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Characterisation of brown-rot decay in the historic Lejonström bridge using X-ray tomography and molecular identification of associated fungi

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The deterioration of wooden heritage structures requires regular monitoring, particularly when pressure-impregnated Scots pine is exposed to moisture and biological degradation. This study assessed fungal degradation of structural elements of the Lejonström bridge in Skellefteå, Sweden's oldest wooden bridge and a culturally significant monument. Non-destructive X-ray tomography identified internal decay based on reduced density, brown-rot characteristics, and microbial colonisation. Culturable fungi were isolated from decayed wood and identified by ITS-based Sanger sequencing. In total, 37 pure cultures representing 17 fungal species from 11 genera were obtained. Most isolates were saprotrophic, mould, or wood-associated ascomycetes typical of weathered or decayed wood. Two basidiomycetes, *Amyloporia xantha* and *Crustoderma* sp., were associated with areas showing brown-rot symptoms, suggesting their contribution to timber degradation. *A. xantha* was the most frequently isolated basidiomycete. These findings improve understanding of fungal communities involved in biodegradation and support monitoring and preservation strategies for wooden heritage structures in Sweden.

Historical wooden structures are an important element of the cultural heritage of every society, representing both the engineering capabilities of ancestors and their identity, and often contributing substantially to local tourism and cultural economies. That is why their long-term preservation, which includes periodic recoveries and maintenance, should be fully ensured[1]. The preservation of wooden historical heritage requires a multi-faceted approach that encompasses architectural authenticity and integrity, structural safety, and the assessment of causes and the prevention of deterioration[1,2]. Wood is a widely used building material both in the past and today, but it is biodegradable. Given this, historic wooden structures built without accounting for modern technologies to ensure greater durability are at increased risk of deterioration and require special monitoring and protection[3]. Most wooden structures built more than a century ago are protected as historical heritage and accordingly require various levels of renovation, including the addition of reinforcing elements or the partial replacement of degraded sections with compatible materials[4,5]

Wood is a biologically degradable material and therefore susceptible to long-term deterioration under favourable environmental conditions. In wooden structures, degradation results from the combined effects of weathering, sunlight (Ultraviolet (UV)), atmospheric chemicals, high temperatures, mechanical wear[6], and biotic agents, primarily fungi and bacteria, while algae mainly contribute to surface colonisation and discoloration[7,8]. Among these, filamentous fungi, especially basidiomycetes and some ascomycetes, are the main organisms responsible for structural wood decay. Their activity depends strongly on wood moisture because free water is required for fungal growth, enzyme transport, and the diffusion of degradation products. When moisture conditions are favourable, wood-decay fungi colonise the cell walls and degrade the main structural polymers of wood - cellulose, hemicellulose and, depending on the decay type, lignin[8,9].

Recent studies increasingly recognise microbial biodegradation of historical wooden objects, particularly by wood-decay fungi, as a major

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threat to cultural heritage[10–13]. This may intensify under ongoing climate change, as altered temperature and moisture regimes can favour microbial growth, shift wood-associated microbial communities, and place additional stress on heritage structures, thereby reducing their durability[14–16].

Wood-decay fungi are commonly classified according to their degradation mechanisms and resulting decay patterns into white rot, brown rot and soft rot fungi[6,17]. White-rot fungi enzymatically degrade all major wood cell-wall components, including cellulose, hemicellulose and lignin, whereas brown-rot fungi primarily depolymerise cellulose and hemicellulose through combined oxidative and enzymatic mechanisms while modifying lignin residues[6,17]. Comparative genomic studies have demonstrated major differences between white- and brown-rot fungi in genes encoding lignin-degrading enzymes and carbohydrate-active enzymes (CAZymes), although some overlap in decay mechanisms exists[8,9]. Soft-rot fungi, mainly ascomycetes, degrade cellulose within the secondary cell wall and produce characteristic cavity or erosion patterns under persistently moist conditions. In contrast, mould and staining fungi usually colonise wood surfaces or nutrient-rich tissues and mainly cause discolouration and aesthetic damage rather than substantial loss of mechanical strength loss[6,17,18].

However, the characteristics and intensity of wood biodegradation, particularly in historic structures, are determined not only by the presence of wood-decaying microorganisms but also by factors such as wood anatomy, porosity, extractive composition, moisture dynamics and water permeability. The characteristics of the wood also affect its durability, with heartwood and sapwood exhibiting different resistance to biodegradation, as do different tree species and origins[8]. That is why an important problem is not only the repair of damaged parts of wooden heritage structures, but also the effective study of wood decay features to develop more effective methods for preventing and protecting them from future deterioration.

Because fungal degradation often develops internally before severe external symptoms become visible, reliable assessment of hidden structural damage is essential for the preservation of historic wooden constructions. Traditional visual inspection methods are frequently insufficient for detecting internal decay zones or evaluating the extent of density loss within large timber elements. Therefore, non-destructive techniques capable of identifying internal wood deterioration are increasingly important for monitoring the structural integrity of heritage buildings and wooden infrastructure.

Today, a powerful approach to in-depth analysis of wood is computed tomography (CT) scanning, a non-destructive, non-invasive technology originally developed for medical diagnostics[19]. CT scanning is widely used to assess wood properties in the context of assessment of wood quality and optimising the manufacturing of wood products[20,21], and allows for assessing wood density, moisture content, annual growth, resin accumulation, and location of branch knots[22–27]. CT scanning was first implemented in 2012 at sawmills in Sweden to detect internal wood defects and reduce yield losses[21], and now has potential for high-resolution, non-destructive visualisation of decay patterns and their distribution[28,29]. In particular, several studies have been conducted to assess the density of wood degraded by microorganisms, namely fungi[28,30,31], thereby providing a more complete understanding of CT capabilities in the context of this study.

The gradual deterioration of historic wooden structures is a significant conservation challenge, particularly in environments where timber is exposed to moisture, weathering, and biological degradation. Despite the cultural and historical importance of the Lejonström Bridge, Sweden's oldest wooden bridge, limited information is available regarding the extent of internal wood decay and the fungal communities associated with its biodegradation. Therefore, this study aimed to characterize the decay of the bridge's structural timber elements by combining non-destructive X-ray computed tomography (CT) scanning with culture-based fungal analysis. CT scanning was employed to detect and localise internal decay and density loss within the timber, while fungal isolation and ITS sequencing were used to identify fungal species associated with the degraded wood. By integrating structural assessment with microbiological characterisation, the study provides new insights into the biodegradation processes affecting this important heritage structure and contributes knowledge that can support future monitoring, maintenance, and preservation strategies for historic wooden bridges.

