Received: 16 February 2023 | Accepted: 23 February 2024

DOI: 10.1111/1365-2745.14295

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Stem decomposition of temperate tree species is determined by stem traits and fungal community composition during early stem decay

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Funding information
the C. T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC); The Nora Croin Michielsen Fonds 2018; The China Scholarship Council, Grant/Award Number: 201706910085

Handling Editor: Giovanna Battipaglia

Abstract

1. Dead trees are vital structural elements in forests playing key roles in the carbon and nutrient cycle. Stem traits and fungal community composition are both important drivers of stem decay, and thereby affect ecosystem functioning, but their relative importance for stem decomposition over time remains unclear.
2. To address this issue, we used a common garden decomposition experiment in a Dutch larch forest hosting fresh logs from 13 common temperate tree species. In total, 25 fresh wood and bark traits were measured as indicators of wood accessibility for decomposers, nutritional quality and chemical or physical defence mechanisms. After 1 and 4 years of decay, we assessed the richness and composition of wood-inhabiting fungi using amplicon sequencing and determined the proportional wood density loss.
3. Average proportional wood density loss for the first year was 18.5%, with further decomposition occurring at a rate of 4.3% year^{-1} for the subsequent 3 years across tree species. Proportional wood density loss varied widely across tree species in the first year (8.7–24.8% year^{-1}) and subsequent years (0–11.3% year^{-1}). The variation was directly driven by initial wood traits during the first decay year, then later directly driven by bark traits and fungal community composition. Moreover, bark traits affected the composition of wood-inhabiting fungi and thereby indirectly affected decomposition rates. Specifically, traits promoting resource acquisition of the living tree, such as wide conduits that increase accessibility and

high nutrient concentration, increased initial wood decomposition rates. Fungal community composition, but not fungal richness explained differences in wood decomposition after 4 years of exposure in the field, where fungal communities dominated by brown-rot and white-rot Basidiomycetes were linked to higher wood decomposition rate.

4. *Synthesis*: Understanding what drives deadwood decomposition through time is important to understand the dynamics of carbon stocks. Here, using a tailor-made experimental design in a temperate forest setting, we have shown that stem trait variation is key to understanding the roles of these drivers; initially, wood traits explained decomposition rates while subsequently, bark traits and fungal decomposer composition drove decomposition rates. These findings inform forest management with a view to selecting tree species to promote carbon storage.

KEYWORDS
bark traits, density loss, ecosystem function and services, fungal community, physical–chemical traits, saprotrophic fungi, wood decomposition, wood traits

1 | INTRODUCTION

Globally, forests act as "carbon sinks" by absorbing more than 1 Pg C per year (Pan et al., 2011). Most of the stored carbon will be slowly released to the atmosphere as CO_2 once the trees die and subsequently decompose. The dynamic in the carbon- and nutrient cycling process in forest ecosystems depends on the speed of deadwood decomposition. Stem decay process is determined by both intrinsic and extrinsic drivers (Cornwell et al., 2009; Kahl et al., 2017) and can strongly differ between tree species (Villéger et al., 2008; Yang, Sterck, et al., 2022). Species-specific anatomical and chemical wood and bark traits are documented to have strong afterlife effects (Freschet et al., 2012). Stem traits can shape the richness and composition of wood-inhabiting fungi (Yang et al., 2021), bacteria and arthropods (Andringa et al., 2019), thus affecting wood decomposition rate and biogeochemical cycling (Kahl et al., 2017; Zuo et al., 2016). Wood decomposition is also driven by biotic interactions between stem traits, the different decomposers and their priority effects (van der Wal et al., 2016; Weedon et al., 2009), and by abiotic conditions (temperature, moisture and light) that determine the decomposer abundance and activity (Edman et al., 2021; Hu et al., 2017). However, we still have little knowledge of the combined and relative effects of these multiple drivers in determining wood decomposition rate and outcomes throughout the decomposition trajectory (but see Kahl et al., 2017; Zuo et al., 2021).

Physical, chemical and anatomical traits of different stem compartments (bark and wood) determine the accessibility and substrate quality for different wood decomposers (Baldrian et al., 2016; Rajala et al., 2012). Bark represents the first line of defence; it comprises up to 20% of above-ground tree biomass, differs greatly from wood in terms of physical–chemical traits (Yang, Sterck, et al., 2022), and serves as an environmental filter for the decomposer community assembly (Ulyshen et al., 2016). Bark can inhibit decomposers' access because of the high content of defence compounds (Jones et al., 2020) or, alternatively attracting decomposers by its high nutrient and by creating locally favourable conditions for wood decomposition (Wu et al., 2021). As a result, the effect of bark on wood decay is often tree species- and stem size-specific (Dossa et al., 2016; Tuo et al., 2021). Nutritional stem traits, like high nutrient and non-structural carbohydrate concentrations, generally stimulate fungal growth (Sinsabaugh et al., 1993), whereas a high C/N ratio or low initial N concentration may cause microbial N limitation and reduce microbial metabolic activity and wood decomposition rate (Bonanomi et al., 2021; Weedon et al., 2009). Chemical defence traits such as toxic phenols and tannins reduce the decomposability of stem cells (Kahl et al., 2017; Viotti et al., 2021). Physical defence traits, such as bark physical toughness, wood density and lignin concentration also determine fungal richness and community composition (Hoppe et al., 2016; Krah et al., 2018). Less attention has been paid to anatomical traits such as parenchyma fraction and conduit size, which may increase access and spread of wood-decaying organisms, thereby regulating nutrient and carbon availability (Lee & Hawkes, 2021; Zanne et al., 2015). Therefore, how this complex of stem traits, in combination with fungi infestation, drives wood decay over time and differs across tree species remains poorly studied.

Fungi are the primary decomposers of dead wood because they can actively decompose lignin and other recalcitrant compounds (Boddy, 2001; Stokland et al., 2012). Three main wood decomposing fungal functional groups are known to break down the major wood polymers cellulose, hemi-cellulose and lignin (Kirk et al., 1987; van der Wal et al., 2013). White-rot Basidiomycetes degrade cellulose, hemicelluloses and recalcitrant lignin with the aid of extracellular lignocellulolytic enzymes; brown-rot Basidiomycetes degrade cellulose and hemicelluloses by depolymerisation while partially modifying lignin through non-enzymatic process, e.g. by demethoxylation (Niemenmaa et al., 2008); and soft-rot Ascomycetes degrade

cellulose and hemicelluloses by secreting cellulase (Schmidt, 2006). Fungal richness can increase wood decomposition via increased niche partitioning, or facilitative interactions among fungal species (Tiunov & Scheu, 2005; Van Der Wal et al., 2015). Yet, this positive richness effect can saturate at rather low fungal richness because of redundancy in metabolic abilities of fungi (Dang et al., 2005; van der Wal et al., 2013) or because of intense competition among fungi (Fukami et al., 2010; Nielsen et al., 2011). Therefore, further studies are necessary to fully understand the effects of fungi on wood decomposition and their role in maintaining the balance of forest ecosystems and the carbon cycle.

