

## Article

# Fungi Occurring in Norway Spruce Wood Decayed by *Heterobasidion parviporum* in Puszcza Borecka Stands (Northeastern Poland)

Andrzej Szczepkowski <sup>1,\*</sup>, Waldemar Kowalczyk <sup>2</sup>, Katarzyna Sikora <sup>3</sup>, Marta Damszel <sup>4</sup> and Zbigniew Sierota <sup>5</sup>

<sup>1</sup> Department of Forest Protection, Institute of Forest Sciences, Warsaw University of Life Sciences—SGGW, ul. Nowoursynowska 159, 02-776 Warszawa, Poland

<sup>2</sup> EKOSYSTEM S.C., ul. Wspaniała 1, 05-400 Otwock, Poland; ekosystem@ekosystem.waw.pl

<sup>3</sup> Department of Forest Protection, Forest Research Institute, Sękocin Stary, ul. Braci Leśnej 3, 05-090 Raszyn, Poland; K.Sikora@ibles.waw.pl

<sup>4</sup> Department of Entomology, Phytopathology and Molecular Diagnostics, University of Warmia and Mazury, ul. Prawocheńskiego 17, 10-720 Olsztyn, Poland; marta.damszel@uwm.edu.pl

<sup>5</sup> Department of Forestry and Forest Ecology, University of Warmia and Mazury in Olsztyn, Plac Łódzki 2, 10-727 Olsztyn, Poland; zbigniew.sierota@uwm.edu.pl

\* Correspondence: andrzej\_szczepkowski@sggw.edu.pl

**Abstract:** In many spruce stands, trees are frequently attacked by the pathogen *Heterobasidion parviporum*, albeit without visible symptoms in the crown. In the present work, the results of the presence of stem rot, assessed by PICUS Sonic Tomography, and the fungal biota on trees and stumps in eight plots in the Puszcza Borecka Forest are described. The plots were located in stands on original forest soil (4) and on post-agricultural soil (4), where around a stump with *H. parviporum* symptoms (signs of internal rot and basidiocarps), 30 trees were selected and examined for internal rot. Wood samples were collected from two selected trees for fungal molecular analysis. A total of 79 fungal taxa were found, including 57 taxa in plots on post-agricultural soil and 45 on forest soil. There were 395 fungal records on stumps and 22 records on trees, therein, from the inner parts of felled trunks. Significant differences in the Chao-1 diversity index indicate that the origin of the soil—post-agricultural or forest soil—influenced the alpha diversity of the fungal communities in the forests studied. The values of the Shannon and Simpson indices show that the two communities were similar in terms of species numbers. The presence of basidiomata of *H. parviporum* and two species of *Armillaria* (mainly *A. cepistipes*) in samples on all plots is striking, although *Armillaria* spp. was detected more frequently. Most of the species identified were typical saprotrophs, although rare species were also found, such as *Entoloma byssisedum*, *Onnia tomentosa*, *Physisporinus vitreus*, *Postia ptychogaster*, and *Ramaria apiculata*. The presence of *H. parviporum* in the inner woody parts was confirmed by PCR analysis, and decay was detected even up to a stem height of 6 m. *Armillaria* was the dominant genus in the studied stands, and *H. parviporum* plays a significant and underestimated role in heartwood decay of old spruce trees in Puszcza Borecka Forest.

**Keywords:** *Picea abies* dieback; conifer root rot and butt rot; coexisting fungi; Borecka Forest; PICUS 3 Sonic

**Citation:** Szczepkowski, A.; Kowalczyk, W.; Sikora, K.; Damszel, M.; Sierota, Z. Fungi Occurring in Norway Spruce Wood Decayed by *Heterobasidion parviporum* in Puszcza Borecka Stands (Northeastern Poland). *Forests* **2022**, *13*, 229. <https://doi.org/10.3390/f13020229>

Academic Editors: Jolanta Behnke-Borowczyk, Jacek Piętka, Piotr Łakomy, Lassaâd Belbahri and Tomasz Oszako

Received: 13 December 2021

Accepted: 26 January 2022

Published: 3 February 2022

**Publisher's Note:** MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



**Copyright:** © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

In spruce (*Picea abies* (L.) H. Karst.) stands, the pathogen *Heterobasidion parviporum* (Niemela & Korhonen) is an important wood destroyer [1–4]. Together with *H. annosum* (Fr.) Bref. and *Armillaria solidipes* Peck = *A. ostoyae* Romagn. (Herink), it is one of the main causal agents of diseases in harvested forests in the Northern Hemisphere [1,5–7]. Wood-inhabiting fungi, both pathogens and saprotrophs, decompose cellulose and lignin in the

cell walls through oxidoreduction enzymes secreted extracellularly during substrate colonization [8]. The decomposition of wood leads to the release of D-glucose and its oxygenation, binding water and carbon dioxide [9–12]. These processes produce large amounts of energy and various metabolites, including nitrogen compounds, that can be used by other organisms [13–18]. As a result of the infection of live spruce trees by *H. parviporum* and the associated persistent decomposition of the heartwood, also after the felling of the trees [19,20], attempts to detect the presence of wood rot on standing trees at an early stage have been made, albeit with varying degrees of success [21–23]. For example, computed tomography allows the assessment of both changes in tree structure and the extent of wood loss caused by *H. parviporum* [24–26].

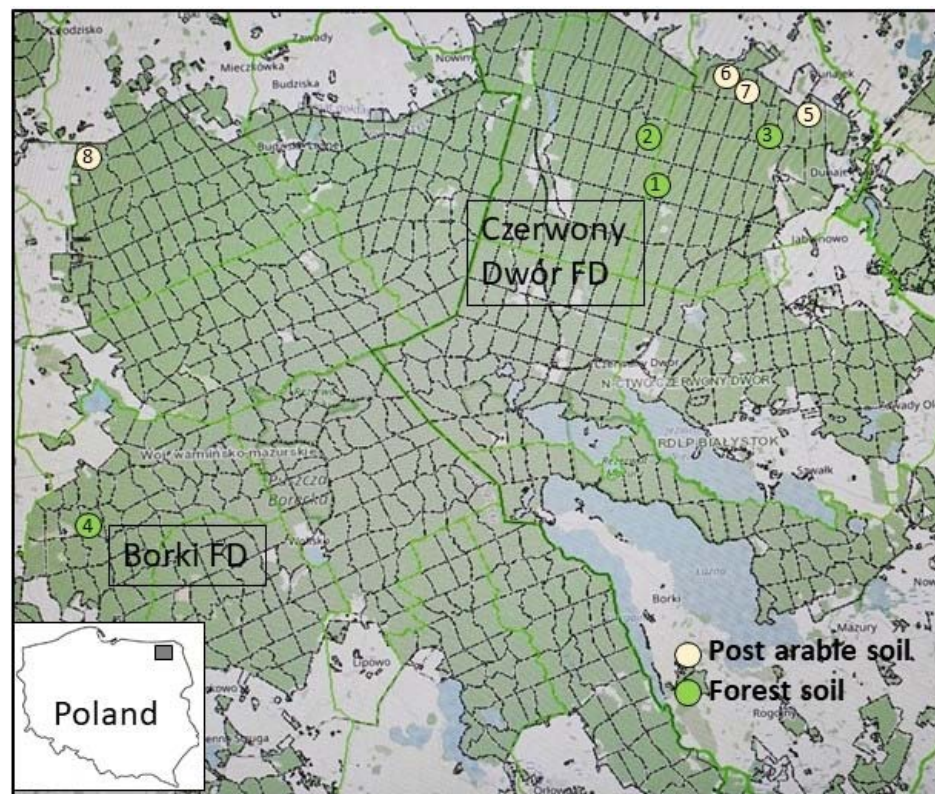
Decomposing tissue appears to provide favorable conditions for the colonization by other fungi along with natural succession [27,28]. Fungi that decompose spruce wood have been largely described in terms of their distribution at different sites [29], the infectivity of root residues [30], the genetic aspects of infection [31,32], or root endophytes as potential biocontrol agents [33], among other issues. However, the biota accompanying *H. parviporum* in decaying wood [34,35] have rarely been recorded, with only 95 search results in Google Scholar.

Since *H. parviporum* is a major cause of infection and death of mature trees in spruce stands in many countries [36–38], the aim of the present study was to determine the proportion of this pathogen in commercial spruce stands over 50 years old in the Borecka Forest, northeastern Poland, that have previously been infested by *H. parviporum*. We determined the fungal biota inhabiting the wood of trees and stumps in selected stands growing on old forest sites and on post-agricultural sites. We hypothesized that: (i) infection with *H. parviporum* can be detected early by tomographic examination of the logs, and (ii) stumps of felled and dead trees with internal rot are, on post-agricultural soil, a more adequate food source for various fungi of different trophic groups than stumps on old forest soil.

## 2. Materials and Methods

### 2.1. Research Plots

The study was performed in summer 2018 (PICUS examination) and autumn 2021 (stumps examination) in spruce stands (over 50 years old) in northeastern Poland (Figure 1) in the Borki and Czerwony Dwór Forest Districts (FDs), which belong to the Białystok Regional Directorate. Both FDs are mainly located in the Borecka Forest, a large forest complex (230 km<sup>2</sup>) in the lake area of the 842.86 Elk Lake District (Masurian Lakeland) [39]; part of Borecka Forest is a dedicated nature reserve. According to the annual reports of the State Forests [40], both forest areas show significant damage by fungal pathogens, mainly *Heterobasidion* spp. and *Armillaria ostoyae*. Based on personal communication with foresters and an inventory, eight threatened stands were selected, four on former agricultural land and four old forest stands (Figure 1, Table 1). The old forest stands were selected randomly, whereas the stands on former agricultural sites were located on the edge of Borecka Forest. The numbers of the compartments were obtained from the Forest Data Bank [41].

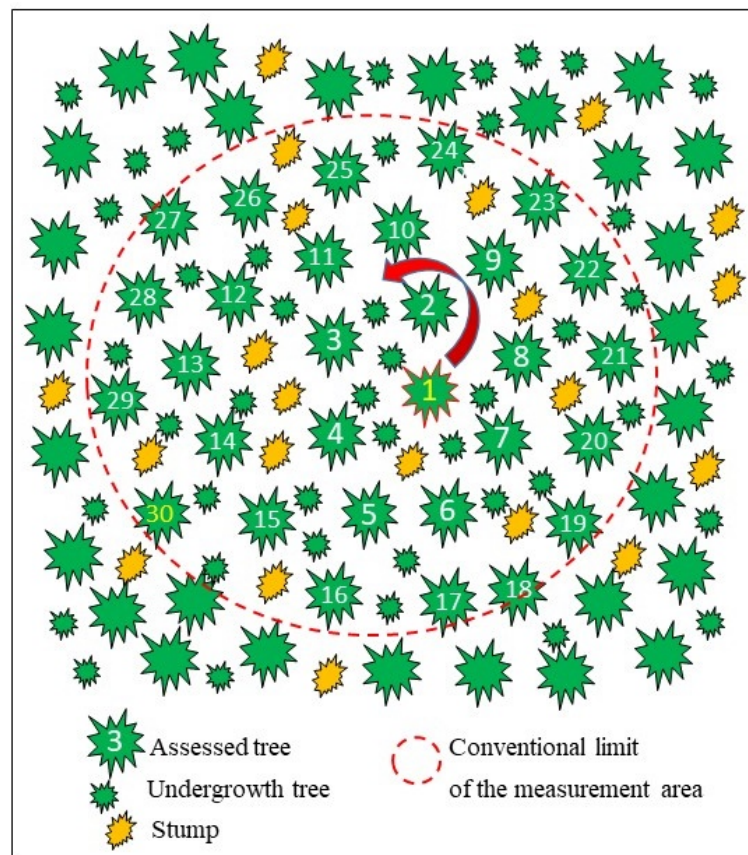


**Figure 1.** Localization of the eight evaluated plots in Czerwony Dwór and Borki Forest Districts in Poland (Map source: [41]).