Methods

Study site and wood material description

Lejonström bridge (Lejonströmsbron) is the oldest wooden bridge in Sweden, built in 1737, that crosses the Skellefte River in Skellefteå, Västerbotten County (Fig. 1a, b) (64°44′59″N 20°54′47″E). It is also the second-longest wooden bridge in Sweden, measuring 207.5 m long and 5 m wide. Since 1994, the bridge has been an architectural monument protected by the state and therefore cannot be rebuilt, moved, or altered[32]. Today, the Lejonström bridge looks much the same as it did in the 1870s and is also open to automobile traffic[33].

Throughout the bridge's existence, numerous reconstructions have been carried out; in particular, the most recent occurred in 2009–2011, 2017, and 2025. During 2009–2011, most of the bridge's load-bearing beams were replaced with heartwood-rich Scots pine (*Pinus sylvestris* L.) derived from old-growth trees as one of the most durable natural wooden building materials[32]. In August-October 2025, the bridge was partially renovated due to significant wear on the roadway and some of the frame timbers[34]. Scots pine timbers with visible symptoms of wood decay (Fig. 1c) were removed from the bridge by workers of the Skellefteå Municipality in September 2025 and then replaced with new ones. Degraded parts were delivered to the Division of Wood Science and Engineering at Luleå University of Technology for further analysis. Immediately after dismantling, the timbers with visible symptoms of wood decay were wrapped in plastic bags and transported to the laboratory, where they were stored for 1 day at room temperature. The next day, wood fragments from timbers were first separated for microbiological analysis in separate sterile bags, and then the samples were scanned using CT according to the protocol described below. Figure 1c–e shows a general view of damaged timbers that were studied.

Computed tomography (CT) scanning of wood samples

The wood samples shown in Fig. 1d, e were scanned in the longitudinal direction using a Microtec Mito CT scanner equipped with a cone-beam X-ray source and dual-angle flat-panel detectors. Prior to scanning, the samples were naturally dried for 1 month indoors at 20°C. The scanning parameters were set to 180 kV tube voltage and 5.5 mA X-ray tube current. The spatial resolution of the scan was 0.5 × 0.5 × 0.5 mm per voxel.

The acquired TIFF image stack was processed in Python 3.12.7 (Python Software Foundation, https://www.python.org/). and converted into NRRD format for three-dimensional reconstruction and visualisation in 3D Slicer (version 5.1.0). Density estimation and image analysis were carried out using the Fiji distribution of ImageJ 1.54p[35].

Isolation and cultivation of fungi from decayed wood

Five wood fragments (10 × 20 mm) were manually separated from each of four timber parts with visible signs of wood decay using a knife. The surface of the knife blade was wiped with 70% ethanol before separating each wood fragment. Sampling was carried out 50 mm beyond the damage edge to obtain wood with potential for active growth of wood-decaying fungi. To isolate representatives of the fungal community, wood fragments were surface sterilised in a 1% sodium hypochlorite solution (Merck KGaA, Germany) for 1 min, followed by 30 s in 70% ethanol, and then three washes in sterile distilled water. Wood samples were transferred to Petri dishes (Ø 90 mm) containing sterile culture medium and incubated for 7 days at 25 °C and 90% humidity in the laboratory chamber HPP260eco (Memmert, Germany). As a culture medium, Malt extract agar (MEA) (Merck KGaA, Germany) was used, prepared according to the manufacturer's recommendations and then sterilised for 15 min at 121 °C. After partial cooling, 50 µg/mL streptomycin (Sigma-Aldrich, USA) was added to sterile MEA medium, and 25 mL of medium was poured into each sterile plastic Petri dish. Verification and selection of potential isolates were carried out daily, starting on the 3rd day, once visible mycelial growth was observed.

