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Rare plant species of the natural forest stands in the Feofania tract and their phytocoenotic association (Kyiv, Ukraine)

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Abstract. Clarifying the current state of distribution of plant species included in the Red Data Book of Ukraine, in particular in the territory of the Feofania tract, is becoming especially relevant, since they are sensitive markers of the level of anthropogenic impact and changes occurring in ecosystems. The aim of the study was to identify new habitats of rare plant species in natural forest stands of the Feofania tract (Kyiv, Ukraine) and to clarify their phytocenotic localisation. Monitoring and geobotanical studies were conducted within the tract during the growing seasons of 2009-2012 and 2021-2024. The structure and condition of the forest stands were also assessed as part of the study. A decline in mature *Quercus robur* and *Carpinus betulus*

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trees was observed, reflecting ongoing ecological changes within the forest ecosystem. As a result, new localities of *Lilium martagon*, *Neottia nidus-avis* were established, and *Epipactis helleborine* was also found for the first time. It is mentioned that *Cephalanthera longifolia*, found on the territory of the Feofania tract in the 80s of the 20^{th} century, apparently disappeared from the studied area. It has been noted that anthropogenic impact on the location of rare species is increasing. This is confirmed by the penetration of invasive species, in particular Impatiens parviflora, into the phytocoenoses where they occur. Here in the first decade of the 21^{st} century such species from the Red Data Book of Ukraine as *Allium ursinum*, *Crocus heuffelianus*, *Erythronium dens-canis*, *Galanthus plicatus*, G. nivalis, Gymnospermium odessanum were successfully introduced. Phytocoenoses with the participation of Neottia nidus-avis were detected in the territory of the second compartment (the 6^{th} subcompartment) of the Feofania Monument Park with a stock of wood of the first and second tiers of about 380 m^3/ha and the third compartment (the 6^{th} subcompartment) with a stock of wood of two tiers of about 330 m^3/ha. Regionally rare species Convallaria majalis and Corydalis cava also occur on the territory of the tract. The information obtained will be useful for biomonitoring, distribution and dynamics of these species and phytocoenoses in which they occur

Keywords: rare species; *Epipactis helleborine*; *Lilium martagon*; *Neottia nidus-avis*; protection; anthropogenic impact

Introduction

Parks, squares, gardens and other objects of the green zone play an important role in megalopolises and cities being their integral component. Artificial green spaces, natural forests, floodplain and dry meadows, swamps and other plant complexes not only surround cities, but also are the part of their urban landscapes. They directly influence on the microclimate, purify the air from dust and gases and saturate it with oxygen, delay winds and precipitation, reduce surface runoff, prevent excessive evaporation of moisture and formation of dust storms. In addition, they are of strategic importance, as they are stocks of wood, medicinal, edible and fodder plants, as well as a natural obstacle for enemies. For city dwellers, the green zone is a place of rest and interaction with nature in order to learn about it and obtain aesthetic and intellectual satisfaction. However, large cities are characterised by a high level of anthropogenic load on the flora, which negatively affects the floristic diversity of woodlands, parks and other green areas. In such conditions rare species are sensitive indicators of the state of the environment, including the natural forest stands in which they occur. Therefore, detecting their presence or disappearance is extremely relevant for understanding the state of forest ecosystems.

The study by S. Koniakin & L. Gubar (2022) focused on the spontaneous flora of the Feofania tract (Kyiv, Ukraine). The authors carried out an inventory of vascular plants, determined the floral structure by life forms and ecological groups, and assessed the degree of anthropogenic transformation of the vegetation cover. The paper identified species listed in the Red Data Book of Ukraine and outlined changes in the flora under urbanisation pressure. The results provide a basis for further monitoring of rare species and assessment of the ecological condition of Feofania habitats. P. Marinov & M. Mihailova (2024) drew attention to the importance of preserving and creating forest areas in modern cities, as they are an important and effective tool for solving problems related to urbanisation and climate change. J.P. Schmit *et al*. (2025) investigated the impact of urban development and human economic activity on forest tree composition, diversity, and structure and pointed to the impoverishment of the age structure and species diversity of forest ecosystems surrounded by urbanised and agricultural areas. In their research M. Baker *et al*. (2025) noted that Urban woodlands require rapid, iterative assessment of their composition, structure, and condition at the local government level.

In their study, N.F. Sonti *et al*. (2024) pointed out the importance of continuous monitoring and protection of forest natural areas given their unique contribution to ecosystem services and taking into account the increasing anthropogenic impact and climate change. O.I. Shynder *et al*. (2024) did floristic research in the territory of Kyiv City and its environs (in the adjacent territories of Kyiv Region). The authors found five new taxa for the flora of Ukraine. Among all discovered taxa there were rare aboriginal and expansive alien. The results confirm the high level of the richness of the studied flora and its rapidly changing character. N.A. Pashkevych (2020) studied the biotopes of the Feofania Gardens. The author pointed out the main aspects of recreational impact on the natural vegetation of Feofania. The impact was regular and unlimited. The study gave an example of the interpretation of park and semi-natural forest vegetation due to the habitat concept.

However, these studies did not mention rare species and their confinement to a specific biotope. Thus, previous studies did not allow to establish the phytocenotic confinement of natural rare plant species, their belonging to a specific habitat, as well as to use these materials for further monitoring. Thus, the purpose of the study was to supplement existing biodiversity databases, which allows to clarify the current state and development trends of forest ecosystems in Feofania Park, and to promote effective biomonitoring of rare species and their habitats in the future.

Materials and Methods

Geobotanical studies of the vegetation cover of the Feofania tract (Kyiv, Ukraine) were conducted using the floristic classification approach of J. Braun-Blanquet in combination with general floristic surveys (Fig. 1). Field investigations were carried out during the vegetation periods from late April to August in two stages: 2009-2012 and 2021-2024. During the first stage, more than 120 geobotanical relevés were made, while additional 84 – during the second one. Alongside the geobotanical surveys, regular monitoring of previously documented habitats of rare plant species was undertaken, and systematic field inspections were conducted to identify additional localities. Data were collected on species composition, the vertical structure of forest stands, and the distribution of rare plant species within different forest communities. During the second study period, repeated surveys of forest stands were performed to document changes in species composition and stand structure under conditions of increasing anthropogenic pressure, climatic variability, the spread of tree diseases and pests, and the decline of old-growth trees. Particular attention was paid to the phytocoenotic affiliation of rare species, allowing their occurrence to be assessed within the context of forest community structure.

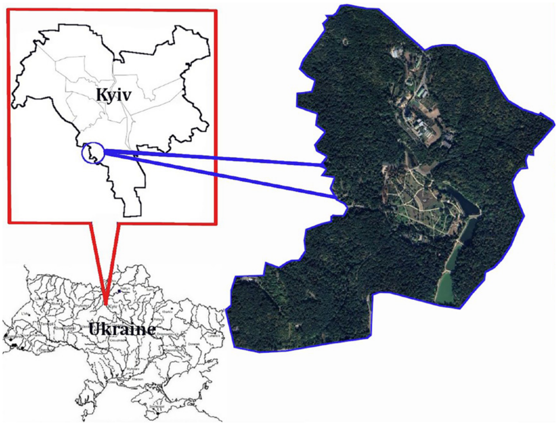

Figure 1. Location of the Feofania tract
Source: developed by the authors with using Google Earth Pro and GNU Gimp 2.10.18

The research was conducted in compliance with ethical standards (Convention on Biological Diversity, 1992). Latin names of species followed the nomenclature of S. Mosyakin & M. Fedoronchuk (1999). The names of syntaxa followed the nomenclature of D. Dubyna *et al.* (2019). Photographs of rare species included in national red lists (Red Data Book of Ukraine, 2009; Order of the Ministry..., 2021), together with their geographic coordinates, were uploaded to the iNaturalist platform (Kozyr, 2024). This allowed the integration of new records into species-specific databases and the supplementation of existing data on distribution and abundance, which may be used in further monitoring and analyses of distribution patterns. In addition, the uploaded georeferenced photographs enabled verification of taxonomic identification. Links to species records on the iNaturalist (n.d.) platform are provided in the text as of early 2025. Devices equipped with integrated GPS modules were used for coordinate recording. Positioning accuracy, according to navigation software (Android Speedometer, GPS Test), ranged from 1 to 7 m. Coordinates were recorded in decimal degrees. At locations where rare species occurred, test plots measuring 25 × 25 m were established to clarify the phytocoenotic affiliation of these sites.

