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Patterns of natural fungal community assembly during initial decay of coniferous and broadleaf tree logs

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Abstract. Community assembly processes do not only influence community structure, but can also affect ecosystem processes. To understand the effect of initial community development on ecosystem processes, we studied natural fungal community dynamics during initial wood decay. We hypothesize that fungal community assembly dynamics are driven by strong priority effects of early-arriving species, which lead to predictable successional patterns and wood decay rates. Alternatively, equivalent colonization success of randomly arriving spores has the potential to drive stochastic community composition and wood decay rates over time. To test these competing hypotheses, we explored the changes in fungal community composition in logs of two tree species (one coniferous and one broadleaf) during the early stages of wood decomposition in a common garden approach. Initial communities were characterized by endophytic fungi, which were highly diverse and variable among logs. Over the first year of decomposition, there was little evidence for priority effects, as early colonizers displaced the endophytic species, and diversity fell as logs were dominated by a few fungal species. During this period, the composition of colonizing fungi was related to the decomposition rates of sapwood. During the second year of decomposition, fungal community composition shifted drastically and the successional dynamics varied considerably between tree species. Variation in fungal community composition among coniferous (*Larix kaempferi*) logs increased, and there remained no evidence for any priority effects as community composition became stochastic. In contrast, early colonizers still dominated many of the deciduous (*Quercus rubra*) logs, with a temporally consistent impact on community composition. For both tree species, wood decay rates levelled off and the relationship with fungal community composition disappeared. Our results indicate that priority effects are relatively minimal in naturally occurring fungal community assembly processes. Instead, fungal successional dynamics are governed predominantly by combative abilities of colonizing fungi, and factors that shape fungal communities over time can differ considerably between tree species. Our results indicate that an increased focus of competitive strength among species, rather than priority effects, may be key to predict community assembly and the ecosystem process they provide.

Key words: competitive strength; endophytic fungi; 454 pyrosequencing of ITS; fungal interactions; LOGLIFE; natural fungal community assembly; priority effects; succession; wood decomposition; wood traits.

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Introduction

One of the major goals in ecological research is to understand and predict ecosystem functioning. As communities control ecosystem processes, the relationship between community structure and ecosystem functioning received more attention the past decade (Hooper et al. 2005, Nemergut et al. 2013). The composition of biotic communities is suggested to be largely driven by community assembly history (the timing of species arrival) (Chase 2003). The identity and interactions of species that colonize first may affect colonization success of later arriving species. For example, gaining early access to resources or the occupation of space inside a habitat may lead to competitive exclusion of later arriving species. This effect is often referred to as a priority effect (Fukami et al. 2010). Priority effects may be especially important in wood and litter decay systems as leaf and wood senescence results in large substrate inputs on top of established saprotrophic communities (Cline and Zak 2015).

In this study, we focused on natural fungal community dynamics during initial wood decay. Understanding the link between fungal community assembly processes and wood decomposition is crucial to predict global C cycling, under current and predicted climate change scenarios (Bradford et al. 2014). Dead wood alone represents a global C-store of approximately 73 ± 6 Pg (Pan et al. 2011), and its decomposition directly influences atmospheric C pools.

Plant traits, such as lignin content and C:N ratio, are currently regarded as the dominant predictors of wood and litter decomposition rates within biomes or ecosystems (e.g., Cornwell et al. 2009, Fortunel et al. 2009, Weedon et al. 2009). This implicitly assumes that decomposition rates are governed mostly by substrate quality and are largely independent of the attributes of the resident decomposer community. However, a growing body of research highlights the importance of microbial community composition in determining decomposition rates under controlled laboratory conditions (e.g., Strickland et al. 2009, McGuire and Treseder 2010, Hättenschwiler et al. 2011). Interspecific variation in fungal-mediated decomposition rates can be exceptionally high (Boddy 2001), and this was recently shown to explain some of the variation in decomposition rates of English oak (*Quercus robur*) tree stumps and Norway spruce logs (Kubartová et al. 2015, van der Wal et al. 2015). This decomposer-dependent variation in wood decay may contribute to the gap between observed and predicted wood decay rates in current decomposition models (Cornwell et al. 2009), with the potential to alter C cycle predictions at local and global scales (Bradford et al. 2014).

Despite the growing appreciation for the importance of fungal community composition in governing wood decay (Crowther et al. 2014), our capacity to incorporate this information into predictive models is still limited by our poor understanding of the fungal community assembly process. The initial establishment and organization of fungal communities are expected to be a major determinant of the subsequent community structure and functioning (Lindner et al. 2011). Experimental manipulations of early-colonizing saprotrophic fungi can, for example, have strong priority effects, with long-term consequences for fungal communities and wood decomposition rates (Fukami et al. 2010, Hiscox et al. 2015*a*). These manipulative studies can highlight potential mechanisms regarding fungal community dynamics, but it is difficult to identify the importance of these priority effects relative to other community assembly processes.

In natural communities, the assembly process is expected to begin prior to tree death. Before a tree dies, through natural senescence or sudden disturbance (e.g., windthrow, logging), the wood has generally already been colonized by endophytic fungi, which might have the potential to influence the colonization success of later arriving decomposer species (Parfitt et al. 2010). These endophytes may enter from the woody stem tissue, via infection of leaf surfaces, and some visually healthy trees may contain heart rot fungi that colonized the tree via the roots (Parfitt et al. 2010, Gonthier and Nicolotti 2013). They can remain in the sapwood without further development until the tree dies, resulting in different fungal communities along the stem length. Following this initial fungal establishment, later colonizers have to employ combative mechanisms to gain territory, and clear hierarchies of combative ability have been revealed among fungi (Boddy 2000). Fungal–fungal interactions as well as interactions with other wood inhabitants continue to take

