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Article

Survey of the Trunk Wood Mycobiome of an Ancient *Tilia × europaea* L.

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Abstract

The genus *Tilia* (Malvaceae) comprises long-lived broadleaf trees of considerable ecological, cultural, and historical importance in temperate Europe and Asia. Among these, *Tilia × europaea* L. is a key native species in Central and Northern Europe, with individuals documented to live for several centuries. While the external and soil-associated microbiomes of linden have been studied, the internal fungal communities inhabiting ancient trees remain poorly understood. Wood-inhabiting fungi (the wood mycobiome) include endophytes, saprotrophs, and potential pathogens that can strongly influence host vitality and ecosystem processes. Advances in high-throughput amplicon sequencing (HTAS) now provide unprecedented opportunities to characterize these hidden communities. In this study, we investigated the trunk wood mycobiome of an ancient *Tilia × europaea* L. individual using a culture-independent HTAS approach. The results reveal a diverse fungal assemblage, including taxa like *Arthrinium* or *Phialemonium* not previously reported from living linden wood, and highlight potential implications for tree health and longevity. This work provides a first baseline characterization of the internal mycobiome of ancient *Tilia* trees and contributes to broader efforts to conserve their biological and cultural value.

Keywords: fungi; linden tree; *Tilia*; mycobiome; ITS sequencing; high-throughput sequencing

1. Introduction

The genus *Tilia* L. (Malvaceae), commonly referred to as linden trees, comprises long lived broadleaf species widely distributed across temperate regions of Europe and Asia. *Tilia × europaea* L. is a prominent native hybrid species in Central and Northern Europe, with significant ecological, cultural, and historical value. Dendrological studies using DBH based models have shown a strong correlation ($r^2 = 0.926$) between trunk diameter and age, indicating that *Tilia* sp. individuals can live for several centuries with high estimation accuracy (<10 % error) [1]. Genetic analyses using SSR markers further revealed that some historically valuable specimens of *T. cordata* are aged between 400 and 1000 years [2].

Fungal communities inhabiting the internal woody tissues of trees, the so-called wood mycobiome, play critical roles in host physiology, wood decay, and broader ecosystem function. These communities include both saprotrophic and endophytic fungi, some of which may be latent pathogens or opportunistic invaders under stress. For instance, pyrotag sequencing of ITS2 has been successfully applied to characterize the deadwood mycobiome, demonstrating correlation between fungal community composition, host species, and wood properties [3]. Moreover, long read PacBio sequencing of fungal ITS regions in deadwood revealed rich taxonomic and functional diversity, including endophytes, saprotrophs, and pathogens, reinforcing the complexity of wood inhabiting mycobiomes [4].

Despite the growing interest in tree-associated microbiomes, knowledge of the internal mycobiome of ancient linden trees remains sparse. Most studies to date have emphasized foliar pathogens or soil fungal communities, whereas endophytic and wood-colonizing fungi within long-lived linden trees are largely unexplored. This knowledge gap persists even as methodological advances, particularly high-throughput amplicon sequencing (HTAS) of the ITS ribosomal DNA region, offer unprecedented resolution in characterizing fungal diversity in woody substrates.

In this study, we surveyed the wood mycobiome of the trunk of an ancient linden tree using a culture-independent high-throughput sequencing approach. Our objectives were (i) to characterize the taxonomic composition of the internal fungal community, (ii) to document the presence of fungal taxa not previously reported from living linden wood, and (iii) to assess whether these fungi represent potential threats to the health and longevity of the ancient tree. This work provides a baseline for understanding the hidden fungal diversity of old-growth *Tilia* tree and contributes to broader efforts aimed at conserving their ecological and cultural value.

2. Materials and Methods

2.1. Linden Tree

Tilia × europaea L. is located in Lednice in from of Mendeleum area (Faculty of Horticulture, Mendel university in Brno) GPS 48.7936175N, 16.7984311E. This tree makes a first tree of Bezučova Alley. Bezručova Alley is a straight, over 6-kilometre-long linden and chestnut tree avenue that connects the towns of Valtice and Lednice in the Břeclav District. The alley was planted in 1715 as a link between the Liechtenstein chateaux of Valtice and Lednice, and it is part of the Lednice-Valtice Cultural Landscape, a UNESCO World Heritage Site. The tree is approximately 150 years old, based on the trunk circumference of the linden tree is 3.5 m and height 18 m. We used this formula: Age (in years) \approx trunk circumference (in cm) \div average annual circumference inkrement.