We examined the relative importance of stem traits and fungal decomposer community structure, as well as their interactions, on wood density loss over 4 years of decay in the field. We sought to address three hypotheses. First, wood density loss will be positively correlated with anatomical trait values that increase accessibility for decomposers (e.g. larger conduit size) and nutritional quality (i.e. N, P), and negatively correlated with values for physical (e.g. high wood density) and chemical defence traits (e.g. high lignin and phenolic concentrations) that inhibit the activity of wood decomposers (Cornwell et al., 2009; Lee et al., 2020). Moreover, the importance of initial stem traits may decrease with ongoing decay as many metabolites of the substrate may be decomposed or have changed. Second, Basidiomycete white-rot and brown-rot fungi will become more important in wood degradation later in the decomposition trajectory, owing to their ability to degrade recalcitrant polymers that remain after initial decomposition stages (Blanchette, 2000; Boddy, 2001). Third, based on the two commonly tested mechanisms: niche complementary (Loreau & Hector, 2001; Tilman et al., 1997) and the mass ratio hypothesis (Grime, 1998), we expect that fungal richness is correlated with wood density loss in the early decay period, because the fungal species that are initially present may be complementary in their niches, while later stages are likely dominated by a narrow range of specialists, thereby eliminating any expected effects of fungal richness (Tiunov & Scheu, 2005; van der Wal et al., 2013). For testing these hypotheses, we took advantage of a common garden experiment (LOGLIFE), in which similar-sized coarse logs of 13 temperate tree species were placed in a Dutch forest and monitored for 4 years (Cornelissen et al., 2012). This design allows for showing the potential effects of species-specific stem traits and their interactions with fungi on wood decay, largely without confounding effects of environmental conditions.

2 | MATERIALS AND METHODS

2.1 | Site and tree species

A common garden experiment was carried out in a Dutch forest, located at the Schovenhorst Estate in the Veluwe region of the Netherlands (52.25 N, 5.63 E). Mean annual temperature is 10.8°C and mean annual precipitation is 829 mm (Royal Netherlands Meteorological Institute [KNMI]). This forest site has a Pleistocene sandy soil that is well-drained and acidic (pH of ca. 4). The experiment was established within a light-open *Larix kaempferi* plantation with a ground layer of *Vaccinium myrtillus* and patches of *Deschampsia flexuosa*. Details of the study site are presented in Cornelissen et al. (2012).

In total, 13 tree species consisting of six angiosperm and seven gymnosperm species were included in this study (see tree species list in Table S1), and these species are commonly planted in Dutch forests. Notably, all conifer species but one (*Picea abies*) have been introduced in Europe, while five broadleaved species are native to European/Dutch forests. Trees of nine species were extracted from a Dutch forest in Schovenhorst, the other four species were harvested from a forest in Flevoland, the Netherlands (52.46 N, 5.42 E). This selection was made to include a broad range of wood traits across species, for which we also include broadleaved species that generally cannot be found in the Schovenhorst forest. Though the two forests differ markedly in soil conditions, growing conditions in the two forests had inferior effects on the stem traits of the harvested trees (Yang, Sterck, et al., 2022).

2.2 | Experimental design

We took advantage of the LOGLIFE project (Cornelissen et al., 2012), in which freshly cut stems of 13 temperate tree species have been left to decompose in a common garden experiment. Ten tree species were incubated in February, 2012, and three tree species were added in February, 2015. First, five individual trees were cut for each tree species and distributed to five blocks (i.e. forest plots) to decay. From trunk parts without major side branches five logs were cut per individual tree and treated as replicates, each with 1 m length and a diameter of 25 ± 3 cm, thus assuring a similar exposed stem cross-sectional area and substrate volume accessible to decomposers (Figure S1). These logs obtained from the same tree shared similar physical–chemical traits. One of the five logs was randomly harvested after 1 and 4 years of decay, respectively, and used for wood density measurement and molecular sampling. Each block measured approximately 12 m by 12 m, with a minimum distance of 20 m between blocks. Each block was surrounded by a 1.2-m high fence to exclude wild boars that are abundant in this area. Within each block, the logs were positioned 30 cm apart on the soil surface, assuring good contact with the soil to harmonize micro-site conditions for all logs, while mimicking natural conditions and allowing fungal access, also from the soil exposed side. In total, 325 logs (13 tree species × 5 individuals × 5 logs) were incubated. More information is given in Cornelissen et al. (2012).

2.3 | Sample preparation and measurements

Stem traits of different tree species and compartments (wood and bark) create different substrates for wood decomposers. To quantify stem traits and wood density loss, a 2-cm thick stem disk was sawn

from the stem base of each individual tree for initial trait measurements (Figure S1). In total, 25 physical–chemical traits were measured in wood and bark samples of all 13 temperate tree species. These traits are associated with hydraulic conductivity, hydraulic safety, storage, metabolism, chemical defence and physical strength. The basic information on these stem traits is given in Table S2, and details on the measurements are given in Yang, Sterck, et al. (2022). Initial wood density was measured by averaging the wood density of six 1.5 cm^3 blocks extracted along the diameter of the base disks. The wood density ($g\,cm^{-3}$) of each block was determined by the water displacement method as mass (g) after drying at 105°C divided by fresh volume (cm^3). Wood density of decaying wood was also determined over time to allow us to assess proportional density loss during decay. After 1 year (T1) and 4 years (T4) of decay, one log of each tree species was extracted from the five blocks at each harvest, resulting in a total of five logs per tree species for each harvest time (T1 & T4). Specifically, for the 10 tree species incubated in 2012, the tree log harvest was conducted in 2013 (T1) and 2016 (T4). For the other three species incubated from 2015, the tree log harvest was conducted in 2016 (T1) and 2019 (T4). It is worth noting that inconsistent incubation and harvest times might impact the effects of the fungal community on wood decomposition rate because of varying climate conditions between years. In a former LOGLIFE study based on the same tree species, Yang et al. (2021) have tested whether annual means of selected climate variables significantly affect fungal diversity and composition based on fruiting body survey. It was found that annual means of temperature, amount of precipitation and number of frost days had little effect on fungal communities (Figures S2 and S3). Therefore, we assume that the inconsistent incubation periods of the tree species had a limited effect on the decomposition experiment. Each harvested tree log was cut into two equal parts, one part (ca. 50 cm) was returned to its original location in the field for later investigation, and the other part was used for quantifying the wood density and fungal community, and for other analyses. It was tangentially divided into two parts (each being one quarter of the original 1 m-length tree log), disks from the middle of each half log were extracted. To obtain representative samples for assessing the fungal communities in the decaying logs, samples were collected immediately after the T1 and T4 harvests from the top (upper, air exposed side) and bottom (soil contact side) of the stem disks, pooled and stored at −20°C for further molecular analysis (Figure S1). We acknowledge the limitation that extracting samples from the middle part of a deadwood segment may not allow for detecting the fungal communities completely, but we decided for this sampling strategy for three reasons: (1) fungi can access dead wood not only from the end exposed sides, but also through bark (exposed to both air and soil); (2) avoid including mosses and fungal propagules that are not related to wood decomposition but are attached to the outer part (cf. Van Der Wal et al., 2015); (3) not all end exposed sides were available for all studied species, so we did not include the end side in order to keep consistency and avoid unbalanced comparison. Moreover, a 3-cm thick plank was sawn from the middle of one part and used for wood density determination. Dry wood density of each plank was determined as the ratio of dry wood weight (based on fresh weight and moisture content) and plank volume (based on plank size and thickness). Proportional density loss is widely assessed to represent wood decomposition rate (Fukasawa, 2018; Kahl et al., 2017; Shorohova et al., 2016). To obtain a more accurate wood decomposition rate, it is important that density of decaying wood is expressed on the basis of the initial volume (Chang et al., 2020). However, in this study, the volume was estimated based on the subsamples of decaying wood, so the proportional density loss method used in this study may not be directly comparable to the measure based on volume-corrected mass loss. To test whether the data are robust, we correlated the density loss measures after 4 years of decay and the volume-corrected mass loss obtained from Chang et al. (2020), based on the same tree species incubated at the same site (Cornelissen et al., 2012). We found that the two wood decay measures were highly correlated ($r=0.86$, $n=10$, $p<0.05$; Figure S4), possibly because little change in volume was observed during the first 4 years of decay (Chang et al., 2020). Therefore, we believe that in this study, using wood density loss to estimate wood decay rate is reasonable during the early decay stage. However, wood fragmentation may occur during later decay stage. We suggest to use the novel approach proposed by Chang et al. (2020) to reconstruct the initial volume of decaying deadwood. This approach can help reduce the error and uncertainty of estimation.

