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Phellinus hartigii in the structure of the pathological background of fir stands

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Abstract. *Phellinus hartigii* is a xylotrophic basidiomycete widely associated with coniferous species; however, its functional role in the processes affecting the biotic stability of coniferous tree species, particularly *Abies alba* in the Carpathian region, remains insufficiently understood. The aim of this study was to determine the pathological significance of *Phellinus hartigii* as a factor contributing to the structural and physiological destabilisation of stands involving *Abies alba* within the Pokuttia Carpathians. The research was based on the results of phytosanitary surveys of forest stands using the sample plot method. Species identification of mycopathogens was carried out according to the morphological characteristics of basidiomes and mycelium, as well as the nature of wood damage. It was established that *Phellinus hartigii* causes heart rot and heartwood-sapwood white corrosive rot, characterised by distinct demarcation zones and the formation of a fibrous wood structure at the early stages of decay. The pathological process was localised mainly in the middle section of the stem, affecting sapwood tissues and spreading basipetally towards the base of the tree with subsequent transition into the root section of the stem. Such changes lead to a substantial reduction in the mechanical stability of trees and

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increase their susceptibility to windbreak and windthrow. The development of rot was found to be closely associated with areas of prior anatomical and physiological destabilisation of tissues, particularly canker lesions and zones altered by bacterial infections. The interaction of fungal and bacterial pathologies forms a complex pathological background. The activity of the pathogen is manifested not only in the destruction of wood in individual trees but also in the formation of structural changes within forest stands, which is of considerable importance for assessing the stability of forest ecosystems. The practical value of the study lies in the use of the identified pathological features for the early diagnosis of *Phellinus hartigii* infection during forest pathological monitoring and for predicting the loss of mechanical stability in fir stands, thereby providing a basis for substantiating sanitary and silvicultural measures

Keywords: *Abies alba*; wood-decaying fungi; white rot; degradation; pathological changes

Introduction

The forests of the Ukrainian Carpathians are one of the most resilient and valuable components of Europe's mountain forest ecosystems, performing important ecological, conservation and economic functions on a biospheric scale. They are characterised by a complex vertical and horizontal structure, a high level of biodiversity and the capacity for self-regulation, which ensures their relative stability under natural conditions. However, in the 2010s and 2020s, even in forests developing under optimal growing conditions, processes of tree weakening, disruption of stand integrity and an increase in the frequency/scale of natural disturbances are being recorded with increasing frequency, consistent with pan-European trends of deteriorating tree vitality indicators (in particular, as indicated by defoliation and damage indicators in the European monitoring system) (Michel *et al.*, 2024).

One of the key, yet often underestimated, causes of such phenomena is the development of stem and root rot caused by wood-decaying fungi. These pathogens affect the trunk, root system and the area around the base of the tree, disrupting water and mineral exchange, reducing mechanical stability and creating conditions for windthrow, windbreak, and premature mortality (Palm-Hellenurm *et al.*, 2024). For a long time, such pathologies remain latent, which complicates timely diagnosis and assessment of their actual impact on the condition of the stands (Bledý *et al.*, 2024). Recent review articles on the issues facing Carpathian forests, notably by M. Soroka *et al.* (2019) and D. Kholiavchuk *et al.* (2023), that changes in the condition of tree stands are shaped by a complex of factors – ranging from management history to climate-driven environmental changes and disturbance regimes – and within this system, biotic agents can act as "triggers" and "amplifiers". In this context, recent studies indicate that climate change increases the risk of disruption to the physiological stability of trees and contributes to an increase in their susceptibility to pathogenic organisms (Hartmann *et al.*, 2022), creating the conditions for a change in the nature of the interaction between trees and disease-causing agents.

Xylotrophic basidiomycetes are a natural component of forest biocenoses and play a key role in the organic matter cycle. At the same time, recent studies of *Abies alba* trees highlight that damage to wood integrity (ranging from discolouration as an early stage to rot) can be caused by both fungi and bacteria, and their combined effect manifests as a deterioration in the mechanical stability of stands (Bledý *et al*., 2024). In the context of wind damage, it is important to note that susceptibility to windthrow is determined not only by meteorological extremes but also by the tree's trunk strength and stand structure; in a synthesis of windthrow dynamics, these factors are considered as key predictors of damage (Esperon-Rodriguez *et al.,* 2022). Furthermore, K. Palm-Hellenurm *et al*. (2024) demonstrated that the presence of pathogens causing decay processes (in particular, the *Phellinus* spp. group alongside other genera) reduces mechanical stability and may increase the proportion of trees damaged or destroyed by wind.

Among xylotrophic pathogens, *Phellinus hartigii* attracts particular attention – a perennial member of the Hymenochaetaceae family, known as the causative agent of "heart rot of fir" and primarily associated with firs, including *Abies alba* (Fischer, 2023). For the Carpathian region, it is important that rot in the root/base zone of fir trunks and other coniferous species is documented in field studies and may have direct consequences for tree stability (in particular through the involvement of the root system) (Baranowska *et al.,* 2023). In the literature, P. *hartigii* is traditionally described as the causative agent of white rot, with predominant damage to the inner wood zones; O.M. Bohoslavets & M.P. Prydiuk (2023), in their work on the biota of the Carpathians and wood-decaying fungi, emphasise the high regional specificity and sensitivity of such processes to the conditions of old-growth forests and local microenvironments, which justifies the need for region-specific studies of pathogenesis.

