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The problem of biotic stability of Carpathian forests under the influence of climate change: Theoretical analysis

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Abstract. The problem of preserving the biotic stability of forest ecosystems in the context of climate change is particularly relevant for the Ukrainian Carpathians, where climatic anomalies and anthropogenic influences exacerbate pathological processes and reduce the adaptive capacity of forest communities. The aim of the study was to theoretically summarise and critically analyse scientific ideas on the problem of biotic stability of Carpathian forests under the influence of climate change, with an emphasis on the role of climate-induced disturbances and internal biotic factors in the formation of pathological processes. The methodological basis of the study was a systematic and comparative analysis of scientific publications, a conceptual synthesis of literature data, and a generalisation of modern theoretical approaches in the field of forestry, ecology, and forest phytopathology. As a result, it was established that climate change is an active factor in reducing the biotic stability of forest ecosystems in the Ukrainian Carpathians, causing maladaptation of woody plants, disruption of competitive relationships

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between species, and an increase in the frequency of natural disturbances. It has been shown that climate-induced hydrothermal stresses create conditions for the realisation of the pathogenic potential of phytopathogenic organisms and play a decisive role in the formation of epiphytotic processes. It is substantiated that an important internal factor in the reduction of biotic stability is endophytic myco- and microbiota, in particular pathogenic obligates, which, under conditions of disruption of the homeostasis of the host plant, transition from a latent existence to active pathogenicity. It has been shown that the combination of climatic stresses and the presence of hidden infectious reservoirs causes the sudden and massive nature of many pathological phenomena in the Carpathian forests. The practical value of the work lies in the possibility of using the theoretical generalisations obtained to assess the level of biotic stability of forest ecosystems, predict phytopathological risks and develop adaptive forest management strategies aimed at maintaining and restoring their biotic stability in the context of climate change

Keywords: adaptive capacity of ecosystems; phytosanitary status; climate-induced stress; endophytic microorganisms; vital obligates; epiphytotic processes

Introduction

Global climate change is considered one of the key factors in the transformation of terrestrial ecosystems, particularly forests, leading to a decline in biodiversity, disruption of ecosystem functions and an increase in the frequency of destructive processes. Climate change is seen not only as a long-term trend, but also as an active catalyst for ecological instability, the consequences of which are increasingly manifested in the form of large-scale disturbances in the structure and functioning of forest ecosystems. Mountain regions, which are characterised by high biodiversity, complex spatial and temporal organisation, and limited opportunities for natural adaptation to rapid climate change, occupy a special place in this context. Mountain forests perform key climate regulation, soil protection and water conservation functions, and their degradation has regional and interregional environmental consequences.

According to the generalised assessments of IPBES (2019), FAO (2020) and the European Forest Institute (2022), climate change combined with biotic disturbances is considered one of the main drivers of the decline in the resilience of European forest ecosystems, with microbiotic complexes, including endophytic and opportunistic organisms, playing a key role in shaping the adaptive response of forests. Scientists P. Tretyak & Yu. Chernevyy (2022) investigated the impact of forest biomass growth on evaporation intensity and possible regional climate change. The authors analysed how changes in forest cover can affect the water balance in regions and contribute to changing climatic conditions, which has important implications for forest management and climate change forecasting.

The Ukrainian Carpathians are one of the key centres of biodiversity in Europe, but the current state of their forest ecosystems is shaped by a combination of long-term anthropogenic pressure and climate change. A number of studies show that these factors not only cause structural changes in forests, but also significantly alter the nature of biotic interactions, particularly between woody plants and microorganisms, including phytopathogens. A comprehensive analysis of the state of the mycobiota of protected ecosystems in the Ukrainian Carpathians is presented in the work of Ya.Yu. Bublyk & O.S. Klymyshyn (2023), which shows the high taxonomic diversity of xylotrophic ascomycetes and emphasises their role in wood destruction processes. At the same time, the phytopathogenic potential of individual taxa in this work is considered only briefly, without a detailed analysis of their impact on the weakening of living tree stands. The functional and spatial heterogeneity of forest ecosystems in the Carpathian region was analysed in detail by Yu.I. Chernevyi (2023), who showed that the current structure of forests is the result of the interaction of natural succession processes and long-term anthropogenic influence. The author emphasises the increasing vulnerability of forests to external stress factors, but the role of phytopathogenic and endophytic microorganisms in these processes remains outside the scope of special consideration.

The problems of preserving fungal diversity within nature conservation areas are summarised in the work of I.O. Dudka *et al*. (2019), which, despite its broader time frame, remains methodologically important for contemporary research. The authors emphasise the need to combine inventory and ecological approaches, while the phytopathogenic aspect of mycobiota and its relationship with the condition of woody plants requires further development. Among contemporary phytopathological studies, the works of I. Matsiakh (2021) occupy an important place among contemporary phytopathological studies, in which invasive pathogens are considered one of the key threats to the biodiversity of Ukrainian forests, and it is shown that climate change contributes to the spread of new disease agents and increases the susceptibility of woody plants to infections. These findings were experimentally confirmed in the work of I. Matsiakh *et al*. (2023), where the susceptibility of *Betula pendula* and *Alnus glutinosa* to species of the genus *Phytophthora* was studied under natural conditions in Western Ukraine, and it was proven that the intensity of damage is largely determined by the physiological stress state of plants. At the same time, both studies focus mainly on invasive pathogens and do not take into account the participation of autochthonous and endophytic mycobiota in the formation and modification of pathological processes in forest ecosystems.

