ISSN 2079-0864, Biology Bulletin Reviews, 2025, Vol. 15, Suppl. 1, pp. S104–S113. © Pleiades Publishing, Ltd., 2025.

Current Trends in Alien Mycobiota of Woody Plants in Boreal Russia

A. G. Shiryaev[a, *], T. S. Bulgakov[b], O. S. Shiryaeva[a], and I. V. Zmitrovich[c]

[a] *Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, Russia*

[b] *Federal Research Centre the Subtropical Scientific Centre of the Russian Academy of Sciences, Sochi, Russia*

[c] *Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg, Russia*

**e-mail: anton.g.shiryaev@gmail.com*

Received April 7, 2025; revised May 6, 2025; accepted May 25, 2025

Abstract—Over the past century, the species richness of alien mycobiota associated with trees and shrubs in the boreal regions of Russia has increased exponentially. This is due to the rapid growth in the number of introduced host plant species, which is due to increased trade volumes and global warming. New data are coming in, thanks to which catastrophic scenarios for the spread of new plant diseases are being corrected. The problem of uncontrolled greening of cities is being discussed, as a result of which botanical gardens, parks, and gardening centers are recognized as foci of concentration and penetration of new diseases deep into the continent.

Keywords: anthropocene, biodiversity, climate change, invasion, monitoring, phytopathogenic fungi, urbanization

DOI: 10.1134/S2079086425600638

INTRODUCTION

In recent decades, the world has seen an unprecedented expansion of the ranges of alien organisms, including fungi (Capinha et al., 2015; Petrosyan et al., 2023). An alarming "sign of the Anthropocene" is the acceleration of invasions and epiphytotic spread of new diseases of woody plants in natural and artificial phytocenoses, which often cause enormous economic and ecological damage to forestry, urban landscaping, and private gardening (Purahong et al., 2022; Theodorou, 2022; IPBES..., 2023).

The vast majority of invasive fungal species (and oomycetes) in the Holarctic, including the European part of Russia, are phytopathogens, many of which have formed secondary habitats and have a significant impact on the state and stability of forest and anthropogenic ecosystems (*Samye opasnye*..., 2018). The history of phytopathology is, in essence, the history of the study of the migrations of phytopathogenic organisms (Crandall and Gravatt, 1967; Gorlenko, 1975; Dyakov and Levitin, 2018). In the 20th century, our country was hit by epiphytotics caused by invasive phytopathogens such as oak powdery mildew (the pathogen *Erysiphe alphitoides* (Griffon et Maubl.) U. Braun et S. Takam.), Dutch elm disease (*Ophiostoma ulmi* (Buisman) Nannf. and *O. novo-ulmi* Brasier), coccomycosis of stone fruits and bird cherry (*Blumeriella jaapii* (Rehm) Arx), and cryphonectrian necrosis of true chestnut (*Cryphonectria parasitica* (Murrill) M.E. Barr), not counting the spread of many pathogens of agricultural and ornamental plants (Gorlenko, 1975; Zhukov, 2010; Dyakov and Levitin, 2018; Selikhovkin et al., 2020). Since the beginning of the 21st century, ash tree necrosis (*Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz et Hosoya) has spread in the European part of the country; Siberia and the Urals were engulfed by an epiphytoty of fir bark necrosis (*Grosmannia aoshimae* (Ohtaka, Masuya et Yamaoka) Masuya et Yamaoka) (Zvyagintsev et al., 2023; Baranchikov et al., 2024). There are local outbreaks of red spot of pine needles (*Dothistroma pini* Hulbary et *D. septosporum* (Dorogin) M. Morelet) and the emergence and spread of sooty bark disease of maples (*Cryptostroma corticale* (Ellis et Everh.) P.H. Greg. et S. Waller) in the southern part of the European part of Russia (Musolin et al., 2016; Gninenko et al., 2023; Bulgakov, 2024a), boxwood cylindrocladium (*Calonectra pseudonaviculata* (Crous, J.Z. Groenew. et C.F. Hill) L. Lombard, M.J. Wingf. et Crous) and American moniliosis (*Monilinia fructicola* (G. Winter) Honey), and a number of harmful alien powdery mildew fungi (*Erysiphe corylacearum* U. Braun et S. Takam., *E. elevata* (Burrill) U. Braun et S. Takam., *E. flexuosa* (Peck) U. Braun et S. Takam., *E. salmonii* (Syd. et P. Syd.) U. Braun et S. Takam., and others) in the European part of Russia (Selikhovkin et al., 2020; Bulgakov, 2024a). It is quite possible that dangerous pathogens such as the causative agent of fusarium wilt of pine trees (*Fusarium circinatum* Nirenberg et O'Donnell) (which are already known in European countries), American poplar rust (*Melampsora medusa* Thüm.), alder blight (*Phytoph-*

thora alni Brasier et S.A. Kirk), walnut cancer (*Ophiognomonia clavigignenti-juglandacearum* (V.M.G. Nair, Kostichka et J.E. Kuntz) Broders et G.J. Boland), and a number of other fungal pathogens of woody plants (Bulgakov, 2024b) will appear in Russia.