Thus, against the backdrop of increasing pathological mortality in fir stands, there exists a need for an in-depth analysis of the role of *Phellinus hartigii* as a component of a complex myco-bacterial pathological complex and a factor in the structural destabilisation of forests.

Materials and Methods

Field studies on the distribution and characteristics of the pathological process caused by *Phellinus hartigii* on the stems of *Abies alba* Mill. were conducted during 2025-2026 within the forest stands of the Pokuttia Carpathians in the territory of the Kolomyia Superforestry fund of the State Specialised Economic Enterprise "Forests of Ukraine". Centres of fir infection by Hartig's bracket fungus were identified and surveyed within six compartments of the Kosiv Forestry, specifically compartment 11 (subcompartments 2, 22, 39), compartment 12 (subcompartments 21, 23, 47, 48, 49, 56, 57, 53), compartment 14 (subcompartments 48, 74), compartment 29 (subcompartment 5), compartment 30 (subcompartments 9, 22, 23), compartment 31 (subcompartment 15), and compartment 35 (subcompartments 5, 9, 11, 14). The selected sites represent typical forest site conditions of the region and differ in their principal silvicultural and mensurational characteristics.

To ensure the representativeness of the study, a network of 22 research plots was established in uneven-aged stands (58-118 years old) and in stands differing in species composition but dominated by *Abies alba*. The stands were characterised by high site quality classes (predominantly I-IA), variable stand density (0.35-0.70), and belonged to the forest types D_3-beech-fir, D_3-beech-spruce-fir, C_3-beech-fir-spruce, C_3-fir-spruce, and C_2-fir-beech, which made it possible to encompass a broad range of ecological growth conditions. On each sample plot, either complete or selective phytopathological surveys of trees were carried out, with recording of the presence of fruiting bodies of *Phellinus hartigii*, external symptoms of infection, and signs of wood destruction. Sampling included fungal fruiting bodies, mycelium, and fragments of affected wood, which were subsequently used for morphological analysis.

Species identification of *Phellinus hartigii* and associated mycopathogens was carried out on the basis of macromorphological characteristics of basidiomes (shape, structure, colouration, and surface characteristics); microscopic features of mycelium and tissues (using light microscopy); and the type and morphology of wood damage (nature of rot, presence of demarcation zones, and structural changes). The research was conducted at the Educational, Scientific and Production Laboratory of General Forestry and Forest Protection of the National University of Life and Environmental Sciences of Ukraine.

Analysis of the pathological process was performed with consideration of the spatial localisation, direction of spread, and intensity of wood destruction. The localisation of infection was determined according to the structural zones of the stem (heartwood, sapwood, and butt section), with recording of the vertical position of rot centres. The direction of pathological spread was assessed according to the pattern of destruction development (acropetal/basipetal), including determination of the degree of transition of infection into the butt section and root system. The type of wood destruction was established according to the morphological characteristics of rot (fibrous structure, presence of demarcation zones, and the nature of tissue degradation), with a qualitative assessment of the intensity of infection. Features of mycelial penetration and spread were analysed according to the nature of primary infection courts (mechanical injuries, canker lesions, and necrotic zones) and the subsequent dynamics of rot development in the wood. The presence of associated pathologies was assessed according to visual symptoms of bacterial infection (wetwood, necrotic tissue changes, and exudation), as well as their spatial association with zones of fungal infection. The synergistic interaction of fungal and bacterial pathogens was determined on the basis of co-localisation of lesions, the degree of overlap of pathological zones, and the nature of wood modification. Such interaction was regarded as an indicator of the formation of a complex pathological background and the intensification of degradation processes in fir stands. Latin names of fungi are provided in accordance with the Index Fungorum database (n.d.). The study was conducted in compliance with international environmental standards, including the provisions of the Convention on Biological Diversity (1992) and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (1973).

Results

Species identification and taxonomic classification of *Phellinus hartigii*. In recent years, forests of the Carpathians have exhibited a deterioration in the sanitary condition of stands involving *Abies alba*, manifested in reduced increment, premature mortality of individual trees, and the formation of centres of pathological decline. Detailed investigations made it possible to identify the principal factors responsible for destabilisation of the studied forests. The leading position is occupied by the epiphytotic spread of bacterial wetwood (caused by the phytopathogenic polybiotrophic bacterium *Lelliottia nimipressuralis* (Carter 1945) (Brady *et al.*, 2013), ulcerative tumour-like disease (caused by the heteroecious fungus with a complete life cycle *Melampsorella caryophyllacearum* J. Schröt.), and a mycocomplex in which the order Polyporales is the most abundant, corresponding to stage IV of the five principal stages of homeostasis loss in woody plants of *Abies alba*. This stage involves the colonisation of weakened trees by secondary phytopathogens and stem insect pests and continues until complete stand mortality. Typical visual symptoms include the presence of fruiting bodies of aphyllophoroid macromycetes, consequences of the activity of wood-staining fungi, formation of a false star-shaped heartwood, galleries of cambio- and xylophagous insects, and related features. As a consequence, gradual stand degradation is expected. However, an atypical dynamic phenomenon of the mass collapse of visually healthy mature and overmature *Abies alba* trees was recorded (Fig. 1). Detailed examination revealed destruction of the root system and enabled the identification of stem rot, mycelium, and fruiting bodies of *Phellinus hartigii*.

a b

Figure 1. Wind-damaged *Abies alba*
Note: a – root system damage; b – damage to the base of the trunk caused by wood-decaying fungi
Source: photo by the authors

Phellinus hartigii (Allesch. & Schnabl) Pat., 1903) is a representative of the group of xylotrophic basidiomycete fungi whose ecological strategy combines features of facultative parasitism and saprotrophic nutrition. Such trophic plasticity determines the ability of the species to function both within the tissues of weakened yet still living trees and in dead wood, which is fundamentally important for understanding its role in the dynamics of forest ecosystems.

