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REGULAR ARTICLE

Early chemical changes during wood decomposition are controlled by fungal communities inhabiting stems at treefall in a tropical dry forest

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Abstract
Purpose A better knowledge of how deadwood decomposes is critical for accurately characterizing carbon and nutrient cycling in forests. Fungi dominate this decomposition process, but we still have limited understanding of fungal community structuring that ultimately controls the fate of wood decomposition. This is particularly true in tropical ecosystems. To address this knowledge gap, our study capitalized on an extreme storm event that caused a large and synchronized input of deadwood to the forest floor.
Methods Here we report data for the first year of wood decomposition of trees in a Puerto Rican dry forest for nine tree species that were snapped by Hurricane Maria in 2017. We measured wood properties and the associated fungal communities after 12 months of decomposition and compared them with initial wood properties and stem-inhabiting fungal communities to identify the best predictors of wood decomposition rates and chemical changes.
Results Changes in wood chemistry were primarily explained by rapid xylan losses, the main hemicellulose component for the studied tree species. Fungal communities were dominated by saprotrophic and plant pathogenic fungi and showed moderate changes over time. The initial relative abundances and ratios of different fungal functional guilds were significant predictors of both xylan and glucan losses, with plant pathogenic fungi accelerating cellulose and hemicellulose decomposition rates compared to saprotrophs.
Conclusion Our results confirm that fungi present at the time of treefall are strong drivers of wood decomposition and suggest that plant pathogenic fungi might act as efficient early decomposers of hemicellulose in dry tropical forests.

Keywords Wood-inhabiting fungi · Fungal functional guild · Trunk pathogenic fungi, wood chemistry · Decay type

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Introduction

Deadwood plays many critical roles in forests (Harmon et al. 1986). Coarse woody debris represent a key reservoir of diversity for fauna (Skelton et al. 2019), bacteria (Johnston et al. 2016), and fungi (Hoppe et al. 2016), as well as an important regeneration niche for plant germination (Harmon and Franklin 1989). Deadwood also significantly influences forest biogeochemical cycles (Chambers et al. 2000), with nutrients liberated from decomposing wood contributing to soil fertility and forest productivity (Baldrian and Lindahl 2011). Additionally, coarse woody debris constitutes one of the primary carbon (C) pools (Magnússon et al. 2016) that could become impacted by climate change (Davidson and Janssens 2006).

In tropical forests, where deadwood represents up to 20% of the total aboveground and belowground C (Murphy and Lugo 1986a; Oswalt et al. 2008; Pan et al. 2011), hurricanes can drastically increase deadwood stocks (Harmon et al. 1995). Despite the relative regularity of these disturbances, the impact of hurricanes on forest C cycling remains unresolved (Lugo 2008). Lugo (2008) proposed that the maintenance of tropical forests as C sinks after hurricane events depends on the decomposition rates of new organic matter and aboveground biomass recovery speed. Consequently, understanding the dynamics of deadwood decomposition in hurricane-prone tropical forests is critical to predicting ecosystem C cycling and adapting post-hurricane forest management practices.

Fungi are central actors in wood decomposition (Van der Wal et al. 2014) and degrade wood using different mechanisms (Riley et al. 2014). White rot fungi cause a final substantial removal of wood carbohydrates (both hemicellulose and cellulose) in parallel with lignin (Eriksson et al. 1990). Conversely, brown and soft rot fungi selectively degrade carbohydrates with predictably less lignin removal than white rot fungi (Eslyn et al. 1975; Riley et al. 2014; Schilling et al. 2020). These different wood decomposition mechanisms may drive major differences in the forest nutrient and C cycles. In particular, brown and soft rot decay types might increase forest C stocks by generating recalcitrant particulate lignin (Stutz et al. 2017). By contrast, the white rot decay type may increase nutrient availability due to the complex cascading effects of lignin depolymerization (del Cerro et al. 2021; Stutz et al. 2019).

High-throughput sequencing (HTS) technologies have improved the characterization of in situ fungal communities associated with wood decomposition (Hoppe et al. 2016; Mäkipää et al. 2017; Purahong et al. 2014, 2018a, b; Rajala et al. 2012). Wood-inhabiting fungal communities were revealed to be more diverse and specialized than initially suspected from sporocarp inventories and culture-based studies (Leonhardt et al. 2019; Purahong et al. 2018a, b). Recent HTS-based results have primarily focused on characterizing wood-inhabiting fungal communities in boreal and temperate forests, and similar efforts in tropical forests remain limited (Purahong et al. 2017). By characterizing chemical decomposition signatures in wood, however, Schilling et al. (2015a) was able to show that white rot fungi were mainly responsible for decay of eight tree species in a tropical dry forest in Costa Rica. In line with these results, Maillard et al. (2020) found a very high relative abundance of *Schizophyllum,* a white-rot fungal genus inhabiting tree stems and potentially acting as a latent saprotroph in a Puerto Rican dry forest.

There is growing recognition that fungi belonging to the saprotrophic functional guild can inhabit the stems of living trees without causing apparent damage (Boddy et al. 1989; Parfitt et al. 2010). These fungal pre-colonizers can initiate wood decomposition and defend their territory, in some cases by creating visible pseudosclerotial plates (spalting) soon after tree death (Hiscox et al. 2015; Pearce 1990). The early presence of these latent saprotrophs often modifies the interaction outcomes with secondary fungal colonizers, directly or indirectly, through the modification of wood properties (Cline et al. 2018; Song et al. 2015). Recent studies of stem-associated fungal communities in tropical trees have shown a co-dominance of two main functional guilds; plant pathogenic fungi and saprotrophic fungi (Maillard et al. 2020; Sadeghi et al. 2019; Skaltsas et al. 2019; Singh et al. 2017). Tree species may be predisposed to faster decay rates after death if their endophytic fungal communities have higher proportions of saprotroph pre-colonizers compared to plant pathogens (Hiscox et al. 2015). It is usually hypothesized that tree species presenting a close phylogenetic proximity would harbor more similar wood-inhabiting fungal communities by comparison with phylogenetically distant tree species (Lee et al. 2019). However, how tree species identity affects the wood-associated fungal communities has been poorly studied in tropical forests, with research usually being done on a limited number of tree species and yielding inconsistent results (Jones et al. 2018; Purahong et al. 2017).

In this study, we assessed the early dynamics of wood decomposition for nine tree species located in a tropical dry forest in Puerto Rico. Trees were snapped by Hurricane Maria in 2017, which caused widespread forest damage (Hu and Smith 2018; Uriarte et al. 2019). Quickly after this disturbance, we collected snapped stems and sampled them for initial fungal community composition (using high-throughput DNA metabarcoding of the ITS2 fungal marker) and wood chemistry (density, lignin and carbohydrate contents). The remaining stem sections were left to decompose for one year in the Guánica Commonwealth Forest and Biosphere Reserve and then re-evaluated with the same measures. We tested the following hypotheses: H1) Increasing tree phylogenetic distance will be positively correlated with greater dissimilarity in wood chemistry and fungal community composition; H2) The effect of tree species identity on fungal community composition will decrease with time; H3) Lignin loss rates will indicate white rot-dominant decay after one year of incubation; H4) Tree species with initial stem-inhabiting fungal communities enriched with saprotrophic fungi will present faster decay relative to tree species having fungal communities enriched with plant pathogenic fungi.

