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Detailed analysis of fungal communities in Norway spruce logs reveals stochastic fine-scale patterns of species and detects lichen forming fungi without their photobionts☆

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ABSTRACT

Fungal ecologists have long been intrigued by the mechanisms behind the high fungal species richness in dead wood at small and large spatial scales. We identified processes resulting in fine-scale fungal community patterns with a network analysis based on a detailed metabarcode mapping of fungi in and on the surfaces of eight naturally fallen Norway spruce logs in northern Sweden. Our results show that (1) dominant species and communities of fungi vary significantly among the logs, (2) wood inside and on log surfaces has distinct and diverse fungal compositions and (3) consistent co-occurrences of fungi in wood are rare. These patterns suggest priority effects favouring primary colonizing species are important for determining which becomes the dominant species, and that colonization of the rest of the community and fungal co-occurrences are largely shaped by stochastic processes. Furthermore, lichen-forming fungi were detected without their photobionts in wood, indicating possible free-living stages.

1. Introduction

Dead wood is a key component for forest biodiversity supporting many species, in particular insects and fungi. In Fennoscandia, wood-inhabiting fungi have previously been estimated to represent at least 10 % of the more than 25 000 forest species (Siitonen, 2001; Stokland et al., 2012), and metabarcoding studies of fungal diversity indicate this estimate to be low (e.g. Ottosson et al., 2015). Compared with the few tree species and the low level of tree diversity (Tingsted et al., 2018), wood-inhabiting fungi form highly species rich communities. For example, Norway spruce, (*Picea abies*), constituting about 40 % of the trees and the volume of dead wood in Fennoscandia, hosts thousands of different wood-inhabiting fungal species (Kubartová et al., 2012; Ovaskainen et al., 2013; Rajala et al., 2015; Mäkipää et al., 2017; Runnel et al., 2021).

Questions of fungal diversity are often addressed at the level of logs, forest stands, landscapes, or larger spatial scales, e.g. in a nature conservation context (e.g. Junninen and Komonen, 2011; Nordén et al., 2013; Runnel et al., 2021). However, this diversity is rooted in strikingly high species richness even within small units of dead wood. A single log contains hundreds of fungal species and minute wood samples from inside the logs may contain tens of species; the variation of fungal compositions seems to be high (Kubartová et al., 2012; Ottosson et al., 2015; Rajala et al., 2015; Runnel et al., 2021). Thus, better insights into this fine scale diversity, its dynamics, and underlying mechanisms are needed to achieve a better understanding of the community ecology of wood-inhabiting fungi.

Wood-inhabiting fungi decay and deplete the substratum in which they grow, feed and are enclosed in. Those substrata are patchily formed and distributed in space and time in the form of either attached or fallen twigs or branches, standing, felled, or fallen trunks and buried roots. As a result, diversity of fungal species and dead wood types occur spatially

☆ Footnotes: Detailed spatial analysis of fungal communities in Norway spruce logs.

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nested within forest stands and landscapes (Abrego, 2022). The temporary and patchy fungal communities in dead wood makes them a particularly interesting case for studying community assembly patterns and processes. However, these characteristics make identifying general patterns in the processes shaping wood-inhabiting communities challenging. The assembly of fungal communities is not a straightforward pathway but rather a complex and dynamic mosaic with deterministic and stochastic components (Boddy, 2001; Boddy and Hiscox, 2016; Abrego, 2022). It appears to be a highly stochastic process with largely unpredictable dispersal and colonization-extinction dynamics (cf. Hubbell, 2001) where deterministic environmental filtering seems to provide only limited predictive power (Norberg et al., 2019). In terms of wood-inhabiting communities, observable deterministic species-environment interactions reveal that certain species are better adapted to specific environmental conditions, foremost relating to the types and amount of wood in forests and impacted by the landscape context (e.g. Nordén et al., 2013; Krah et al., 2018; Kärvemo et al., 2021; Runnel et al., 2021). Within wood, both space and abiotic properties (e.g. type of dead wood, decay stage, moisture, the tree's cause of death) determine the nature and scale over which individual mycelium meet and interact (O'Leary et al., 2021). At the finer scale, the community members' traits and overall fitness relating to resource acquisition, competitive exclusion, and facilitation influence community structuring and diversity (Dawson et al., 2019; Boddy, 2021). Mycelial establishment and territorial occupation of wood by the primary colonizer species strongly influences the assembly of the later-arriving community. This is called priority effect and repeatedly reported from surveys and experimental studies in wood-inhabiting communities (Fukami et al., 2010; Lindner et al., 2011; Dickie et al., 2012; Ottosson et al., 2014; Hiscox et al., 2015).

Fungi are present already in the wood of living trees. With increasing tree age, heart rot fungi may colonize and spread through roots and basal trunk, and similarly wounds and broken branches may over time result in multiple establishments of spatially restricted fungi (eg. Renvall, 1995; Boddy, 2021). A sparse mycobiome of endophytic latent wood decay fungi, ascomycetes and basidiomycetes causing white, brown and soft rot, is also present in the sap and heart wood of living trees, potentially many years before the sapwood becomes dysfunctional and available for establishment and spread (e.g. Roll-Hansen and Roll-Hansen, 1979; Gilmartin et al., 2022). In that way, wood-inhabiting fungi may gradually accumulate in living trees prior to their death, affecting the subsequent fungal colonization and developing community. Furthermore, random natural processes impact which species establish from spores due to spatiotemporal interspecific variation in sporocarps, number of spores and whether spores are dispersed by wind or insects (Boddy, 2001; Norros et al., 2012; Norberg et al., 2019). As a result, the composition of species and how communities develop will be different among and within individual woody resource units. Nonetheless, general driving forces for community development pathways can be discerned (Boddy, 2021; Abrego, 2022). To enhance our understanding of and pose hypotheses for the role played by deterministic and stochastic processes in shaping wood-inhabiting communities, empirical evidence on the spatially detailed distribution and co-occurrence of fungi within wood is needed. A challenge for studying this arises from the predominantly hidden nature of community assembly as mycelia and the inevitable destructive sampling needed to identify and analyze fungal occurrences and activities in wood.

Culture dependent techniques of mycelia shed light on the distribution of individual species within wood by tracing interaction zones between species, mycelial individuals, and different types of rot (Rayner and Boddy, 1988; Boddy, 2021). When whole communities have been studied by molecular methods, most studies have primarily relied on several pooled wood samples to better represent the community within wood units (Rajala et al., 2012; Ovaskainen et al., 2013; Runnel et al., 2021); only a few studies were based on individually analyzed samples (Kubartová et al., 2012; Kubart et al., 2016; Ovaskainen et al., 2010). Such individual samples spanning from the outer to the inner part of a log reports tens of coexisting species and different community composition between the outer and inner parts of the logs. Yet, more detailed spatial distribution is poorly known. The outer surface sapwood and the heartwood at the center of a tree present distinct environmental conditions, chemical properties and presence of latent species, influencing fungal species that colonize and establish in different locations of the wood (Boddy, 2001). The upper and lower parts of downed logs may also harbor different communities, considering reported interactions between soil- and wood-inhabiting fungal communities (Rajala et al., 2012; Ottosson et al., 2014; Mäkipää et al., 2017). The increase in fungal species richness during decomposition is partly associated with the gain of mycorrhizal and some soil-saprotroph species (Mäkipää et al., 2017). Also, the way a tree has died has a major influence on the wood-inhabiting fungal community (Saine et al., 2024).

An interesting observation is that saproxylic lichen-forming fungi have been detected in low abundance several centimeters into logs and also in veteranized trees raising the question of whether they may have a free-living life cycle phase (Kubartová et al., 2012; Menkis et al., 2022). Traditionally, lichen-forming fungi have been considered to form obligate symbioses with photobionts and to be confined to the surface of their growing substratum. A re-analysis of both fungal and algal DNA data from Kubartová et al. (2012) could not exclude that dominant *Cladonia* DNA in these logs originates from vegetative propagules or thallus fragments dispersed into the logs through cracks or by animals or water (Tuovinen et al., 2015). The frequency of occurrence and biological significance of lichen-forming fungi in wood is yet to be determined, holding the potential to unveil insights into the mechanisms governing colonization and establishment.

Exploring the ecological roles of wood-inhabiting fungi, not limited to wood-decomposing fungi but also including lichen-forming, mycorrhizal, parasitic and other saprotrophic fungi, contributes to a broader perspective on the dynamic interplay of these ecological groups. The spatial pattern of ecological groups of species may be less dynamic than the species themselves, as these likely are more tightly connected to the underlying mechanisms governing species distributions and community changes (Rajala et al., 2012; Violle et al., 2007). An understanding of the spatial distribution of fungi within wood may enhance our insights into the establishment, distribution, and co-occurrences of fungi having different ecological roles.

Our aim with this study was to analyze fine-scale spatial patterns of wood-inhabiting fungal communities in logs; including the relative abundance, richness, composition, co-occurrence networks, the species' ecological roles and search for presence of free-living lichen-forming fungi. As we wanted to investigate well-developed fungal communities, we selected naturally fallen logs of Norway spruce of intermediate decay within an old-growth forest in northern Sweden. Fungal identifications were made from DNA metabarcoding of wood samples taken from cross-sectional discs sampled throughout the logs. We expected to find nearby logs being dominated by different fungi and having varied fungal communities (Renvall, 1995; Edman and Jonsson, 2001; Kubartová et al., 2012), and most species to potentially occur in the same niches or microhabitats within the logs (Piché-Choquette et al., 2023). We hypothesized.

1. Species, except the few most abundant ones, to occur randomly and rarely in fixed co-occurrences,
2. Fungal communities in the log surface and inside the logs to differ, largely consisting of different species,
3. Lichen-forming fungi to occasionally occur in the wood without their photobionts indicating a possibly free-living life stage, and
4. Fungal ecological roles largely to be restricted to different parts of the logs, reflecting their niches and mode of colonization, e.g. lichen-forming fungi and non-wood-decomposing saprotrophs close to the log surfaces and mycorrhizal fungi at the bottom of logs, entering by mycelia and connected to tree roots.

2. Materials and methods

2.1. Study site and design

The study was conducted at Sveaskog's Ekopark Ledfat, Arvidsjaur, in northern Sweden (65°32.706′ N; 018°27.863′ E). The stand is an old growth forest dominated by Norway spruce. We selected two sites located 250 m apart with 25–50 and 50–80 naturally formed Norway spruce logs/ha, respectively. Site 1 was a drier forest of *Vaccinium-myrtillus*-type (Påhlson, 1994) where the logs sampled had little ground contact. Site 2 was moister (*Vaccinium* spp. – *Sphagnum* spp. type; Påhlson, 1994), located at a mire edge and the logs had more ground contact. Four logs were selected at each site. We aimed for logs without visible cracks to avoid detection of lichen fragments carried into the wood from the log surface, allowing for the search for potential free-living lichen-forming fungi. The selected logs were dry with a hard surface (i.e., limited signs of decay of the outer surface wood; decay stage 2 according to Renvall, 1995), largely debarked, without moss cover but with abundant lichen cover, especially of *Parmeliopsis* and *Xylographa* species. All logs had fallen by butt breakage.

