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# Mycobiota of Alien Plants in Siberian Arctic: A Case Study in Norilsk

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**Abstract**—Rapid climate warming in the Arctic contributes to an increase in the number of fungal species. However, the long-term dynamics of alien mycobiota, especially in Siberia, has been studied fragmentarily. In one of the largest industrial centers of the Arctic, the Norilsk city and nearby settlements in the Taymyrsky Dolgano-Nenetsky District of Krasnoyarsk krai, 78 species of fungi and pseudofungi (Ascomycota, Basidiomycota, and Oomycota) have been collected on alien plants over a 100-year period. Of these, 59 species are new to the district, 32 of which are noted in the Russian Arctic for the first time. Fungi are associated with 57 species of alien woody and herbaceous plants, 8 of which are included in the Black Book of Siberian Flora; 50 species of fungi were found on woody plants and 38 on herbaceous plants. The richest mycocomplexes are associated with *Populus tremula* (seven species of fungi), *Acer negundo*, and *Prunus padus* (five species each). Most of the alien fungi species (69.2%) are taxa widespread in Siberian forests, which, thanks to alien host plants, were able to expand their range to the north, while 7.7% are invasive for the entire territory of the Arctic and Siberia. The primary ranges of 24 fungi species are located in America, East Asia, and Europe. All alien fungal species were brought to district unintentionally. The main vectors of dispersal are the development of transport infrastructure and the movement of transport, people, and related goods during the economic development of territories. The first results indicate the absence of a correlation between the number of aphyllophoroid fungi species with the age and area of cities, but a reliable relationship has been established with the number of residents. A detailed study of other territories will allow the development of a Black List of Russian Arctic mycobiota.

**Keywords:** Taymyr, fungi, global warming, flora, biodiversity, alien species, invasion vector, forest tundra, *Acer negundo*

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## INTRODUCTION

The Arctic is warming about four times faster than other regions of the planet (Rantanen et al., 2022). In response to rapid temperature increases, profound changes are being observed in terrestrial Arctic ecosystems, such as borealization of flora, northward advance of the tree line, growth of woody phytomass, and increased species richness of mycobiota (Kauserud et al., 2008; Shiyatov, 2009; Walker et al., 2012). Fungi, including symbionts, pathogens, and decomposers, play a leading role in plant community dynamics and nutrient cycling in terrestrial ecosystems. Despite their ecological importance, the response of Arctic fungi to climate warming is unknown, as is their potential role in driving observed and projected changes in high-latitude biota (Diez et al., 2013).

With the rise in temperature in the north, anthropogenic activity has intensified: the construction of economic infrastructure from imported lumber is underway, and the rate of introduction of woody and herbaceous plants is accelerating in order to green populated areas (Morozova and Tishkov, 2021; Pis'markina et al., 2022). In turn, the emergence of many alien plant species in the Arctic is the cause of associated biological invasions that affect local, regional, and global biodiversity (Wasowicz et al., 2020). Warming and the introduction of plants have allowed alien fungi to spread to regions where they could not previously survive and reproduce (Dahlberg and Bültmann, 2013). The increasing rate of emergence of alien fungal species in the north, as in more southern regions, will probably contribute to changes in plant communities, especially when alien phytopathogenic species penetrate local ecosystems (Diez et al., 2013; Khimich et al., 2020). In the Arctic, the number of indoor fungi is growing, which destroy infrastructure built from imported wood building materials and also cause allergies in the local population (Shiryaev et al., 2020; Schertler et al., 2024).

The alien mycobiota of the European Arctic has been studied for at least 30 years, making it possible to establish the principles of spatiotemporal dynamics of invasive species and invasion vectors (Karatygin et al., 1999; Shiryaev and Mukhin, 2010; Shiryaev et al., 2020). The alien mycobiota of Siberian territories has been studied. Fragmentary data are known for the West Siberian and Yakut sectors (*Otchet*..., 1992; Shiryaev et al., 2018; Shiryaev et al., 2020). In high-latitude regions, at least 90% of alien fungal species were found on alien plants, as well as on anthropogenic building materials (Kotiranta and Mukhin, 2000; Khimich et al., 2020; Shiryaev et al., 2020). Data on the alien mycobiota of the vast Taymyrsky Dolgano-Nenetsky District of Krasnoyarsk krai are rare (Karatygin et al., 1999; Shiryaev, 2011, 2024).

The Norilsk industrial region is one of the largest agglomerations in the Russian Arctic, with more than a century of industrial development history (Erts, 2004; Open..., 2024). In 1938, a state-owned agricultural enterprise was established in the region that included two farms: Norilsk and Valkovskaya. For cows and pigs, hay and feed were brought in from the "mainland." In the mid-1940s, the state farm grew a number of "exotic" plants in the open ground: turnips, potatoes, three types of cabbage, rutabagas, turnips, radishes, lettuce, carrots, peas, beets, dill, sorrel, and green onions. In order to grow heat-loving crops, greenhouses and hothouses were built (Erts, 2004; State..., 2024). In the 1980s, the Norilsk state farm grew flowers; cucumbers, tomatoes, eggplants, bell peppers, lettuce, spinach, parsnips, watermelons, melons, green onions, and table greens ripened in greenhouses, and champignons and oyster mushrooms were also grown (*Otchet*..., 1992; Sevastyanov et al., 2014). However, in the 1990s, most agricultural products were already delivered from the "mainland," and in 2005, the Norilsk farm was abolished (Sevastyanov et al., 2014).

Norilsk lacks green spaces. Landscaping is of an island nature: lawns and flower beds are common; shrubs are present along roads and in public places (*Postanovlenie*..., 2015; State..., 2024). In 2012, the central part of Norilsk was renovated. Meadow bluegrass and red fescue, blue spruce, juniper and flowering shrub species, and decorative larch shrubs (dogwood, serviceberry, Japanese spirea, and cinquefoil) were planted on lawns. In 2013, about 100000 seedlings of various flower crops were grown in a Norilsk greenhouse: several types of marigolds, coleus, ageratum, and sage (*Postanovlenie*..., 2015). Since the beginning of the 2020s, perennial herbs have been planted in the Central District of the city and shrubs such as rose hips, spirea, rhododendrons, and bergenia. In populated areas, the greening of living spaces is actively taking place with a wide range of trees, shrubs, and herbaceous plants, the primary habitat of which is located far from Taymyr (*Postanovlenie*..., 2015; Filatova and Sergeeva, 2021; Yanchenko and Filatova, 2021; Pospelova and Pospelov, 2023).