Most often, phytopathogenic fungi penetrate into Russia through coastal territories with a relatively mild climate, especially in the presence of large ports with a large cargo flow (Selikhovkin et al., 2020; Zvyagintsev et al., 2023): Leningrad oblast in the Northwest, Krasnodar krai in the South, and Primorsky krai in the Russian Far East. At the same time, data on the expansion of secondary ranges of alien fungi deep into Russia are extremely fragmentary. Identification and analysis of natural prerequisites for biological invasions, i.e., those biological features that allow a species to penetrate beyond its original range, adapt to new conditions, successfully compete with local species, and become a malicious alien pathogen, is one of the most important problems of modern biology, which has not only fundamental but also practical significance.

The globalization of forest plant pathology problems requires consolidation of efforts to solve them (Mulenko et al., 2010; Yu et al., 2021). The appearance of alien fungi (neomycetes) in Europe dates back to the time of the Great Geographical Discoveries (which began with Columbus' expeditions to America), i.e., the starting point is the end of the 15th–beginning of the 16th centuries (Voglmayr et al., 2023). Species that spread before this time are proposed to be called archaeomycetes (Schertler et al., 2024). In European countries, the task of inventorying invasive fungal species has now become a priority (Voglmayr et al., 2023; Schertler et al., 2024). In 2022, economic losses from alien species in Europe amounted to US$140 billion, and worldwide reached almost US$0.5 trillion per year (IPBES..., 2023).

In Russia, the history of the dispersal and the biodiversity of alien fungi have been poorly studied compared to Europe; detailed information is available mainly on fungal pathogens of important crop plants, such as cereals, vegetables, and some fruit and industrial crops (Gorlenko, 1975; Dyakov and Levitin, 2018). For most regions, there are no lists of alien phytopathogens; the time and vector of invasions of species causing economic damage to forestry are unknown (Selikhovkin et al., 2020; Bulgakov and Shiryaev, 2022; Bulgakov, 2024b). At the same time, Russia's economic losses are growing: from 2017 to 2019, damage from biological invasions cost the country's budget at least US$51.5 billion, of which at least 9% is due to the activity of phytopathogenic fungi (Kirichenko et al., 2021).

At the same time, in Europe, as long ago as 2000–2010, the results of studies of alien fungi associated with woody and herbaceous plants, living in the soil, and parasitizing animals were published (Mulenko et al., 2010; Voglmayr et al., 2023). Updated lists of alien species have been published in Austria, Germany, Switzerland, and a number of other countries (Voglmayr et al., 2023; Schertler et al., 2024). In Russia, similar complete lists have not yet been compiled for any region. This is largely due to the lesser study of fungi and the general lag in mycological research in Russia: in Europe, the scientific study of alien fungi began in the 18th century, but in Russia, it began only in the second half of the 19th century and was interrupted several times because of catastrophic wars and historical upheavals of the 20th century. The longest history of research, almost one and a half centuries, is characteristic of St. Petersburg and Leningrad oblast, Moscow and Moscow oblast, and Yekaterinburg and Sverdlovsk oblast (Gorlenko, 1975; Dyakov and Levitin, 2018; Shiryaev and Kiseleva, 2023).

LONG-TERM DYNAMICS OF SPECIES RICHNESS ALIEN FUNGI

As a model region, we will consider Sverdlovsk oblast, in which the first results of the study of alien mycobiota developing on woody and shrubby plants have been summarized. In the largest city, Yekaterinburg, information on the development of alien pathogenic fungi on local and introduced plants has been accumulating for 160 years (Shiryaev et al., 2010, 2022; Bulgakov and Shiryaev, 2021, 2022). Since the 1860s, 297 species of alien fungi and fungus-like organisms (Ascomycota, Basidiomycota, Oomycota) have been identified on 453 species of native and alien trees and shrubs in the region.

The list of the TOP-100 most dangerous invasive species in Russia (Dgebuadze et al., 2018) includes four species of fungi, and all of them were found in Moscow oblast. Three species have been collected in Sverdlovsk oblast (*Ophiostoma novo-ulmi*, *Melampsoridium hiratsukanum* S. Ito ex Hirats. f., *Aphanomyces astaci* Schikora), and the fourth (*Batrachochytrium dendrobatidis* Longcore, Pessier et D.K. Nichols) is most likely present in this region (Trubetskaya, 2011; Burakova and Vershinin, 2013). For other regions, one or two species are indicated.