**Table 1.** Description of the assessed compartments in the two forest types.

Forest District	Plot No. Subdistrict	Soil Type	Stand Age	No. of Trees on Survey Plot	Trees with Decay by PICUS (%)	No. of Stumps/with Decay Symptoms (Including Stumps with Hollows and Basidiomata of <i>H. parviporum</i> and <i>Armillaria</i> spp.)
Czerwony Dwór	1—Dunajki 102l	Forest	53	144	13.3	39/33 (13)
	2—Kaliniszki 85h	Forest	63	118	33.3	43/36 (10)
	3—Dunajki 59k	Forest	74	82	56.7	35/29 (12)
	5—Dunajki 58c	Arable	53	109	36.7	64/44 (11)
	6—Dunajki 44a	Arable	63	117	33.3	51/43 (20)
	7—Dunajki 43g	Arable	74	129	13.3	55/53 (19)
	Borki	4—Knieja Ł. 49b	Forest	111	51	70.0
8—Lipowa G. 6a		Arable	109	71	73.3	18/18 (15)
Average		Forest			43.3	37.8/32.5 (11.3)
number of stumps		Arable			39.2	47.0/39.5 (16.3)

In each of these stands, spruce stumps with symptoms of internal decay typical of *H. parviporum* or with basidiomata were searched. One randomly selected stump served as the reference for further evaluation, and the tree closest to it was selected as the plot center (No. 1 in Figure 2). Subsequently, 30 consecutive trees were selected in a spiral and numbered (1–30). The trees showed no signs of crown thinning or dieback. The undergrowth and the small trees in the lower floors of the plot were omitted. The diameter of this area was measured and represented the survey plot (Figure 2). Within each plot, all spruce stumps and all trees were counted and examined for the presence of sporocarps (Table 1).



**Figure 2.** Diagram showing the selection and location of 30 trees and stumps within the conventional survey plot.

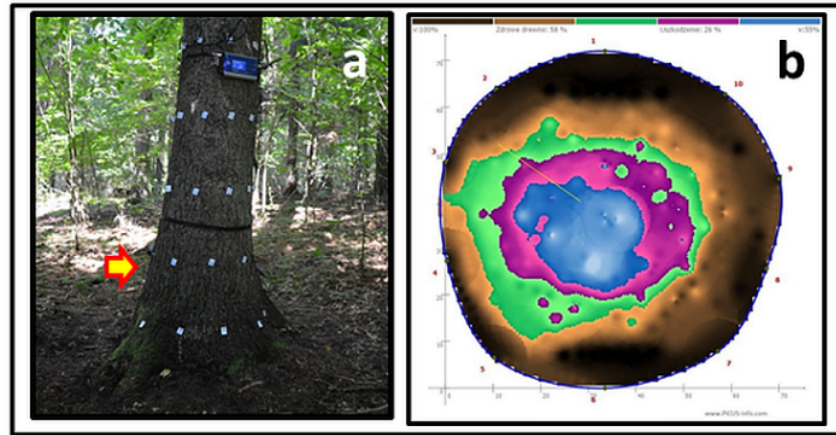
### 2.2. Computed Tomographic Analysis

All 240 trees (30 trees in each of the 8 plots) were examined with PICUS Sonic® to determine the presence or absence of internal rot (Figure 3).



**Figure 3.** One of the trees cut down for DNA analysis of fungi inside the spruce trunk. The crown of the tree showed no symptoms of defoliation or discoloration, whereas evaluation via PICUS Sonic Tomography showed the presence of stem internal rot. Photo by M. Damszel.

Tomographic assessment of wood decay inside the tree trunk [42,43] was performed at a height of 0.1 and 0.6 m above the ground (Figure 4), using the Sonic Tomograph—PICUS 3 Q74 EXP and the PICUS GMS Calliper 3 measuring device [26].



**Figure 4.** Measurement with PICUS Sonic (a), and tomogram of the trunk presented in Figure 3 at a height of 0.6 m (b). Photo by W. Kowalczyk.

### 2.3. Assessment of Sporocarps

The collected specimens, growing in the root necks of all standing trees and on tree stumps within each plot, were identified using standard mycotaxonomic methods [44]. Species were identified using keys [45–49], and dried specimens were stored in the fungarium of the Forest Protection Department of the Warsaw University of Life Sciences (SGGW). The nomenclature of fungi followed the Index Fungorum database [50]. Threat categories were assigned according to the “Red List of Macrofungi in Poland” [51]; endangered and rare fungal species were listed according to Kujawa et al. (2021) [52].

### 2.4. Preparation of Pure Cultures and Molecular Analyses

Two trees showing signs of decay previously indicated by PICUS were randomly selected from the measurement plots (one from forest plot 49b and the other from arable site plot 6a). The trees were felled in October 2020. After debarking the trunk, five replicates of wood samples were cut at a height of 0.1 and 0.6 m, placed in sterile glass tubes, and stored in the refrigerator prior to further analyses. In the laboratory, the samples were surface-sterilized, cut into small inocula, and placed on 2% malt extract agar (MEA) supplemented with 50 mg/L streptomycin. Cultures were incubated at 22 °C for 7 days and sub-cultured as necessary. The resulting colonies were transferred to plates containing 2% MEA to obtain pure cultures for DNA analyses.

Fungal genomic DNA from mycelium, rhizomorphs, and sporocarps was extracted according to Kubiak et al. (2016) [53]. For the identification of fungal isolates obtained from decaying wood, the ITS rDNA region was amplified and sequenced using the primers ITS1F and ITS4 [54,55]. Identification of *Heterobasidion* specimens was performed by species-specific PCR with the primer pairs MJ-F/MJ-R (*H. annosum*) and KJ-F/KJ-R (*H. parviporum*) [56]. Identification of *Armillaria* species was performed based on sequencing of a portion of the translation elongation factor 1 alpha (tef 1-alpha, amplified according to Szewczyk et al. (2015) [57]. The amplified regions had a size of 100 bp (*H. annosum*), 350 bp (*H. parviporum*), and 600–650 bp (tef 1-alpha). Both strands of PCR products of the ITS region and the tef 1-alpha gene were sequenced using a 3730XL DNA analyzer (Applied Biosystems, Waltham, MA, USA) at Genomed (Warsaw, Poland). Nucleotide sequences were read and edited using FinchTV v. 1.4.0 (Geospiza Inc., Seattle, WA, USA) and aligned with sequences publicly available in GenBank (<http://www.ncbi.nlm.nih.gov>, accessed on

12 January 2022), using the BLASTn algorithm to confirm the taxonomy of the fungi studied.

### 2.5. Statistical Analyses

To determine the species diversity in the studied groups, several indices were calculated: Chao1, Ace, Shannon, Simpson, and Fisher. Alpha biodiversity was analyzed using the phyloseq package R [58]. Statistical analysis of the selected indices was performed using the R function pairwise.wilcox.test as Wilcoxon sum in pairs. Chi-square statistical analysis was performed for the frequencies presented in Tables 2 and 3. Statistical analysis was performed using the Pearson chi-square test, and differences were considered statistically significant at  $p < 0.1$ . Correlation analysis for some of the tested results was performed using the ggpvr library of the R package. The method chosen was the non-parametric Spearman correlation. The alpha biodiversity of community samples describing individual taxa within a defined area or a collective list of species present in a given area was assessed. Both ACE and Chao1 are richness estimators, whereas Shannon and Simpson are diversity indices. The Fisher index was theoretically adjusted for sampling bias.

**Table 2.** Frequency (%) of fungal taxa on Norway spruce stumps within plots on old forest sites (1–4) and post-agricultural sites (5–8) (trophic categories: E—ectomycorrhizal fungi, M—mycoparasites, P—parasites, S—saprotrophs).

Stand Location Site No.	Forest Soil/Old Forest					Arable Soil/Post-Agricultural Soil					Number of Stands with Taxa Present
	1	2	3	4	Mean 1–4	5	6	7	8	Mean 5–8	
<b>Number of Stumps</b>	<b>39</b>	<b>43</b>	<b>35</b>	<b>34</b>	<b>38</b>	<b>64</b>	<b>51</b>	<b>55</b>	<b>18</b>	<b>47</b>	
<i>ASCOMYCOTA</i>											
<i>Helotiales</i>											
<i>Gelatinodiscaceae</i>											
<i>Ascocoryne cylichnium</i> (Tul.) Korf S	7.7	7.0	0	0	3.7	3.1	13.7	3.6	5.6	6.5	6
<i>Hypocreales</i>											
<i>Hypocreaceae</i>											
<i>Hypocrea citrina</i> (Pers.) Fr. S	0	0	0	0	0	0	0	1.8	0	0.5	1
<i>Hypocrea pulvinata</i> Fuckel M	0	2.3	0	0	0.6	0	0	0	0	0	1
<i>Pezizales</i>											
<i>Helvellaceae</i>											
<i>Helvella macropus</i> (Pers.) P. Karst. E	0	0	0	0	0	0	2.0	0	0	0.5	1
<i>Pyronemataceae</i>											
<i>Scutellinia scutellata</i> (L.) Lambotte S	0	0	0	0	0	0	0	0	5.6	1.4	1
<i>BASIDIOMYCOTA</i>											
<i>Agaricales</i>											
<i>Crepidotaceae</i>											
<i>Crepidotus malachus</i> Sacc. var. <i>trichifer</i> Hesler & A.H. Sm. S	0	0	0	0	0	0	2.0	0	0	0.5	1
<i>Entolomataceae</i>											
<i>Clitopilus hobsonii</i> (Berk.) P.D. Orton S	0	4.7	0	0	1.2	0	0	0	0	0	1