In the vicinity of Norilsk, the number of recreational complexes (recreation centers, sports and health facilities, tourist centers, and summer cottages) is increasing, where landscaping with introduced woody and herbaceous plants is being carried out. The Norilsk Lake District became the basis for the formation of a recreational area approximately 30 km in length (along the Norilsk-Talnakh highway), where 38 recreational complexes created in the second half of the 20th and early 21st centuries are located (Sevastyanov et al., 2014). In landscaping, there are woody and herbaceous introduced species, such as *Bergenia crassifolia* (L.) Fritsch, *Iris sibirica* L., *Populus tremula* L., and *Sorbaria sorbifolia* (L.) A. Braun. Climate warming and the desire of local residents for personal garden plots have led to the introduction of a large number of plants. In the Valek region, the number and area of garden plots is growing. The number of greenhouses where seasonal crops are grown is increasing: cucumbers, tomatoes, peppers, zucchini, onions, dill, and parsley (Sevastyanov et al., 2014). According to E.B. Pospelova and I.N. Pospelova (2007, 2023), 54 species of alien plants are known in Taymyr.

The first information about the discovery of alien, cryptogenic species of fungi and pseudofungi (hereinafter simply referred to as fungi) of Taymyr dates back to 1912, when oomycetes (*Peronospora chenopodii* Schltdl.) were collected in the vicinity of Dudinka on the leaves of an alien *Chenopodium album* L. (Lavrov, 1926, cited from Karatygin et al., 1999). At the same place, on the leaves of *Rumex acetosella* L., ascomycete *Cladosporium allicinum* (Fr.) Bensch, U. Braun & Crous was collected (Lind, 1934, cited by Karatygin et al., 1999). In 1968, a new species of alien fungi *Rhizoctonia solani* J.G. Kühn was collected on potatoes and tomatoes at the Norilsk state farm (*Otchet*..., 1992). In the 1970s, three types of microscopic pathogens were identified: *Cladosporium cucumerinum* (Fr.) Bensch, U. Braun & Crous, *Golovinomyces artemisiae* (Grev.) VP Heluta, and *Pseudoperonospora cubensis* (Berk. & M.A. Curtis) Rostovzev. In 1980, the *Phytophthora infestans* (Mont.) de Bary developed massively on potatoes and tomatoes and *Septoria petroselini* Desm. on parsley in greenhouses. In the 1990s and 2000s, no new species of fungi were discovered, but in the 2010s, the macromycete *Typhula ishikariensis* S. Imai was collected (*Otchet*..., 1992; Shiryaev, 2024). By the start of this research in 2024, nine species of alien fungi developing on alien plants were known in Taymyr. In the 1980s, there were attempts to grow champignons (Agaricus spp.) and oyster mushrooms (Pleurotus sp.) in greenhouses, but this turned out to be economically unprofitable. These species are excluded from this study.

The aim of this study is to establish the number of fungal species developing on alien plants of Taymyr and identify the trophic and biogeographic structure of mycobiota and the routes of penetration of invasive species.

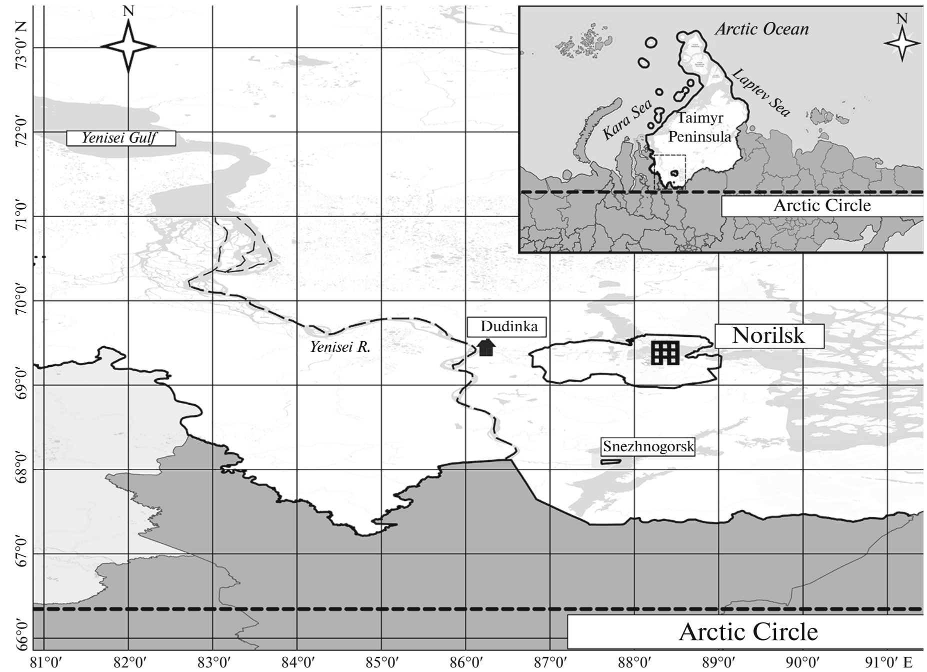


**Fig. 1.** Map of Taymyrsky Dolgano-Nenetsky District. The rectangle marks the research area.

## MATERIALS AND METHODS

The Taymyrsky Dolgano-Nenetsky District is located in the far north of Krasnoyarsk krai, north of the Arctic Circle (*Krasnaya kniga*..., 2022). Cape Chelyuskin, the northernmost point of Eurasia, is located on the Taymyr Peninsula (Fig. 1). The territory belongs to the Central Siberian floristic subprovince of the North Angara province of the Hypoarctic belt (Yurtsev, 1966). In the far north of Taymyr, arctic deserts are widespread, and most of the region is covered with tundra vegetation. The Arctic forest boundary runs through the region of Dudinka and Norilsk. Forest tundra and mountain northern taiga forests are widespread to the south.

The area of the region is 879900 km$^2$. The capital is the city of Dudinka, located on the right bank of the Yenisei River (69°24′ N, 86°10′ E). The largest city in the Taymyrsky Dolgano-Nenetsky District is Norilsk (69°21′ N, 88°11′ E), with a population of 235000 people. It is the second largest city in Krasnoyarsk krai by population (Open..., 2024).

According to data from the Dudinka weather station (Reference and information..., 2024), the climate in the Norilsk region is subarctic continental. The average annual air temperature in the middle of the 20th century was –9.4 to –10.5°C (Fig. 2). Since the 1980s, there has been warming, and in the current decade the average annual air temperature is –6.4°C. Therefore, over 50 years the temperature has increased by 4.4°C; i.e., it is increasing at a rate of 0.88°C/10 years. On average, 341 mm of precipitation falls per year.