Results and Discussion

The Feofania tract is one of the well-preserved unique objects of the green zone of the Holosiiv district in Kyiv. In the past the tract was the only large forest massif along with Lysa Gora and Holosiivsky forest (Goncharenko *et al.*, 2013). Its area is 150 hectares, of which about 130 hectares are natural massifs mainly formed by oak-hornbeam-maple, oak-hornbeam, hornbeam and other phytocoenoses of forest vegetation, which occur less often than the previous ones. Because of the active urban development of the metropolis, the number of visitors has increased significantly (in general, recreational load has been increasing every year since the 1980s (Goncharenko *et al.*, 2013). Various impacts on vegetation and animal life have accordingly increased. Because of construction close to the park, trampling, walking of domestic animals, laying of paths and roads, and natural changes in phytocoenoses, alien species displace gradually natural ones. Rare species of plants suffer the most from this, since the localities of their population in the studied territory are already insignificant. Therefore, the updating of information on rare species of flora will make it possible to provide measures for the protection and monitoring of the population of rare species and the phytocoenosis in which they grow and, thus, to preserve the floristic and phytocoenotic wealth of the tract.

According to a study by Yu. Kleopov (1990), herbaceous plants are an important component of forests. Some of these plants are indicators of forest vegetation conditions (Pogrebnyak, 1955). Rare and endangered herbal species of such phytocoenoses, particularly of the Feofania tract, are sensitive indicators of the ecological balance of forest ecosystems. The disappearance of their localities indicates risks and disturbances that can lead to irreversible changes in the biodiversity of the forest ecosystem and, as a result, the impoverishment of its gene pool.

During studies of the Feofania tract, new habitats of natural species included in the Red Data Book of Ukraine were found: *Lilium martagon*, *Neottia nidus-avis*, *Epipactis helleborine* (this species was found for the first time in the park and had not been mentioned here before). Since significant attention is being paid to the protection of habitats where species exist, as one of the ways to protect rare species in particular and biodiversity in general, the main idea of the research was to establish the phytocoenotic localisation of the found rare species. This is because the habitats are based on phytocoenoses in one way or another, and therefore, the establishment of communities in which rare species grow will allow for the establishment of habitats, more effective protection of biodiversity in general. So, in total 15 habitats of rare species were found where it was made geobotanical relevés. Of these, 9 involved *Lilium martagon*, *Neottia nidus-avis* was present in 5 relevés, and *Epipactis helleborine* was noted in only one (Table 1).

Table 1. Locations of rare plant species recorded during the 2021-2024 monitoring period

Species name	Coordinates of location	Conservation status/degree of vulnerability	Phytocoenosis name	Degree and type of anthropogenic impact	Presence of individuals
Epipactis helleborine	50.347275°N, 30.493608°E	RDBU CITES	*Aceri platanoidis-Fraxinetum excelsioris*	R	+
Lilium martagon	50.336967°N, 30.485952°E	RDBU	*Aceri platanoidis-Fraxinetum excelsioris*	R	–
	50.343257°N, 30.496245°E	–//–	–//–	R	–
	50.342685°N, 30.484599°E	–//–	–//–	R	+
	50.344381°N, 30.483819°E	–//–	–//–	R	+
	50.342945°N, 30.485174°E	–//–	–//–	R	+
	50.344555°N, 30.480988°E	–//–	–//–	R	+
	50.345112°N, 30.482742°E	–//–	–//–	R	+
	50.343193°N, 30.482908°E	–//–	–//–	R	+
	50.343403°N, 30.495335°E	–//–	–//–	R	+

Table 1, Continued

Species name	Coordinates of location	Conservation status/degree of vulnerability	Phytocoenosis name	Degree and type of anthropogenic impact	Presence of individuals
Neottia nidus-avis	50.344028°N, 30.485397°E	RDBU, CITES	*Aceri platanoidis-Fraxinetum excelsioris*	R	+
	50.336578°N, 30.489725°E	–//–	*Galeobdolo lutei- Carpinetum*	R	+
	50.336417°N, 30.491606°E	–//–	–//–	R	+
	50.344261°N, 30.492887°E	–//–	–//–	R	+
	50.343399°N, 30.493150°E	–//–	–//–	R	+

Note: R – recreation, CITES – Convention on International Trade in Endangered Species of Wild Fauna and Flora, RDBU – Red Book of Ukraine
Source: developed by the authors

Based on an analysis of published sources and original data, four natural rare species included in the Red Data Book of Ukraine (Didukh, 2009) were documented within the Feofania tract during the study period: *Epipactis helleborine, Neottia nidus-avis, Lilium martagon, Cephalanthera longifolia*. Two of them are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (1983): *E. helleborine* and N. nidus-avis. V. Lyubchenko (1983) and Y. Shelyag-Sosonko *et al.* (2009) mentioned the occurrence of *Cephalanthera longifolia*, but no locations of this species have been recorded since 1983. Rare introduced plant species are also found here: *Allium ursinum, Crocus heuffelianus, Erythronium dens-canis, Galanthus nivalis, Galanthus plicatus, Gymnospermium odessanum*. In addition to those already listed, regionally rare species for the city of Kyiv – *Convallaria majalis, Corydalis cava* – occur in abundance on the territory of Feofania (Andrienko & Peregrym, 2012).

Epipactis helleborine (Orchidaceae) is a polymorphic species with a wide ecological and cenotic amplitude, a hemicryptophyte, its conservation status is unvalued (Order of the Ministry..., 2021). The species is native to the Palearctic. It has also been naturalised in North America. In Ukraine, it occurs in forest, forest-steppe, steppe zones, the Carpathians, and the Mountainous Crimea. It is known in all administrative regions of Ukraine. For the first time the only location of *Epipactis helleborine* was discovered by on the territory of the tract at the end of May 2024 on a small slope of western exposure in a hornbeam-oak forest near the road (Kozyr, 2024). In Information on the habitat of this and other rare species currently noted for convenience was summarised in Table 1.

The coenosis has a four-tier structure with 26 identified species of higher vascular plants. The first tier formed by *Quercus robur* and *Acer plathanoides* is up to 25 m high with a crown density (c. d.) of 0.2 and 0.15, respectively. The second tier formed by *Carpinus betulus* (crown density 0.45) is up to 18 m high. The undergrowth represented by *Euonymus europaeus*, *E. verrucosus* is weak, up to 1 m tall, and has a projective coverage of 3-5%. The fourth, grassy tier has a projective coverage of 80% and is up to 30 cm tall. In terms of species composition, it is typical of oak-hornbeam forests, but due to significant anthropogenic impact, 3/4 of the projective coverage at the end of spring – the beginning of summer is occupied by *Impatiens parviflora*. The number of *I. parviflora* per 1 m^2 is over 30, although every year at the beginning of spring there is an early spring synusia here, consisting of species common to similar plant communities. The phytocoenosis belongs to the association *Aceri platanoidis-Fraxinetum excelsioris* Onyshchenko 1998 (Dubyna *et al.*, 2019). In general, *Epipactis helleborine* is typical for forest phytocoenoses in Kyiv. Researchers noted it in the forest areas of the Holosiivskyi Forest, located a few kilometers north of the Feofania tract (Parnikoza & Shevchenko, 2007; Parnikoza *et al.*, 2008; Gubar & Koniakin, 2021). According to the assumption, the species spread from the territory of the National Natural Park "Holosiivskyi".

According to Order of the Ministry of Environmental Protection and Natural Resources of Ukraine No. 111 (2021) *Lilium martagon* (Liliaceae) is a geophyte with a disjunctive range. Its conservation status is unvalued. The species' range is European-Siberian. In Ukraine, it is known in Polissya, the Forest-Steppe, the Carpathians, Transcarpathia, Ciskarpattia, Opilla, and Roztochchy. Administratively, the species is present everywhere except Crimea, Luhansk, Donetsk, Zaporizhzhia, Kherson, Mykolaiv and Dnipropetrovsk regions (Didukh, 2009). On the territory of the tract, the species were noted in 9 localities, however, in two of them it has not been recorded for several years (50.336967°N, 30.485952°E; 50.343257°N, 30.496245°E). Coordinates of the points where the species is present as of 2024 are the following (Fig. 1): 1) 50.342685°N, 30.484599°E; 2) 50.344381°N, 30.483819°E; 3) 50.342945°N, 30.485174°E; 4) 50.344555°N, 30.480988°E; 5) 50.345112°N, 30.482742°E; 6) 50.343193°N, 30.482908°E; 7) 50.343403°N, 30.495335°E (Kozyr, 2024). Phytocoenoses in which *L. martagon* grows usually have 2-3 woody tiers, an understory tier, and a grass tier. The first tier, up to 23-27 m tall, is formed by *Quercus robur* (c. d. 0.15-0.35) with an admixture of *Tilia cordata* (c. d. up to 0.3), *Acer platanoides* (c. d. 0.1-0.2), and *Carpinus betulus* (c. d. up to 0.75). The second tier, up to 20 m tall, is represented by *A. platanoides* (c. d. 0.1-0.2), *C. betulus* (c. d. 0.1-0.45), sometimes with an admixture of *T. cordata* (c. d. 0.05). The third tier, 15 m tall, is less pronounced and is formed by *A. platanoides* (c. d. up to 0.1), *C. betulus* (c. d. up to 0.23). The undergrowth, up to 1-2.5 m tall and with a projective coverage of up to 20%, is formed by *Sambucus nigra*, *Euonymus europaea*, and *E. verrucosa*. Typical representatives of oak-hornbeam forests form a grass tier up to 30-40 cm tall and with a projective coverage of 6-88%. It is important to note that *Impatiens parviflora* is present in most communities (sometimes it has a projective coverage of up to 45%, the number of individuals per 1 m^2 can be more than 20-30), which clearly indicates excessive anthropogenic impact. Phytocoenoses with the participation of *L. martagon* in the territory of the tract usually occur in groups of the association *Aceri platanoidis-Fraxinetum excelsioris* Onyshchenko 1998. It is necessary to recall the statement of V.M. Lubchenko (1983) that *L. martagon* is a typical species and often occurs in groups of oak-hornbeam forests of the Middle Dnieper region. In 2007, the species was noted in the forests of the Feofania tract in only two localities. Thus, the frequency of occurrence of the species is unstable and fluctuates from year to year, or since 2007, conditions for the growth and spread of the species have improved. The forest biota is closely associated with rare plant species. In Svyatoshynskyi Forest Park near *Formica rufa* anthills the population of *L. martagon* occurs.