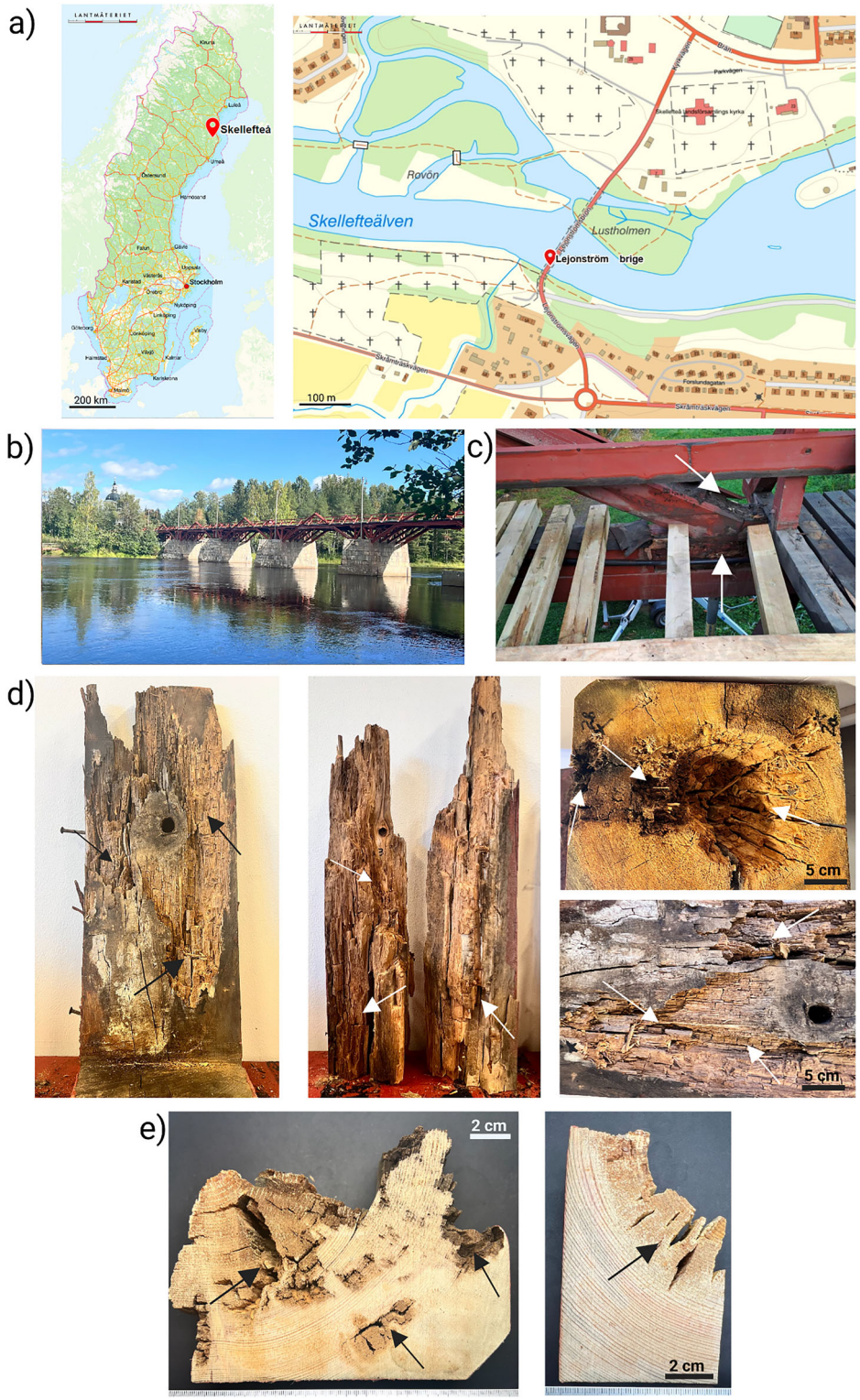

Fig. 1 | Lejonström bridge and its removed timber parts with wood-decay symptoms. Geographic location (**a**) and general view of the bridge (**b**), location of decayed timbers on the bridge (**c**), general view of damaged timbers (red parts) (**d**) and their cross-sections (**e**). Decayed wood areas are marked with arrows.

Mycelium fragments with different morphologies were transferred to separate Petri dishes containing MEA with 50 µg/ml streptomycin and cultured at 25 °C and 90% humidity in the laboratory chamber for 1–2 weeks, depending on the growth rate of the mycelium of the isolated fungi. This step was repeated as necessary until a single pure culture was obtained. For visualisation of the surfaces of wood samples and fungal colonies, a Digital Microscope System Olympus DSX1000 with 3 and 10x magnification lenses (Evident Scientific, Japan) was used.

To isolate the fungi causing brown rot of wood, five additional wood fragments (10 × 20 mm) from each of four timber parts with visible signs of wood decay were separated using a knife, carried out 50 mm beyond the damage edge. The knife surface was wiped with 70% ethanol before separating each wood fragment. Wood fragments were briefly flame-sterilised (5 s from all sides) to reduce contamination by fast-growing surface fungi. Afterwards, the wood fragments were transferred to Petri dishes containing sterile MEA cultivation medium with 50 µg/ml streptomycin

and cultured for 3 weeks at 20 °C and 90% humidity in the laboratory chamber HPP260eco (Memmert, Germany).

Because most brown-rot fungi associated with the structural timber parts belong to Basidiomycota, visible mycelia were examined microscopically for clamp connections, a characteristic feature of many basidiomycetes. The mycelium was stained with 0.4% trypan blue solution (Sigma-Aldrich, USA) for 5 min. Clamp contact detection was performed with a Nikon Eclipse Ni-U microscope (Japan) equipped with a 100× oil-immersion objective (VWR Chemicals, USA). If clamp connections were found on the mycelium, the mycelium was transferred to a separate Petri dish containing MEA medium and cultured under the conditions described above. If necessary, additional transfers of fungi were made to obtain a single pure, isolated culture. To ensure sterile conditions, all work on isolating fungi was carried out in a biosafety cabinet BSC-700II-I (HMC-Europe, Germany) using pre-sterilised instruments (tweezers, needles, loops, etc.).

DNA extraction, ITS amplification, and Sanger sequencing

Total genomic DNA was isolated from pure fungal culture using the cetyltrimethylammonium bromide (CTAB) method[36,37] with minor modifications. A mycelial fragment 50–100 mg (fresh weight) was homogenised in a 2 mL tube with sterilised CTAB buffer (200 mM Tris-HCl, 200 mM Na-EDTA, 1.4 M NaCl w/v, 2% CTAB w/v, pH 7.5 (Merck KGaA, Germany)), 100 mg mixture of silica gel 60H - celite 545 (2:1) (Merck KGaA, Germany), and a metal ball (Ø 2.4 mm) using a Bead Mill MAX homogeniser (VWR Chemicals, USA) for 1 min at 13.000 rpm. After incubation (65 °C, 1.5 h), 500 µL of chloroform (VWR Chemicals, USA) was added to each sample, mixed vigorously, and then centrifuged (13,000 RPM, 5 min, room temperature). After chloroform extraction and centrifugation, the aqueous phase was transferred to clean tubes, and the extraction step was repeated once. Then, 800 µL of cold isopropanol was added, and the mixture was incubated at −20 °C overnight. The next day, the samples were centrifuged (13,000 rpm, 5 min, −4 °C). The supernatant was removed, and the obtained DNA pellet was washed with 500 µL cold 70% ethanol, followed by final centrifugation (13,000 rpm, 5 min, −4 °C). After removal and evaporation of residual ethanol, the DNA pellet was dissolved in 50 µL TE buffer (10 mM Tris, 10 mM Na-EDTA, pH 8.0 (Merck KGaA, Germany)). DNA concentration was measured using a Qubit Flex fluorometer (Thermo Fisher, USA) with a Qubit dsDNA BR Assay Kit (Thermo Fisher, USA) according to the manufacturer's protocol. DNA was diluted in TE buffer to 10 ng/µl and stored at 4 °C until further use.

Identification of isolated fungi was performed by amplifying the Internal Transcribed Spacer (ITS) region via Polymerase Chain Reaction (PCR) and further Sanger sequencing. PCR was performed using ITS1 (5'-TCCGTAGGTGAACCTGCGG-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3') primers[38]. Each mixture (30 µL) contained 15 µLof DreamTaq PCR Master Mix (2×) (Thermo Fisher, USA), 10 pmole of forward and reverse primers (1 µL of each) (Merck KGaA, Germany), 10 ng genomic DNA (1 µL), and 12 µL nuclease-free water (Thermo Fisher, USA). PCR was performed using a Thermo Cycler T100 (Bio-Rad, Germany) according to the following protocol: an initial denaturation (2 min, 95 °C), followed by 35 cycles of a denaturation (45 s at 95 °C), a primer annealing (30 s, 55 °C), and an elongation (1 min, 72 °C). The final elongation (72 °C) was 4 minutes, and storage was at 4 °C. The size of the target fragments ranged from 450 to 600 bp.