A separate area of contemporary research concerns the role of endophytic mycobiota. The work of I.M. Kulbanska *et al*. (2022) shows that bacterial endophytes can act as direct pathogens of forest tree plants, in particular *Abies alba*, under conditions of disturbance of the physiological state of the host plant. This confirms the concept of hidden infections and points to the need for a comprehensive analysis of endophytic microbial communities. The practical consequences of phytopathogenic processes in the Carpathian forests are demonstrated in the work of I. Sopushynskyi *et al*. (2021), which found a significant deterioration in the quality of *Abies alba* wood due to infection with the fungus *Phellinus hartigii*. At the same time, the study focuses mainly on the characteristics of biological damage to wood and does not analyse the prerequisites for the development of pathology at the level of the forest biocenosis. In general, an analysis of scientific publications shows that studies of forest ecosystems in the Ukrainian Carpathians cover individual aspects of climate change, the structural organisation of forests, the diversity of mycobiota and phytopathological processes. At the same time, the issue of the relationship between climate-induced disturbances, structural transformation of forest communities, and the role of endophytic myco- and microbiota in the formation of mass (epiphytotic) pathologies of woody plants remains insufficiently generalised and systematically analysed, which determines the relevance of this study.

The aim of this article was to summarise and critically analyse scientific ideas about the transformation of forest ecosystems in the Ukrainian Carpathians under conditions of climate change, with an emphasis on the catalytic role of climatic factors in the development of phytopathological processes and the importance of endophytic myco- and microorganisms in the formation of mass pathologies of woody plants.

The research methodology was based on a review approach to the analysis of scientific literature on the impact of forest biomass growth on evaporation intensity and regional climate change. A systematic review method was used, which involves the selection, classification and analysis of publications from various sources to identify the main trends and factors that determine the relationship between forest biomass and climate change. A comparative analysis method was used to identify key patterns in climate change under the influence of forest ecosystems at the regional level.

Retrospective analysis of the transformation of forest vegetation in the Carpathians under the influence of climate change

Global climate change is currently considered one of the key factors in the transformation of biota and the decline in species biodiversity. The relevance of this issue was emphasised in the materials of the UN Conference on Environment and Development (Rio de Janeiro, 1992), the Conference of Environment Ministers (Sofia, 1995), the World Summit on Sustainable Development (Johannesburg, 2002), the International Botanical Congress (Vienna, 2005), the Rio+20 conference (2012) and other international forums (Didukh & Chornei, 2016). Research by Ya.P. Didukh & I.I. Chornei (2016) records a dynamic decline in the number of rare species, the expansion of adventive taxa, the transformation of biotopes, the disruption of consortium links and the degradation of cenoses. In this regard, climatologists and ecologists have proposed a number of scenarios for future climate change and corresponding changes in biotopes, with the aim of minimising expected ecological losses and preserving biodiversity. Mountainous natural complexes are particularly sensitive to climatic fluctuations, as they are characterised by high levels of biodiversity, the presence of unique types of biotopes and complex spatial and temporal organisation. The Carpathian region is one of the key centres of biodiversity in Europe, but at the same time it has been subjected to prolonged and intense anthropogenic impact. As noted by B.M. Bahniuk & Ya.P. Didukh (2002), the transformation of Carpathian ecosystems is caused by a combination of large-scale economic activity and climate change, which makes it difficult to distinguish between individual abiotic, biotic and anthropogenic factors. The works of L.M. Felbaba-Klushyna (2009) emphasise that one of the key ecological consequences of these processes is a decrease in forest cover and a disruption of the protective functions of forests, in particular soil protection, climate regulation and water regulation.

S.M. Stoiko (2018) draws attention to significant changes in the species structure of Carpathian forests, linking them to the large-scale replacement of native beech and fir-beech forests with artificial spruce plantations. This trend is also confirmed by studies by L.M. Felbaba-Klushyna (2009) and V. Parpan *et al*. (2014), which point to a decrease in the resistance of such plantations to biotic and climatic stresses. According to the generalisation by M.A. Holubets (2016), the structural restructuring of forests is accompanied by the active spread of invasive tree species, in particular *Quercus rubra* L., in the lower altitude zone, which further complicates the conservation of natural forest ecosystems in the Carpathians (Didukh & Chornei, 2016). Irrational logging technologies and excessive logging in the Carpathian region have become one of the key factors in the degradation of mountain ecosystems. B.M. Bahniuk & Ya. P. Didukh (2002) showed that intensive forest use led to the development of erosion processes with soil loss of up to 300 t/ha, and during 1960-2000, logging volumes exceeded scientifically based norms by approximately 20 million m^3 of wood. The authors emphasise that such violations have a long-term negative impact on the stability of forest ecosystems and their ability to regenerate naturally. The transformation of natural biotopes has also led to an increase in phytoinvasions. The study by V.V. Protopopova *et al*. (2010) provided a detailed analysis of the processes of phytocenosis impoverishment, insularisation of native species populations and hybridisation with alien taxa. The authors emphasised that invasive species significantly alter the structure of plant communities and disrupt trophic chains, reducing the ecological stability of forest biocenoses.