According to Order of the Ministry of Environmental Protection and Natural Resources of Ukraine No. 111 (2021), *Neottia nidus-avis* (Orchidaceae) is a sciophyte with an unvalued conservation status. A saprophytic (symbiomycotrophic) type of nutrition and a complex developmental biology characterizes the plant. The range is Western Eurasian. In Ukraine, it is known in Polissya, in the Forest-Steppe, in the northern part of the Steppe, in the Carpathians, and in the Mountainous Crimea (Didukh, 2009). It has been recorded the species in five locations on the territory of the tract: 1) 50.344028°N, 30.485397°E; 2) 50.336578°N, 30.489725°E; 3) 50.336417°N, 30.491606°E; 4) 50.344261°N, 30.492887°E; 5) 50.343399°N, 30.493150°E (Kozyr, 2012). It is worth noting that locations 1 and 2 are given for the first time. The literature only cites point 3 and the approximate area where it was noted location 4 (Padun, 1985; Shelyag-Sosonko *et al.*, 2009; Radchenko *et al.*, 2019). In the same area, A. Kuzemko (2021; 2024) noted two more locations of this rare species. In the first location, 1 blooming individual was noted, in the second – 4 blooming and 5 dry, in the third – 5 dry, in the fourth – about 30 individuals (dry and blooming), in the fifth – 1 blooming.

Phytocoenoses in which *Neottia nidus-avis* occurs usually have 1-3 tree tiers, an understory layer, and a grass tier. The first tier, up to 23-27 m tall, is mainly formed by *Quercus robur* (c. d. 0.05-0.5), *Tilia cordata* (c. d. up to 0.05), *Acer platanoides* (c. d. 0.1), *Carpinus betulus* (c. d. 0.55-0.7). The second tier, up to 20-22 m tall, is represented mainly by *C. betulus* (c. d. 0.1-0.55), *T. cordata* (c. d. 0.05). The third tier is 15-18 m tall. It is less pronounced and formed by *C. betulus* (c. d. 0.1). The undergrowth is up to 1.5-2.5 m tall with a projective coverage of up to 23%. It is formed by *Sambucus nigra*, *Euonymus europaea*, *E. verrucosa*, and *Acer campestre*. A grass tier is up to 30-40 cm tall with a projective coverage of 8-87%. Typical representatives of oak-hornbeam forests form it. *Impatiens parviflora* is gradually beginning to penetrate some phytocoenoses, and the number of individuals per 1 m^2 can be more than 30. Phytocoenoses with the participation of Neottia nidus-avis on the territory of the tract usually occur in groups of two associations *Aceri platanoidis-Fraxinetum excelsioris* Onyshchenko 1998, *Galeobdolo lutei-Carpinetum* Shevchik, Bakalina et Solomakha 1996. The associations *Aceri platanoidis-Fraxinetum excelsioris* and *Galeobdolo lutei-Carpinetum* were discovered in the second compartment of the Feofania Monument Park (the 6th subcompartment, area 9.7 ha). In general, the first tier stand is formed by *Quercus robur* (predominant) and *Carpinus betulus* (vegetative origin), the second tier is formed by *Acer platanoides* and *Carpinus betulus* (predominant), the underwood is *Sambucus nigra*. The slope is southern exposure, about 10 degrees. The total litter is about 29 m^3 per subcompartment. The incidence of *Fomes fomentarius* is about 10% with a low degree of damage. In the first tier, the average age of *Quercus robur* is 197 years, 29 m high, trunk diameter is 88 cm, the tree wood of the first tier is about 200 m^3/ha. The percentage of the *Quercus robur* lumber is 20%. In the second tier, the age of *Acer platanoides* and *Carpinus betulus* is 62 years. On average, *Acer platanoides* is 25 m tall, and *Carpinus betulus* is 24 m. The diameter of the trunk of *Carpinus betulus* is on average 32 cm, and of the *Acer platanoides* is 34 cm. The tree wood of the second tier is about 180 m^3/ha. The percentage of *Carpinus betulus* lumber is 20%, of the *Acer platanoides* is 40%. An economic measure is proposed – clearing of litter. The grass layer contains *Aegopodium podagraria, Anemone ranunculoides, Asarum europaeum, Chelidonium majus, Convallaria majalis, Corydalis cava, C. solida, Ficaria verna, Gagea lutea, Galium aparine, G. odoratum, Geranium robertianum, Geum urbanum, Lamium galeobdolon, L. maculatum, Mercurialis perennis, Polygonatum latifolium, Polygonatum multiflorum, Pulmonaria obscura, Rabelera holostea, Urtica dioica*.

The *Galeobdolo lutei-Carpinetum* association was discovered in the third compartment of the Feofania Monument Park (the 6th subcompartment, area 1.4 ha). In general, the first-tier stand is formed by *Quercus robur*, *Tilia cordata*, *Carpinus betulus*, the second – *Carpinus betulus*, *Acer platanoides*, *Tilia cordata*. The underwood consists of *Corylus avellana* and *Sambucus nigra*. The slope is eastern exposure, 10 degrees. The total litter is 37 m^3 per subcompartment. The incidence of *Fomes fomentarius* is about 10% with a low degree of damage. In the first tier, the age of *Quercus robur* is 187 years, *Carpinus betulus* and *Tilia cordata* is 97 years. The height of *Quercus robur* is 30 m, *Tilia cordata* is 28 m, *Carpinus betulus* is 26 m, on average, the diameter of the trunk of *Quercus robur* is 78 cm, *Tilia cordata* is 50 cm, *Carpinus betulus* is 42 cm. On the average the first-tier tree wood is 210 m^3/ha, on a subcompartment – 3.67 thousand m^3. The first-tier timber of *Quercus robur* is 40%, of *Tilia cordata* – 30%, and of *Carpinus betulus* – 10%. In the second-tier, the age of *Carpinus betulus*, *Acer platanoides* and *Tilia cordata* is 55 years. The height of *Acer platanoides* is 25 m, *Tilia cordata* is 24 m, and *Carpinus betulus* is 22 m. On average, the diameter of the trunk of *Carpinus betulus* is 32 cm, *Acer platanoides* is 36 cm, and the *Tilia cordata* is 34 cm. On average, the second tier tree wood is 120 m^3/ha, the subcompartment tree wood is 2.08 thousand m^3. The second-tier timber is 40% of *Carpinus betulus*, 50% of *Acer platanoides*, and 40% of *Tilia cordata*. The proposed management measures are clearing of litter and care for the underwood. The grass layer contains *Aegopodium podagraria, Anemone ranunculoides, Asarum europaeum, Corydalis solida, Ficaria verna, Lamium galeobdolon, Polygonatum multiflorum, Pulmonaria obscura, Rabelera holostea*.

A number of rare species were also introduced into the area, namely: *Allium ursinum, Crocus heuffelianus, Erythronium dens-canis, Galanthus plicatus, G. nivalis, Gymnospermium odessanum* (Bayrak & Hrytsay, 2009; Koniakin & Gubar, 2022). It should be noted that all of the above species have taken root well, and the number of individuals in their populations is increasing. This is especially true for *Allium ursinum*, which was planted in 2000 by Y.V. Dubrovsky (Radchenko *et al.*, 2019) in two areas of hornbeam forest (one with planting material from Cherkasy region, and the other from Kyiv region). During the study period this species has spread throughout Feofania Park and is already recorded in five localities (Fig. 1). Therefore, D.A. Davydov's assumption about the naturalisation of this species is correct (Shynder *et al.*, 2024).

