WOOD QUALITY THREATS FOR ECONOMICALLY IMPORTANT TREE SPECIES IN LATVIA: FINDINGS ON WOOD COLONIZING FUNGI

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Abstract
This study investigated the wood colonization by rot, blue stain or discoloration causing fungi, focusing on the quality of roundwood assortments of several economically important tree species in Latvia. A total of 105 trees were analysed across Latvia, including *Pinus sylvestris* (34), *Picea abies* (22), *Betula pendula* (10), *Alnus glutinosa* (29), and *Populus tremula* (10). Trees were randomly selected during or after felling based on visible signs of fungal infection: wounds, blue stain, wood discolouration, stem rot, cracks, and other symptoms. Wood-inhabiting fungi were isolated from different zones of one disc per tree (340 wood samples in total). Fungi were identified based on their morphological characteristics and molecular analysis (ITS region sequencing with primers ITS4 and ITS1F). A total of 56 fungal taxa were isolated from the wood samples. Among the rot-causing fungi, *Heterobasidion* spp. was frequently isolated from conifers; *Porodaedalea pini* and *Stereum sanguinolentum* were isolated specifically from pine and *Amylostereum areolatum* - from spruce. *Xanthoporia radiata* and *Eutypella cerviculata* were frequently isolated from black alder; while - *Phellinus tremulae* - from aspen wood. The blue stain causing fungi *Ophiostoma* spp. were isolated from pine, spruce and birch wood, while *Diplodia* spp. – only from spruce. This work was funded by JSC Latvia's State Forests (project No. 5-5.5.1_0009_200_24_7) and Forest4LV (project No. VPP-ZM-VRIIILA-2024/2-0002).
Keywords: *Picea abies*, *Pinus sylvestris*, deciduous trees, rot-causing fungi, blue stain fungi.

Introduction

Latvia's forests cover approximately 52% of the country's territory, making them a crucial component of the nation's landscape, biodiversity, and economy (Latvian State Forest Service, 2024). These forests are dominated by both coniferous and broadleaf tree species, 51% of the whole forest land is dominated Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, 30% is silver birch *Betula pendula*, 7% is European aspen *Populus tremula* and 4% is black alder *Alnus glutinosa* (Latvian State Forest Service, 2024). Given their economic and ecological importance, these tree species play a fundamental role in supporting forest biodiversity, regulating the carbon cycle, and providing valuable timber resources (Wani et al., 2021).

Forest ecosystems contribute significantly to soil stabilization and habitat formation, making them essential for global and regional environment. However, forest health is increasingly threatened by various biotic stress factors, including fungal pathogens that cause wood decay. Wood-decay fungi reduce the viability of trees and the commercial value of wood by causing structural damage, discoloration, and decomposition. These fungi include both saprotrophic species that degrade dead wood and pathogenic species that infect living trees and accelerate decay and mortality.

In Latvia, one of the biggest threats to coniferous forests are rot-causing pathogens, such as *Heterobasidion* spp., *Stereum sanguinolentum*, *Armillaria* spp. and *Porodaedalea pini* (Burņeviča et al., 2016; Szewczyk et al., 2016; Zaļuma et al., 2022; Klavina et al., 2023). Among these, *Heterobasidion* spp. is one of the most aggressive pathogens in whole Northern Europe, particularly affecting Scots pine and Norway spruce by causing root and butt rot, which leads to high tree mortality, reduced timber quality, and substantial economic losses (Asiegbu et al., 2005; Gaitnieks et al., 2008). In Europe alone, the estimated annual losses of *Heterobasidion* root rot is about one billion euro (Kovalchuk et al., 2022). *Porodaedalea pini* is a significant pathogen of Scots pine, causing heartwood decay that causes stem rot, and makes timber commercially unsuitable (Szewczyk et al., 2016). *Stereum sanguinolentum* is one of the most frequently isolated decay fungi in damaged spruce wood, following thinning operations in young stands across Central and Northern Europe (Mäkinen et al., 2007).

For deciduous trees common in Latvia, some studies have focused on rot fungi in grey and black alder stands (Arhipova et al., 2011; Arhipova et al., 2012). Recently, there have been sporadic studies about birch and aspen wood inhabiting fungi (Ciseļonoka et al., 2024, Miklašēvičs et al., 2024). The main rot-causing agents vary by species: *Xanthoporia radiata* (formely *Inonotus radiatus*) often colonizes alders, *Phellinus tremulae* is a primary agent of white trunk rot in European aspen, significantly reducing wood quality and shortening tree lifespan (Wikström, 1976), while *Armillaria* may cause root rot to several deciduous tree species (Guillaumin & Legrand, 2013).

Other problem, which cause decrease in wood quality, especially during timber storage is wood blue stain, discoloration and wood molding, caused by various Ascomycota genera (Highley, 2004; Uzunovic et al., 2008). This study aims to investigate fungal species associated with economically important tree species in Latvia, focusing on roundwood-colonizing fungi that cause blue stain, discoloration, rot and decay to strengthen the knowledge base of forest workers about fungal damage in timber.