<i>Entoloma byssisedum</i> (Pers.) Donk S	0	0	0	0	0	0	2.0	0	0	0.5	1
<i>Hymenogastraceae</i>											
<i>Galerina marginata</i> (Batsch) Kühner S	5.1	0	5.7	0	2.7	1.6	3.9	1.8	0	1.3	5
<i>Galerina triscopa</i> (Fr.) Küh- ner S	0	2.3	0	8.6	2.7	0	0	1.8	0	0.5	3
<i>Galerina</i> sp. S	2.6	2.3	0	0	1.2	0	0	1.8	0	0.5	3
<i>Gymnopilus penetrans</i> (Fr.) Murrill S	5.1	7.0	2.9	8.8	6.0	1.6	0	0	16.7	4.6	6
<i>Gymnopilus picreus</i> (Pers.) P. Karst. S	0	0	0	5.9	1.5	0	2.0	0	5.6	1.9	3
<i>Incertae sedis</i>											
<i>Cystoderma carcharias</i> (Pers.) Fayod S	0	0	0	0	0	0	2.0	0	0	0.5	1
<i>Tricholomopsis rutilans</i> (Schaeff.) Singer S	0	0	0	0	0	0	2.0	1.8	0	1.0	2
<i>Lycoperdaceae</i>											
<i>Apioperdon pyriforme</i> (Schaeff.) Vizzini S	0	2.3	3.7	5.8	3.0	6.3	2.0	1.8	22.2	8.0	7
<i>Macrocytidiaceae</i>											
<i>Macrocytidia cucumis</i> (Pers.) Joss. S	0	0	0	0	0	0	2.0	0	0	0.5	1
<i>Marasmiaceae</i>											
<i>Gymnopus androsaceus</i> (L.) Della Magg. & Trassin. S	0	0	0	0	0	1.6	0	0	0	0.4	1
<i>Mycenaceae</i>											
<i>Mycena galericulata</i> (Scop.) Gray S	0	0	0	0	0	1.6	2.0	1.8	0	1.4	3
<i>Mycena galopus</i> (Pers.) P. Kumm. S	2.6	0	0	2.9	1.4	3.1	2.0	1.8	0	1.7	5
<i>Mycena</i> sp. S	2.6	4.7	5.7	2.9	4.0	6.3	0	3.6	0	2.5	6
<i>Pleurotaceae</i>											
<i>Pleurotus pulmonarius</i> (Fr.) Quél. S	0	0	0	0	0	0	2.0	0	0	0.5	1
<i>Pluteaceae</i>											
<i>Pluteus atromarginatus</i> (Konrad) Kühner S	0	0	2.9	2.9	1.5	0	0	0	0	0	2
<i>Pluteus pouzarianus</i> Singer S	2.6	0	8.6	0	2.8	0	0	0	0	0	2
<i>Physalacriaceae</i>											
<i>Armillaria borealis</i> * Marxmüller & Korhonen P	0	48.8	0	0	12.2	0	0	0	0	0	1
<i>Armillaria cepistipes</i> * Velen. P	56.4	0	34.3	5.9	24.2	39.1	62.7	10.9	5.6	29.6	7
<i>Schizophyllaceae</i>											
<i>Schizophyllum commune</i> Fr. S	0	0	0	2.9	0.7	0	0	0	0	0	1
<i>Strophariaceae</i>											

<i>Hypholoma capnoides</i> (Fr.) P. Kumm. S	7.7	9.3	8.6	0	6.4	12.5	2.0	3.6	0	4.5	6
<i>Hypholoma fasciculare</i> (Huds.) P. Kumm. S	10.3	0	0	4.7	3.8	6.3	0	7.3	11.1	6.2	5
<i>Hypholoma lateritium</i> (Schaeff.) P. Kumm S	0	2.3	0	0	0.6	0	0	0	0	0	1
<i>Kuehneromyces mutabilis</i> (Schaeff.) Singer & A.H. Sm. S	0	0	0	0	0	3.1	0	0	0	0.8	1
<i>Pholiota flammans</i> (Batsch) P. Kumm. S	0	0	0	0	0	1.6	3.9	0	0	1.4	2
<i>Atheliales</i>											
<i>Atheliaceae</i>											
<i>Amphinema byssoides</i> (Pers.) J. Erikss. S	0	0	0	2.9	0.7	0	0	0	0	0	1
<i>Auriculariales</i>											
<i>Auriculariaceae</i>											
<i>Exidia nigricans</i> (With.) P. Roberts S	0	0	0	0	0	0	0	0	5.6	1.4	1
<i>Uncertain position</i>											
<i>Pseudohydnum gelatinosum</i> (Scop.) P. Karst. S	0	2.3	2.9	0	1.3	0	0	0	0	0	2
<i>Boletales</i>											
<i>Coniophoraceae</i>											
<i>Coniophora arida</i> (Fr.) P. Karst. S	0	4.7	0	0	1.2	0	0	0	0	0	1
<i>Hygrophoropsidaceae</i>											
<i>Hygrophoropsis aurantiaca</i> (Wulfen) Maire S	0	0	0	5.9	1.5	0	0	1.8	5.6	1.9	3
<i>Paxillaceae</i>											
<i>Paxillus involutus</i> (Batsch) Fr. E	0	2.3	0	0	0.6	0	0	0	0	0	1
<i>Dacrymycetales</i>											
<i>Dacrymycetaceae</i>											
<i>Calocera viscosa</i> (Pers.) Fr. S	0	2.3	0	5.9	2.05	1.6	0	0	0	0.4	3
<i>Dacrymyces stillatus</i> Nees S	5.1	7.0	2.9	8.8	6.0	7.8	0	0	0	2.0	5
<i>Gloeophyllales</i>											
<i>Gloeophyllaceae</i>											
<i>Gloeophyllum odoratum</i> (Wulfen) Imazeki S	0	0	0	2.9	0.7	0	0	0	0	0	1
<i>Gomphales</i>											
<i>Gomphaceae</i>											
<i>Ramaria apiculata</i> (Fr.) Donk S	0	0	0	11.8	2.9	0	0	0	0	0	1
<i>Hymenochaetales</i>											
<i>Hymenochaetaceae</i>											
<i>Onnia tomentosa</i> (Fr.) P. Karst. P	0	0	0	2.9	0.7	0	0	0	0	0	1
<i>Hyphodontiaceae</i>											



<i>Hyphodontia arguta</i> (Fr.) J. Erikss. S	0	0	0	0	0	0	0	0	11.1	2.8	1
<i>Hyphodontia pallidula</i> (Bres.) J. Erikss. S	0	0	0	0	0	0	0	0	5.6	1.4	1
<i>Incertae sedis</i>											
<i>Trichaptum abietinum</i> (Pers. ex J.F. Gmel.) Ryvarden S	0	0	0	2.9	0.7	0	0	0	0	0	1
<i>Schizoporaceae</i>											
<i>Xylodon flaviporus</i> (Berk. & M.A. Curtis ex Cooke) Riebesehl & Langer S	0	0	0	0	0	1.6	0	1.8	0	0.9	2
<i>Xylodon nesporii</i> (Bres.) Hjortstam & Ryvarden S	0	0	0	0	0	0	0	0	5.6	1.4	1
<i>Polyporales</i>											
<i>Dacrybolaceae</i>											
<i>Postia ptychogaster</i> (F. Ludw.) Vesterh S	7.7	0	0	5.9	3.4	0	0	1.8	5.6	1.9	4
<i>Postia tephroleuca</i> (Fr.) Jülich S	0	0	0	0	0	1.6	0	0	0	0.4	1
<i>Fomitopsidaceae</i>											
<i>Fomitopsis pinicola</i> (Sw.) P. Karst. P	0	4.7	0	0	1.2	1.6	0	1.8	0	0.6	3
<i>Hyphodermataceae</i>											
<i>Hyphoderma roseocremeum</i> (Bres.) Donk S	2.6	0	0	0	0.7	0	0	0	0	0	1
<i>Incertae sedis</i>											
<i>Amaropostia stiptica</i> (Pers.) B.K. Cui, L.L. Shen & Y.C Dai P	0	2.3	2.9	0	1.3	0	0	0	5.6	1.4	3
<i>Incrustoporiaceae</i>											
<i>Skeletocutis amorpha</i> (Fr.) Kotl. & Pouzar S	0	0	0	2.9	0.7	0	0	0	0	0	1
<i>Meruliaceae</i>											
<i>Phlebia tremellosa</i> (Schrad.) Nakasone & Burds. S	0	0	0	0	0	0	0	1.8	0	0.5	1
<i>Physisporinus vitreus</i> (Pers.) P. Karst. S	0	0	2.9	0	0.7	0	0	0	0	0	1
<i>Rigidoporus sanguinolentus</i> (Alb. & Schwein.) Donk S	0	0	0	2.9	0.7	0	0	0	0	0	1
<i>Phanerochaetaceae</i>											
<i>Bjerkandera adusta</i> (Willd.) P. Karst. S	0	0	0	0	0	0	2.0	0	0	0.5	1
<i>Phlebiopsis gigantea</i> (Fr.) Jülich S	2.6	0	0	2.9	1.4	0	0	0	0	0	2
<i>Polyporaceae</i>											
<i>Cyanosporus caesius</i> (Schrad.) McGinty P	5.1	2.3	0	0	1.9	6.3	0	1.8	0	2.0	4
<i>Xenasmataceae</i>											

<i>Xenasmatella vaga</i> (Fr.) Stalpers S	0	0	2.9	5.9	2.2	0	0	1.8	16.7	4.6	4
					<i>Russulales</i>						
					<i>Stereaceae</i>						
<i>Heterobasidion parviporum</i> * Niemelä & Korhonen P	5.1	4.7	5.7	11.8	6.8	1.6	9.8	7.3	11.1	7.5	8
					<i>Bondarzewiaceae</i>						
<i>Stereum sanguinolentum</i> (Alb. & Schwein.) Fr. P	2.6	2.3	0	2.9	2.0	4.7	3.9	3.6	5.6	4.5	7
					<i>Thelephorales</i>						
					<i>Thelephoraceae</i>						
<i>Tomentella bryophila</i> (Pers.) M.J. Larsen E	0	0	0	0	0	0	0	0	5.6	1.4	1
<i>Tomentella radiosa</i> (P. Karst.) Rick E	0	0	0	0	0	0	0	0	11.1	2.8	1
					<i>Trechisporales</i>						
					<i>Hydnodontaceae</i>						
<i>Trechispora hymenocystis</i> (Berk. & Broome) K.H. Larss. S	0	0	0	0	0	0	2.0	5.5	0	1.9	2
<i>Trechispora nivea</i> (Pers.) K.H. Larss. S	2.6	0	0	0	0.7	0	0	0	5.6	1.4	2
<i>Trechispora mollusca</i> (Pers.) Liberta S	0	0	0	0	0	0	2.0	0	0	0.5	1
					<i>Tremellales</i>						
					<i>Tremellaceae</i>						
<i>Tremella encephala</i> Pers. M	0	0	0	0	0	0	0	0	5.6	1.4	1
Total: 69 taxa ( <i>Ascomycota</i> —5, <i>Basidiomycota</i> —64)											
Total: 69 taxa (S—55, P—8, E—4, M—2)											
Total: 395 records	forest soil—185					arable soil—210					
S—218 records	forest soil—105					arable soil—113					
P—170 records	forest soil—78					arable soil—92					
E—5 records	forest soil—1					arable soil—4					
M—2 records	forest soil—1					arable soil—1					

\* from basidiomata, mycelium, or rhizomorphs (PCR-confirmed).

**Table 3.** Frequency (%) of fungal taxa on Norway spruce trees within plots on old forest (1–4) and post-agricultural soils (5–8) (trophic categories: P—parasites and S—saprotrophs); \* W—in wood inside trunk (PCR-confirmed).