In August 2019, sawdust samples of different stem compartments (heartwood/inner wood, sapwood/outer wood and bark; when available) were collected using an electric drill. Before extracting the DNA, the sawdust samples were further ground into fine powder with a Retsch MM400 ball mill (Retsch, Haan, Germany). Specifically, sawdust samples and a metal ball (20 mm) were first put into a stainless-steel beaker (50 mL) allowing the sawdust to fill 30% to 40% of the beaker. We then closed the beaker, put it in liquid nitrogen until frozen, after which the sawdust was ground for 3 min at 30 Hz. Finally, the sample powder was stored at −20°C prior to further analysis. Notably, the drill bit used in the sawdust preparation process, and the beaker and metal ball used in the grinding process were all thoroughly disinfected with ethanol between samples to prevent sample cross-contamination.

2.4 | DNA extraction, PCR amplification and sequencing

DNA was isolated from 0.10 to 0.25 g fresh weight of ground samples using the PowerSoil DNA Isolation Kit (MO BIO Laboratories, Inc.). The total DNA quantity and quality was determined using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA). All DNA extractions were stored at −80°C prior to downstream analyses.

We used the primer pair ITS1F (5′-CTTGGTCATTTAGAGGAA GTAA-3′) (Gardes & Bruns, 1993) and ITS2 (5′-GCTGCGTTCTTC ATCGATGC-3′) (White et al., 1990) to amplify the fungal internal transcribed spacer (ITS) region. Amplifications were performed in

25 μL volumes with the Qiagen HotStar Taq master mix (Qiagen Laboratories Inc.) using the following conditions: denaturation period of 15 min at 96°C followed by 33 cycles of 96°C for 30 s, 52°C for 30 s, 72°C for 1 min and a final elongation step at 72°C for 10 min. Product quality was verified on a 2% agarose gel. Quantification of each amplicon was performed with Quant-iT™ PicoGreen® dsDNA Assay Kit (Life Technologies). The library was then generated by pooling the same quantity (ng) of each amplicon. The pool (or library) was cleaned up with sparQ PureMag Beads (from Quantabio). The library was quantified using Kapa Illumina GA with Revised Primers-SYBR Fast Universal Kit (Kapa Biosystems). Average fragment size was determined using a LabChip GX (PerkinElmer) instrument. Before sequencing, 15% of the Phix control library was added to the amplicon pool (loaded at a final concentration of 9 pM) to improve the unbalanced base composition on the flowcell. Subsequently, paired-end (2 × 250 bases) sequencing was performed with the MiSeq Reagent Kit v2 on an Illumina MiSeq System (Illumina Inc.).

2.5 | Bioinformatics

We followed the standard ITS pipeline (https://benjjneb.github.io/dada2/ITS_workflow.html) with a modification: in "filter and Trim" section; we changed "multithread = TRUE" to "multithread = 12" to avoid overloading the server. The fungal community structure was determined by filtering, denoising, and assigning taxonomy to paired amplicons with the package DADA2 v.1.8 (Callahan et al., 2016). DADA2 does not throw away singleton reads, however, we did not include the amplicon sequence variants (ASVs) that are only supported by a single read in this study, because singletons are assumed too difficult to differentiate from errors (Callahan et al., 2016). In total, 268 samples were sequenced. First, primers from the reads were removed using a specialized primer/adapter removal tool—cutadapt. The quality of the sequence reads was checked according to the DADA2 workflow. After inspecting the read quality profiles, fungal reads with more than two expected errors (maxEE = 2) and shorter than the length of 50 base-pairs (minLen = 50, minimum length 50 bp was used to remove spurious very low-length sequences) were discarded by the "filterAndTrim" function. Then, amplicon sequence variants (ASVs), which can be utilized to classify groups of species based on DNA sequences, were inferred for each sample, forward and reverse reads were merged and a sequence frequency table was generated. After chimera removal, the taxonomy of the ASVs was assigned with the UNITE database, v. 8.2 (Abarenkov et al., 2010). Ultimately, taxonomic identities were assigned to 100% of ASVs (i.e. 1987 fungal ASVs) at the kingdom level, 91.0% phylum, 79.1% class, 74.8% order, 64.8% family, 57.7% genus and 39.8% at species level.

FungalTraits (Põlme et al., 2020) is a user-friendly trait database of fungi, which combines the information from the databases of FUNGuild (Nguyen et al., 2016) and Fun^{Fun} (Zanne et al., 2020) together with expert knowledge. Based on this FungalTraits database, we assigned the fungal guilds according to their primary lifestyles, among which saprotrophs and plant pathogens were the most common in terms of the number of genera. Therefore, in this study, all detected fungal ASVs were grouped into (1) saprotrophs—receiving nutrients by breaking down dead host cells, which were further divided into "white-rot", "brown-rot", "soft-rot" and other, undefined saprotrophs based on decay types in FungalTraits database; (2) "plant pathogens"—receiving nutrients by harming host cells; and (3) other fungal primary lifestyles (i.e. endophytes, lichenized and ectomycorrhizal fungi).

2.6 | Calculations and data processing

To test for the differences in wood density loss across tree species and different decomposition time, we calculated annual proportional wood density loss (WDL) as:

$$WDLxy = -\frac{WDy - WDx}{WDx \bullet (y - x)}$$

where WDx gives the dry wood density of the sample at the time x and WDy denotes dry wood density at a later decay time y; (y-x) is the decomposition time. In this study, two proportional density losses were calculated. WDL_{01}: wood density loss during the first year of decay (T0–T1); WDL_{14}, wood density loss between decay year one and year four (T1–T4). WDL was first calculated for each replicate, and then averaged over the five replicates of each tree species.

A principal component analyses (PCA) was performed in CANOCO 5.0 using mean species values of 21 wood traits as data points. Two multivariate wood trait axes were generated based on the ordination scores of the first and second wood PCA axis and coined "Wood_PC1" and "Wood_PC2". Similarly, another PCA was conducted using mean species values of 17 bark traits as data points and the multivariate bark trait spectra were generated based on the first two ordination scores of bark PCA, and coined "Bark_PC1" and "Bark_PC2". These four multivariate trait axes were then used for further analyses.

Given the dominant role of saprotrophic fungi in wood decomposition, here we only included saprotrophic fungi in measurements of fungal richness as calculated in the R package "phyloseq", function "estimate_richness" (McMurdie & Holmes, 2013). Notably, all determined fungal richness and saprotrophic fungal richness was highly correlated ($r = 0.89$, $p < 0.05$, Figure S5), and fungal richness per tree species was illustrated in Figure S6. We used centred log-ratio (CLR) transformation converting compositional sequence data to correct for compositional effects and differences in sequencing depth by recasting relative count data with respect to a reference—the sample geometric mean, thereby allowing application of multivariate analyses (Gloor et al., 2017; Sisk-Hackworth & Kelley, 2020). Since CLR transformation requires the replacement of zeros, we replaced the zeros in the dataset by using the "czm" method in the "zCompositions" R package (Palarea-Albaladejo & Martín-Fernández, 2015) before CLR transformation (Gloor et al., 2017). To quantify how fungal community composition varied across different tree species at T1 and T4, two PCAs were performed (one for T1 and the other for

T4). We used mean fungal abundance of each tree species as data points and proportions of different fungal functional groups (i.e. saprotrophs, pathogens and other) as supplementary variables. The ordination scores of the first two PCA axes were obtained and used to present fungal community composition, and coined "Fungi_PC1" and "Fungi_PC2".