2.2. Sampling

Wood samples, specifically sawdust, were collected from the tree trunk. A sample of sawdust was taken using an increment borer with a diameter of 1.0 cm and a length of 70 cm. The drilled holes in the trunk are depicted on the Figure 1. To ensure the highest possible reliability of the sample from infected tissues, sawdust was collected from three points of the trunk at a height of approximately 1 meter above ground, 27th March 2023. One sample thus consisted of sawdust from three boreholes, perpendicular to each other. Each borehole was treated with a grafting balm. The tools used were disinfected between each sampling. The collected wood samples were cooled on site.



Figure 1. Linden tree (*Tilia × europaea* L.), A-habitus of the tree; B-sampling using increment borer; C-drilled holes in the trunk of the linden tree.

2.3. High-Throughput Amplicon Sequencing

Samples were homogenized to a fine powder using a pestle and subsequently used for DNA extraction following the protocol of the commercial NucleoSpin Tissue kit (Macherey-Nagel, Düren, Germany). DNA concentration was measured using the SPECTROstar Nano (BMG Labtech, Offenburg, Germany), we obtained total DNA in concentration $12.52 \text{ ng} \cdot \mu\text{l}^{-1}$. Genomic libraries were prepared by amplifying a fragment of the internal transcribed spacer (ITS) region (~500–600 bp) using the primers gITS7 (GTG AAT CAT CGA ATC TTT G) and ITS4 (TCC TCC GCT TAT TGA TAT GC). The thermal cycling conditions included an initial denaturation at 95 °C for 10 minutes, followed by 35 cycles of 94 °C for 20 seconds, 47 °C for 30 seconds, and 72 °C for 20 seconds, with a final elongation step at 72 °C for 7 minutes. PCR was carried out in 50 μL reaction volumes containing 25 μL of Q5® High-Fidelity 2× Master Mix (NEB, Ipswich, UK), 2.5 μL of each primer (10 μM), 2 μL of template DNA, and 18 μL of nuclease-free water. Library preparation followed the Nextera XT protocol (Illumina, San Diego, CA, USA). The final library was subjected to a quality check using a Fast qPCR Library Quantification Kit (MCLAB, San Francisco, CA, USA) and sequenced using MiniSeq (Illumina) (2 × 150 paired-end reads) with a MiniSeq Mid Output Kit (300 cycles) (Illumina). To evaluate potential contamination, negative controls were included during the extraction, amplification, and sequencing to evaluate potential contamination throughout the entire process.

2.4. Bioinformatics and Data Evaluation

The quality of the sequences was assessed using FastQC v0.12.1 [5]. Trimming and merging of paired-end reads were performed with CLC Genomics Workbench v6.5.1 (CLC Bio, Aarhus, Denmark), applying a quality score threshold of Q30. Only reads longer than 100 nucleotides were retained for further analysis. The expected fragment size for trimming and merging was set between 150 and 300 nucleotides. Primer and Illumina adapter sequences were removed during trimming. The resulting FASTQ files were clustered using the SCATA pipeline (<https://scata.mykopat.slu.se/>). Clustering parameters were as follows: clustering distance 0.015; minimum alignment for clustering 0.95; mismatch penalty 0.1; gap open penalty 0; gap extension penalty 1; end gap weight 0; homopolymers collapsed at 3; downsample sample size 0; removal of low-frequency genotypes 0; Tag-by-Cluster Max 10,000,000; BLAST E-value cutoff 1e-60; clustering engine USERACH; number of representative sequences reported: 50. CBS isolates were used as reference sequences. Singleton operational taxonomic units (OTUs) were discarded. Non-singleton OTUs were represented by a consensus sequence and identified using the BLASTn algorithm against the NCBI GenBank reference database (version 2.2.30+). OTUs that matched mitochondrial, Viridiplantae, or chloroplast sequences, or those lacking kingdom-level classification, were excluded. Also the mapping of the total raw reads was done with CLC Genomics Workbench v6.5.1 to see the percentage of linden tree sequences, the mapping was done with parameters „No masking“, „Linear gap cost“, „Global alignment“ and „Map randomly“. Additionally, OTUs represented by fewer than 50 reads in total were removed from the dataset [6]. Richness and diversity metrics were calculated from the final curated sample.

2.5. Fungal Diversity and Statistical Analysis

Alpha-diversity was calculated by analyzing the Chao1 richness and Shannon diversity in PAST version 2.17c. Good's coverage values were also calculated.

