termites driving changes in fungal communities, recent studies also reported similar finding. Termites can indirectly alter wood decomposition through changes in fungal composition (Cheesman et al., 2018; Ulyshen et al., 2016). Termites may aid in dispersal-colonization for fungi by introducing fungal spores specific microclimates within the woody debris.

4.5. Overall view from structural equation modeling

Our structural equation modeling (SEM) extended the results from linear mixed effects modeling. Notably the SEM showed that the effects of wood species identity and termites on WSG loss were mediated by the abundance of soft rot fungi. We also found that soft rot fungi and white rot abundances led to an increase of saprotroph abundance. The negative effect of soft rot fungi abundance on WSG loss may arise from a shift in function or it could arise from increased competition for resources (Maynard et al., 2017), as the diversity of fungi was correlated with soft rot abundance.

In conclusion, we showed that: (1) the strong wood species effect observed on wood decay rates may be due to both differences in the wood properties that result in differences in fungal communities (Lee et al., 2020), (2) the lack of a difference in decay rates observed across the disturbance gradient probably resulted from functional redundancy at the landscape scale due to the dissimilarities in fungal community composition among habitats, and (3) decay rates change with time which likely reflects changing substrate quality and fungal community composition. Future studies should investigate the roles of fungal functional traits and rot types, particularly those of Ascomycete fungi whose functional traits and roles in wood decay are still poorly characterized (Lee et al., 2020), as well as effects of bark traits on dynamics of fungal decomposers over time.

Ethics approval and consent to participate

Not applicable.

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Authors' contributions

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 field data; Y.Q.Y., W.H., and K.E.B. Conducted DNA extraction and molecular analyses; W. M. and KEB conducted bioinformatics analyses; G.G.O.D., W.H., K.E.B.,

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.

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 data

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References

Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecological Monographs 83, 557–574. https://doi.org/10.1890/12-2010.1.

Bartlett, M.S., 1937. Properties of sufficiency and statistical tests. Proceedings of the Royal Society A: Mathematical, Physical & Engineering Sciences 113–126. https://doi.org/10.1007/978-1-4612-0919-5_8.

Bills, G.F., Gonzalez-Menendez, V., Martin, J., Platas, G., Fournier, J., Persoh, D., Stadler, M., 2012. Hypoxylon pulicicidum sp. nov. (Ascomycota, Xylariales), a pantropical insecticide-producing endophyte. PloS One 7, e46687. https://doi.org/10.1371/journal.pone.0046687.

Blanchette, R.A., Held, B.W., Jurgens, J.A., Mcnew, D.L., Harrington, T.C., Duncan, S.M., Farrell, R.L., 2004. Wood-destroying soft rot fungi in the historic expedition huts of Antarctica. Applied and Environmental Microbiology 70, 1328–1335. https://doi.org/10.1128/AEM.70.3.1328.

Caporaso, J.G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F.D., Costello, E.K., Fierer, N., Peña, A.G., Goodrich, J.K., Gordon, J.I., Huttley, G. a, Kelley, S.T., Knights, D., Koenig, J.E., Ley, R.E., Lozupone, C. a, Mcdonald, D., Muegge, B.D., Pirrung, M., Reeder, J., Sevinsky, J.R., Turnbaugh, P.J., Walters, W. a, Widmann, J., Yatsunenko, T., Zaneveld, J., Knight, R., 2010. Correspondence QIIME allows analysis of high- throughput community sequencing data Intensity normalization improves color calling in SOLiD sequencing. Nature Publishing Group 7, 335–336. https://doi.org/10.1038/nmeth0510-335.

Chao, A., 1984. Nonparametric estimation of the number of classes in a population author. Scanadinavian Journal of Statistics 11, 265–270. https://doi.org/10.1214/aoms/1177729949.

Cheesman, A.W., Cernusak, L.A., Zanne, A.E., 2018. Relative roles of termites and saprotrophic microbes as drivers of wood decay: a wood block test. Austral Ecology 43, 257–267. https://doi.org/10.1111/aec.12561.

Dossa, G.G.O., Paudel, E., Cao, K., Schaefer, D., Harrison, R.D., 2016. Factors controlling bark decomposition and its role in wood decomposition in five tropical tree species. Scientific Reports 6, 34153. https://doi.org/10.1038/srep34153.

Dossa, G.G.O., Paudel, E., Schaefer, D., Zhang, J., Cao, K.-F., Xu, J.-C., Harrison, R.D., 2020. Quantifying the factors affecting wood decomposition across a tropical forest disturbance gradient. Forest Ecology and Management 468.