The further development of degradation processes in the Carpathian forests is associated with the spread of invasive pests and disease pathogens. According to I. Matsiakh (2021), the formation of epiphytotic foci is accompanied by a massive weakening and dieback of tree stands, which, in turn, leads to an increase in the frequency of windbreaks and windfalls. The author considered these phenomena as a complex consequence of anthropogenic pressure and a decrease in the biotic stability of forests. The formation of the forest cover of the Ukrainian Carpathians took place during the Holocene under the decisive influence of climatic fluctuations. In the early Holocene, forest-tundra and boreal communities dominated, with the participation of *Betula pendula*, *Pinus sylvestris* and *Picea abies*, which, according to H. Krynytskyi & P. Tretiak (2003), was due to colder post-glacial climatic conditions. During the Atlantic phase of the Holocene (8-4.5 thousand years ago), thermophilic broad-leaved forests spread, including species of the genera *Quercus*, *Ulmus*, *Acer*, *Fraxinus* and *Corylus*, which almost completely replaced the boreal vegetation. During the sub-boreal and sub-Atlantic periods, *Carpinus betulus*, *Fagus sylvatica* and *Abies alba* spread, leading to the formation of the modern altitudinal zonation of the Carpathian forests. As emphasised by S.M. Stoiko & Yu.P. Yermolenko (1976) and M.A. Holubets (2016), it was the combination of climatic changes and subsequent anthropogenic influence that determined the modern structure and spatial differentiation of the region's vegetation cover.

Anthropogenic impact on the vegetation of the Ukrainian Carpathians has a long history and can be traced back to the 8th-9th centuries. According to A.H. Soldatov *et al*. (1960) and S.A. Hensiruk (2002), the initial forms of economic development were local in nature, but in the 18th-19th centuries, anthropogenic pressure increased sharply as a result of massive deforestation of mountain forests. The authors point out that this period was a turning point in the transformation of the natural structure of the Carpathian landscapes. Intensive forest use resulted in the disruption of natural processes. A.V. Melnyk (1999) showed that the reduction in forest cover contributed to the intensification of erosion processes, the development of mudslides, floods and windfalls, which significantly increased natural hazards in mountainous areas. At the same time, phytosanitary problems have intensified: S.A. Hensiruk (2002) and I. Kruhlov *et al.* (2018) noted the spread of root rot and mass damage to artificially created spruce cultures in the foothill areas, which the authors associate with a violation of the principles of typological correspondence of species and low biotic resistance of monocultures.

Individual components of the mountain landscape that performed important ecosystem functions have also undergone significant transformations. In particular, I.P. Kovalchuk & A.B. Mykhnovych (2004) note the degradation of crooked forests, which has led to a disruption of water regulation and snow retention functions and an increased risk of flooding. The marsh and floodplain complexes of the Transcarpathian lowlands have also undergone significant changes, which, according to L.M. Felbaba-Klushyna (2009), are due to drainage and land development, resulting in a loss of biodiversity and simplification of ecosystem structures. The deterioration of the soil cover is another consequence of anthropogenic impact. B.M. Bahniuk & Ya.P. Didukh (2002) found that intensive land use is accompanied by processes of salinisation, secondary swamping, ogleisation and active humus leaching, which significantly limits the regenerative potential of plant communities and increases the overall vulnerability of landscapes. The increase in anthropogenic pressure in the foothill areas, associated with recreational activities, transport infrastructure, urbanisation and agricultural development, further exacerbates the fragmentation of natural biocenoses, where in some areas the proportion of arable land exceeds 20% (Felbaba-Klushyna, 2009).

Structural changes in the forest fund of the Carpathian region are confirmed by statistical data. According to O.I. Furdychko (2002), as of 1996, the area of forest land was 2,267,900 hectares (40.1% of the territory), while forested land accounted for 36.7% and mature and overmature stands accounted for only 4.6%. According to estimates by H. Krynytskyi & P. Tretiak (2003), average timber reserves amounted to about 250 m^3/ha, while in mature forests they amounted to 390-480 m^3/ha, which indicates an imbalance in the age structure and complicates the provision of sustainable forest use. Contemporary studies by I. Kruhlov *et al*. (2018) Yu.I. Chernevyi (2023) are aimed at predicting the future evolution of forest landscapes in the Carpathians under various climate scenarios using simulation models, in particular LANDIS-II, for the main forest-forming species – oak, beech, spruce, hornbeam, fir and maple. The results obtained form the scientific basis for the development of adaptive strategies for the management and preservation of the biotic stability of forest ecosystems in the Carpathian region. The structural and functional changes in the forest vegetation of the Carpathians identified in the retrospective analysis indicate the growing role of climatic factors in the transformation of modern phytocenoses. Changes in temperature, moisture regime and frequency of extreme weather events not only affect the species composition and productivity of plantations, but also create conditions for the disruption of their phytosanitary status and the intensification of phytopathological processes.

Climate change as a catalyst for phytosanitary disturbances and the development of phytopathological processes in forest communities

Climate change has a significant impact on the functioning of forest ecosystems, primarily due to disturbances in the hydrothermal regime and an increase in the frequency of extreme weather events. For long-lived organisms, particularly woody plants, the pace of modern climate change significantly exceeds their ability to adapt, leading to maladaptation of forests and a decline in their ecological stability (Seidl & Lexer, 2013). Under current conditions, climate-induced disturbances in forest ecosystems are seen not only as individual stress factors, but as catalysts for deeper structural and functional changes in forest communities. D. Thom *et al*. (2017) showed that droughts, floods and sharp temperature fluctuations disrupt the physiological balance of forest trees, reducing the effectiveness of their defence mechanisms. In turn, P. Tretyak & Yu. Chernevyy (2022) emphasised that shifts in seasonal precipitation patterns create favourable conditions for the activation of phytopathogenic organisms, which is particularly dangerous for weakened tree stands.