3. Results

This section may be divided by subheadings. It should provide a concise and precise description of the experimental results, their interpretation, as well as the experimental conclusions that can be drawn.

3.1. High-Throughput Amplicon Sequencing

After paired-end alignments, quality filtering and deletion of chimeras and singletons, a total of 6,102,452 sequences were generated per read from one direction, R1 reads, an example is depicted on Figure 2, 47 % GC bases were generated. The R2 dataset also comprised 6,102,452 reads. In general, we obtained 12,204,904 reads. We mapped the reads on the ITS of linden tree (Acc. No. KF897521), and 3,642,227 reads were successfully mapped on this sequence, that is approx. 30 % of the total reads. Eight genera were identified in the DNA sample. According to Good's coverage, 94.2% of the total genera richness was represented in the fungal communities (Table 1). The Chao1 richness estimator was 8, and the Shannon diversity estimator was 1.813. High-throughput amplicon sequencing (HTAS) data were deposited in NCBI GenBank under BioProject accession number PRJNA1270958, BioSample: SAMN48846729.

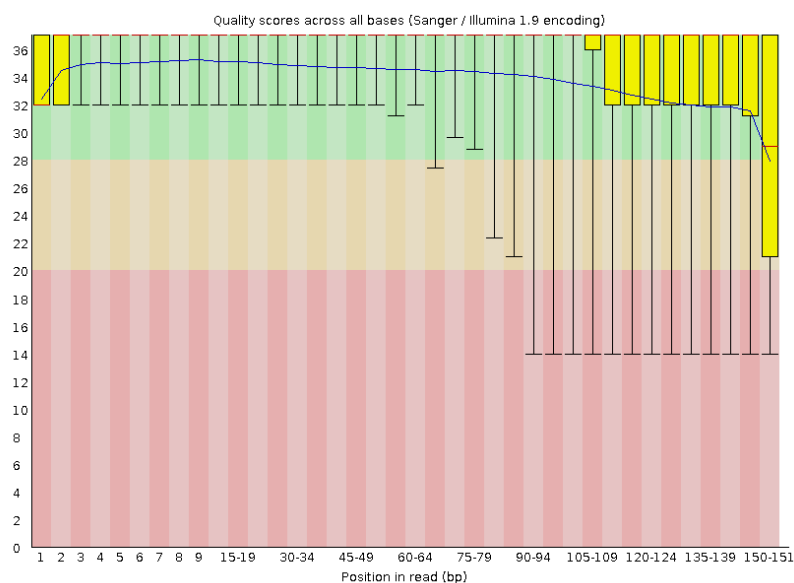


Figure 2. Quality scores across all nucleotide bases (Sanger / Illumina 1.9 encoding), R1 reads, generated by FastQC v0.10.1.

3.2. Taxonomy

Ascomycota dominated the fungal phyla (7 from 8 genera), one genus was identified as Basidiomycota, *Symmetrospora* – Basidiomycota (Cystobasidiomycetes) that reached 17 % abundance. The rest belongs to Ascomycota: *Alternaria* – Ascomycota (Dothideomycetes), *Arthrinium* – Ascomycota (Sordariomycetes), *Cladosporium* – Ascomycota (Dothideomycetes), *Didymocyrtis* – Ascomycota (Dothideomycetes), *Phoma* – Ascomycota (Dothideomycetes), *Phialemonium* – Ascomycota (Sordariomycetes), *Septoriella* – Ascomycota (Dothideomycetes). The most abundant genus was *Arthrinium* that reached 23 % abundance, followed by *Phialemonium* with 22 %. (Figure 3, 4).

Table 1. Estimates of sample coverage and diversity indices at the genus level for fungal profiles.

Diversity indices	Value
Taxa_S	8
Individuals	9262
Dominance_D	0.1798
Simpson_1-D	0.8202
Shannon_H	1.813
Evenness_e^H/S	0.7662
Brillouin	1.81

Menhinick	0.08313
Margalef	0.7664
Equitability_J	0.8719
Fisher_alpha	0.8618
Berger-Parker	0.2333
Chao-1	8