Materials and Methods

While the age of the trees sampled in 2024 was not specifically determined as the study prioritized the analysis of visible symptoms, the investigation aimed to identify potential root rot and evaluate if it could degrade wood quality to the point of excluding it in the use of structural buildings. The wood disc samples were taken from 105 mature livingtrees (34 Scots pine *Pinus sylvestris* (average disc diameter – 30 cm), 22 Norway spruce *Picea abies* (average disc diameter – 28 cm), 29 black alder *Alnus glutinosa* (average disc diameter – 36 cm), 10 European aspen *Populus tremula* (average disc diameter – 39 cm) and 10 birch *Betula pendula* (average disc diameter – 32 cm). Trees were randomly selected during or after felling based on visible signs of fungal infection: wounds, blue stain, wood discolouration, stem rot, cracks, and other symptoms. From each tree, a single 2-3 cm thick wood disc was dissected from the cutting surface. Discs were marked, stored separately in plastic bags, and transported to the laboratory for pathogen identification. In the laboratory, 0.5-1 cm wood pieces were extracted from the wood discs, using a flame-sterilised chisel (Vasiliauskas & Stenlid, 1998). The top layer of wood was carefully removed from the disc's surface then sterilized again, and small pieces of the discolored and symptomatic wood were collected at one to five points per disc, depending on the disc size and the decay extent. The extracted samples were then flame sterilised with disinfected tweezers and placed on a sterile Petri dishes with Hagem agar media (5 g glucose, 0.5 g NH_4NO_3, 0.5 g $MgSO_4$ $7H_2O$, 5 g malt extract, 20 g agar, 1000 mL distilled H_2O at pH 5.5). Petri dishes with wood samples were incubated at room temperature (21 °C) and monitored every two days for fungal mycelium growth. Fungal colonies that could not be identified microscopically and were potentially associated with wood decay were individually subcultured on separate Petri dishes with Hagem agar media (5 g glucose, 0.5 g NH_4NO_3, 0.5 g KH_2PO_4, 0.5 g $MgSO_4$, 5 g malt extract, 20 g agar, 1000 mL distilled H_2O at pH 5.5) and subjected for molecular identification.

For molecular identification, fungal aerial mycelium was carefully scraped from pure cultures using a flame-sterilized scalpel and transferred into a 2 mL tubes. DNA extraction was performed at the LSFRI Silava Genetic Resource Center using a modified CTAB method (Arhipova, 2012). PCR reactions were performed in a volume of 10 µl containing approximately 50 ng DNA, 2 µl HOT FIREPol® Blend Master Mix (Solis BioDyne) (containing 10 mM $MgCl_2$), 0.3 µM the fungal-specific forward primer ITS1F (5'-CTTGGTCATTTAGAGGAAGTAA-3') and reverse primer ITS4 (5'-TCCTCCGCTTATTGATATGC-3') (White et al., 1990; Gardes & Bruns, 1993). PCR was carried out in a thermocycler (Eppendorf Mastercycler epgradient) using the following protocol: initial predenaturation step at 95 °C for 12 min, followed by 35 cycles of 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 45 s and a final extension step of 72 °C for 7 min. The ITS region was Sanger sequenced in both directions using the same primers - ITS4 and ITS1F at the LSFRI Silava Genetic Resource Center. Nucleotide sequences were analyzed using the BLAST function in the UNITE and NCBI platforms (Altschul et al., 1997; Nilsson et al., 2018). The criteria to assign taxonomy for representative sequences was based on BLAST thresholds: family-level > 85%, genus-level > 90%, and species-level > 97%. Taxa falling below these thresholds were considered unidentified fungi at the respective taxonomic levels. To assign ecological functions and primary lifestyle to each fungal genus, FungalTraits database was used (Põlme et al., 2020).

The obtained sequences were deposited in GenBank with the accession number PV351336-PV351394.

We analysed percentage (%) of wood samples and proportion of wood discs colonized by each fungal species. Incidence of each fungal species was calculated for each tree species separately.

Results and Discussion

From the analysis of 105 wood discs and their corresponding 340 wood samples (116 from pine, 87 from black alder, 63 from spruce, 40 from aspen, and 34 from birch) a total of 56 fungal taxa were identified (Table 1 and 2). The most frequently isolated fungi across all tree species were from phylum Ascomycota such as *Alternaria*, *Cladosporium* and *Trichoderma.* These genera include saprotrophic, endophytic, and parasitic species, some of which are also plant pathogens (Põlme et al., 2020; Stępniewska et al., 2021). For example, some species of the genus *Alternaria* are widespread pathogens of leaves and young shoots (Matić et al., 2020). Additionally, several species from genera *Cladosporium* and *Fusarium* can become pathogenic to the plant under stress conditions such as prolonged drought, heat, or frost (Photita et al., 2004). *Ascocoryne* is very often present in spruce wounds as an endophyte or saprotroph (Vasiliauskas & Stenlid, 1998; Burneviča et al., 2016). *Schizophillum commune* was also identified; it is a common saprotroph in Latvia that grows on already dead deciduous wood, causing white rot but occasionally infects weakened living trees (Arhipova et al., 2011).