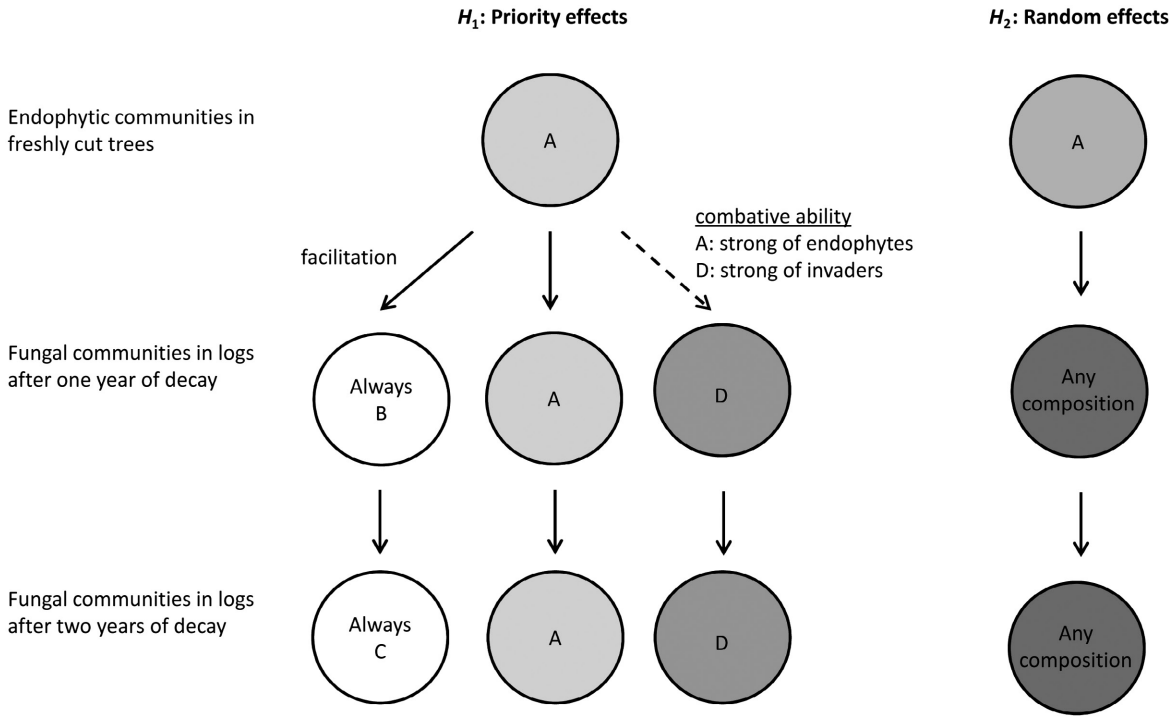


Fig. 1. Hypothesized fungal community assembly processes during log decay. Letters refer to a hypothesized fungal community composition. H_1: During wood decay, previously established fungi affect the probability of successful colonization by invaders via facilitation (left circles). Alternatively, strong combative abilities of endophytic fungi will result in their persistence over time (middle circles). Finally, strong combative abilities among newly arriving fungi will result in high relative abundance of the best competitor (right circles). Broken arrow indicates no priority effect. All of these processes can be considered as priority effects leading to predictable successional patterns. H_2: Randomly arriving fungal spores have equal success to colonize the community, resulting in stochastic community composition over time.

place potentially affecting fungal community development and wood decomposition (Hiscox et al. 2015*b*). Despite these long-standing ideas about the fungal assembly process in dead wood, no study to date has explored the temporal changes in natural fungal community dynamics during the initial stages of decomposition, and the relative importance of different community assembly mechanisms in the actual forest remains untested.

In this study, we make use of high within-site replication of freshly cut logs to study the fungal community dynamics during the first 2 yr of wood decomposition in two contrasting (deciduous and coniferous) tree species in a common garden experiment in a forest stand. This approach allows us to investigate the relation between wood quality, dynamics of decomposer fungal communities, and decay rates during natural colonization of logs by fungi while minimizing the effects of abiotic environmental variation. The early years represent a particularly important phase of the decomposition process, characterized by the highest rates of decomposition (e.g., Krankina and Harmon 1995, van der Wal et al. 2015). In addition, during this period assembly processes are expected to be highly dynamic as fungal pioneer species will be replaced by secondary saprotrophic wood-decaying fungi (Ottosson et al. 2014). We hypothesize that fungal community assembly processes are influenced by priority effects caused by the presence of early colonizers, resulting in predictable successional patterns (Fig. 1, Hypothesis 1). Primary communities can modify the chemical and physical properties of wood, which could facilitate certain

secondary species (Fig. 1, left circles). Alternatively, strong combative abilities of endophytic fungi could result in their persistence over time by reducing the availability of space and resources for secondary colonizers (Fig. 1, middle circles). Finally, strong combative abilities among newly arriving fungi will result in high relative abundance of the best competitor (Fig. 1, right circles). Our alternative hypothesis is that randomly arriving spores have equal success to colonize the community, resulting in stochastic community composition over time (Fig. 1, Hypothesis 2). Using a deciduous and a coniferous tree species, we will explore whether fungal assembly processes and the relationship with wood decay rates are consistent despite strong differences in wood traits.

Materials and Methods

Research site and experimental design

We established a field experiment in a forest located at the Schovenhorst estate in the Veluwe region, in the central part of the Netherlands (52.25 N, 5.63 E) in February 2012. This experiment concerns an in-depth study on microbial decomposition of two tree species and is located adjacent to the LOGLIFE experiment which focuses on the effects of wood traits of many different tree species on decomposition rates (Cornelissen et al. 2012). The site consists of postglacial loamy sand (elevation approximately 30 m above sea level) in which well-drained, acidic (pH ~4) podzolic soils of low fertility have been formed. The plot (±150 × 150 m) is a relatively light-open *Larix kaempferi* (Lambert) Carrière stand with low understory dominated by the grass *Deschampsia flexuosa* and mosses and patches of bilberry (*Vaccinium myrtillus*). Around the plot, deciduous trees (*Quercus robur* and *Quercus rubra* L.) are also present. In this forest, eight individual needle-leaved trees of *L. kaempferi* (subsequently referred to as *Larix*) and eight broadleaf trees of *Q. rubra* L. (subsequently referred to as *Quercus*) were cut. These two contrasting tree species (deciduous and coniferous) were chosen to be able to determine the close-to-maximum extent of the effect of different wood qualities on fungal community assembly processes and the impact thereof on wood decay rates. Trees were selected based on apparent health and trunk diameter at breast height (approximately 25 cm diameter). From each individual tree, 18 sections of 30 cm length were sampled using a chain saw. In addition, two 2 cm thick disks at the bottom and at the upper side of the stem were sawn out for the determination of tree diameter and width of heartwood and sapwood. Next, from each disk a wedge-shaped piece was separated into bark, sapwood, and heartwood (Fig. 2A). Sapwood and heartwood were analyzed for initial wood moisture content, wood density, and composition of wood-inhabiting fungal communities (see below). Logs were randomized per tree species and thin branches were cut off. For each tree species, 16 subplots (2 × 2 m) were created, each subplot hosting nine logs (Fig. 2C, D). Logs within subplots were placed 50 cm apart and subplots were at least 15 m apart. During the incubation, every six weeks the field experiment was visited to check the position of the logs. In a few subplots, wild boars had moved some of the logs and plowed the soil underneath. Disturbed logs were recorded and placed back to their original position. For this study, only undisturbed logs were included for analyses.

Sampling of the field experiment

After the first and second years of incubation (subsequently referred to as T1 and T2, respectively), one log from each subplot was randomly chosen and taken to the laboratory for analyses. From the middle part of each log, a disk of 2 cm thickness was collected with a chain saw. These wood disks were used to determine tree diameter, size of heartwood and sapwood zones, and condition of the bark (intact or peeled off). Next, for each disk, two wedge-shaped pieces representing as much as possible all fungal decay patterns (e.g., interaction zones, type of wood decay) present in the whole disk were cut out and separated into sapwood, heartwood and, if still present, bark. One piece was collected from the part of the log that had been in contact with the soil, and the other piece was collected from the upper side (Fig. 2B). For each year, we thus collected 32 logs, and from these logs, 64 wedge-shaped pieces and 64 sawdust samples (see below) were extracted. Wood samples were stored in plastic bags at −20°C until analyses.