Stand Location	Forest Soil/Old Forest				Arable Soil/Post-Agricultural Soil				Number of Stands with Taxa Present
Site No.	1	2	3	4	5	6	7	8	
Number of Trees	144	118	82	51	109	117	129	71	
<b>ASCOMYCOTA</b>									
<i>Helotiales</i>									
<i>Hamatocanthoscyphaceae</i>									
<i>Xenopolyscytalum pinea</i> Crous S	0	0	0	0	0	0	0	1.4 * W	1
<i>Incertae sedis</i>									
<i>Scytalidium lignicola</i> Pesante P	0	0	0	0	0.9 *	0	0	0	1
<i>Hypocreales</i>									

			<i>Nectriaceae</i>							
<i>Mariannaea pinicola</i> L. Lombard & Crous S	0	0	0	0	0	0	0	1.4*	1	
								W		
			<b>BASIDIOMYCOTA</b>							
			<b>Agaricales</b>							
			<i>Physalacriaceae</i>							
<i>Armillaria cepistipes</i> Velen. P	0	0	0	0	0	0	0	0.9*	1	
								W		
			<i>Pleurotaceae</i>							
<i>Pleurotus dryinus</i> (Pers.) P. Kumm. P	0	0	0	0	0.9	0	0	1.4	2	
<i>Pleurotus ostreatus</i> (Jacq.) P. Kumm. P	0	0	0	0	0	0.9	0	0	1	
			<i>Strophariaceae</i>							
<i>Hypholoma capnoides</i> (Fr.) P. Kumm. S	0	0	0	0	0	0.9*	0	0	1	
<i>Hypholoma fasciculare</i> (Huds.) P. Kumm. S	0	0	0	0	0	0.9	0	0	1	
<i>Pholiota squarrosa</i> (Vahl) P. Kumm. P	0	0.8	0	0	0	0	0	0	1	
			<b>Cantharellales</b>							
			<i>Hydnaceae</i>							
<i>Sistotrema brinkmannii</i> (Bres.) J. Erikss. S	0.7*	0	0	2.0*W	0	0	0	0	2	
			<b>Dacrymycetales</b>							
			<i>Dacrymycetaceae</i>							
<i>Dacrymyces stillatus</i> Nees S	0	0	0	0	0.9	0	0	0	1	
			<b>Hymenochaetales</b>							
			<i>Hymenochaetaceae</i>							
<i>Onnia tomentosa</i> (Fr.) P. Karst. P	0	0	0	5.9	0	0	0.8	0	2	
			<i>Incertae sedis</i>							
<i>Trichaptum abietinum</i> (Pers. ex J.F. Gmel.) Ryvarden S	0	0.8	0	0	0	0	0	0	1	
			<i>Oxyporaceae</i>							
<i>Oxyporus ravidus</i> (Fr.) Bondartsev & Singer P	0	0	0	0	0	0.9	0	0	1	
			<b>Incertae sedis</b>							
			<i>Incertae sedis</i>							
<i>Resinicium bicolor</i> (Alb. & Schw. ex Fr.) Parm. P	0	0	0	0	0	0.9*	0	0	1	
			<b>Polyporales</b>							
			<i>Incertae sedis</i>							
<i>Amaropostia stiptica</i> (Pers.) B.K. Cui, L.L. Shen & Y.C Dai P	0	0	1.2	0	0.9	0	0	0	2	
			<b>Russulales</b>							
			<i>Bondarzewiaceae</i>							
<i>Heterobasidion parviporum</i> * Niemelä & Korhonen P	0	0	0	2.0*	0	0.9*	0.8*	0	3	
				W						
			<b>MUCOROMYCOTA</b>							
			<b>Mucorales</b>							
			<i>Mucoraceae</i>							

<i>Mucor hiemalis</i> Wehmer S	0	0	0	0	0	0	0	0	1.4 *	1
									W	
<b>Total: 18 taxa</b> ( <i>Ascomycota</i> —3, <i>Basidiomycota</i> —14, <i>Mucoromycota</i> —1)										
<b>Total: 18 taxa</b> (S—8, P—10)										
<b>Total: 22 records</b>	forest soil—8				arable soil—14					
S—7 records	forest soil—3				arable soil—4					
P—15 records	forest soil—5				arable soil—10					

\* from basidiomata, mycelium, or rhizomorphs (PCR-confirmed).

### 3. Results

Computed tomographic analysis of the stems showed the presence of internal rot in 13.3–73.3% of the trees studied (Table 1). On average, the percentage of trees with internal damage was 43.3% on forest sites and 39.2% on former agricultural sites. For both soil types, the differences in the proportions of trees in which *H. parviporum* was detected by PICUS were not significant (pchi-sq. > 0.05).

The average percentage of stumps with decay symptoms (hollow) and/or basidiomata of both pathogens was 11.3 and 16.3%, respectively (Table 1). In both categories, the proportion of stumps with rot increased with stand age. It is noteworthy that the crowns of all trees with internal wood decay found by tomography showed no signs of thinning or discoloration of the needles.

In the eight studied plots representing the economic spruce stands of Borecka Forest, a total of 79 fungal taxa were found. In total, 417 records (395 on stumps and 22 on trees), including from the inner parts of the felled trunks, were obtained (Tables 2 and 3). The occurrence of fungi inhabiting the wood of spruce growing on former agricultural sites (57 taxa) was higher than that of spruce growing on forest sites (45 taxa), with 224 versus 193 records.

The taxa found belonged to *Ascomycota* (8 species) and *Mucoromycota* (1), but mainly to *Basidiomycota* (70 taxa), with the representative orders *Agaricales* (30) and *Polyporales* (13) predominating. The sporocarps belonged to a total of 18 orders and 45 families at least. Among the identified taxa (59 saprotrophs, 14 parasites), four species (*Helvella macropus*, *Paxillus involutus*, *Tomentella bryophila*, *T. radiosa*) are classified as ectomycorrhizal fungi, and two species (*Hypocrea pulvinata*, *Tremella encephala*) are mycoparasites (Tables 2 and 3).

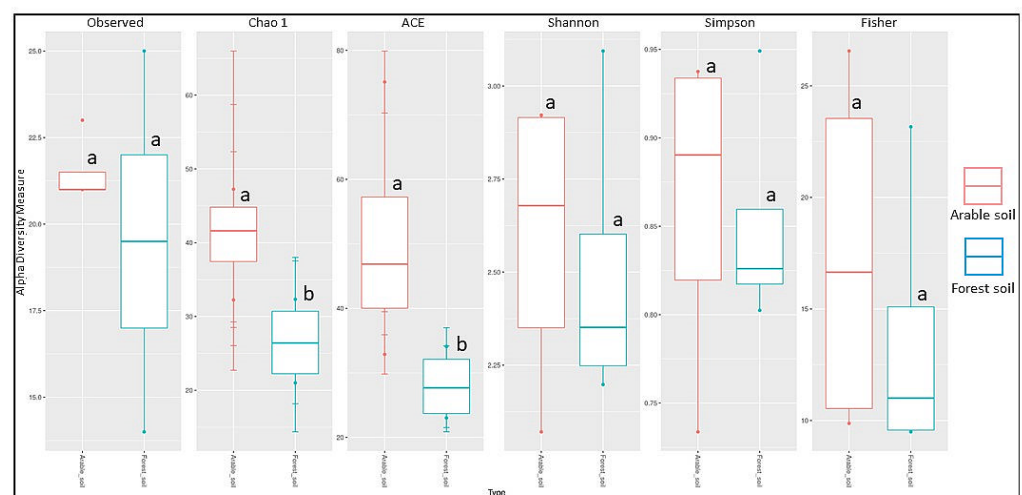
In the old forest sites, 45 species were identified, of which 21 were only found in these sites (e.g., *Amphinema byssoides*, *Armillaria borealis*, *Gloeophyllum odoratum*, *Phlebiopsis gigantea*, *Pholiota squarrosa*, *Pluteus pouzarianus*, *Pseudohydnum gelatinosum*, or *Sistotrema brinkmannii*), whereas 57 species were recorded in the post-agricultural sites, of which 34 taxa only occurred in these sites (e.g., *Bjerkandera adusta*, *Kuehneromyces mutabilis*, *Mycena galericulata*, *Pholiota flammans*, *Pleurotus dryinus*, *P. ostreatus*, *P. pulmonarius*, *Trichomolopsis rutilans*, *Xylodon flaviporus*). Overall, 24 species occurred on both site types (e.g., *Amaropostia stiptica*, *Armillaria cepistipes*, *Cyanosporus caesius*, *Heterobasidion parviporum*, *Hypoholoma capnoides*, *H. fasciculare*, *Onnia tomentosa*, *Postia ptychogaster*, *Stereum sanguinolentum*). Only three species were found on the wood of spruce trees growing on both soil types: *Amaropostia stiptica*, *Heterobasidion parviporum*, and *Onnia tomentosa*. For the post-agricultural soils, 15 species were recorded, whereas in the forest soils, we found 6 species (Tables 2 and 3).

Significant differences in the Chao1 diversity index indicate (Table 4) that the origin of the soil—farm or forest soil—influences the alpha diversity of the fungal communities in the studied forests. The values of the Shannon and Simpson indices showed that the two communities were similar in terms of species number, with  $p = 0.88$ . The probability for the Chao1 index, which counts singletons and doubletons, was at the 0.05 limit, indicating a difference between the groups in the low-identified species (where we had one or two of the stumps). Regarding the ACE indicator, which is a non-parametric method

for estimating the total number of species based on the coverage (size) of the sample, a probability at the 0.05 limit means that between groups of samples, the distribution of coverage (size) varies (Figure 5). Fungi belonging to four trophic groups were found on the studied tree stumps: saprotrophs (55 taxa), parasites (8), ectomycorrhizal (4), and mycoparasites (2) based on 395 records (185 in forest soil, 210 in arable soil). On the examined trees, 8 saprotrophs and 10 parasites were found based on 22 records (8 in forest soil, 14 in arable soil) (Tables 2 and 3).

**Table 4.** Values of some ecological indices describing the fungal communities in the forest (s1–s4) and arable (s5–s8) soils.

Soil Type	Observed	Chao1	se.chao1	ACE	se.ACE	Shannon	Simpson	Fisher
s1	18	22.6667	4.4832	23.913	2.4033	2.2652	0.8024	9.5999
s2	21	30.1667	7.3707	31.4436	2.7365	2.4383	0.8298	12.4085
s3	14	21	6.6296	23.0175	2.1613	2.1979	0.8222	9.4903
s4	25	32.3333	5.6718	34.0909	2.9108	3.094	0.9491	23.1609
s5	21	32.25	9.5328	32.8689	3.0501	2.444	0.8482	9.8691
s6	21	47.25	18.7364	75.0972	4.8122	2.0708	0.7337	10.7594
s7	23	44	14.7299	51.2985	3.8028	2.9218	0.9325	22.5337
s8	21	39.2	13.1381	42.4181	2.939	2.9131	0.9375	26.5619



**Figure 5.** Alpha diversity in arable soil (red) and forest soil (blue) taxa groups based on the number of observed species, Chao1, ACE, Shannon, Simpson, and Fisher index; a, b indicate significant differences between groups.

In the saprotroph group, three fungal species of the genus *Hypholoma* were found, among others: *H. capnoides* and *H. fasciculare* occurred in six plots and *H. lateritia* in one plot (Tables 2 and 3). The shares of stumps with basidiomata of *H. capnoides* were similar for post-agricultural soil (11 stumps) and forest soil (10 stumps). *Hypholoma fasciculare* basidiomata were found more frequently on stumps in post-agricultural soil (10 stumps) compared to stumps in forest soil (6 stumps) (Table 2).