Our team identified alien plants and mycobiota in July–September 2024. We use the term "alien plants" (and fungi) in a broad sense: species that are absent from the natural flora of the region or are highly likely to have been introduced (Pyšek et al., 2015). For example, like in the work (Pospelova and Pospelov, 2023), we classify *Chenopodium album*, *Pinus sibirica* Du Tour, *Populus tremula*, and *Tanacetum vulgare* L., et al., as alien plants.

The location of primary habitats allows us to divide alien plants into three groups:

(A) Exotic, whose primary range is located in America, East and Central Asia, and Europe: *Acer negundo* L., *Beta vulgaris* L., *Cucumis sativus* L., *Cucurbita pepo* L., *Hydrangea arborescens* L., *Lupinus polyphyllus* Lindl., *Malva thuringiaca* (L.) Vis., *Petroselinum crispum* (Mull.) Fuss, *Ribes uva-crispa* L., *Solanum tuberosum* L. *S. lycopersicum* L., *Solidago canadensis* L., *Sorbaria sorbifolia*, *Symphyotrichum novi-belgii* (L.) G.L.Nesom, *Syringa josikaea* J. Jacq. ex Rchb., *Ulmus pumila* L., *Vitis vinifera* L., and others.

(B) Siberian (Eurasian), distributed in the south of Siberia, but not north of the Arctic Circle: *Bergenia crassifolia*, *Cotoneaster lucidus* Schltdl. [=*C. acutifolius* Turcz.]. *Lonicera xylosteum* L., *Pinus sylvestris*, *Populus alba* L., *Populus laurifolia* Ledeb., *Prunus padus* L., *Rubus idaeus* L., *Spiraea chamaedryfolia* L., and others.

(C) Northern, the range limits of which are located on the border of Taymyr: *Dasiphora fruticosa* (L.) O. Schwarz., *Hordeum jubatum* L., *Pinus sibirica*, *Populus tremula*, etc.

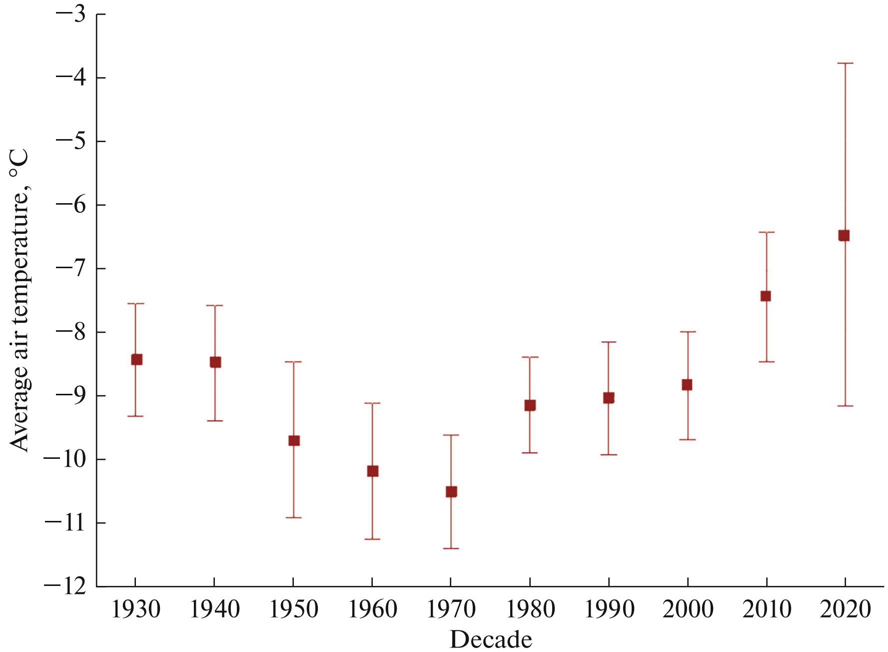


**Fig. 2.** Changes in average annual air temperature at the Dudinka weather station (1930–2020). The mean value and 95% confidence interval are given.

The names of plant species are given according to the Plants of the World (2024) database.

Plants collected in Taymyr are stored in the Biological Museum of the Institute of Plant and Animal Genetics, Ural Branch, Russian Academy of Sciences (SVER) (Yekaterinburg).

The fungal samples are stored in the collection of the Institute of Plant and Animal Ecology, Yekaterinburg (SVER(F)). The names of fungi species are given according to the IndexFungorum database (2024).

The work separately analyzes the distribution of two model groups of fungi in anthropogenic territories: aphyllophorales and powdery mildews.

A number of plants showed signs of damage by pathogenic fungi, but there was no sporulation. Such plants and fungi are excluded from the work.

In Taymyr, some genera of host plants (Artemisia, Vicia, Urtica, etc.) are found in natural conditions, so associated micromycetes can be considered native for the region (*Erysiphe baeumleri* (Magnus) U. Braun & S. Takam.; *E. polygonum* DC. s.str.; *E. urticae* (Wallr.) S. Blumer; *Golovinomyces artemisiae*; *G. macrocarpus* (Speer) U. Braun; and *G. bolayi* S. Takam., Lebeda & M. Götz). However, in the course of previously conducted studies, it was not possible to identify them, or they were associated with anthropogenic habitats (Karis and Pyldmaa, 1974; Karatygin et al., 1999). Due to the uncertainty of their geographic origin, such species are classified as cryptogenic, i.e., probably introduced (Voglmayr et al., 2023). In the future, such fungi are considered together with alien fungi.

When comparing data arrays, Spearman's rank correlation coefficient ($r_{SP}$), Sørensen's index of species similarity ($I_{CS}$), and the Kruskal–Wallis criterion (KW-H) were used. The Shannon (H') and Menhinick ($D_{Mn}$) diversity indices were calculated. The dendrogram was constructed using Ward's method and Euclidean distance. Calculations were performed using the Statistica 10.0 program.

The description of the fungal species in the annotated list is given in the following order:

The letter (A) denotes new species for the Russian Arctic; the asterisk (*) denotes new species for the Taymyrsky Dolgano-Nenetsky District.

The synanthropic status of fungal species is formed from two components: geographical group (I is alien and II is native). Alien species are divided into three subgroups (Richardson et al., 2000): accidental (Ia), naturalized (Ib), and invasive (Ic). Native species, in relation to the anthropogenic factor, are divided into three subgroups (Mukhin and Ushakova, 2005): anthropophobes (IIa), anthropotolerants (IIb), and anthropophiles (IIc).

Trophic group of fungi: M indicates a mycorrhiza-forming organism, P indicates a pathogen, and S indicates a saprotroph.

The number of fungal finds is given.

Geographic groups of plants: A is exotic, B is Siberian, and C is northern.

$^{A}$*Species name [=synonym]—Ia–IIc, MS, number of fungi found on alien substrates: description of locality, substrate (biogeographic group of plants: A–C), date of discovery, collection number in SVER(F) or (link to a literary source).