2.2. Sampling

From each log, four 8 cm thick discs were sampled from areas with a rich epiphytic lichen cover, to test whether the same lichen-forming fungi would be detected in wood. The distance between the discs was on average 60 cm (range 26–170 cm). For each disc, the position on the log together with the direction of the log, was recorded. Identity of epiphytic lichens on the discs and 15 cm extending on both sides of the disc were recorded. A log surface sample was collected as a wood shaving of the uppermost 2–5 mm of the log surface from four positions on each disc with a clean knife (Fig. 1, Fig. S1) before detaching the disc with a chainsaw. The samples were transported to the laboratory and frozen within 48 h until they were further processed. The average circumference of the disc closest to the base was 60 cm and 46 cm for the disc closest to the top.

In the laboratory, debris was cleaned from the surface of each disc with pressured air, after which the disc was packed tightly in aluminum foil leaving one cut surface to be exposed and sampled (Fig. S1). The exposed surface was sterilized with a gas burner and covered with plastic wrap. Wood drill dust were taken using a sterilized 6 mm drill bit down to 2 cm depth in three directions from the disc center, each with four samples evenly spread from about 1 cm below the log surface to the

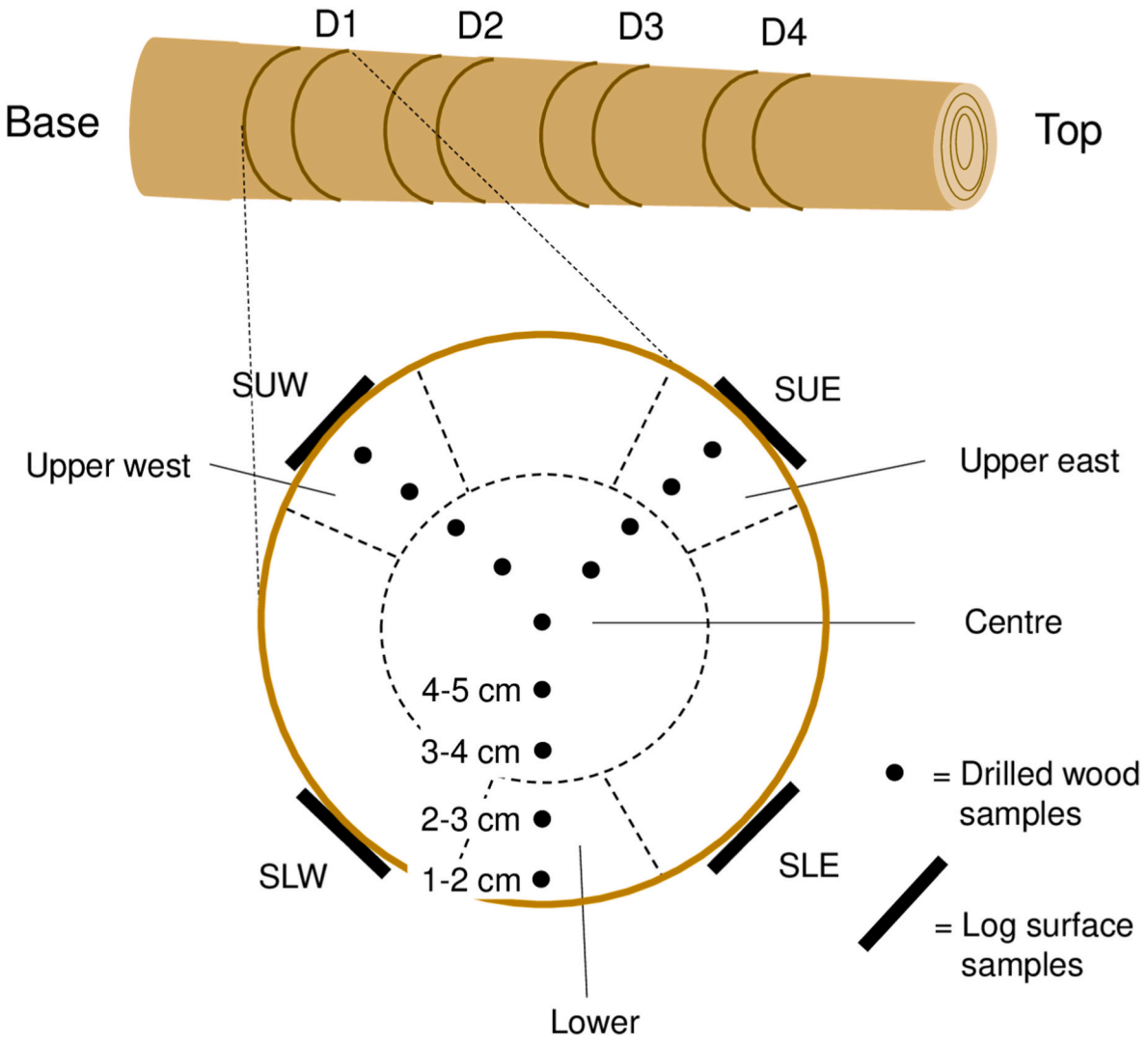

Fig. 1. Study design showing sampling points for each log; four wood discs (from base toward top D1-D4), each with 13 drilled wood samples analyzed in four groups (lower, centre, upper east and upper west) and the four log surface samples (SUW= Surface upper west; SUE= Surface upper east; SLW= Surface lower west; SLE= Surface lower east). The 13 wood samples were taken at 1–2, 2–3, 3–4, 4–5 cm depth from the surface and in the middle of the disc.

center, resulting in 13 samples from each disc, upper two quadrants towards the center and from the center vertically towards the bottom of the log facing the ground (Fig. 1, Fig. S1). Each sample was collected into a separate 15 ml Falcon tube.

The surface of the plastic, the drill and the bench were sterilized with 5 % NaClO solution and the drill bit was washed and burned with EtOH between each drilling. The minimum amount of drill dust collected was 2 ml. If drill dust was spread under the plastic during the sampling, the plastic was removed, the surface re-burned and covered with a new plastic before taking the remaining samples. If taking the samples from the predetermined spot was not possible due to a crack, the samples were shifted right clockwise as close as possible to the original spot. Each drill dust sample was hand-shaken, thereafter two technical replicates were taken to fill up $^1/_3$ of a 2 ml screw-cap tube and two metal nuts were added into each tube. The tubes were shaken with a FastPrep (Precellys) at 3000 rpm for 30 s to grind the samples for DNA-extraction. In total, 414 wood samples (13 drilled samples x 4 discs × 8 logs, except for 12 samples for two discs which were so decayed inside that the 13th sample could not be collected, log 4 D2 and log 8 D4) were collected resulting in a total of 828 samples for DNA extraction including the technical replicates.

The log surface samples (the wood shavings) were prepared for DNA extractions in a laminar flow hood. First, any macrolichens were removed as their presence was recorded already in the field. Then, the surface of the wood chip was moistened with $_{dd}H_2O$ and a 4 cm^2 surface area of max 1 mm deep was scraped off with a sterilized scalpel, put in a 2 ml tube with screwcap and ceramic beads from NucleoSpin soil kit (Machinery-Nagel) and ground similar to the drill dust samples. In order to detect fungi growing both in and on the thin wood shavings, these samples were not sterilized. Hence, fungal propagules deposited as spores or environmental debris on the surfaceare also contributing to the fungal community in the log surface. In total, 128 log surface samples (4 shavings x 4 discs × 8 logs) were collected. Both wood and log surface samples were stored at −20 °C until the DNA extraction.

2.3. Molecular analyses and bioinformatics

The NucleoSpin soil kit was used for the DNA extractions of all samples following the manufacturer's protocol, with SL2 and enhancer SX buffers. The fungal internal transcribed spacer 2 (ITS2) was PCR amplified from all of the DNA extractions with tagged primers gITS7, ITS4A and ITS4 (Ihrmark et al., 2012) in 50 μl reactions with DreamTaq Green polymerase (Thermo Scientific), annealing at 56 °C and an extension step of 5 min. These primers also amplify the most common green algal lichen photobionts (e.g. *Trebouxia, Asterchloris*). The DNA replicates from each wood sample were amplified with the same tag pair included in the PCR primers. 25–33 PCR cycles were run based on the signal strength of the amplicons run on a 1 % agarose gel, as similar strength of the bands was selected for (medium) (Lindahl et al., 2013). PCR-products were cleaned with AMPure (Agencourt Beckman Coulter Inc., Brea, CA, USA) and the final concentrations measured by Qubit (Life Technologies). First, the cleaned PCR amplicons from each DNA extraction replicate were pooled together in an equimolar concentration, as they were tagged with the same tag pair. Then, the samples were pooled to four equimolar pools of 104 samples, except for the fourth pool that had 103 samples. The amplicons from the log surface samples were pooled to two equimolar pools of 64 samples. Each pool was sequenced on one PacBio flow cell at SciLifeLab, Uppsala.

The raw reads obtained were quality filtered and clustered using SCATA pipeline (http://scata.mykopat.slu.se/). Short sequences (<200 bp) were removed, and the other parameters were set as described in Kubart et al. (2016) with few modifications. Specifically, we used 3 as threshold for minimum base quality and 0.9 for proportional primer match. Operational taxonomic units (OTUs) with less than 2 sequences were excluded from downstream analyses. Eight wood samples and 1 log surface sample were removed from the dataset due to a missing tag match after sequencing. A total of 422 370 sequences passed the quality filtering and were clustered in 1447 OTUs. Each OTU was then BLAST searched against reference sequences in the UNITE (Abarenkov et al., 2010) and GenBank databases (NCBI). The taxonomic ranks were delimited according to ITS2 sequence similarity at 98–100 % for species, 90–97 % for genus, 85–89 % for family and 75–84 % for order level. The OTUs that were not assigned to fungal taxa were excluded from the dataset. Finally, to avoid sequencing depth bias in the analyses, each of the six pools was rarefied according to the pool with lowest number of reads, leading to the exclusion of 49 rare OTUs.

2.4. Statistical analyses

Community structure of wood and log surface samples was analyzed with non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances using package "vegan" in R software (v3.6.2) (Oksanen et al., 2019; R Core Team, 2019). One wood sample was excluded from the analysis as it turned out to be a clear outlier in the ordination diagram, limiting the statistical validity of subsequent analysis. We used a non-parametric multivariate analysis of variance (PERMANOVA) followed by pairwise comparison on Bray-Curtis distances with 9999 permutations to test the differences in fungal community structure between sites, logs, discs and locations for both wood and log surface samples using "adonis" function. Prior to the analysis we designed locations in discs according to their position as follows: Lower, Centre, Upper east and Upper west (see Fig. 1). Upper and lower wood samples were defined as the outermost two samples (1–3 cm depth), and the remaining samples in the middle as centre samples (>3 cm depth).

For the fine-scale analysis, we analyzed the most abundant OTUs representing 80 % of the mapped reads. Heatmaps were generated for each log separately as well as one including all the samples using "vegan", "readr", "dplyr", "taxa" and "qgraph" packages (Epskamp et al., 2012; Foster et al., 2018; Oksanen et al., 2019; Wickham and Hester, 2020; Wickham et al., 2020). They were scaled by column and only the 15 most abundant OTUs were displayed for clarity. For each of the logs, Pearson's correlation was calculated to measure the correlation between these OTUs and each location. Besides, Pearson co-occurrence correlation networks of the most abundant OTUs were generated for each log with the "qgraph" package using the graph = "cor" option. OTUs repartition between discs and between locations that appeared in the networks was calculated after normalization by mean and only significant ($p < 0.05$) correlations were displayed. Relative abundance refers to the relative number of amplicons of a species in relation to all amplicons of all species. The relative frequencies refer to the relative number of occurrences in samples of a species in relation to the total number of samples analyzed.