Separation and visualisation of the resulting PCR amplicons were performed using 1% agarose gel electrophoresis (Bio-Rad, Germany) with staining using SYBR Safe DNA Gel Stain (Thermo Fisher, USA). If a single target DNA fragment was visualised in the 450–600 bp range on the agarose gel, then PCR product purification was performed by adding 0.5 µL Exonuclease I (Thermo Fisher, USA) and 1 µL FastAP Thermosensitive Alkaline Phosphatase (Thermo Fisher, USA) for every 5 µL of unpurified PCR product[39]. The resulting mixture was incubated (15 min, 37 °C), followed by inactivation of enzyme activity (15 min, 85 °C).

Pure DNA fragments were sent to Macrogen Europe (Amsterdam, Netherlands, https://www.macrogen-europe.com/) for sequencing. The resulting sequences were manually analysed, and the sequence similarity was compared with the sequences available in the GenBank database at the National Center for Biotechnology Information (NCBI) using the Basic Local Alignment Search Tool (BLAST) (http://www.ncbi.nlm.nih.gov/BLAST/). Taxonomic identification was assigned based on ITS sequence similarity and query coverage, with ≥98% similarity considered species-level identification and 94–97% considered genus-level identification[40]. The obtained sequences were submitted to GenBank under accession numbers PZ161136-PZ161152. Phylogenetic analysis of the identified fungi was performed by the Maximum Likelihood method using 1000 bootstrap replicates in MEGA 12 software[41]. Prior to phylogenetic analysis, ITS sequences were aligned using the ClustalW algorithm[42].

Results

CT scanning of decayed wood timbers

The CT images of a selected wood sample are presented in Fig. 2. Figure 2a shows an overview of the three-dimensional reconstructed CT image; Fig. 2b presents a cross-section in the Tangential × Radial direction; and Fig. 2c shows a longitudinal section in the Radial × Longitudinal direction. The image in Fig. 2b clearly distinguishes between intact and decayed regions within the wood sample. Derived from the image analysis, the density decreases from approximately 600 kg/m^3 in the sound region to 450 kg/m^3 in the decayed region, indicating substantial degradation of the wood tissue (yellow dashed boxes in Fig. 2b). The density was lower at one end of the sample and became higher further along the longitudinal section in Fig. 2c. This suggests that the decay developed from one side of the sample and progressed inward, likely facilitated by long-term moisture exposure. The bright vertical object corresponds to a nail, whose presence may have influenced local moisture retention through suction from the end-cross area of the timber part and thereby affected wood decay.

Figure 2d demonstrates one more example of wood decay on another scanned timber with the true-colour (RGB) image (left) and the corresponding CT image (right). The central cavity, located in the heartwood region of the wood sample, seems to be formed via the complete decay of wood close to the wood pith (black box in Fig. 2d). The surrounding decayed region had a lower density of 330 kg/m^3, while the sound region had a density of about 520 kg/m^3 (yellow dashed boxes in Fig. 2d).

The degraded areas with lower density in all scanned timbers corresponded to areas showing characteristic brown-rot features, including cubical cracking and brittle wood texture[17,18]. In particular, the wood in the affected area appeared cracked, brittle, and dry, like cubes. The areas around the decayed zones of the timbers were chosen for subsequent mycological diversity analysis.

Culturable fungi isolated from decayed bridge timbers

Fungal isolation was performed from wood samples showing advanced decay symptoms and reduced wood density detected by CT scanning. At this stage, 37 pure fungal cultures were isolated from wood samples and identified using ITS marker sequencing. In total, representatives of 11 genera were defined (Fig. 3a), belonging to the *Ascomycota*, *Basidiomycota*, and *Mucoromycota* divisions. The most common genera were *Trichoderma*, *Penicillium* and *Amyloporia*. At the same time, the genera *Sugiyamaella*, *Mucor*, *Crustoderma*, *Aureobasidium*, and *Apiospora* were represented by only one fungal isolate.

The representatives of *Trichoderma* sp., which are typical saprotrophs, exhibited a significantly higher rate of colony growth on Petri dishes than all other identified mycobiome representatives. The *Trichoderma* sp. colony covered the entire surface of the medium within 3–4 days, with intensive sporulation, and rapidly overgrew culture plates during incubation.

Of the 37 isolated fungal cultures, 25 were identified to the species level and 12 to the genus level. Among the representatives of the genus *Trichoderma*, *Trichoderma harzianum*, *Trichoderma koningiopsis*, *Trichoderma pseudokoningii* and one unidentified species of *Trichoderma* sp. were detected (Fig. 3b). The genus *Penicillium* was represented by *Penicillium corylophillum*, *Penicillium jejuense*, *Penicillium spinulosum* and two