Within the framework of modern ecological theory, the idea of disturbances as a driving force for the reorganisation of ecosystems is becoming increasingly widespread. The conceptual basis for this approach was laid by L.H. Gunderson & C.S. Holling (2001), who view disturbances as a mechanism for ecosystems to transition into a phase of reorganisation, where structural and functional relationships are restructured. Developing this idea, S.A. Pulsford *et al*. (2016) showed that climate-induced disturbances can change competitive relationships between species, increase resource availability, and promote the formation of new, potentially more climate-adapted communities.

However, for forest ecosystems in the Carpathian region, the implementation of such adaptive scenarios is significantly complicated by the effects of long-term anthropogenic influence. R. Seidl & M.J. Lexer (2013) emphasised that simplifying the age and spatial structure of tree stands reduces their adaptive capacity and resistance to external disturbances. J.F. Johnstone *et al*. (2016) reached similar conclusions, noting that under conditions of reduced structural diversity, climatic disturbances do not stimulate recovery but, on the contrary, accelerate degradation processes, in particular the mass weakening and dieback of woody plants, the formation of persistent pathological foci and the development of epiphytotics.

Climate change also significantly affects the dynamics of interaction between the host plant and the phytopathogen. C. Brasier *et al*. (2004) showed that changes in temperature and humidity can modify the aggressiveness and virulence of disease pathogens. F.J. Ruiz-Gómez *et al*. (2019) supplemented these data, emphasising the change in the level of innate and acquired resistance of forest trees under climatic stress. In a regional context, I. Matsiakh *et al.* (2023) found that disruptions in the biological synchronisation of plant and pathogen life cycles lead to atypical pathological processes and increased intensity, which is an additional factor in reducing the biotic resilience of forests. The triggers for epiphytotics in forest ecosystems are usually prolonged droughts or excessive moisture. In particular, rising temperatures and reduced rainfall in the summer increase the vulnerability of trees to root rot caused by representatives of the *Phytophthora* and *Armillaria* genera, and also facilitate the colonisation of weakened trees by xylophagous insects, which accelerates their death and the formation of pathological foci.

Thus, climate change should be considered a key catalyst for phytopathological processes in the forest communities of the Carpathian region, the effect of which is realised through the disruption of the physiological balance of woody plants, changes in the ecological niches of phytopathogens, and the weakening of the self-regulating capacity of forest ecosystems. In these conditions, it is particularly important to analyse the role of endophytic myco- and microbiota, which are capable of transitioning from a latent existence to active pathogenicity under conditions of climate-induced stress.

Participation of endophytic myco- and microbiota in the formation of epiphytotic pathologies of forest tree species under climatic stress conditions

In modern forest phytopathology, tree diseases are traditionally interpreted as the result of external (exogenous) infection. The pathological process is described through inoculation (infection), incubation period and the disease itself, which may result in the death or complete/incomplete recovery of the plant. The incubation period is defined as the time from the exogenous penetration of the phytopathogen (obligate or facultative) to the appearance of the first symptoms. Its duration varies from several days (diseases of seeds, fruits, needles, leaves) to several years, for example, in pathologies associated with aphylophoroid macromycetes of the xylocomplex (*Phellinus igniarius*, *Ph. robustus*, *Ph. pini*, etc.). The idea of a hidden (latent) period of the disease, which actually meant the presence of myco- and microorganisms in visually healthy plants (including seeds), was expressed by A.L. Shcherbyn-Parfenenko during his research on bacteriosis, but without experimental confirmation (Shcherbyn-Parfenenko, 1963).

Experimental results, on the contrary, support the concept of an endogenous vector of pathologies through endophytic auto-myco- and microbiota (the biota of healthy plants and their organs), including the participation of phytopathogenic components (Goychuk & Rozenfeld, 2011). Central to this approach is the concept of "vital obligates" – microorganisms that normally perform protective, life-supporting and regulatory functions in plants. When systemic interactions in plants are disrupted, primarily metabolic processes under the influence of various factors, including abiotic ones (recently, hydrothermal stress has been considered a catalyst for the activity of vital obligates), pathogenic vital obligates are capable of initiating disease without the involvement of external infection, which is consistent with the manifestations of epiphytotic dieback of forest species, in particular *Pinus sylvestris* L. and *Picea abies* (L.) H. Karst. (Goychuk & Rozenfeld, 2011; Kulbanska *et al.,* 2022). Accordingly, if pathogenic vital obligates are part of the endophytic biota (even in minor quantities), a visually healthy plant is potentially infected: there are no symptoms, but the pathogenic component is in an "incubation" state, accompanying the plant throughout its ontogenesis and can be transmitted between generations, maintaining mutualistic relationships with other components of the automycota and microbiota and with the host plant.

An important methodological limitation is that plant-pathogen interactions are often considered in pairs, with minimal consideration of the role of the broader endophytic community. At the same time, it is the endophyte community that can determine the progression of the disease and/or the plant's immune response, especially in the case of complex diseases, when several phytopathogens act simultaneously, and saprotrophs and weak pathogens can synergise the primary infection and accelerate the dieback of the host plant. In the forest biocenosis, myco- and microorganisms are an integral functional component that accompanies woody plants at all stages of growth and development and participates in the utilisation of dead matter. Among their groups, phytopathogenic endophytes of various trophic specialisation occupy a special place, capable of causing significant ecological, economic and social damage, as confirmed by mass pathologies and tree dieback both in Ukraine and beyond its borders (Kulbanska *et al*., 2022). Endophytic microorganisms include both representatives of the kingdom Fungi (Mycota) and representatives of prokaryotes – Bacteria (Gouda *et al*., 2016).