Materials and methods

Experimental site

The Guánica Forest and Biosphere Reserve is located in southwestern Puerto Rico (18°N 66°55'W). The central part of the reserve is a mature tropical dry forest that has been protected from extensive cutting since at least 1919 (Murphy and Lugo 1986b). The forest boundaries were expanded in 1948, adding stands that were previously farmed or housing and are currently dominated by secondary forests with some stands dominated by non-native species including *Leucaena leucocephala* (Colón and Lugo 2006; Lugo et al. 1996). Thus minimum stand ages range from 60 to 130 years. From 1931 to 2018, annual rainfall averaged 824 mm, annual temperatures averaged 25.1 °C, and potential evapotranspiration averaged >1200 mm (Murphy and Lugo 1986b; Wolfe et al. 2019). Typically, rainfall is bimodally distributed into spring and fall wet seasons, but specific timing and amount of rains are highly variable. Soils are classified mollisols developed from limestone parent material, with pH >7.5 and low available P (Murphy and Lugo 1986b). The dry conditions with low soil fertility result in slow tree growth, with average diameter increases being <1 mm per year (Van Bloem, unpublished data). Many species have dense wood (0.8–1.2 g cm^3) but a few species do have relatively light wood (<0.4) (Colón and Lugo 2006). Hurricane Maria battered the forest with 105 km per hour winds (Category 1) on September 20, 2017. The previous hurricane to affect the forest was Hurricane Georges in 1998, with 180 km per hour winds (Van Bloem et al. 2005).

Sampling

Fallen trees were sampled along roads and trails in Guánica Forest approximately one month after Hurricane Maria (when research access was first permitted). Stem sections were cut from snapped trees with a chainsaw. Sections were 1–1.5 m in length and included the snap point. We selected stems with diameters ranging from 2.5–15 cm, a diameter range which comprises > 99% of the trees in the forest (Murphy and Lugo 1986b). We targeted nine tree species representing frequently snapped stems: *Bucida buceras*, *Bursera simaruba*, *Coccoloba diversifolia*, *Colubrina arborescens*, *Gymnanthes lucida*, *Leucaena leucocephala*, *Pisonia albida*, *Pithecellobium unguis-cati* and *Swietenia mahogany* (see Table 1 for the number of samples for each tree species). The tree species represent a gradient in wood density and are among the most abundant in the forest. Wood discs of ~2 cm thickness were cut from stem sections, either at the mid-sections of boles or at the first knot-free section to yield intact discs near the site of snap. Wood discs were frozen immediately at −20 °C after sampling, shipped overnight to Minnesota with freezer packs and without noticeable thaw, and then stored frozen until analyses. These disc samples represent the year 0 treatment (i.e.,time zero or initial). The remaining sections of the stems were then placed at a single location near a long-term research plot in mature dry forest, far enough from roads to minimize edge or forest fragmentation effects. Stem sections were placed on the ground approximately 1 m apart in east-west orientation on either side of a 50 m transect. All sections were left to decay for one year, after which discs ca. 3 cm thick were cut from the butt ends, after first cutting a 'face' disc of approximately 4 cm thickness and discarding. This confines the dynamics to within the wood rather than having any end grain (where decay will be more advanced). The disc samples, which represent the year one treatment, were frozen, shipped overnight with freezer packs to Minnesota, and frozen at −80 °C before DNA extraction and sequencing.

Fungal community analyses

Shavings from each frozen wood disc were collected from three spots randomly chosen using an autoclave-sterilized drill bit. Total genomic DNA was extracted from the wood shavings for each sample with the DNEasy Powerlyzer PowerSoil Kit (Qiagen, Hilden, Germany) following manufacturer's instructions. Prior to the first step in the protocol, all samples were bead-beat for 15 s (BioSpec Products, Bartlesville, OK, USA) to facilitate homogenization. Fungal DNA was amplified for high throughput sequencing using a two-step PCR process. For the first PCR, the ITS 5.8-Fun (5′-AACTTTYRRCAAYGGATCWCT-3′) and ITS4-Fun (5′-AGCCTCCGCTTATTGATATGCTTAART-3′) primer pair (Taylor et al. 2016), which targets the ITS2 region, was used. Samples, including a synthetic mock community (Palmer et al. 2017) and negative controls, were amplified in individual 20 μl reactions containing 10 ul of Phusion Hot Start II High-Fidelity PCR Master Mix (Thermo Scientific, Waltham, MA, USA), 0.5 ul of each 20 mM primer, 1 μl of DNA template and 8 μl of PCR-grade water. Thermocycling conditions were as follows: 1. 98 °C for 30 s, 2. 98 °C for 10 s, 3. 55 °C for 30 s, 4. 72 °C for 30 s, repeat steps 2–4 34 times, 5. 72 °C for 10 min and 6. infinite hold at 4 °C. For the second PCR, a second set of forward and reverse primers with unique Golay barcodes and Illumina adaptors were used. Reaction and thermocycling conditions were identical to the first PCR. Following the second PCR, all samples were cleaned and normalized using the Charm Just-A-Plate kit (Charm, San Diego, CA, USA) following manufacturer's instructions. Samples were then quantified on a Qubit fluorimeter (Thermo Scientific, Waltham, MA, USA), mixed at an equimolar concentration (3 nM) into a single sequencing library, and sequenced using Illumina MiSeq 2 × 300 bp v3 chemistry at the University of Minnesota Genomics Center.

The raw demultiplexed .fastq files were processed using the AMPtk pipeline outlined in Palmer et al. (2017). Briefly, primers were removed and sequences trimmed to 250 bp. Sequences were then denoised using UNOISE3 (Edgar 2016) and clustered into operational taxonomic units (OTUs) at 97% similarity. Read counts in the OTU x sample matrix were adjusted by accounting for index bleed present in the synthetic mock community. Taxonomy was assigned using a hybrid algorithm that integrates results from a USEARCH global alignment against the UNITE database (v8, Nilsson et al. 2018) and both UTAX and SINTAX classifiers. Sequence read counts of any OTUs present in PCR and DNA controls were summed and then subtracted from counts of those same OTUs in all samples.

Based on the assigned taxonomy, fungal OTUs were assigned to saprotrophic, pathogenic, and symbiotrophic trophic modes using FUNGuild (Nguyen et al. 2016). Saprotrophic fungi were further parsed between soft rot and white rot fungi, with the remaining OTUs were classified as other saprotroph (no brown rot fungi were detected). Pathogenic fungi were parsed between plant pathogen and animal pathogen fungi. All the OTUs without FUNGuild assignment were manually blasted against the NCBI database. If additional taxonomic identification was found, this was passed through FUNGuild to reassign the OTUs to the corresponding functional guild.

Wood property analyses

Using one cut half (through the pith) of each disc, wood density (g cm^{-3}) was measured at fresh volume (cm^3) using water displacement, followed by oven drying for 48 h at 103 °C and weighing (g). The dried half was then ground to a powder through 20-mesh in a Wiley mill. Wood lignin was measured as the acid-insoluble (Klason) fraction using the standard gravimetric ASTM procedure (2001), and those values, as well as the carbohydrate values below, were adjusted by multiplying by density fraction remaining after decay to reflect component loss per original content. The 72% sulfuric acid-dissolved hydrolysate was then analyzed via high-performance liquid chromatography (HPLC) for carbohydrates (glucose, xylose, arabinose, galactose and mannose acid-dissolved monomer) as in Schilling et al. (2015a) for xylan-rich angiosperm woods.