The ecological role of identified taxa was assigned using FUNGuild v1.0 database (https://github.com/UMNFuN/FUNGuild) and complemented by information reported in recent literature. Eight groups were defined as follows: lichen-forming fungi (Li); mycorrhizal (My); possible lichen-forming fungi (Pli); plant pathogen (Pp); saprotroph (Sa); both saprotroph and parasitic (Sp); unknown ecology (Unk); wood decomposer (Wd). When assigning an OTU the ecological role of lichen-forming fungi, the sequence similarity to previously sequenced lichen taxa (from types or curated by taxonomic experts of the group) was set to ≥ 98,5 % and 100 % query coverage. The OTUs that have a previously sequenced lichen-forming fungus as a closest BLAST hit but similarity <98,5 % were assigned as "possible lichen-forming fungi".

Spatial analysis using Inverse Distance Weighting (IDW) with GIS (ArcMap 10 – http://www.esri.com) was performed to visualize the distribution of OTUs with different ecological role within wood discs based on abundance data. Canonical correspondence analysis (CCA) followed by a Monte Carlo permutation test based on 999 permutations was used to correlate the lichens occurrences with sampling locations within the discs and on log surface.

3. Results

After random subsampling and removal of plant reads (4 %), the final matrix consisted of 246 423 reads clustered in 1038 OTUs, of which 21 % could be identified to the species level, 23 % to the genus level and in total 56 % to the level of order or higher. Basidiomycetes formed 258 OTUs and accounted for 46 % of the reads, ascomycetes made up 636 OTUs and formed 51 % of the reads, while other and unidentified fungi accounted together for the remaining 3 % of the reads (144 OTUs).

3.1. Fungal communities in wood

In total, 645 OTUs were identified from the drilled wood samples, with on average 10 OTUs (range: 1–49) and 404 reads (range: 1–2078) per sample from the 164 287 analyzed reads. Basidiomycetes accounted for 65 % of the reads and 184 OTUs, and Ascomycota for 33 % of the reads and 397 OTUs. The three most abundant OTUs (*Antrodia serialis, Porodaedalea abietina* and *Veluticeps abietina*) accounted for 35 % of the reads, and together the 95 most abundant OTUs made up 80 % of the reads (Table S1a and b). The most abundant OTUs belonged to order Hymenochaetales (25 % of reads), Helotiales (19 %) and Polyporales (16 %) being present in 57, 65 and 38 % of the wood samples, respectively (Fig. 2, Fig. S2 for relative frequencies).

The data imply that fungal communities differed significantly in composition between the two sites and among the eight logs (PERMANOVA: $p < 0.01$; Fig. S3). Moreover, community composition differed horizontally within the individual logs between wood discs as well as with upper, lower and center locations within wood discs (PERMANOVA: $p < 0.01$; Table S2). The fungal communities in the upper wood did not differ significantly between the east and west sides (PERMANOVA $p = 0.051$, Table S2).

3.2. Fine-scale distribution patterns of fungi in wood

Three of the eight logs were dominated by single different OTUs throughout their interior, while the other logs had a few more abundant OTUs (Figs. 3–5, Fig. S4–9, Table S1ab, Table S3). *Porodaedalea abietis* dominated the fungal community in log 8 where it accounted for 96 % of reads (Table S4). Similarly, *Neoantrodia serialis* and *Veluticeps abietina* dominated in log 1 and 7, respectively, accounting for 57 % and 50 % of the reads. These three fungi were also present in most other logs, but at low frequencies and low abundances (Fig. 3). In the other logs (log 2, 3, 4, 5 and 6), the contribution of the most abundant OTUs was smaller, constituting 15–35 % of the reads. Considering all logs, the ten most abundant OTUs in each log accounted for 70–99 % of the reads (Table S4). The recorded average OTU richness per log was 176 (range: 61–257). The most abundant OTUs in individual logs; *N. serialis, Coniophora puteana, Amylocystis lapponica, V. abietina, Phellopilus nigrolimitatus,* and *Porodaedalea abietis* predominantly occupied the center of the logs and often occurred from the bottom disc 1 and all the way to the utmost disc 4 (Figs. 3 and 4, and Fig. S4–S9).

A general pattern was that the frequent and dominant taxa were mostly present in all discs and in most to all parts of the disc (Figs. 4 and 5 and Figs. S4–S9). The occurrence of less frequent taxa was often confined to a few or specific discs and to certain areas of the logs. Log 1 is an example of a log with a marked dominance of *N. serialis*. The heatmap and network analysis showed this species to be spread in all discs, significantly related to the log center ($p < 0.05$; Fig. 4a), but also present in the outer parts in all discs (Fig. 4b). The lower occurrence of *N. serialis* in the outer parts corresponds to the presence of other OTUs and with a significant negative co-occurrence with Rhytismataceae1 in one location. Other common OTUs, such as *Sarea difformis, Coniophora olivacea,* Stictidaceae and *Gloeophyllum sepiarium,* occupied localized outer parts of the log and typically in single discs (Fig. 4ab). The network analyses showed all logs to have groups of co-occurring OTUs clustered within and among wood-discs (Fig. 4b–5b, Fig. S4b–S9b). These OTU groups were typically localized predominantly at one part of one disc and were often unique to each log (Fig. 4b–5b, Fig. S4b–S9b). The clustered structure in the co-occurrences network shows that certain, often less common OTUs, frequently co-occurred in a certain location within a log (Fig. 4b). As an example, *Tubulicrinis* sp1 (OTU number 122) and *Dacrymycetes* sp. (138) were part of a well-defined cluster occurring mainly in the upper west part of log 1 of disc 1. Similarly, *Phialocephala virens* (26) and *Hyphodontia pallidula1* (11) were only found in the center of the disc 4 of the log. However, this could just be random as it was single locations.

Log 4 represents a log with more even community diversity and no single dominant fungal OTU (Fig. 5). However, besides having three co-dominating OTUs, the aggregated pattern of co-occurring less common OTUs resembled log 1. *Hyphodontia pallidula* (disc 1-3) occurred mainly in the center of the log ($p < 0.05$; Fig. 5a) while *Phialocephala virens*, *Cadophora* sp1 and Rhytismataceae1 mainly occurred in the outer parts. The upper part of the log was characterized by the prevalence of Sordariomycetes1, Rhytismataceae1, Phialocephala sp1, Hyaloscyphaceae1 and *Trichaptum abietinum*. Co-occurrences showed a cluster of few OTUs that occurred in the upper east part of disc 1 which includes *N. serialis* (3), *P. nigrolimitatus* (5) and *Xeromphalina campanella* (36) (Fig. 5b). Other clusters were e.g. *T. abietinum* (72) and Eurotiales1 (43; upper west of Disc 1) and Helotiaceae1 (20) and Basidiomycota2 (25; upper east of Disc 3).

The total dominance of *P. abietis* throughout log 8, in 50 of 52 samples, is a special case (Fig. S9a). Here only two samples at the lower part of the log at two different discs were occupied with other OTUs (Fig. S9b). This log was the largest and most decayed in the study.

Only a few of the most abundant OTUs were significantly related to the same location in multiple logs (Fig. 4a–5a; Fig. S4a–9a). OTUs

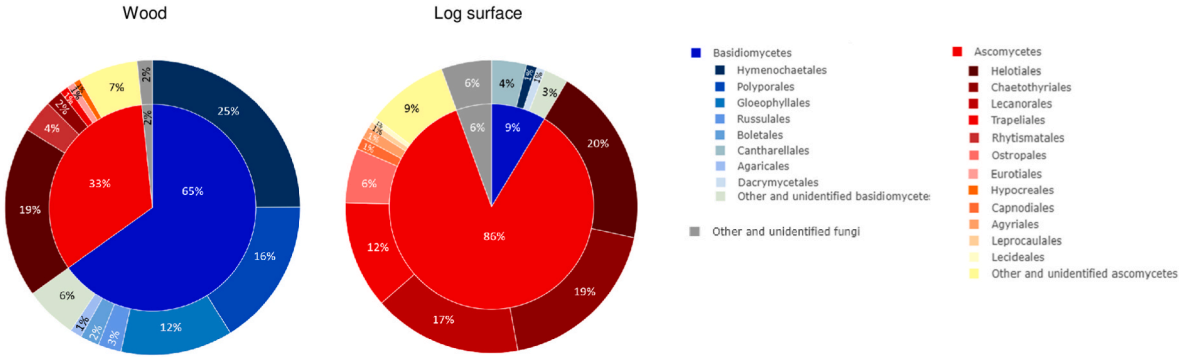

Fig. 2. The relative abundance of fungal orders in the wood and log surface.
The relative abundance of each order was calculated as the percentage of all OTU reads from 407 wood and 127 log surface samples, respectively, from 8 Norway spruce logs.

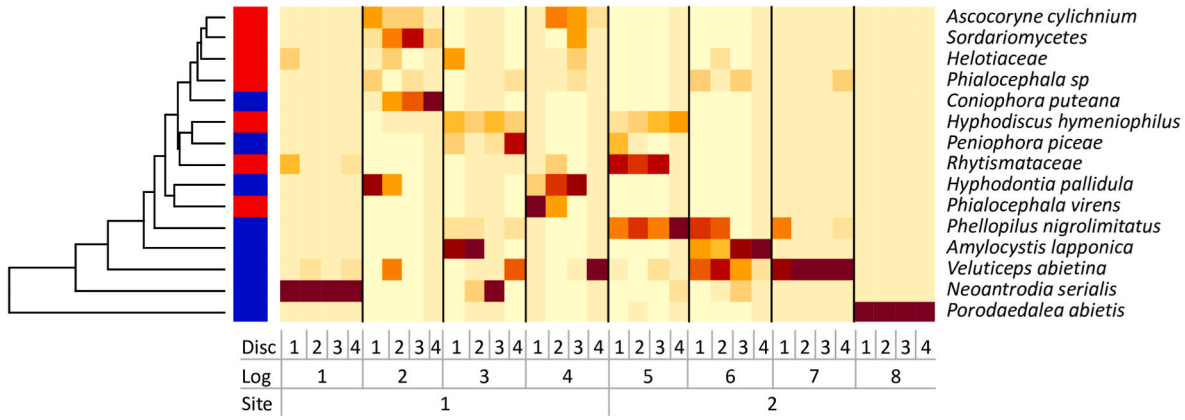

Fig. 3. Heatmap of the 15 most abundant OTUs in the wood for the discs (1–4) from each log (1–8) at the two sites. Darker brown indicates higher relative abundances. In the dendrogram, fungal taxa belonging to Ascomycota and Basidiomycota are represented by red and blue, respectively.