Dossa, G.G.O., Schaefer, D., Zhang, J.-L., Tao, J.-P., Cao, K.-F., Corlett, R.T., Cunningham, A.B., Xu, J.-C., Cornelissen, J.H.C., Harrison, R.D., 2018. The cover uncovered: bark control over wood decomposition. Journal of Ecology 106, 2147–2160. https://doi.org/10.1111/1365-2745.12976.

Edgar, R.C., Flyvbjerg, H., 2015. Error filtering, pair assembly and error correction for next-generation sequencing reads. Bioinformatics 31, 3476–3482. https://doi.org/10.1093/bioinformatics/btv401.

Edgar, R.C., Haas, B.J., Clemente, J.C., Quince, C., Knight, R., 2011. UCHIME improves sensitivity and speed of chimera detection. Bioinformatics 27, 2194–2200. https://doi.org/10.1093/bioinformatics/btr381.

Ferrer, A., Heath, K.D., Canam, T., Flores, H.D., Dalling, J.W., 2020. Conribution of fungal and invertebrate communities to wood decay in tropical terrestrial and aquatic habitats. Ecology. https://doi.org/10.1093/acprof:oso/9780199575299.003.0003.

Fukami, T., Dickie, I.A., Paula Wilkie, J., Paulus, B.C., Park, D., Roberts, A., Buchanan, P. K., Allen, R.B., 2010. Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecology Letters 13, 675–684. https://doi.org/10.1111/j.1461-0248.2010.01465.x.

Gohl, D.M., Vangay, P., Garbe, J., MacLean, A., Hauge, A., Becker, A., Gould, T.J., Clayton, J.B., Johnson, T.J., Hunter, R., Knights, D., Beckman, K.B., 2016. Systematic improvement of amplicon marker gene methods for increased accuracy in microbiome studies. Nature Biotechnology 34, 942–948. https://doi.org/10.1038/nbt.3601.

Gora, E.M., Lucas, J.M., 2019. Dispersal and nutrient limitations of decomposition above the forest floor: evidence from experimental manipulations of epiphytes and macronutrients. Functional Ecology 33, 2417–2429. https://doi.org/10.1111/1365-2435.13440.

Hagge, J., Bassler, C., Gruppe, A., Hoppe, B., Kellner, H., Krah, F., Müller, J., Seibold, S., Stengel, E., Thorn, S., 2019. Bark coverage shifts assembly processes of microbial decomposer communities in dead wood. Proceedings of the Royal Society B: Biological Sciences 286.

Halme, P., Ódor, P., Christensen, M., Piltaver, A., Veerkamp, M., Walleyn, R., Siller, I., Heilmann-Clausen, J., 2013. The effects of habitat degradation on metacommunity structure of wood-inhabiting fungi in European beech forests. Biological Conservation 168, 24–30. https://doi.org/10.1016/j.biocon.2013.08.034.

Hiscox, J., Boddy, L., 2017. Armed and dangerous – chemical warfare in wood decay communities. Fungal Biology Reviews 31, 169–184. https://doi.org/10.1016/j.fbr.2017.07.001.

Hiscox, J., Savoury, M., Müller, C.T., Lindahl, B.D., Rogers, H.J., Boddy, L., 2015. Priority effects during fungal community establishment in beech wood. The ISME Journal 1–15. https://doi.org/10.1038/ismej.2015.38.

Hu, W., Strom, N., Haarith, D., Chen, S., Bushley, K.E., 2018. Mycobiome of cysts of the soybean cyst nematode under long term crop rotation. Frontiers in Microbiology 9. https://doi.org/10.3389/fmicb.2018.00386. Article 386.

Ives, A.R., 2015. For testing the significance of regression coefficients, go ahead and log-transform count data. Methods in Ecology and Evolution 6, 828–835. https://doi.org/10.1111/2041-210X.12386.

Jones, J.M., Heath, K.D., Ferrer, A., Brown, S.P., Canam, T., James, W., 2019. Wood decomposition in aquatic and terrestrial ecosystems in the tropics: contrasting biotic and abiotic processes. FEMS Microbiology Ecology 95, fiy223.

Jones, J.M., Heath, K.D., Ferrer, A., Dalling, J.W., 2020. Habitat-specific effects of bark on wood decomposition: influences of fragmentation, nitrogen concentration and microbial community composition. Functional Ecology 34, 1123–1133. https://doi.org/10.1111/1365-2435.13547.

Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., Buscot, F., Floren, A., Heibl, C., Hessenmöller, D., Hofrichter, M., Hoppe, B., Kellner, H., Krüger, D., Linsenmair, K.E., Matzner, E., Otto, P., Purahong, W., Seilwinder, C., Schulze, E.D., Wende, B., Weisser, W.W., Gossner, M.M., 2017. Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. Forest Ecology and Management 391, 86–95. https://doi.org/10.1016/j.foreco.2017.02.012.

Koljalg, U., Nilsson, R.H., Abarenkov, K., Tedersoo, L., Taylor, A.F.S., Bahram, M., 2014. Towards a unified paradigm for sequence-based identification of fungi. Molecular Ecology 22, 5271–5277. https://doi.org/10.1111/mec.12481.

Krah, F.-S., Seibold, S., Brandl, R., Baldrian, P., Muller, J., Bassler, C., 2018. Independenteffects of host and environment on the diversity of wood-inhabiting fungi. Journal of Ecology 106. https://doi.org/10.1111/ijlh.12426.

Lee, M., Oberle, B., Olivas, W., Young, D.F., Zanne, A.E., 2020. Wood construction more strongly shapes deadwood microbial communities than spatial location over five years of decay. Environmental Microbiology. https://doi.org/10.1111/1462-2920.15212.

Lee, M.R., Powell, J.R., Oberle, B., Cornwell, W.K., Lyons, M., Rigg, J.L., Zanne, A.E., 2019. Good neighbors aplenty: fungal endophytes rarely exhibit competitive exclusion patterns across a span of woody habitats. Ecology. https://doi.org/10.1002/ecy.2790.

Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution 7, 573–579. https://doi.org/10.1111/2041-210X.12512.

Lenth, R., Love, J., Herve, M., 2020. Estimated Marginal Means, Aka Least-Squares Means. Package ' Emmeans ' Version 1.1.2 for R. License. https://doi.org/10.1080/00031305.1980.10483031>.

Leonhardt, S., Hoppe, B., Stengel, E., Noll, L., Moll, J., Bassler, C., Dahl, A., Buscot, F., Hofrichter, M., Kellner, H., 2019. Molecular fungal community and its decomposition activity in sapwood and heartwood of 13 temperate European tree species. PloS One e0212120, 1–21.

Lustenhouwer, N., Maynard, D.S., Bradford, M.A., Lindner, D.L., Oberle, B., 2020. A trait-based understanding of wood decomposition by fungi. Proceedings of the National Academy of Sciences 117, 11551–11558. https://doi.org/10.1073/pnas.1909166117.

Maillard, F., Andrews, E., Moran, M., Kennedy, P.G., Van Bloem, S.J., Schilling, J.S., 2020. Stem-inhabiting fungal communities differ between intact and snapped trees after hurricane Maria in a Puerto Rican tropical dry forest. Forest Ecology and Management 475, 118350. https://doi.org/10.1016/j.foreco.2020.118350.

Mäkipää, R., Rajala, T., Schigel, D., Rinne, K.T., Pennanen, T., Abrego, N., Ovaskainen, O., 2017. Interactions between soil- and dead wood-inhabiting fungal communities during the decay of Norway spruce logs. The ISME Journal 11, 1964–1974. https://doi.org/10.1038/ismej.2017.57.

Maynard, D.S., Crowther, T.W., Bradford, M.A., 2017. Competitive network determines the direction of the diversity – function relationship. Proceedings of the National Academy of Sciences 114, 11464–11469. https://doi.org/10.1073/pnas.1712211114.

Mckinnon, A.C., Saari, S., Nicolai, M.E.M., Meyling, N.V., Raad, M., Glare, T.R., 2017. Beauveria bassiana as an endophyte : a critical review on associated methodology and biocontrol potential. Biological Control 62, 1–17. https://doi.org/10.1007/s10526-016-9769-5.

Naranjo-Ortiz, M.A., Gabald, T., 2019. Fungal evolution : diversity , taxonomy and phylogeny of the Fungi. Biological Reviews 94, 2101–2137. https://doi.org/10.1111/brv.12550.

Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecology 20, 241–248. https://doi.org/10.1016/j.funeco.2015.06.006.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2018. Vegan: Community Ecology Package. R Package.

Paudel, E., Dossa, G.G.O., Blécourt, M. de, Beckschäfer, P., Xu, J., Harrison, R.D., de Blécourt, Marleen, Beckschafer, P., Xu, J., Harrison, R.D., 2015. Quantifying the factors affecting leaf litter decomposition across a tropical forest disturbance gradient. Ecosphere 6, 267.

Pinheiro, J., Bates, D., Debroy, S., Sarkar, D., Team, R.D.C., 2013. Nlme: linear and nonlinear mixed effects models. R package version 3, 1–101.