Figure 2. Distribution of rare species in the Feofania tract included in the Red Data Book of Ukraine
Source: developed by the authors with using Google Earth Pro and GNU Gimp 2.10.18

It should be noted separately that in the last few years, the phytocoenoses of the Feofania tract have been undergoing changes due to the significant extinction and decline of old *Quercus robur* specimens, and the few large specimens of *Pinus sylvestris* here. There have also been more cases of *Carpinus betulus* trees falling. This is due not only to a change in climate to a more arid one, but also to the massive spread of tree pests. It is because of the almost complete disappearance of red forest ants *Formica rufa* from the forest territory of the studied object. In 2014 there were 89 nests here, which were divided into 3 large complexes (colonies), and in 2023 – only 3 single anthills. The results of the present study confirm the ongoing transformation processes within the forest ecosystems of the Feofania tract, which are reflected not only in the floristic composition and structure of the phytocoenoses but also in the condition of associated faunal complexes. Similar tendencies were documented by S. Stukalyuk *et al.* (2016), who monitored the nest complexes of *Formica rufa* within the Feofania Natural Park. Their research indicated that in 2014 there were 89 anthills grouped into three large colonies, demonstrating the previously stable state of the red wood ant populations, which play an important role in maintaining the ecological balance of the forest ecosystem. However, more recent findings by S. Stukalyuk *et al.* (2023) revealed a drastic decline in the number and structural integrity of nest complexes of *Formica rufa* and *F. polyctena* in urban forests of Kyiv, including Feofania. The authors attributed this decline to increasing anthropogenic pressure, habitat fragmentation, and the degradation of mature oak–hornbeam stands. These conclusions are consistent with the observations obtained during the 2021-2024 monitoring period in the present study, where the loss of dominant tree species (*Quercus robur*, *Carpinus betulus*) and a reduction in understory vitality were accompanied by a visible decrease in ant activity and the near disappearance of red wood ant colonies.

Ant species of the genus *Formica* have been documented as key ecological components of forest ecosystems in Ukraine, with a well-established role in trophic interactions and soil processes. According to A.G. Radchenko (2016), ants of the *Formica rufa* group not only regulate populations of forest pests but also actively engage in seed dispersal and soil modification, thereby influencing understory vegetation dynamics. In the present study, a marked decline in *Formica rufa* and *F. polyctena* was observed within the Feofania tract, which corresponded with reduced occurrences of myrmecochorous plant species such as *Lilium martagon*. This concordance suggests that the loss of functionally important ant assemblages could be linked to altered seed dispersal and community structure in urban forest patches. However, whereas A.G. Radchenko (2016) provided a comprehensive faunistic and ecological overview of ant distribution across Ukraine, the current findings extend this understanding by demonstrating how the absence of these ants in a specific urban protected area may correlate with changes in rare plant populations and phytocoenotic conditions.

The loss of the dominants of the first tier leads to the formation of large areas of several hundred square meters, which will contribute to changes in the vegetation cover in the places of their formation. Therefore, this may lead to the transformation of existing phytocoenoses into others that are not typical of this area, and a gradual complete or partial replacement of the species composition of phytocoenoses. The loss of dominant tree species in the first tier, particularly *Quercus robur* and *Carpinus betulus*, leads to the formation of open areas covering several hundred square meters. Such canopy gaps promote changes in the vegetation cover within their boundaries. These processes can cause the transformation of existing phytocoenoses into new ones that are not typical for the given locality, resulting in the gradual partial or complete replacement of their species composition. During the 2021-2024 monitoring period, signs of this transformation were recorded in the Feofania tract. The decline of mature oak and hornbeam stands has initiated successional shifts towards mesophilous and nitrophilous communities dominated by *Acer platanoides* and *Tilia cordata*. These structural changes appear to reflect both natural successional dynamics and the influence of anthropogenic factors and pest outbreaks.

The growing number of visitors who often come here for leisure activities leads to disturbance of the herbaceous layer due to trampling, digging, uprooting or damaging plants, making bonfires, etc. The same applies to rare species that grow here. It has been repeatedly observed trampled, broken or torn out specimens of *Allium ursinum*, *Convallaria majalis*, *Corydalis cava, Lilium martagon, Neottia nidus-avis*. In this regard, it is recommendable the need to implement measures aimed at reducing the impacts of anthropogenic origin on the habitats of rare species. As such, it is recommended to carry out zoning of the territory and take measures aimed at reducing visits to the habitats of rare species. In addition, to track the status of the populations of these species, it is necessary to monitor them throughout the entire tract and directly in the noted places in accordance with Ukraine's international obligations (Association Agreement..., 2014; European Commission, 2020; Convention on Biological Diversity, 2022). In the future, it is advisable to conduct research into the possibilities of artificial propagation of these plants using all available biotechnological methods. For associations with rare species, it is worth using various silvicultural measures according to the specific situation, including landscape felling of maintenance, selective sanitary felling, elimination of littering, care for underwood, pruning of hanging dry branches from trees, felling of emergency trees along roads and trails, clearing of cross rides (Resolution..., 1995, 2007).

The study of rare plant species in the Feofania tract highlights their critical role as indicators of ecological balance and anthropogenic impact within urban forest ecosystems. The identification of new habitats for species such as *Epipactis helleborine*, *Lilium martagon*, and *Neottia nidus-avis*, alongside the observed decline of mature trees and the spread of invasive species like *Impatiens parviflora*, underscores the ongoing environmental changes in the region. The successful introduction of RDBU species, such as *Allium ursinum* and *Galanthus nivalis*, demonstrates the potential for conservation efforts to bolster biodiversity. These findings provide a foundation for enhanced biomonitoring and targeted conservation strategies to protect the tract's floristic diversity. In conclusion, the research emphasises the need for continued monitoring and management to mitigate anthropogenic pressures and preserve the ecological integrity of the Feofania tract.

Conclusions

For the first time in the territory of the Feofania tract, the *Epipactis heleborine* habitat was discovered. Presumably, the seeds of the plant were brought from the Holosiivskyi Forest National Park, the distance to which is less than 1 km. The obtained geobotanical data showed that *E. heleborine* is confined to the *Aceri platanoidis-Fraxinetum excelsioris* Onyshchenko 1998 association. Other rare species occured on the territory of the tract: *Lilium martagon* and *Neottia nidus-avis*, but quite rarely, and in some known habitats, individuals have disappeared and not recorded for several years in a row. This is due to a number of factors: climate change, loss of dominants of the woody layer, phytocenotic changes, increased anthropogenic load, penetration of transformant species into phytocoenoses, as well as the mass disappearance of *Formica rufa and F. polyctena ants*. In particular, climate change adversely affects both individual plants and phytocoenoses, as reduced precipitation throughout the year, significant warming in winter, and frosts in spring negatively affect plant life, inhibit their development, allow more pests to survive, and contribute to the spread of plant and animal diseases. The loss of dominants of the woody layer contributes to increased evaporation of moisture from the soil and the rapid appearance of other species and new phytocenosis in these places.

Such changes in forest structure will cause a change in the microclimate and species composition, which will negatively affect rare species due to allelopathic effects. Anthropogenic pressure, which manifests itself in trampling and breaking plants, paving roads, compacting substrates, and picking flowers, also leads to a decrease in populations of rare species. The penetration of alien transformative species (for example, *Impatiens parviflora*) into phytocoenoses will lead to severe shading of rare species, as well as their allelopathic effect. Another negative factor in the number decreasing of rare species is the disappearance of *Formica rufa* and *F. polyctena* ants from the park. These insects not only fought pests but also contributed to the spread of seeds of rare species (for example, *L. martagon* seeds have an edible appendage that ants eat when transporting the seeds along the way to the anthill).

Regarding phytocenotic localisation, *L. martagon* occured in the *Aceri platanoidis-Fraxinetum excelsioris* Onyshchenko 1998 association. While *N. nidus-aves occurs* in the coenoses of two associations: *Aceri platanoidis-Fraxinetum excelsioris* Onyshchenko 1998 and *Galeobdolo lutei-Carpinetum* Shevchik, Bakalina et Solomakha 1996. It had not previously noted the rare species *Cephalantera longifolia* from the Central Ukraine Reserve, which is presented here. It has completely disappeared from the studied area. In the first decade of the 21st century, a number of rare plants were introduced into the Feofania tract, including 6 species listed in the Central Ukrainian Plant Conservation Register: *Allium ursinum, Crocus heuffelianus, Erythronium dens-canis, Galanthus plicatus, G. nivalis, Gymnospermium odessanum.* These species have taken root well and actively spread throughout the area. This is especially true for *A. ursinum*, which has been recorded in several localities at a considerable distance from the place of their planting.