The literature often focuses on the beneficial functions of endophytic fungi, but pathogenic species have not been sufficiently studied. At the same time, among the listed taxa there are facultative saprotrophs and pathogens (obligate pathogens among representatives of the auto-microbiota of woody plants, according to the literature, have not been noted), in particular Coelomycetes and representatives of *Leptostroma* spp., *Phomopsis* spp., *Phyllosticta* sp., *Phoma* sp., *Venturia ditricha*, etc., which are capable of colonising healthy organs and surviving when the plant dies (Schouten, 2019). The lack of information on aphylophore endophytic fungi is particularly emphasised: the nature of some pathologies and the formation of basidia in wood-destroying species indicates the need for in-depth study of *Polyporaceae*, in particular the causative agents of mixed stem rot (*Fomes fomentarius*, *Piptoporus betulinus*, etc.)

Endophytic fungi are considered important components of plant microbiota, capable of positively influencing the physiological state of the host plant. Many endophytes produce indoleacetic acid and other phytohormone-like compounds, participate in the secretion of stress-adaptive metabolites, and synthesise a wide range of biologically active substances. N. Radic & B. Strukelj (2012) demonstrated the ability of endophytic fungi to produce antibacterial compounds, while F. Uzma *et al*. (2018) reported the synthesis of anticarcinogenic molecules by endophytes, indicating their high biosynthetic potential.

A separate group of studies is devoted to the role of endophytes in the regulation of secondary plant metabolism. According to H.A. El Enshasy *et al.* (2019), association with endophytic fungi can stimulate the synthesis of essential oils, indicating the involvement of microorganisms in the modification of host plant metabolic pathways. In the context of phytosanitary stability, J. Poveda (2021) and J. Wen *et al.* (2022) emphasised the role of endophytes in the biocontrol of phytopathogens and stimulation of plant growth, as well as in the formation of induced systemic resistance to biotic stresses. Similarly, R. Cui *et al*. (2021) showed that endophytic fungi can increase plant tolerance to abiotic factors, particularly temperature and water stress. The interaction between the plant and endophytes is mutually beneficial. As noted by K.A. Odelade & O.O. Babalola (2019), the plant provides microorganisms with nutrients and a stable habitat, while endophytes enhance the adaptive potential of the host plant.

The results of studies of the endophytic microbiota of Scots pine (*Pinus sylvestris*) seeds are indicative in this context. A. Goychuk & V. Rozenfeld (2011) isolated micromycetes of the genera *Mucor, Trichoderma, Aspergillus, Penicillium, Alternaria, Acremonium* and yeast from healthy seeds, which exhibited selective antagonistic activity against bacterial endophytes of pine and collection strains. *Penicillium autogriseum* and *Alternaria alternata* showed the highest antagonistic activity, indicating their potential role in regulating the microbial balance of seeds. The same authors established that the limitation of the colonisation of *P. sylvestris* seeds by phytopathogenic bacteria is primarily associated with the action of microfungi and spore-forming bacteria, while among bacterial endophytes, including vital obligates, no antagonists promising for use as biological pesticides were found. Importantly, no components of the automicrobiota capable of stimulating the growth of phytopathogenic bacteria were found, confirming the protective function of the endophytic complex of seeds.

At the level of the forest biocenosis, fungi play a systemic role in the formation of consortia and xylolysis processes. A significant proportion of fungi are xylobionts, present at all stages of wood decomposition – from the damage of living woody plants to the complete mineralisation of plant residues. Another group of species is associated with soil and forest litter, including mycorrhizal fungi, with the spectrum of fungal interactions with woody plants ranging from neutral to strongly antagonistic. At the same time, the mycobiota of forests includes not only functionally important or “useful” species, but also dangerous phytopathogens capable of latently weakening living trees for a long time and initiating the formation of rot. The mycobiota of the Ukrainian Carpathians has been studied unevenly, but the available generalisations allow to assess the scale of its diversity and identify priority areas for conservation. Thus, according to the results of a comprehensive analysis by Ya.Yu. Bublyk & O.S. Klymyshyn (2023), the xylotrophic ascomycota of nature conservation sites in the region includes 406 *Ascomycota* taxa, represented by 190 genera, 66 families, 26 orders, 10 subclasses and 6 classes. The authors showed that the specialisation of wood-destroying ascomycetes in terms of substrates significantly depends on the life forms and species diversity of woody plants, which emphasises the close connection between mycobiota and the structure of forest communities.

A separate block of studies is devoted to the mycobiota of nature conservation areas. For the Hutsulshchyna National Nature Park (NNP), a number of studies (Fokshei & Derzhypilskyi, 2021; Bohoslavets & Prydiuk, 2023) confirm a high level of taxonomic diversity of fungi. According to the generalised data of M.V. Pasailiuk (2022), as of 1 January 2022, more than 1,000 species of fungi and fungus-like organisms have been identified in the park's forest communities, 23 of which are listed in the Red Book of Ukraine. This indicates the high conservation value of the region's mycobiota and its vulnerability to anthropogenic and climatic changes.