The etymology of the generic name *Phellinus* derives from the Greek *φελλός* (*phellos*) meaning "cork", reflecting the characteristic consistency and structure of the fruiting bodies. The specific epithet *hartigii* honours Robert Hartig, one of the founders of forest phytopathology, whose work established the foundations of modern understanding of the pathogenesis of wood-decaying fungi. The very establishment of the species within scientific nomenclature highlights its historically recognised economic and ecological significance.

In the literature, the species appears under a number of synonymous names (The world of mushrooms in Ukraine, n.d.), reflecting the complex history of its taxonomic interpretation: *Polyporus hartigii* – Allesch. & Schnabl, 1890; *Fomes hartigii* – Allesch. & Schnabl, Bres., 1897; *Phellinus robustus f. hartigii* – Allesch. & Schnabl, Bourdot & Galzin, 1925; *Phellinus robustus var. hartigii* – Allesch., Bourdot & Galzin, 1925; *Fomitiporia hartigii* – Allesch. & Schnabl, Fiasson & Niemelä, 1984; *Fomitiporella hartigii* – Allesch. & Schnabl, Teixeira, 1992; *Polyporus fulvus* – Quél., 1872; *Trametes lutescens* – Lázaro Ibiza, 1916. Such nomenclatural variability is typical for members of the family Hymenochaetaceae and is associated with the revision of genus boundaries following the accumulation of morphological and molecular data (Index Fungorum, n.d.).

According to its systematic position, *Phellinus hartigii* belongs to the division Basidiomycota, class Agaricomycetes, order Hymenochaetales, family Hymenochaetaceae, genus *Phellinus* (Zerova *et al*., 1972). At the same time, molecular phylogenetic studies have significantly transformed the understanding of the systematics of this group of fungi. It has been shown that the genus *Phellinus*, in its classical, morphologically oriented sense, is polyphyletic, i.e. it unites taxa of different evolutionary origins. This has led to the establishment of new genera (*Fuscoporia, Phellinopsis, Fomitiporia*, etc.) and a revision of diagnostic criteria (Zhu *et al*., 2018; Wu *et al*., 2022). Despite these changes, *Phellinus hartigii* occupies a relatively stable position within the family Hymenochaetaceae. Molecular data indicate the formation of a distinct, phylogenetically well-supported clade, associated predominantly with coniferous species (Kumari *et al.,* 2021; Gafforov *et al.,* 2025). This genetic distinctiveness correlates with the species' pronounced substrate specialisation, primarily with *Abies alba*.

The identified phylogenetic autonomy allows *P. hartigii* to be regarded not only as a morphologically defined taxon, but as an evolutionarily stable ecological unit with a clearly defined trophic niche. This is of fundamental importance for interpreting its biology: high association with *Abies alba* may indicate a long-term co-evolutionary "pathogen – host" interaction; the stability of genetic markers is consistent with the relative conservatism of morphological traits; ecological specialisation potentially determines the nature of pathogenesis and the rate of wood decay (Vazquez-Armenta *et al*., 2022).

From a phytopathological perspective, the taxonomic stability of the species has not only nomenclatural but also practical significance. Correct species identification directly influences the diagnosis of rot types in stands, the assessment of risks of structural degradation of trees, the prediction of stand stability, and the interpretation of interactions with other biotic agents. Given the transitional state of the genus's systematics, within the scope of this study it is appropriate to use the name *Phellinus hartigii* (Allesch. & Schnabl) Pat. with a broad interpretation of the genus (*Phellinus sensu lato*) (He & Zhao, 2022). This approach is consistent with current practice in applied phytopathological and forest ecological research, where the key factor is not so much the formal generic status as the biological and ecological identity of the pathogen.

Thus, *Phellinus hartigii* should be regarded as an evolutionarily distinct, ecologically specialised xylotrophic organism, whose functional role in fir stands extends beyond that of a typical saprotrophic component. Its presence in stands potentially reflects not only the processes of wood decomposition and the age-related stage in the formation of the pathological background of fir, but also structural changes in the biotic stability of *Abies alba*.

The natural range and distribution patterns of *Phellinus hartigii* in fir stands in the Carpathians. The distribution range of *Phellinus hartigii* is Holarctic in character and covers extensive areas of Eurasia and North America. The species has been recorded in various parts of Europe (Świderski *et al*., 2025), Asia (Gafforov *et al*., 2025) and North America (Andjièrèyir *et al.,* 2024), indicating its ecological plasticity within coniferous forest ecosystems. Within Eurasia, the fungus occurs from the Far East, including Sakhalin, to the western regions of the continent (Gafforov *et al*., 2025). At the same time, the species' distribution is distinctly patchy, manifesting as uneven representation in individual geographical zones. In the central regions of Eastern Europe, *P. hartigii* is characterised by limited occurrence, whereas in mountainous and foothill areas its presence is significantly more stable. This pattern is consistent with the species' bioecological specialisation and its association with fir and mixed fir-beech forests (Świderski *et al.,* 2025). In Ukraine, the species' range is clearly associated with the natural distribution area of *Abies alba*. The main centres of the fungus's occurrence are confined to the Carpathian region and the Precarpathians, where silver fir is one of the community-forming species. Such spatial localisation indicates a close link between the pathogen's distribution and the structure and age dynamics of fir stands.