Several pathogenic fungi were identified, including *Botrytis cinerea* (Ascomycota), which causes grey mold (Williamson et al., 2007). While not a primary pathogen of adult conifers, it causes moldy needles in seedlings in nurseries (Lilja, 1986; Lilja et al., 2010). The pathogenic fungus *Neonectria tsugae* was also isolated from several samples. While this fungus does not cause wood decay, it is associated with canker formation in conifers, which weakens trees and increases their susceptibility to secondary infections

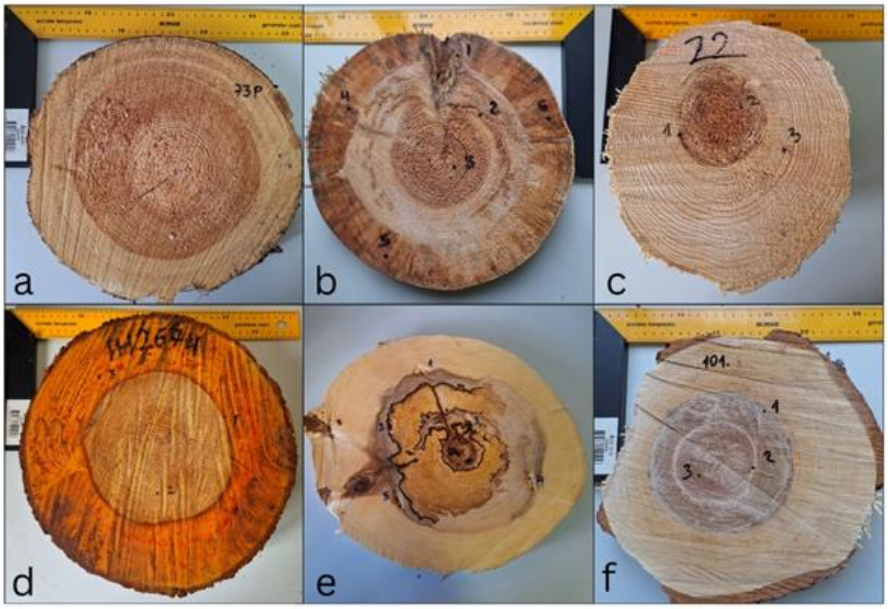
and environmental stress (González & Chaverri, 2017; Durodola et al., 2023).

Among the analyzed species, several blue-stain fungi of the genus *Ophiostoma* were isolated from Scots pine and European aspen samples. Another fungus *Aureobasidium pullulans* associated with blue-stain was isolated from Scots pine, European aspen and silver birch wood samples. *Aureobasidioum pullulans* is more widely known as black yeast that can penetrate wood surface coatings (Deshpande et al., 1992; Bardage, 1998). *Diplodia* sp. was also detected as blue stain causing for conifers (Brodde et al., 2019; Brodde, 2023). While these fungi do not cause mechanical degradation, they reduce the aesthetic and commercial value of the wood due to discoloration (Deshpande et al., 1992; Bardage, 1998; Brodde, 2023).

Eight wood-decaying and rot-causing fungi were identified in Scots pine and Norway spruce samples: *Amylostereum areolatum*, *Bjerkandera adusta*, *Cylindrobasidium evolvens*, *Heterobasidion* spp., *Porodaedalea pini*, *Sistotrema brinkmannii*, *Stereum sanguinolentum*, and *Trametes versicolor*, of which *Heterobasidion* spp., *P. pini* and *S. sanguinolentum* is considered one of the most severe pathogens of conifers. *Heterobasidion* spp. is among the most aggressive tree pathogens in Northern Europe, causing root and butt rot ʻFigure 1a'. *P. pini* is often referred to as ʻred-ring rot' due to the characteristic reddish-brown discoloration of the wood ʻFigure 1b'. It primarily infects the lower trunk, leading to significant structural weakening and rendering the timber commercially unsuitable (Szewczyk et al., 2016).

Figure 1

Evaluated wood discs: a - Scots pine (Heterobasidion spp. - white rot agent isolated), b - Scots pine (Porodaedalea pini - brown rot/red-ring rot agent isolated), c - Norway spruce (Amylostereum areolatum - white rot causing fungus isolated), d - black alder (Chondrostereum purpureum isolated), e - European aspen (Phellinus tremulae - white rot causing fungus isolated), f - e – silver birch (Pholiota spp. - white rot causing fungus isolated)



It spreads rapidly within the wood, with studies in Poland reporting that decay affects an average of 40% of the total trunk volume and nearly half of the cross-sectional area at the infection site. This leads to a significant reduction in the tree's mechanical stability and disrupts its physiological processes (Čermák et al., 2004). *Amylostereum areolatum* infects conifers, especially pines, causing white rot in living trees ʻFigure 1c'. This fungus primarily spreads via the invasive woodwasp *Sirex noctilio*, which inoculates trees with fungal spores while creating oviposition tunnels in the bark and laying their larva, making this a symbiotic relationship (Thomsen & Koch, 1999). Although neither *A. areolatum* nor the woodwasp currently cause widespread tree mortality in Northern Europe, they are considered to be a problem for the pine and spruce plantations in Central and Southern Europe (Vasiliauskas & Stenlid, 1999). In Latvia and Lithuania, *A. areolatum* is frequently isolated from damaged wood (Vasiliauskas, 1999; Burņeviča et al., 2016).