Purahong, W., Pietsch, K.A., Lentendu, G., Schöps, R., 2017. Characterization of unexplored deadwood mycobiome in highly diverse subtropical forests using culture-independent molecular technique. Frontiers in Microbiology 8, 574. https://doi.org/10.3389/fmicb.2017.00574.

R Foundation for Statistical Computing, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Rajala, T., Tuomivirta, T., Pennanen, T., Makipaa, R., 2015. Habitat models of wood-inhabiting fungi along a decay gradient of Norway spruce logs. Fungal Ecology 18, 48–55. https://doi.org/10.1016/j.funeco.2015.08.007.

Reay, S.D., Brownbridge, M., Gicquel, B., Cummings, N.J., Nelson, T.L., 2010. Isolation and characterization of endophytic Beauveria spp . (Ascomycota : Hypocreales) from Pinus radiata in New Zealand forests. Biological Control 54, 52–60. https://doi.org/10.1016/j.biocontrol.2010.03.002.

Schilling, J.S., Ayres, A., Kaffenberger, J.T., Powers, J.S., 2015. Initial white rot type dominance of wood decomposition and its functional consequences in a regenerating tropical dry forest. Soil Biology and Biochemistry 88, 58–68. https://doi.org/10.1016/j.soilbio.2015.05.002.

Schilling, J.S., Kaffenberger, J.T., Held, B.W., Ortiz, R., Blanchette, R.A., Waring, B.G., 2020. Using wood rot phenotypes to illuminate the " gray " among decomposer fungi. Frontiers in Microbiology 11, 1–12. https://doi.org/10.3389/fmicb.2020.01288.

Schloss, P.D., Westcott, S.L., Ryabin, T., Hall, J.R., Hartmann, M., Hollister, E.B., Lesniewski, R.A., Oakley, B.B., Parks, D.H., Robinson, C.J., Sahl, J.W., Stres, B., Thallinger, G.G., Van Horn, D.J., Weber, C.F., 2009. Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. Applied and Environmental Microbiology 75, 7537–7541. https://doi.org/10.1128/AEM.01541-09.

Song, Z., Kennedy, P.G., Liew, F.J., Schilling, J.S., 2017. Fungal endophytes as priority colonizers initiating wood decomposition. Functional Ecology 31, 407–418. https://doi.org/10.1111/1365-2435.12735.

Stier, A.C., Geange, S.W., Hanson, K.M., Bolker, B.M., 2013. Predator density and timing of arrival affect reef fish community assembly. Ecology 94, 1057–1068. https://doi.org/10.1890/11-1983.1.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Dead Wood. Cambridge, UK.

Tomao, A., Antonio Bonet, J., Castaño, C., de-Miguel, S., 2020. How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi. Forest Ecology and Management 457, 117678. https://doi.org/10.1016/j.foreco.2019.117678.

Ulyshen, M.D., Diehl, S.V., Jeremic, D., 2016. Termites and flooding affect microbial communities in decomposing wood. International Biodeterioration & Biodegradation 115, 83–89. https://doi.org/10.1016/j.ibiod.2016.07.017.

van der Wal, A., Geydan, T.D., Kuyper, T.W., de Boer, W., 2012. A thready affair: linking fungal diversity and community dynamics to terrestrial decomposition processes. FEMS Microbiology Reviews 1–18. https://doi.org/10.1111/1574-6976.12001.

van Der Wal, A., Ottosson, E., De Boer, W., 2015. Neglected role of fungal community composition in explaining variation in wood decay rates. Ecology 96, 124–133. https://doi.org/10.1890/14-0242.1.

Williamson, G.B., Wiemann, M.C., 2010. Measuring wood specific gravity…Correctly. American Journal of Botany 97, 519–524. https://doi.org/10.3732/ajb.0900243.

Xu, J., Lebel, L., Sturgeon, J., 2009. Functional links between biodiversity, livelihoods, and culture in a Hani swidden landscape in southwest China. Ecology and Society 14, 20.

Yang, Chunyan, Schaefer, D.A., Liu, W., Popescu, V.D., Yang, Chenxue, Wang, X., Wu, C., Yu, D.W., 2016. Higher fungal diversity is correlated with lower CO 2 emissions from dead wood in a natural forest. Scientific Reports 6, 1–10. https://doi.org/10.1038/srep31066.

Zhu, H., Yong, C., Zhou, S., Wang, H., Yan, L., 2015. Vegetation , floristic composition and species diversity in a tropical mountain nature reserve in southern Yunnan , SW China , with implications for conservation. Tropical Conservation Science 8, 528–546.