Analysis of field observations allows to identify a number of characteristic features of the distribution of *Phellinus hartigii* in Carpathian forests. The fungus is predominantly associated with mature and overmature stands. This age-related distribution is likely linked to the accumulation of structural defects, micro-damage and physiological weakening in the wood, which creates favourable conditions for infection. Infection is more frequently recorded in trees showing signs of reduced vitality. This suggests that *P. hartigii* functions primarily as a facultative parasite, using physiologically weakened trees as its primary substrate. At the same time, the development of rot may have a prolonged latent phase, which complicates the early diagnosis of the pathological process. The spatial distribution of affected trees is markedly uneven. Fungal foci often form in stands with elevated levels of stress factors – mechanical damage, water regime disturbances, and the influence of abiotic extremes. This indicates the significant role of environmental conditions in the realisation of the species' pathogenic potential.

An important ecological feature is that the presence of *Phellinus hartigii* in a stand does not always correlate directly with visible symptoms of weakness. Since the fungus causes internal wood decay, its impact on tree stability may remain hidden until mechanical instability or tree collapse occurs. From an ecosystem perspective, the species' biology allows to be regarded as a specific structure-forming factor in the dynamics of fir forests. On the one hand, the fungus participates in the processes of natural wood decomposition and the organic matter cycle. On the other hand, under conditions of mass development, it can act as an agent accelerating tree degradation and the transformation of stands. That is, the range of *Phellinus hartigii* in the Carpathian region is determined not only by the geographical limits of the host species' distribution, but also by a complex of ecological and coenotic factors. The pattern of fungal distribution indicates its functional integration into the processes of weakening and structural transformation of fir stands.

Morphological characteristics of basidiomes and their diagnostic significance. *Phellinus hartigii* forms perennial basidiomes of the sessile type, appearing as laterally attached caps. This morphological organisation is typical of members of the Hymenochaetaceae family and reflects the prolonged nature of the fungus's generative structures within a single substrate. The fruiting bodies are characterised by their considerable size: the diameter of the basidiome is usually 15-25 cm, and the thickness can reach 20 cm. At early stages of development, the basidiomes possess a nodular form, whereas in the mature state they acquire a console-shaped or hoof-shaped configuration. The lower surface is often uneven, with a stepped structure reflecting the perennial layering of tubular strata (Fig. 2).

Basidiomycetes are firmly attached to the substrate by a broad base and usually grow singly. Occasionally, several specimens are found growing together, which is likely due to a local concentration of mycelium or the specific characteristics of wood colonisation. The surface of the fruiting bodies is rough, with faint concentric zoning, and is sometimes cracked. The colour varies from yellow-brown in the early stages to dirty grey or almost black in older basidiomes. A characteristic feature of ageing basidiomes is the growth of green algae on them, indicating that the fruiting bodies have remained for a long time in the stable microclimate of the trunk.

Figure 2. Basidiomes of *Phellinus hartigii* on a living (*left*) and dead (*right*) trunk of *Abies alba*
Source: photo by the authors

The margin of the basidiome is usually blunt, rounded, and yellow-brown or light reddish in colour. The relative stability of the growth zone's colour can be regarded as an indicator of the fungus's physiological activity. The hymenophore is tubular and multilayered. The tubes vary in length, and between the individual annual layers there are interlayers of sterile tissue, coloured similarly to the flesh. This structure reflects the cyclical nature of fruit body growth and correlates with the pathogen's long-term activity within the infected wood. The pores are small (0.1-0.15 mm), rounded or slightly angular, with a high density (4-6 pores per 1 mm). This micro-morphology of the hymenophore is a diagnostically significant feature for species identification and allows *P. hartigii* to be distinguished from morphologically similar polypores. The spore print is yellowish. The spores are small, predominantly round or broadly ovoid in shape, colourless or faintly yellowish. The tissue of the fruiting bodies is woody, extremely hard, distinctly zoned, with a characteristic rusty-red or yellow-brown colour. A silky sheen is often observed on the fracture surface, which is a typical feature of members of the Hymenochaetaceae.

The diagnostic and phytopathological significance of morphological characteristics. The morphology of the basidia of *Phellinus hartigii* has not only taxonomic but also practical significance in phytopathological surveys. The perennial nature of the fruiting bodies indicates the prolonged nature of the infectious process. The presence of well-developed basidiomes generally correlates with the late stages of wood destruction, when the pathological process becomes structurally irreversible. The considerable size and high tissue density of the fruiting bodies indirectly reflect the intensity of substrate colonisation. This allows the basidiomes to be regarded as a kind of indicator of the extent of internal trunk degradation. The localisation of basidiomes on the trunk often corresponds to zones of maximum mycelial activity. In the practice of forest pathology diagnosis, this is significant for assessing the mechanical stability of trees and predicting the risk of their collapse. It is important to emphasise that the formation of fruiting bodies is a relatively late stage in the pathogen's development. The absence of basidiomes does not rule out the presence of rot, whereas their presence almost always indicates profound structural changes in the wood.