In black alder samples, the fungal pathogen *Chondrostereum purpureum* was detected ʻFigure 1d'. This species causes white rot and wood discoloration and is more commonly associated with birch. Although rarely considered a primary pathogen, it can significantly contribute to the decline of already weakened trees (Wall, 1991). The white-rot fungus *Xanthoporia radiata* was also identified. This species

is predominantly saprotrophic and does not typically pose a threat to healthy trees (Germain et al., 2002). However, some studies have reported its presence in frost-damaged or decayed alder trees, suggesting potential pathogenicity under specific conditions (Kodrík et al., 2006; Arhipova et al., 2011). Both *X. radiata* and *C. purpureum* have been frequently isolated in Latvia and Lithuania (Arhipova et al., 2011; Iršėnaitė et al., 2013). Overall, no serious pathogens or rot-causing fungi were detected in black alder tree samples.

European aspen samples were found to be infected with the white-rot fungus *Phellinus tremulae*, a primary agent of trunk rot that infects both sapwood and heartwood ʿFigure 1e'. The structural degradation of the wood caused by the fungus significantly shortens tree lifespan and reduces its commercial value (Wikström, 1976).

Silver birch samples revealed colonization of *Pholiota* sp., a wood saprotroph occasionally reported as a secondary root pathogen causing white rot ʿFigure 1f', and *Trametes versicolor*, predominantly saprotrophic but occasionally pathogenic in weakened trees (Terho et al., 2007; Bari et al., 2019; Kymäläinen et al., 2022). *Botrytis cinerea* was also isolated from silver birch samples, though it primarily affects conifer seedlings in nurseries rather than birch (Lija et al., 2010).

Bacteria were isolated from most of wood discs of all tree species. Some authors noted that bacteria could be involved in decay and discoloration processes in tree wood (Shortle et al., 1978; Clause, 1996; Zhang et al., 2022), but more researches needed to fully understand those impact to decay processes and interaction with decay causing fungi. However, not all causes of wood discoloration could be attributed to decay-cousin microorganisms or bacteria, as some symptomatic wood discs had not yielded any fungal or bacterial growth, remaining sterile, even after repeated samplings: 40% of birch and 40% of aspen wood disks, 17% of pine discs and 10% of spruce disks. Discoloration of wood, caused by factors other, than pathogens, previously reported for several tree species. For example, photochemical discoloration (caused by UV light) could occur in some species of pine, spruce and oak; biochemical discoloration is typical for alders; chemical (in contact with iron) occurs in oak wood; brownstain can develop in western hemlock, true firs and ponderosa pines after tree felling (Kreber, 1994). Also, discoloration could be associated with tree aging and stem injuries (Shigo & Hillis, 1973). Discoloration caused by factors other than fungal activity usually have an impact only on timber visual quality, but have no or little influence for mechanical wood properties, which made such discoloured wood suitable for many purposes, not only as firewood or pulpwood.

In sawmills, the quality assessment of timber for building structures is important, as it will be reflected later in the lifetime of the structure. When staining is detected, the sawn timber is often assessed to lower quality. If the cause of the staining is wrongly identified as a fungal decay that damages the wood structure, it causes economical losses which could be reduced with more precise identification and detection of decay type. Improved understanding of wood discoloration causing factors, as well as identification tool for different kind of discoloration is needed to help workers of forestry sector to evaluate timber assortment more precisely, thus reducing losses of valuable timber.

Table 1

Basidiomycetes and Mucorales fungi isolated from wood samples from five tree species (pine, spruce, alder, birch and aspen) in Latvia. Additional information about analysed material

Fungal species	***Pinus sylvestris***	***Picea abies***	***Alnus glutinosa***	***Betula pendula***	***Populus tremula***
	% of wood samples from which the fungus were isolated / % of wood discs from which the fungus were isolated				
Basidiomycota (decay causing fungi)					
Amylostereum areolatum	-	3.2/10.0	-	-	-
Bjerkandera adusta	0.9/2.8	-	2.3/6.9	-	5.0/10.0
Chondrostereum purpureum	-	-	1.1/3.4	-	-
Cylindrobasidium evolvens	-	1.6/5.0	1.1/3.4	8.8/10.0	-
Heterobasidion sp.	6.0/5.6	17.4/25.0	-	-	-
Phellinus tremulae	-	-	-	-	7.5/30.0
Phlebiopsis gigantea	2.6/5.6	-	-	-	-
Pholiota sp.	-	-	-	8.8/20.0	-
Porodaedalea pini	7.8/16.7	-	-	-	-

Fungal species	***Pinus sylvestris***	***Picea abies***	***Alnus glutinosa***	***Betula pendula***	***Populus tremula***
	% of wood samples from which the fungus were isolated / % of wood discs from which the fungus were isolated				
Schizophyllum commune	-	-	-	2.9/10.0	-
Sistotrema brinkmannii	0.9/2.8	4.8/5.0	-	-	2.5/10.0
Stereum sanguinolentum	0.9/2.8	-	-	-	-
Trametes versicolor	0.9/2.8	-	-	2.9/10.0	-
Xanthoporia radiata	-	-	29.9/58.6	-	5.0/9.1
Mucorales					
Mucor sp.	3.4/11.1	4.8/5.0	4.6/13.8	-	2.5/10.0
Umbelopsis sp.	5.2/13.9	6.3/15.0	12.6/34.5	2.9/10.0	-
Other data					
Bacteria	41.4/69.4	65.1/90	87.4/96.6	58.8/90.0	47.5/80.0
No fungal or bacterial growth detected	6.0/16.7	4.8/10	-	17.6/40.0	10.0/40.0
Number of samples/number of trees	116/34	63/20	87/29	31/10	43/10