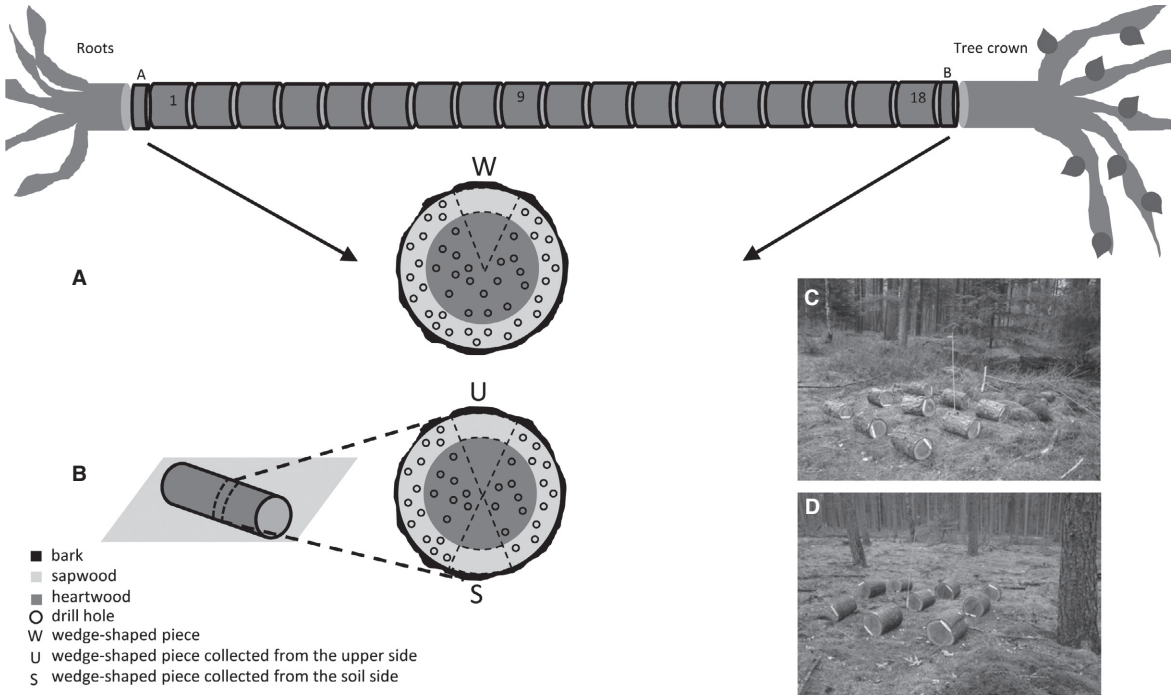


Fig. 2. Sampling design for (A) an individual tree at the start of the experiment and (B) an individual log after each time interval. (A) Logs 1–18 are randomized and placed in different plots. Wood disks (A, B) are used for initial analyses. At the start of the experiment, one wedge-shaped piece (W) in the wood disk was cut out and separated into heartwood, sapwood, and bark, and for every separate piece, the moisture content and density were determined. Drill holes were made to extract sawdust for further laboratory analyses (see *Materials and Methods*). (B) Every year, wood disks were sampled from the middle part of the log and two wedge-shaped pieces were cut out and drill holes were made to extract sawdust. Wedge-shaped pieces and sawdust were processed as described at (A). (C) Picture of a subplot with nine *Larix kaempferi* logs at the start of the field experiment. (D) Picture of a subplot with nine *Quercus rubra* logs at the start of the field experiment.

Wood density, mass loss, and moisture content analyses

Volumes of sapwood and heartwood were calculated using Archimedes' volume displacement method. All samples were then oven-dried at 70°C for 3 d, and the density of each segment was calculated as dry weight per unit volume (g/cm^3). Moisture content (%) was calculated as ((mass wet wood − mass dry wood)/dry wood) × 100%.

Densities of wood samples taken from the basal side and from the upper side of the stem for both *Larix* and *Quercus* were averaged to calculate the initial density for both wood types in each tree. Next, mass loss for every wood type in each sample was calculated as ((density of wood type in corresponding tree at the time of cutting − density of wood type at the time of sampling)/density of wood type in corresponding tree at the time of cutting) × 100%.

Sample preparation

From each disk, sawdust samples were taken using an electric drill (bit diameter 8 mm) in the laboratory. Disks were drilled on a metal plate, and plate and drill bit were thoroughly sterilized with ethanol and water between samples. Sawdust from sapwood and heartwood was separately collected. At least 15 holes were drilled into both heartwood and sapwood. The resulting sawdust samples were pooled resulting in two samples per disk: one from heartwood and one from sapwood. Samples were stored at −20°C until further analyses (Fig. 2A, B).

DNA extraction, amplification, and sequencing

Sapwood and heartwood sawdust samples were frozen in liquid nitrogen and ground into a fine powder. DNA was isolated from 0.15 g fresh weight of sawdust samples using the PowerSoil DNA Isolation Kit according to the manufacturer's instructions (MO BIO Laboratories, Carlsbad, California, USA), with some modifications: After adding solution C1 (causing cell lysis), samples were incubated at 60°C for 30 min, and after adding solution C6 (releasing DNA from spin filter), samples were incubated at 30°C for 10 min. The nuclear rDNA internal transcribed spacer (ITS) region was amplified using the fungal-specific primer pair fITS9 and ITS4 (Ihrmark et al. 2012). Adapter sequences were added to the primers as recommended by Roche as well as 6-bp tags specific for each sample. PCRs were performed in 25 μL reaction mixtures and contained 400 μmol/L of each dNTP, 1 U of FastStart Expand High Fidelity Polymerase (Roche Applied Sciences, Indianapolis, Indiana, USA), 2.5 μL 10× PCR buffer with $MgCl_2$, 10 μmol/L of each of the two primers, 2.5 μL BSA (4 mg/mL), and 1 μL DNA (1–10 ng). The temperature cycling PCR conditions were as follows: denaturation at 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, 56°C for 30 s, and 72°C for 1 min. The final extension step was 72°C for 10 min. After confirming the presence of expected sizes of PCR products by agarose-gel electrophoresis, PCR products from four reactions were pooled per sample and purified using a QIAquick PCR Purification Kit (Qiagen, Venlo, the Netherlands). DNA in samples was quantified by a fluorescence-based method (PicoGreen assay; Life Technologies, Bleiswijk, the Netherlands), and each PCR sample was normalized to 50 ng and pooled together for multiplex sequencing. The samples were sequenced (Macrogen Company, Seoul, South Korea) on a Roche 454 automated sequencer and GS FLX system using titanium chemistry (454 Life Sciences, Branford, Connecticut, USA).

Bioinformatics

Sequences and quality information were extracted from the Standard Flowgram Format (SFF) files using the SFF converter tool in the Galaxy interface (Goecks et al. 2010). The 454 SFF files are deposited in the European Nucleotide Archive (http://www.ebi.ac.uk/ena/data/view/PRJEB9030). Sequences were analyzed as described in van der Wal et al. (2015). The sequences passing the quality control thresholds were clustered into operational taxonomic units (OTUs) using USEARCH version 5.2.236 (Edgar 2010) with a minimum sequence identity cutoff of 97%. The average length of the ITS sequences passing the filtering step was 363 bp. For each operational taxonomic unit (OTU), the most abundant sequence was selected as a representative for all sequences assigned to that OTU. Taxonomic assignment was performed for the representative sequences by comparing them with known reference sequences in the UNITE and GenBank (NCBI) database using the Blastn algorithm. Sequences were, whenever possible, identified to the species (>98% similarity) or genus (94–97% similarity) level. The relative abundance of each OTU was calculated by dividing the number of sequences per OTU by the total number of sequences per sample. We refer to dominant OTUs when they account for ≥10% of all the sequences in each sample, and frequent OTUs when they occur in at least two logs.