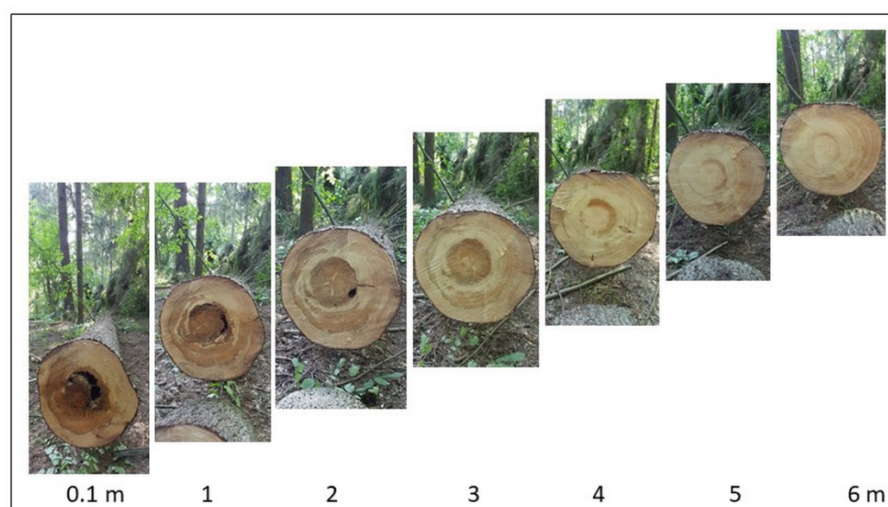
The presence of root pathogens (*H. parviporum* and two species of *Armillaria*) in stumps and trees on all plots is striking, although *Armillaria* spp. were detected more frequently (122 stumps and trees versus 25 stumps and trees). Although the presence of *A. borealis* was confirmed via mycelium under bark and basidiomata with PCR (NCBI sequences OL634955 and –56), only in spruce stumps in one plot (No. 2) on forest soil, *A. cepistipes* was detected in most plots (Tables 2 and 3), both in forest (NCBI sequences OL652577, –80) and agricultural soils (NCBI sequences OL652578, –79, –81, –82, –83).

There was no significant correlation between the presence of a particular taxa in arable soil or forest soil, while the highest correlation was found for *Armillaria* spp. ( $R = 0.8$ ,  $p = 0.33$ ), all fungi  $R = -0.77$ ,  $p = 0.23$ ) and *H. parviporum* + *Armillaria* spp. stumps ( $R = -0.63$ ,  $p = 0.37$ ). Weak correlations were detected for Fungi on stumps vs. All stumps ( $R = 0.58$ ,  $p = 0.13$ ), and PICUS+ vs. All stumps ( $R = -0.49$ ,  $p = 0.21$ ). The analyzes performed also showed a strong negative correlation ( $p < 0.1$ ) between trees with rot confirmed tomographically (PICUS+) (n) and the number of trees in the study plot ( $R = -0.96$ ,  $p = 0.00011$ ), and a positive correlation between trees with rot (PICUS+) (n) and stand age (Table 5).

**Table 5.** Correlation coefficient and Spearman  $p$ -values for the compared variables (counts).

Counts		All stumps	PICUS+trees	<i>H. parviporum</i> + <i>Armillaria</i> spp. stumps
Fungi on stumps	-	$R = 0.58$ , $p = 0.13$	$R = -0.09$ , $p = 0.83$	$R = -0.096$ , $p = 0.82$
Counts	Fungi on stumps	All stumps	PICUS+trees	<i>H. parviporum</i> + <i>Armillaria</i> spp. stumps
Forest soil vs. Arable soil	$R = -0.77$ , $p = 0.23$	$R = 0.2$ , $p = 0.92$	$R = 0.2$ , $p = 0.92$	$R = -0.63$ , $p = 0.37$
Counts	<i>Armillaria</i> spp.		<i>Hypholoma</i> spp.	<i>H. parviporum</i>
Forest soil vs. Arable soil	$R = 0.8$ , $p = 0.33$		$R = 0.4$ , $p = 0.75$	$R = -0.26$ , $p = 0.74$
Counts	No. of trees on survey plot		Trees with decay by PICUS (n)	
Forest soil vs. Arable soil	$R = 0.2$ , $p = 0.92$		$R = 0.2$ , $p = 0.92$	
Counts	No. of trees on survey plot		Stand age	
Trees with decay by PICUS (n)	$R = -0.96$ , $p = 0.00011$		$R = 0.63$ , $p = 0.097$	

Basidiomata were found more frequently on stumps than in the root necks of standing trees. In wood samples taken from different sections of two felled trees that showed symptoms of wood decay on tomographic examination, genetic analysis confirmed the presence of the DNA of the pathogens with 100% identity: *H. parviporum* (NCBI sequence OL691107-OL691110), *A. cepistipes* (see above), both at 0.1 and 0.6 m, as well as *Sistotrema brinkmannii* (NCBI sequence OL691111) and *Resinicium bicolor* (NCBI sequence OL691112). On the other hand, the presence of *H. parviporum* was not confirmed at a height of 6.0 m, despite visible symptoms of wood decay (Figure 6). The presence of both pathogens, whose sequences were submitted to GenBank, was confirmed from both perimeters of the surface.



**Figure 6.** Symptoms of heartwood rot caused by *H. parviporum* on successive 1-m sections of a spruce trunk. Photo by M. Damszel.

The six species collected were red-listed fungi. Two of them (*Onnia tomentosa*, *Pleurotus pulmonarius*) are listed in the threatened category and described as vulnerable (V), whereas four species (*Entoloma byssisedum*, *Galerina triscopa*, *Physisporinus vitreus*, and *Postia ptychogaster*) are rare (R). Of the identified species, 20 (*Amphinema byssoides*, *Armillaria borealis*, *A. cepistipes*, *Clitopilus hobsonii*, *Entoloma byssisedum*, *Galerina triscopa*, *Hyphoderma roseocremeum*, *Hyphodontia arguta*, *H. pallidula*, *Onnia tomentosa*, *Physisporinus vitreus*, *Pleurotus pulmonarius*, *Pluteus pouzarianus*, *Postia ptychogaster*, *P. tephroleuca*, *Ramaria apiculata*, *Sistotrema brinkmannii*, *Trechispora hymenocystis*, *T. nivea*, and *T. mollusca*) are included in the “Register of Protected and Endangered Fungal Species in Poland (GREJ)”.

#### 4. Discussion

In this study, the presence of fungi was identified by classical methods. Root pathogens were detected using genetic methods, both on 821 trees, including 240 PICUS-trees, and on 339 stumps in both site types (four stands on old forest soil and four stands on post-agricultural soil). Based on our results, the wood of both standing spruce with living crowns and stumps is commonly colonized by fungi belonging to different trophic groups, with different interactions among them [59–61]. The difference in the occurrence of different taxa (values of Chao1 and ACE) may be caused by differences in the structure of spruce wood due to different soil fertility levels (arable was made fertile in the past) [62,63].

A similar number of wood-inhabiting species (58), compared to our study (57), in spruce stands on former agricultural land was found in a 3-year study in Slovakia in spruce stands aged 21–51 years [64]. It is worth noting that in the cited studies, typical spruce pathogens, such as *Armillaria* spp. and *Heterobasidion* spp., only sporadically occurred, in contrast to our results. We detected numerous species of pathogens (*Heterobasidion parviporum* and *Armillaria* spp.) as well as saprotrophs and symbiotrophs. Kubart et al. (2016) [65] point out that the presence of stump fungi is common in spruce stands in different regions of Sweden, whereas saprotrophic fungi, especially *Resinicium bicolor*, *Fomitopsis pinicola*, and *Hyphodontia* spp., which were also found in our studies, are present in large numbers.

It is interesting to note that the occurrence of fungi on spruce stumps and trees growing on an old arable soil was more numerous and diverse than on forest soils. This is probably due to the greater fertility of arable soils, which favors the formation of a wider annual increment [66,67], as well as to different fungal communities present in the environment of both types of stands in the past and today [68,69].

The analysis showed the strong negative correlation between the number of trees with tomographically confirmed decay and all stumps on the plots and positive correlation with stand age, which can be attributed to the systematic removal of dead trees by the forest administration and thus the increasing number of stumps. The weak correlation between all stumps and the number of inhabiting taxa is understandable. It is surprising that communities frequency within a dense forest complex, i.e., a Borecka forest, differ considerably depending on the type of soil (forest or arable) on which the stands grow. For similar trends in colonization of stumps and logs in a habitat, see Kubartova et al. (2012) [70].

Among the identified fungi, several taxa are effective competitors of food root pathogens (including *Hypholoma*, *Pleurotus*, and *Phlebiopsis*) and have therefore been studied and used in the biological protection against these pathogens [71–75]. The relatively high proportion of *Hypholoma* species suggests that fungi of this genus are widespread and important organisms that can limit the population of root pathogens in spruce stands [76,77].

Interestingly, several fungi described by Wojewoda and Ławrynowicz (2006) [51] as threatened/vulnerable (*Onnia tomentosa*, *Pleurotus pulmonarius*) or rare (*Entoloma byssisedum*, *Galerina triscopa*, *Physisporinus vitreus*, *Postia ptychogaster*) were identified in this study. In Poland, *O. tomentosa* is known from about a dozen sites, mainly from large, well-

preserved forest complexes in the mountains (in the south of the country) and in the north [78,79]; this species has not been reported from the Borecka Forest. According to Ryvardeen et al. (2017) [49], terrestrial basidioma often develop in large numbers from roots in old spruce stands. In our study, basidiocarps were found in both old (111 years old, forest plot 4) and a much younger, 74-year-old tree stand (arable plot 7). *P. pulmonarius* is known from numerous sites in Poland [79] and does not seem to be a threat to any species. It grows on various deciduous trees and in North America also on conifers, e.g., on *Abies* [80,81]. In Poland, *P. pulmonarius* has rarely been reported on conifers, e.g., *Picea abies* [82,83], and recently, it has been found on the trunk of a fallen *Pinus sylvestris* in a wind-damage area in Kampinos National Park [84]. The occurrence of numerous rare fungal species in spruce stands, both in managed and old forests, has been reported previously [85–89].

Gori et al. (2013) [90] found that in the Alps, spruce infection and wood rot can last for up to 80 years, with variable growth decline depending on climatic altitudes and the effects of drought [91]. The trees tested showed extensive heartwood decay, suggesting that infection began in the younger age classes. In the Borecka Forest, the proportion of *H. parviporum*-positive trees was 13.3–70.3%, although the trees were older than 50 years. The large number of undergrowth trees in the studied plots indicates a high density of root systems and an easy penetration of the mycelium of both root pathogens (*H. parviporum* and *Armillaria* spp.) into the trees due to numerous secondary infections through the roots [37,92–94]. In Norway, significant threats are caused by both *Heterobasidion* fungi, with a high proportion of *H. parviporum*, 98.5% [95]. The authors found that 68.2% of the trees were infected in 44-year-old regenerated spruce stands.

The *Armillaria* species found here (*A. cepistipes* and *A. borealis*) are mainly described as weak pathogens of deciduous trees and as opportunistic pathogens or saprotrophs of conifers [96–99]. In the current study, *A. cepistipes* was identified by genetic analyses of DNA from underneath bark, rhizomorphs, and basidiocarps collected in all stands studied, but surprisingly, more frequently in stands established on post-agricultural soils than on forest soils, which is described by other authors [100–102].

In a previous study, both *H. parviporum* and *A. cepistipes* have also been re-isolated from within the wood after felling standing trees whose crowns showed no symptoms of disease [103]. This confirms the thesis that without computed tomographic assessment of the interior of the wood, trees infected with the pathogen can grow unproductively for decades as commodities in managed spruce stands [19,37,104,105]. Another question is their ecological role in the ecosystem, where the pathogen and the resulting decomposition of wood during forest succession can provide suitable opportunities for the development of other organisms such as other fungi, birds, bats, insects, and squirrels [106–110].