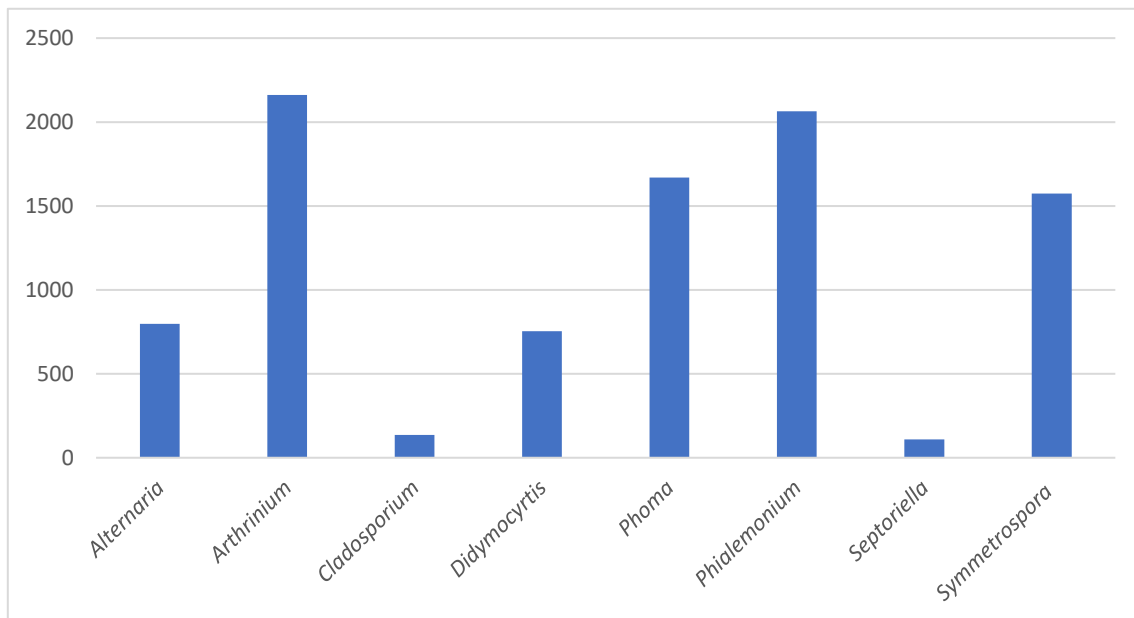


Figure 3. Graph of the numbers of paired Illumina reads associated with the fungal genera.

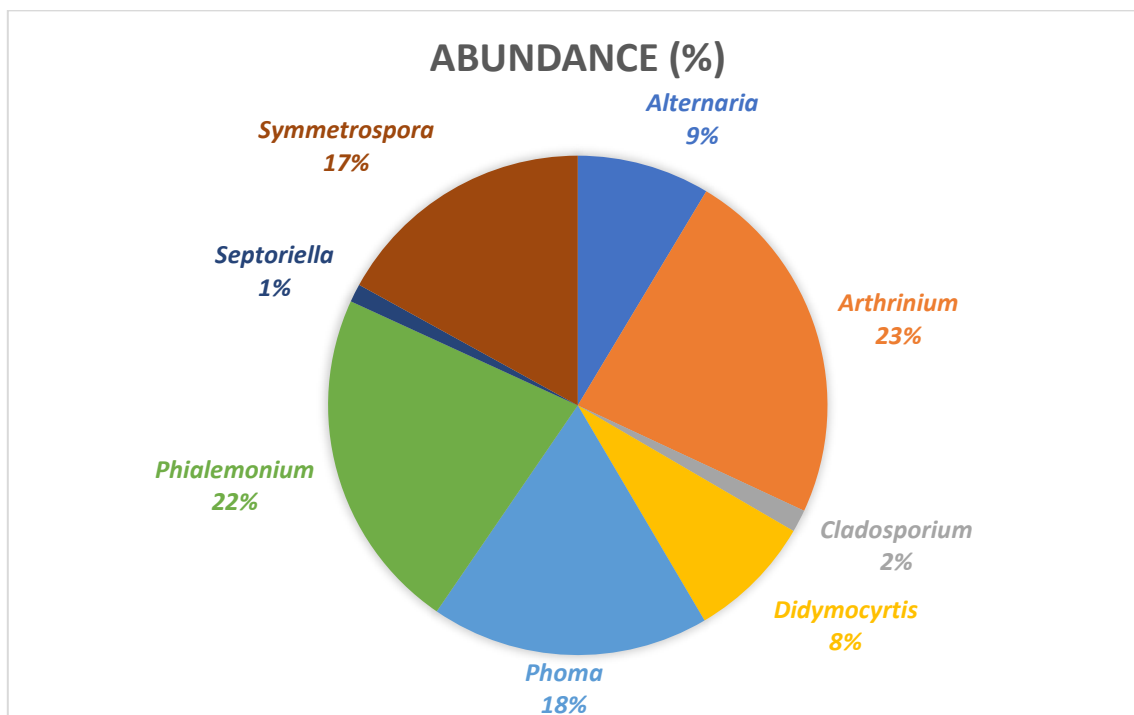


Figure 4. Percentage of the Illumina reads abundance associated with the particular fungal genera.