Enzyme assays

Enzyme activities (laccase, manganese peroxidase, cellulase, and hemicellulase) were assayed spectrophotometrically in the same extracts according to van der Wal et al. (2007). Briefly, 8 mL of MilliQ water (Millipore BV, Etten-Leur, the Netherlands) was added to 1 g of sawdust and shaken for 1 h at room temperature, and then, the slurry was pressed over a stainless steel filter (containing pores with a diameter of 2 mm). The supernatants were kept at −20°C until analysis of enzyme activities.

Data analysis and statistics

Relationships between the percentage of mass loss, wood moisture content, tree diameter, ratio between width of heartwood and sapwood, OTU richness, fungal diversity, and fungal evenness were calculated by linear regression. Differences in mass loss between tree species, wood type, and sample year were tested by analysis of variance (ANOVA) or by the nonparametric Mann–Whitney *U* test. Statistical significance was set at $P < 0.05$, and analyses were performed using SPSS (version 20.0.0; Chicago, Illinois, USA).

Ordination analyses were performed in Canoco version 4.5 (ter Braak and Šmilauer 2002). Canonical correspondence analysis (CCA) was used to explore the relationships between fungal community composition and tree species, stem height, percentage of mass loss, tree diameter, wood moisture content, and extracellular enzyme activities. Significance of canonical axes was assessed by the forward approach using Monte Carlo permutation tests under the reduced model. Canonical correspondence analysis was performed separately on the samples collected from T1 and T2.

Fungal diversity was calculated as the Shannon index $H' = -\Sigma(p_i \times \ln p_i)$, where p_i represents the relative abundance of species (OTU) i, and the Shannon's equitability (evenness) $E_H = H'/\ln S$, where S represents the total number of species (OTUs) present in the community.

Spatial distances between *Larix* and *Quercus* subplots were manually determined in the field using a measuring tape. Next, to examine the correlation between spatial distance and the degree of similarity in fungal communities, the Bray–Curtis similarity measure between each pair of samples was calculated for use in the Mantel tests (Horner-Devine et al. 2004, Fierer and Jackson 2006). All analyses were calculated per tree species and performed in Past v.2.16 (Hammer et al. 2001). Bray–Curtis similarity measure was used for fungal community data and Euclidean distances for spatial data.

Results

Wood densities and bark loss

At the start of the experiment, there were no differences between densities of wood samples taken from the basal side and from the upper side of the stem ($P > 0.12$) for either *Larix* or *Quercus*. The average densities of *Larix* heartwood and sapwood were 0.51 ± 0.05 and 0.58 ± 0.05 g/cm^3, respectively. For *Quercus*, the average densities of heartwood and sapwood were 0.62 ± 0.04 and 0.69 ± 0.06 g/cm^3, respectively. After 1 and 2 yr of decomposition on the forest floor, there were no differences between wood mass loss of

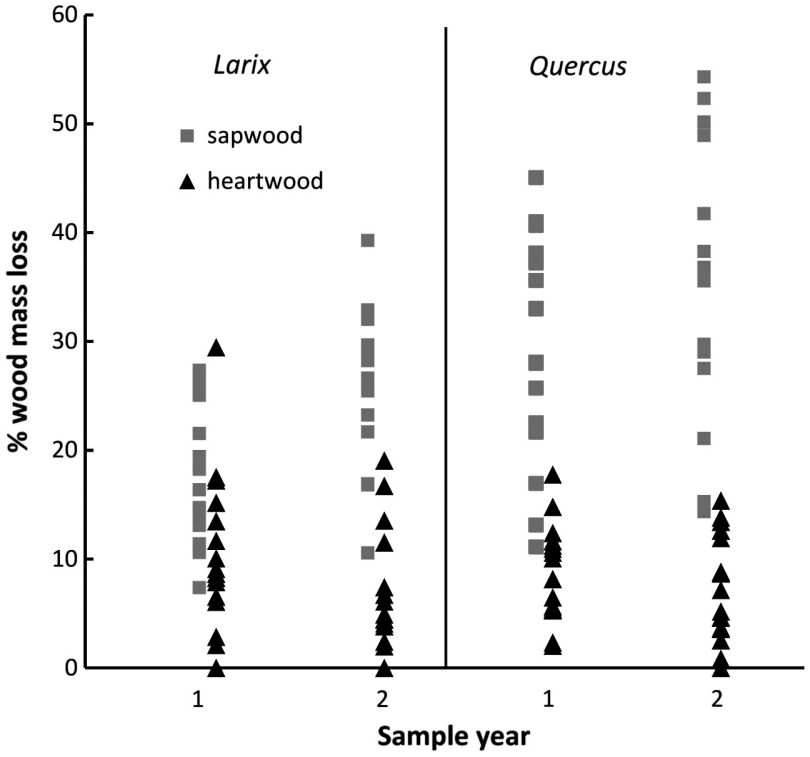


Fig. 3. Wood mass loss (%) of heartwood (black pyramids) and sapwood (gray squares) from *Larix* and *Quercus* logs after 1 and 2 yr of decomposition.

samples taken from the upper side and from the soil side of logs ($P > 0.05$) for both heartwood and sapwood and for both *Larix* and *Quercus*. Therefore, densities of wood sampled from the soil side and upper side of the log were grouped to calculate differences in mass loss for heartwood and sapwood per tree species.

After 2 yr, decay rates (mass loss) of *Larix* sapwood and heartwood were 25.7 ± 6.7% and 7.1 ± 5.2% (average ± SD), respectively. During the same period, mass losses of *Quercus* sapwood and heartwood were 34.9 ± 12.1% and 7.3 ± 4.8%, respectively. For both wood types and both tree species, variation among samples was considerable (Fig. 3). After the first year, mass loss varied over a range of more than threefold for both tree species and for both wood types. After the second year, this range had increased to almost fourfold differences in mass loss. In general, sapwood decomposed faster than heartwood ($P < 0.01$), although in *Larix* this was only visible after the second year (Fig. 3). Differences in decay rates between tree species were found; *Quercus* sapwood decomposed faster than *Larix* sapwood at T1 and T2 ($P < 0.01$). Remarkably, there were no significant differences in mass loss for both heartwood and sapwood between T1 and T2 ($P > 0.15$), except for *Larix* sapwood that showed a small increase in decay in the second year ($P < 0.01$). This indicates that most wood decay took place in the first year and thereafter leveled off.

Bark was still present on all logs after 1 yr of decay, but after 2 yr of decomposition, 44% of the *Larix* logs and 38% of the *Quercus* logs were losing their bark. No relationship could be found between loosening of bark and mass loss for either of the wood types ($P > 0.07$).

Relationships between wood decay, moisture content, and log characteristics

After 1 yr of decomposition on the forest floor, *Quercus* heartwood and sapwood samples taken from the soil side of the log were more moist than samples from the upper side of the log ($P < 0.01$). This was not the case for *Larix* wood ($P > 0.63$). In the second year, all wood that was sampled from the soil side of the log had a higher moisture content ($P < 0.03$), except for *Quercus* sapwood ($P = 0.07$). Because moisture contents in wood samples from the soil side were at least in some cases higher, mass loss of wood samples from the soil side and upper side of the logs was separately analyzed to determine the relationship between mass loss and moisture content. Overall, there was a significant positive relationship between mass loss and moisture content ($P < 0.01$, $n = 256$). A positive relationship was also found between sapwood decay and log diameter after 2 yr of decay ($P < 0.01$).