Data analyses

Statistical analyses and data visualizations were performed using R (R Core Team 2016) and considered significant at $P \le 0.05$. To account for variation in total

Table 1 The number of replicates for the nine studies tree species depending on the treatment (year zero and year one) and the mean diameter (±S.D.) of the logs

Genus species	Code	Plant family	Number of samples: year 0	Number of samples: year 1	Average stem diameter (cm)
Bucida buceras	Bub	Combretaceae	5	5	12.05 (4.45)
Bursera simaruba	Bus	Burseraceae	5	5	8.67 (4.15)
Coccoloba diversifolia	Cod	Polygonaceae	4	4	7.03 (2.75)
Colubrina arborescens	Coa	Rhamnaceae	5	5	5.47 (2.72)
Gymnanthes lucida	Gyl	Euphorbiaceae	5	5	6.33 (1.57)
Leucaena leucocephala	Lel	Fabaceae	4	4	5.775 (0.15)
Pisonia albida	Pia	Nyctaginaceae	6	6	8.07 (2.25)
Pithecellobium unguis-cati	Piu	Fabaceae	5	5	5.14 (1.60)
Swietenia mahogani	Swm	Meliaceae	4	4	6.7 (1.74)

sequence read counts across samples, all fungal community analyses were based on counts rarefied to 1298/sample. The 76 samples had a total of 51,920 sequences and 381 fungal operational taxonomic units (OTUs) present in the final quality-controlled and rarefied dataset. Fungal OTU richness per sample was calculated in the vegan package (Oksanen et al. 2013). To determine the independent and interactive effects of time and tree species on wood properties (i.e. density, lignin, glucan, xylan, mannan and arabinan contents) and fungal OTU composition a series of permutational multivariate analyses of variance (PerMANOVA, Anderson 2001) were applied. The variation in samples based on cumulative wood properties and fungal OTU composition were visualized with non-metric multi-dimensional scaling (NMDS) plots based on Euclidean and Bray-Curtis dissimilarity matrices, respectively. The specificity of the fungal OTUs to tree species was visualized using Gephi (Bastian et al. 2009). Tree species phylogenetic distances were calculated using rbcL gene (Kang et al. 2017). Briefly, rbcL sequences of the nine tree species were downloaded from the NCBI database (http://www.ncbi.nlm.nih.gov/)(Table S1), aligned using ClustalW, and a phylogenetic tree was inferred with the Maximum Likelihood in MEGA (Fig. S1; Kumar et al. 2018; Tamura and Nei 1993). Pairwise phylogenetic distances were then calculated and associations between tree species phylogenetic distances and wood property dissimilarity as well as fungal OTU composition dissimilarity were determined using Spearman's Rank-Order correlations. The effects of time and tree species on wood property quantities and the fungal community relative abundances (i.e. fungal OTU richness and Ascomycota, Basidiomycota, plant pathogen, total saprotroph, undefined saprotroph, white rot and soft rot) were assessed using two-way analyses of variance (ANOVA) for paired-samples. Prior to the ANOVAs, variance homoscedasticities were tested using Cochran's test and data were log-transformed if necessary. All higher abundance fungal OTUs (representing a cumulative sum of 80% of relative abundances) were evaluated for significant association with time and tree species using Indicspecies package (De Caceres and Legendre 2009). Finally, associations between wood chemistry change over time (% change between year zero and year one), initial wood properties and initial and final fungal community features were assessed using Spearman's Rank-Order correlations.

Results

Wood properties

When all nine species were considered together, there were strong differences in wood properties following one year of decomposition (Fig. 1a), with time significantly affecting wood chemistry ($F_{1,58} = 3.73$, $P \leq 0.001$). When each tree species was assessed separately, the effect of time on the wood properties remained significant ($P \leq 0.05$) for all the tree species except for *L. leucocephala* (Fig. 1b). This effect was mostly due to a significant loss in xylan for all tree species ($F_{1,29} = 284.140$, $P \leq 0.001$), ranging from 30.2 to 76.9% across species (Fig. 2). Wood properties were also significantly influenced by tree species identity ($F_{8,58} = 3.73$, $P \leq$

0.001), but only at year one (Fig. 1b). The tree species effect was significant ($P \leq 0.05$) for all wood properties measured except for lignin ($P \leq 0.1$). In addition, there was a significant interaction between time * tree species on wood density ($F_{8,29} = 284.140$, $P \leq 0.001$) and glucan content ($F_{8,29} = 284.140$, $P = 0.001$). This interaction was mainly caused by the high density and glucan losses respectively of 50.6% and 64.0% measured for *B. simaruba*. In contrast, mannan content increased for *C. arborescens*, *G. lucida,* and *P. albida*. Notably, *B. simaruba* had much lower initial density and lignin content in comparison with the other species.

Fungal community structure

NMDS analysis of fungal OTU composition revealed that the effect of time depended on tree species. This was confirmed by the PERMANOVA results showing a significant time * tree species interaction ($F_{8,58} = 1.30$, $P \leq 0.001$) (Fig. 1c). The effect of time on fungal OTU composition was significant ($P \leq 0.05$) for *B. buceras*, *B. simaruba*, *C. diversifolia,* and *P. albida*, but not *C. arborescens*, *G. lucida*, *L. leucocephala, P. unguis-cati, and S. mahagoni* (Fig. 1d). Tree species identity appeared to be the main factor affecting fungal community structure ($F_{8,58} = 2.75$, $P \leq 0.001$), explaining 22% of the variance in OTU composition and being significant ($P \leq 0.05$) at both sampling times. Summed by tree species, a high proportion of OTUs were specific to only one tree species: 50% at year zero (Fig. 3a and b) and 75% at year one (Fig. 3c and d). Tree species specificity was also observed when OTUs were grouped by guild, with saprotrophic fungi being more specialized (i.e. being detected in only one tree species) than plant pathogenic fungi at both sampling times. OTU richness ranged from 18 to 42 per tree species, and was significantly impacted by the time treatment ($F_{1,29} = 4.553$, $P \leq 0.05$). OTUs richness decreases were significant ($P \leq 0.05$) for *C. arborescens* (−50.9%), *P. albida* (−33.7%), and *P. unguis-cati* (−46.5%) (Fig. 4).

For both time points, fungal communities were dominated by phylum Ascomycota, representing more than 65% of the total sequences across tree species. Fungi in the phylum Basidiomycota were second most abundant, ranging from 0 to 30% of the total depending on tree species. The relative abundances of both phyla were not significantly influenced by time or tree species identity. In terms of functional guild composition, both plant pathogenic and saprotrophic fungi were abundant, with each guild being significantly influenced by tree species identity (plant pathogen: $F_{8,29} = 4.77$, $P \leq 0.001$; saprotroph: $F_{8,29} = 4.175$, $P \leq 0.01$) but not time. The saprotrophic fungi were mostly comprised of white rot fungi and undefined saprotrophs, with soft rot fungi only detected in *B. simaruba*. Tree species identity also significantly affected the abundances of these saprotrophic subgroups (white-rot: $F_{8,29} = 3.382$, $P \leq 0.01$; undefined saprotroph: $F_{8,29} = 2.828$, $P \leq 0.05$), but not time.

Most of the abundant fungal OTUs persisted across the two sampling times (Fig. 5) and could be considered as generalists because they were detected in multiple tree species. For example, the most abundant OTU, *Lasidioplodia* (OTU1), a plant pathogenic fungus, was detected in all tree species. Other plant pathogenic fungi were also found in multiple tree species, such as *Albonectria rigidiuscula* (OTU46), *Cytospora* (OTU24), *Cytospora rhizophorae* (OTU11), and *Phaeocremonium rubrigenum* (OTU161 and OTU657). Similarly, *Schizophyllum commune* (OTU4), a white rot fungal OTU, was detected in eight of the nine studied tree species. Interestingly, a suite of other OTUs that were significantly associated with year zero sampling strongly or fully disappeared after 12 months, such as *Clonostachys rosea* (OTU35), *Fusarium* (OTU49 and OTU143), *Albonectria rigidiuscula* (OTU 46) and *Phaeoacremonium rubrigenum* (OTU161).

Relationships between tree phylogenetic distance, wood properties, and fungal community structure

There was a significant negative correlation between tree phylogenetic distance and wood chemistry dissimilarity ($r = -0.33$, $P \leq 0.05$) at year zero (Fig. 6), whereas tree phylogenetic distance and fungal community dissimilarity were significantly positively correlated at year one ($r = 0.43$, $P \leq 0.01$).