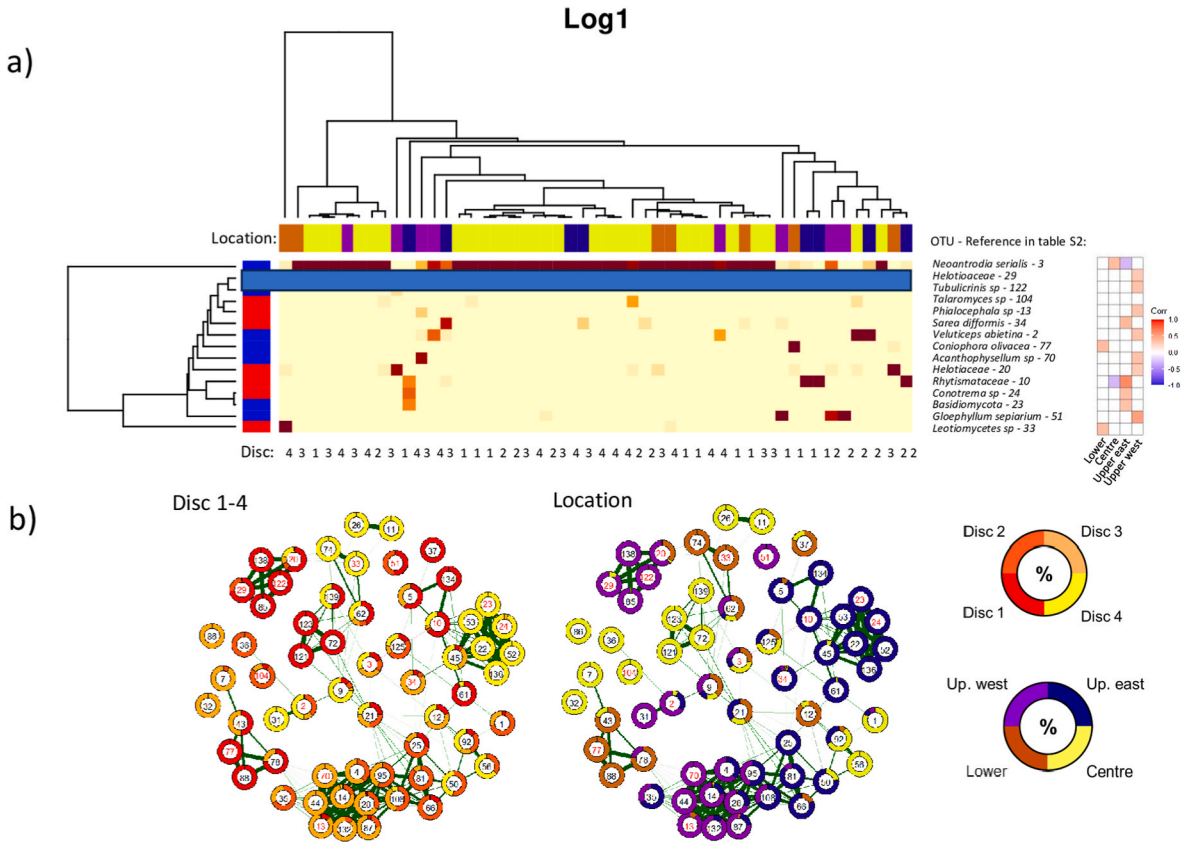

Fig. 4. a) Heatmap of the relative abundance of the 15 most abundant OTUs for each wood sample in log 1. Higher relative abundances are indicated by darker brown color. The belonging of fungal OTU to Ascomycota and Basidiomycota is shown by red and blue, respectively. Dendrograms represent hierarchical clustering based on similarity in OTU composition: columns (discs) are clustered based on OTU abundance profiles, and rows (OTUs) are clustered based on their distribution across samples. The color of the upper dendrogram shows the location in the disc for each sample (see legend for b). Pearson's correlation table next to the OTUs names shows significant correlations ($p < 0.05$) between OTUs and wood locations. Positive and negative coefficients are indicated by red and blue, respectively. b) Co-occurrence networks of most abundant fungal taxa with correlation strength indicated by lines thickness, only significant ($p < 0.05$) positive (green edge) and negative (red edge) co-occurrences are displayed. The colors in the left network indicate the OTU's relative abundance along the log (disc 1 to 4). The colors in the right network indicate the OTU's relative abundance within the discs (location Lower, Centre, Upper west, Upper east). Numbers next to OTUs names and within network circles refer to OTUs name as listed in Supplementary Table S2. Red numbers in network circles refer to the 15 most abundant OTUs reported in the heatmap and listed in the Pearsons's correlation table (a).

preferentially occurring in the same location in at least two logs were *Cadophora luteo-olivacea* (OTU reference 32 in Table S1ab and S3) (Lower); Helotiaceae1 (20), Basidiomycota2 (25) and *Sarea difformis* (34) (Upper west); Chaetothyriales2 (50) and Stictidaceae (24) (Upper east); Rhytismataceae1 (10) (Upper east and Lower).

Co-occurrence clusters across logs were composed of different assemblages, except in few cases (Fig.. 4b–5b; Fig. S4b–S9b). *Exophiala bergeri* (87) + Pezizomycotina1 (28) co-occurred in 6 of 8 logs. *Exophiala bergeri* (87) + Chaetothyriales1 (4) and *Exophiala* sp1 (87) + Lecanoromycetes1 (66) both co-occurred in 5 logs. *Exophiala* bergeri (87) also

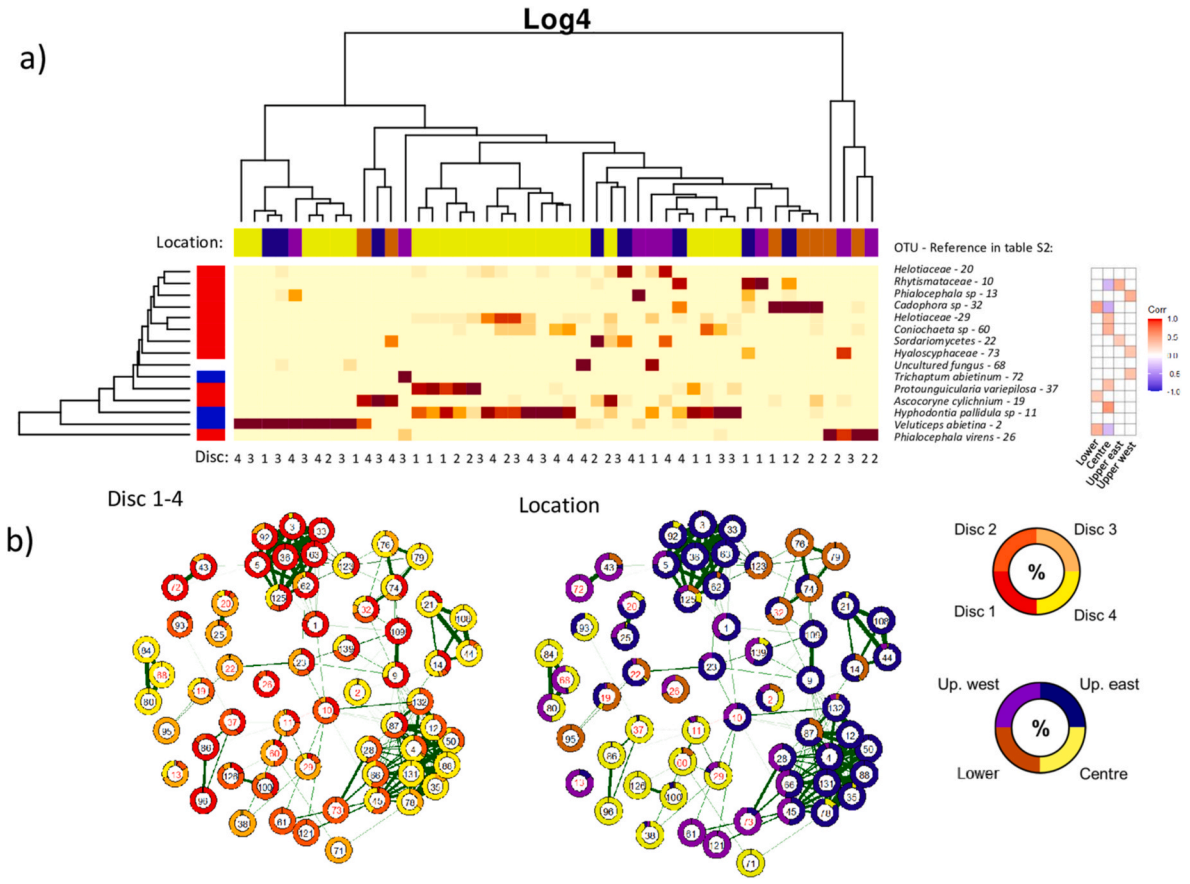

Fig. 5. a) Heatmap of the relative abundance of the 15 most abundant OTUs for each wood sample in log 4 and b) co-occurrence networks of most abundant fungal OTUs in the same log. Correlation strength is indicated by lines thickness, only significant ($p < 0.05$) co-occurrences are displayed. For further plot details, see legend in Fig. 4.

co-occurred with Pezizomycotina1 (28) + Chaetothyriales1 (4), with Lecanoromycetes1 (66) + Pezizomycotina1(28), and with Chaetothyriales1 (4) + Lecanoromycetes1 (66) in four different logs.

3.3. *The fungal communities on the log surface*

65 320 reads clustered into 598 OTUs with an average of 647 reads (range: 4-1145) and 40 OTUs per sample (range: 4–110) from the log surface. Basidiomycetes accounted for 26 % of the OTUs and 20 % of the reads and ascomycetes for 64 % of the OTUs and 70 % of reads. The fungal communities were dominated by ascomycetes, with OTUs from Helotiales, Chaetothyriales and Lecanorales, accounting for 55 % of the reads (Fig. 2). Chaetothyriales was the most frequent fungal order present in all samples, followed by Helotiales (99 % of samples) and Lecanorales (97 %) (Fig. S2). The most abundant OTUs on the log surface were an OTU from Chaetothyriales (Chaetothyriales1), *Xylographa parallela*, and *Micarea misella.* The fungal communities on the log surface differed significantly from the communities in the wood (PERMANOVA $P = 0.001$; Figs. 2 and 6, Fig. S2).

The fungal communities differed between the upper and the lower surface of the logs, but not between the different sides (PERMANOVA $p > 0.05$, Table S1ab). Samples from the lower part of the log had higher OTU richness (average 50 OTUs per sample) compared to the upper samples (average 30 OTUs). The community structure was similar between discs along the log (PERMANOVA: $p > 0.05$; Table S1ab). The most common OTUs in the wood were absent or only sporadically recorded on the log surface, e.g. *Veluticeps abietina* occurred in 5 samples, while *Porodaedalea abietis* was not recorded at all (Table S1ab).