General pattern and taxonomic results of fungal communities in wood

In total, 1,119,561 high-quality sequences were obtained from 33 wood samples at T0 (mainly *Larix*), 60 wood samples at T1, and 60 wood samples at T2. The mean number of sequences per sample was 7317. We identified in total 1565 different OTUs. Of these OTUs, 950 belonged to Ascomycota, 407 to Basidiomycota, 20 to Zygomycota, 16 to Chytridiomycota, and 12 to Glomeromycota, and 160 OTUs could not be classified to known phyla (Appendices S1, S2, and S4). In general, fungal communities differed clearly between wood collected from freshly cut trees, T1 and T2 logs (Appendix S3). In addition, fungal communities were very different between *Quercus* and *Larix* logs. Below we discuss the fungal community dynamics in more detail.

Based on the relative abundance of OTUs, a clear shift from a 5:1 ratio of OTUs assigned to Ascomycota and Basidiomycota in fresh *Larix* trees toward an equal ratio of OTUs assigned to Ascomycota and Basidiomycota in logs decaying for 1 and 2 yr was observed. After 1 yr of decomposition, the dominance of Basidiomycota in sapwood was even larger than in heartwood (Appendix S1). In *Quercus* logs, a 3:1 ratio of OTUs assigned to Ascomycota and Basidiomycota was observed for both years (Appendix S2). For both tree species, a slight increase of OTUs assigned to Zygomycota was observed after 2 yr of decomposition.

Fungal community composition in relation to stem height at the time of tree cutting

At the time of tree cutting, there were significant differences in fungal communities inhabiting the basal and the upper part of the *Larix* tree stem ($P < 0.01$), but there were no differences in fungal community composition between sapwood and heartwood ($P > 0.74$; Fig. 4A). At the basal part of the tree, most dominant and frequent OTUs were identified as *Serpula himantioides*, *Heterobasidion annosum*, *Phaeomollisia piceae*,

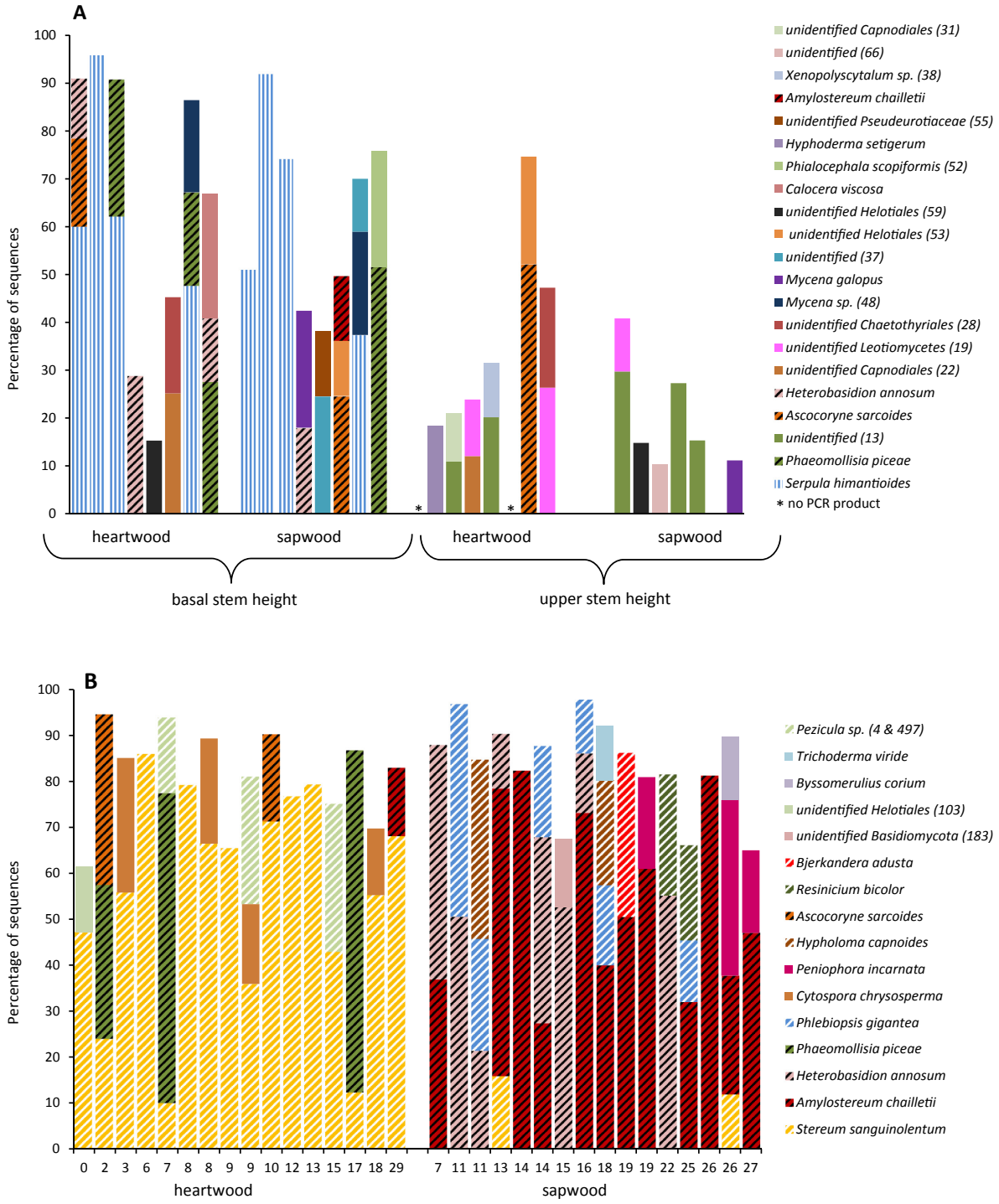


Fig. 4. Percentage of most abundant operational taxonomic units (OTUs) in samples collected from *Larix* trees or logs.