Relationships between wood decomposition rates, initial and final wood properties, and fungal community features

The percent changes in wood density were significantly positively correlated with initial lignin content ($r = 0.70$, $P \leq 0.05$) and xylan ($r = 0.70$, $P \leq 0.05$) (Fig. 7) and

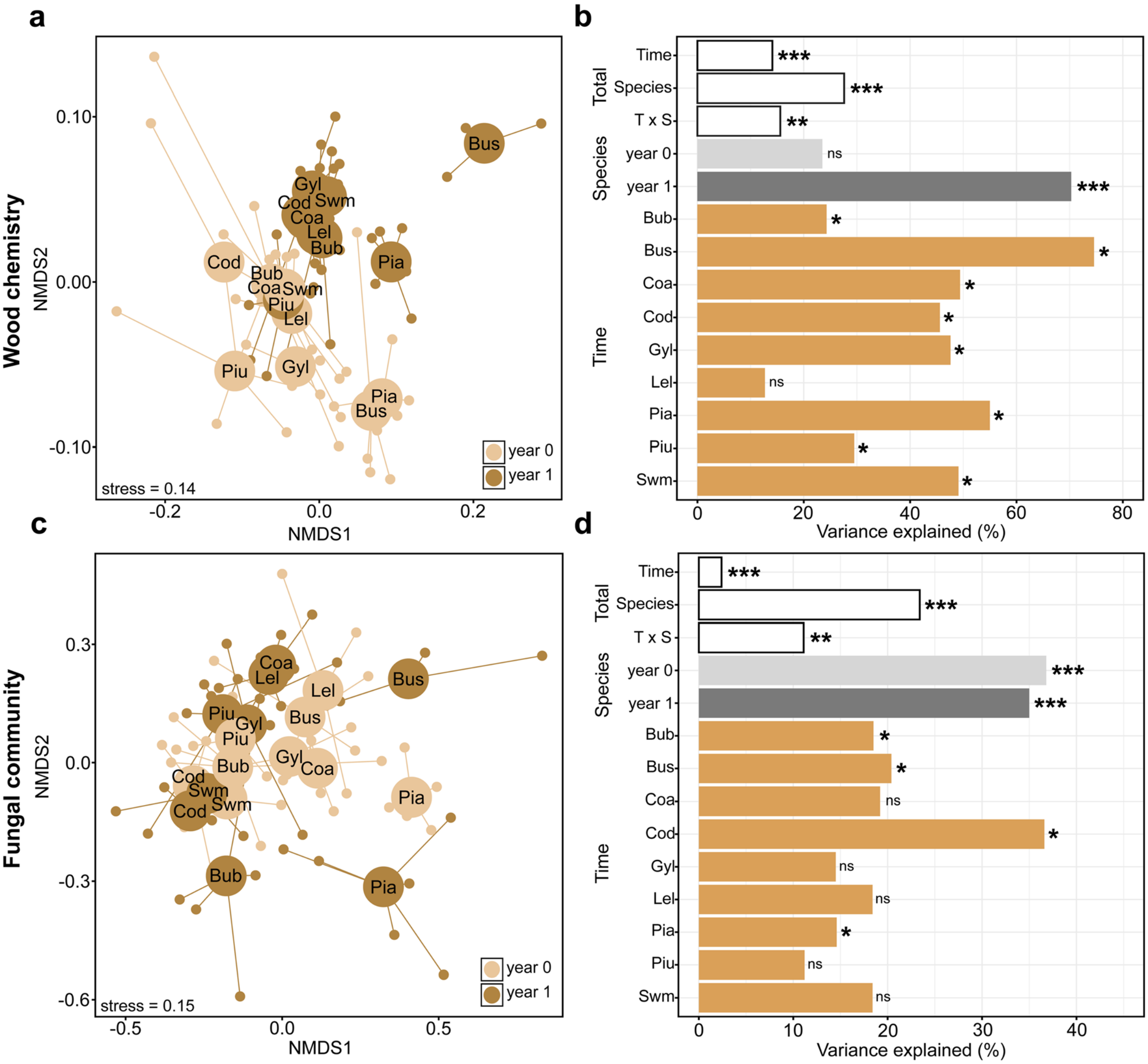


Fig. 1 Non-metric multidimensional scaling (NMDS) and PerMANOVA (**P* ≤ 0.05; ***P* ≤ 0.01; ****P* ≤ 0.001) analys es for the (**a**, **b**) wood chemical properties of the logs depending the time and the tree species treatments based on Euclidean dissimilarity and for the (c, d) the fungal communities of the logs based on OTUs composition depending on time and the tree species treatments based on Bray-Curtis dissimilarity

significantly negatively correlated with the saprotroph/plant pathogen ratio at year one (r = −0.75, P ≤ 0.05). Additionally, both glucan and xylan percent changes were significantly positively correlated with the relative abundance of the undefined saprotrophs at year zero (glucan: r = 0.82, P ≤ 0.01; xylan: r = 0.75, P ≤ 0.05) and saprotroph/plant pathogen ratio at year zero (glucan: r = 0.73, P ≤ 0.05; xylan: r = 0.72, P ≤ 0.05).

Discussion

Recent studies using high-throughput sequencing technologies have illuminated our understanding of the role of the fungal community in wood decomposition. However, in comparison with temperate and boreal forests, tropical forests have remained understudied, particularly in the dry tropics. This study explored the simultaneous changes in wood properties and fungal communities