Thus, the morphological features of *Phellinus hartigii* basidia should be regarded as a key element of field diagnosis, allowing external signs to be linked to the nature and stage of the pathological process.

Features of pathogenesis and the type of wood destruction. *Phellinus hartigii* is characterised by a pronounced substrate specificity towards coniferous species, among which *Abies alba* is the dominant host plant. However, it can also infect Siberian fir, Caucasian fir, white-barked fir, and, less frequently, European spruce, Scots pine and European yew. The fungus develops predominantly on living trees, although it can remain active in dead wood – on fallen trunks and stumps. This ecological strategy indicates the species' facultative parasitic nature, in which primary colonisation is often associated with physiologically weakened trees.

The pathogen causes heart rot or heartwood-sapwood rot of the corrosive type. Affected wood acquires a pale yellow or white colouration and is distinctly separated from intact tissues by narrow sinuous dark lines. The formation of such demarcation zones reflects the complex interaction between the fungus and the defence responses of the tree and indicates the prolonged, chronic character of the pathological process (Fig. 3).

Figure 3. Mycelium of *Phellinus hartigii* (*left*) and demarcation zones in the stem wood of *Abies alba* (*right*)

Source: photo by the authors

The structural transformation of the wood is typical of white rot. During the decomposition process, there is selective breakdown of the lignin, with the cellulose framework remaining relatively intact in the early stages, resulting in the formation of a fibrous, flaky texture. As the rot progresses, the integrity of the vascular and mechanical elements is compromised, leading to a sharp decline in the physical and mechanical properties of the trunk. A fundamentally important feature of the pathogenesis of *Phellinus hartigii* is the spread of rot from the heartwood into the sapwood. This transition involves the inclusion of functionally active tissues in the pathological process, which has a dual effect: a reduction in the mechanical stability (strength) of the trunk and disruption of the water-conducting and assimilation functions. It is precisely the involvement of the sapwood that largely explains the increased susceptibility of infected trees to windthrow and windbreak damage. The affected wood loses its elasticity and resistance to dynamic loads, which is particularly critical in mountain ecosystems with strong winds. In the later stages of rot development, characteristic macroscopic signs form on the surface of the *Abies alba* trunk – localised indentations, cracks and deformations of the bark. The appearance of perennial fruiting bodies reflects the completed stages of substrate colonisation and is, in fact, an indicator of deep internal destruction.

Spatially, the rot is usually localised in the middle sections of the trunk, most often within the second and third thirds. Such localisation is of fundamental importance for the mechanical stability of the tree, as it is precisely these zones that play a key role in load redistribution. At the same time, a modified pattern of rot development caused by *Phellinus hartigii* was observed in the studied fir trees – basipetal spread with a transition to the base and root parts of the tree. This pattern of infection indicates a region-specific transformation of the pathogenesis, which may be linked to the specific ecological conditions of the Carpathians, the age structure of the stands, and prior anatomical and physiological destabilisation of the tissues. The involvement of the root system in the destruction process significantly alters the functional consequences of the infection, as it disrupts not only the conductive and mechanical functions of the trunk but also the stability of the tree's supporting structure.

According to the results of the research, the average extent (length) of the rot reaches up to 8 metres, indicating the pathogen's high destructive potential. It has been established that infection of silver fir trees by *Phellinus hartigii* occurs primarily through breaches in the integrity of the outer tissues. The most likely routes of entry are sites of dead or broken branches, mechanical damage to the bark and cambium, as well as canker lesions of various aetiologies (including bacterial).

The role of secondary pathological processes in the formation of "infection courts" deserves particular attention. Ulcerative and tumour-like formations associated with *Melampsorella caryophyllacearum*, as well as lesions associated with bacterial water rot (*Lelliottia nimipressuralis*), significantly alter the anatomical and physiological state of the tissues. Destruction of the parenchyma, disruption of the water balance and local necrosis create favourable conditions for the colonisation of wood by xylotrophic fungi. In this context, *Phellinus hartigii* should be regarded as a component of a complex pathological process, in which fungal infection occurs against a background of prior physiological or structural weakening of the tree. Such interaction is consistent with current understanding of the multifactorial nature of tree degradation in natural stands.

In the surveyed stands, the distribution of infected silver fir trees is predominantly scattered. At the same time, within established foci, the proportion of infected trees can be significant (typical signs of *Phellinus hartigii* infection are observed in 6 out of 10 surveyed trees), particularly in mature and overmature stands. The predominant infection of trees of larger diameters (32 cm and above) is ecologically and coenotically significant, as it leads to changes in the vertical and horizontal structure of the stand, the formation of gaps and the redistribution of resources within the stand.

The development of rot is accompanied by a progressive decline in the mechanical and physiological resilience of fir trees. The likelihood of windthrow and windbreak increases, as does the level of litter accumulation, which, in turn, creates favourable conditions for secondary biotic agents, primarily stem pests. Thus, the pathogenic activity of *Phellinus hartigii* in fir stands is systemic in nature and manifests itself not only in the destruction of the wood of individual trees, but also in the transformation of the structural and functional stability of the stands.