Ectomycorrhizal mycobiota also has an important functional significance. For the Western Carpathians, E. Luptáková & I. Mihál (2020) list 51 species of ectomycorrhizal fungi, among which *Ramaria formosa, Hygrophorus pustulatus, Lactarius aurantiacus, L. rufus, Paxillus involutus*, and others dominate. The authors emphasised the role of these species in succession processes, particularly during the reforestation of former agricultural land, which indicates their participation in the restoration of ecosystem functions. In addition to purely biocenotic aspects, modern research also draws attention to the applied ecological significance of fungi. In particular, M. Senila *et al*. (2024) demonstrated the ability of wild edible fungi (*Cantharellus cibarius, Boletus edulis, Amanita rubescens*) to accumulate toxic metals in the mountainous regions of the Western Carpathians. The results obtained emphasise the need to consider mycobiota not only as a component of forest ecosystems, but also as a potential indicator of ecological status and a risk factor for humans.

The problems of studying the diversity of fungi in the Ukrainian Carpathians and preserving their gene pool are considered closely interrelated in modern research. As noted by I.O. Dudka *et al.* (2019), establishing the boundaries of the range, degree of endemism and ecological specialisation of species is key to correctly assessing their actual rarity, as well as the sensitivity of forest phytocenoses to anthropogenic and climatic changes. This approach allows to move from a formal list of species to an assessment of their functional and conservation significance. In this context, considerable attention is paid to nature conservation areas. For the Hutsulshchyna National Nature Park, S.I. Fokshei & L.M. Derzhypilskyi (2021) provided a list of rare mushroom species included in the Red Book of Ukraine, as well as taxa that are rare on a national scale. These data confirm the high biological value of the park's forest communities and the need for their targeted protection.

Along with the nature conservation aspects, studies of mycobiota emphasise its functional role in forest ecosystems. In particular, Ya.Yu. Bublyk & O.S. Klymyshyn (2023) emphasised the importance of xylotrophic ascomycobiota in the processes of dead wood destruction, which is an important component of the cycle of substances. At the same time, these same communities may include phytopathogenic species capable of affecting the condition of living trees. Thus, in the process of beech wood destruction in the Hutsulshchyna National Nature Park, M.V. Pasailiuk (2022) identified 50 species of fungi and fungus-like organisms, which indicates the complex and multi-component nature of mycobiotic succession.

The practical aspect of the problem is illustrated by studies on the impact of fungi on wood quality. I. Sopushynskyi *et al*. (2021) analysed changes in the trunk wood of *Abies alba* affected by *Phellinus hartigii*, showing a significant decrease in its technical characteristics. Similar results are supplemented by data from the Gorgany Nature Reserve, where O.M. Bohoslavets (2023) found 25 species of fungi on woody substrates, including a number of valuable and significant finds. Taken together, these studies indicate that although the species composition of fungi in the Carpathian region has been broadly outlined, questions regarding phytopathogenic species, their ecological and trophic specialisation, and their role in the transformation of forest ecosystems remain insufficiently explored. This justifies the need for further systematic and structural studies, in particular of the mycobiota of forests with *Abies alba* in the Pokuttia and Bukovyna Carpathians.

Endophytic bacteria of woody plants are generally less studied than endophytes of agricultural crops, where the focus is on their benefits (Izumi, 2011). At the same time, it has been reported that important tree genera, including *Pinus, Populus*, and *Picea*, contain bacterial endophytes of the genera *Bacillus, Paenibacillus*, and *Pseudomonas*, which potentially contribute to nitrogen fixation and biomass increase (Puri *et al*., 2017). Among the main groups of endophytic bacterial communities of many tree species are *Pseudomonas, Bacillus, Actinobacteria, Acinetobacter*, and *Sphingomonas* (Izumi, 2011). It has been shown that endophytes can suppress disease development through the synthesis of structural compounds and fungitoxic metabolites and the induction of acquired systemic resistance (Sturz & Nowak, 2000). The growth-stimulating mechanisms of endophytes are associated with the production of IAA, solubilisation of mineral phosphate, acid phosphatase activity, the presence of the ACC deaminase gene, nitrogen fixation and degradation of biopolymers (War Nongkhla & Joshi, 2014), and the phenotypes of plant-endophyte interactions are plastic depending on environmental conditions, nutrition, genetic predisposition, etc. (Anand *et al*., 2006). A range of isolated endophytic bacteria (*Bacillus, Erwinia, Flavobacterium, Pseudomonas, Cytophaga, Leuconostoc, Micrococcus, Xanthomonas*) has been described for *Picea abies* seeds (Cankar *et al*., 2005), and phytopathogenic (*Pseudomonas syringae, Pectobacterium caratovorum, Enterobacter (Lelliottia) nimipressurallis*), conditionally pathogenic (*P. fluorescens, Paenibacillus polymyxa, Pantoea agglomerans*) and saprotrophic bacteria (*Bacillus subtillis, B. pumillus*), as well as fungi (Goychuk, & Rozenfeld, 2019). J.K. Stone *et al*. (2000) conceptually describe "endophytic" infections as inconspicuous: the tissues of the host plant remain asymptomatic for some time, and colonisation is proven histologically, by isolation from superficially disinfected tissues, or molecularly (DNA amplification). Thus, endophytic bacteria are a functionally important component of woody plants, but the pathogenic component of endophytic automycota and microbiota can be a powerful vector in the development of epiphytotic forest pathologies.