From the list of "100 major alien fungal and fungus-like oomycete pathogens" (Schertler et al., 2024), 28 species were identified in Sverdlovsk oblast: 14 species develop on woody-shrubby plants (hereinafter referred to as WSP), of which six species were collected on local plants: *Cronarthium ribicola* H.A. Dietr., *Erysiphe alphitoides*, *E. corylacearum*, *Lachnellula willkommii* (R. Hartig) Dennis, *Melampsoridium hiratsukanum*, *Ophiostoma novo-ulmi*; and 11 species develop on introduced trees: *Calonectra pseudonaviculata*, *Cronarthium ribicola*, *Dothistroma septosporum*, *Erysiphe corylacearum*, *E. necator*, *Hymenoscyphus fraxineus*, *Monilinia fructicola*, *Ophiostoma novo-ulmi*, *Plasmopara viticola* (Berk. et M.A. Curtis) Berl. et De Toni, *Diplodia sapinea* (Fr.)

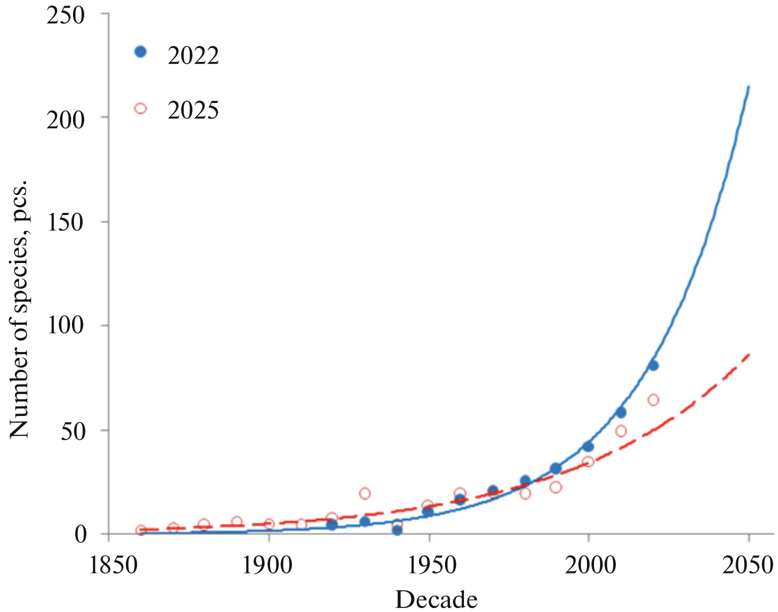

Fig. 1. Long-term dynamics of accumulation of species richness of newly identified alien fungal species in Sverdlovsk oblast. Models are built on the basis of data for 2022—solid line (y = 2E – 210$x^{64.05}$, $R^2 = 0.92$, $n = 11$), and for 2025—dashed line (y = 4E – 122$x^{37.23}$, $R^2 = 0.90$, $n = 17$).

P. Karst., *Venturia inaequalis* (Cooke) G. Winter. The following were collected from local and alien species: *Cronarthium ribicola*, *Erysiphe corylacearum*, *Ophiostoma novo-ulmi*. Ten species of fungi have been identified on herbaceous plants: *Blumeria graminis* (DC.) Speer, *Phytophthora infestans* (Mont.) de Bary, *Pseudoperonospora cubensis* (Berk. et M.A. Curtis) Rostovzev, *P. humuli*, *Puccinia graminis* Pers., *Pyrenophora tritici-repentis* (Died.) Drechsler, *Tilletia caries* (DC.) Tul. et C. Tul., *T. laevis* J.G. Kühn, *Urocystis tritici* Körn., *Verticillium dahlia* Kleb. Four species parasitize native animal species: *Aphanomyces astaci*, *Batrachochytrium dendrobatidis*, *Nosema ceranae* I. Fr., F. Feng, J.A. da Silva, S.B. Slemenda et N.J. Pieniazek, *Pseudogymnoascus destructans* (Blehert et Gargas) Minnis et D.L. Lindner (Martinkova et al., 2018; Shiryaev et al., 2022, 2023).

An example of rapid spread in the taiga zone of Russia, including the Urals, is Dutch elm disease (*Ophiostoma novo-ulmi*). This disease was absent in Yekaterinburg 10 years ago, and in 2022 in the central part of the city per 1 km^2 on average, eight trees of the species *Ulmus glabra* Huds., *U. laevis* Pall., and *U. minor* Mill. were already infected (Shiryaev and Kiseleva, 2023). Currently, in the region, *Grosmannia aoshimae* is actively expanding its range, and the number of finds in parks of *Diplodia sapinea* and other species of phytopathogens exotic for the Urals will increase (Shiryaev et al., 2021, 2023; Baranchikov et al., 2024).