Rigerte et al. (2019) [34] found 11 taxa described only as fungal root endophytes in spruce, none of which were identified in the present study. Numerous saprotrophs and symbiotrophs found on stumps and trees indicate that trees formerly infested by root pathogens are still attractive as food sources and are not discriminated against by the enzymes and metabolites of the pathogens [111].

## 5. General Conclusions

Our results show that trees older than 50 years, regardless of the type of soil on which the spruce stands grow (forest, post-agricultural), are subjected to advanced internal wood rot. This means that the infection of the roots took place many years earlier and that the development of the pathogen, detected by tomography inside the trunk, takes at least a dozen years. Consequently, in some valuable spruce stands, the degree of infestation of spruce with root pathogens should be determined by computed tomography at the age of 30–40 years.

Trees or stem sections showing advanced heartwood decay could be termed “dead-wood”, and some of them should be left in the stand from an ecological point of view to contribute to an increased biodiversity.



Because of the significant proportion of fungi of the genus *Armillaria* in the studied stand, which is generally underestimated in risk assessments, monitoring methods for assessing the presence of these pathogens in spruce stands need to be revised, including the severity of rhizomorph occurrence in the soil.

**Author Contributions:** A.S., M.D., K.S. and Z.S. substantially contributed to the conceptualization, resources, writing of the original draft, review and editing of the text; W.K., A.S. and M.D. performed the field experiments; K.S. and A.S. analyzed the data. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was partially supported by the Warmia and Mazury University in Olsztyn, Poland (Project No. 30.610.019-110).

**Data Availability Statement:** Sequences OL634955-56; OL652577-83; OL691107-OL691112 are available at <http://www.ncbi.nlm.nih.gov> (accessed on 12 January 2022).

**Acknowledgments:** The authors thank Agata Młodzińska, Bioidea Poland, for her constructive bioinformatic additions, the Czerwony Bór and Borki Forest Districts administration for help in the field works and the anonymous reviewers for their valuable comments and suggestions.

**Conflicts of Interest:** The authors declare no conflict of interest.

## References

- Woodward, S.; Stenlid, J.; Karjalainen, R.; Hüttermann, A. *Heterobasidion Annosum. Biology, Ecology, Impact and Control*; CAB International: Wallingford, UK, 1998.
- Asiegbu, F.O.; Adomas, A.; Stenlid, J. Conifer root and butt rot caused by *Heterobasidion annosum* (Fr.) Bref. *s.l. Mol. Plant Pathol.* **2005**, *6*, 395–409, <https://doi.org/10.1111/J.1364-3703.2005.00295.x>.
- Garbelotto, M.; Gonthier, P. Biology, epidemiology, and control of *Heterobasidion* species worldwide. *Annu. Rev. Phytopathol.* **2013**, *51*, 39–59, <https://doi.org/10.1146/annurev-phyto-082712-102225>.
- Żółciak, A.; Bohacz, J. Ligninolytic activity of *Heterobasidion parviporum* isolates in cultivation on Norway spruce wood. *Sylvan* **2016**, *160*, 1027–1035, <https://doi.org/10.26202/sylvan.2016032>.
- Burdsall, H.H., Jr.; Volk, T.J. *Armillaria solidipes*, an older name for the fungus called *Armillaria ostoyae*. *North. Am. Fungi* **2008**, *3*, 261–267, <https://doi.org/10.2509/naf2008.003.00717>.
- Oliva, J.; Bernat, M.; Stenlid, J. Heartwood stump colonisation by *Heterobasidion parviporum* and *H. annosum* s.s. in Norway spruce (*Picea abies*) stands. *For. Ecol. Manag.* **2013**, *295*, 1–10, <https://doi.org/10.1016/j.foreco.2013.01.005>.
- Sierota, Z.; Grodzki, W.; Szczepkowski, A. Abiotic and Biotic Disturbances Affecting Forest Health in Poland over the Past 30 Years: Impacts of Climate and Forest Management Forests. *Forests* **2019**, *10*, 75, <https://doi.org/10.3390/f10010075>.
- Boddy, L. Fungal community ecology and wood decomposition processes in angiosperms: From standing tree to complete decay of coarse woody debris. *Ecol. Bull.* **2001**, *49*, 43–56, <https://www.jstor.org/stable/20113263>.
- Chapin III, F.S.; Matson, P.A.; Mooney, H.A. *Principles of Terrestrial Ecosystem Ecology*; Springer-Verlag: New York, NY, USA, 2002.
- Hammel, K.E.; Kapich, A.N.; Jensen, K.A., Jr.; Ryan, Z.C. Reactive oxygen species as agents of wood decay by fungi. *Enzym. Microb. Technol.* **2002**, *30*, 445–453, [https://doi.org/10.1016/S0141-0229\(02\)00011-X](https://doi.org/10.1016/S0141-0229(02)00011-X).
- Hietala, A.M.; Dörsch, P.; Kvaalen, H.; Solheim, H. Carbon dioxide and methane formation in Norway spruce stems infected by white-rot fungi. *Forests* **2015**, *6*, 3304–3325, <https://doi.org/10.3390/f6093304>.
- Sierota, Z.; Żółciak, A.; Małecka, M.; Sikora, K.; Damszel, M. An approach to calculate CO<sub>2</sub> release through Norway spruce wood decay by *Heterobasidion parviporum*. *Dendrobiology* **2018**, *79*, 91–96, <https://doi.org/10.12657/denbio.079.008>.
- Swift, M.J. The roles of fungi and animals in the immobilisation and release of nutrient elements from decomposing branchwood. In *Soil Organisms as Components of Ecosystems*; Lohm, U. Persson, T., Eds.; Swedish Natural Science Research Council: Stockholm, Sweden, 1977; Volume 25, pp. 193–202.
- Harmon, M.E.; Franklin, J.F.; Swanson, F.J.; Sollins, P.; Gregory, S.V.; Lattin, J.D.; Anderson, N.H.; Cline, S.P.; Aumen, N.G.; Sedell, J.R.; et al. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **1986**, *15*, 133–302.
- Hendrickson, O. Abundance and activity of N<sub>2</sub>-fixing bacteria in decaying wood. *Can. J. For. Res.* **1991**, *21*, 1299–1304, <https://doi.org/10.1139/x91-183>.
- Zimmerman, J.K.; Pulliam, W.M.; Lodge, D.J.; Quinones-Orfila, V.; Fetcher, N.; Guzman-Grajales, S.; Parrotta, J.A.; Asbury, C.E.; Walker, L.R.; Waide, R.B. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. *Oikos* **1995**, *72*, 314–322, <https://doi.org/10.2307/3546116>.
- Metzler, B. Quantitative assessment of fungal colonization in Norway spruce after green pruning. *Eur. J. For. Path.* **1997**, *27*, 1–11, <https://doi.org/10.1111/j.1439-0329.1997.tb00848.x>.
- Eriksson, K-E.L.; Blanchette, R.A.; Ander, P. *Microbial and Enzymatic Degradation of Wood and Wood Components*; Springer-Verlag: Berlin/Heidelberg, Germany, 2012, <https://doi.org/10.1007/978-3-642-46687-8>.

19. Nagy, N.E.; Ballance, S.; Kvaalen, H.; Fossdal, C.G.; Solheim, H.; Hietala, A.M. Xylem defense wood of Norway spruce compromised by the pathogenic white-rot fungus *Heterobasidion parviporum* shows a prolonged period of selective decay. *Planta* **2012**, *236*, 1125–1133, <https://doi.org/10.1007/s00425-012-1664-4>.
20. Klavina, D.; Bruna, L.; Zaluma, A.; Burnevica, N.; Polmanis, K.; Gaitnieks, T.; Piri, T. Infection and Spread of Root Rot Caused by *Heterobasidion parviporum* in *Picea abies* Stands after Thinning: Case Studies on Former Pasture and Meadow Lands. *Environ. Sci. Proc.* **2021**, *3*, 2, <https://doi.org/10.3390/IECF2020-07950>.
21. Shortle, W.C.; Smith, K.T. Electrical properties and rate of decay in spruce and fir wood. *Phytopathology* **1987**, *77*, 811–814.
22. Mattheck, C.G.; Bethge, K.A. Detection of decay in trees with the Metriguard Stress Wave Timer. *J. Arbor.* **1993**, *19*, 374–378.
23. Sierota, Z.; Wrzosek, M.; Małecka, M.; Zólcziak, A. Decay indices for evaluating wood decomposition activity. *Biocontrol Sci. Technol.* **2016**, *26*, 163–173, <https://doi.org/10.1080/09583157.2015.1085000>.
24. Nicolotti, G.; Socco, L.V.; Martinis, R.; Godio, A.; Sambuelli, L. Application and comparison of three tomographic techniques for detection of decay in trees. *J. Arboric.* **2003**, *29*, 66–78.
25. Chomicz, E. Bezinwazyjne metody wykrywania defektów wewnątrz pni drzew stojących (Tomograf PiCUS Sonic and PiCUS Treetronic). *Leś. Pr. Bad.* **2007**, *3*, 117–122.
26. Szczepkowski, A.; Kowalczyk, W. Nowe stanowisko *Perenniporia fraxinea* (Polyporaceae, Basidiomycota) w Polsce i tomograficzna analiza drewna porażonego drzewa. *Przegląd Przym.* **2018**, *29*, 116–121.
27. Nilsson, K.; Bjurman, J. Chitin as an indicator of the biomass of two wood-decay fungi in relation to temperature, incubation time, and media composition. *Can. J. Microbiol.* **1998**, *44*, 575–581, <https://doi.org/10.1139/w98-039>.
28. Lindahl, B.D.; Finlay, R.D. Activities of chitinolytic enzymes during primary and secondary colonization of wood by basidiomycetous fungi. *New Phytol.* **2006**, *169*, 389–397, <https://doi.org/10.1111/j.1469-8137.2005.01581.x>.
29. Piri, T.; Korhonen, K. Spatial distribution and persistence of *Heterobasidion parviporum* genets on a Norway spruce site. *For. Pathol.* **2007**, *37*, 1–8, <https://doi.org/10.1111/j.1439-0329.2007.00482.x>.
30. Piri, T.; Hamberg, L. Persistence and infectivity of *Heterobasidion parviporum* in Norway spruce root residuals following stump harvesting. *For. Ecol. Manag.* **2015**, *353*, 49–58, <https://doi.org/10.1016/j.foreco.2015.05.012>.
31. Oliva, J.; Rommel, S.; Fossdal, C.G.; Hietala, A.M.; Nemesio-Gorrioz, M.; Solheim, H.; Elfstrand, M. Transcriptional responses of Norway spruce (*Picea abies*) inner sapwood against *Heterobasidion parviporum*. *Tree Physiol.* **2015**, *35*, 1007–1015, <https://doi.org/10.1093/treephys/tpv063>.
32. Zeng, Z.; Sun, H.; Vainio, E.J.; Raffaello, T.; Kovalchuk, A.; Morin, E.; Duplessis, S.; Asiegbu, F.O. Intraspecific comparative genomics of isolates of the Norway spruce pathogen (*Heterobasidion parviporum*) and identification of its potential virulence factors. *BMC Genom.* **2018**, *19*, 220, <https://doi.org/10.1186/s12864-018-4610-4>.
33. Terhonen, E.; Sipari, N.; Asiegbu, F.O. Inhibition of phytopathogens by fungal root endophytes of Norway spruce. *Biol. Control* **2016**, *99*, 53–63, <https://doi.org/10.1016/j.biocontrol.2016.04.006>.
34. Rigerte, L.; Blumenstein, K.; Terhonen, E. New R-Based Methodology to Optimize the Identification of Root Endophytes against *Heterobasidion parviporum*. *Microorganisms* **2019**, *7*, 102, <https://doi.org/10.3390/microorganisms7040102>.
35. Awan, H.U.M.; Asiegbu, F.O. Interspecific interactions within fungal communities associated with wood decay and forest trees. In *Forest Microbiology: Tree Microbiome: Phyllosphere, Endosphere and Rhizosphere*; Asiegbu, F.O., Kovalchuk, A. Eds.; Academic Press: Cambridge, MA, US, 2021; Volume 1, pp. 75–108, <https://doi.org/10.1016/B978-0-12-822542-4.00020-6>.
36. Gonthier, P.; Garbelotto, M.; Nicolotti, G. Swiss stone pine trees and spruce stumps represent an important habitat for *Heterobasidion* spp. in subalpine forests. *For. Pathol.* **2003**, *33*, 191–203, <https://doi.org/10.1046/j.1439-0329.2003.00323.x>.
37. Piri, T.; Valkonen, S. Incidence and spread of *Heterobasidion* root rot in uneven-aged Norway spruce stands. *Can. J. For. Res.* **2013**, *43*, 872–877, <https://doi.org/10.1139/cjfr-2013-0052>.
38. Honkaniemi, J.; Ojansuu, R.; Piri, T.; Kasanen, R.A.O.; Lehtonen, M.; Salminen, H.; Kalliokoski, T.; Mäkinen, H. Hmodel, a *Heterobasidion annosum* model for even-aged Norway spruce stands. *Can. J. For. Res.* **2014**, *44*, 796–809, <https://doi.org/10.1139/cjfr-2014-0011>.
39. Solon, J.; Borzyszkowski, J.; Bidlasik, M.; Richling, A.; Badora, K.; Balon, J.; Brzezińska-Wójcik, T.; Dobrowolski, R.; Grzegorzczak, I.; Jodłowski, M.; et al. Physico-geographical mesoregions of Poland: Verification and adjustment of boundaries on the basis of contemporary spatial data. *Geogr. Pol.* **2018**, *91*, 143–170, <https://doi.org/10.7163/GPol.0115>.
40. Szmidla, H. Warunki pogodowe w 2020 r. In *Krótkoterminowa Prognoza Występowania Ważniejszych Szkodników i chorób Infekcyjnych Drzew Leśnych w Polsce w 2021 roku*; Jabłoński, T., Ed.; Instytut Badawczy Leśnictwa: Sękocin Stary, Poland, 2021; pp. 13–18.
41. Bank danych o lasach. Available online: <https://www.bdl.lasy.gov.pl/> (accessed on 11 November 2021).
42. Gilbert, E.A.; Smiley, E.T. Picus Sonic Tomography for the quantification of decay in white oak (*Quercus alba*) and hickory (*Carya* spp.). *J. Arboric.* **2004**, *30*, 277–281.
43. Deflorio, G.; Fink, S.; Schwarze, F.W.M.R. Detection of incipient decay in tree stems with sonic tomography after wounding and fungal inoculation. *Wood Sci. Technol.* **2008**, *42*, 117–132, <https://doi.org/10.1007/s00226-007-0159-0>.
44. Clemençon, H. *Methods for Working with Macrofungi. Laboratory Cultivation and Preparation of Larger Fungi for Light Microscopy*. IHW-Verlag: Eching, Germany, 2009.
45. Breitenbach, J.; Kränzlin, F. *Fungi of Switzerland, Ascomycetes*; Verlag Mykologia: Luzern, Switzerland, 1984; Volume 1.
46. Bernicchia, A. *Polyporaceae s.l. Fungi Europaei 10*; Edizioni Candusso: Alassio, Italy, 2005.
47. Bernicchia, A.; Gorjón, S.P. *Corticaceae s.l. Fungi Europaei 12*; Edizioni Candusso: Alassio, Italy, 2010.