## RESULTS

### *Annotated list*

### *Ascomycota*

*Blumeria graminis* (DC.) Speer sl – IIb, P, 4: Dudinka, on cereals (Põldmaa and Raitvir, 1972); Norilsk, lawn on Leninsky prospekt, on leaves of *Phleum pratense* L. (B), August 22, 2024, SVER(F) 86563; ibid., lawn, on *Festuca pratensis* Huds., August 7, 2024, SVER(F) 86631; Talnakh, lawn near the bus station, on *Hordeum jubatum* (C), August 4, 2024, SVER(F) 86589.

A**Cercospora beticola* Sacc. – Ic, P, 3: Valek, garden plots, on leaves of *Beta vulgaris* (A), August 29, 2024, SVER(F) 86588.

A**Cercospora hydrangeae* Ellis & Everh. – Ia, P, 1; Norilsk, greenhouse, Valekskoe shosse 1, on living leaves *Hydrangea arborescens* (A), August 29, 2024, SVER(F) 86630.

*Cladosporium allicinum* (Fr.) Bensch, U. Braun & Crous [= *Mycosphaerella allicina* (Fr.) [Vestergr.] – Ia, P, 1: env. Dudinki, on the leaves of *Rumex acetosella* L. (B) (Lind, 1934).

A**Cladosporium iridis* (Fautrey & Roum.) GA de Vries – Ia, P, 1: Valek, garden plot, on leaves of *Iris sibirica* (A), August 8, 2024, SVER(F) 86562.

**Coleosporium tussilaginis* (Pers.) Lev. – Ia, P, 1: Talnakh, st. Baumanskaya, on *Tussilago farfara* L. (B), September 9, 2024, SVER(F) 86632.

A**Colletotrichum malvarum* (A. Braun & Casp.) Southwest. – Ia, P, 1: Valek, garden plots, on leaves of *Malva thuringiaca* (A), July 7, 2024, SVER(F) 86629.

A**Cryptosporium lonicerae* Cooke & Ellis – Ib, P, 1: Norilsk, greenhouse, on branches of *Lonicera xylosteum* (B), September 1, 2024, SVER(F) 86550.

**Epichloe typhina* (Pers.) Brockm. – Ia, P, 1; Norilsk, lawn on Leninsky prospekt, on *Phleum pratense* (B), August 7, 2024, SVER(F) 86590.

A**Erysiphe adunca* (Wallr.) Link – Ia, P, 1: Snezhnogorsk, on the leaves of *Populus tremula* (C), September 2, 2024, SVER(F) 86587.

**Erysiphe baeumleri* (Magnus) U. Braun & S. Takam. – Ib, P, 6: Norilsk, lawns, on leaves of *Vicia sepium* L. (B), September 7, 2024, SVER(F) 86633; Talnakh, ul. Maslova, on *V. sepium*, August 31, 2024, SVER(F) 86564.

A**Erysiphe convolvuli* DC. – Ia, P, 1: Valek, Norilsk Rublevka, on leaves of *Convolvulus arvensis* L. (A), September 3, 2024, SVER(F) 86628.

A**Erysiphe ehrenbergii* (Lev.) U. Braun, M. Bradshaw & S. Takam. – Ic, P, 1: Norilsk, greenhouse, on leaves of *Lonicera xylosteum* (B), September 9, 2024, SVER(F) 86676.

A**Erysiphe macleayae* R.Y. Zheng & GQ Chen – Ia, P, 2: Valek, garden plots, on leaves of *Chelidonium majus* L. (A), September 18, 2024, SVER(F) 86685; Dudinka, on *Ch. majus*, August 5, 2024, SVER(F) 86675.

**Erysiphe polygonum* DC. s.str. – Ib, P, 3: Norilsk, former state farm, on leaves of *Persicaria maculosa* Gray. (B), September 14, 2024, SVER(F) 86627; same place, TPP-1, on *Polygonum aviculare* L., September 14, 2024, SVER(F) 86586.

A**Erysiphe russellii* (Clinton) U. Braun & S. Takam. – Ia, P, 1: Valek, garden plots, on leaves of *Oxalis stricta* L. (A), September 12, 2024, SVER(F) 86591.

A**Erysiphe syringae-japonicae* (U. Braun) U. Braun & S. Takam. – Ic, P, 2: Norilsk, Lake Dolgoe Park, on leaves of *Syringa josikaea* (A), August 6, 2024, SVER(F) 86634.

**Erysiphe trifoliorum* (Wallr.) U. Braun – Ib, P, 1: Talnakh, Ogni tundry tourist center, on leaves of *Lupinus polyphyllus* Lindl. (A), September 6, 2024, SVER(F) 86561.

**Erysiphe urticae* (Wallr.) S. Blumer. – Ib, P, 3: Dixon, on leaves of *Urtica dioica* L. (B), August 4, 2024, SVER(F) 684; Norilsk, near the greenhouses, on *U. dioica*, September 3, 2024, SVER(F) 86674.

*Golovinomyces artemisiae* (Grev.) VP Heluta – Ib, P, 14: Norilsk, lawn on Leninsky prospekt, on leaves of *Artemisia vulgaris* L. (B), July 30, 2024, SVER(F) 86635; Dudinka, on *A. vulgaris*, August 8, 1967, (Karis, Pyldmaa, 1974); Talnakh, on leaves of *A. vulgaris*, August 4, 2024, SVER(F) 86592.

A**Golovinomyces asterum* var. *asterum* (Switzerland.) U. Braun – Ia, P, 1: Valek, Norilsk Rublevka, on leaves of *Symphyotrichum novi-belgii* (A), September 3, 2024, SVER(F) 86585.

A**Golovinomyces asterum* var. *solidarity* (Switzerland.) U. Braun - Ia, P, 1: Valek, on leaves of *Solidago canadensis* L. (A), September 3, 2024, SVER(F) 86565.

A**Golovinomices bolayi* S. Takam., Lebeda & M. Got – Ic, P, 3: Norilsk, Lake Dolgoe Park, on living leaves of *Petunia* × *atkinsiana* (Sweet) D.Don ex WHBaxter (A), September 3, 2024, SVER(F) 86677; Talnakh, campsite, on *P.* × *atkinsiana*, August 27, 2024, SVER(F) 86625.

A**Golovinomyces latisporus* (U. Braun) P.-L. Qiu & S.Y. Liu – Ia, P, 1: Valek, garden plots, on leaves of *Helianthus tuberosus* L. (A), September 10, 2024, SVER(F) 86626.

**Golovinomyces macrocarpus* (Speer) U. Braun – Ia, P, 2: Norilsk, near the greenhouse, on leaves of *Tanacetum vulgare* (C), September 3, 2024, SVER(F) 86593.