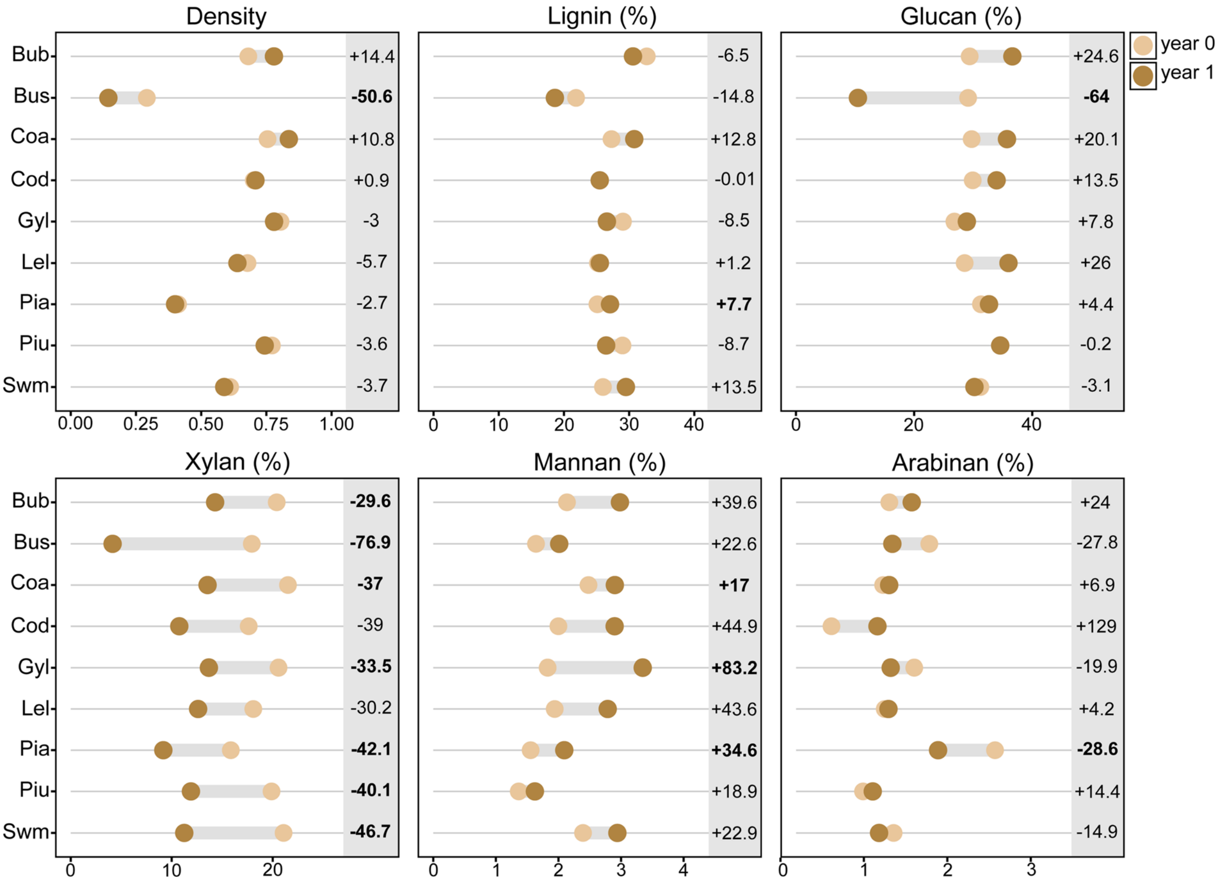


Fig. 2 Wood chemical properties in the nine studied tree species depending on time. Associated values represent the % changes at year one by comparison with year zero. The % change values represented in bold indicate a significant difference between year zero and year one based on t-test for paired samples ($P \leq 0.05$)

during the early stages of decomposition in a tropical dry forest following a major hurricane. We showed that tree species identity had a strong effect on the structure of both the stem-associated and deadwood-associated fungal communities. Additionally, the fungal species, and notably the saprotrophic fungi, harbored a high degree of specialization for deadwood substrates. Further, we found a rapid and consistent diminution of the wood carbohydrate content, and notably the xylan, without important lignin losses. Finally, we demonstrated that fungal communities represented the main factor explaining rates of cellulose and hemicellulose degradation during the early stages of wood decomposition.

Wood-inhabiting fungal community structure is associated with tree phylogenetic signal

As phylogenetic distance increased among tree species their fungal communities were less similar, confirming our hypothesis (H1). Surprisingly, this relationship between tree phylogenetic distance and fungal community structure was significant after one year of decomposition but not at time zero. If plants filter their associated microbial communities, a proposed explanation of why closely related taxa might present similar microbiomes, we might have expected a stronger signal at year zero than year one (Hacquard et al. 2017; Jones et al. 2019). Our result contrasts with the recent study of Lee et al. (2019), who found a significant relationship between tree species phylogenetic distance and the fungal endophytic community structure of tree stems. One mechanism that might explain links between tree phylogeny and associated microbiota is the similarity in wood properties, but we did not find a significant correlation between tree phylogeny and wood properties or wood properties and fungal community after one year of decomposition. Lee et al. (2019) also measured this lack of tree phylogenetic and wood properties

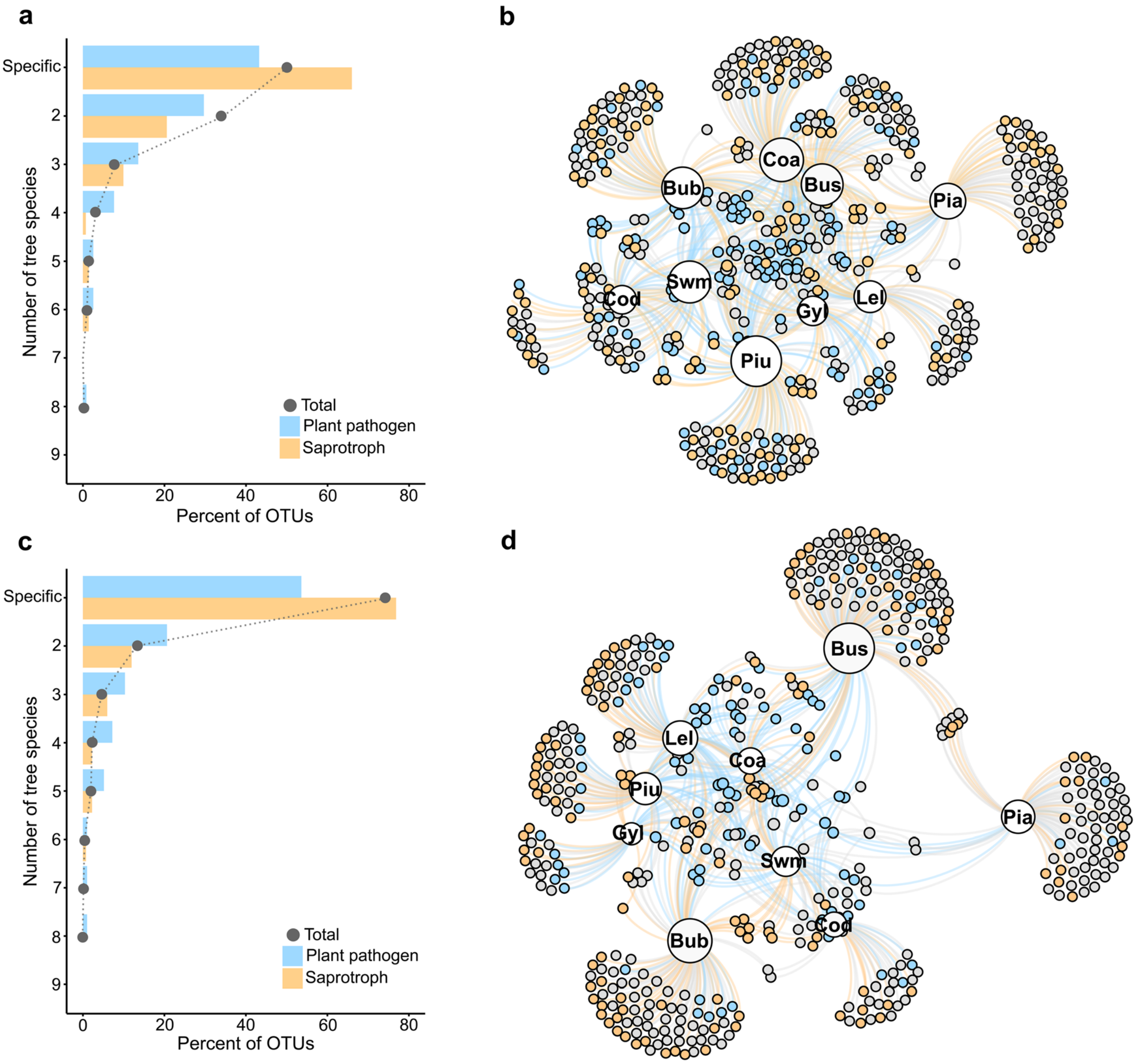


Fig. 3 Percent of the specific and shared fungal OTUs in the nine studied tree species (**a**) at year zero and at (**c**) year one for the total OTUs and depending on their functional guild assignment (plant pathogen and saprotroph). Networks showing the association of the fungal OTUs with the nine studied tree species (**b**) at year zero and (**d**) at year one. Large nodes represent the tree species (see Table 1 for the tree species code) and small nodes represent the fungal OTUs. All the OTUs are represented. A link between a tree species and an OTU indicate that this OTU was detected in this tree species. OTUs and their associated links are colored depending on their functional guild assignment (blue for plant pathogens, orange for saprotroph and grey for other and unclassified). The size of the tree species nodes is proportional to the total number of associated OTUs

association with living trees. We suspect our results may have been driven by wood chemical and anatomical parameters we did not assess in this study, such as the pH, water content, micronutrients, and the secondary wood chemistry, which are often described as structuring factors of the fungal communities (Baldrian et al. 2016; Kotowska et al. 2020; Purahong et al. 2016).