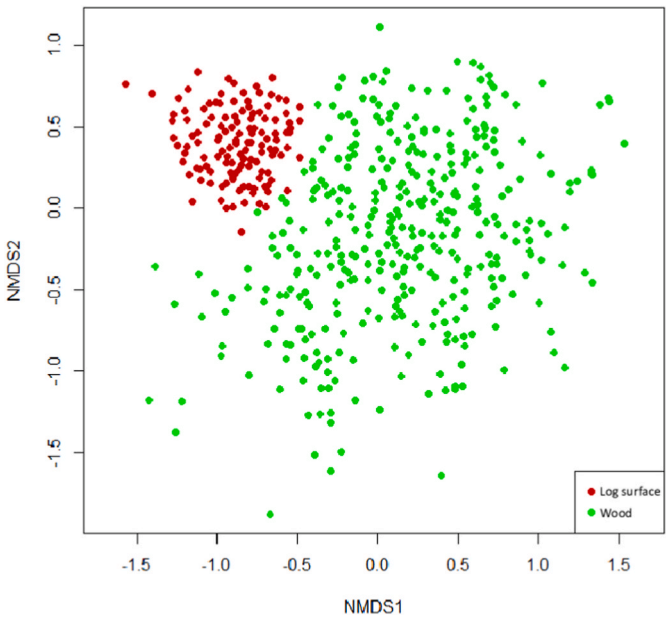

Fig. 6. NMDS ordination of the community structure of fungi in the wood and on log surface, stress = 0.16.

3.4. Occurrence of lichen-forming fungi without their photobionts in wood samples

Among the OTUs present in wood samples, eight (1 % of the total number of OTUs and 0.02 % of the total number of reads) could be assigned to lichen-forming fungi with certainty, i.e., with high sequence similarity to previously sequenced lichen-forming fungi (Table 1). In addition, nine OTUs that are possible lichen-forming fungi were recorded. The most frequently detected, with certainty, identified lichen-forming fungal OTUs were *Parmeliopsis ambigua* and *Xylographa parallela*, which were also frequently visually identified on the log surface. Notably, two possibly lichen-forming OTUs belonging to *Elixia* were detected from 10 % of all wood samples and at least one of the OTUs was present in each log, but they were mostly not detected in the log surface samples or in the visual inventory (Table S4). In addition, *Micarea* sp. 4 (Pli), *Frutidella* sp. (Pli), and *Hypogymnia tubulosa* (Li), were detected from more than one sample. Ten (59 %) of the lichen-forming or possible lichen-forming taxa were recorded only from one sample (Table 1), but in total lichen-forming fungi were recorded from 58 samples (14 % of all wood samples). At least one lichen-forming fungal OTU was detected from the wood samples in each log. Two lichen-forming OTUs were recorded only from the wood samples once and not recorded in the lichen inventory or sequenced from the log surface: *Scoliciosporum umbrinum* (Li) and *Elixia* sp1 (Table 1). Most of the lichen-forming OTUs were recorded 1–2 cm from the surface (33 % of upper samples and 28 % of lower samples), but all locations had at least one occurrence of lichen-forming or possibly lichen-forming fungi (Table 1, Fig. 7). No known lichen photobionts were detected from the wood samples with detected lichen-forming taxa. In contrast, lichen photobionts (e.g. *Trebouxia, Asterochloris*), were frequently sequenced from the log surface samples verifying that the primers also amplify photobionts when they are present (data not shown).

Lichen-forming fungi belonging to *Lecanorales* and *Trapeliales* constituted the most abundant and frequent taxa on the log surface (Fig. 2). Most lichen-forming fungi identified from the log surface were not detected in wood (61 OTUs, 78 %) (Table S5). DNA from 34 possible lichen-forming fungal OTUs were recorded in the log surface that were not observed in the field inventory of lichens (Table S5). Several of the lichen-forming or possible lichen-forming OTUs that were detected in wood were also detected from the surface of the same disc (*Catinaria* sp1., *Cladonia pleurota*, *Frutidella* spp., *Micarea* sp3., *Elixia* spp., *Parmeliopsis ambigua and Xylographa parallela*). Two OTUs were recorded both from wood and log surface but not from the same disc, (*Hypogymnia tubulosa*, *Tuckemannopsis chlorophylla*) (Table S5). Ultimately, the community structure of lichen-forming OTUs was related to location within the upper 2 cm wood and especially associated to log surface samples, but with some OTUs occurring occasionally also in other wood locations (e.g. *Cladonia* sp1 and Trapaleliaceae in log surface and in wood center (Table 1).

3.5. Distribution of putative ecological roles

Classification of the OTUs into ecological roles revealed known wood decomposers to be concentrated in the center of the logs, other saprotrophs, pathogens, and mycorrhizal fungi in the outer parts of the logs, while lichen-forming fungi were confined to upper and outer parts of the log (Fig. 7).

4. Discussion

Our analyses of fine-scale patterns of wood-inhabiting fungal communities show that most species occurred in seemingly haphazard fine-scale patterns throughout the naturally formed Norway spruce logs, and that different dominating fungi and differing fungal communities are present even in nearby logs. Although highly variable assemblages of wood-inhabiting fungi are well described (Kubartová et al., 2012; Baldrian et al., 2016; van der Wal et al., 2016; Norberg et al., 2019), their distribution had not previously been investigated in such fine-scale as reported here. In accordance with known influence of microclimate and wood qualitiy on fungi (Baldrian et al., 2016; Krah et al., 2018; Birkemoe et al., 2022), we also found that the outer log surface communities differed substantially from that in the wood. We also detected several lichen-forming fungal OTUs in wood, indicating the ability of some of them to have a saprotrophic life-cycle stage.

Table 1
The number of samples where lichen-forming OTUs were recorded in wood and their presence in log surface samples. The assigned ecological role is marked as a superscript. Li = Lichens, with ≥98,5 % similarity and 100 % query coverage to well-curated lichen sequences in GenBank; Pli = Possible lichens, with <98,5 % similarity and 100 % query coverage to well-curated lichen sequences in GenBank.

Taxon	Wood										Log surface		
	Upper		Lower		Centre			Present in no. of			No. of samples		
	1–2 cm	2–3 cm	1–2 cm	2–3 cm	3–4 cm	4–5 cm	center	samples	discs	logs	Upper	Lower	In total
Cladonia crispata li						1		1	1	1	2	3	5
Cladonia pleurota li				1				1	1	1	9	21	30
Frutidella furfuracea li					1			1	1	1	26	23	49
Hypogymnia tubulosa li	1	1						2	2	2	4	2	6
Parmeliopsis ambigua li	2				3	1		6	5	4	58	49	107
Scoliciosporum umbrinum li [a]			1					1	1	1			
Tuckermannopsis chlorophylla li			1					1	1	1	1	2	3
Xylographa parallela li	2		2			2		6	6	4	50	40	90
Catinaria sp*1 pli*		1						1	1	1	8	22	30
Cladonia sp*1 pli*							1	1	1	1	6	12	18
Elixia sp*1 pli* [a]				1				1	1	1			
Elixia sp2 pli	12	3	4	3		1		23	17	8		3	3
Elixia sp3 pli	6	3	3	1	1	4	1	19	10	6		2	2
Frutidella sp. pli	3							3	3	2	25	36	61
Micarea sp*3 pli*	2			2	2			6	5	4	42	56	98
Xylographa sp*1 pli*							1	1	1	1			
Xylographa sp2 pli	1							1	1	1	6	3	9
N of samples with lichens	21	6	8	5	6	9	3	58	26	8	64	61	
Total no of samples	32	32	29	31	31	31	29	405	32	8	64	63	
% of samples with lichens	66	19	28	16	19	29	10	14	81	100	100	97	

[a] Not recorded from log surface or inventoried.

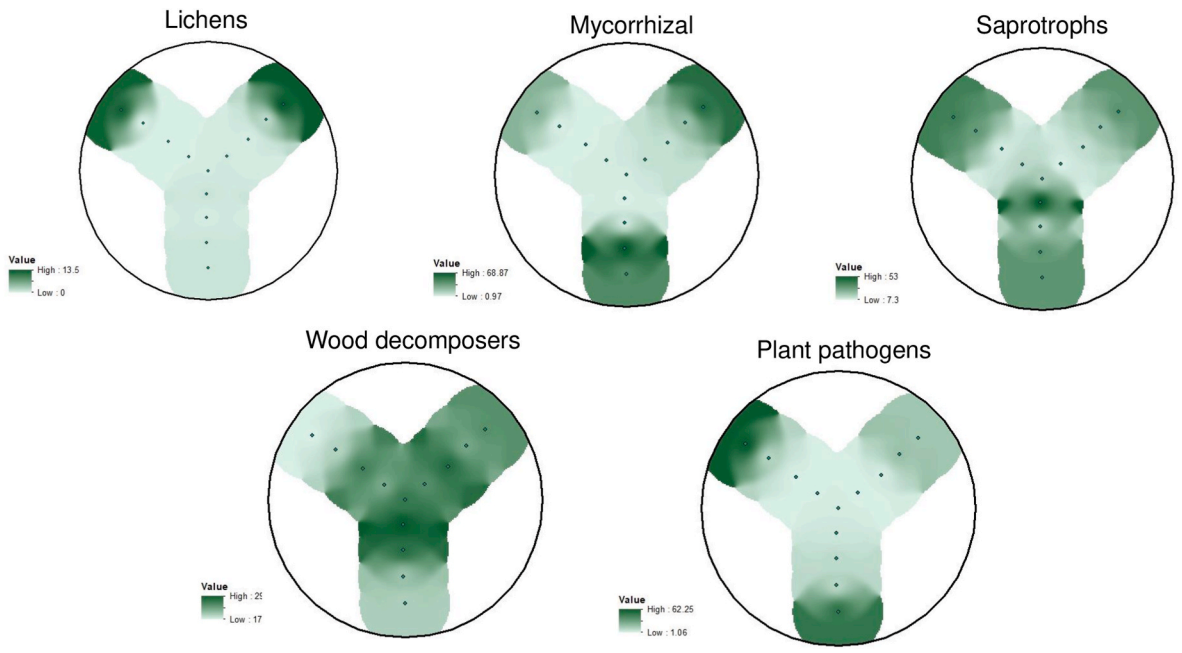

Fig. 7. Maps of interpolated abundances of fungal ecological groups within wood discs using Inverse Distance Weighting (IDW) in GIS. Saprotrophs refers to saprotrophs except known wood-decomposers. Higher abundances are represented by darker shaded circles (dots represent the sampling points as in Fig. 1).

4.1. Logs dominated by different fungi

The composition of the fungal communities varied significantly between the logs and the two nearby sites within the forest. Individual logs were typically dominated by one or few OTUs, which also were different between the logs. Three of the logs were dominated by a single species, while the other five were dominated by a handful of species. The pattern that the majority of the OTUs are less frequent and recorded only in few or single logs, and that only a few OTUs are widespread and abundant, is in accordance with earlier reports (Renvall, 1995; cf. Norikorpi, 1979; Kubartová et al., 2012; Ovaskainen et al., 2013). Although potentially exposed to the same local pool of species, fungal communities differ among dead wood units within a site (Edman and Jonsson, 2001; Kubartová et al., 2012; Baldrian et al., 2016; van der Wal et al., 2016; Norberg et al., 2019). This is probably due to a combination of stochasticity, priority effects and environmental filtering due to microclimatic variations in temperature and humidity (eg. Krah et al., 2018; Brabcová et al., 2022) with subsequent downstream impacts on wood qualities. Establishment and mycelial development of potential colonizing successor species, i.e. their fitness, is affected by the combative abilities of the species already established and their alteration of physical wood conditions and chemistry (Boddy, 2001; Fukami et al., 2010; van der Wal et al., 2013). Thus, dead wood characteristics (e.g. cause of death, type of breakage, and whether standing dead prior to fall) may play a more important role for fungal establishment than interspecific interactions per se (Renvall, 1995; Edman and Jonsson, 2001; Ottosson et al., 2015).