Therefore, the received materials gave possibility to conduct ecomonitoring in the future and track changes that will occur in the populations of the species described above and the phytocoenoses in which they grow.

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Conflict of Interest

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Раритетні види рослин природних лісових насаджень урочища Феофанія та їхня фітоценотична приуроченість (Київ, Україна)

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Анотація. З'ясування сучасного стану поширення видів рослин, які включені в Червону книгу України, зокрема на території урочища Феофанія, набувають особливої актуальності, оскільки вони є чутливими маркерами рівня антропогенного навантаження та змін, що відбуваються в екосистемах. Метою дослідження було виявлення нових місцезростань рідкісних видів рослин природних лісових насаджень урочища Феофанія (Київ, Україна) та з'ясування їхньої фітоценотичної приуроченості. У межах урочища проводились моніторингові та геоботанічні дослідження упродовж вегетаційних сезонів 2009-2012 рр. та 2021-2024 рр. Також у межах дослідження було оцінено структуру та стан лісових насаджень. Виявлено зниження життєздатності старих дерев *Quercus robur* і *Carpinus betulus*, що відображає триваючі екологічні зміни в межах лісової екосистеми. У результаті встановлено нові локалітети *Lilium martagon*, *Neottia nidus-avis*, а також вперше знайдено *Epipactis helleborine*. Згадується, що *Cephalanthera longifolia* знайдений на території урочища Феофанія у 80-ті рр. XX ст. очевидно зник із дослідженої території. Відмічено, що на місцезнаходження рідкісних видів зростає антропогенний тиск. Це підтверджується проникненням у фітоценози, де вони трапляються, інвазійних видів, зокрема *Impatiens parviflora*. Тут у першому десятиріччі XXI ст. було успішно інтродуковано ще такі види із Червоної книги України як *Allium ursinum*, *Crocus heuffelianus*, *Erythronium dens-canis*, *Galanthus plicatus*, G. *nivalis*, *Gymnospermium odessanum*. Фітоценози з участю Neottia nidus-avis виявлено на території другого кварталу (виділ 6) парку-пам'ятки «Феофанія» із запасом деревини першого та другого ярусів близько 380 $м^3$ / га та третього кварталу (виділ 6) із запасом деревини двох ярусів близько 330 $м^3$ / га. На території урочища також трапляються регіонально рідкісні види *Convallaria majalis* та Corydalis cava. Отримані відомості будуть корисними для біомоніторингу, поширення та динаміки цих видів і фітоценозів, у яких вони трапляються

Ключові слова: раритетні види; *Epipactis helleborine*; *Lilium martagon*; *Neottia nidus-avis*; охорона; антропічне навантаження

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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 8^{th}-9^{th} 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 18^{th}-19^{th} 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. Boholavets (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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Conflict of Interest

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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 облігати, 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 облігати; епіфітотійні процеси

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Anatomical study of *Shorea* species in Sri Lanka

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Abstract. The six *Shorea* species native to Sri Lanka Beraliya dun (*S. disticha*), Navada dun (*S. stipularis*), Dun (*S. zeylanica*), Yakahalu dun (*S. trapezifolia*), Yakal dun (*S. astylosa*), and Thiniya dun (*S. congestiflora*) are commercially valuable timbers within the Dipterocarpaceae family, yet their close morphological resemblance creates substantial difficulties in accurate species-level identification across field, trade, and processing contexts. This study aimed to establish reliable wood anatomical criteria for distinguishing these six *Shorea* species through microstructural analysis and its quantitative relationship with timber density. Permanent sections in transverse, radial, and tangential planes were prepared and examined under light microscopy, with vessel diameter and ray dimensions measured using Micrometrics SE Premium imaging software, while timber density was determined through the water displacement principle. All six species exhibited solitary and multiple vessel arrangements, with mean vessel diameters differing considerably across taxa, providing a primary basis for microscopic discrimination. Ray structure ranged from uniseriate to multiseriate configurations, with measurable variation in ray height and width offering additional diagnostic value. Axial parenchyma patterns including paratracheal and apotracheal forms differed consistently among species, reinforcing anatomical boundaries

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at the cellular level. A statistically significant negative correlation was identified between wood density and vessel diameter, indicating that species with greater density characteristically develop narrower conducting elements. By integrating vessel arrangement, ray morphology, parenchyma distribution, and density values, a dichotomous identification key was constructed that successfully and unambiguously separates all six taxa. The anatomical framework and dichotomous key developed in this study offer timber inspectors, foresters, and wood processing industries a scientifically grounded, practical tool for the accurate identification of Sri Lankan dun timbers in both raw and processed forms

Keywords: anatomical features; wood density; wood anatomy; timber identification; vessel characteristics; microscopic features; dichotomous key

Introduction

Timber remains a critical natural resource in sustainable construction due to its renewability, aesthetic value, and favourable mechanical properties. In many tropical countries, including Sri Lanka, it continues to play an essential role in both traditional and modern building practices. However, increasing pressure on natural forests and growing demand for high-quality timber have intensified concerns regarding species authentication and resource management. Nearly 300 local timber species are available in Sri Lanka, as reported by I.G. Chathushaki *et al*. (2025), but only 30 species are commonly available in the timber market. Timber has been a popular construction material in Sri Lanka since ancient times and, according to M.C. Anuruddha *et al*. (2025), it is considered one of the most valuable raw materials in the country because of its multipurpose usage. Though replacement for the wood which comes from steel and concreate doesn't bear the same structural properties, timber is a natural structural material whose strength properties and other characteristics vary considerably. These variations occur not only within the same family, species even from tree to tree it may occur. The strength of timber depends on its species and the effects of certain growth characteristics, as explained by J.P. Cabral *et al*. (2022).

Dipterocarpaceae is a taxonomically diverse family comprising 17 genera, including five monotypic genera. The genus *Shorea* is the largest, containing 186 species, of which 121 are threatened. The Sri Lankan endemic genus Stemonoporus has 26 species, all of which are assessed as threatened, as noted by K. Atapattu *et al*. (2022). In Sri Lanka, the genus *Shorea* is represented by 15 species, of which 13 are endemic to the country, with 10 species found specifically in the wet zone. However, the existence of different classification systems for this genus, proposed by several authors, has created some taxonomic complexity, as discussed by A. Musa *et al*. (2024).

In the Sri Lankan timber market, there are venders will sell low maturity products with low-grade timber species that considered as below the. Buyers who cannot identify the authenticity of timber species are easily misled by forged documents and misidentified timber. The authenticity percentage is very low for both local and imported timber species, although local timber species have a higher authenticity percentage compared to imported species, according to G.W.C. But *et al.* (2023). A study of Sri Lankan timber species, including *Shorea spp*., has linked properties to four categories: building construction, furniture/joinery, light construction, and miscellaneous, promoting evidence-based selection over traditional species-oriented practices, as reported by A.J. Duffy (2024). Previous research by P. Chalise *et al*. (2022) conducted a detailed anatomical investigation of *Shorea robusta*, commonly known as Sal, which P. Chalise *et al*. (2022) described as one of the major multipurpose timber trees in Nepal. The main objective of this study is to identify six *Shorea* species by anatomical features and prepare a dichotomous key.

Timber remains one of Sri Lanka's most valued construction materials, yet the marketplace is increasingly vulnerable to misidentification and fraud. As emphasised by C.K. Muthumala *et al*. (2024; 2025), low-grade or immature timber is substituted for premium species under falsified documentation. Among the commercially traded species, the genus *Shorea* the largest within the Dipterocarpaceae family presents a particular identification challenge, as its 15 Sri Lankan representatives share strikingly similar external appearances, grain patterns, and colouration, making visual discrimination unreliable even for experienced traders. Despite the ecological and economic significance of these species, no dedicated anatomical identification framework exists for the six lesser-studied Sri Lankan *Shorea* timbers *S. disticha, S. stipularis, S. zeylanica, S. trapezifolia, S. astylosa,* and *S. congestiflora* leaving a critical gap in both taxonomic science and timber authentication practice. Although anatomical studies of *Shorea* robusta have previously been conducted in neighbouring regions by P. Chalise *et al*. (2022), systematic wood anatomical investigations targeting Sri Lanka's endemic *Shorea* species remain absent from the literature. Current identification methods rely predominantly on macroscopic traits and field expertise, neither of which provides reproducible or legally defensible results in market or forensic contexts. This underscores the urgent need for a scientifically robust, microscopy-based identification approach that can differentiate these species at the cellular level and support evidence-based timber authentication across trade, construction, and conservation sectors. This study sought to identify reliable wood anatomical features that can differentiate these six *Shorea* species by analysing their microstructure and examining its quantitative association with timber density.