Synergy between fungal and bacterial plant pathogens. The infection process in the trunks of *Abies alba* occurs primarily through the disruption of the integrity of the epidermal and vascular tissues. The most common routes of pathogen entry are dead or broken knots, mechanical damage to the bark and cambium, as well as canker lesions. The latter are of particular pathogenetic significance, as they form stable zones of structural destabilisation of the wood. Ulcerative-tumour-like formations were observed on virtually all the wind-damaged fir trees examined, serving as evidence of the localisation of "infection courts" for the penetration of wood-destroying fungi. Ulcerative-tumour-like deformations associated with *Melampsorella caryophyllacearum* are accompanied by disruption of the normal anatomical organisation of tissues, hypertrophy and necrosis of individual areas. Such changes create localised areas of physiological and mechanical vulnerability, which can function as long-term "infection courts" for xylotrophic fungi.

Pathological processes associated with bacterial water rot caused by *Lelliottia nimipressuralis* play a similar role. The development of bacterial infection is accompanied by changes in the water balance of tissues, exudate secretion, local maceration of cellular structures, and alterations in the physicochemical properties of the wood. As a result, the barrier function of the tissues is significantly reduced and the likelihood of wood colonisation by fungal pathogens increases. Another possible pathway of infection of fir trees by *Phellinus hartigii* is the penetration of fungal hyphae through fused roots of neighbouring trees, a phenomenon recorded in many windthrown trees. From the perspective of pathogenesis, it is advisable to consider fungal and bacterial infections not as isolated phenomena, but as interrelated components of a single pathological complex (Fig. 4). Within such a complex, infectious agents form a sequential and mutually reinforcing continuum, in which each link alters the structural and physiological characteristics of the substrate in such a way as to create favourable conditions for the subsequent colonisation and persistence of other microorganisms.

A primary bacterial infection caused by *Lelliottia nimipressuralis* can trigger physiological destabilisation of fir tissues through disruption of xylem hydraulic conductivity, local maceration of the parenchyma, and a weakening of the tree's defence mechanisms. Dysfunction of the vascular system, changes in water potential and redox conditions (oxidative-reductive conditions), as well as the formation of canker and necrotic zones, reduce the efficiency of compartmentalisation (spatial separation of processes) and create anatomical "infection courts" for xylotrophic basidiomycetes. Under such conditions, the invasion of *Phellinus hartigii* occurs against a backdrop of already reduced biotic resistance, which enhances the pathogen's competitive advantage in the altered ecological niche.

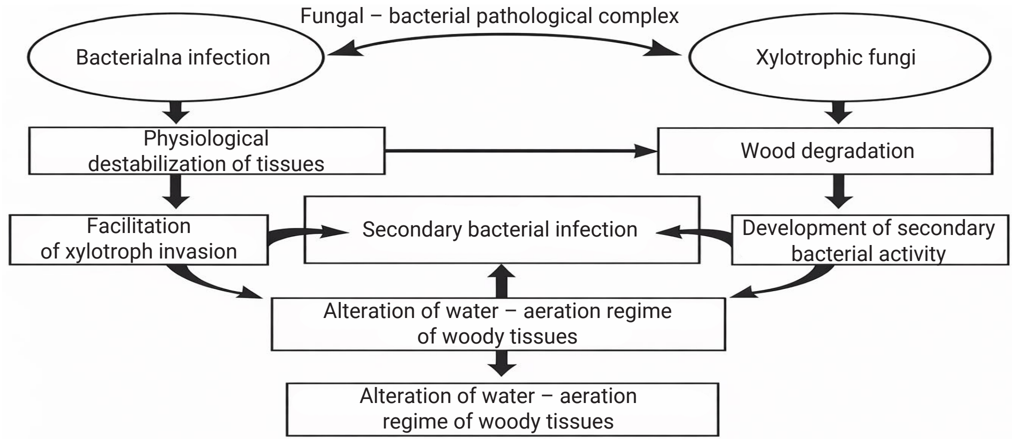

Figure 4. Mechanism of interaction within the fungal-bacterial pathological complex of *Abies alba*

Source: compiled by the authors

Further wood degradation, characteristic of white rot, acts as a key mechanistic "switch" in the system. The degradation of lignin and hemicellulose is accompanied by changes in porosity, the fibrous structure, and the formation of demarcation zones, reflecting the tree's response to the spread of the mycelium. At the same time, the destruction of cell walls leads to a significant reduction in mechanical strength and a disruption of the stability of the trunk and, in the event of basipetal spread of the process, the root collar and root system. Thus, the pathogenesis extends beyond local trunk rot and transforms into a factor destabilising the tree's supporting structure.

Destructive changes to the substrate are inevitably accompanied by a transformation of the water-air regime of the wood tissues. Increased porosity and the appearance of microcavities create a mosaic of microecological niches in which a secondary bacterial microbiota forms. Consequently, rot destruction not only reduces the mechanical properties of the wood but also initiates a succession-driven restructuring of microbial consortia. Secondary bacterial colonisation, in turn, may intensify maceration processes and sustain the chronic nature of the pathology, forming a self-sustaining pathological cycle.

The spread of *P. hartigii* rot into the root collar and root zone, as observed in the Carpathians, indicates a modification of the classical model of the process's localisation. The involvement of the root system means that destabilisation affects not only the conductive and mechanical functions of the trunk, but also the structural integrity of the root system, which directly increases the risk of windthrow and windbreak. Such a scenario may be caused by pre-existing anatomical and physiological weakness of the tissues, cancerous lesions, or specific hydrothermal conditions of mountain ecosystems that promote changes in microbial consortia.