The realisation of the pathogenic potential of microbiota in forest ecosystems is closely related to the physiological state of woody plants and the effectiveness of their defence mechanisms. Thus, further analysis should be focused on revealing the physiological basis of plant biotic resistance, in particular the processes of stress adaptation, immune response formation and resistance in conditions of climate change.

Physiological and biochemical foundations of biotic stability in woody plants: Stress, immunity and resistance in a changing climate

Infection of plants with phytopathogenic organisms, as well as the action of physical, chemical, biotic and mechanical environmental factors, cause corresponding protective reactions in the plant organism. These reactions manifest themselves in the strengthening of cell walls, the synthesis of signalling compounds and phytoalexins, the formation of hypersensitivity reactions and other immune response mechanisms. When the sensitivity threshold is exceeded, the impact of such factors becomes stressful and can lead to the development of pathological, including irreversible, processes (Scheel, 1998).

Adverse factors that exceed background values are defined as stressors, and the response of a plant organism to deviations from optimal conditions is defined as stress. For plants, stress is considered to be external conditions that negatively affect growth, development, and productivity (Verma *et al.*, 2013). Depending on the intensity and duration of stressors, either specific resistance mechanisms or non-specific reactions, which are often destructive in nature, are formed (Bessonova & Yakovlieva-Nosar, 2014). Within the classical concept of H. Sele (2016), stress was considered as a general non-specific adaptive response of the organism to the action of adverse environmental factors. The set of changes that occur in response to stress is described as an adaptation syndrome, within which the phases of anxiety, recovery, exhaustion and regeneration are distinguished (Kosakivska, 2008). The anxiety phase is accompanied by a decrease in viability and a violation of functional norms; the recovery phase includes adaptive and reparative processes and the formation of increased resistance. With excessive intensity or duration of stressors, a phase of exhaustion occurs, ending in the chronic development of disease or death of the plant. After the cessation of stress factors, restoration of functions and partial or complete regeneration are possible, leading to acclimatisation.

For a more correct use of the concept of stress, the term "phytostress" has been proposed, which refers to the reaction of a plant to any deviation from optimal conditions of existence (Prysedskyi, 2017). During the acclimatisation process, resistance to the stressor is formed; acclimatisation is not inherited. In scientific literature, the term adaptation is often used as a synonym, which means a state of increased resistance to repeated exposure to the same or another factor (cross-adaptation). Hereditary fixation of adaptive traits is referred to as genetic adaptation, accompanied by changes in gene expression: inhibition of growth and photosynthesis genes and activation of genes for the synthesis of protectors, adaptogens and stress proteins. The stability of the functioning parameters of a plant organism under conditions of minor environmental fluctuations is ensured by homeostatic mechanisms. Homeostasis V.P. Bessonova & V.P. Yakovlieva-Nosar (2014) considered homeostasis to be the ability of biological systems to maintain relative stability of the internal environment through autoregulation and control of metabolic processes.

The concept of plant resistance is interpreted ambiguously in scientific literature, which is due to the multilevel nature of the phenomenon itself. In most definitions, resistance is considered as the ability of a plant organism to withstand the effects of adverse environmental factors and preserve its morphological structure and functional properties. This interpretation is characteristic of the physiological and ecological approach presented in the works of M.M. Musiienko (2005) and Yu.H. Prysedskyi (2017), where the emphasis is on maintaining plant homeostasis under stress conditions. At the same time, a number of researchers emphasise the genetic nature of resistance. From the perspective of evolutionary biology, V.P. Bessonova & V.P. Yakovlieva-Nosar (2014) considered it as a result of the co-evolution of plants and pathogens, which is realised through complementary gene pairs of the "virulence – resistance gene" type. Within this approach, resistance is interpreted not as a static trait, but as a dynamic result of the interaction of genotypes in a changing environment.

An important characteristic of resilience is its variability throughout ontogenesis and dependence on environmental conditions. As experimental and theoretical studies show, it is often realised as a potential property that manifests itself only under the influence of stressful or extreme factors. This indicates a close connection between stability and the adaptive capabilities of plant organisms and the plasticity of their regulatory systems. The theoretical foundations of the modern understanding of plant stability are linked to ideas about the functioning of living systems as open, nonlinear, and self-regulating. In this context, M.D. Yevtushenko *et al.* (2004) consider resilience through the prism of thermodynamics and synergetics, emphasising the role of self-organisation and maintenance of structural order under conditions of constant exposure to external factors. This systematic approach has made it possible to integrate physiological, genetic and ecological aspects of stability into a single conceptual model.

In response to abiotic factors, specialised types of resistance (winter hardiness, heat resistance, drought resistance, salt tolerance, etc.) are formed, which may be of a compromising nature. Of particular importance is disease resistance, which determines the ability of a plant to prevent or limit the development of an infectious agent and influence the course of pathogenesis. Pathogens exert their influence through phytotoxins and hydrolytic enzymes, which destroy cell walls, forming “infection gateways” and facilitating penetration into plant tissues. Resistance is ontogenetically variable: it is minimal at the seed germination stage, increases during the formation of vegetative organs, and decreases in the generative phase; its maximum level is characteristic of the state of anabiosis (spores, seeds) (Bessonova & Yakovlieva-Nosar, 2014).