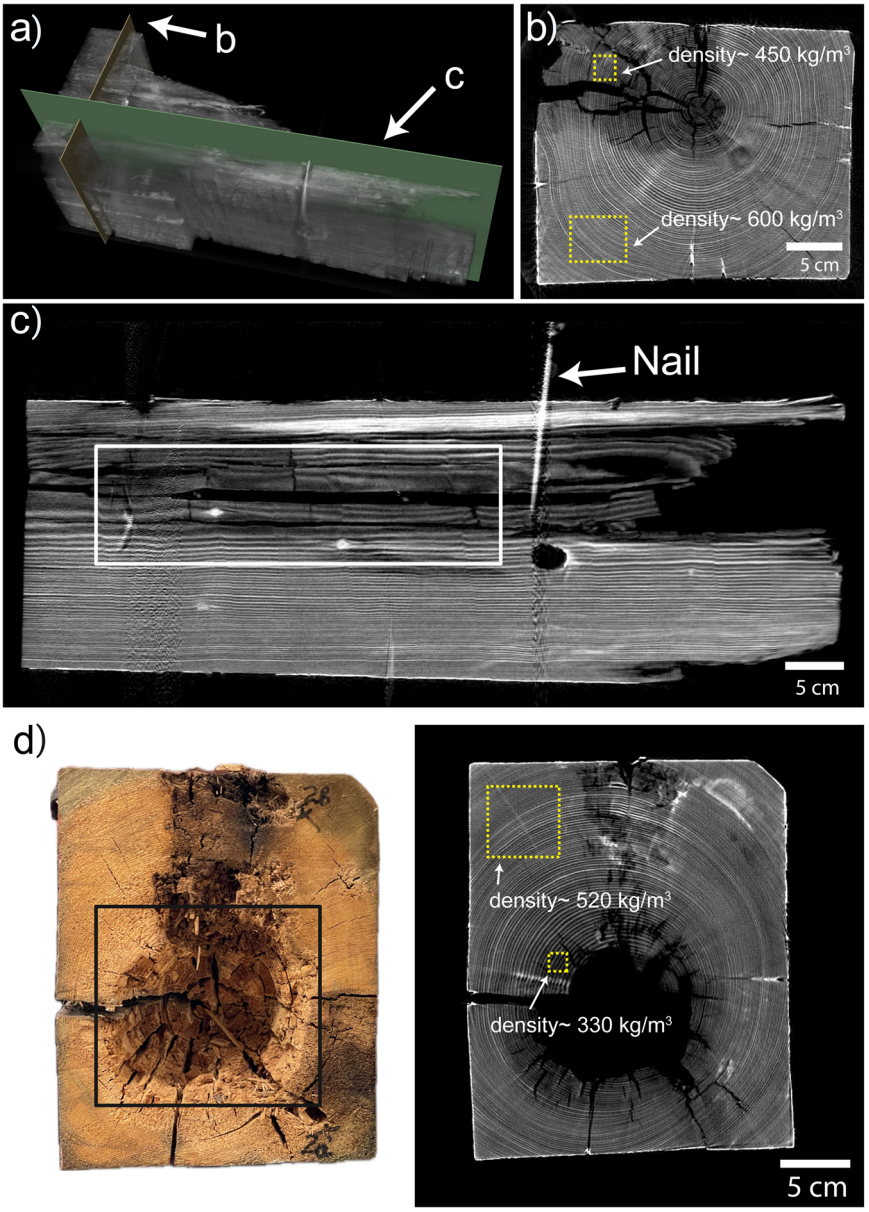

Fig. 2 | X-ray computed tomography (CT) analysis of timbers removed from the Lejonström bridge showing internal deterioration and density variation. a 3D reconstruction of a timber specimen illustrating the orientation of the cross-sectional (**b**) and longitudinal (**c**) planes used for analysis. **b** Representative cross-sectional CT image showing differences in wood density between sound and deteriorated regions, with selected regions of interest (yellow dashed boxes) used for density measurements. **c** Longitudinal CT section revealing internal decay, cracking (white box), and the presence of a metal nail embedded in the timber. **d** Comparison between the external appearance of a deteriorated timber cross-section (left) and the corresponding CT image (right), demonstrating extensive internal degradation (black box). Representative density values (kg/m³) measured in sound and degraded wood are shown.

unidentified isolates of *Penicillium* sp. (Fig. 3c). *Apiospora arundinis*, *Aureobasidium pullulans*, *Mucor circinelloides* and *Sydowia polyspora* were the only species found within their respective genera. At the same time, the ITS sequence data did not allow identification of species belonging to the genera *Coniochaeta, Crustoderma, Sugiyamaella* and *Eurotiales*.

Among all these fungal species, the study focused on the isolated basidiomycetes associated with brown-rot decay of the bridge timbers. Using a slightly modified isolation protocol (see Materials and Methods), 7 pure cultures of *Amyloporia xantha* were isolated and identified. Figure 4 shows the general appearance of a 1-month colony, macro- and microphotographs of *A. xantha*. The growth of the mycelium of this fungus was characterised as significantly slower compared to other representatives of the fungal community. Given this, only a more intensive surface sterilisation by flame treatment allowed this fungus to be isolated into pure culture.

During this study, another representative of Basidiomycetes was also isolated, namely *Crustoderma* sp., which is likely associated with brown-rot decay of wood[43,44]. Only one culture of this fungus was obtained. It was not possible to reliably determine the species of this basidiomycete using the ITS marker, so an additional marker gene is required for further detailed identification.

Phylogenetic analysis (Fig. 5) revealed a clear separation of the identified mycobiome representatives across the main fungal groups. *Ascomycota* fungi form a separate cluster with strongly supported, monophyletic *Trichoderma* and *Penicillium* groups, which are visualised with 85–100% bootstrap support. The clade *Sydowia–Aureobasidium* formed separately from other ascomycetous fungi, with 95% bootstrap support *A. xantha* clustered with *Crustoderma* sp., since only these two species belong to the class *Dothideomycetes* of which both are closely related. *A. xantha* and *Crustoderma sp.* clustered within the basidiomycete lineage with strong bootstrap support (96%). The single representative of the *Mucoromycota*, *M. circinelloides*, is separated into a lineage distinct from the *Ascomycota* and *Basidiomycota*, with 99% bootstrap support. In addition, a separate lineage was formed by the sole yeast-like fungus *Sugiyamaella* sp., clearly separated from all filamentous fungi included in the phylogenetic analysis. More detailed information about all identified fungal species is presented in Table 1.

Discussion

This study provides one of the first integrated assessments of fungal-associated biodegradation in the historic Lejonström bridge using both non-