Materials and Methods

This investigation was conducted from June to September 2025 in the lowland wet agro-ecological zone of Ratnapura District, Sri Lanka, where six *Shorea* species naturally occur. Three mature, healthy trees per species were randomly selected yielding 18 specimens in total using simple random sampling to ensure equal probability of inclusion and minimise selection bias. Selected trees were free from visible disease, mechanical damage, and abnormal growth deformities, and were positively identified at the species level by a qualified taxonomist prior to sampling, consistent with established practice in descriptive wood anatomy where three to five individuals per species are considered sufficient when intraspecific variation is low (Wheeler *et al*., 1989). Defect-free heartwood blocks of approximately 2 cm × 2 cm × 5 cm were extracted at breast height (1.3 m above ground level) and oriented for sectioning in the transverse, radial, and tangential planes to standardise the anatomical region examined and eliminate height-related structural variability. The six *Shorea* species selected for this study are presented in Table 1.

Table 1. Selected timber species for the study

Common name	Scientific name
Beraliya dun	*Shorea disticha*
Navade dun	*Shorea stiplaris*
Yakal dun	*Shorea astylosa*

Table 1, Continued

Common name	Scientific name
Dun	*Shorea zeylanica*
Yakahalu dun	*Shorea trapezifolia*
Thiniya dun	*Shorea congestiflora*

Source: compiled by authors

All anatomical examinations were carried out at the Wood Science Laboratory, State Timber Corporation, Battaramulla, Sri Lanka. All sampling procedures were conducted in accordance with the principles of the Convention on Biological Diversity (1992) to ensure ethical and sustainable utilisation of biological resources. The anatomical study of timber species followed standard protocols as outlined by E.A. Wheeler *et al*. (1989) and A. Laskowska *et al*. (2021). Preparation of wood samples for microscopic examination included sectioning of wood samples in transverse, radial, and tangential planes, followed by preparation of thin sections suitable for microscopic observation. Staining and mounting procedures were conducted according to established protocols, after which microscopic examination and documentation of anatomical features were performed. Anatomical characteristics evaluated included vessel arrangement and dimensions, parenchyma distribution, fiber characteristics, and ray structure, following standard wood anatomical terminology and measurement protocols.

Samples were collected from heartwood portion of wood. Wood block of 2 cm × 2 cm × 2 cm was taken for the slide preparation, representing Transverse, Tangential and Radial section of the wood. After taking the sample from the tree, it was socked in the water before preparation of the slides. Samples were prepared as blocks of approximately 8 mm × 8 min size with anatomical orientation for microtome sectioning.

Sliding microtome (Model LEICA SM 2000R-SCHITTEN MIKROTOM) was used to produce section cut from the wood species. This microtome has a wedge shape sharp blade. The piece of wood sample and the knife were flooded with 30% Ethanol during section cutting to facilitate fine sectioning. The wood specimens were taken from transverse, radial and tangential sections at the range of 10-15 mm thickness by using sliding microtome, in here mainly consider about transverse section cutting of the wood samples (Fig. 1).

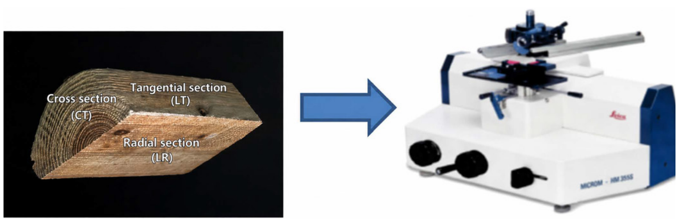

Figure 1. Section cutting and procedure of preparing slides (Model LEICA SM 2000R-SCHITTEN MIKROTOM)

Source: created by authors

Preparation of wood samples for microscopic examination included sectioning of wood samples in transverse, radial, and tangential planes, followed by preparation of thin sections suitable for microscopic observation. Sections were mounted permanently with Canada Balsam following a standardised dehydration and staining protocol. The procedure involved initial dehydration in 50% alcohol for 5 minutes, followed by staining with safranin in 50% alcohol for 15 minutes to remove moisture and impart colour to the sections. The stained sections were then washed in alcohol and subjected to a graded dehydration series: 70% alcohol for 5-10 minutes, 90% alcohol for 10 minutes, and absolute alcohol for 10 minutes with covers to prevent evaporation. The dehydrated sections were then transferred to an absolute alcohol and xylene mixture for 10 minutes, where the appearance of milkiness indicated incomplete dehydration, necessitating repetition of the previous stage. Finally, sections were cleared in xylene for 10 minutes under cover and permanently mounted in Canada Balsam. Transverse, tangential, and radial sections were prepared for comprehensive anatomical examination and documentation.

The light microscope was used to make anatomical observations on both qualitative and quantitative parameters at 4 × 10 magnifications. Micrometrics SE Premium 4 software and anatomical images were used to get measurements. Quantitative wood anatomical characteristics were measured, such as the mean tangential diameter of the vessel Lumina. Qualitative factors were found, including the vessel's morphology, the presence of deposits within it, and the organisation of the parenchyma. According to the 1989 IAWA list, slides were made and measurements were made for every sample. (Baas *et al.*, 2004). A handheld microscope Toontor TE013 was used to examine wood samples in order to see the vessel number and Ray number that fit in 25 mm^2. Within a 25 mm^2 area, anatomical observations were made at 20 magnifications.

Wood density was measured using Archimedes' principle. Wood samples were selected from each timber species and thoroughly cleaned to remove sawdust and other debris. Each sample was soaked in water for approximately three days to ensure complete saturation, with the assumption that all vessels and pores were filled with water within this period. A water-filled beaker was placed on an electrical balance and its initial weight (w_1) was recorded. The water-soaked wood sample was then submerged in the beaker to a constant depth using a thin stick attached to a stand, and the final weight of the beaker (w_2) was measured. Following this, the timber samples were placed in an oven at 103°C for 48 hours to remove all available moisture, with samples maintained in the oven until a constant weight was achieved. After 48 hours, the timber samples were transferred to a desiccator to cool down, and the oven-dry weight (g) of each sample was measured (checked it with the classification of density as in Table 2). This consistent procedure was maintained for all wood samples, and density was calculated using the following formulas. The wet weight of the timber sample was calculated by the following formula

$$x = w_1 - w_2, \tag{1}$$

where x represents timber weight, w_1 –internal beaker weight and w_2 –final beaker weight.

The density at 0% moisture level, was calculated by the following formula:

$$\rho = m \times \rho_w \text{ (1,000 kg/m}^2\text{)}, \tag{2}$$

where ρ represents density, m –oven dry weight of timber sample and ρ_w –density of water.

Table 2. Classification of density at 12% MC, kg/m^3

Density class	Density range
Very high	> 840
High	641-840
Medium	500-640
Low	500 <

Source: compiled by authors

Observations and measurements of anatomical features were systematically recorded for all six *Shorea* species. Using Micrometrics SE Premium 4 software, which is accessible at the State Timber Corporation's Research Division, the Mean Vessel Diameter (Tangential Diameter) of six timber species was measured in a 5 × 5 mm cross section. Number of vessels were measured in 5 mm × 5 mm cross section, of six *Shorea* timber species cross section number of Ray height was measured using Tangential section of 06 timber species using Micrometrics SE Premium 4 software available at Research Division of the State Timber Corporation. Number of rays were measured in 5mm × 5mm cross section, of six *Shorea* timber species cross section number of Ray height was measured using Tangential section of 06 timber species using Micrometrics SE Premium 4 software available at Research Division of the State Timber Corporation. Selected Six *Shorea* timber species were studied considering their anatomical features by microscope. Vessels, Rays, Parenchyma and other anatomical properties were used for construction of Identification keys in accordance with E.A. Wheeler *et al*. (1989).

Results

The wood anatomy of six *Shorea* species native to Sri Lanka *S. disticha* (Beraliya Dun), *S. stipularis* (Navada Dun), *S. zeylanica* (Dun), *S. trapezifolia* (Yakahalu Dun), *S. astylosa* (Yakal Dun), and *S. congestiflora* (Thiniya Dun) was systematically examined across transverse, radial, and tangential sections. Key qualitative and quantitative parameters vessel features, ray dimensions, axial parenchyma patterns, and intercellular canal distribution were assessed for their diagnostic value in species-level identification. Photographic representations of anatomical sections for all six species are presented in Figure 2.