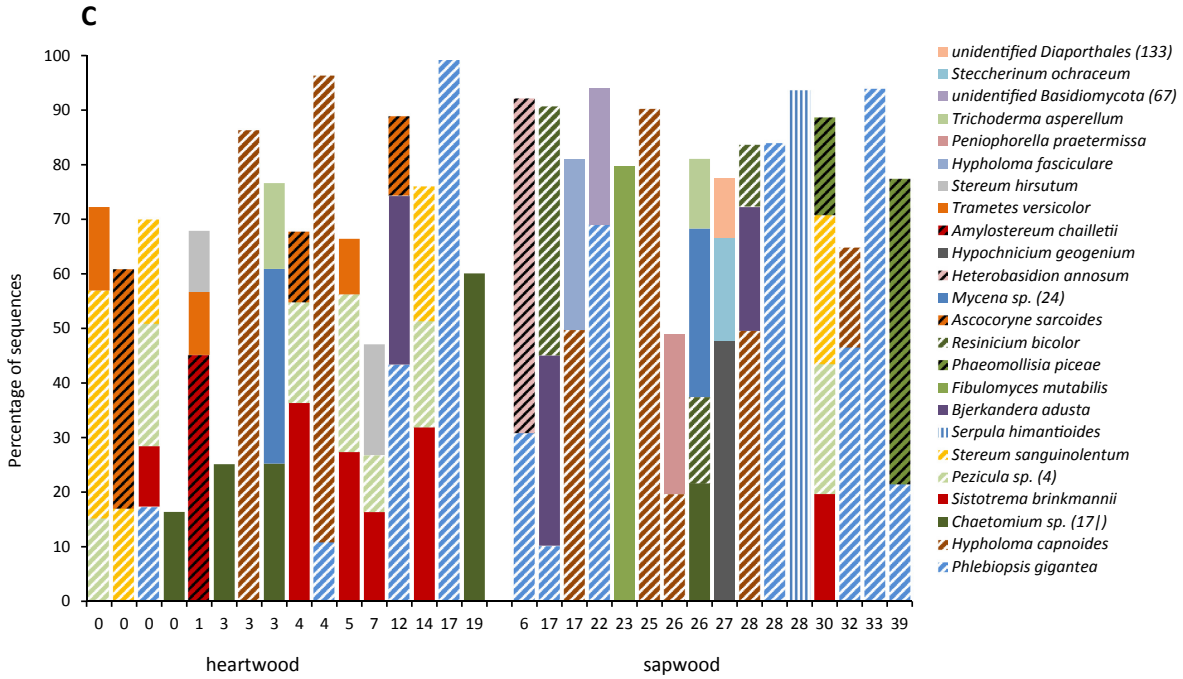


Fig. 4. Continued.
Numbers between brackets indicate OTU number of OTUs that could not be identified to the species level. On the horizontal axis the type of wood (heartwood, left or sapwood, right) is presented. Black hatched bars represent fungal OTUs that were found in freshly cut trees and logs that had decayed for 1 and 2 yr on the forest floor. Vertical striped bars represent fungal OTUs that were found in freshly cut trees and logs that had decayed for 2 yr. (A) Percentage of most abundant OTUs in samples collected from freshly cut *Larix* trees. On the horizontal axis, the stem height (basal stem or upper stem height) is presented. (B) Percentage of most abundant OTUs in samples collected from *Larix* logs that had decayed for 1 yr on the forest floor. On the horizontal axis, the percentage mass loss per sample is presented. (C) Percentage of most abundant OTUs in samples collected from *Larix* logs that were decaying for 2 yr on the forest floor. On the horizontal axis, the percentage mass loss per sample is presented.

Ascocoryne sarcoides, and *Mycena* sp. At the upper part of the stem tree, the most dominant and frequent OTUs were assigned to an unidentified *Leotiomycetes* and an unidentified OTU. The number of OTUs was large; at the basal stem height 513 OTUs and at the upper part of the tree 745 OTUs were found.

No relationships were found between the spatial distance of the trees (location where they were cut) and endophytic fungal community composition (lower and upper parts of the stem separately tested, $P > 0.32$). Thus, living trees that were growing more closely together were not more similar in endophytic fungal community composition than trees growing further away.

It was only possible to determine the fungal community composition in sapwood of three freshly cut *Quercus* trees; from other samples, we were not able to obtain any PCR products (data not shown). This was probably due to the presence of inhibiting toxic compounds in oak heartwood (Schmidt 2006), and a very low endophytic fungal biomass in the freshly cut trees (Saikkonen et al. 1998).

Fungal community dynamics over 2 yr of Quercus *and* Larix *log decomposition*

After 1 yr of decomposition, the fungal community composition in *Larix* logs had completely changed compared to the communities found in freshly cut trees. The relationship with stem height had disappeared ($P = 0.08$) and significantly different fungal communities were found in heartwood and sapwood ($P < 0.01$; Fig. 4B). In heartwood, dominant and frequent OTUs could be assigned to *Stereum sanguinolentum*, *Phaeomollisia piceae*, *Ascocoryne sarcoides*, *Pezicula*

sp., and *Cytospora chrysosperma*. In sapwood, dominant and frequent OTUs could be assigned to *Amylostereum chailletii*, *Heterobasidion annosum*, *Phlebiopsis gigantea*, *Hypholoma capnoides*, *S. sanguinolentum*, *Peniophora incarnata*, and *Resinicium bicolor*. After 2 yr of *Larix* decomposition, the fungal community composition had again completely changed (Fig. 4C). The differences between heartwood and sapwood communities had disappeared ($P > 0.16$) and no effect of stem height could be found ($P > 0.09$). In heartwood, dominant and frequent OTUs could be assigned to *Pezicula* sp., *S. sanguinolentum*, *Trametes versicolor*, *A. sarcoides*, *P. gigantea*, *Sistotrema brinkmannii*, *Chaetomium* sp., and *H. capnoides*. In sapwood, dominant and frequent OTUs belonged to *P. gigantea*, *Bjerkandera adusta*, *R. bicolor*, *H. capnoides*, and *Phaeomollisia piceae*.

After 1 and 2 yr of decomposition of *Larix* logs, a few dominant OTUs determined the fungal communities (Fig. 4B, C) and this coincided with a drastic drop in H' diversity and species evenness over time: Overall, in heartwood the average H' diversity and evenness changed from 2.63 (at T0) to 1.23 and finally to 1.99 at T2, and from 0.55 to 0.35 to 0.49 at T2, respectively. In sapwood, the average H' diversity and evenness decreased from 3.00 to 1.32 to 1.27, and from 0.59 to 0.44 to 0.39. Thus, the biggest reduction in fungal diversity and evenness occurred during the first year of decomposition ($P < 0.01$).

The absence of sequence information of freshly cut *Quercus* trees prevented the comparison of fungal community composition between logs at T0 and T1. However, a similar differentiation between fungal community composition in heartwood and sapwood was found ($P < 0.01$), and also, here we could not detect a relation between fungal community composition and stem height ($P > 0.07$; Fig. 5A). In heartwood, dominant and frequent OTUs could be assigned to *Pezicula* sp., *Penicillium thomii*, *P. carneum*, *P. corylophilum*, *Cadophora* sp., and *C. chrysosperma*. In sapwood, dominant and frequent OTUs could be assigned to *T. versicolor*, *Cadophora malorum*, *Diatrype stigma*, *P. incarnata*, and *B. adusta*. After 2 yr of *Quercus* decomposition, the fungal community composition had changed compared to communities found at T1 (Fig. 5B). Differences between heartwood and sapwood communities disappeared ($P > 0.71$), and no effect of stem height could be found ($P > 0.51$). Clearly, *T. versicolor* and *Pezicula* sp. still dominated, now both in heartwood and in sapwood. *Moristroma* sp. always co-occurred with *Pezicula* sp. and *Phlebia radiata* became dominant as well (Fig. 5B).

Also in *Quercus* logs, a few dominant OTUs determined the fungal community composition (Fig. 5). The average H' diversity and evenness in heartwood were 1.43 and 0.41 at T1, and 1.92 and 0.59 at T2. In sapwood, the average H' diversity and evenness decreased from 3.93 (based on three samples at T0) to 1.85 to 1.53 at T2, and from 0.84 at T0 to 0.49 to 0.41 at T2. Thus, as in *Larix*, the biggest reduction in fungal diversity and evenness in sapwood appeared to occur during the first year of decomposition ($P < 0.01$).