Table 2

Ascomycetes isolated from wood samples from five tree species (pine, spruce, alder, birch and aspen) in Latvia

Fungal species	***Pinus sylvestris***	***Picea abies***	***Alnus glutinosa***	***Betula pendula***	***Populus tremula***
	Fungi (% of wood samples from which the fungus were isolated /% of wood discs from which the fungus were isolated)				
Blue-stain causing Ascomycota					
Aureobasidium pullulans	0.9/2.8	1.6/5.0	2.3/6.9	2.9/10.0	2.5/10.0
Ceratocystis minor	0.9/2.7	-	3.4/10.3	-	-
Leptographium piriforme	-	-	-	-	7.5/9.1
Ophiostoma sp.	4.3/8.3	-	-	-	5.0/20.0
Other Ascomycota					
Alternaria sp.	0.9/2.8	4.8/15.0	-	5.9/20.0	2.5/10.0
Ascocoryne sp.	6.0/13.9	3.2/10.0	4.6/10.3	-	7.5/30.0
Aspergillus sp.	-	-	1.1/3.4	-	-
Botrytis cinerea	-	-	-	2.9/10.0	-
Cadophora sp.	0.9/2.8	-	1.1/3.4	-	-
Cladosporium sp.	1.7/2.8	3.2/10.0	8.0/17.2	2.9/10.0	10.0/40.0
Cosmospora sp.	-	-	-	-	2.5/10.0
Cosmospora viridescens	-	-	1.1/3.4	-	-
Cytospora phialidica	-	-	-	2.9/10.0	-
Cytospora sp.	0.9/2.8	1.6/5.0	-	-	-
Diatrype sp.	-	-	-	-	2.5/10.0
Didymella sp.	-	-	1.1/3.4	-	-
Dydimellaceae sp.	5.2/16.7	-	3.4/10.3	5.9/20.0	5.0/20.0
Diplodia sp.	0.9/2.8	3.2/5.0	-	-	-
Endoconidiophora polonica	-	1.6/5.0	-	-	-
Epicoccum nigrum	-	3.2/5.0	-	5.9/10.0	-
Eutypella cerviculata	-	-	2.3/6.9	-	-
Fusarium sp.	0.9/2.8	1.6/5.0	-	-	2.5/10.0

Fungal species	***Pinus sylvestris***	***Picea abies***	***Alnus glutinosa***	***Betula pendula***	***Populus tremula***
	Fungi (% of wood samples from which the fungus were isolated /% of wood discs from which the fungus were isolated)				
Fusarium tricinctum	1.7/5.6	-	-	-	-
Hormonema sp.	-	1.6/5.0	-	2.9/10.0	-
Ilyonectria sp.	-	-	-	2.9/10.0	-
Leptodontidium trabinellum	-	-	-	-	7.5/20.0
Lophium arboricola	-	1.6/5.0	-	-	-
Neonectria tsugae	0.9/2.8	9.5/20.0	-	2.9/10.0	-
Penicillium sp.	13.8/36.1	25.4/55.0	26.4/72.4	8.8/30.0	30.0/70.0
Parafenestella sp.	-	-	1.1/3.4	-	-
Phialocephala dimorphospora	0.9/2.8	-	1.1/3.4	-	-
Pseudogymnoascus hyalinus	2.6/8.3	1.6/10.0	-	-	-
Pyrenochaeta xanthriae	-	-	-	-	2.5/10.0
Sordariaceae sp.	-	-	-	-	5.0/10.0
Sordariales sp.	-	-	5.7/13.7	-	-
Thyronectria cucurbitula	0.9/2.8	-	-	-	-
Thyronectria sp.	-	-	1.1/3.4	2.9/10.0	-
Trichoderma sp.	23.3/36.1	14.3/30.0	3.5/10.3	11.8/20.0	15.0/30.0
Truncatella angustata	-	1.6/5.0	1.1/3.4	-	-
Xylariaceae sp.	-	-	-	-	2.5/10.0

Conclusions

1. The analysis of fungal communities across five tree species revealed a diverse assemblage of fungal taxa. White-rot fungi were the most frequently isolated wood-decaying organisms across all studied tree species, suggesting their dominant role in wood decomposition processes in Latvian forests.
2. Prevalence of *Heterobasidion* spp. in Norway spruce and *Porodaedalea pini*, in Scots pine samples underscores the substantial economic and ecological impact of these fungi, particularly in conifer-dominated forests.
3. The presence of *Amylostereum areolatum* in Norway spruce samples also indicates potential threats to forest health. Furthermore, the presence of blue-stain fungi such as *Ophiostoma* spp. and *Aureobasidium pullulans* highlights their importance in timber quality assessments. Moreover, wood discoloration caused by factors other than fungal activity, is also abundant in several tree species (mostly birch, aspen and pine).
4. Further research should focus on understanding the interactions between wood-decaying fungi and various host trees and age classes, as well as forest management strategies to mitigate these threats and sustain forest vitality and productivity.