A**Golovinomyces sonchicola* U. Braun & RTA Cook – Ib, P, 2: Norilsk, near TPP-1, on *Sonchus arvensis* L. (B), SVER(F) 86673; Talnakh, near the bus station, on *S. arvensis*, August 27, 2024, SVER(F) 86678.

A**Golovinomyces sordidus* (L. Junell) VP Heluta – Ia, P, 1: Norilsk, on leaves of *Plantago major* L. (B), September 10, 2024, SVER(F) 86594.

A**Melampsora populnaea* (Pers.) P. Karst.sl – Ia, P, 2: Norilsk, greenhouse, on leaves of *Populus alba* (B), August 7, 2024, SVER(F) 86566; Snezhnogorsk, on *P. tremula* (C), August 6, 2024, SVER(F) 86636.

**Nectria cinnabarina* (Today) Fr. – Ia, P, 2: Norilsk, lawn on Leninsky prospekt, on a dead branch of *Spiraea hypericifolia* (B), August 3, 2024, SVER(F) 86624; ibid., greenhouse, on a dying branch of *Prunus padus* (B), August 5, 2024, SVER(F) 86672.

*Podosphaera aphanis* (Wallr.) U. Braun & S. Takam. – IIb, P, 1: Valek, garden plots, on leaves of *Dasiphora fruticosa* (C), September 10, 2024, SVER(F) 86584.

*Podosphaera fusca* (Fr.) U. Braun & Shishkoff [=*Podosphaera xanthii* (Castagne) U. Braun & Shishkoff) – IIc, P, 2: Dudinka, greenhouse, on leaves of *Cucurbita pepo* (A), August 3, 2024, SVER(F) 86671; Valek, garden plots, on leaves of *Calendula officinalis* L. (A), September 4, 2024, SVER(F) 86679.

A**Podosphaera tridactyla* (Wallr.) de Bary s.str. – Ia, P, 1: Norilsk, greenhouse, on leaves of *Prunus padus* (B), September 10, 2024, SVER(F) 86560.

A**Polystigma rubrum* (Pers.) DC. – Ia, P, 1: Norilsk, greenhouse, on *Prunus padus* (B), September 1, 2024, SVER(F) 86670.

A**Pseudocercospora cotoneastri* (Katsuki & Tak. Kobay.) Deighton – Ia, P, 1: Norilsk, Lake Dolgoe Park, on *Cotoneaster lucidus* (B), September 1, 2024, SVER(F) 86623.

A**Pseudocercospora puderi* BH Davis ex Deighton – Ia, P, 1: Valek, garden plots, on *Rosa rugosa* (A), September 4, 2024, SVER(F) 86595.

**Puccinia urticata* (Link) F. Kern s.l. – Ia, P, 1: Norilsk, next to the greenhouse, on *Urtica dioica* (B), August 28, 2024, SVER(F) 86551.

A**Ramularia bergeniae* Vasyag. – Ib, P, 2: Norilsk, lawn on Leninsky prospekt, on leaves of *Bergenia crassifolia* (B), July 31, 2024, SVER(F) 86637.

A**Sawadaea bicornis* (Wallr.) Homma – Ia, P, 3: Norilsk, lawn, on *Acer negundo* (A), August 1, 2024, SVER(F) 596; same place, greenhouse, August 5, 2024, SVER(F) 86567.

*Septoria petroselini* Desm. – Ib, P, 2: Norilsk, greenhouse, on living leaves of *Petroselinum crispum* (Mill.) Fuss (A), August 1986, (Report ..., 1992).

A**Septoria phlogis* Sacc. & Speg. – Ia, P, 1; Valek, Norilskskata rublevka, on living leaves of *Phlox paniculata* L. (A), September 2, 2024, SVER(F) 86622.

A**Sporocadus rosarum* (Henn.) F. Liu, L. Cai & Crous – Ia, P, 1: Valek, garden plots, on *Rosa rugosa* (A), August 29, 2024 SVER(F) 86638.

A**Titaeosporina tremulae* (Lib.) Luijk – Ia, P, 1: Talnakh, on *Populus tremula* (C), September 5, 2024, SVER(F) 86597.

*Basidiomycota*

**Athelia rolfsii* (Curzi) CC Tu & Kimbr. – Ia, P, 1: Norilsk, greenhouse, on the bases of living and dying stems of *Cucumis sativus* (A), August 27, 2024, SVER(F) 86583.

*Basidiodendron cinereum* (Bres.) Luck-Allen – Ib, P, 4: Norilsk, lawn on Leninsky prospekt, on the base of a seedling *Pinus sibirica* (C), September 2, 2024, SVER(F) 86620; Talnakh, Zharki tourist center, on *Pinus sibirica*, September 9, 2024, SVER(F) 86639.

**Bovista furfuracea* Persian. – Ia, S, 1: Norilsk, trash can next to greenhouses, on dead cucumber tops mixed with soil (A), September 1, 2024, SVER(F) 86598.

**Chondrosteroneum purpureum* (Pers.) Pouzar – Ia, P, 1: Snezhnogorsk, on the trunk of a living *Populus tremula* (C), August 20, 2024, SVER(F) 86668.

**Coprinellus micaceus* (Bull.) Vilgalys, Hopple & Jacq. Johnson – Ia, S, 1: Norilsk, greenhouse, on the base of a dead *Hydrangea arborescens* trunk (A), September 10, 2024, SVER(F) 86569.

**Gymnopilus penetrans* (Fr.) Murrill – Ia, S, 1: Norilsk, greenhouse, on the base of a dead *Ulmus pumila* trunk (A), September 10, 2024, SVER(F) 86600.

A**Intextomyces contiguus* (P. Karst.) J. Ericss. & Ryvarden – Ia, S, 1: Norilsk, greenhouse, on the base of *Populus alba* (B), September 14, 2024, SVER(F) 86558.

*Kneiffiella barba-jovis* (Bull.) P. Karst. – IIa, S, 1: Norilsk, greenhouse, on *Ulmus pumila* (A), August 5, 2024, SVER(F) 86655.

*Marasmius oreades* (Bolton) Fr. – Ia, S, 1: Talnakh, lawn near the bus station, at the base of the stems *Hordeum jubatum* (C), August 4, 2024, SVER(F) 86580.

*Mutinus ravenelii* (Berk.) E.Fisch. – Ia, S, 2: Norilsk, greenhouse, on the base of dead *Acer negundo* trunks (A) and Salix sp.; September 12, 2024, SVER(F) 86602; ibid., August 1984 (*Otchet*..., 1992).