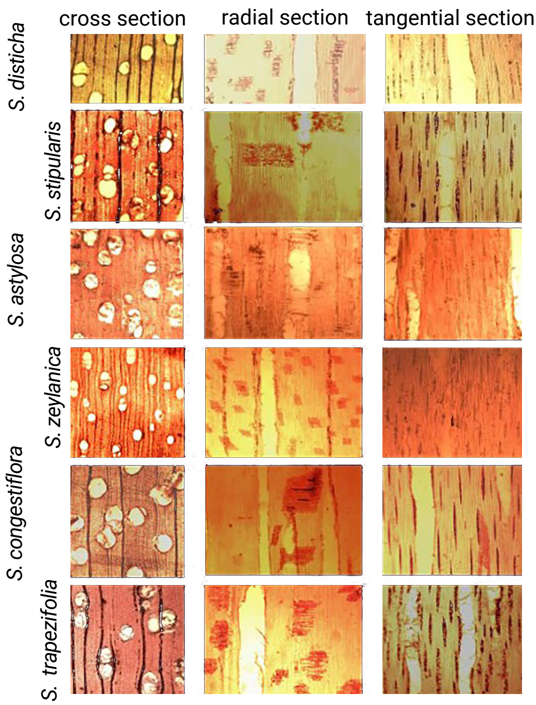

Figure 2. Tree section of anatomical slides photos

Source: created by authors

Macroscopic characteristics: heartwood colour. Heartwood colour provided an initial, macroscopic basis for preliminary distinction among the six species (Table 3). *S. zeylanica* (Dun) and *S. congestiflora* (Thiniya Dun) both exhibited red to reddish-brown heartwood, while *S. disticha* (Beraliya Dun) and *S. trapezifolia* (Yakahalu Dun) shared brown tones. *S. astylosa* (Yakal Dun) was distinctive with yellow heartwood, and *S. stipularis* (Navada Dun) was the only species to display white to grey colouration. However, given that some species share similar hues, colour alone was insufficient for reliable identification, and microscopic features were essential for unambiguous discrimination.

Table 3. Colour of heartwood of the selected *Shorea* species

Species name	Colour of the heartwood
Beraliya Dun	Brown or shades of brown
Navanda Dun	White to grey
Yakal Dun	Yellow or shades of yellow
Dun	Red or shade of red
Yakahal Dun	Brown or shades of brown
Thiniya Dun	Red or shade of red

Source: compiled by authors

Vessel features. Vessel characteristics showed pronounced variation across the six species, providing the most discriminatory microscopic features for identification (Table 4). All species exhibited oval or round vessel shapes and predominantly solitary arrangement; however, *S. zeylanica*, *S. trapezifolia*, and *S. congestiflora* additionally formed radial vessel multiples of two to three, distinguishing them from the exclusively solitary arrangement observed in *S. disticha*, *S. stipularis*, and *S. astylosa*.

Table 4. Key anatomical features (Vessels) of selected *Shorea* species

Species	Vessels				
	Shape	Grouping	Tangential lumen diameter, mean (μm)	Vessels per 25 mm²	Tyloses and deposits in vessels
Beraliya (Shorea disticha)	Oval	exclusively solitary	152	116	Absent
Nawadadun (Shorea stipularis)	Oval	exclusively solitary	156	99	Absent
Yakal (Shorea astylosa)	Round Oval	exclusively solitary	169	115	Present
Dun (Shorea ceylanica)	Oval	solitary and radial multiples of two to three	100	154	Present
Yakahaludun (Shorea trapezifolia)	Oval	solitary and radial multiples of two to three	172	187	Present
Thiniyadun (Shorea congistiflora)	Wood diffuse-porous	solitary or radial multiple of two	231	161	Present

Source: compiled by authors

Mean tangential lumen diameter differed substantially among species, ranging from 100 μm in *S. zeylanica* to 231 μm in *S. congestiflora* a more than twofold difference. *S. congestiflora* had the widest vessels and the second highest vessel frequency (161 per 25 mm²), while *S. zeylanica* had the narrowest vessels despite its relatively high vessel density (154 per 25 mm²). This inverse relationship between vessel diameter and vessel frequency reflects the established negative correlation between vessel size and wood density. *S. trapezifolia* had the highest vessel frequency (187 per 25 mm²) paired with a wide mean diameter (172 μm), indicating that vessel grouping into multiples may partially compensate for the density-diameter trade-off in this species. Tyloses and vessel deposits were absent in *S. disticha* and *S. stipularis* but consistently present in the remaining four species, providing an additional diagnostic character.

Ray structure. Ray dimensions and cellular composition varied consistently among species, offering additional reliable criteria for identification (Table 5). Ray frequency ranged from 27 per 5 mm in *S. trapezifolia* the species with the highest vessel density to 46 per 5 mm in *S. disticha*. This inverse relationship between ray frequency and vessel frequency is consistent with the structural trade-off between conducting and storage tissue in hardwoods. Ray width (seriation) ranged from 1-2 seriate in *S. disticha* to 1-4 seriate in *S. astylosa*, *S. zeylanica*, and *S. congestiflora*. Notably, ray cell type provided a clear binary distinction: *S. disticha* and *S. astylosa* possessed heterogeneous rays comprising both procumbent and upright/square cells whereas the remaining four species exhibited homogeneous rays composed exclusively of procumbent cells. This character aligned with intercellular canal distribution and was incorporated as a key discriminating feature in the dichotomous identification key.

Axial parenchyma and intercellular canals. Axial parenchyma patterns differed markedly among species and proved highly diagnostic (Table 5). *S. congestiflora* was immediately separable by the near absence of axial parenchyma a character unique among the six taxa. *S. stipularis* exhibited a combination of scanty paratracheal, vasicentric, and winged-aliform parenchyma; *S. astylosa* and *S. zeylanica* both displayed aliform and confluent forms, with *S. zeylanica* additionally showing aliform-confluent parenchyma. *S. disticha* and *S. trapezifolia* presented the more restricted scanty paratracheal and vasicentric patterns respectively, further differentiating them from species with more elaborate parenchyma configurations. Intercellular canals in long tangential lines were present in five of the six species and are characteristic of the Dipterocarpaceae family. The sole exception was *S. stipularis* (Navada Dun), in which intercellular canals were entirely absent. This single feature unambiguously separates *S. stipularis* from all other species examined and serves as the primary dichotomous branch point in the identification key.

Table 5. Key anatomical features rays, parenchyma and intracellular canals of selected *Shorea species*

Species	Rays			Parenchyma	Intercellular canals
	Rays per 5 mm	Ray width	Type of ray cells		
Beraliya (*Shorea disticha*)	46	Ray width 1 to 2 seriate	Heterogeneous	Axial parenchyma scanty and paratracheal	Axial canals in long tangential lines
Nawadadun (*Shorea stipularis*)	35	Ray width 1 to 3 seriate	Homogeneous	Axial parenchyma scanty paratracheal Axial parenchyma vasicentric Axial parenchyma winged-aliform	Not present

Table 5, Continued

Species	Rays			Parenchyma	Intercellular canals
	Rays per 5 mm	Ray width	Type of ray cells		
Yakal (*Shorea astylosa*)	35	Ray width 1 to 4 seriate	Heterogeneous	Axial parenchyma Aliform Axial parenchyma confluent	Axial canals in long tangential lines
Dun (*Shorea ceylanica*)	37	Ray width 1 to 4 seriate	Homogeneous	Axial parenchyma confluent Axial parenchyma scanty and vasicentri Axial parenchyma aliform confluent	Axial canals in long tangential lines
Yakahaludun (*Shorea trapezifolia*)	27	Ray width 1 to 3 seriate	Homogeneous	Axial parenchyma scanty and vasicentric	Axial canals in long tangential lines
Thiniyadun (*Shorea congistiflora*)	33	Ray width 1 to 4 seriate	Homogeneous	Axial parenchyma absent or rare	Axial canals in long tangential lines

Source: compiled by authors

Relationship between vessel diameter and wood density. A statistically significant negative correlation was identified between mean vessel diameter and wood density across the six species. Species with narrower vessels notably *S. zeylanica* (100 μm) exhibited higher wood density, while *S. congestiflora* with the widest vessels (231 μm) showed comparatively lower density values. This pattern reflects the hydraulic-mechanical trade-off in wood structure: denser woods invest proportionally more in thick-walled fibres and smaller lumina, resulting in narrower conducting elements. This density-vessel diameter relationship reinforces the diagnostic utility of vessel diameter measurements, linking functional wood properties to species identity in a quantitatively verifiable manner.

Dichotomous identification key. The anatomical features selected for the dichotomous key axial parenchyma pattern, intercellular canal presence, vessel arrangement, and ray cell type were chosen because they showed the most consistent, qualitatively clear, and species-exclusive variation across all six taxa (Dormontt *et al*., 2015). Quantitative characters such as vessel diameter and ray frequency, while diagnostically informative, were used as supporting evidence rather than primary key characters due to overlapping ranges. The resulting key successfully and unambiguously separates all six Shorea species and is presented below. It is designed for practical use with light microscopy and does not require specialised equipment beyond standard anatomical slide preparation, making it directly applicable to timber inspection, forensic identification, and trade verification contexts.