The species dominant in single logs, e.g. *Porodaedalea abietis, Neoantrodia serialis* and *Veluticeps abietina* were also present in most other logs, but at significantly lower abundances. *P. abietis* is a widespread weak pathogen in northern Europe causing heart rot in living old Norway spruce and continuing as a decomposer after the tree has died and fallen (Norikorpi, 1979; Edman and Jonsson, 2001; Recoder, 2022). In forests older than 150 years, the average extent of the decay column caused by *P. abietis* is reported to be 3 m and 6 m if formed by butt rot or originating from a stem wound, respectively (Norikorpi, 1979). The frequency of decay from *P. abietis* depends primarily on the age of trees. In natural forests, butt rot begins to occur when Norway spruce trees are 50–100 years old and is found in almost all trees at an age of 300–400 years (Norikorpi, 1979). At our moist study site (site 2) two of the logs (7 and 8) were massively and predominantly colonized by single fungal species; *P. abietis* and *V. abietina*, respectively. It is likely that they already extensively colonized these logs from the base before tree death, impeding the colonization and establishment of other fungi (Boddy, 2001; Boddy and Heilmann-Clausen, 2008).

We found that the abundant and long-lived basidiomycete fungi (e.g. *P. abietis*, *P. nigrolimitatus*, *Amylocystis lapponica*, *V. abietina*) typically dominated the inner parts of the logs from the base to the top disc, suggesting that they established in the trunk before tree death and fall. Similarly to our findings, Alfredsen et al. (2014) and Kurbatová et al. (2012) report *A. lapponica* to occur in the inner part of logs. Earlier studies have shown that it is a weak competitor in interaction experiments (Holmer & Stenlid,1997) and a weak colonizer of logs in the field (Moor et al., 2021). Hence, its success and apparent commonness in coarse naturally fallen logs in old-growth forests may rely on the establishment of mycelia in trunks before tree death and tree fall, rather than later establishment from spores (Alfredsen et al., 2014).

4.2. Highly variable fine-scale spatial fungal community patterns

The network analyses revealed a fine-scale fungal community pattern with different occurrences and compositions of fungi within logs. Fungal assemblages varied within and among wood discs from different parts of a log, from the outer to the inner part of the log, and between upper and lower sides of the logs. Several fungal taxa occurred at the same time even in minute volumes of wood throughout the logs. On average, we identified 10 species in our minute wood dust-samples (range 1–49). The dominant species were characteristically present in the center of the trunk throughout the log and often also extending to the outer parts. Occurrences of less common species were spatially restricted.

The origin of these fine-scale patterns is probably due to a combination of processes. First, we suggest that the dominant species were often established in the living trees and successively occupied larger volumes by mycelial spread as the tree aged, condition deteriorated, and eventually died and fell, as exemplified with the species described above. Second, throughout the lifespan of a tree, numerous fungi may establish through damage resulting in either smaller restricted areas of a

fungus or survival as endophytes, where both may develop as the tree's resilience declines (Boddy, 2021). Potentially, yet unknown, dying and dead branches collecting fungi may act like Trojan horses, where established mycelia in the dead branches may extend into the trunk and survive until the conditions may allow extension, or become overgrown (Zabel and Morrell, 2020). This route could be a significant inlet in Norway spruce, which forms annual branch whorls that successively die as the tree grows and becomes old, especially in dense stands. Third, fungi may also colonize and establish after the tree has died from either wind or insect-dispersed spores, or soil mycelia at the base of the trunk or where logs have ground contact. We assume that fungal assemblages in naturally and successively dying trees partly will differ from felled trees as sudden loss of moisture from such wood favour species selected to different conditions. Hence, fungal colonization of wood in roots and trunks of trees that died naturally may differ from man-made stumps and logs due to priority effects and subsequent downstream successional impacts.

The patterns of random and spatially restricted occurrence of rarer species supports the idea that for taxa that share niches and microhabitat requirements, stochastic processes are more decisive for the occurrence and composition of fungal communities in wood than deterministic processes such as environmental filtering (Hubbell, 2001; Norberg et al., 2019). These findings also suggest that producing many spores at appropriate times and thereby increasing the probability of becoming established, may be more crucial than niche differentiation and interspecific interactions for species mainly colonizing from spores (Boddy, 2001; Boddy and Hiscox, 2016). Our results also suggest that primary decayers and other fungi present in the lower parts of the logs may significantly establish by mycelial spread from the ground where species interactions and niche differentiation will take place.

The fungal community composition differed significantly between the upper and lower parts of the logs, demonstrating differential niches between species. An example is represented by the widespread *Hyphodiscus hymeniophilus* that was significantly related to the upper part in multiple logs, while *Phialocephala* sp. from a genus considered to be root endophytes was mainly found in the lower part. The species' occurrences for different parts of a log were presumably associated with different microclimatic environmental conditions since the wood in the lower part of a log is less exposed for deposition of spores and close to mycelia of soil fungi, cooler and more humid, while the upper part experiences periods which are significantly warmer and dryer (Lindhe et al., 2004; Krah et al., 2018).

4.3. Fungal co-occurrences were rare

Among the 15 most abundant OTUs for each log, few positive occurrences at the expense (i.e. negative occurrence) of other abundant species were detected within specific wood locations. For example, the positive correlative occurrence of early colonizers (e.g. *V. abietina*) did not coincide with negative occurrences of other abundant species, which could suggest that the succession of wood fungi was substantially driven by primary abundant decomposers and priority effects (Ovaskainen et al., 2010). However, negative co-occurrences are statistically harder to detect since they require more data to infer than positive associations (Ovaskainen et al., 2016). Species' co-occurrences may indicate similar or dissimilar environmental niches as well as interspecific interactions (Pan & May 2009). This is especially hard to disentangle in our study where we analyzed raw occurrence data that did not account for the effects of environmental conditions (Abrego et al., 2017, 2020; Saine et al., 2020). Some wood-inhabiting fungi may have co-occurred merely due to shared responses to certain abiotic conditions (Saine et al., 2020).

Co-occurrence patterns were highly stochastic as different OTUs clustered together, often including less abundant species, in each log, disc and location. We only identified a few common spatial co-occurrence networks for some of the taxa, which were clustered across a variety of spatial fine scales. However, to appropriately detect co-occurrences, a much higher number of replicates would be needed for all spatial scales. Nevertheless, across logs, we found positive co-occurrences between Exophiala sp1 and Pezizomycotina1, as well as groups Helotiales and Chaetothyriales. Similarly to our findings, Abrego et al. (2020) reported two groups of endophytic ascomycetes to positively co-occur in root-associated fungal communities, suggesting that such pattern may reflect facilitative or trophic interactions.

A species' competitive ability is linked to the size of its occupied territory within the wood (Holmer and Stenlid, 1997). Our methods do not allow us to identify whether occurrences of the same species within logs belong to the same genet or not, nor if mycelial genets were continuous or fragmented into ramets. However, as the inherent nature of wood fungi is to expand their domains by mycelial growth, nearby occurrences likely belong to the same genotype. Mycelia of some wood-inhabiting basidiomycete species may with time extend from decimeters to several meters (Boddy, 2021), making it likely that the records of the most abundant basidiomycetes species consisted of one genet in each log. On the contrary, mycelia of other species, in particular ascomycetes, inherently are smaller (Boddy, 2021). Many ascomycetes occurred in relatively low abundances in different locations of the wood, and their spatially constrained mycelia in the wood likely make them susceptible to replacement by more abundant species and stochastic extinction events.

4.4. Different fungi on and inside logs

As expected, the log surfaces and the wood hosted distinctly different fungal communities. Ascomycetes dominated the surfaces and basidiomycetes dominated the wood. Most likely, part of this difference is due to the contribution of fungal progagules of deposited as spores or environmental debris to the log surface fungal communities as the thin surface samples were not sterilized. However, the common species in the wood were not present on the log surface (e.g. *P. abietis*), and only exceptionally species in the outer wood samples were detected on the surface (e.g. *Hyaloscypha aureliella* in log 5, *Rhinocladiella atrovirens* in log 7). It could be expected that the log surface could be an important gateway for colonization of fungi in the wood. Over time, perhaps particularly early in the decay, it may be influential. However, the dissimilar environmental conditions between the log surface and wood in combination with the outcome of biotic interactions may lead to the formation of significantly different communities. In other words, log surfaces form a special habitat with distinct assemblages of fungi and other biota. This does not exclude fungi on the log surfaces to be a source for some fungi to colonize the wood. Hagge et al. (2019) report species richness of wood fungi to be about 30 % higher if cut trees were debarked after 1.5 years, confirming colonization to take place from the wood surface. Their study implies that wood-inhabiting fungi may largely originate from already established endophytic fungi also in freshly created wood. Establishment from log surfaces may necessitate more extended time periods compared to colonization via mycelia from the soil or through the root system. This is because early colonizers already present in wood often possess antagonistic properties that can hinder the spread of species with lower competitive abilities (Boddy and Hiscox, 2016). The community composition on the upper and lower sides of log surfaces was significantly different but were similar along the logs across the log base-to-top discs. As discussed, these variations may be attributed to microclimatic differences and potential colonization pathways of the upper and lower parts of the logs.

4.5. Rare occurrence of lichen-forming fungi in wood

Deadwood surfaces represent an important niche for lignicolous lichens (Svensson et al., 2016). We recorded lichen-forming and possible lichen-forming fungi in 14 % of the wood samples; however, their occurrence was infrequent and sparse in abundance (0.02 %). The most common of the recorded seventeen taxa, *Elixia* sp2, was detected in 6 %

of the wood samples, while ten taxa were recorded from single wood samples only. This pattern of most species being rare and only a few being more common may correspond well to the general pattern of species frequences in communities of different groups of organisms. In our sampling design, we deliberately aimed to minimize the likelihood of lichen propagules in the wood samples. Consequently, we successfully eliminated thallus propagules from the samples, as no lichen photobionts were detected in the same wood samples as the lichen-forming fungi. This outcome underscores the effectiveness of our sampling strategy in achieving its intended purpose.