3.3. Morphological Evaluation of the Linden Tree

The linden tree was estimated to be 150 years old, with a trunk circumference of 3.5 m and a height of 18 m. It is a solitary specimen, with a crown height of 15 m and an average crown diameter of 13 m. Its overall health was good, although about 10% of the young branches were dried out. The

tree was infested with *Viscum album* L., but generally appeared healthy (Figure 1). Several younger branches extending from the main crown show visible signs of drying shrinkage. No visible damage was observed. Operational safety was assessed as average, and the tree's maintenance state was unkempt. From a biological perspective, the estimated remaining lifespan is likely more than 15 years. Both the biological and landscape values were considered very high.

4. Discussion

Authors should discuss the results and how they can be interpreted from the perspective of previous studies and of the working hypotheses. The findings and their implications should be discussed in the broadest context possible. Future research directions may also be highlighted.

To best of our knowledge, we do not know about any study using the HTAS analysis of the living linden wood mycobiome. We detected *Arthrinium* genus in abundance 23%. *Apiospora* was previously known as the sexual morph of the genus *Arthrinium* [7,8](Ellis 1963; Seifert *et al.* 2011). According to the International Code of Nomenclature for Algae, Fungi, and Plants (ICN) [9] (McNeil *et al.* 2012), *Apiospora* was a synonym of *Arthrinium* due to the early introduction of *Arthrinium* and it was more commonly used in the literature [10] (Crous and Groenewald 2013). As endophytes, plant pathogens and humus, *Apiospora* is ubiquitous in a wide range of terrestrial environments, such as soil, atmosphere and even marine substrates, but its main hosts are still plants, especially Poaceae [11] (Yan *et al.* 2019). *Apiospora* is widely distributed throughout the world, and usually identified as endophytes, pathogens or saprobes. Ai *et al.* [12] described six strains that were isolated from Bambusaceae sp., *Prunus armeniaca* L., *Salix babylonica* L. and saprophytic leaves in Shandong Province, China. These fungi were isolated from the leaves, not from the wooden tissues. According to Gerin *et al.* [13], *Arthrinium marii* is capable of colonizing the wood of olive trees and has been identified as a widespread fungal species involved in severe dieback of olive trees in southern Italy. *Phialemonium* was detected at the genus level in abundance 22%, as the second most abundant genus. *Phialemonium* is a genus of ascomycetous fungi, morphologically intermediate between *Acremonium* and *Phialophora* (Gams and McGinnis 1983) [14]. According to Manici *et al.* [15], who investigated fungal communities colonizing the wood of poplar, black locust, and willow, *Phialemonium* was most frequently isolated from willow. It was grouped within the complex of tree decay fungi, together with *Neocucurbitaria*, *Neofusicoccum*, and *Botryosphaeria*. *Daldinia childiae* co-colonized undecomposed willow wood samples alongside the endophytes *Botryosphaeria dothidea*, *Neofusicoccum parvum*, and *Phialemonium*, suggesting that these ascomycetes were not antagonistic. Members of the Botryosphaeriaceae family and *Phialemonium* colonized willow at early stages and subsequently shifted to a pathogenic phase, compromising plant health and facilitating further colonization by *Daldinia* as the main ligninolytic taxon. The potential use of *P. curvatum* as a biological control agent against *Ophiostoma crassivaginatatum*, wood pathogen on aspen, was previously investigated [16] (Hiratsuka and Chakravarty 1999). The growth of the pathogen *Ophiostoma crassivaginatatum* was significantly suppressed *in vitro* [16] (Hiratsuka and Chakravarty 1999). The symptoms observed on the linden tree may be linked to *Phialemonium*, which was identified as the most abundant species according to the references discussed. *Phoma* species are environmentally widespread fungi, frequently associated with soil and aquatic habitats, primarily recognized as plant pathogens. *Phoma* spp. have been isolated from various sources, including water, food, and agricultural crops. Its well known saprophyte or opportunistic pathogen but endophyte too. *Phoma* spp. was isolated from the wood of *Taxus wallachiana*, the fungus was present among the plant cells of xylem [17] (Yang *et al.* 1994). But its not understood as a typical colonizing fungi of the wood. On the other hand, interveinal chlorosis, presence of ash-grey areas on withered trees, and wilting with salmon-pink or orange-red discolouration of the wood of citrus trees is a characteristic feature of the mal secco disease caused by *Phoma tracheiphila* [18,19] (Migheli *et al.* 2009; Nigro *et al.* 2011). The ash-grey or lead-grey areas indicate the presence of pycnidia produced underneath the trees. To our best our knowledge, we did not find any information about *Phoma* fungus in a living wooden tissues of *Tilia* spp. *Symmetrospora* genus was unveiled in abundance 17% in the linden wood. *Symmetrospora* genus is a red yeast from