After 1 yr of decomposition for both tree species, the variation in fungal communities among logs was exceptionally low, and few OTUs were almost dominating the total fungal community (Figs. 4B and 5A). After 2 yr of decomposition, the variation in fungal communities among logs greatly increased in *Larix* logs, but only slightly in *Quercus* logs (Figs. 4C and 5B). Comparing dominant fungal OTUs between *Larix* and *Quercus* logs reveals that certain OTUs are almost exclusively found in one tree species. In *Larix* logs, *P. piceae*, *A. chailletii*, *H. annosum*, *P. gigantea*, and *H. capnoides* were dominantly and frequently present, but represented less than 1% of all the sequences in *Quercus* logs. On the other hand, in *Quercus* logs, *C. malorum*, *D. stigma*, *P. carneum*, *P. corylophilum*, *Cadophora* sp., *P. radiata*, and *Moristroma* sp. were dominantly and frequently present, but represented less than 1% of all the sequences in *Larix* logs (Figs. 4 and 5 and Appendix S5). However, there were also dominant and frequent OTUs present in logs of both tree species; in heartwood of *Larix* and *Quercus* logs, OTUs assigned to *Pezicula* sp., *C. chrysosperma*, and *T. versicolor* were found. In sapwood of both tree species, OTUs assigned to *P. incarnata* and *Pezicula* sp. were observed.

Fungal community composition in relation to wood decay rates

After 1 yr of *Quercus* decomposition, the H' diversity and evenness were negatively related to sapwood decay ($P < 0.03$), whereas after 2 yr of *Quercus* decomposition, OTU richness was positively related to heartwood decay ($P = 0.01$). Other relationships between fungal diversity and wood decay were not found.

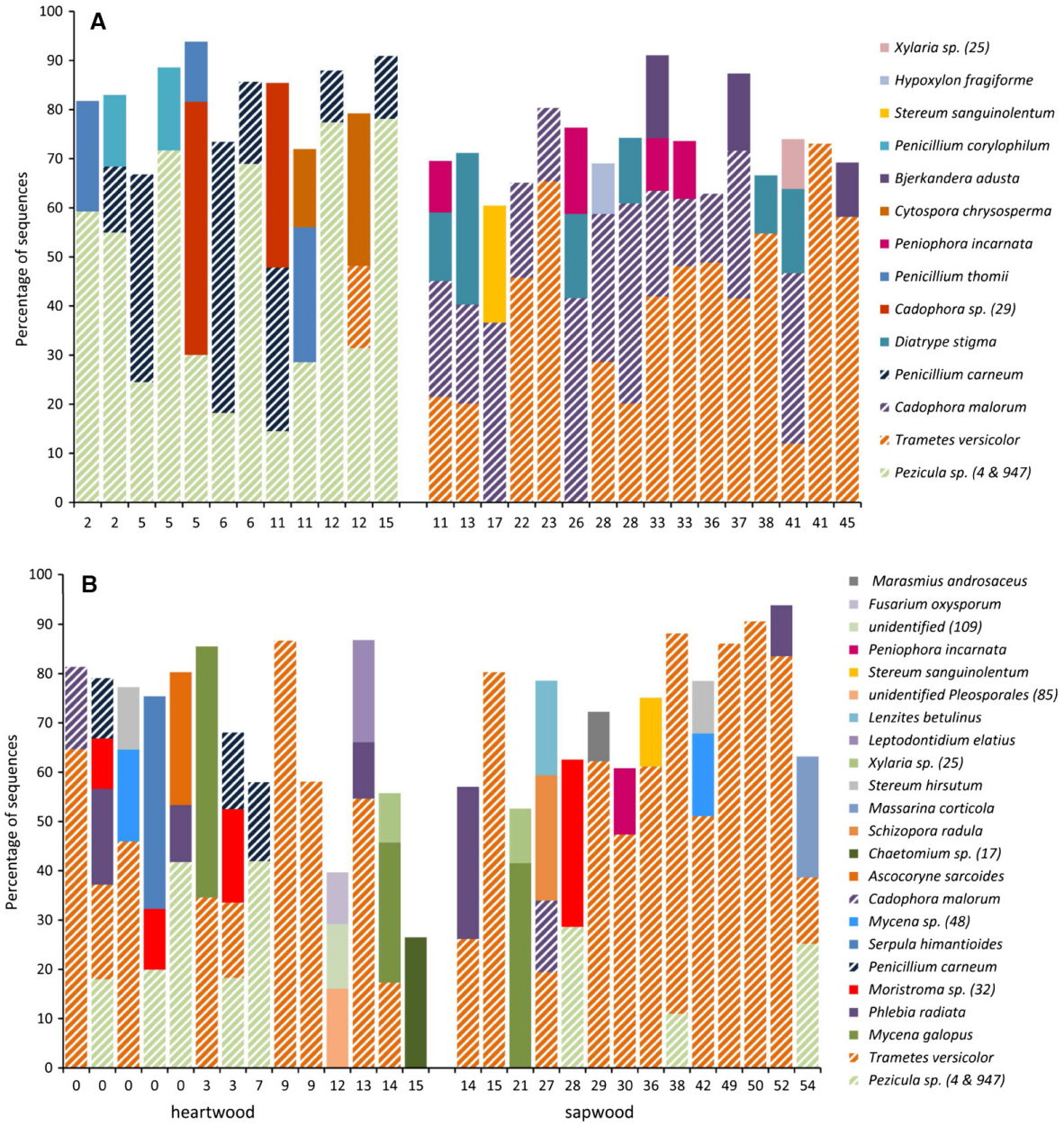


Fig. 5. Percentage of most abundant operational taxonomic units (OTUs) in samples collected from *Quercus* logs that had decayed for 1 yr (A) or 2 yr (B) on the forest floor. Numbers between brackets indicate OTU number of OTUs that could not be identified to the species level. On the horizontal axis, the type of wood (heartwood or sapwood) and percentage mass loss per sample are presented. White hatched bars represent fungal OTUs that were both found in logs that had decayed for 1 and 2 yr.

The fungal community composition in heartwood of *Larix* logs was not related to wood decomposition ($P > 0.55$) after 1 yr of decomposition. There was a positive trend between fungal community composition and sapwood decay ($P = 0.058$). Logs that were decomposing more quickly harbored the dominant OTU identified as *P. incarnata* (Fig. 4B). *A. chailletii*, however, dominated in sapwood of almost every log without any relation with sapwood decay. After 2 yr

of *Larix* decomposition, the fungal community composition was not related to heartwood or sapwood decay ($P > 0.34$). Fig. 4C shows that variation in fungal communities among logs increased, showing no clear pattern with mass loss; for example, *P. gigantea* was abundant in several logs showing different mass losses.

Also for *Quercus* logs, similar patterns between fungal community composition and wood decay rates were observed. After 1 yr of decomposition, no relationship between fungal community composition and heartwood decay could be observed ($P > 0.58$); however, fungal community composition was significantly correlated with sapwood decay ($P = 0.03$). Fig. 5A shows that one of the abundant OTUs in logs that had decomposed more strongly consisted of *B. adusta*. After 2 yr of *Quercus* decomposition, fungal community composition was not related to heartwood or sapwood decay ($P > 0.20$). *T. versicolor* was very abundant throughout all logs with different decomposition rates (Fig. 5B).

For both tree species and time points, other variables (moisture content and log diameter) were not significantly related to fungal community composition ($P > 0.08$).