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References

Altschul, S. F., Madden, T. L., Schaffer, A. A., Zhang, J., Zhang, Z., Miller, W., & Lipman, D. J. (1997). Gapped BLAST and PSI-BLAST: A new generation of protein database search programs. *Nucleic Acids Research*, 25, 3389–3402. https://doi.org/10.1093/nar/25.17.3389

Arhipova, N. (2012). *Heart rot of spruce and alder forests in Latvia – impact and possibilities for silvicultural control* [Doctoral thesis], Uppsala, Swedish University of Agricultural Sciences, 48 pp.

Arhipova, N., Gaitnieks, T., Donis, J., Stenlid, J., & Vasaitis, R. (2011). Decay, yield loss and associated fungi in stands of grey alder (*Alnus incana*) in Latvia. *Forestry*: *An International Journal of Forest Research*, *84*(4), 337–348. https://doi.org/10.1093/forestry/cpr018

Arhipova, N., Gaitnieks, T., Donis, J., Stenlid, J., & Vasaitis, R. (2012). Heart-rot and associated fungi in *Alnus glutinosa* stands in Latvia. *Scandinavian Journal of Forest Research, 27(*4), 327–336. https://doi.org/10.1080/02827581.2012.670727

Asiegbu, F. O., Adomas, A., & Stenlid, J. (2005). Conifer root and butt rot caused by *Heterobasidion annosum* (Fr.) Bref. s.l. *Molecular Plant Pathology*, *6*(4), 395–409. https://doi.org/10.1111/j.1364-3703.2005.00295.x

Bardage, S. L. (1998). Susceptibility of painted wood to *Aureobasidium pullulans*: fungal stain and growth patterns. *Holz als Roh- und Werkstoff*, 56, 359–364. https://doi.org/10.1007/s001070050333

Bari, E., Daryaei, M. G., Karim, M., Bahmani, M., Schmidt, O., Woodward, S., …, & Sistani, A. (2018). Decay of *Carpinus betulus* wood by *Trametes versicolor* - An anatomical and chemical study. *International Biodeterioration & Biodegradation,* 137, 68–77. https://doi.org/10.1016/j.ibiod.2018.11.011

Brodde, L. (2023). Diplodia tip blight affecting Scots pine. Factors determining infection and spread in Swedish forests [Doctoral thesis 2023: 43], Uppsala, Swedish University of Agricultural Sciences, 106 pp.

Brodde, L., Adamson, K., Camarero, J. J., Castaño, C., Drenkhan, R., Lehtijärvi, A., …, & Oliva, J. (2019). Diplodia tip blight on its way to the north: Drivers of disease emergence in Northern Europe. *Frontiers in Plant Science*, 9. https://doi.org/10.3389/fpls.2018.01818

Burneviča, N., Jansons, Ā., Zaļuma, A., Kļaviņa, D., Jansons, J., & Gaitnieks, T. (2016). Fungi Inhabiting Bark Stripping Wounds Made by Large Game on Stems of *Picea abies* (L.) Karst. in Latvia. *Baltic Forestry*, *22*(1), 2-7.

Ciseļonoka, L., Kļaviņa, D., Zaļuma, A., Kenigsvalde, K., Striķe, Z., Liepiņš, K., …, & Menkis, A. (2024). The urea treatment of silver birch (*Betula pendula* Roth) logs promotes wood decay and wood discoloration. *Wood Material Science & Engineering*, 1–8. https://doi.org/10.1080/17480272.2024.2353792

Čermák, P., Jankovský, L., & Glogar, J. (2004). Progress of spreading *Stereum sanguinolentum* (Alb. et Schw.: Fr.) Fr. wound rot and its impact on the stability of spruce stands. *Journal of Forest Science*, *50*(8), 360–365. https://doi.org/10.17221/4662-jfs

Clausen, C. A. (1996). Bacterial associations with decaying wood: a review. *International Biodeterioration & Biodegradation*, *37*(1-2), 101-107. https://doi.org/10.1016/0964-8305(95)00109-3

Deshpande, M. S., Rale, V. B., & Lynch, J. M. (1992). *Aureobasidium pullulans* in applied microbiology: a status report. *Enzyme and Microbial Technology*, *14*(7), 514-527. https://doi.org/10.1016/0141-0229(92)90122-5

Durodola, B., Blumenstein, K., Akinbobola, A., Kolehmainen, A., Chano, V., Gailing, O., & Terhonen, E. (2023). Beyond the surface: Exploring the mycobiome of Norway spruce under abiotic stress and with *Heterobasidion parviporum*. *BMC microbiology*, *23*(1), 350. https://doi.org/10.1186/s12866-023-03099-y

Gaitnieks, T., Arhipova, N., Donis, J., Stenlid, J. & Vasaitis, R. (2008). Butt rot incidence and related losses in Latvian *Picea abies* (L.) Karst. stands. *Proceedings of the 12th International Conference on Root and Butt Rot of Forest trees*. USA, The University of California: Berkley, 177–179. https://nature.berkeley.edu/matteolab/downloads/iufro/IUFROText.pdf#page=189