**Peniophora cinerea* (Pers.) Cooke – Ia, S, 1: Norilsk, Lake Dolgoe Park, on a dead branch of *Cotoneaster lucidus* (B), September 13, 2024, SVER(F) 86642.

**Peniophora limitata* (Chaillet ex Fr.) Cooke – Ia, S, 1: Norilsk, greenhouse, in pots on the base of dead *Hydrangea arborescens* (A), August 5, 2024, SVER(F) 86654.

**Phellinus tremula* (Bondartsev) Bondartsev & P.N. Borisov – Ib, P, 1: Snezhnogorsk, on the trunk of living *Populus tremula* (C) (Shiryaev, 2024).

**Phragmidium rubi-idaei* (DC.) P. Karst. – Ia, P, 1: Valek, garden plots, on leaves of *Rubus idaeus* (B), September 4, 2024, SVER(F) 86615.

A**Pleurotus calyptratus* (Lindblad ex Fr.) Sacc. – Ia, S, 1: Dudinka, greenhouse, on the base of a dead *Vitis vinifera* tree trunk (A), August 3, 2024, SVER(F) 86643.

**Podofomes stereoides* (Fr.) Gorjon – Ia, S, 1: Norilsk, at the base of a dead stem of *Artemisia vulgaris* (B), August 7, 2024, SVER(F) 86614.

**Pseudotomentella nigra* (Höhn. & Litsch.) Svrček – Ia, M, 1: Norilsk, greenhouse, on the root and root collar of *Ribes uva-crispa* (A), August 5, 2024, SVER(F) 86604.

**Ramariopsis tenuiramosa* Corner – Ia, S, 1: Norilsk, greenhouse, in a tub on the root collar of *Populus laurifolia* (B), moss covered, August 5, 2024, SVER(F) 86557.

A**Rhizoctonia fusispora* (J. (Schroed.) Oberw., R. Bauer, Garnica & R. Kirschner – Ib, P, 3: Norilsk, Lake Dolgoe Park, on the base of *Spiraea hypericifolia* (B), August 1, 2024, SVER(F) 86644; Valek, Norilskaya rublevka, on *Dasiphora fruticosa* (C), September 10, 2024, SVER(F) 86571; Valek, Norilskaya rublevka, on the root collar *Fragaria × ananassa* (A), September 10, 2024, SVER(F) 86573.

*Rhizoctonia solani* JG Kühn – Ib, P, 3: Norilsk (*Otchet…*, 1992); Dudinka, vegetable garden, on stems and tubers of *Solanum tuberosum* (A), August 3, 2024, SVER(F) 86653; Valek, garden plots, on Brassica sp. (A) September 4, 2024, SVER(F) 86613.

*Schizophyllum commune* Fr. – Ia, S&P, 2: Norilsk, greenhouse, in a tub at the base of a living *Populus laurifolia* (B), August 5, 2024, SVER(F) 86605; same place, on a dead branch of *Syringa josikaea* (A), August 5, 2024, SVER(F) 86681.

**Sistotrema raduloides* (P. Karst.) Donk – Ib, S, 3: Norilsk, greenhouse, on the base of *Lonicera xylosteum* (B) and on the neighboring *Prunus padus* (B), August 5, 2024, SVER(F) 86682; Valek, garden plots, on dead *Rubus idaeus* bushes (B), September 1, 2024, SVER(F) 86611.

**Thelephora palmata* (Scop.) Fr. – Ia, M, 2: Norilsk, lawn on Leninsky prospekt, on the basis of living *Sorbaria sorbifolia* (A), August 7, 2024, SVER(F) 86651; Talnakh, tourist center, on the root collar of *Rubus idaeus* (B), September 2, 2024, SVER(F) 86606.

**Tomentella badia* (Link) Stalpers – Ia, M, 1: Talnakh, Gora Otdel'naya ski resort, on the dead part of the base of *Populus tremula* trunk (C), August 6, 2024, SVER(F) 86648.

*Trametes hirsuta* (Wulfen) Lloyd – IIb, S, 2: Norilsk, greenhouse, on a dead *Acer negundo* tree trunk (A), August 27, 2024, SVER(F) 86556; Valek, garden plots, on a dead *Rosa rugosa* bush (A), September 6, 2024, SVER(F) 86610.

*Trechispora cohaerens* (Switzerland.) Jülich & Stalpers – IIa, S, 1: Norilsk, lawn on Leninsky prospekt, on the base of a dead seedling *Pinus sibirica* (C), August 7, 2024, SVER(F) 86574.

*Trechispora microspora* (P. Karst.) Liberta – IIb, S, 1: Valek, garden plots, near greenhouses, on fallen dead *Rubus idaeus* trees (B), September 4, 2024, SVER(F) 86577.

*Typhula ishikariensis* S. Imai – Ib, P, 2: Dudinka (Shiryaev, 2024); Norilsk, lawn on Leninsky prospekt, on *Festuca pratensis* (B), August 7, 2024, SVER(F) 86607.

*Typhula micans* (Pers.) Berthier – IIb, S, 3: Dudinka, trash near the port, on dead stems of *Cannabis ruderalis* Janisch. (B), August 3, 2024, SVER(F) 86554; Valek, garden plots, on *Persicaria maculosa* (B), September 6, 2024, SVER(F) 86649; Norilsk, greenhouse, on a fallen branch of *Acer negundo* (A), August 5, 2024, SVER(F) 86649.

**Typhula trifolii* Rostr. – Ia, S, 2: Norilsk, trash can near greenhouses, on leaves of *Trifolium montanum* L. (B), August 7, 2024, SVER(F) 86683; Dudinka, lawn near the administration of the Taymyrsky Dolgano-Nenetsky District, on leaves of *Trifolium pratense* L. (B), August 3, 2024, SVER(F) 86650.

A**Xenasma tulasnelloideum* (Höhn. & Litsch.) Donk – Ia, S, 1: Norilsk, lawn on Moskovsky Prospect, on the basis of a seedling *Acer negundo* (A), August 6, 2024, SVER(F) 86608.

**Xenasmatella alnicola* (Bourdot & Galzin) KH Larss. & Ryvarden – Ia, S, 1: Dudinka, greenhouse, on the base of a dead *Vitis vinifera* tree trunk (A), August 3, 2024, SVER(F) 86609.

**Xylodon detriticus* (Bourdot) KH Larss., Viner & Spirin – Ib, S, 2: Snezhnogorsk, on the litter under *Populus tremula* (C), September 5, 2022 SVER(F) 86575.

*Oomycota*

*Peronospora chenopodii* Schltdl. – Ia, P, 1: the environs of Dudinka, on leaves of *Chenopodium album* (B), July 20, 1912 (Lavrov, 1926, cited from Karatygin et al., 1999).