The first dataset covering a 100-year period of research (1920–2020) of alien fungi developing on trees and shrubs in Sverdlovsk oblast was analyzed in 2022 (Fig. 1). From 1920 to 1940, 2–6 new species of alien fungi for the region were identified in each decade; from 1950 to 1980, from 11 to 25 species; and from 1990 to the current decade, there has been a sharp increase from 31 to 81 species. Consequently, the fact of an exponential increase in species richness has been established.

New data have been obtained in the three years since 2022. The materials of the collection of the Ural Society of Natural Science Lovers (UOLE), which contains samples of fungi collected in the region in 1860–1910 (the first sample dates back to 1864, the last to 1916), were analyzed. Consequently, compared to the 1920s, the range of available data has shifted back 60 years. We were also given phytopathological collections of an agricultural organization that worked in the region in the 1920s–1950s. Thus, the 2025 data differ from 2022 in terms of the historical depth of research and distribution of the analyzed material.

This affected the shape of the species richness accumulation curve constructed using the data available in 2025 (Fig. 1). An important result was discovered: species of fungi that in 2022 were considered to have been collected for the first time in the Sverdlovsk region in recent decades (1990–2020) were found among samples from the early and mid-20th century, as well as from the 19th century. In the new dataset, the largest number of species were collected in the

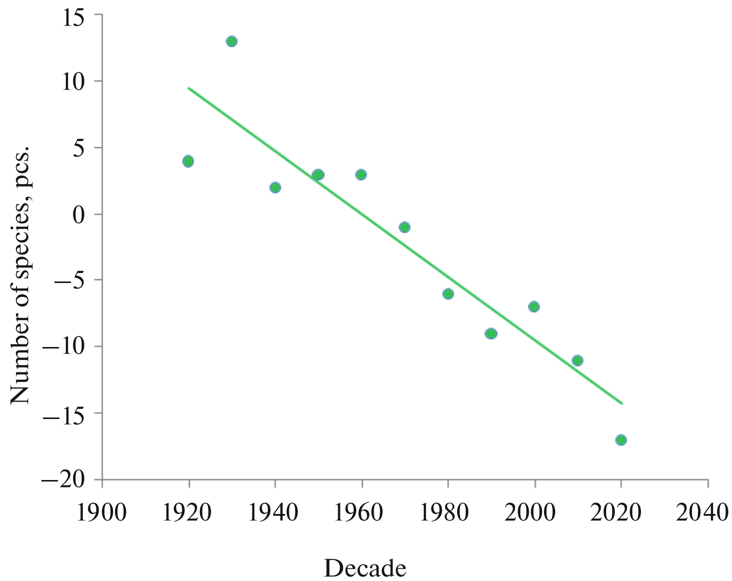

Fig. 2. Change in species richness of newly identified alien fungi in Sverdlovsk oblast in each decade in comparison between the model built using data for 2025 and the model for 2022 ($y = -0.24x + 465.06$, $R^2 = 0.91$, $n = 11$).

1880s–1890s, probably thanks to the Siberian-Ural Industrial Exhibition held in Yekaterinburg in 1887, which resulted in the creation of new parks in the city with a large number of new species of introduced plants. Also from this time onwards, city dwellers began to create gardens abundantly, and the number of greenhouses with exotic plants increased. In this regard, the power function of the exponential trend line from the "catastrophic" version of 2022 acquired a more "optimistic" appearance. However, in both cases, there is a sharp, linear increase in the species richness of phytopathogenic mycobiota, which began in the 1980s–1990s and continues to the present day.

The described redistribution of the number of species by decades between the data for 2022 and 2025 is expressed in the fact that, as we approach the present time, the difference between the first and second forecasts decreases, and then it becomes a negative value. In each decade from 1920 to 1960, the number of species in the 2025 model increased by 2–13 species compared to the 2022 model, and from the 1970s to the current decade, this number decreased by 1–17 species (Fig. 2).

Compared to the data for 2022, the number of species first identified in the 1930s has increased the most. This is due to the rapid increase in the number and area of parks and botanical gardens, in which the range of introduced alien trees and shrubs, the main substrates for the development of alien mycobiota, has expanded dramatically. During these years, the first wave of mass imports of East Asian plants took place, whereas before this, planting material came mainly from Europe. For the 1940s, the previously known list was expanded by only one new species. In contrast, the largest decline in species richness corresponds to the last two decades (2010 and 2020), when species were redistributed to earlier decades.

According to the forecast obtained on the basis of data for 2022, with a probability of 95%, about 215 new alien species may appear in Sverdlovsk oblast in 2050, and according to the second scenario, with a probability of 87%, the number of new alien species may be about 86, i.e., 2.5 times less (Fig. 1). Thanks to this, the "catastrophic" scenario of rapid spread of alien fungi in Sverdlovsk oblast can be corrected. However, in both scenarios, a rapid increase in neomycetes is expected. It is worth noting that both forecasts may change thanks to the receipt of new data, owing to the fact that there is still half of the second decade of the 21st century ahead, during which new species of fungi will be discovered.