Gardes, M. & Bruns, T. D. (1993). ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Molecular Ecology*, *2*(2), 113–118. https://doi.org/10.1111/j.1365-294x.1993.tb00005.x

Germain, H., Laflamme, G., Bernier, L., Boulet, B., & Hamelin, R. C. (2002). DNA polymorphism and molecular diagnosis in *Inonotus* spp. *Canadian Journal of Plant Pathology*, *24*(2), 194–199. https://doi.org/10.1080/07060660309506995

Guillaumin J.-J. & Legrand P. (2013). *Armillaria* root rots. In Gonthier, P. & Nicolotti, G. (Eds.). *Infectious Forest Diseases*. CABI, Wallingford.

González, C. D. & Chaverri, P. (2017). Corinectria, a new genus to accommodate *Neonectria fuckeliana* and *C. constricta* sp. nov. from *Pinus radiata* in Chile. *Mycological Progress*, *16*(11–12), 1015–1027. https://doi.org/10.1007/s11557-017-1343-8

Higley, T. L. (2004). Wood formation and properties: biological deterioration of wood. In: Barley, J. (Eds.). *Encyclopedia of Forest Sciences*, pp. 1846-1851.

Iršėnaitė, R., Adamonytė, G., Daniele, I., Kasparavičius, J., Kutorga, E., & Stončius, D. (2013). Macromycetes and myxomycetes of Asveja Regional park (Lithuania). *Botanica Lithuanica*, *19*(1), 8–21. https://doi.org/10.2478/botlit-2013-0002

Klavina, D., Tedersoo, L., Agan, A., Zaluma, A., Bitenieks, K., Polmanis, K., …, & Drenkhan, R. (2023). Effect of stand thinning, former land use and individual tree parameters on wood inhabiting fungal community composition in young living Norway spruce. *Fungal Ecology*, 65. https://doi.org/10.1016/j.funeco.2023.101281

Kodrík, J., Kodrík, M., & Hlaváč, P. (2006). The occurrence of fungal and insect pests in riparian stands of the central Hron and Slatina rivers. *Journal of Forest Science*, *52*(1), 22–29. https://doi.org/10.17221/4483-JFS

Kreber, B. (1994). *Understanding wood discoloration helps maximize wood profits*. Vancouver, Forintek Canada Corp, 72 – 76.

Kymäläinen, M., Belt, T., Seppäläinen, H., & Rautkari, L. (2022). Decay resistance of surface carbonized wood. *Materials*, *15*(23), Article 8410. https://doi.org/10.3390/ma15238410

Lilja, S. (1986). Disease and pest problems on *Pinus sylvestris* nurseries in Finland 1. *EPPO Bulletin*, *16*(3), 561–564. https://doi.org/10.1111/j.1365-2338.1986.tb00323.x

Lilja, A., Poteri, M., Petäistö, R. L., Rikala, R., Kurkela, T., & Kasanen, R. (2010). Fungal diseases in forest nurseries in Finland. *Silva Fennica*, *44*(3), 525-545. https://doi.org/10.14214/sf.147

Matić, S., Tabone, G., Garibaldi, A., & Gullino, M. A. (2020). Alternaria Leaf Spot Caused by Alternaria Species: An Emerging Problem on Ornamental Plants in Italy. *Plant Diseases*, 104, 2275–2287. https://doi.org/10.1094/PDIS-02-20-0399-RE

Mäkinen, H., Hallaksela, A., & Isomäki, A. (2007). Increment and decay in Norway spruce and Scots pine after artificial logging damage. *Canadian Journal of Forest Research*, *37*(11), 2130–2141. https://doi.org/10.1139/x07-087

Miklašēvičs, Z., Burnēviča, N., Iejavs, J., & Šķēle, K. (2024). Evaluation of aspen (*Populus tremula*) wood structure infected by fungi (*Phellinus tremulae*) and opportunities for wider use of timber in structural elements. *ETR, 1*, 242–250. https://doi.org/10.17770/etr2024vol1.7944

Möttönen, V. & Katri, L. (2004). Discolouration of sawn birch (*Betula pendula*) timber from plantation forests during drying. Part 1. Effect of growing site, felling season and storage of logs on discolouration. *Baltic Forestry*, *10*(2), 31-38.