48. Knudsen, H.; Vesterholt, J. *Funga Nordica. Agaricoid, Boletoid, Clavarioid, Cyphelloid and Gastroid Genera*, 2nd ed.; Nordsvamp: Copenhagen, Denmark, 2012.
49. Ryvarde, L.; Melo, I. *Poroid Fungi of Europe*, 2nd ed.; Fungiflora AS: Oslo, Norway, 2017.
50. Index Fungorum. Available online: <http://www.indexfungorum.org/authorsoffungalnames.htm> (accessed on 11 November 2021).
51. Wojewoda, W.; Ławrynowicz, M. Red list of the macrofungi in Poland. In *Red List of Plants and Fungi in Poland*; Mirek, Z., Zarzycki, K., Wojewoda, W., Szela, Z., Eds.; Polish Academy of Sciences: Kraków, Poland, 2006; pp. 53–70.
52. Kujawa, A.; Gierczyk, B.; Ślusarczyk, T. GREJ - Rejestr gatunków grzybów chronionych i zagrożonych. [Register of protected and endangered fungi species in Poland]. In *Atlas grzybów Polski [Fungi of Poland]*; Snowarski, M. Ed. Available online: <http://www.grzyby.pl/rejestr-grzybow-chronionych-i-zagrozonych.htm> (accessed on 11 November 2021).
53. Kubiak, K.; Damszel, M.; Sikora, K.; Przemieniecki, S.; Małeczka, M.; Sierota, Z. Colonization of fungi and bacteria in stumps and roots of Scots pine after thinning and treatment with Rotstop. *J. Phytopath.* **2016**, *165*, 143–156, <https://doi.org/10.1111/jph.12534>.
54. Gardes, M.; Bruns, T.D. ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. *Mol. Ecol.* **1993**, *2*, 113–118, <https://doi.org/10.1111/j.1365-294x.1993.tb00005.x>.
55. White, T.J.; Burns, T.; Lee, S.; Taylor, J.W. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR Protocols: A Guide to Methods and Applications*, Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J., Eds.; Academic Press: New York, NY, USA, 1990; pp. 315–322.
56. Hantula, J.; Vainio, E. Specific primers for the differentiation of *Heterobasidion annosum* (s.str.) and *H. parviporum* infected stumps in northern Europe. *Silva Fenn.* **2003**, *37*, 181–187, <https://doi.org/10.14214/sf.500>.
57. Szewczyk, W.; Kwaśna, J.; Behnke-Borowczyk, J. Populations of *Armillaria* species in pine plantations in west-central Poland. *Dendrobiology* **2015**, *74*, 95–108, <https://doi.org/10.12657/denbio.074.010>.
58. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Available online: <https://www.r-project.org/> (accessed on 15 July 2019).
59. Boddy, L. Interspecific combative interactions between wood-decaying basidiomycetes. *FEMS Microbiol. Ecol.* **2000**, *31*, 185–194, <https://doi.org/10.1111/j.1574-6941.2000.tb00683.x>.
60. Jönsson, M.T.; Edman, M.; Jonsson, B.G. Colonization and extinction patterns of wood-decaying fungi in a boreal old-growth *Picea abies* forest. *J. Ecol.* **2008**, *96*, 1065–1075, <https://doi.org/10.1111/j.1365-2745.2008.01411.x>.
61. Boddy, L.; Hiscox, J. Fungal ecology, principles and mechanisms of colonisation and competition by saprotrophic fungi. *Microbiol. Spectr.* **2016**, *4*, 4–6, <https://doi.org/10.1128/microbiolspec.FUNK-0019-2016>.
62. Bujoczek, L.; Zięba, S.; Banaś, J. Effect of site conditions and site index for the dominant tree species on the amount of deadwood in managed forests. *Sylvan* **2016**, *160*, 320–327, <https://doi.org/10.26202/sylvan.2015094>.
63. Piętko, S.; Sotnik, A.; Damszel, M.; Sierota, Z. Coarse woody debris and wood-colonizing fungi—differences between a reserve stand and a managed forest in the Taborz region of Poland. *J. For. Res.* **2019**, *30*, 1081–1091, <https://doi.org/10.1007/s11676-018-0612-y>.
64. Mihál, I.; Luptáková, E.; Pavlík, M. Wood-inhabiting macromycetes communities in spruce stands on former agricultural land. *J. For. Sci.* **2021**, *67*, 51–65, <https://doi.org/10.17221/107/2020-JFS>.
65. Kubart, A.; Vasaitis, R.; Stenlid, J.; Dahlberg, A. Fungal communities in Norway spruce stumps along a latitudinal gradient in Sweden. *For. Ecol. Manag.* **2016**, *371*, 50–58, <https://doi.org/10.1016/j.foreco.2015.12.017>.
66. Tomczak, A.; Jelonek, T. Radial variation in the wood properties of Scots pine (*Pinus sylvestris* L.) grown on former agricultural soil. *For. Res. Pap.* **2013**, *74*, 171–177, <https://depot.ceon.pl/handle/123456789/5290>.
67. Cukor, J.; Zeidler, A.; Vacek, Z.; Vacek, S.; Šimůnek, V.; Gallo, J. Comparison of growth and wood quality of Norway spruce and European larch: Effect of previous land use. *Eur. J. For. Res.* **2020**, *139*, 459–472, <https://doi.org/10.1007/s10342-020-01259-7>.
68. Lauber, C.L.; Strickland, M.S.; Bradford, M.A.; Fierer, N. The influence of soil properties on the structure of bacterial and fungal communities across land-use types. *Soil Biol. Biochem.* **2008**, *40*, 2407–2415, <https://doi.org/10.1016/j.soilbio.2008.05.021>.
69. Balami, S.; Vašutová, M.; Košnar, J.; Karki, R.; Khadka, C.; Tripathi, G.; Cudlín, P. Soil fungal communities in abandoned agricultural land has not yet moved towards the seminatural forest. *For. Ecol. Manag.* **2012**, *491*, 119181, <https://doi.org/10.1016/j.foreco.2021.119181>.
70. Kubartova, A.; Ottosson, E.; Dahlberg, A.; Stenlid, J. Patterns of fungal communities among and within decaying logs, revealed by 454 sequencing. *Mol. Ecol.* **2012**, *21*, 4514–4532, <https://doi.org/10.1111/j.1365-294X.2012.05723.x>.
71. Pratt, J.E.; Niemi, M.; Sierota, Z.H. Comparison of three products based on *Phlebiopsis gigantea* for the control of *Heterobasidion annosum* in Europe. *Biocontr. Sci. Techn.* **2000**, *10*, 469–479, <https://doi.org/10.1080/09583150050115052>.
72. Chapman, B.; Xiao, G. Inoculation of stumps with *Hypholoma fasciculare* as a possible means to control *Armillaria* root disease. *Can. J. Bot.* **2000**, *78*, 129–134, <https://doi.org/10.1139/b99-170>.
73. Zhang, J.; Ju, Y.; Zhao, B. Advances in the research of *Pleurotus* poison to nematodes and the potential use for *Pleurotus* in controlling pine wilt disease. *Acta Agric. Univ. Jiangxi.* **2002**, *4*, 441–444, Available online: [https://en.cnki.com.cn/Article\\_en/CJFDTotal-JXND200204004.htm](https://en.cnki.com.cn/Article_en/CJFDTotal-JXND200204004.htm) (accessed on 11 November 2021).
74. Hoff, J.A.; Klopfenstein, N.B.; McDonald, G.I.; Tonn, J.R.; Kim, M.-S.; Zambino, P.J.; Hessburg, P.F.; Rogers, J.D.; Peever, T.L.; Carris, L.M. Fungal endophytes in woody roots of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). *For. Pathol.* **2004**, *34*, 255–271, <https://doi.org/10.1111/j.1439-0329.2004.00367.x>.