In well-studied European countries, the results of repeated studies of the species composition of neomycetes obtained after 10–20 years have been published. For example, in Austria, the list of alien fungal species has grown by 4.6 times over two decades, and the lists of individual taxonomic groups of fungi have increased significantly. The curve of accumulation of species richness in European countries is close to that obtained in Sverdlovsk oblast according to data for 2022. The main differences between the analyzed datasets in European countries and Sverdlovsk oblast are that, in Europe, the first samples of alien fungi were collected in the middle of the 18th century, while in the Middle Urals, they were collected a century later. It is worth noting that, in Lithuania and Poland, there are opinions that the curve of accumulation of

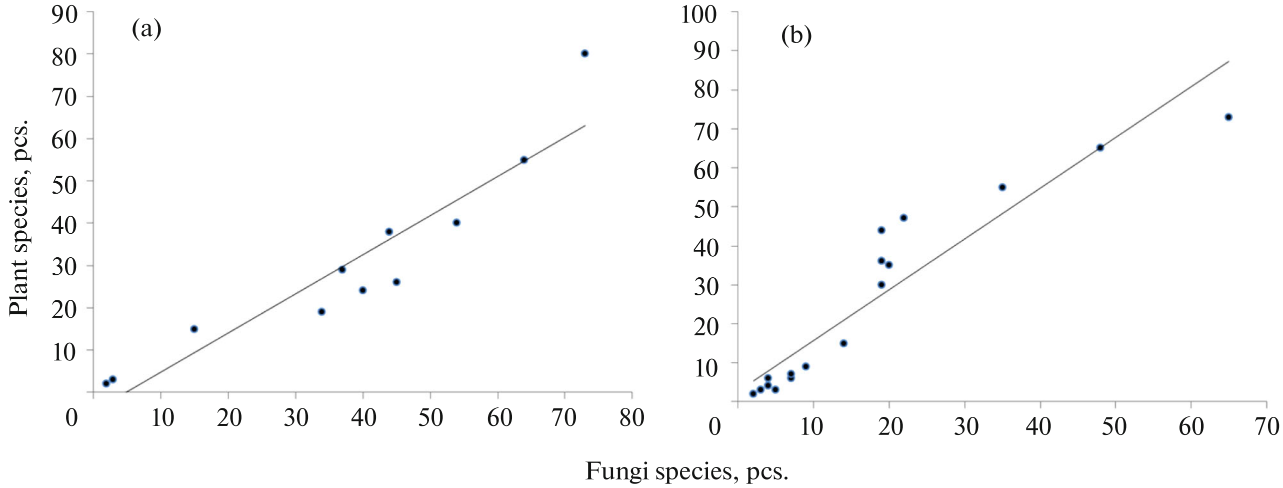

Fig. 3. The relationship between the number of newly identified species of alien fungi and trees and shrubs by decades in Yekaterinburg. Data for ten-year periods: (a) data for 2022, (b) data for 2025.

species richness of alien fungi is reaching a plateau (Mulenko et al., 2010).

For other regions and cities of Russia, the results of similar studies are still being summarized. At the same time, the initial results indicate, that in well-studied regions of the European part of Russia, such as Moscow (including Moscow), Leningrad (including St. Petersburg), and Rostov oblasts and in Krasnodar krai, an increase in the number of neomycete species is still observed (Bulgakov et al., 2014; Bulgakov, 2024a, 2024b). It can be assumed that this belated (compared to Europe) growth is associated with Russia's transition to a market economy in the 1990s and the beginning of the widespread import of planting material from other countries in the 2000s. This led to a sharp acceleration in the penetration of many alien species in the first two decades of the 21st century—including those species that had already spread to Western and Central Europe before the 1990s.

Using the example of a model group of aphyllophoroid fungi, it was found that over 100 years of research in Yekaterinburg, the total number of species increased from 196 to 304, i.e., by 1.6 times (Shiryaev and Kiseleva, 2023). At the same time, the number of local species did not change significantly ($p > 0.05$), while the number of alien species increased from 4 to 98, i.e., by 24 times. In the first half of the 20th century, 1.4 times more species of aphyllophoroid fungi were identified in the city compared to natural landscapes. The number of alien species in the city is 12 times higher than in natural landscapes. A similar trend was found for the proportions (%) of alien fungal species: over 100 years in Yekaterinburg, the proportion of alien species has increased by 13.5 times and is currently 9 times higher than in natural landscapes. The number of species and the proportion of pathogens in natural landscapes are currently similar to the parameters typical for Yekaterinburg in the period from the 1920s to the 1940s. For phytopathogenic species, as well as for alien species, an increase in the number of species and their proportion (%) has been established in general: over 100 years, the number has increased by 7 times, while the proportion has increased by 3.5 times. Both indicators for pathogenic fungi of woody and shrubby plants in modern natural landscapes are close to the levels identified for the mycobiota of Yekaterinburg in the period from the 1920s to the 1940s (Shiryaev and Kiseleva, 2023).