the subphylum Pucciniomycotina in the phylum Basidiomycota [20] (Wang *et al.* 2015). *Symmetrospora pseudomarina* SA42 was isolated from decaying wood, Louisiana, USA [21] (Haelewaters *et al.* 2020). *Symmetrospora* was also detected in a high abundance on the bamboo samples [22] (An *et al.* 2023) and in citrus tissue samples, however not in the wood [23] (Xi *et al.* 2023). Our study proved that *Symmetrospora* genus could colonize a linden tree wood. *Alternaria* was identified in 9% abundance. *Alternaria malorum* was identified as a causal agent of bark canker on walnut trees [24] (Bagherabadi and Zafari 2022). *Alternaria tenuissima* was identified in the wood of *Cedrus atlantica* L. in Morocco. Several studies have identified *A. tenuissima* as an aggressive pathogen of apple trees in South Africa and pecan in China, and as the causal agent of leaf spot in *Datura metel* L. and black chokeberry (*Aronia melanocarpa* L.) in Korea. The fungus also produces metabolites, including mycotoxins, that can degrade various plant tissues [25] (Chauiyakh *et al.* 2023). *Didymocyrtis* was identified in abundance of 8 %. The fungal genus *Didymocyrtis* Vain., long overlooked since its original description, has recently been resurrected and now encompasses lichenicolous species that were previously placed under *Diederichia* D. Hawksw., *Diederichomyces* Crous & Trakun., *Leptosphaeria* Ces. & De Not. and *Phoma* Sacc. [26,27] (Trakuningcharoen *et al.* 2014; Ertz *et al.* 2015) but also some foliicolous [28,29] (Crous *et al.* 2017, 2018) and terricolous species [30] (Das *et al.* 2021). The genus belongs to the family Phaeosphaeriaceae M.E. Barr. It was identified on *Banksia sessilis* var. *cygnorum* or *Brachylaena discolor*. *Cladosporium* has been reported as an endophyte in the wood (xylem, sapwood, and heartwood) of numerous tree species. In contrast to *Alternaria*, which is primarily recognized as a foliar pathogen, *Cladosporium* species are commonly associated with the internal woody tissues of both healthy and stressed trees. These fungi exhibit a remarkably broad ecological amplitude, occurring on diverse substrates and a wide range of hosts, either as biotrophs or colonizers of dead and senescing tissue. Contrary to earlier assumptions, only a few species are truly plurivorous, cosmopolitan saprobes, such as *C. herbarum*, *C. cladosporioides*, and *C. oxysporum*, which show little evidence of strong environmental preferences [31] (Bensch *et al.* 2012). This fungus was detected in abundance of 2%. *Septoriella* was detected in abundance of 1%. This genus is usually found as saprobic on dead wood. However, the wood that was extracted from the old trunk of linden tree was not dead.

5. Conclusions

Based on the analytical pipeline, high-throughput sequencing of the ITS amplicon revealed eight fungal genera; however, this method does not allow for reliable species-level identification. The most abundant genera were *Arthrinium* and *Phialemonium*. All eight determined fungal taxa were identified in living linden wood for the first time. Given the nature of these genera, the detected fungi are not considered to pose any threat to this ancient linden tree based on current knowledge. The described diagnostic pipeline provides a fast and precise approach for plant diagnostics. Beyond this case study, the methodology can be applied to the analysis of wood mycobiota in other tree species, opening new perspectives for plant pathology and biodiversity research.

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Conflicts of Interest: The authors declare no conflicts of interest.

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