*Phytophthora infestans* (Mont.) de Bary – Ic, P, 5: Norilsk, on leaves of and fruits *Solanum tuberosum* (A) (*Otchet…*, 1992); Valek, garden plots, on leaves of *S. tuberosum* and *S. lycopersicum* (A), August 27, 2024, SVER(F) 86576.

A**Plasmopara viticola* (Berk. & M.A. Curtis) Berl. & De Toni – Ia, P, 1: Dudinka, greenhouse, on leaves of *Vitis vinifera* (A), August 3, 2024, SVER(F) 86555.

*Pseudoperonospora cubensis* (Berk. & M.A. Curtis) Rostovzev – Ic, P, 3: Norilsk, greenhouse, on leaves of *Cucumis sativus* (A), August 1975 (*Otchet…*, 1992).

Over 120 years, from the 1910s to the 2020s, 78 species of fungi were collected on alien plants in Norilsk and neighboring settlements: seven local (8.9% of the total number of species) and 71 alien species (91.1%). In the annotated list, 41 species (52.6% of the total) are Ascomycota, 33 species are Basidiomycota (42.3%), and four species are Oomycota (5.1%) (Fig. 3). If only alien species are taken into account, the Ascomycota

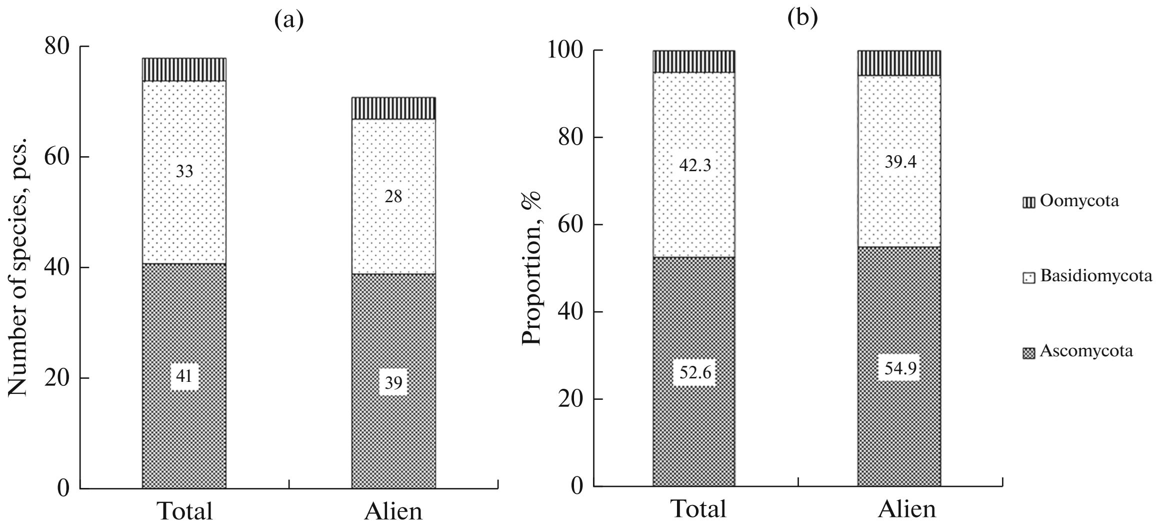


**Fig. 3.** Number of species (a) and proportion (b) of three divisions of fungi in the general list and the alien group.

division includes 39 species (54.9%), Basidiomycota 28 species (39.4%), and Oomycota 4 species (5.6%).

In 2024, 73 species of fungi were collected on alien plants, 69 of which were collected on alien plants for the first time (Fig. 4). Of these, 59 species are new to Taymyr, and 32 were discovered for the first time in the Russian Arctic. None of the species are included in the Red Data Book of Krasnoyarsk krai (2022). In contrast, five species were found (*Blumeria graminis*, *Lachnellula willkommii*[1], *Phytophthora infestans*, *Plasmopara viticola*, and *Pseudoperonospora cubensis*) from the list of 100 most dangerous pathogenic fungi on the planet (Schertler et al., 2024).

Of the nine species collected from 1910 to the 2010s, only six were recorded in 2024; hence the similarity coefficient is low ($I_{CS} = 0.11$). The average similarity between the eight decades (in which the fungi were collected) is also low: 0.14 (min–max. 0–0.29).

The diversity of the alien fungal fraction, including 71 species and 127 samples ($D_{Mn} = 6.3$), is almost twice as high as the native one, which includes 7 species and 15 samples ($D_{Mn} = 3.8$). This conclusion is also confirmed by the Shannon Index (H' = 3.02 vs. 1.96), which is significantly higher for the alien fraction ($t = 3.6$, $p < 0.001$).

The abundance of the five most common fungal species (>4 samples) is 22.5% of the total number of samples (142), while 46 species are represented by only one sample. Among the mass species, there is one local species (*Blumeria graminis*, 4 samples), and four are alien (*Basidiodendron cinereum*, *Erysiphe baeumleri*, *Golovinomyces artemisiae*, and *Phytophthora infestans*, 29 samples).

[1] *Lachnellula willkommii* is a local species that develops on larch trees. It is not included in the article.

In Taymyr, the proportion of alien species was calculated for two model groups of fungi. Currently, 290 species of aphyllophoran fungi are known, of which 12.4% are alien species (Table 1). For the life forms of aphyllophoran fungi—poroid and corticioid fungi—the proportion of alien species is 8.4 and 12.8%, respectively. The proportion of alien aphyllophorans forming basidiomes on wood is 9.6%, on litter 7.3%, and on soil 5.4%.

For the second model group, powdery mildew fungi, 19 alien species are taken into account in this study. Previously, 12 native species were known in the region (Karatygin et al., 1999), and we collected another one, *Phyllactinia betulae* (DC.) Fuss (Budimirov, personal data). Thus, at present, in Taymyr, 59.4% of the total list of the group are alien species. On woody plants, 71.4% of powdery mildew fungi species are alien, and on herbaceous plants, 56% are alien.

When studying the mycobiota of the settlements of Dudinka, Norilsk (center), Talnakh, and Snezhnogorsk, there was no correlation between the number of fungal species with the age and area of the settlements or the number of residents ($p > 0.01$). For the model group—aphyllophoral fungi—in well-studied cities of the Russian Arctic (Murmansk, Vorkuta, Labytnangi, Salekhard, Dudinka, and Norilsk (center)), there is no correlation between the number of fungal species with age and the area of the city, but there is with the number of residents ($r_{SP} = 0.832$, $p = 0.039$).