RELATIONSHIP BETWEEN SPECIES RICHNESS OF ALIEN FUNGI AND PLANTS

Phytopathogenic fungi are coevolutionarily associated with plants; therefore, one can expect a high level of connection between the number of emerging plant species and the fungi parasitizing them (Dyakov and Levitin, 2018). With each decade, the increase in the number of alien fungal species strongly positively correlates with the growing number of host plants (Fig. 3a), which, in turn, is due to rapid climate warming—an increase in the average annual temperature in the region, which over the past 100 years amounted to 3.8°C (Shiryaev and Kiseleva, 2023). Calculations showed that, with an increase in average annual temperature by 1°C in Yekaterinburg, the list of alien species of fungi on trees and shrubs increased by 76.1 species. Climate warming increases the likelihood of introduction into culture and naturalization of host plants of phytopathogens that did not exist in Yekaterinburg 50 years ago. Every year, 5–8 new species of trees and shrubs appear in the city (Shiryaev and Kiseleva, 2023).

Data analysis shows that the models obtained for the two analyzed periods represent linear functions (Fig. 3). For 2022 data, this is $y = 0.95x - 4.42$, $R^2 = 0.88$, $n = 11$, and for data for 2025, $y = 1.36x + 2.84$, $R^2 = 0.98$, $n = 17$. Thus, according to the first model, on average, for every 10 new plant species there are 7.8 ± 2.8 species of new fungi, and according to the second model, there are 8.3 ± 2.4 species of fungi.

The increase in the number of fungal species is associated not only with an increase in the number of plant species but also with an increase in aboveground phytomass (Shiryaev and Kiseleva, 2023). In Yekaterinburg, over the past 50 years, the structure of woody plants with the largest volume of phytomass has changed significantly. In 1968, the first two places were occupied by local plants—*Betula pendula* Roth (probably together with *B. pubescens* Ehrh.) and *Pinus sylvestris* L., and in third place was *Polulus balsamifera* L. s.l. The following changes have occurred over the years. Currently, the leading three are formed exclusively by North American plants: *Acer negundo* L., *P. balsamifera* s.l., and *Fraxinus pensilvanica* L. Thus, over 50 years, the phytomass of local woody plants has decreased to the maximum extent—*Pinus sylvestris* (2 times) and *Betula pendula* (1.6 times), on which no alien species of fungi were detected. The phytomass of *Populus balsamifera* remained similar, which allowed this species to remain in the top three leading plants. The greatest growth was noted for *Fraxinus pennsylvanica* (3.2 times), and also *Acer negundo*, *Prunus maackii* Rupr., and *Salix* × *fragilis* L. (1.6 times). The rapid growth of aboveground phytomass (and their areas) of alien woody plants is one of the leading factors in the increase in the number of xylotrophic fungi species.

URBAN PROTECTED NATURES—CONCENTRATORS OF NEOMYCETES

In order to control the rapid growth of alien fungi and plants in Sverdlovsk oblast, a number of measures have been developed. These include monitoring and recording of alien species, destruction of hotbeds of invasive species, development of legislation regulating the import and use of alien host plants, and educational work with the population about the harm of invasive plants. When preparing materials for inclusion in the upcoming reprint of the Red Book of Sverdlovsk Oblast, it is necessary to clearly distinguish between rare local and alien species (Shiryaev and Kiseleva, 2023).

Specially protected natural areas (OOPT) are areas of land and water surface where natural complexes and objects are located that have special environmental and scientific significance. The most important tasks of protected areas are the preservation of regional biodiversity, including rare, endangered, and economically and scientifically valuable objects of biota. In Russia, the area of nature reserves and national parks within old-growth forests and untouched tundra and steppe regions is increasing (Faterina, 2023). This is due to the awareness of the problem of preserving biodiversity in connection with the growth of economic activity.

Over the past 20 years, more and more urban areas have acquired the status of protected areas (Zaitsev and Polyakov, 2015). Botanical gardens and dendrological parks are being created, among other things, to form special collections of plants in order to preserve the plant world and its diversity. Within the boundaries of such urban protected areas, a number of rare species are purposefully introduced, and, more importantly, those included in various Red Books. This highlights the importance of protected areas for the protection of local biodiversity. Along with elements of local flora, botanical gardens also contain the maximum number of alien plant species. Many groups of living organisms, including fungi, are coevolutionarily related to plants. Some of them are adapted to development on a wide range of substrates, but many are obligately associated with a specific genus or species of plants.