Tree species identity effect persists after one year of decomposition

The effect of tree species identity on fungal community composition was initially significant at year zero but persisted at year one at a similar magnitude, which did not support our second hypothesis (H2). Tree species

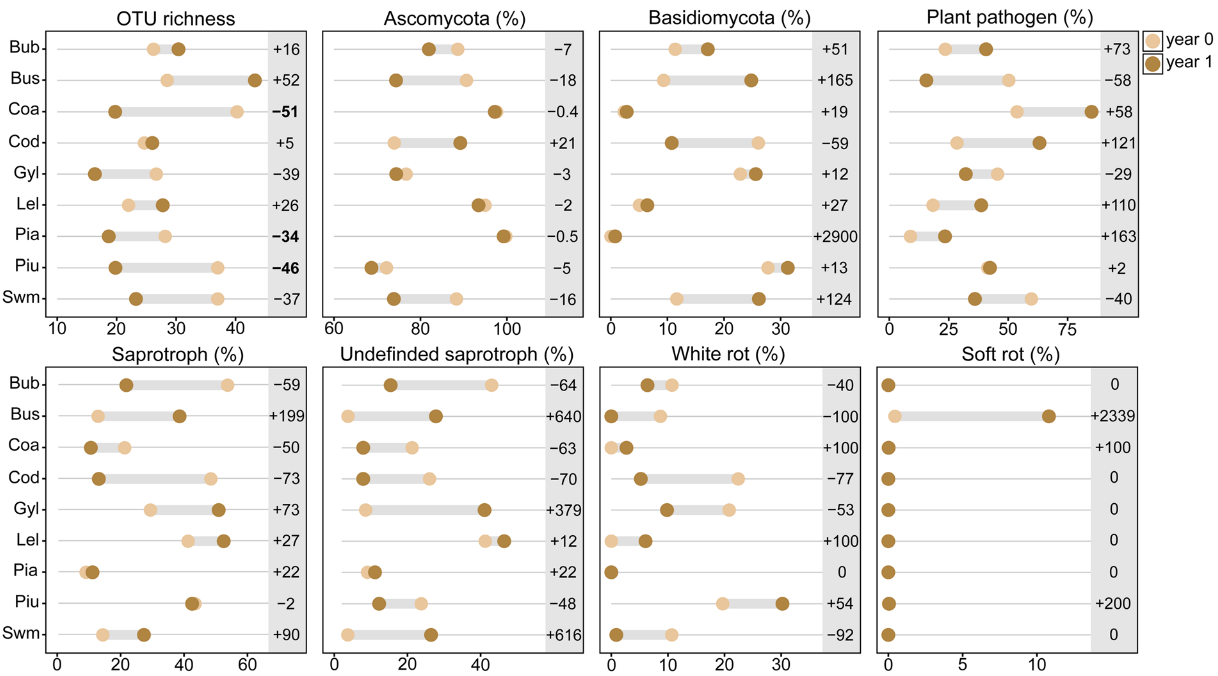


Fig. 4 Fungal community features in the nine studied tree species depending on time. Associated values represent the % changes of fungal community features at year one by comparison with year zero. The % change values represented in bold indicate a significant difference between year zero and year one based on t-test for paired samples (P ≤ 0.05)

identity has been well described as a factor structuring the stem-inhabiting fungal communities of living trees (Lee et al. 2019; Maillard et al. 2020; Skaltsas et al. 2019) as well as fungal community structure in deadwood in temperate forests (Baldrian et al. 2016; Leonhardt et al. 2019; van der Wal et al. 2016). To date, the results in tropical forests are less clear, with both a significant effect of tree identity (Dossa et al. 2021; Purahong et al. 2017) and no effect of tree identity (Jones et al. 2018). Previous observational and culture-based experiments conducted in temperate and tropical forests have also reported a low specificity of wood-inhabiting communities (Lee et al. 2020; Lodge 1997). Here, using HTS, we found a very high specificity of the fungal communities for the tree species, increasing with time, which contradicts Lodge (1997). However, almost all the abundant OTUs in our study were shared between multiple tree species, indicating that most specific OTUs were present at low relative abundance. The fact that rare OTUs were the ones that tended to be to be specific might explain why culture-based studies did not find these results, as rare species are usually difficult to capture by isolation approaches compared with metabarcoding (Ferrer and Gilbert 2003). Paralleling our results, Purahong et al. (2017) recently found a very high proportion of deadwood-associated fungal OTUs exhibiting a strong tree species preference in a temperate forest. The fact that saprotrophic fungi were more specialized than plant pathogenic fungi might suggest greater adaptation of these fungi for deadwood. In particular, the potential specialization of the fungi for their wood substrates might be related to functional traits involved in decomposition, tolerance for toxic wood compounds, or intra- and inter-kingdom interactions with fungi, bacteria, oomycetes, or wood-associated insects (Lee et al. 2020; Skelton et al. 2019; Song et al. 2015).

The lack of white rot decomposition chemical signature

Most of the chemical changes measured in this study were associated with a decrease in xylan content over time, indicating that hemicellulose degradation was remarkably consistent across the nine tree species. These results contradict our third hypothesis (H3), in which we expected a simultaneous decrease in both carbohydrates as well as lignin contents over time. While these results run counter to the white rot dominance observed in Schilling et al. (2015a), it should be noted that white rot fungi can degrade hemicellulose without affecting