2.7 | Statistical analyses

To test how proportional wood density loss differed across tree species, one-way ANOVAs were conducted with the wood density loss WDL_{01} or WDL_{14} as dependent variables followed by Tukey's HSD post-hoc test. The normality of the residuals was checked with the Shapiro test and Q-Q plots. To compare the wood density loss at the two decay times (i.e. T1 and T4), a pairwise *t*-test was conducted. T-tests were carried out to compare how wood density loss varies between the two tree groups (conifer vs. broadleaf), and between the two decomposition times.

Linear regression models were conducted to test the effect of stem traits (i.e. wood_PC1, wood_PC2, bark_PC1 and bark_PC2) or fungal communities (i.e. fungal richness, fungi_PC1 and fungi_PC2) on the wood density loss. To test how stem traits and fungal communities jointly affect wood decomposition process, and test whether and how the important drivers of wood density loss change over time, we performed structural equation models (SEMs) separately for the two decomposition periods (i.e. T1 and T4). The models were evaluated using the "sem" function of the "lavaan" package in R (Rosseel, 2012), with all data being standardized (i.e. z-transformed) prior to analysis. The models were accepted when the Chi-square (χ^2) statistic was insignificant ($p > 0.05$). All statistical analyses were performed using R v. 3.6.1 (R Core Team, 2019) and CANOCO 5.0 (ter Braak & Smilauer, 2012).

3 | RESULTS

Wood density loss differed significantly among tree species (one-way ANOVAs, $F_{12,52} = 5.24$ for WDL_{01}, $F_{12,50} = 5.59$ for WDL_{14}, $p < 0.05$). Overall, wood decomposed more rapidly during both periods for broadleaved species ($WDL_{01} = 22.3\%$, $WDL_{14} = 5.8\%$ $year^{-1}$) as compared to coniferous species ($WDL_{01} = 15.2\%$, $WDL_{14} = 3.1\%$ $year^{-1}$) (*t*-test, $p < 0.05$; Figure 1). With time, the average wood density loss across all tree species declined significantly, from 18.5% $year^{-1}$ (T0–T1) to 4.3% $year^{-1}$ (T1–T4) (*t*-test, $p < 0.05$, Figure 1).

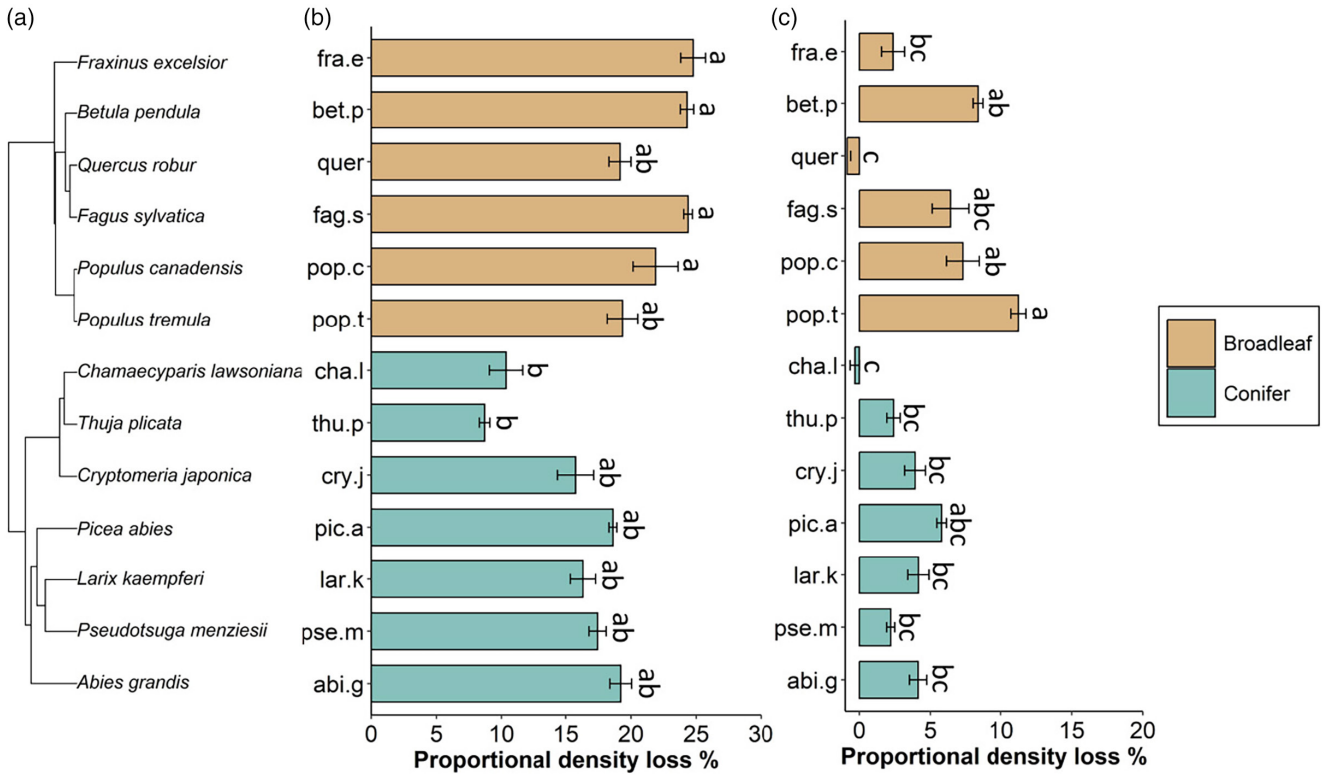

FIGURE 1 Proportional wood density loss varies across 13 tree species at two decay periods, the first year T0–T1 (WDL_{01}) and three follow up years T1–T4 (WDL_{14}). (a) The species phylogeny of tree species. (b, c) The annual proportional density loss for the different species in the first year (b) and three follow-up years (c). For both decay periods, one-way ANOVAs were conducted to test how proportional wood density loss varied across tree species. Bars show mean proportional wood density loss per tree species, and bars accompanied by a different letter are significantly different (Tukey's HSD post-hoc test, $p < 0.05$). Error bars represent the standard error of the mean ($N = 5$, individuals per tree species).

Principal component analyses were conducted to describe variation in wood and bark traits (Figure 2a,b) and fungal community composition across the 13 tree species (Figure 2c,d). For wood traits, the first PCA axis (Wood_PC1) described 67% of the variation and was generally driven by differences between coniferous species with high concentrations of carbon and lignin and broadleaved species with high wood accessibility (i.e. conduit size, ray parenchyma fraction) and nutrient concentrations. The second PCA axis (Wood_PC2) explained 21% of the variation and was negatively associated with pH and positively with antifungal substances (i.e. phenols & tannins; Figure 2a). For bark traits, the first PCA axis (Bark_PC1) explained 58% of the variation and was negatively associated with inner bark thickness, lignin and phenolic concentrations, while the second axis (Bark_PC2) was associated with high pH and nutrient concentrations and low C/N and N/P ratios, and cellulose concentrations (Figure 2b).