The two most frequently recorded lichen-forming species, *Xylographa parallela* and *Parmeliopsis ambigua,* are common epiphytes on *Picea abies* and were detected in 3 % of the samples and half of the studied logs. *Xylographa parallela*, characterized as a crustose, obligate lignicolous species with primarily sexual reproduction (Spribille et al., 2015), may maintain a saprotrophic capacity as a survival strategy in cases where suitable photobionts are unavailable to. Notably, *Xylographa parallela* was detected in samples both near the surface and deeper within the wood. However, it was never recorded twice from the same disc, posing a challenge in predicting the penetration depth of its hyphae from the lichen growing on the log surface. *Parmeliopsis ambigua* forms a common foliose lichen mainly growing on wood. In our data, records of *P. ambigua* from wood were restricted to the upper side of the log but found even 4–5 cm deep. Similarly, *Cladonia crispata*, *Elixia* sp3, *Frutidella furfuracea* and *Micarea* sp3 were found deep in wood. These records could be indicative of hyphae penetrating from the epiphytic lichens or indicate a saprotrophic life stage. Specific staining of the individual hyphae could be one approach to confirm if they belong to the same individuals that grow epiphytic on the surface. However, the presence of several epiphytic lichens and lichen-forming fungal OTUs on the log surfaces suggests that if their hyphae were regularly penetrating deep into the wood, more of their DNA would likely be captured in barcoding studies. Resl et al. (2022) demonstrated that many lichen-forming fungi have the genomic arsenal for breaking down wood. Although rare, the occurrences of lichen-forming fungi deep in the wood suggest that optional lichenization may be more widespread across lichen-forming fungi than currently acknowledged, but the significance of such strategies in the life cycle of lichen-forming fungi remains unknown. Interestingly, species belonging to *Elixia* were frequent in wood samples but rarely detected from surface samples of the same discs. *Elixia* is a genus with currently two described crustose lichens living on wood or bark (Spribille and Lumbsch, 2010). The OTUs detected in this study could be previously undescribed lichen-forming members of the genus, or closely related saprotrophs. We note that previous reports of Umbilicariales from wood samples (e.g. Ottosson et al., 2015) may likely be closely related to *Elixia* species detected in our study, which could now be identified because of a large recent increase of well-curated wood--inhabiting lichen sequences in GenBank (Vondrak et al., 2023).

4.6. Asymmetric spatial distribution of fungi with different ecological roles

Grouped into ecological roles, OTUs occurred spatially partitioned to various niches in the wood. This indicates that environmental filtering influenced fine-scale assemblages of OTUs of certain ecological roles more than OTUs of a specific identity, likely because fungal ecological roles are more tightly connected to underlying mechanisms relating to colonization, resource use and successional stage (Dawson et al., 2019; Zanne et al., 2020). Wood decomposers predominantly occupied the center of logs, confirming what we observed for single abundant species (e.g. *P. abietis*). Wood decomposers include long-lived white rot and brown rot fungi known to often colonize wood before tree death and develop large mycelia which prevent other species from spreading throughout inner wood parts (Ottosson et al., 2015). After tree death, the abiotic conditions in sapwood change rapidly and fungi with other ecological roles can establish via wood wounds or bark loss and by insect vectors (Boddy, 2001). This pathway is supported by our results showing mycorrhizal, saprotrophic and plant pathogenic groups inhabiting mainly the outer parts of the logs. As expected, the lower outer parts of wood were associated with a higher abundance of mycorrhizal and some soil-saprotroph species (Mäkipää et al., 2017). Lichen-forming taxa were mainly distributed in the upper 2 cm of the logs indicating a possible colonization route from the surface samples where they were more abundant and diverse.

CRediT authorship contribution statement

Anders Dahlberg: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Silvia Pioli:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Mari Jönsson:** Writing – review & editing. **Florian Barbi:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Göran Thor:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Veera Tuovinen Nogerius:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

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Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2025.101458.

References

Abarenkov, K., Nilsson, R.H., Larsson, K.H., Alexander, I.J., Eberhardt, U., Erland, S., Høiland, K., Kjøller, R., Larsson, E., Pennanen, T., Sen, R., Taylor, A.F.S., Tedersoo, L., Ursing, B.M., Vrålstad, T., Liimatainen, K., Peintner, U., Kõljalg, U., 2010. The UNITE database for molecular identification of fungi – recent updates and future perspectives. New Phytol. 186, 281–285. https://doi.org/10.1111/j.1469-8137.2009.03160.x.

Abrego, N., 2022. Wood-inhabiting fungal communities: opportunities for integration of empirical and theoretical community ecology. Fungal Ecol 59, 101112. https://doi.org/10.1016/j.funeco.2021.101112.

Abrego, N., Norberg, A., Ovaskainen, O., 2017. Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. J. Ecol. 105, 1070–1081. https://doi.org/10.1111/1365-2745.12722.

Abrego, N., Roslin, T., Huotari, T., Tack, A.J.M., Lindahl, B.D., Tikhonov, G., Somervuo, P., Schmidt, N.M., Ovaskainen, O., 2020. Accounting for environmental

variation in co-occurrence modelling reveals the importance of positive interactions in root-associated fungal communities. Mol. Ecol. 29, 2736–2746. https://doi.org/10.1111/mec.15516.
Alfredsen, G., Rolstad, J., Solheim, H., Rolstad, E., Storaunet, K.O., 2014. Is fungal species richness and composition related to the occurrence of the old-growth associated wood-decaying *Amylocystis lapponica*? Nord. J. Bot. 32, 330–336. https://doi.org/10.1111/j.1756-1051.2013.00130.x.
Baldrian, P., Zrůstová, P., Tláskal, V., Davidová, A., Merhautová, V., Vrška, T., 2016. Fungi associated with decomposing deadwood in a natural beech-dominated forest. Fungal Ecol 23, 109–122. https://doi.org/10.1016/j.funeco.2016.07.001.
Birkemoe, T., Nybakken, L., Andelic, M., Tangnæs, M.-J., Sverdrup-Thygeson, A., Kauserud, H., Jacobsen, R.M., 2022. Secondary metabolites and nutrients explain fungal community composition in aspen wood. Fungal Ecol 59, 101115. https://doi.org/10.1016/j.funeco.2021.101115.
Boddy, L., 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecol. Bull. 49, 43–56.
Boddy, L., 2021. Fungi and Trees. their Complex Relationships. Arboricultural Associations, Gloucestershire.
Boddy, L., Heilmann-Clausen, J., 2008. Chapter 12 basidiomycete community development in temperate angiosperm wood. Br. Mycol. Soc. Symp. 28, 211–237. https://doi.org/10.1016/S0275-0287(08)80014-8.
Boddy, L., Hiscox, J., 2016. Fungal ecology: principles and mechanisms of colonization and competition by saprotrophic fungi. Microbiol. Spectr. 4 (6). https://doi.org/10.1128/microbiolspec.funk-0019-2016.
Brabcová, V., Tláskal, V., Lepinay, C., Zrůstová, P., Eichlerová, I., Štursová, M., Müller, J., Brandl, R., Bässler, C., Baldrian, P., 2022. Fungal community development in decomposing fine deadwood is largely affected by microclimate. Front. Microbiol. 13, 835274. https://doi.org/10.3389/fmicb.2022.835274.
Dawson, S.K., Bodd, L., Halbwachs, H., Bässler, C., Andrew, C., Crowther, T.W., Jönsson, M., 2019. Handbook for the measurement of macrofungal functional traits: a start with basidiomycete wood fungi. Funct. Ecol. 33, 372–387. https://doi.org/10.1111/1365-2435.13239.
Dickie, I.A., Fukami, T., Wilkie, J.P., Allen, R.B., Buchanan, P.K., 2012. Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. Ecol. Lett. 15, 133–141. https://doi.org/10.1111/j.1461-0248.2011.01722.x.
Edman, M., Jonsson, B.G., 2001. Spatial pattern of downed logs and wood-decaying fungi in an old-growth *Picea abies* forest. J. Veg. Sci. 12, 609–620. https://doi.org/10.2307/3236900.
Epskamp, S., Cramer, A.O.J., Waldorp, L.J., Schmittmann, V.D., Borsboom, D., 2012. Qgraph: network visualizations of relationships in psychometric data. J. Stat. Software 48, 1–18. https://doi.org/10.18637/jss.v048.i04.
Foster, Z.S.L., Chamberlain, S., Grundwald, N.J., 2018. Taxa: an R package implementing data standards and methods for taxonomic data. F1000Res 7 (272). https://doi.org/10.12688/f1000research.14013.2.
Fukami, T., Dickie, I.A., Wilkie, P.J., Paulus, B.C., Park, D., Roberts, A., Buchanan, P.K., Allen, R.B., 2010. Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecol. Lett. 13, 675–684. https://doi.org/10.1111/j.1461-0248.2010.01465.x.
Gilmartin, E.C., Jusino, M.A., Pyne, E.J., Banik, M.T., Lindner, D.L., Boddy, L., 2022. Fungal endophytes and origins of decay in beech (*Fagus sylvatica*) sapwood. Fungal Ecol 59, 101161. https://doi.org/10.1016/j.funeco.2022.101161.
Hagge, J., Bässler, C., Gruppe, A., Hoppe, B., Kellner, H., Krah, F., Müller, J., Seibold, S., Stengel, E., Thorn, S., 2019. Bark coverage shifts assembly processes of microbial decomposer communities in dead wood. Proc. R. Soc. A B. 286, 20191744. https://doi.org/10.1098/rspb.2019.1744.
Hiscox, J., Savoury, M., Muller, C.T., Lindahl, B.D., Rogers, H.J., Boddy, L., 2015. Priority effects during fungal community establishment in beech wood. ISME J. 9, 2246–2260. https://doi.org/10.1038/ismej.2015.38.
Holmer, L., Stenlid, J., 1997. Competitive hierarchies of wood decomposing basidiomycetes in artificial systems based on variable inoculum sizes. Oikos 79, 77–84.
Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.
Ihrmark, K., Bödeker, I.T.M., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandström-Durling, M., Clemmensen, K.E., Lindahl, B.D., 2012. New primers to amplify the fungal ITS2 region – evaluation by 454-sequencing of artificial and natural communities. FEMS Microbiol. Ecol. 82, 666–677.
Junninen, K., Komonen, A., 2011. Conservation ecology of boreal polypores: a review. Biol. Conserv. 144, 11–20.
Kärvemo, S., Jönsson Hekkala, A.-M., Sjögren, J., Strengbom, J., 2021. Multi-taxon conservation in northern forest hot-spots: the role of forest characteristics and spatial scales. Landsc. Ecol. 36, 989–1002.
Krah, F.S., Seibold, S., Brandl, R., Baldrian, P., Müller, J., Bässler, C., 2018. Independent effects of host and environment on the diversity of wood-inhabiting fungi. J. Ecol. 106, 1428–1442. https://doi.org/10.1111/1365-2745.12939.
Kubart, A., Vasaitis, R., Stenlid, J., Dahlberg, A., 2016. Fungal communities in Norway spruce stumps along a latitudinal gradient in Sweden. For. Ecol. Manag. 371, 50–58.
Kubartová, A., Ottosson, E., Dahlberg, A., Stenlid, J., 2012. Patterns of fungal communities among and within decaying logs, revealed by 454 sequencing. Mol. Ecol. 21, 4514–4532. https://doi.org/10.1111/j.1365-294X.2012.05723.x.
Lindahl, B.D., Nilsson, R.H., Tedersoo, L., Abarenkov, K., Carlsen, T., Kjoller, R., Koljalg, U., Pennanen, T., Rosendahl, S., Stenlid, J., Kauserud, H., 2013. Fungal community analysis by high-throughput sequencing of amplified markers - a user's guide. New Phytol. 199, 288–299. https://doi.org/10.1111/nph.12243.
Lindhe, A., Åsenblad, N., Toresson, H.G., 2004. Cut logs and high stumps of spruce, birch, aspen and oak – nine years of saproxylic fungi succession. Biol. Conserv. 119, 443–454. https://doi.org/10.1016/j.biocon.2004.01.005.
Lindner, D.L., Vasaitis, R., Kubartová, A., Allmér, J., Johannesson, H., Banik, M.T., Stenlid, J., 2011. Initial fungal colonizer affects mass loss and fungal community development in *Picea abies* logs 6 yr after inoculation. Fungal Ecol 4, 449–460. https://doi.org/10.1016/j.funeco.2011.07.001.
Mäkipää, R., Rajala, T., Schigel, D., Rinne, K.T., Pennanen, T., Abrego, N., Ovaskainen, O., 2017. Interactions between soil- and dead wood-inhabiting fungal communities during the decay of Norway spruce logs. ISME J. 11, 1964–1974. https://doi.org/10.1038/ismej.2017.57.
Menkis, A., Redr, D., Bengtsson, V., Hedin, J., Niklasson, M., Nordén, B., Dahlberg, A., 2022. Endophytes dominate fungal communities in six-year-old veteranisation wounds in living oak trunks. Funct. Ecol. 59, 101020. https://doi.org/10.1016/j.funeco.2020.101020.
Moor, H., Nordén, J., Penttilä, R., Siitonen, J., Snäll, T., 2021. Long-term effects of colonization–extinction dynamics of generalist versus specialist wood-decaying fungi. J. Ecol. 109, 491–503. https://doi.org/10.1111/1365-2745.13526.
Norberg, A., Halme, P., Kotiaho, J.S., Toivanen, T., Ovaskainen, O., 2019. Experimentally induced community assembly of polypores reveals the importance of both environmental filtering and assembly history. Fungal Ecol. 41, 137–146. https://doi.org/10.1016/j.funeco.2019.05.003.
Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. J. Ecol. 101, 701–712. https://doi.org/10.1111/1365-2745.12085.
Norikorpi, Y., 1979. Old Norway spruce stands, amount of decay and decay-causing microbes in northern Finland. Commun. Inst. For. Fenn. 97, 1–77.
Norros, V., Penttilä, R., Suominen, M., Ovaskainen, O., 2012. Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. Oikos 121, 961–974. https://doi.org/10.1111/j.1600-0706.2012.20052.x.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. Vegan: community ecology package. https://www.researchgate.net/publication/313502495_Vegan_Community_Ecology_Package#fullTextFileContent.
O'Leary, J., Journeaux, K.L., Houthuijs, K., Engel, J., Sommer, U., Viant, M.R., Eastwood, D.C., Müller, C., Boddy, L., 2021. Space and patchiness affects diversity–function relationships in fungal decay communities. ISME J. 15, 720–731. https://doi.org/10.1038/s41396-020-00808-7.
Ottosson, E., Nordén, J., Dahlberg, A., Edman, M., Jönsson, M., Larsson, K., Olsson, J., Penttilä, R., Stenlid, J., Ovaskainen, O., 2014. Species associations during the succession of wood-inhabiting fungal communities. Fungal Ecol 11, 17–28. https://doi.org/10.1016/j.funeco.2014.03.003.
Ottosson, E., Kubartová, A., Edman, M., Jönsson, M., Lindhe, A., Stenlid, J., Dahlberg, A., 2015. Diverse ecological roles within fungal communities in decomposing logs of *Picea abies*. FEMS Microbiol. Ecol. 9, 1–15. https://doi.org/10.1093/femsec/fiv012.
Ovaskainen, O., Hottola, J., Siitonen, J., 2010. Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. Ecology 9, 2514–2521. https://doi.org/10.1890/10-0173.1.
Ovaskainen, O., Schigel, D., Ali-Kovero, H., Auvinen, P., Paulin, L., Nordén, B., Nordén, J., 2013. Combining high-throughput sequencing with fruitbody surveys reveals contrasting life-history strategies in fungi. ISME J. 7, 1696–1709. https://doi.org/10.1038/ismej.2013.61.
Ovaskainen, O., Abrego, N., Halme, P., Dunson, D., 2016. Using latent variable models to identify large networks of species-to-species associations at different spatial scales. Methods Ecol. Evol. 7, 549–555. https://doi.org/10.1111/2041-210X.12501.
Pan, J.J., May, G., 2009. Fungal-fungal associations affect the assembly of endophyte communities in maize (*Zea mays*). Microb. Ecol. 58, 668–678. https://doi.org/10.1007/s00248-009-9543-7.
Påhlson, L., 1994. Vegetationstyper I Norden. Nordiska Ministerrådet, Copenhagen, p. 630.
Piché-Choquette, S., Tláskal, V., Vrška, T., Jiráska, L., Větrovský, T., Baldrian, P., 2023. Continuous microhabitats as crossroads of fungal communities in a primeval temperate forest. Soil Biol. Biochem. 187, 109187. https://doi.org/10.1016/j.soilbio.2023.109187.
R Core Team, 2019. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Rajala, T., Peltoniemi, M., Pennanen, T., Mäkipää, R., 2012. Fungal community dynamics in relation to substrate quality of decaying Norway spruce (*Picea abies* [L.] Karst.) logs in boreal forests. FEMS Microbiol. Ecol. 81, 494–505. https://doi.org/10.1111/j.1574-6941.2012.01376.x.
Rajala, T., Tuomivirta, T., Pennanen, T., Mäkipää, R., 2015. Habitat models of wood-inhabiting fungi along a decay gradient of Norway spruce logs. Fungal Ecol 18, 48–55. https://doi.org/10.1016/j.funeco.2015.08.007.
Rayner, A.D.M., Boddy, L., 1988. Fungal Decomposition of Wood: Its Biology and Ecology. John Wiley & Sons, Ltd, Chichester.
Recoder, M.G., 2022. Spruce Associated *Porodaedalea* Species Distribution in Sweden. Uppsala University, Sweden. Master Thesis. http://uu.diva-portal.org/smash/get/diva2:1673828/FULLTEXT01.pdf.
Renvall, P., 1995. Community structure and dynamics of wood-rotting basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35, 1–51. https://doi.org/10.29203/KA.1995.309.
Resl, P., Bujold, A.R., Tagirdzhanova, G., Meidl, P., Rallo, S.F., Kono, M., Fernández-Brime, S., Gudmundsson, H., Andrésson, O.S., Muggia, L., Mayrhofer, H., McCutcheon, J.P., Wedin, M., Werth, S., Willis, L.M., Spribille, T., 2022. Large