The introduction of plants into new regions promotes the dispersal of associated alien fungi (Dyakov and Levitin, 2018). Most of them are "harmless" saprotrophs, mycorrhizal fungi, or harmless phytopathogens. However, owing to the growth of international trade and the popularity of exotic plants for urban landscaping, aggressive alien phytopathogens that cause serious plant diseases are penetrating new territories; they are also penetrating regions where they could not settle without human assistance (Zvyagintsev et al., 2023). According to a number of researchers, botanical gardens contain more alien and invasive fungi, thereby protecting rare and endangered species (Voglmayr et al., 2023). Let us consider whether this statement is fair using the example of the Botanical Garden of the Ural Branch of the Russian Academy of Sciences (Yekaterinburg) and the Peter the Great Botanical Garden of the Botanical Institute of the Russian Academy of Sciences (St. Petersburg).

Four species of fungi protected in Sverdlovsk oblast were found in the Botanical Garden of the Ural Branch of the Russian Academy of Sciences, which makes up 10.8% of the number of species in the Red Book of Sverdlovsk Oblast (*Krasnay kniga*..., 2018). Also collected here are 39 species of aphyllophoroid fungi, which have been assigned IUCN categories (Shiryaev et al., 2010): two species with category CR, two species with category EN, and three species with category VU, and the largest number belongs to category LC (38.5%). Thus, the Botanical Garden of the Ural Branch of the Russian Academy of Sciences protects 40 species of rare and endangered fungi for Sverdlovsk oblast. On the other hand, 52 species of aphyllophoroid fungi that are not found in the natural conditions of the Middle Urals have been identified here. Twenty-seven species of them are obligate and facultative phytopathogens that affect alien and native plants (Shiryaev et al., 2022, 2023; Baranchikov et al., 2024).

Also, 166 species of alien microscopic fungi were identified in the Botanical Garden of the Ural Branch of the Russian Academy of Sciences—specialized phytopathogens of specific plant species developing on leaves, needles, branches, and wood (Bulgakov and Shiryaev, 2021; Shiryaev et al., 2022, 2023, 2024). This is the most dangerous fraction of alien species. A number of them are generally recognized invasive species (Shiryaev and Kiseleva, 2023). It is worth noting that, in the Botanical Garden of the Ural Branch of the Russian Academy of Sciences, the area of which is 0.5 km^2, 204 species were identified (Shiryaev and Kiseleva, 2023; Shiryaev et al., 2024), i.e., 68.7% of the total number of species of alien fungi known in Sverdlovsk oblast.

Ten percent of the species of fungi included in the Red Book of St. Petersburg (2018) have been identified in the Peter the Great Botanical Garden. A number of these seven species are indicators of biologically valuable forests. In total, 41 species of fungi can be characterized as rare in St. Petersburg (Bondartseva et al., 2014; Morozova et al., 2014). On the other hand, more than 120 species of alien fungi have been identified in the Peter the Great Botanical Garden, including a number of invasive phytopathogens that are obligately associated with specific plant species (Lebedeva, 1924; Melnik, 2011; Firsov et al., 2016).

It is obvious that plantings of introduced species facilitate the penetration of many previously unknown species of alien fungi, including potentially invasive ones, into taiga regions. The overwhelming majority of identified species of alien fungi cannot develop in the current natural and climatic conditions of the studied regions because of the lack of the necessary substrate. Alien fungi go through an adaptation stage within botanical gardens and parks, and in the future, when favorable conditions are formed, they can expand their secondary range into the natural conditions of the corresponding regions (Melnik, 2011; Shiryaev and Kiseleva, 2023). It can be assumed that, owing to the presence of many exotic substrates within the city's protected areas, alien fungi are gradually moving deeper into continental Russia. About 20 years ago, it was impossible to imagine the discovery of many exotic phytopathogens in the harsh continental climate of Yekaterinburg. However, a study of collections of fungi collected in St. Petersburg and Yekaterinburg suggests the leading role of urban protected areas in the spread of alien species of fungi deep into the country.

It is worth noting that, owing to the rapid growth in the volume of imported seedlings from Europe and nurseries in Moscow and Moscow oblast, over the past 10 years, about 160 species of alien fungi previously unknown in the Urals have been discovered in Yekaterinburg. Many of the new plant species are being planted in city parks and also developed by private investors. These plants bring into the city corresponding plant diseases that were previously absent in the region. In this regard, the Botanical Garden of the Ural Branch of the Russian Academy of Sciences, thanks to its wide range of woody plant species, performs the function of "sentinel plantings," allowing many phytopathogens to be identified before they pass the naturalization stage and begin to cause damage to the city's greenery.