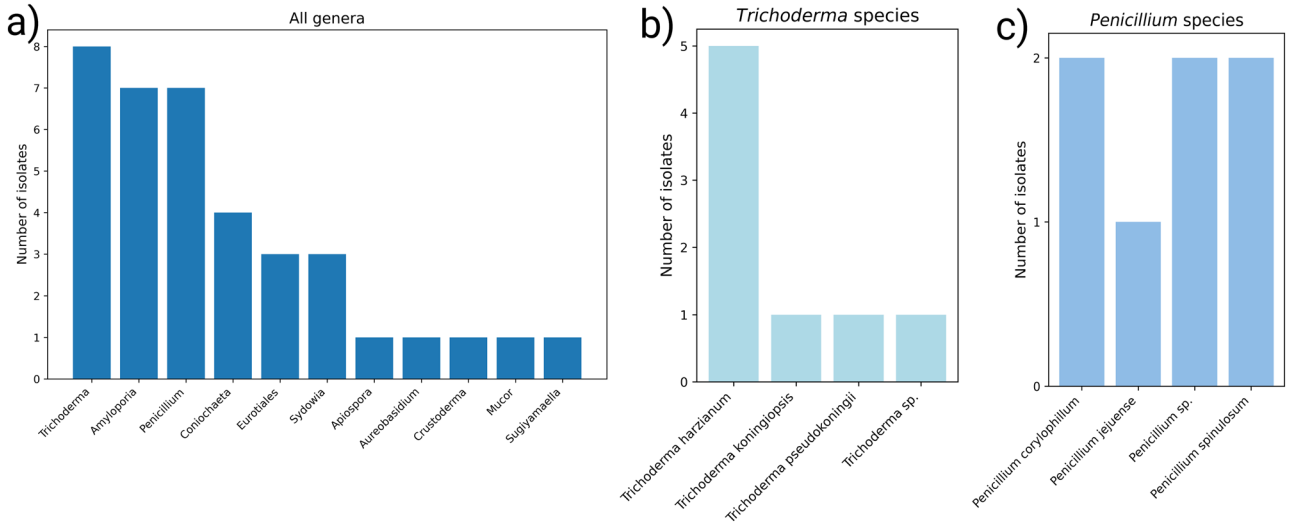

Fig. 3 | Culturable fungal taxa associated with decayed wood detected on Lejonström bridge. All genera of isolated fungi represented in the library (**a**), species diversity of *Trichoderma* (**b**) and *Penicillium* (**c**) genus separately.

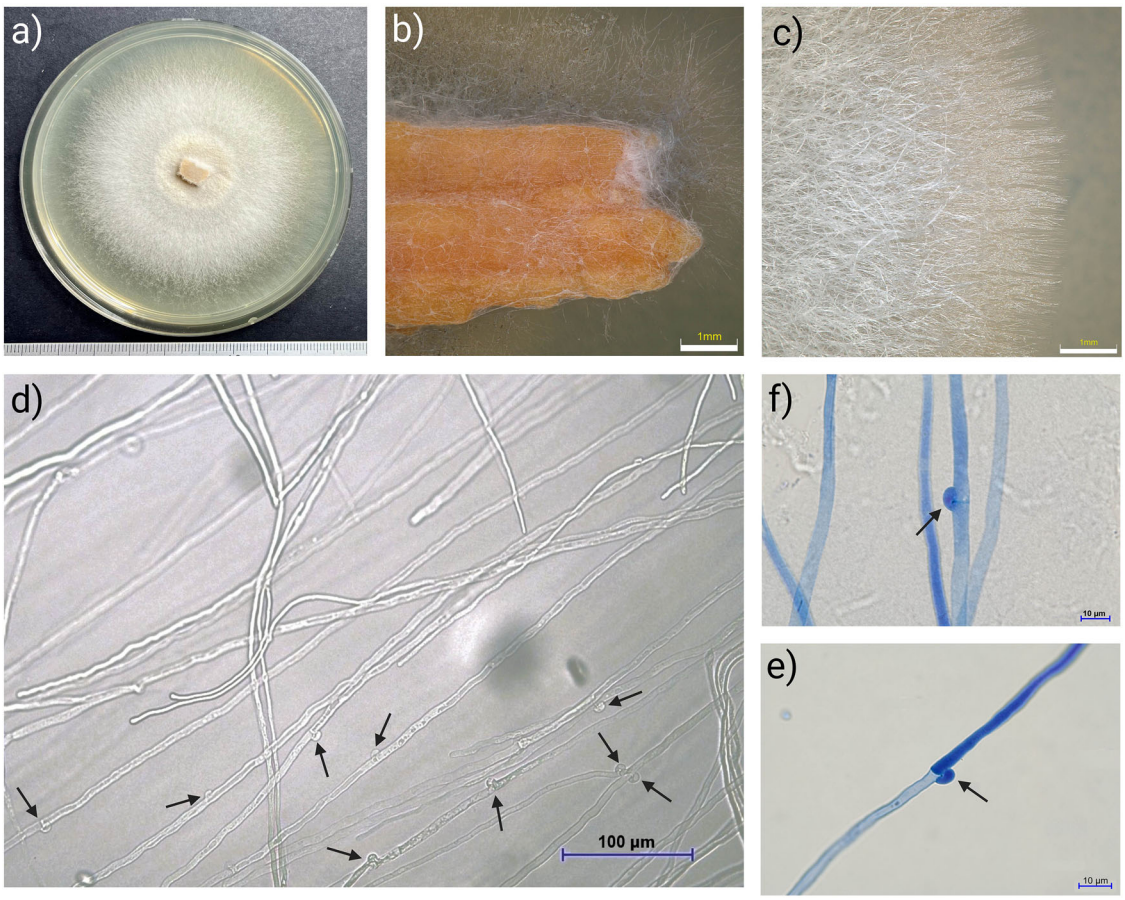

Fig. 4 | *Amyloporia xantha* isolated from Lejonström bridge timbers showing brown-rot decay. General view of the colony on MEA medium after 1-month cultivation (**a**), mycelium growing on a fragment of wood after 2-weeks cultivation (**b**), fragment of a 3-week isolated fungal colony during intensive growth on the surface of the MEA medium (**c**), hyphal structures (**d**–**f**) of the mycelium with clamp contacts (marked with arrows).

destructive CT imaging and culture-based fungal analysis. The results demonstrate that substantial internal wood deterioration developed within structural bridge timbers and was associated with characteristic brown-rot features, including cubical cracking and pronounced density loss. The combination of CT scanning and fungal isolation proved effective for linking structural deterioration with biologically active decay zones and identifying fungal taxa associated with advanced wood decay in this culturally important heritage structure.[6–8,33].