Dichotomous key to six Sri Lankan Shorea species based on wood anatomical features:

1a. Axial parenchyma absent or rare – Thiniya Dun (*S. congestiflora*)

1b. Axial parenchyma present → (2)

2a. Intercellular canals absent – Navada Dun (*S. stipularis*)

2b. Intercellular canals present (tangential lines) → (3)

3a. Axial parenchyma aliform or confluent → (4)

3b. Axial parenchyma not aliform or confluent → (5)

4a. Vessels exclusively solitary; ray cells heterogeneous – Yakal Dun (*S. astylosa*)

4b. Vessels in radial multiples; ray cells homogeneous – Dun (*S. zeylanica*)

5a. Ray cells heterogeneous; rays 1-2 seriate – Beraliya Dun *(S. disticha*)

5b. Ray cells homogeneous; rays 1-3 seriate – Yakahalu Dun (*S. trapezifolia*)

Discussion

The findings of this study demonstrate that microscopic wood anatomy provides a reliable and practical basis for distinguishing six *Shorea* species native to Sri Lanka that are otherwise difficult to separate by external morphology alone. This outcome is consistent with established practice in tropical timber identification, where vessel arrangement, ray structure, and axial parenchyma patterns form the core of species-level diagnostic frameworks (Wheeler & Baas, 1988; Wheeler *et al*., 1999). The qualitative stability and consistency of these cellular characters across individuals makes them particularly well-suited for discrimination within genera characterised by close morphological affinity, such as *Shorea* (Helmling, 2020).

Vessel features proved to be the most discriminatory category of characters examined. The mean tangential lumen diameter ranged from 100 μm in *S. zeylanica* to 231 μm in *S. congestiflora*, a range consistent with values reported for other *Shorea* species across Southeast Asia, where vessel diameters of 81-270 μm have been documented within the white meranti group (Helmling, 2020). The exclusively solitary vessel arrangement observed in *S. disticha*, *S. stipularis*, and *S. astylosa* contrasts with the radial multiples found in *S. zeylanica*, *S. trapezifolia*, and *S. congestiflora*, providing a clear binary character at the microscopic level. These grouping patterns are broadly analogous to those described in related dipterocarp genera, where radial vessel multiples are associated with species of higher vessel frequency (Ohashi *et al*., 2014). The presence of tyloses and vessel deposits in four of the six species absent only in *S. disticha* and *S. stipularis* further extended the suite of vessel-based criteria available for identification.

The statistically significant negative correlation identified between vessel diameter and wood density supports a widely documented functional trade-off in angiosperm wood anatomy. Wood density correlates negatively with vessel diameter and positively with vessel packing density across tropical tree species (Fajardo *et al*., 2022), reflecting the hydraulic efficiency–mechanical safety trade-off whereby denser woods invest proportionally more in thick-walled fibres and correspondingly narrower lumina. Within the Dipterocarpaceae specifically, N. Malik *et al*. (2025) reported that wood density was negatively correlated with axial parenchyma abundance across five dipterocarp species, consistent with the pattern observed here in *S. congestiflora*, which combined the widest vessels with near-absent parenchyma. The density-vessel diameter relationship identified in this study thus has both practical and functional significance: it provides a quantitative parameter that reinforces the qualitative anatomical distinctions and links species identity to measurable differences in timber mechanical properties relevant to end-use classification.

Ray and axial parenchyma characters provided complementary discrimination at finer taxonomic resolution. The distinction between heterogeneous rays found in *S. disticha* and *S.astylosa* and the homogeneous rays present in the remaining four species constitutes a reliable qualitative character that is consistent with broader patterns in *Shorea* systematics (Musa *et al*., 2024). Axial parenchyma patterns, ranging from scanty paratracheal in *S. disticha* to the near-complete absence in *S. congestiflora*, showed species-specific consistency throughout the sampled material and matched configurations documented for the genus in the

Dipterocarpaceae wood anatomy literature (Erwin *et al.*, 2025). The complete absence of intercellular canals in *S. stipularis* is particularly noteworthy, given that axial intercellular canals in long tangential lines are regarded as a diagnostic feature of the family Dipterocarpaceae (Erwin *et al.*, 2025). This absence represents a taxonomically informative deviation that is immediately detectable under light microscopy and serves as the most decisive branch point in the constructed dichotomous key.

The dichotomous key constructed from these combined anatomical criteria successfully and unambiguously separates all six *Shorea* species. By prioritising qualitative characters axial parenchyma pattern, presence of intercellular canals, vessel arrangement, and ray cell type the key minimises the dependence on quantitative measurements that may exhibit intraspecific variability. This approach mirrors that taken in identification keys for other morphologically similar tropical genera, where stable structural characters are preferred over metric thresholds (Wheeler & Baas, 1998). The key is operable using standard light microscopy on permanent anatomical sections, without recourse to molecular or chemical methods, making it directly applicable in field laboratories, timber yards, and customs inspection settings. Given the commercial importance of Sri Lankan dun timbers and the ongoing risk of misidentification in the regional timber trade, the availability of a verified anatomical key represents a tangible contribution to sustainable forest resource management and timber trade governance.

Conclusions

The six Sri Lankan *Shorea* species *S. disticha, S. stipularis, S. zeylanica, S. trapezifolia, S. astylosa,* and *S. congestiflora* although morphologically similar, exhibit sufficiently distinct wood anatomical characteristics to permit reliable species-level identification. Variation in vessel diameter, ray dimensions, and axial parenchyma patterning across transverse, radial, and tangential sections provided clear microstructural boundaries among taxa. The statistically significant negative correlation between vessel diameter and wood density further strengthened the discriminatory framework, linking functional wood properties to anatomical organisation. The dichotomous identification key constructed from these integrated criteria successfully and unambiguously separates all six species, offering a practical and scientifically grounded tool applicable across field, trade, and processing contexts. These findings address a longstanding challenge in the accurate identification of commercially important dun timbers in Sri Lanka, where visual similarity frequently leads to misidentification. The anatomical reference criteria and key established in this study provide timber inspectors, foresters, and wood processing industries with a reliable resource for species verification in both raw and processed timber forms, ultimately supporting sustainable timber trade, forest resource management, and conservation of native Dipterocarpaceae in Sri Lanka. The prospects for future research include expanding the anatomical database to additional Sri Lankan *Shorea* species, integrating molecular and chemical identification techniques with wood anatomy, and evaluating the influence of environmental and ecological factors on anatomical variation and timber properties to strengthen forensic timber identification and sustainable forest management practices.

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Conflict of Interest

None.

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Анатомічне дослідження видів *Shorea* у Шрі-Ланці

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Анотація. Шість видів роду Shorea, ендемічних для Шрі-Ланки – Beraliya dun (*S. disticha*), Navada dun (*S. stipularis*), Dun (*S. zeylanica*), Yakahalu dun (*S. trapezifolia*), Yakal dun (*S. astylosa*) та Thiniya dun (*S. congestiflora*) – є комерційно цінними породами деревини родини Dipterocarpaceae. Водночас їхня близька морфологічна подібність створює значні труднощі для точного визначення виду на рівні виду в польових умовах, торгівлі та під час переробки. Метою цього дослідження було встановити надійні анатомічні критерії деревини для розрізнення цих шести видів Shorea шляхом мікроструктурного аналізу та оцінки його кількісного зв'язку з щільністю деревини. Постійні зрізи в поперечній, радіальній та тангенціальній площинах були підготовлені та досліджені за допомогою світлової мікроскопії, при цьому діаметр судин і розміри променів вимірювалися за допомогою програмного забезпечення Micrometrics SE Premium, а щільність деревини визначалася методом витіснення води. Усі шість видів демонстрували як одиночне, так і групове розташування судин, при цьому середні діаметри судин суттєво відрізнялися між таксонами, що стало основною основою для мікроскопічного розрізнення. Будова променів варіювала від однорядної до багаторядної, а вимірювані відмінності у висоті та ширині променів мали додаткову діагностичну цінність. Патерни осьової паренхіми, включаючи паратрахеальні та апотрахеальні форми, послідовно відрізнялися між видами, підсилюючи анатомічні межі на клітинному рівні. Було виявлено статистично значущу негативну кореляцію між щільністю деревини та діаметром судин, що свідчить про те, що види з більшою щільністю характеризуються формуванням вужчих провідних елементів. Шляхом інтеграції розташування судин, морфології променів, розподілу паренхіми та значень щільності було побудовано дихотомічний визначальний ключ, який успішно та однозначно розрізняє всі шість таксонів. Розроблена в цьому дослідженні анатомічна структура та дихотомічний ключ пропонують інспекторам деревини, лісівникам і деревообробній промисловості науково обґрунтований практичний інструмент для точного визначення деревини дунових порід Шрі-Ланки як у необробленому, так і в обробленому вигляді

Ключові слова: анатомічні особливості; щільність деревини; анатомія деревини; ідентифікація деревини; характеристики судин; мікроскопічні особливості; дихотомічний ключ

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