Fungal composition on decaying stems was described after one and 4 years of decay. After 1 year of decay, the first fungal PCA axis

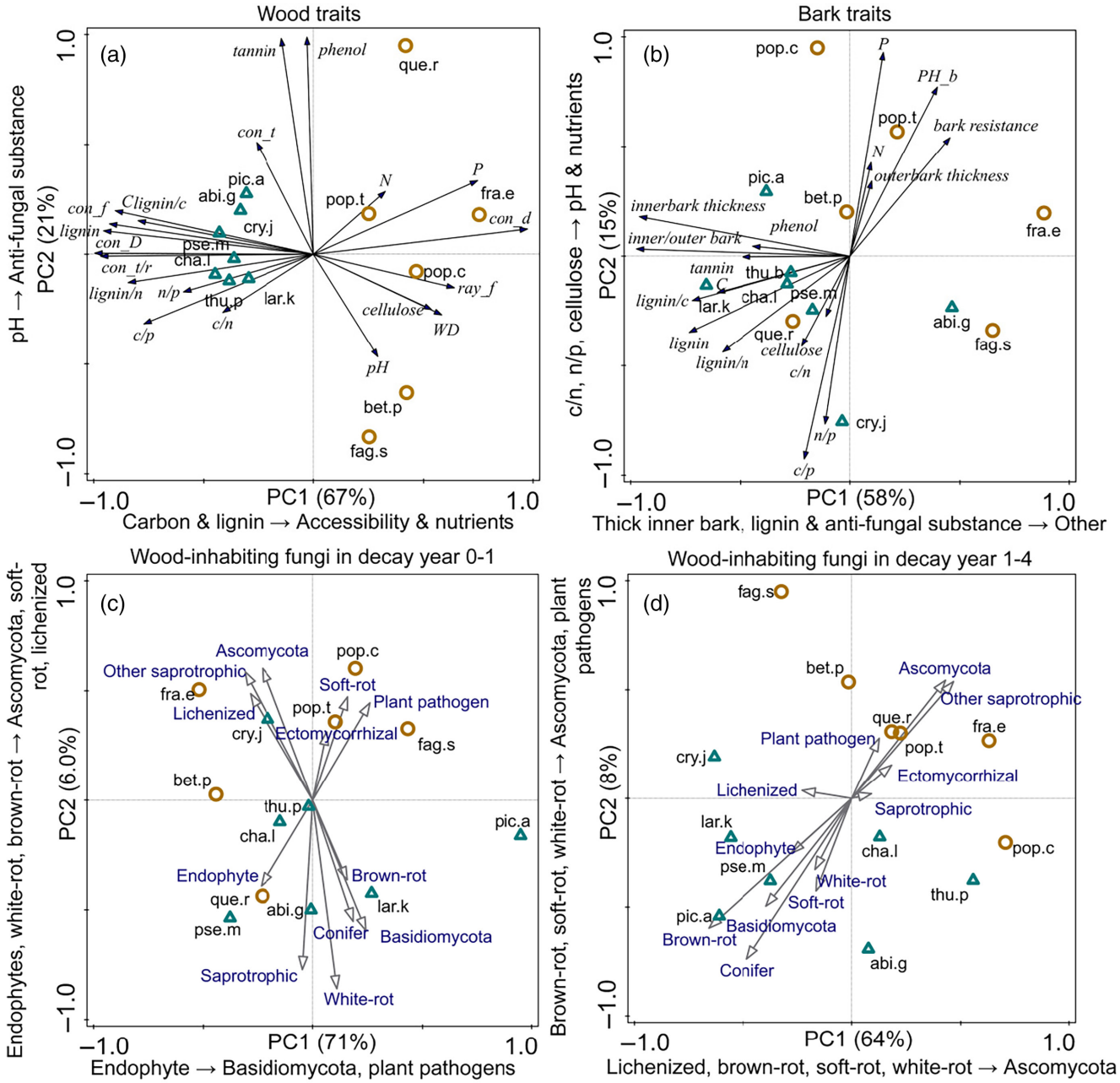

FIGURE 2 Principal component analyses showing the associations among multiple wood (a) and bark (b) traits of 13 tree species and showing how wood-inhabiting fungi vary among 13 tree species at two decaying periods: T1 (decay year 0–1, c) and T4 (decay year 1–4, d); the proportion of different fungal ecotypes was detected and plotted as supplementary variables. Scores of first two PCA axes were extracted and used for further analyses. Blue triangles indicate coniferous species while brown circles indicate broadleaved species. The full species names of the abbreviations were shown in Table S1, and the stem traits are grouped according to different functions: hydraulic conductivity, hydraulic safety, storage, metabolism, chemical defence and physical strength, as shown in detail in Table S2.

(i.e. Fungi_PC1_T1) described 71% of the species variation and was associated with a low proportion of endophytes and high proportions of Basidiomycota and plant pathogens. The second axis (i.e. Fungi_PC2_T1) explained 6.0% and was negatively associated with endophytes, white-rot and brown-rot fungi, but positively associated with Ascomycota, soft-rot and lichenized fungi, which associate with algae or cyanobacteria for energy sources (Figure 2c). After the fourth year, the first fungal PCA axis (i.e. Fungi_PC1_T4) described 64% of the variation and was associated with low proportions of lichenized, brown-rot, soft-rot fungi and high proportions of Ascomycota. The second axis (i.e. Fungi_PC2_T4) explained 8.0% and distinguished between proportions of brown-rot, soft-rot, white-rot fungi versus Ascomycota and plant pathogens (Figure 2d). The results along these first two axes of these PCAs were extracted to represent fungal composition and then used to test their effects on wood density loss over time.

Pairwise linear regressions reflected wood density loss was significantly affected by stem traits but not the fungal communities (Figure 3 and Figure S7). During the first year of decay, stem decomposition rate of 13 temperate tree species increased with the first PCA axis for wood traits (Wood_PC1) (Figure 3a). This relationship was largely driven by the contrast between heartwood-forming