CONCLUSIONS

In conclusion, we would like to reduce the drama by recalling that research on biological invasions focuses on anthropogenically transformed landscapes, often urbanized ones. Such territories are incomparable in area with the vast taiga plateaus, which have been resistant to the climate changes of the last four decades. Oligotrophic and acidophilic taiga mosaics, characterized by a slow turnover of generations, do not allow potential broadleaf forest invaders (neutrophils and often calciphiles by nature) to penetrate and remain on soils where the capillary fringe reaches the root zone in summer. These species irradiate into taiga ecosystems along steep river banks, characterized by intensive erosive-accumulative activity of watercourses and soil dynamics, but we cannot yet accurately predict the possibilities and period of continuous reproduction of invaders in the context of ecosystem dynamics. Experience shows that most invaders are eliminated in the second or third generation. Approximately the same number of generations are required to replace zonal small-leaved species with coniferous cenosis-forming species, which have a complex age structure in such forests (Fedorchuk et al., 1998). In vast areas of taiga, subclimax forests are monodominant (spruce, fir, larch in different sectors of the taiga), and on flat areas, they tend to become swampy. Thus, on the "Map of Restored Vegetation of Central and Eastern Europe" (Gribova and Neuhäusl, 1989), reconstructed in conjunction with the tendency of reestablishment of vegetation and with mechanical composition of soils and drainage properties of the landscape, on the territory of St. Petersburg and its environs, we could observe only (1) northern European spruce forests (*Picea abies* L.) with a marsh shrub-moss cover with the participation of *Linnaea borealis* L. and *Moneses uniflora* L., (2) Northern European hydrophytic spruce forests with marsh shrub-grass cover (*Vaccinium uliginosum* L., *Equisetum sylvaticum* L., *Carex globularis* L., *Sphagnum* spp., *Polytrichum commune* Hedw.), and (3) Northern European hydrophytic pine forests with *Betula pubescens* and moss-shrub cover (*Vaccinium myrtillus* L., *V. uliginosum*, *Ledum palustre* L., *Polytrichum commune*, *Sphagnum* spp.)—without any niches for *Quercus robur* L., *Tilia europaea* L., *Fraxinus excelsior* L., *Acer platanoides* L., and *Ulmus laevis*, widely represented today in urban landscaping.

To this day, 600-year-old pines and 300-year-old spruces, which emerged before instrumental observations of climate change, are preserved in taiga forest stands and continue to perform their cenosis-forming functions against the backdrop of global warming. In addition to the forest stands themselves, which determine the rhythm of ecosystems, taiga plateaus contain a number of depots that help mitigate the effects of the current warming trend. Thus, in the European taiga, one of the consequences of global warming is the July waterlogging of soils (Nikolaev, 2024). If in non-upland conditions, for example, river terraces, this kind of moisture can lead to localized decay of forest stands and landslides, then on uplands excess moisture is deposited by peatlands, having virtually no effect on tree stands—their growth or degradation.

The second question about biological invasions in the taiga zone that has not yet been sufficiently studied is the distinction between the influence of climatic and water reclamation components on them. For this purpose, it is necessary to reconstruct the cultigenic ranges of the main introduced species in certain locations of the taiga zone both in space and in time.

The third little-studied issue is the global cyclicality of epiphytoties and the factors influencing it. Interesting material is provided by the spore-pollen diagrams of the European Plain: at the boundary of the Atlantic and Subboreal periods of the Holocene, a sharp and radical decrease in the proportion of pollen of *Ulmus* spp. is observed in all spectra, so-called "Ulmus decline." Further research has shown that fossil wood from the Ulmus decline period contains remains of bark beetles *Scolytus scolytus* Fabricius and *S. multistriatus* Marsham, modern transmitters of Dutch elm disease, as well as fungal spores (Innes et al., 2003; Clark and Edwards, 2004); i.e., some pathogens similar to the causative agents of Dutch elm disease affected European species of *Ulmus* long before the period of anthropogenic biological invasions, after which their representation in ecosystems increased again.

Despite these unresolved issues and the optimistic view expressed on the inertial processes of undisturbed upland forests, it is nevertheless necessary to note that the trends of biological invasions observed in anthropogenically transformed territories of the taiga biome are "a reality happening before our eyes." To more clearly allocate these trends, it is necessary to study the history of introduction of plants, if possible, in a century-long retrospective. Here, botanical collections can be an important resource, as they can reveal both the generative structures of micromycetes and the characteristic symptoms caused by these organisms.

This study calls for closer attention to urban protected areas, such as botanical gardens, parks, and arboretums, which act as an accumulator of alien species of fungi, the number of which sometimes exceeds the list of local species requiring protection. Urban protected areas of the taiga zone are a reserve for the invasion of alien species of fungi into some natural biotopes (including non-upland ones), the results of which require careful study.

FUNDING

This study was carried out with financial support from the Russian Science Foundation (project no. 25-26-00338).

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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