Consequently, fungal-bacterial co-infection in fir stands should be interpreted as an integrated system of interactions, within which primary tissue destabilisation, xylotrophic destruction and secondary bacterial colonisation form a single mechanism of progressive degradation. This approach allows for a deeper explanation of the spatial dynamics of the damage and the mechanisms of loss of mechanical stability in *Abies alba* under the conditions of the Carpathian region. It is worth noting that during a detailed phytosanitary survey, associated species of mycelia associated with life on silver fir trees were identified – *Fomitopsis pinicola* (Sw.) – P. Karst. 1881; *Gloeophyllum abietinum* (Fr.) – P. Karst. 1882; *Hericium flagellum* (Scop.) – Pers. 1797; *Heterobasidion abietinum* – Niemelä & Korhonen, 1988; *Melampsorella cerastii* (Pers.) – J. Schröt. 1887; *Trichaptum abietinum* (Dicks.: Fr.) – Ryvarden, 1972 (Index Fungorum, n.d.).

The functional structure of this complex indicates the formation of a multi-level system of xylotrophic organisms, within which different species occupy specific ecological niches. Some fungi are predominantly associated with dead wood, whilst others are associated with living but weakened trees. This mosaic nature of the mycofauna reflects the sequence and duration of wood degradation processes. The presence of several species of wood-decaying fungi within a single tree or stand may indicate the chronic nature of pathological processes, the structural heterogeneity of the damage, and the long-term dynamics of wood decomposition. In this context, *Phellinus hartigii* functions as one of the key agents of destruction; however, its pathogenic effect is realised in interaction with other components of the biotic environment. The formation of such pathogenic consortia is a typical feature of weakened and degrading stands.

Thus, the interaction of fungal and bacterial infections in the tissues of *Abies alba* is complex in nature and can be regarded as one of the mechanisms underlying the disruption of the biotic stability of fir stands. The combination of various pathological processes creates a cumulative effect, manifested in accelerated wood degradation, reduced mechanical stability of trees, and increased susceptibility to damage. The results obtained indicate that *Phellinus hartigii* in the fir stands of the Pokuttia Carpathians acts as a key factor in the structural destabilisation of *Abies alba*, rather than merely a component of the xylotrophic mycofauna. The established basipetal nature of the spread of rot, with progression into the root collar and root regions of the tree, fundamentally alters the understanding of the pathogenesis of this species. This model helps explain the observed phenomenon of mass tree dieback without pronounced external signs of weakness.

Discussion

As noted by S. Senf & R. Seidl (2021), the mechanical stability of trees is determined primarily by the integrity of the supporting structure, and not merely by the physiological condition of the crown. The work of M. Esperon-Rodriguez *et al.* (2022) shows that windthrow occurs due to a combination of internal weakening of the wood and external loads caused by wind. Similar conclusions are drawn by K. Palm-Hellenurm *et al.* (2024), emphasising the role of hidden defects in the root zone in the formation of windthrow. In this context, the localisation of *P. hartigii* rot in the root zone is critical, as it is precisely this that determines the loss of the tree's mechanical stability. The significant extent of the rot (up to 8 m) indicates the pathogen's prolonged latent development and its high destructive potential. As noted by F. Wu *et al.* (2022) and M. Fischer (2023), members of the Hymenochaetaceae are characterised by chronic colonisation of wood, and the formation of basidia corresponds to the late stages of the pathological process. The data presented in this study further clarify this point: in the Carpathian region, *P. hartigii* acts not only as an agent of stem white rot but also as a factor destabilising the root-stem complex.

The observed association of *P. hartigii* with older trees is consistent with the concept of facultative parasitism. As shown in the works of A. Kumari *et al*. (2021) and Y. Gafforov *et al.* (2025), members of the Hymenochaetales are characterised by substrate specialisation and are predominantly active in physiologically weakened trees. In the present study, this manifests as selective infection of trees with larger diameters, indicating a link between the development of rot and the accumulation of structural defects and reduced tree vitality. Of fundamental importance is the established synergistic relationship between *P. hartigii* and other pathogens, in particular *Lelliottia nimipressuralis* and *Melampsorella caryophyllacearum*. As noted by M. Soroka *et al.* (2019), the degradation of *Abies alba* is polyetiological in nature and is shaped by a complex of factors. The results of this study confirm this view and help to clarify the mechanism of interaction: bacterial and canker lesions form stable "infection courts" that reduce the effectiveness of compartmentalisation and create conditions for the colonisation of wood by xylotrophic fungi. Subsequently, white rot caused by *P. hartigii* acts as a key stage that transforms local damage into a phase of systemic mechanical instability.

The data obtained are consistent with current understanding of the state of European forests. As noted by H. Hartmann *et al*. (2022) and M. Bledý *et al.* (2024), the decline in the resilience of *Abies alba* is linked to a combination of climatic stresses and biotic factors. The works of D. Kholiavchuk *et al.* (2023) emphasise that Carpathian forests are undergoing a state of dynamic transformation caused by changing environmental conditions. In this context, the increased activity of *P. hartigii* can be regarded as an indicator of deeper disruptions in the functioning of fir ecosystems. The associated mycocomplex identified in the study confirms the formation of a multi-level system of xylotrophic organisms. As noted by O. Bohoslavets & M. Prydiuk (2023), the mycobiota of coniferous forests is characterised by high structural complexity, and individual species form functional consortia. In this context, *P. hartigii* acts not as an isolated pathogen, but as a component of a system where species interactions determine the rate and nature of wood degradation.