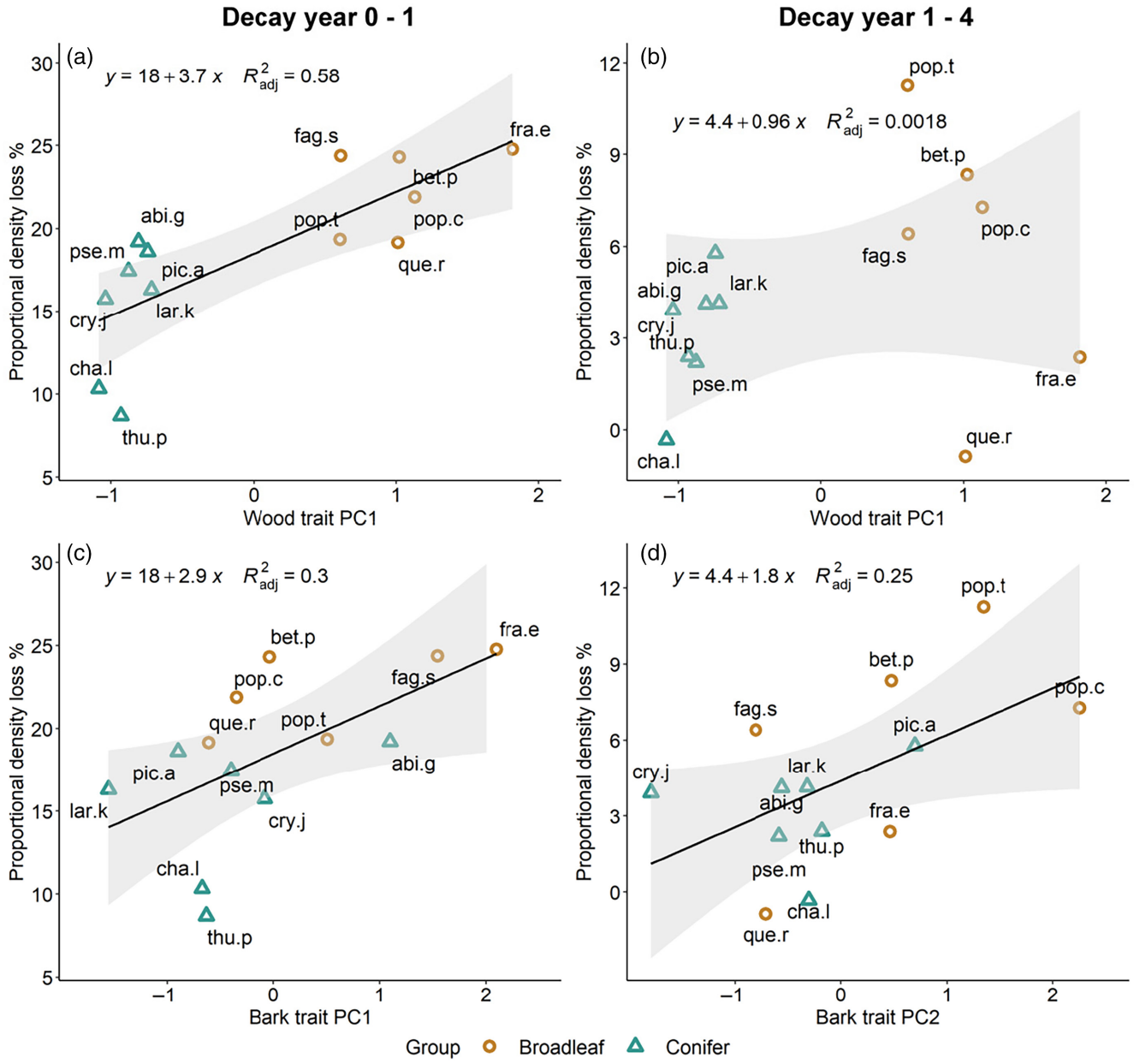

FIGURE 3 Relationships between proportional density loss of 13 tree species and wood (a, b) and bark (c, d) trait values, after one year (T1, left column) and between decay year one and four (T1–T4, right column). Solid line indicates significant relationship ($p < 0.05$). Data of coniferous species are shown as blue triangles and broadleaved species are shown as brown circles. Wood_ trait PC1: high accessibility, nutrients & low carbon, lignin. Bark trait PC1: thin inner bark & low lignin, anti-fungal substance. Bark trait PC2: high pH, nutrients & low c/n, c/p, cellulose.

(exception *Abies grandis*) conifers versus non-heartwood forming (exception *Quercus robur*) broadleaved species, that is broadleaved species with higher wood accessibility and nutrient concentrations had higher decomposition rate. Early wood density loss also increased with the first PCA axis for bark traits (Bark_PC1), namely those traits associated with a thinner inner bark, lower lignin concentrations and lower concentrations of anti-fungal substances (Figure 3c). After 4 years of decay, the effects of wood traits disappeared but bark_PC2 (reflecting high nutrient levels), had a significant positive effect on wood density loss (Figure 3).

Structural equation models provided an integrated picture of how multiple stem traits affect fungal composition and richness, and how stem traits and fungal decomposers jointly impact wood density loss in the 13 temperate tree species (Figure 4). During the first year of decay, wood_PC1 (i.e. wood traits associated with higher wood accessibility and nutrient concentrations) directly impacted wood decomposition rate and explained 78% of the total variation (Figure 4a). Moreover, wood_PC2 (i.e. pH and defence components) was associated with saprotrophic fungal richness and explained 48% of the variation, although without a significant effect on wood

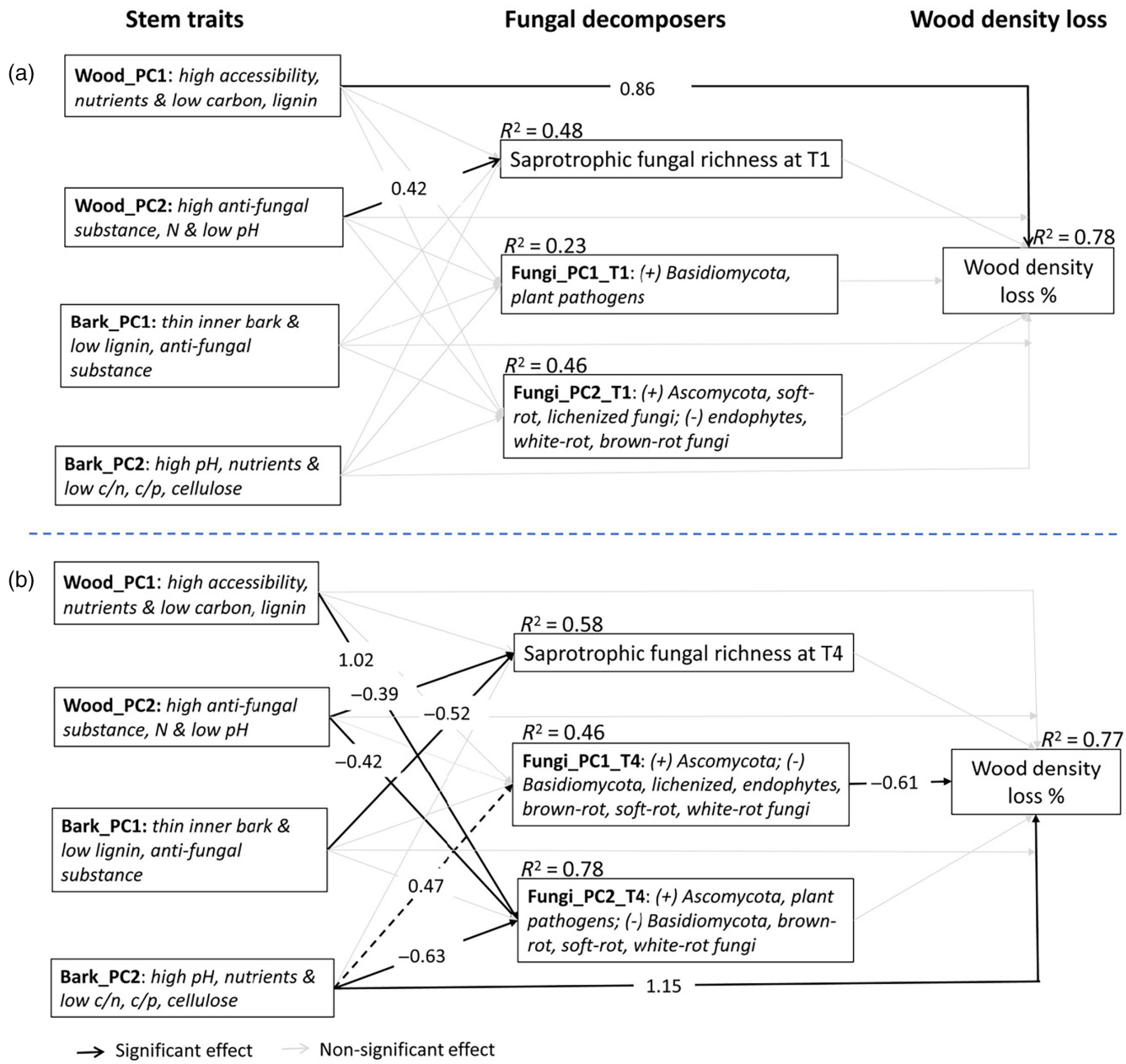

FIGURE 4 Structural equation models for the effects of initial stem traits (wood and bark) and fungal decomposers on wood density loss of 13 species; (a) effect during decay period T0-T1 ($\chi^2_{df=3}=0.64$, $p=0.89$) and (b) effect during decay period T1–T4 ($\chi^2_{df=3}=6.84$, $p=0.08$). Standardized coefficients are shown in the models when significant effects were found. Black arrows indicate significance ($p<0.05$), and dashed line indicate near-significance ($p\leq0.06$).

decomposition rate (Figure 4). No direct effects were found between fungal communities and wood density loss, and the same was true for bark traits (Figure 4a and Table S3).