Nilsson, R. H., Larsson, K. H., Taylor, A. F. S., Bengtsson-Palme, J., Jeppesen, T. S., Schigel, D., … & Abarenkov, K. (2018). The UNITE database for molecular identification of fungi: Handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Research*, *47*(D1), D259–D264. https://doi.org/10.1093/nar/gky1022

Photita, W., Lumyong, S., Lumyong, P., McKenzie, E. H. C., & Hyde, K. D. (2004). Are some endophytes of *Musa acuminata* latent pathogens? *Fungal Diversity*, 16, 131-140. https://www.fungaldiversity.org/fdp/sfdp/16-4.pdf

Põlme, S., Abarenkov, K., Nilsson, R. H., Lindahl, B. D., Clemmensen, K. E., Kauserud, H., …, & Tedersoo, L. (2020). Fungal Traits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Diversity*, *105*(1), 1–16. https://doi.org/10.1007/s13225-020-00466-2

Shigo, A. L. & Hillis, W. E. (1973). Heartwood, discolored wood, and microorganisms in living trees. *Annual Review of Phytopathology*, 11, 197 – 122. https://doi.org/10.1146/annurev.py.11.090173.001213

Shortle, W. C., Menge, J. A., & Cowling, E. B. (1978). Interaction of bacteria, decay fungi, and live sapwood in discoloration and decay of trees. *European Journal of Forest Pathology*, *8*(5-6), 293–300. https://doi.org/10.1111/j.1439-0329.1978.tb00642.x

Stępniewska, H., Jankowiak, R., Bilański, P. & Hausner, G. (2021). Structure and abundance of Fusarium communities inhabiting the litter of beech forests in central Europe. *Forests*, 12, Article 811. https://doi.org/10.3390/f12060811

Szewczyk, W. (2016). Decay of the heartwood in lower and upper trunk of *Pinus sylvestris* by *Porodaedalea pini*. *Acta Scientiarum Polonorum Silvarum Colendarum Ratio et Industria Lignaria*, *15*(3), 185–188. https://doi.org/10.17306/j.afw.2016.3.21

Uzunovic, A., Byrne, T., Gygnac, M. & Yang, D.-Q. (2008). *Wood discolorations and their prevention with an emphasis on bluestein.* Natural Resources Canada, Special Publication SP-50.

Terho, M., Hantula, J., & Hallaksela, A. (2007). Occurrence and decay patterns of common wood-decay fungi in hazardous trees felled in the Helsinki City. *Forest Pathology*, *37*(6), 420–432. https://doi.org/10.1111/j.1439-0329.2007.00518.x

Thomsen, I. M. & Koch, J. (1999). Somatic compatibility in *Amylostereum areolatum* and *A. chailletii* as a consequence of symbiosis with siricid woodwasps. *Mycological Research*, *103*(7), 817-823. https://doi.org/10.1017/S0953756298007783

Vasiliauskas, R. (1999). Spread of *Amylostereum areolatum* and *A. chailletii* decay in living stems of *Picea abies*. *Forestry*: *An International Journal of Forest Research*, *72*(2), 95–102. https://doi.org/10.1093/forestry/72.2.95

Vasiliauskas, R. & Stenlid, J. (1998). Fungi inhabiting stems of *Picea abies* in a managed stand in Lithuania. *Forest Ecology and Management*, *109*(1–3), 119–126. https://doi.org/10.1016/s0378-1127(98)00226-6

Vasiliauskas, R. & Stenlid, J. (1999). Vegetative compatibility groups of *Amylostereum areolatum* and *A. chailletii* from Sweden and Lithuania. *Mycological Research*, *103*(7), 824-829. https://doi.org/10.1017/S0953756298007862

Wall, R. (1991). Pathological effects of *Chondrostereum purpureum* in inoculated yellow birch and beech. *Canadian Journal of Plant Pathology*, *13*(1), 81–87. https://doi.org/10.1080/07060669109500969

Wani, A. M. & Sahoo, G. (2021). Forest ecosystem services and biodiversity. In P. K., Shit, H. R., Pourghasemi, P., Das, & G. S., Bhunia, (Eds.), *Spatial modeling in forest resources management* (pp. 22). Springer. https://doi.org/10.1007/978-3-030-56542-8_22

White, T. J., Bruns, T., Lee, S., & Taylor, J., Innis, M. A., Gelfand, D. H., & Sninsky, J. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In M. A., Innis, D. H., Gelfand, J. J., Sninsky, T. J., White, (Eds.), *PCR Protocols: A Guide to Methods and Applications*. Academic Press Inc., USA, 315–322. https://www.researchgate.net/publication/262687766_Amplification_and_Direct_Sequencing_of_Fungal_Ribosomal_RNA_Genes_for_Phylogenetics

Wikström, C. (1976). The occurrence of *Phellinus tremulae* (Bond.) Bond. and Borisov as a primary parasite in *Populus tremula* L. *Forest Pathology*, *6*(6), 321–328. https://doi.org/10.1111/j.1439-0329.1976.tb00544.x

Williamson, B., Tudzynski, B., Tudzynski, P., & Van Kan, J. A. (2007). *Botrytis cinerea*: the cause of grey mould disease. *Molecular Plant Pathology*, *8*(5), 561-580. https://doi.org/10.1111/j.1364-3703.2007.00417.x

Zaluma, A., Strike, Z., Rieksts-Riekstiņš, R., Gaitnieks, T., & Vasaitis, R. (2022). Long-term pathological consequences of resin tapping wounds on stems of Scots pine (*Pinus sylvestris* L.). *Trees*, 36, 1507–1514. https://doi.org/10.1007/s00468-022-02307-y

Zhang, X., Liu, H., Han, H., Zhang, B., Zhang, C., He, J., Li, S., & Cao H. (2022). Microbial Community Succession Associated with Poplar Wood Discoloration. *Plants (Basel) 2022*, *11*(18), Article 2420. https://doi.org/10.3390/plants11182420