Enzymes

Overall, there was a positive relationship between the activities of all enzymes (cellulase, hemicellulase, laccase, and manganese peroxidase) and mass loss ($P < 0.01$, $n = 128$). Enzyme activities in sapwood were much higher than in heartwood ($P < 0.01$), in accordance with the higher wood decay rate in sapwood (see above). Overall, cellulase activity was higher in *Larix* than in *Quercus* wood ($P < 0.02$), whereas laccase activity was much higher in *Quercus* wood ($P < 0.01$). After 2 yr of decomposition, manganese peroxidase and hemicellulase activity had significantly increased ($P < 0.01$), whereas cellulase and laccase activity remained at similar levels over time. For every year, wood type, and tree species, enzyme activities were not related to fungal community composition (CCA; $P > 0.07$).

Relationship between fungal communities and spatial distances

There were no correlations between spatial distances between plots and differences in fungal community composition among *Larix* and *Quercus* logs for both wood types and time points ($P > 0.25$). Thus, logs that were located closer to each other were not more similar in fungal community composition than logs that were located further away. This indicates that fungal community composition was likely not influenced by local environmental factors, supporting the basic idea for this common garden approach.

Discussion

Our field study reveals some of the controls on the successional community dynamics of fungal species in dead wood and highlights the functional consequences of these changes in community composition. During the first year of decomposition, the basal sections of *Larix* trees differed from the higher sections. Basal sections were dominated by endophytic, pathogenic, and butt rot fungi, such as *Heterobasidion annosum*, *Phaeomollisia piceae*, and *Serpula himantioides*. These fungi typically colonize living trees via the stem that is in contact with the soil, and continue to decay the wood after felling or tree death (Koch and Thomsen 2003). However, although these fungi were dominant at the time of tree cutting, their abundances fell after 1 yr of decomposition, and their influence on overall fungal community composition (i.e., the difference between the composition at the bottom and the top of logs) had diminished by this time (Fig. 4A, B). No clear associations could be found between the highly diverse and different endophytic fungal communities that were initially present in individual trees (in *Quercus* based on three samples) and the low diverse and uniform fungal communities among logs after 1 yr. We reveal little evidence for priority effects of these endophytic fungi as the initial community in both tree species diminished after a year, with little bearing on the subsequent establishment of fungal species. The most likely scenario is that newly arriving saprotrophic fungi with highly combative abilities were able to successfully colonize the dead trees, thereby outcompeting the less competitive endophytic fungi (Boddy 2001). In addition, endophytic fungal biomass can be low or highly localized to infections in the freshly cut trees (Saikkonen et al. 1998), leaving empty niches for

primary wood-rotting fungi that are specialized in colonization of fresh, relatively homogeneous, wood. Colonization of fungal spores with high combative abilities probably occurred via random dispersal, or via dispersal by insect vectors such as in the case of the fungus *Amylostereum chailletii*. This fungus has a symbiotic relationship with siricid woodwasps that inoculate the fungus into sapwood of living trees (Ryan and Hurley 2012). Dispersal of fungal spores by wind may be limited by distance of more than a few hundred meters (Norros et al. 2012); however, the plot is at most 150 × 150 m. No relation between spatial distance between plots and differences in fungal community composition among logs was found, also indicating that there was no or weak dispersal limitation.

After the second year of decomposition, fungal community patterns became less uniform across *Larix* logs. As with the first year, priority effects appeared to be minimal as there were no indications of impact of primary communities on secondary communities. The changes in fungal community composition over the entire 2 yr were considerable. For example, *A. chailletii* dominated in sapwood and *S. sanguinolentum* in heartwood during the first year, but were almost entirely replaced by several different fungi by the end of the second year. Although we sampled the logs destructively, and priority effects could not be tested on exactly the same logs, the high-replication design of our experiment allowed us to show the consistent lack of priority effects (Fig. 4). In contrast to the apparently stochastic community patterns in *Larix* logs, we found evidence for priority effects in *Quercus* logs, as a few early colonizers still dominated the fungal community after 2 yr. *Trametes versicolor* and *Pezicula* sp. were able to persist, and even colonized both heartwood and sapwood. Dominance of *Moristroma* sp. was always in combination with high abundance of *Pezicula* sp., possibly pointing to facilitative interactions. The strong differences in fungal community dynamics are likely to be the result of inherent wood characteristics, and highlight that the importance of early-colonizing fungal species (i.e., the strength of priority effects) can vary considerably between tree species.

The variation in the strength of priority effects among logs contrasts directly with the results of previous manipulative studies, in which the success of late-arriving species depended on the colonization success (established mycelia) of early-arriving species (Holmer and Stenlid 1997, Fukami et al. 2010, Lindner et al. 2011, Hiscox et al. 2015*a*). Our results indicate that these observed relationships are unlikely to be so straightforward under natural conditions, and our capacity to predict fungal successional dynamics from the characteristics of early species will depend on the wood species being colonized and the stage of decomposition.

Fungal community composition also had consequences for the rates of sapwood decomposition, but this effect varied over time. After the first year, fungal community composition was related to the decomposition rate of sapwood in both *Larix* and *Quercus* logs. This initial phase, characterized by high concentrations of sugars, organic acids, pectin, and easily accessible cellulose, was the period in which decomposition rates were the fastest. The importance of fungal community composition during initial decomposition reflects the observations in previous work with decaying oak tree stumps (van der Wal et al. 2015). However, decomposition rates slowed after the first year, as the accessibility of cellulose and hemicellulose decreases and lignin protects hemicellulose and cellulose from further degradation (van der Wal et al. 2007, 2013). Indeed, the patterns in enzyme activities after 2 yr of decomposition shifted toward higher activity of manganese peroxidase and hemicellulose activity, indicating the degradation of recalcitrant molecules such as lignin and hemicellulose. Antagonistic fungal interactions between saprotrophic species can also limit decomposition rates during this latter period of decomposition (Fukami et al. 2010). As decomposition rates slowed, the relationship between fungal community composition and sapwood decay diminished.

Conclusion

Initial patterns of fungal community assembly were similar for both *Larix* and *Quercus* logs, but there were different trajectories for subsequent community development. Endophytic fungal communities, which could only be analyzed well for *Larix*, were found to be highly diverse and variable among trees and had no

apparent effect on fungal community composition in 1-yr-old logs. After 1 yr of wood decay, we found a few dominant fungal species and low variation in community composition among logs, and fungal community composition was related to sapwood decay rates for both tree species. However, as decomposition proceeded, an increase in variation in fungal community composition among *Larix* logs was observed without apparent priority effects. In contrast, in many of the *Quercus* logs the early invaders appeared to persist. For both tree species, wood decay rates levelled off and the relationship with fungal community composition disappeared. This indicates that the impact of fungal composition on wood decay rates can be best predicted during early stages of decomposition when wood decay rates are high and fungal community assembly shows similar patterns. In conclusion, we reveal limited evidence for priority effects of early succession fungi on subsequent fungal succession under natural field conditions. Instead, fungal assembly processes appear to be governed by combative abilities among fungi, and depend on the wood species being colonized as well as the stage of wood decomposition. Community assembly may thus be due to hierarchical differences in species' competitive abilities, as recently shown in plant communities (Kunstler et al. 2012, Roux et al. 2014).

These findings demonstrate that an increased focus of competitive interactions among species, rather than priority effects, may be key to predict community assembly and the ecosystem process they provide.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1393/supinfo