differences in carbohydrate degradation and transport potential among lichen fungal symbionts. Nat. Commun. 13, 2634. https://doi.org/10.1038/s41467-022-30218-6.
Roll-Hansen, F., Roll-Hansen, H., 1979. Microflora of sound-looking wood in *Picea abies* stems. Eur. J. For. Pathol. 9, 308–316. https://doi.org/10.1111/j.1439-0329.1979.tb00693.x.
Runnel, K., Drenkhan, R., Adamson, K., Lohmus, P., Rosenvald, K., Rosenvald, R., Rahn, E., Tedersoo, L., 2021. The factors and scales shaping fungal assemblages in fallen spruce trunks: a DNA metabarcoding study. For. Ecol. Manag. 495, 119381. https://doi.org/10.1016/j.foreco.2021.119381.
Saine, S., Ovaskainen, O., Somervuo, P., Abrego, N., 2020. Data collected by fruit body – and DNA-based survey methods yield consistent species-to-species association networks in wood-inhabiting fungal communities. Oikos 129, 1833–1843. https://doi.org/10.1111/oik.07502.
Saine, S., Penttila, R., Furneaux, B., Monkhouse, N., Zakharov, E.V., Ovaskainen, O., Abrego, N., 2024. Natural deadwood hosts more diverse pioneering wood-inhabiting fungal communities than restored deadwood. Restor. Ecol. 32 (1), e14056. https://doi.org/10.1111/rec.14056.
Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41. https://doi.org/10.2307/20113262.
Spribille, T., Lumbsch, H., 2010. A new species of *Elixia* (Umbilicariales) from Greece. Lichenologist 42, 365–371. https://doi.org/10.1017/S0024282910000058.
Spribille, T., Resl, P., Ahti, T., Pérez-Ortega, S., Tønsberg, T., Mayrhofer, H., Lumbsch, H. T., 2015. Molecular systematics of the wood-inhabiting lichen-forming genus *Xylographa* (Baeomycetales, Ostropomycetidae) with eight new species. Symb. Bot. Ups. 37 (1), 1–87.
Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Dead Wood. Cambridge University Press, UK. https://doi.org/10.1017/CBO9781139025843.
Svensson, M., Johansson, V., Dahlberg, A., Frisch, A., Thor, G., Ranius, T., 2016. The relative importance of stand and dead wood types for wood-dependent lichens in managed boreal forests. Fungal Ecol 20, 166–174. https://doi.org/10.1016/j.funeco.2015.12.010.
Tingsted, L., Grytnes, J.A., Felde, V.A., Juslén, A., Hyvärinen, E., Dahlberg, A., 2018. The potential to use documentation in national Red Lists to characterize red-listed forest species in Fennoscandia and to guide conservation. Global Ecol. Conservat. 15, e00410.
Tuovinen, V., Svensson, M., Kubartová, A., Ottosson, E., Stenlid, J., Thor, G., Dahlberg, A., 2015. No support for occurrence of free-living *Cladonia* mycobionts in dead wood. Fungal Ecol 14, 130–132. https://doi.org/10.1016/j.funeco.2014.12.003.
van der Wal, A., Geydan, T.D., Kuyper, T.W., de Boer, W., 2013. A thready affair: linking fungal diversity and community dynamics to terrestrial decomposition processes. FEMS Microbiol. Rev. 37, 477–494. https://doi.org/10.1111/1574-6976.12001.
van der Wal, A., Gunnewiek, P.J.A.K., Cornelissen, J.C., Crowther, T.W., de Boer, W., 2016. Patterns of natural fungal community assembly during initial decay of coniferous and broadleaf tree logs. Ecosphere 7, e01393. https://doi.org/10.1002/ecs2.1393.
Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional. Oikos 116, 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x.
Vondrak, J., Svoboda, S., Kosnar, J., Malícek, J., Soun, J., Frolov, I., Svensson, M., Novotny, P., Palice, Z., 2023. Martin7: a reference database of DNA barcodes for European epiphytic lichens and its taxonomic implications. Preslia 95, 311–345. https://doi.org/10.23855/preslia.2023.311.
Wickham, H., Hester, J., 2020. Readr: read rectangular text data. R package version 1.4.0. http://doi.org/10.32614/CRAN.package.readr.
Wickham, H., François, R., Henry, L., Müller, K., 2020. Dplyr: a grammar of data manipulation. R package version 1.0.2. https://CRAN.R-project.org/package=dplyr.
Zabel, R.A., Morrell, J.J., 2020. Decays originating in the stems of living trees. In: Chapter 12 in Wood Microbiology: Decay and its Prevention, second ed. Academic Press, pp. 311–337. https://doi.org/10.1016/B978-0-12-819465-2.00012-7.
Zanne, A.E., Abarenkov, K., Afkhami, M.E., Aguilar-Trigueros, C.A., Bates, S., Bhatnagar, J.M., Busby, P.E., Christian, N., Cornwell, W., Crowther, T.W., Moren, H. F., 2020. Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. Biol. Rev. 95, 409–433. https://doi.org/10.1111/brv.12570.