In the later decay stage, initial stem traits had both direct and indirect effects on stem decomposition rate, together with fungal communities, affecting wood decomposition process (Figure 4b). Bark_PC2, that is bark traits associated with high pH and nutrient level and low physical defence can directly accelerate wood decomposition rate (Figure 4b); this finding was also supported by the linear regression analysis (Figure 3). Meanwhile, these bark traits affected the colonization of fungal communities, and thereby indirectly affected the wood decomposition process (Figure 4). Fungal communities with a higher proportion of white-rot, brown-rot, soft-rot and lichenized fungi (Fungi_PC1_T4) significantly accelerated wood density loss. This indicates that wood traits were the main determinants for wood decomposition in the first decay year, but that the composition of wood-inhabiting fungi combined with bark traits, played increasingly important roles in wood decomposition during the subsequent decay years (T1–T4).

4 | DISCUSSION

In this study, we evaluated how wood and bark traits and fungal decomposers affect wood decomposition of 13 temperate tree species during the early decay phase. In general, broadleaved species had stems that have a high nutrition value and better accessibility, and therefore, decomposed more rapidly than the coniferous species that have opposite trait values. After 4 years in the field, also fungal community composition explained variation in wood density loss across tree species. In the discussion below, we will first focus on variation in wood density loss, then discuss the afterlife effects of stem traits on wood-inhabiting fungi, and finally discuss how stem traits and fungal communities jointly affect wood decomposition of the 13 tree species in different phases during the 4-year decay period.

4.1 | Wood density loss varies across tree species

Wood density loss varied significantly across of the 13 temperate tree species, with the included broadleaved species having a higher wood decomposition rate than the coniferous species (Figure 1). Similarly, an experimental decomposition study in Germany found that density loss was faster for the broadleaved species (*Carpinus*, *Fagus* and *Populus*) in comparison to the coniferous species (*Larix* and *Pseudotsuga*) (Kahl et al., 2017). The slower wood decomposition in coniferous species can be explained by a suite of traits. All studied coniferous species except *Abies grandis* produce heartwood that contains a high amount of anti-fungal substances (e.g. phenols and tannins) and inhibits decomposer activity (Cornwell et al., 2009; Noll et al., 2016; Scheffer, 1966). In contrast, all examined broadleaved species, except *Quercus*, lack heartwood. The strong drop in wood density loss of *Quercus* after the first-year decomposition (T0-T1) is thus likely attributed to the switch in decomposing substrate from easy degradable permeable and nutrient rich oak sapwood to resistant, only slowly degrading heartwood. Additionally, coniferous wood consists of narrow (ca. 20 nm) and short conduits (i.e. tracheids), which are less favourable for the axial spread of fungal hyphae compared to the wide (ca. 80 nm) and long conduits of broadleaved species (Boddy, 2001; Yang, Sterck, et al., 2022). Moreover, conifer wood has a higher a lignin concentration than wood of broadleaf species (31% vs. 21%, Yang, Sterck, et al., 2022) and produces guaiacyl lignin, which is known to be resistant to decomposition (Lamlom & Savidge, 2003; Lourenço et al., 2015). This together with high concentrations of condensed tannins (Hernes & Hedges, 2004) and other species-specific phenolic compounds contributes to its decay resistance. These fundamental differences in wood quality may thus explain the consistently slower decay rate in coniferous species compared to non-heartwood forming broadleaved species across studies. It should however be noted that there is also a large degree of variation in density loss within each of these groups (Figure 1), which can be explained by their bark and wood traits (see below).

Wood density loss declined from 18.5% in the first decay year to 4.3% year^{-1} in the following 3 years. During the initial decay year, the nutritious bark was still attached to the stem, which preserves humidity and creates a favourable microenvironment for the colonization and activity of wood decomposers (Chang et al., 2023; Dossa et al., 2016, 2018). In the following decay years, wood density loss declined markedly, since easily degradable bark and sapwood had already been partly decomposed, and the decomposition process had likely progressed towards the more resistant wood; particularly heartwood of some species is considered more recalcitrant to decomposition for the reasons discussed above (Figure 1). In total, wood density loss declined over the 4-year study period and varied significantly among tree species with generally coniferous species decomposing more slowly than the studied broadleaved species.

4.2 | Stem traits affect the richness and composition of wood-inhabiting fungi

We tested how the initial bark and wood trait values of 13 temperate tree species affect the community composition of wood-inhabiting fungi during 4 years of decay. As decay proceeded, initial stem trait values showed stronger afterlife effects on fungal community composition (Figure 4b); high wood lignin concentrations were associated with higher proportions of Basidiomycota in the fungal community. During initial wood decay, labile compounds are rapidly decomposed, leading to an increased relative concentration of recalcitrant substances. As Basidiomycota are the only microbial phylum that can degrade recalcitrant lignin, their relative abundance would be expected to increase over time during decay (Cornwell et al., 2009; Tláskal et al., 2021; Yang, Poorter,

et al., 2022). Remarkably, high phenolic and tannin concentrations in wood were positively associated with richness of saprotrophic fungi during the first year of decomposition (Figure 4a). Perhaps, the degradation of these toxic and recalcitrant substances (Stokland et al., 2012) requires more fungal specialists. During the subsequent 3 years (decay years T2–T4), with the exhaustion of easy decomposable resources, lignin accumulates, allowing more white-rot specialists that can decompose these recalcitrant substances to establish. To conclude, stem traits showed long-lasting afterlife effects by shaping the richness and community composition of deadwood-inhabiting fungi.

4.3 | Wood decomposition is initially driven by wood traits and later by bark traits

We expected that acquisitive trait values for both wood and bark would be associated with increased wood decomposition rate. As expected, wood traits associated with wide conduits and high nutrient concentrations had a positive effect on wood density loss during the first decay year (i.e. T0-T1); this was found in both pairwise regression analysis and SEM (Figures 3a and 4a). Wider conduits may provide favourable moisture and oxygen conditions and thus facilitate the access for saprobic communities (Cornwell et al., 2009; Kahl et al., 2017; Zanne et al., 2015). Macronutrients are critical resources for wood decomposers, thereby playing important roles in wood decomposition processes (Lee et al., 2020). However, the initial "green" wood traits failed to predict wood decomposability at the later decay stage (i.e. T1–T4) (Figure 4b). Probably during decay, the modified "brown" wood traits are more important for wood decomposition than the living "green" traits. This finding is supported by previous studies that found substrate quality could be altered by the physical and enzyme activities of multiple decomposers, which, in turn, had a long-lasting impact on these decomposers leading to alterations in biogeochemical cycling (Fukasawa, 2021; Guo et al., 2022; Hoppe et al., 2016; Noll et al., 2016).

We expected the explanatory power of initial stem traits would decrease with ongoing decay due to the gradual convergence of substrate during decomposition (Lee et al., 2020; Oberle et al., 2020; Sun et al., 2022). This was true for initial wood traits but not for initial bark traits in this study. We found that bark traits were more important after the 4 year of wood decay (i.e. T1–T4). This result is surprising, given the fact that the bark got soon detached from the wood and was partly peeled-off after 4 years of decomposition (Figure 4b). The bark likely serves as an environmental filter for multiple decay agents (e.g. fungi and invertebrates; Eastwood et al., 2011; Ulyshen, 2016; Zuo et al., 2016) that inhabit and consume bark tissues, and then may start to consume the xylem once the bark has decomposed and partly peeled off. We found that nutrient-rich, and less lignified bark was associated with a higher wood decomposition rate (Figure 4b), indicating that the afterlife effects of one organ (i.e. bark) can affect the decomposability of another organ (i.e. wood; cf. Tuo et al., 2021). In total, stem traits had strong-afterlife effects on wood decomposition rate, tree stems with high levels of acquisitive traits showed higher wood decomposability.