A similar term is resistance, which is interpreted as the resistance or immunity of an organism to infectious agents and other external factors (Yevtushenko *et al.*, 2004). According to N.I. Vavilov’s classification, resistance is divided into species (non-specific, horizontal) and varietal (specific, vertical). Species resistance provides plant phytoimmunity, while varietal resistance is controlled by mono- or oligogenes, is race-specific and is often unstable due to the rapid adaptation of pathogens (Kriuchkova *et al.*, 2010). In breeding practice, it is combined with non-specific resistance to increase the duration of the effect. According to H.H. Flor’s (1947) “gene for gene” hypothesis, susceptibility is a recessive trait, while resistance is a dominant trait.

Despite the widespread use of the term “biotic resistance,” there is no single generally accepted definition of this concept in the scientific literature. In most modern works, biotic resistance is considered as the ability of a plant to counteract the negative effects of biotic stressors – bacteria, viruses, fungi, nematodes, insects, and other consumers. In particular, A. Gull *et al.* (2019) and O.B. Umar *et al.* (2021) emphasise that, unlike abiotic factors, biotic agents interact directly with the host plant, consuming its nutrients and disrupting its metabolic balance.

In response to the invasion of biotic agents, plants activate multilevel defence responses. N.J. Atkinson & P.E. Urwin (2012) showed that one of the early responses is the intensive formation of reactive oxygen species, which perform a signalling function, as well as the activation of antioxidant systems to prevent oxidative damage. At the same time, lignification of cell walls increases, which physically limits the penetration of pathogens and reduces the susceptibility of tissues to further invasion. Summarising these approaches, A. Gull *et al*. (2019) considered biotic resistance as an integral property of a plant organism, formed as a result of coordinated morphological, physiological and biochemical regulation. This approach allows biotic resistance to be interpreted not as a separate response to a pathogen, but as the result of a complex interaction of defence mechanisms aimed at maintaining the functional integrity of the plant under conditions of constant biotic pressure.

Thus, the biotic resistance of plants is an integral property that is formed as a result of the coordinated action of morphological, physiological, biochemical, and genetically determined mechanisms in response to constant biotic pressure. Understanding these processes in forest ecosystems is crucial for assessing their stability and predicting the consequences of anthropogenic and climatic changes.

Conclusions

It has been substantiated that endophytic myco- and microbiota are an integral component of forest woody plants and, under conditions of disturbance of the homeostasis of the host plant, can transition from a latent existence to active pathogenicity, forming an internal (endogenous) mechanism for the development of infectious pathologies. Vital obligates are considered an important source of hidden infection, capable of realising pathogenic potential without external signs of damage, which causes the sudden and massive nature of many epiphytotic processes in modern forest ecosystems. Climate-induced stress contributes to the activation of such hidden infectious reservoirs, changes the dynamics of interaction between the host plant and the complex of pathogens, and complicates the course of phytopathological processes, forming complex syndromes of damage to woody plants.

The generalisations obtained indicate the need to rethink traditional approaches to assessing the sanitary condition of forests and to develop adaptive forest management strategies that take into account the role of climate change, endophytic microbiota and hidden infections in the formation of pathological processes and ensuring the biotic stability of forest ecosystems in the Carpathians. Prospects for further research are related to an in-depth study of the structure and functional role of endophytic microbial complexes in different types of forest stands, assessment of their interaction with climatic stressors, and the development of integrated approaches to predicting phytopathological risks in the context of climate change.

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Проблема біотичної стійкості карпатських лісів під впливом кліматичних змін: теоретичний аналіз

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Анотація. Проблема збереження біотичної стійкості лісових екосистем у контексті кліматичних змін набуває особливої актуальності для Українських Карпат, де кліматичні аномалії та антропогенні впливи посилюють патологічні процеси та знижують адаптивні можливості лісових ценозів. Метою роботи було теоретичне узагальнення та критичний аналіз наукових уявлень щодо проблеми біотичної стійкості карпатських лісів під впливом кліматичних змін з акцентом на роль кліматоіндукованих порушень і внутрішніх біотичних чинників у формуванні патологічних процесів. Методологічною основою дослідження були системний і порівняльний аналіз наукових публікацій, концептуальний синтез літературних даних та узагальнення сучасних теоретичних підходів у галузі лісівництва, екології та лісової фітопатології. У результаті встановлено, що кліматичні зміни виступають активним чинником зниження біотичної стійкості лісових екосистем Українських Карпат, спричиняючи дезадаптацію деревних рослин, порушення конкурентних взаємовідносин між видами та зростання частоти природних порушень. Показано, що кліматоіндуковані гідротермічні стреси створюють умови для реалізації патогенного потенціалу фітопатогенних організмів і відіграють визначальну роль у формуванні епіфітотійних процесів. Обґрунтовано, що важливим внутрішнім чинником зниження біотичної стійкості є ендофітна міко- та мікробіота, зокрема патогенні вітальні обліґати, які за умов порушення гомеостазу рослини-господаря переходять від латентного існування до активної патогенності. Показано, що поєднання кліматичних стресів і наявності прихованих інфекційних резервуарів зумовлює раптовий і масовий характер багатьох патологічних явищ у карпатських лісах. Практична цінність роботи полягає у можливості використання отриманих теоретичних узагальнень для оцінки рівня біотичної стійкості лісових екосистем, прогнозування фітопатологічних ризиків та розробки адаптивних стратегій управління лісами, спрямованих на підтримання і відновлення їх біотичної стійкості в умовах кліматичних змін

Ключові слова: адаптивна здатність екосистем; фітосанітарний стан; кліматоіндукований стрес; ендофітні мікроорганізми; вітальні обліґати; епіфітотійні процеси