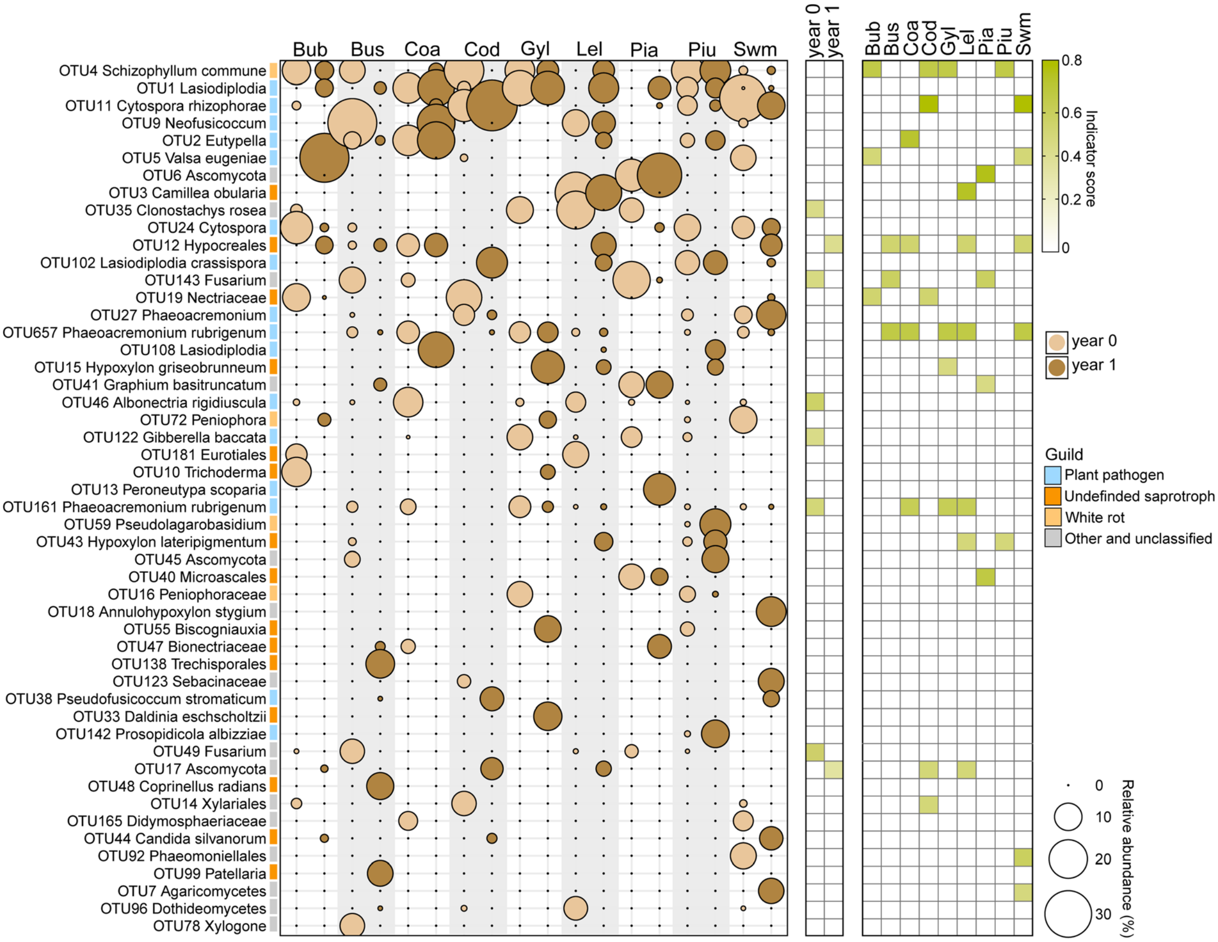
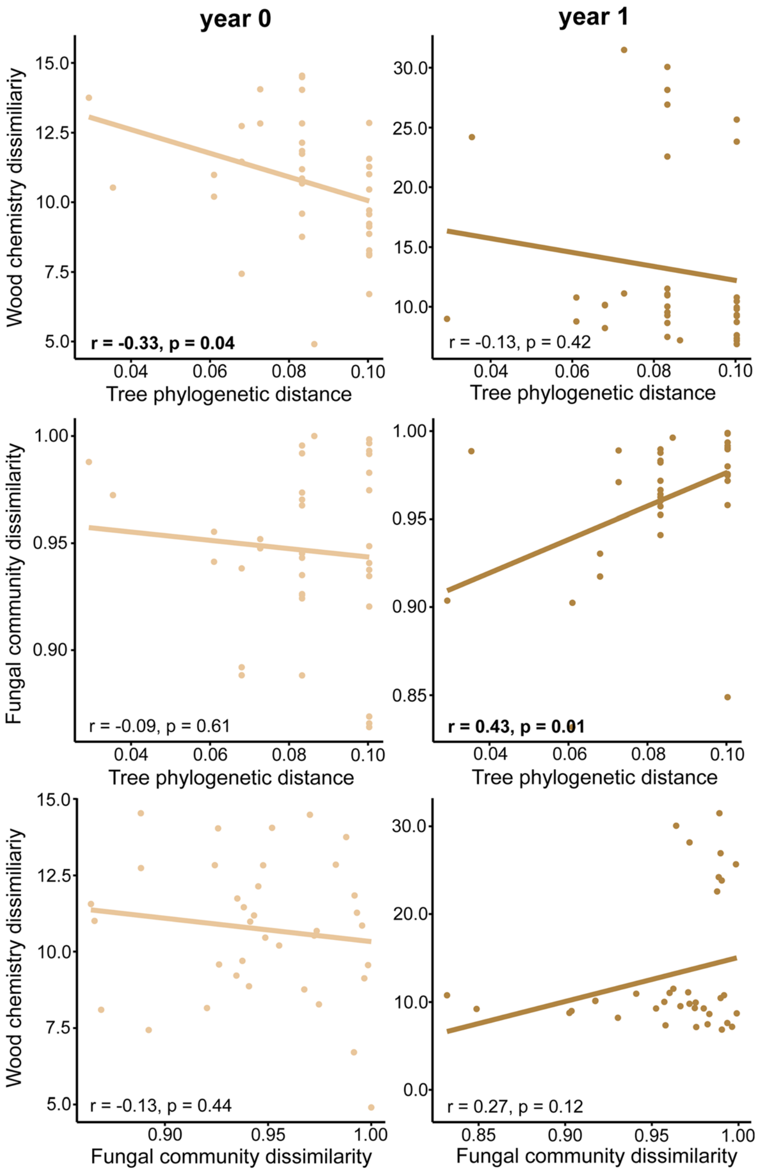


Fig. 5 The relative abundance of the fungal OTUs contributing to 80% of the total sequences depending on the time and tree species treatments. Size of the circles is proportional to the relative abundance of the fungal OTUs. Heatmaps summarize the OTUs defined as significant ($P \leq 0.05$) indicator of the time or the tree species based on the Indicspecies R package

lignin in the early stages of decomposition (Curling et al. 2002). Accordingly, the presence of abundant genera classified as white rot fungi (e.g., *Schizophyllum*, *Peniophora,* and *Pseudolagarobasidium*) in most of the studied tree species might indicate greater lignin removal is likely to occur during more advanced stages of decomposition. On the other hand, controlled wood decay experiments suggested that *Schizophyllum commune,* the most abundant OTU in our dataset, presents limited abilities for lignin degradation for a white rot-classified fungal species (Schilling et al. 2015b). Additionally, the only studied tree species with relatively rapid decomposition dynamics in this study, *B. simaruba,* challenges this possibility of strong chemical shifts associated with lignin degradation. Specifically, *B. simaruba* was the only tree species to exhibit significant decreases in density as well as glucan content, indicating rapid decomposition. The fast decomposition of *B. simaruba* was confirmed in another study and is likely associated with its low density and lignin content by comparison with the other tree species that we studied (Harmon et al. 1995). The lignin loss/density loss ratio (L/D) has been described as a robust proxy of wood decay type with values below 0.80 indicating a brown or soft rot fungi dominance and values above being typical of white rot fungi decomposition mechanisms (Schilling et al. 2015b). On average, we calculated L/D of 0.28 (± 0.15) for *B. simaruba* deadwood indicating a substantial loss of the carbohydrates composing cellulose and hemicellulose (contributing to density loss) while its lignin content only slightly decreased, which is typical of brown or soft rot decay types. Although we did not detect any brown rot fungi in this study, *B. simaruba* was the only tree species in

Fig. 6 Spearman's correlations between the wood chemistry dissimilarity (Euclidean), the fungal community dissimilarity (Bray-Curtis) and the phylogenetic distance of the tree species (based on rbcL phylogenetic tree) at year zero and year one



which we detected soft rot fungi, suggesting they might be responsible for this decomposition pattern. In agreement with our results, Jones et al. (2018) measured a strong diminution of the hemicellulose content for three tree species in a tropical forest in Peru, while the lignin content and the cellulose content remained stable. Additionally, Torres and González (2005) found some visual observations of brown or soft rot decay for wood incubated in the Guánica Dry Forest where we conducted our experiment. More quantitatively, González and Luce (2013) found that dead logs presenting visual signs of brown or soft rot decay were almost twice more frequent than wood debris presenting white rot decay in Puerto Rican dry forests. These inconsistencies between our results and those of Schilling et al. (2015a) might have additional explanations. In particular, the two studies have no overlap in tree species and differ notably in tree age and wood density, which are factors having potential effects on wood decomposition patterns (Zanne et al. 2015). Further, the small stem diameters and high stem density for the Puerto Rican dry forest contrast with larger stem diameters (18 cm. on average) used in the Schilling et al. (2015a) study. Regardless of these differences, our results challenge