CT scanning proved to be an effective approach for detecting decayed areas and demonstrated a significant reduction in wood density, particularly

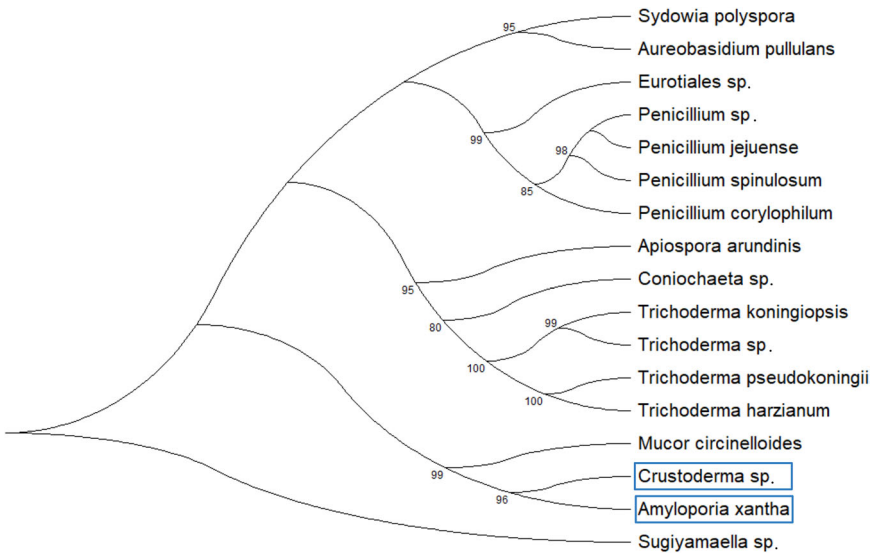

Fig. 5 | Maximum Likelihood phylogenetic analysis of all fungi isolated from the Lejonström bridge based on ITS sequence analysis. The phylogenetic tree was constructed with 1000 bootstrap support, and bootstrap values ≥ 80% are shown near nodes. The blue rectangle indicates fungi that caused the brown rot.

Table 1 | All identified fungal species associated with rotted wood from Lejonström bridge

Species	Division	No of isolates	Lifestyle	Accession number (GenBank)
Amyloporia xantha (Fr.) Bondartsev & Singer ex. Bondartsev	*Basidiomycota*	7	Wood-decay (brown rot)	PZ161152
Apiospora arundinis (Corda) Pintos & Alvarado	*Ascomycota*	1	Plant pathogen, saprotroph	PZ161136
Aureobasidium pullulans (de Bary) Arnaud	*Ascomycota*	1	Saprotroph	PZ161147
Coniochaeta sp.	*Ascomycota*	4	Saprotroph/opportunistic pathogen	PZ161146
Crustoderma sp.	*Basidiomycota*	1	Wood-decay (brown rot)	PZ161151
Eurotiales sp.	*Ascomycota*	3	Saprotroph, mould	PZ161139
Mucor circinelloides (Bruderl.) Schipper	*Mucoromycota*	1	Saprotroph, mould	PZ161150
Penicillium corylophilum Dierckx	*Ascomycota*	2	Saprotroph, mould	PZ161138
Penicillium jejuense Park & Lim	*Ascomycota*	1	Saprotroph, mould	PZ161149
Penicillium sp.	*Ascomycota*	2	Saprotroph, mould	PZ161143
Penicillium spinulosum Thom	*Ascomycota*	2	Saprotroph, mould	PZ161140
Sugiyamaella sp.	*Ascomycota*	1	Saprotrophic yeast	PZ161148
Sydowia polyspora Bref & Tavel	*Ascomycota*	3	Endophyte/saprotroph/opportunistic pathogen	PZ161137
Trichoderma harzianum Rifai	*Ascomycota*	5	Saprotroph/mycoparasite	PZ161144
Trichoderma koningiopsis Samuels, Suarez & Evans	*Ascomycota*	1	Saprotroph	PZ161141
Trichoderma pseudokoningii Rifai	*Ascomycota*	1	Saprotroph	PZ161142
Trichoderma sp.	*Ascomycota*	1	Saprotroph/mycoparasite	PZ161145

in the heartwood zone (Fig. 2). One important finding was the extensive internal deterioration detected in heartwood regions that externally showed only limited visible damage. This highlights the importance of non-destructive diagnostic approaches for heritage timber structures, where destructive sampling is often restricted. CT imaging allowed precise visualisation of density loss and internal decay distribution, demonstrating its strong potential as a monitoring tool for early detection of structurally significant fungal degradation. Although Scots pine heartwood is generally characterised by relatively high natural durability due to resinous extractives, localised moisture accumulation, limited preservative penetration, and prolonged exposure conditions may still permit colonisation by specialised wood-decay fungi. The coastal northern Swedish climate, characterised by prolonged periods of high relative humidity and seasonal moisture fluctuations (65% to 92% relative humidity depending on the month, data available at Weather Atlas, https://www.weather-atlas.com/ and Climate data, https://en.climate-data.org/), likely created favourable conditions for fungal colonisation and progression of wood decay.

Another key stage of this study was to assess the fungal biodiversity associated with the bridge's decayed wood. Isolating pure fungal cultures and subsequently identifying them proved quite effective, allowing the detection of 17 fungal species, including two basidiomycetes that caused brown rot at this heritage site.

The frequent isolation of *A. xantha* strongly suggests that this species represents a major contributor to brown-rot development in the studied bridge timbers. This finding is particularly important because *A. xantha* is a well-recognised conifer-associated brown-rot fungus capable of degrading structural timber in buildings and outdoor wooden constructions across northern Europe[2,18,40,45,46]. Considering that conifers are mainly affected by this fungus and that Northern Europe widely uses conifers as building materials, the problem of *A. xantha* mass spread is undeniable[47]. A detailed

investigation of buildings in Norway demonstrated that this genus of wood-decay fungi most often affects roof and wall constructions (28.6%), roof beams (17.3%), and exterior constructions (23.4%)[48,49]. Another study of wood-destroying fungi in historic buildings built before 1945 in Styria (Austria) demonstrated that fungi of this genus were identified in 10.7% of cases, second only to *Serpula* spp. in prevalence[50]. In addition, studies have shown that *A. xantha* is sensitive to climatic conditions and wood quality[51]. This suggests that environmental conditions and wood characteristics may influence the occurrence and decay potential of this fungus, which is important for predicting the future risk of biodeterioration in historic timber structures.

The detection of *Crustoderma* sp. is also noteworthy because representatives of this genus possess cellulolytic capabilities and have previously been associated with the degradation of conifer wood[43,44]. Although only a single isolate was obtained, its occurrence together with *A. xantha* demonstrates that advanced decay in historical timber may involve more than one basidiomycete species. Compared with *A. xantha*, relatively little is known about the distribution and ecology of the genus *Crustoderma* in Europe[52], partly because many species within this genus are considered rare and of conservation interest. For example, *Crustoderma corneum*, the most frequently reported species in Sweden, is currently classified as Near Threatened on the Swedish Red List[53]. Therefore, the detection of *Crustoderma* in historical timber may be of ecological as well as cultural heritage interest. Its presence may reflect the use of mature heartwood originating from old-growth forests during historical construction or restoration rather than indicating an aggressive colonizer of wooden buildings. Furthermore, previous studies have shown that *Crustoderma* species exhibit limited establishment even under experimental inoculation conditions, suggesting relatively slow growth or low competitive ability[54]. Further investigations are needed to clarify the ecological role and distribution of this genus in historic wooden structures.