75. Thakur, M. Fungi as a Biological Tool for Sustainable Agriculture. In *Agriculturally Important Fungi for Sustainable Agriculture. Fungal Biology*; Yadav, A.N., Mishra, S., Kour, D., Yadav, N., Kumar, A., Eds.; Springer: Berlin/Heidelberg, Germany, 2020; pp. 255–273, [https://doi.org/10.1007/978-3-030-45971-0\\_11](https://doi.org/10.1007/978-3-030-45971-0_11).
76. Nicolotti, G.; Gonthier, P.; Varese, G.C. Effectiveness of some biocontrol and chemical treatments against *Heterobasidion annosum* on Norway spruce stumps. *Eur. J. For. Pathol.* **1999**, *29*, 339–346, <https://doi.org/10.1046/j.1439-0329.1999.00159.x>.
77. Warwell, M.V.; McDonald, G.I.; Hanna, J.W.; Kim, M.-S.; Lalande, B.M.; Stewart, J.E.; Hudak, A.T.; Klopfenstein, N.B. *Armillaria altimontana* Is Associated with Healthy Western White Pine (*Pinus monticola*): Potential in Situ Biological Control of the *Armillaria* Root Disease Pathogen, *A. solidipes*. *Forests* **2019**, *10*, 294, <https://doi.org/10.3390/f10040294>.
78. Wojewoda, W. *Checklist of Polish larger Basidiomycetes*; Polish Academy of Science: Kraków, Poland, 2003.
79. Kujawa, A. Macroscopic fungi of Poland in mycological literature. Available online: <http://www.grzyby.pl/grzyby-makroskopijne-Polski-w-literaturze-mikologicznej.htm> (accessed on 11 November 2021).
80. Hilber, O. *The genus Pleurorus (Fr.) Kummer (2)*; Private: Kelheim, Germany, 1997.
81. Stamets, P. *Growing Gourmet and Medicinal Mushrooms*, 3rd ed.; Ten Speed Press: Berkeley, CA, USA, 2000.
82. Gierczyk, B.; Kujawa, A.; Szczepkowski, A.; Ślusarczyk, T.; Pachlewski, T.; Chachuła, P.; Domian, G. Macrofungi of the Bieszczady Mountains. *Acta Mycol.* **2019**, *54*, 1124, <https://doi.org/10.5586/am.1124>.
83. Chachuła, P.; Dorda, A.; Fiedor, M.; Rutkowski, R. *Grzyby Cieszyna*; Urząd Miejski w Cieszynie: Cieszyn, Poland, 2015.
84. Szczepkowski, A. (Institute of Forest Sciences, Warsaw University of Life Sciences—SGGW, Warsaw, Poland); Gierczyk, B. (Faculty of Chemistry, Adam Mickiewicz University in Poznań, Poznań, Poland); Kujawa, A. (Institute for Agricultural and Forest Environment, Polish Academy of Sciences, Poznań, Poland), Ślusarczyk, T. (Naturalists' Club, Świebodzin, Poland). Unpublished work, 2019.
85. Penttillä, R.; Siitonen, J.; Kuusinen, M. Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. *Biol. Cons.* **2004**, *117*, 271–283, <https://doi.org/10.1016/j.biocon.2003.12.007>.
86. Junninen, K.; Komonen, A. Conservation ecology of boreal polypores: A review. *Biol. Conserv.* **2011**, *144*, 11–20, <https://doi.org/10.1016/j.biocon.2010.07.010>.
87. Norden, J.; Penttillä, R.; Siitonen, J.; Tomppo, E.; Ovaskainen, O. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *J. Ecol.* **2013**, *101*, 701–712, <https://doi.org/10.1111/1365-2745.12085>.
88. Kunttu, P.; Helo, T.; Kulju, M.; Julkunen, J.; Pennanen, J.; Shiryaev, A.G.; Lehtonen, H.; Kotiranta, H. Aphyllophoroid funga (Basidiomycota) of Finland: Range extensions and records of nationally new and rare species. *Acta Mycol.* **2019**, *54*, 1128, <https://doi.org/10.5586/am.1128>.
89. Komonen, A.; Puumala, I.; Várkonyi, G.; Penttilä, R. Wood-decaying fungi in old-growth boreal forest fragments: Extinctions and colonizations over 20 years. *Silva Fenn.* **2021**, *55*, 10491, <https://doi.org/10.14214/sf.10491>.
90. Gori, Y.; Cherubini, P.; Camin, F.; La Porta, N. Fungal root pathogen (*Heterobasidion parviporum*) increases drought stress in Norway spruce stand at low elevation in the Alps. *Eur. J. Forest. Res.* **2013**, *132*, 607–619, <https://doi.org/10.1007/s10342-013-0698-x>.
91. La Porta, N.; Capretti, P.; Thomsen, I.M.; Kasanen, R.; Hietala, A.M.; Von Weissenberg, K. Forest pathogens with higher damage potential due to climate change in Europe. *Can. J. Plant. Pathol.* **2008**, *30*, 177–195, <https://doi.org/10.1080/07060661.2008.10540534>.
92. Rayner, A.D.M.; Boddy, L. *Fungal decomposition of wood. Its biology and ecology*. John Wiley & Sons: Hoboken, NJ, USA, 1988.
93. Gunulf, A.; Wang, L.; Englund, J.-E.; Rönnberg, J. Secondary spread of *Heterobasidion parviporum* from small Norway spruce stumps to adjacent trees. *For. Ecol. Manage.* **2013**, *287*, 1–8, <https://doi.org/10.1016/j.foreco.2012.09.011>.
94. Gaitnieks, T.; Zaļuma, A.; Kenigvalde, K.; Kļaviņa, D.; Brauners, I.; Piri, T. Susceptibility of Small-Diameter Norway Spruce Understory Stumps to *Heterobasidion* Spore Infection. *Forests* **2019**, *10*, 521, <https://doi.org/10.3390/f10060521>.
95. Piri, T.; Korhonen, K.T. The effect of winter thinning on the spread of *Heterobasidion parviporum* in Norway spruce stands. *Can. J. For. Res.* **2008**, *38*, 2589–2595, <https://doi.org/10.1139/X08-103>.
96. Fox, R.T.V. *Armillaria Root Rot: Biology and Control of Honey Fungus*; Intercept Press: Andover, Hampshire, UK, 2000.
97. Prospero, S.; Holdenrieder, O.; Rigling, D. Comparison of the virulence of *Armillaria cepistipes* and *Armillaria ostoyae* on four Norway spruce provenances. *For. Pathol.* **2004**, *34*, 1–14, <https://doi.org/10.1046/j.1437-4781.2003.00339.x>.
98. Lygis, V.; Vasiliauskas, R.; Larsson, K.-H.; Stenlid, J. Wood-inhabiting fungi in stems of *Fraxinus excelsior* in declining ash stands of northern Lithuania, with particular reference to *Armillaria cepistipes*. *Scand. J. For. Res.* **2005**, *20*, 337–346, <https://doi.org/10.1080/02827580510036238>.
99. Heinzemann, R.; Dutech, C.; Tsykun, T.; Labbé, F.; Soularue, J.-P.; Prospero, S. Latest advances and future perspectives in *Armillaria* research. *Can. J. Pl. Path.* **2019**, *41*, 1–23, <https://doi.org/10.1080/07060661.2018.1558284>.
100. Mańka, M.; Łakomy, P. Effect of thinning in Scotch pine (*Pinus sylvestris* L.) stand growing on former arable land, on suppressiveness of soil to *Heterobasidion annosum* (Fr.) Bref. and *Armillaria obscura* (Schaeff.) Herink. *Phytopath. Polon.* **1995**, *9*, 45–51.
101. Kubiak, K.; Żółciak, A.; Damszel, M.; Lech, P.; Sierota, Z. *Armillaria* Pathogenesis under Climate Changes. *Forests* **2017**, *8*, 100, <https://doi.org/10.3390/f8040100>.
102. Przemieniecki, S.W.; Damszel, M.; Ciesielski, S.; Kubiak, K.; Mastalerz, J.; Sierota, Z.; Gorczyca, A. Bacterial microbiome in *Armillaria ostoyae* rhizomorphs inhabiting the root zone during progressively dying Scots pine. *Appl. Soil Ecol.* **2021**, *164*, 103929, <https://doi.org/10.1016/j.apsoil.2021.103929>.

103. Kovalchuk, A.; Mukrimin, M.; Zeng, Z.; Raffaello, T.; Liu, M.; Kasanen, R.A.O.; Sun, H.; Asiegbu, F.O. Mycobiome analysis of asymptomatic and symptomatic Norway spruce trees naturally infected by the conifer pathogens *Heterobasidion* spp. *Environ. Microbiol. Rep.* **2018**, *10*, 532–541, <https://doi.org/10.1111/1758-2229.12654>.
104. Seifert, T. Simulating the extent of decay caused by *Heterobasidion annosum* s. l. in stems of Norway spruce. *For. Ecol. Manag.* **2007**, *248*, 95–106, <https://doi.org/10.1016/j.foreco.2007.02.036>.
105. Möykkynen, T.; Pukkala, T. Optimising the management of a Norway spruce stand on a site infected by *Heterobasidion* coll. *Scand. J. For. Res.* **2009**, *24*, 149–159, <https://doi.org/10.1080/02827580902870508>.
106. Goheen, D.J.; Orosina, W.J. 1998. Characteristics and consequences of root diseases in forests of Western North America. In: Frankel, Susan J., tech. coord. User's guide to the western root disease model, version 3.0. Gen. Tech. Rep. PSW-GTR 165. Albany, CA: U.S. Dept. Agr., For. Serv., Pacific Southw. St.: 3-8.
107. Schwarze, F.W.M.R.; Engels, J.; Mattheck, C. *Fungal Strategies of Wood Decay in Trees*; Springer Verlag: Berlin, Germany, 2000.
108. Lonsdale, D.; Pautasso, M.; Holdenrieder, O. Wood-decaying fungi in the forest: Conservation needs and management options. *Eur. J. For. Res.* **2008**, *127*, 1–22, <https://doi.org/10.1007/s10342-007-0182-6>.
109. Wrzosek, M.; Ruskiewicz-Michalska, M.; Sikora, K.; Damszel, M.; Sierota, Z. The plasticity of fungal interactions. *Mycol. Prog.* **2017**, *16*, 101–108, <https://doi.org/10.1007/s11557-016-1257-x>.
110. Jaworski, T.; Plewa, R.; Hilszczański, J.; Szczepkowski, A.; Horak, J. Saproxylic moths reveal complex within-group and group-environment patterns. *J. Insect Conserv.* **2016**, *20*, 677–690, <https://doi.org/10.1007/s10841-016-9898-2>.
111. Custer, G.F.; van Diepen, L.T.A.; Stump, W.L. Structural and functional dynamics of soil microbes following spruce beetle infestation. *Appl. Environ. Microbiol.* **2020**, *86*, e01984–e02003, <https://doi.org/10.1128/AEM.01984-19>.