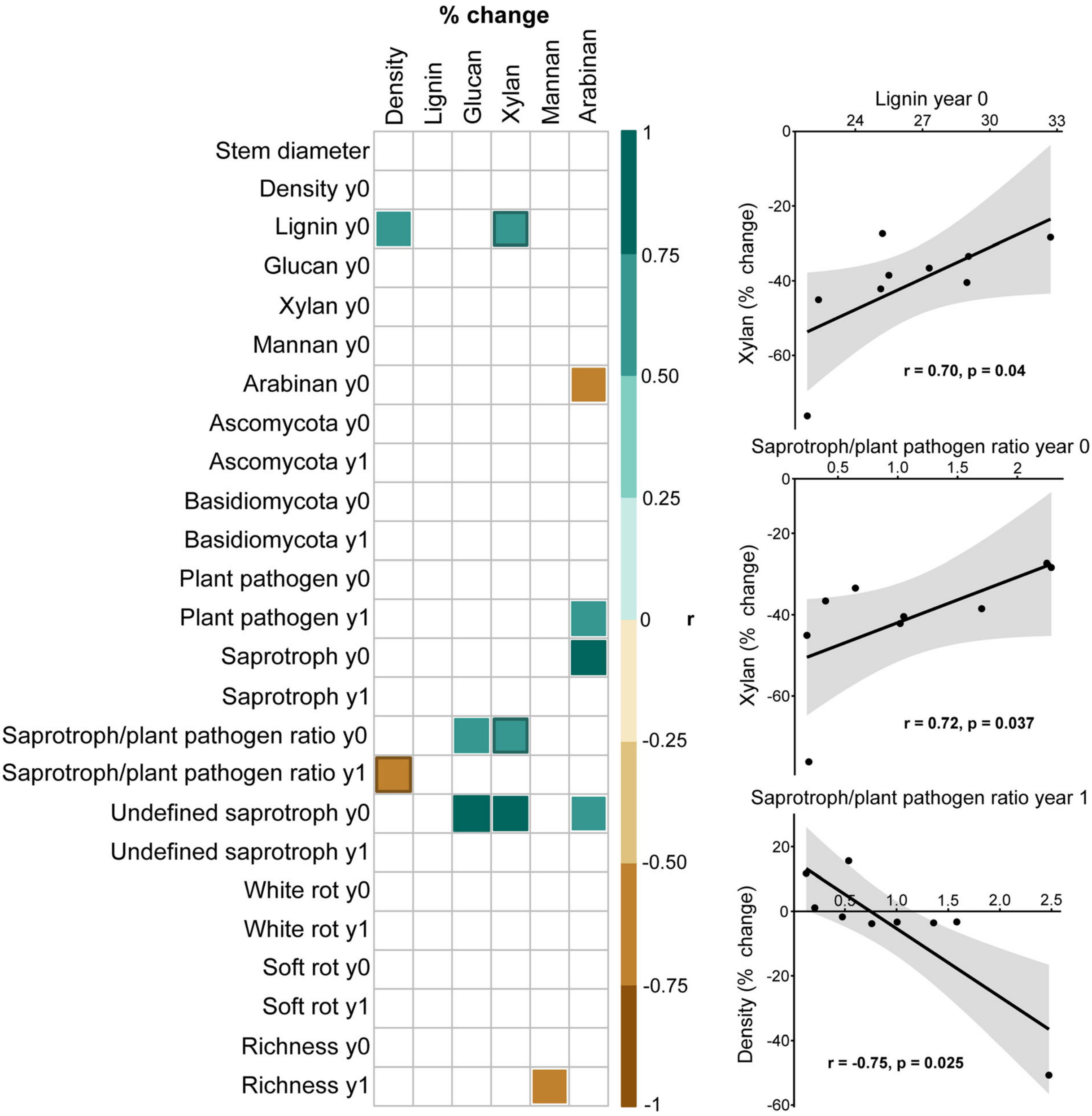


Fig. 7 Spearman's correlations between the wood chemical changes (% change) between year zero (y0) and year one (y1) with the initial wood properties and the initial and final fungal community features. Only significant correlations are shown (P ≤ 0.05). We represented three significant correlations presenting a specific interest to us

the idea that the white rot decay type is dominant in all tropical dry forests, particularly in the early stages of decomposition.

Plant pathogenic Fungi might act as early decomposers

We expected that tree species presenting an initial higher proportion of saprotrophic fungi pre-colonizers would have faster decomposition rates (Hiscox et al. 2015; Song et al. 2015). Surprisingly, we found the opposite pattern, with the tree species having initially low saprotrophic/plant pathogen ratios displaying a significantly higher loss of glucan and xylan contents, contradicting our fourth hypothesis (H4). We described that plant pathogenic fungi were consistently found to be the second most abundant fungal functional guild, and it has been previously proposed that trunk pathogens might have some versatile saprotrophic capacities (Maharachchikumbura et al. 2014; Purahong et al. 2017). While they are suspected of being quickly replaced by new fungal colonizers, Cline et al. (2018) found that *Phaeoacremonium*, a plant pathogenic fungal genus that was also very abundant in our study, persisted in deadwood up to 42 months of field incubation. We suspect that such a long persistence of plant pathogenic fungi in deadwood is related to their ability to degrade wood. Support for this possibility was recently demonstrated in some trunk pathogens, notably *Neofusicoccum*, which was also very abundant in our study, which presents a clear expansion of gene families associated with plant cell wall degradation (Morales-Cruz et al. 2015). Specifically, transcriptomes of trunk pathogens were enriched in CAZymes families coding for cellulose and hemicellulose degradation (GH3, GH5, GH16, GH43, AA3, AA7, and AA9) by comparison with a non-trunk associated pathogenic fungus (Morales-Cruz et al. 2015). These genomic results were confirmed by physiological experiments showing that *Neofusicoccum* was able to degrade carbohydrates present in wood through the secretion of cellulases and hemicellulases (Stempien et al. 2017). *Eutypella*, another plant pathogen that was abundant in our study, has been found to have abilities to decompose wood in controlled conditions (Brglez et al. 2020). Together, these ecological, physiological, and genomic pieces of evidence indicate that trunk pathogens harbor significant wood decomposition abilities.

Why a higher abundance of saprotrophic fungi retarded decomposition in our study is less clear. Studies have suggested that saprotrophic fungi inhabiting living trees may be inactive (Boddy et al. 1989; Hendry et al. 2002; Parfitt et al. 2010) in contrast, to plant pathogenic fungi which are likely active and potentially widespread in plant tissues (Travadon et al. 2013). These potential differences in activity between these two functional guilds may help explain why in our study plant pathogenic fungi seemed to outcompete the saprotrophic fungi for wood decomposition. However, the significant negative correlation we found between the wood density percent change and the saprotroph/plant pathogen ratio indicates that in the more advanced stages of decomposition, saprotrophic fungi became dominant. This is most likely because as decomposition advances wood chemistry becomes more recalcitrant and more efficient decomposition machinery is needed that plant pathogenic fungi do not possess.

Limitations

It is important to note that we only assessed the role of the fungal community in deadwood decomposition. Thus, we might have neglected the contribution of other micro- and macro-organisms in the wood degradation process. Recent studies suggested, for example, a key role of the bacteria in wood decomposition (Tláskal et al. 2021; Viotti et al. 2021). Additionally, in the Guánica forest where we conducted our experiment, it has been shown that both arboreal and subterranean termites were important actors of wood decomposition (Torres and González 2005). Holistic studies will be needed to decipher the respective and interactive roles of the different biotic components of wood decomposition in tropical dry forests.

Conclusion

We have provided evidence suggesting a rapid and consistent decomposition of hemicellulose in downed trunks of nine tree species that were snapped during Hurricane Maria, having potential consequences for the forest C and nutrient cycles in forest ecosystems post-hurricane events. Further, we showed that fungal communities were associated with the tree species phylogeny such that more distantly related tree species also diverged more in their fungal communities and exhibited a very high level of specificity. Finally, we found that tree species presenting wood enriched in plant pathogenic fungi presented an acceleration in the decomposition of the carbohydrates composing the hemicellulose. The mechanisms and long-term consequences of this important wood hemicellulose depletion likely caused by the trunk pathogenic fungi on forest biogeochemical cycles need further investigation.

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Data availability statement Raw .fastq files for each sample were deposited in the NCBI Short Read Archive as accession PRJNA560937.

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Declarations

Conflict of interests The authors declare no conflict of interests.

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