From an applied perspective, the study's results are of direct relevance to forest pathology monitoring. Firstly, the absence of external symptoms does not guarantee the mechanical stability of the tree. Secondly, the presence of *P. hartigii* basidiomes should be regarded as an indicator of late stages of decay. Thirdly, canker lesions, bacterial exudates and mechanical damage should be assessed as key predictors of subsequent xylotrophic colonisation. *Phellinus hartigii* in the fir stands of the Carpathians should be regarded as a functionally significant component of the pathological background, playing a key role in the transition of stands from a state of weakness to the stage of structural collapse. Its pathogenic effect is realised through interaction with other biotic agents and is an important factor in shaping the current dynamics of fir stands.

Conclusions

The article examines the role of *Phellinus hartigii* in the formation of the pathological background of fir stands in the Carpathians and establishes its significance as a factor contributing to the structural destabilisation of *Abies alba*. The aim of the study – to clarify the pathological role of this xylotrophic pathogen under the conditions of the Pokuttia Carpathians – was generally achieved. It was established that *Phellinus hartigii* in fir stands of the Carpathians acts as an ecologically specialised xylotrophic pathogen closely associated with *Abies alba* and predominantly confined to trees of older age classes. The pathogen causes heart rot and heartwood-sapwood white corrosive rot, accompanied by profound structural changes in the wood, the formation of a fibrous texture, and a sharp decline in the physical and mechanical properties of the stem. The spread of rot into the sapwood portion of the wood is of critical importance for the mechanical stability of trees, increasing their susceptibility to windbreak and windthrow. The formation of perennial basidiomes of *Phellinus hartigii* is an indicator of the prolonged course of the pathological process and generally corresponds to the late stages of wood destruction. Tree infection occurs mainly through areas with compromised tissue integrity, particularly canker lesions and zones transformed by bacterial pathologies. The interaction of fungal and bacterial lesions forms a complex pathological background within the forest stands of the Pokuttia Carpathians. The activity of *Phellinus hartigii* in the fir forests of the Carpathians should therefore be regarded as one of the key biotic factors contributing to stand destabilisation and as a potential indicator of processes of ecological transformation.

Thus, the novelty of the study lies in the establishment of a regionally modified model of *Phellinus hartigii* pathogenesis, which includes the basipetal spread of rot involving the root system and substantiates the role of the fungal-bacterial pathological complex as a key factor in the degradation of *Abies alba*. The proposed model makes it possible to explain the discrepancy between the visual condition of trees and their actual mechanical stability. At the same time, it was established that the use of predominantly morphological approaches for pathogen identification limits the possibility of fully revealing the structure of microbial consortia. The absence of molecular verification of the components of the pathological complex determines the need for further studies aimed at molecular profiling of the mycobiome and bacteriome, as well as at assessing the effect of rot on the mechanical properties of wood.

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Phellinus hartigii у структурі патологічного фону ялицевих деревостанів

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Анотація. *Phellinus hartigii* є ксилотрофним базидіоміцетом, широко асоційованим із хвойними видами, однак його функціональна роль у процесах порушення біотичної стійкості хвойних видів дерев, зокрема, *Abies alba* у Карпатському регіоні залишається недостатньо з’ясованою. Метою дослідження було встановлення патологічного значення *Phellinus hartigii* як чинника структурної та фізіологічної дестабілізації деревостанів за участі *Abies alba* у межах Покутських Карпат. Дослідження базувалося на результатах фітосанітарних обстежень деревостанів з використанням методу пробних площ. Видову ідентифікацію мікопатогенів здійснювали за морфологічними ознаками базидіом і міцелію та характером уражень деревини. Встановлено, що *Phellinus hartigii* спричиняє ядрову та ядрово-заболонну білу корозійну гниль, характеризується чіткими демаркаційними зонами та формуванням на ранній стадії гниття волокнистої структури деревини. Патологічний процес локалізується, переважно, в середній частині стовбура, охоплює заболонні тканини та поширюється базіпетально – у напрямку до основи дерева з переходом у кореневу частину стовбура. Подібні зміни призвели до істотного зниження механічної стабільності дерев і підвищення їх схильності до буреломів та вітровалів. Виявлено, що розвиток гнилі тісно пов'язаний із ділянками попередньої анатомо-фізіологічної дестабілізації тканин, зокрема раковими ураженнями та зонами, трансформованими бактеріальними інфекціями. Взаємодія грибних і бактеріальних патологій формує комплексний патологічний фон. Активність патогена проявляється не лише у деструкції деревини окремих дерев, але й у формуванні структурних змін деревостанів, що має суттєве значення для оцінки стабільності лісових екосистем. Практична цінність дослідження полягає у використанні встановлених патологічних ознак для ранньої діагностики уражень *Phellinus hartigii* під час лісопатологічного моніторингу та прогнозування втрати механічної стійкості ялицевих деревостанів, що є основою для обґрунтування санітарно-лісогосподарських заходів

Ключові слова: *Abies alba*; дереворуйнівні гриби; біла гниль; деградація; патологічні зміни