In addition to brown-rot basidiomycetes, numerous saprotrophic and mould-associated fungi were isolated from decayed bridge timbers, including species of *Trichoderma*, *Penicillium*, *Aureobasidium, Mucor* and *Sugiyamaella*. These fungi are commonly associated with weathered or decayed wood and likely represent secondary colonisers occupying nutrient-rich niches created during advanced decomposition[6,55–61]. The rapid growth of *Trichoderma* spp. observed under laboratory cultivation reflects its high growth capacity under the culture conditions used in this study. However, competitive interactions among wood-decay fungi in historical timber are considerably more complex and are influenced by resource availability, environmental conditions, and interspecific interactions, as demonstrated in previous studies on fungal community dynamics in decaying wood[62,63]. Two ascomycete species have been identified that combine characteristics of both saprotrophs and plant pathogens, namely species *A. arundinis, Coniochaeta* sp., and *S. polyspora*. In particular, *A. arundinis* infects a significant number of plant species, including economically important ones[64,65], and is also a saprophyte present on plant debris and decaying wood[66]. *S. polyspora* is a common saprotroph of conifers in genera such as *Pinus*, *Picea*, *Abies*, *Larix* and *Tsuga*[67], which, under the influence of various biotic and abiotic factors, causes various symptoms of plant damage (discolouration, yellowing or necrosis of needles, stem canker, etc.)[68]. In addition, it is a typical representative of the wood mycobiome in Sweden, particularly detected in Skellefteå[61].

In this study, one rotted-wood-associated yeast, *Sugiyamaella* sp., was identified. *Sugiyamaella* species can exhibit wood-decaying activity by producing xylanase, an enzyme that breaks down xylan, a component of hemicellulose[65]. Although these yeasts are usually associated with insects, they have also been isolated from insect habitats, namely rotting wood, soil, and fungi[69,70].

The coexistence of active brown-rot fungi with rapidly growing saprotrophic colonisers suggests complex fungal succession within the decayed timber microhabitat. Since rotten wood represents an ecological niche in which microorganisms, particularly fungi, coexist and compete for space and nutrients[71], it was expected to reveal significant mycobiome biodiversity. The approach of isolating pure fungal cultures and subsequently identifying them by Sanger sequencing with ITS markers proved quite effective, allowing us to discover key representatives of the mycobiome, including wood-decaying species, which was the goal of this study. However, the limitation of the present study is that fungal isolation was performed using a single culture medium (MEA). Although this approach enabled the recovery and identification of the dominant wood-decay fungi, the choice of medium may have influenced the composition of the recovered fungal community by favouring fast-growing species over slower-growing or more demanding taxa. Future studies could benefit from combining different isolation media, including low-nutrient media such as water agar, to improve the recovery of a broader diversity of wood-associated fungi. Although culture-based isolation successfully identified key wood-associated fungi, culture-independent metabarcoding approaches could also provide a more comprehensive understanding of fungal and bacterial communities inhabiting historical timber structures, including slow-growing or unculturable taxa.

In addition to their cultural heritage value, historic timber structures can also provide habitat for specialised wood-dwelling organisms, including fungi, lichens, and other microorganisms. Historic timber has been described as an ecological "time capsule," preserving biological communities that may have disappeared from modern managed landscapes[72]. Although the primary focus of this study was on the biodegradation of timber from a cultural heritage perspective, the fungal diversity documented here may also be of ecological interest and merits further investigation. Integrating cultural heritage conservation with ecological considerations can provide a more complete understanding of historic timber structures and support more sustainable conservation strategies.

Overall, the results demonstrate that biologically driven deterioration poses a substantial threat to historical wooden structures, even in highly durable timber. The integration of CT-based structural assessment with fungal identification provides a valuable framework for early detection and monitoring of decay in culturally important wooden structures. The frequency of monitoring should be determined on a case-by-case basis, considering environmental exposure, moisture conditions, the conservation status of the structure, and local management requirements, rather than applying a universal inspection interval. As climate change is expected to increase average temperatures, alter precipitation patterns, and prolong periods of elevated wood moisture in northern environments, it may promote fungal growth, colonisation, and wood-decay activity. Therefore, long-term surveillance of fungal-associated wood degradation will become increasingly important for the preservation of wooden cultural heritage.

This study demonstrated that significant internal deterioration had developed within structural timbers of the historic Lejonström bridge and was associated with characteristic brown-rot decay features and fungal colonisation. The integration of non-destructive CT scanning and culture-based fungal analysis enabled effective localisation of hidden decay zones and identification of fungal taxa associated with advanced wood degradation, including the brown-rot basidiomycete *A. xantha*. The results highlight the importance of combining structural imaging and mycological approaches for assessing historical wooden infrastructure, particularly when preservation constraints limit destructive sampling. In addition to active wood-decay fungi, many secondary saprotrophic and mould taxa were detected to be associated with rotten wood, suggesting complex fungal succession processes within decayed timber microhabitats. Overall, this study provides a useful framework for monitoring fungal-associated deterioration in important cultural wooden heritage and supports the development of more targeted conservation and maintenance strategies under changing environmental conditions.

Data availability

All data obtained in this study are stored on servers at Luleå University of Technology and are available at the link https://researchdata.se/en/catalogue/dataset/2026-259/1?previewToken=3375354b-2d7a-4292-acf3-

1ce449c70996. The obtained sequences of isolated fungi were submitted to GenBank under accession numbers PZ161136-PZ161152.

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Author contributions

A.P. conducted the microbiological and molecular genetic part of the study, prepared the first version of the manuscript, and corresponded with it. C.F.L and O.B. scanned the samples using CT, processed and visualised the CT data. K.D supported the microbiological and molecular genetic part of the study. O.K. provided academic support for the research supervision and manuscript preparation. O.M. contacted the Skellefteå Municipality and provided supervision of the research and manuscript preparation. All authors reviewed and agreed on the final version of the manuscript.

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Competing interests

The authors declare no competing interests.

Ethics approval and consent to participate

Not applicable.

Additional information

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