4.4 | Wood decomposition in later stage is driven by fungal composition

We found that fungal community composition did not provide any significant explanatory power with respect to the observed wood density loss in the first year. This result may be a reflection of the importance of other decomposers like beetles, which may consume woody debris faster than fungi (Bultman & Southwell, 1976; Zuo et al., 2016). Moreover, initial fungal community composition may be more a reflection of dispersal limitation and chance than determinism (Van Der Wal et al., 2015), as opposed to selection. Over time, the proportion of saprotrophic fungi in the total fungal community increased significantly in this experiment, from 35% after the first decay year to 75% after the fourth decay year (Yang, Poorter, et al., 2022). This result may reflect a shift from a fungal community dominated by endophytic fungi to the one more dominated by saprotrophic fungi during wood decomposition (van der Wal et al., 2016). In later stage, we found that fungal community composition (i.e. fungi_PC1_T4) had negative effects on wood density loss (Figure 4b). However, this SEM finding was not confirmed by the pairwise regression analysis (Figure 3h), where no significant effect was found between fungal community composition and wood density loss. The possible reason for this discrepancy could be that the negative relationship between fungal_PC1_T4 and wood density loss may be compensated by the facilitation effect of bark_PC2 on wood density loss, because bark_PC2 had a direct positive effect on fungal_PC1_T4 (Figure 4b). Our findings implied that fungal community composition may therefore play a more important role in wood decomposition as decomposition increased for logs that were dominated by brown-rot and white-rot fungi (Figure 4b), where especially the latter group can degrade recalcitrant biopolymers of decaying wood (Blanchette, 2000; Tura et al., 2016).

We predicted that during the initial decay year fungal richness would promote wood decomposition rate because of niche complementary (van der Wal et al., 2013), or facilitative interactions (LeBauer, 2010; Loreau et al., 2001), but that during later stages it would likely be dominated by a narrow range of specialists that are able to degrade recalcitrant polymers that remain after initial decomposition year, thereby eliminating any expected effects of fungal richness (Blanchette, 2000). In this study, we found fungal diversity (in terms of richness) did not affect wood density loss, neither in the initial year (with 103 fungal ASVs per tree species) nor in the later decay years (with 58 fungal ASVs per tree species, Figures 3 and 4), which is not consistent with the niche complementarity hypothesis. A possible explanation could be attributed to the mass-ratio mechanism (Grime, 1998), i.e. wood decomposition rate may be determined by the functional traits of the dominant fungal species rather than the diversity of the total fungal

community. Some studies have found that fungal diversity can positively affect plant litter decomposition through niche complementarity, but only when the total fungal richness is relatively low (e.g. 10 species; Gessner et al., 2010; Nielsen et al., 2011). At higher fungal diversity, there may be redundancy in fungal metabolic abilities (Dang et al., 2005; Setälä & McLean, 2004; van der Wal et al., 2013) or increased inter-specific competition among fungal populations, thereby offsetting or outweighing the positive effects of niche complementarity on wood decomposition (Fukami et al., 2010; Nielsen et al., 2011). Overall, the change in fungal composition and transition into more recalcitrant wood explained the role of fungi in explaining wood decay in years T1–T4.

5 | CONCLUSIONS

Wood decomposition rates varied significantly among tree species, with the studied non-heartwood forming broadleaved species generally showing more rapid decomposition rates than conifers. The relatively slow initial wood decomposition rates of heartwood-forming coniferous species suggest that their dead stems allow for longer-term carbon storage than non-heartwood-forming broadleaved species, which has also been confirmed by other studies that monitored decay over longer time periods (Kahl et al., 2017; Weedon et al., 2009). Initial stem traits and fungal communities jointly affected wood decomposition rates as indicated by SEMs (Figure 4). However, although consistent explanatory power was generated at both decay periods, the relative importance of drivers changed over time with a decreasing influence of wood traits and an increasing influence of fungal community composition. Specifically, variation in wood density loss was initially driven by wood traits, and later by bark traits and fungal community composition. Initial stem traits have long-lasting consequences for wood decomposition rate (cf. Lee et al., 2022) with acquisitive trait values (i.e. high nutrient concentrations and accessibility) increasing wood decomposability during the early decomposition phase. Fungal composition, but not fungal richness, was an important driver of wood decay; with fungal communities dominated by brown-rot and white-rot Basidiomycetes showing higher wood decomposition rates after the first year. Because of complicated interactions among multiple wood decomposers, wood substrates change over time (Hiscox et al., 2015; Noll et al., 2016; van der Wal et al., 2013). Future studies should therefore focus more on changes in stem traits during the decay process, and monitor stem decomposition and the abundance of other important decomposers (e.g. bacteria, invertebrates and vertebrates like woodpeckers) over time. By doing so, we can gain a more complete understanding of the process of wood decomposition, and its consequences for forest diversity, carbon storage and nutrient cycling.

AUTHOR CONTRIBUTIONS

Shanshan Yang, Lourens Poorter, Frank J. Sterck, Ute Sass-Klaassen and Johannes H. C. Cornelissen conceived the ideas and designed methodology. All authors made contributions to data collection. Shanshan Yang, Lourens Poorter, Frank J. Sterck and Ute Sass-Klaassen analysed the data. Shanshan Yang led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

The authors thank many participants of the LOGLIFE Team in various years for help with setting up, maintenance and harvesting. The Schovenhorst estate and Staatsbosbeheer Flevoland were very hospitable and helpful with establishing and in hosting LOGLIFE throughout the experimental period. The authors thank Agata Pijl and Mattias de Hollander for their technical support in DNA extraction and bioinformatics, thank Marcio F.A. Leite and Ohana Y.A. Costa for their support in statistical analyses. Financial support was provided by the C. T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC), the Nora Croin Michielsen Fonds, and the China Scholarship Council.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. Johannes H. C. Cornelissen is an Associate Editor of Journal of Ecology but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Sequence data generated for this study have been deposited in the National Centre for Biotechnology Information's Short Read Archive under BioProject PRJNA768246 (https://dataview.ncbi.nlm.nih.gov/object/PRJNA768246). Other data are accessible in the Dryad Digital Repository: https://doi.org/10.5061/dryad.qrfj6q5pw (Yang et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Information of the 13 studied tree species with their name, abbreviation, major phylogenetic group they belong to, collection site, heartwood presence and wood structure.

Table S2. Stem trait definition and related stem functions.

Table S3. Summary table obtained from structural equation models (SEMs).

Figure S1. Experimental design.

Figure S2. Relationships between climate variables and fungal abundance.

Figure S3. Canonical Correspondence Analysis (CCA) ordination diagram showing how fungal composition in Schovenhorst forest site is significantly affected by decay time, phylogenetic group, stem traits and climate variables.

Figure S4. Comparison of volume-corrected wood mass loss versus proportional wood density loss over 4 years of decomposition.

Figure S5. Relationships between all fungal richness and saprotrophic fungal richness.

Figure S6. Boxplots illustrate that fungal richness based on all fungal sequences and saprotrophic fungal sequences vary among tree species and time point.

Figure S7. Relationships between proportional density loss of 13 tree species and stem trait values (a–d), fungal richness (e–f), and fungal composition (g–j), after 1 year of decay (T1, left column) and between decay year 1 and 4 (T1–T4, right column).

How to cite this article: Yang, S., Poorter, L., Sterck, F. J., Cornelissen, J. H. C., van Logtestijn, R. S. P., Kuramae, E. E., Kowalchuk, G. A., Hefting, M. M., Goudzwaard, L., Chang, C., & Sass-Klaassen, U. (2024). Stem decomposition of temperate tree species is determined by stem traits and fungal community composition during early stem decay. *Journal of Ecology*, *00*, 1–16. https://doi.org/10.1111/1365-2745.14295