Among the alien fraction, pathogens predominate—50 species, which is 68.5% of the species richness of the fraction, followed by saprotrophs (20 species/27.4%) and mycorrhiza-forming (3 species/4.1%). The native fraction is characterized by the opposite situation: saprotrophs totally predominate here (6 species/85.6%); there is only one species of phytopathogens, and mycorrhizal fungi are absent (Fig. 5).

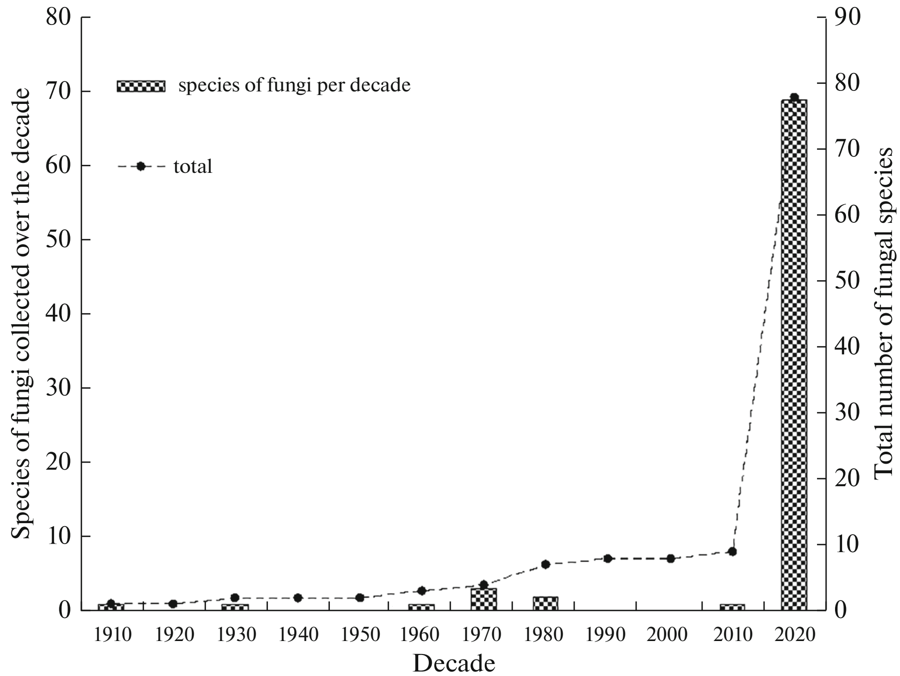


**Fig. 4.** Number of species of alien fungi collected in each decade and the accumulation curve of the number of species identified in the Taymyrsky Dolgano-Nenetsky District, Krasnoyarsk krai, from the 1910s to the 2020s.

Among the alien fraction, the greatest richness was found for pathogens: (random) 31 species in group Ia, which is 64% of the species richness of the group; 14 species in group Ib (83.3%); and 6 species in Ic (100%) (Fig. 6). Among the native fraction, the maximum richness was found for saprotrophs in group IIb (anthropotolerants, four species), then for anthropophobes (IIa, two species), and the least was for anthropophiles (one). Among the three groups of the native fraction, saprotrophs predominate (50–100%).

Fungi were collected on 57 species of alien plants: 18 species of woody plants and 39 species of herbaceous plants. Fifty species of fungi have been identified on woody plants, and 38 species on herbaceous plants. On 46 plant species (80.7%), one to two species of fungi were identified (Fig. 7); three species on *Cucumis sativus*, *Hydrangea arborescens*, *Lonicera xylosteum*, *Pinus sibirica*, *Rosa rugosa*, and *Vitis vinifera*; four on *Rubus idaeus*; and five on *Acer negundo* and *Prunus padus*. The richest mycocomplex is associated with *Populus tremula* (seven). Only on one species of herbaceous plants were three species of fungi identified (*Cucumis sativus*), while on all the others there are no more than two. In general, the species richness of mycocomplexes associated with woody plants is 2.5 times richer than those associated with herbaceous plants (2.91 vs. 1.23); their 95% confidence intervals

**Table 1.** Species richness of native and alien mycobiota in Taymyrsky Dolgano-Nenetsky District and Sverdlovsk oblast

| Group of fungi | Taymyrsky Dolgano-Nenetsky District | | Sverdlovsk oblast |
|---|---|---|---|
| | Native species | Alien species (share %) | Alien species (share %) |
| Aphyllophorales | 254 | 36 (12.4) | 96 (11.3) |
| *Poroid fungi* | 76 | 7 (8.4) | 22 (7.7) |
| *Corticoid fungi* | 156 | 23 (12.8) | 52 (13.8) |
| *On wood* | 234 | 25 (9.6) | 71 (9.0) |
| *On soil* | 35 | 2 (5.4) | 12 (10.2) |
| *On litter* | 39 | 3 (7.3) | 8 (5.7) |
| Powdery mildew (Erysiphales) | 13 | 19 (59.4) | 33 (38.4) |
| *On woody plants* | 2 | 5 (71.4) | 25 (53.5) |
| *On herbaceous plants* | 11 | 14 (56.0) | 8 (19.5) |

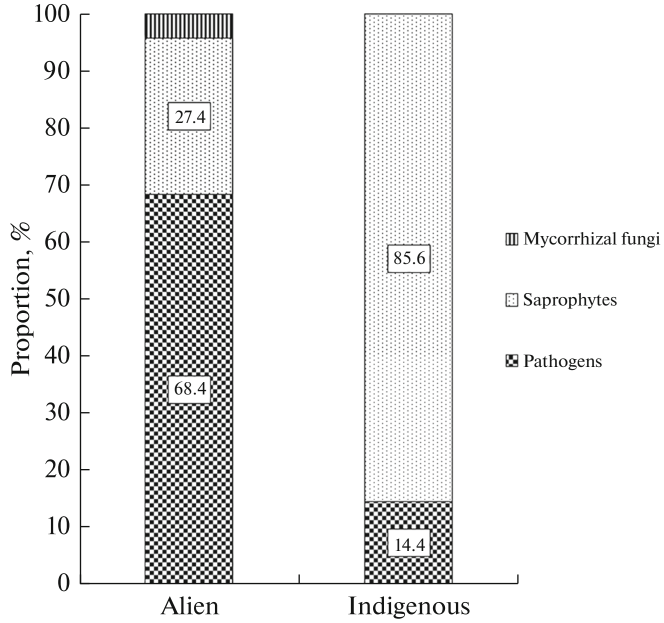


**Fig. 5.** Ratio (%) of trophic groups among alien and native species of fungi developing on alien plants of Taymyr.

do not intersect (Fig. 8). The mycocomplexes of woody plants are reliably richer than those of herbaceous plants: KW-H (1; 57) = 27.19; $p = 0.00001$.

In relation to the natural ecosystem of Taymyr, we classify six species of fungi (Ic) as invasive: *Cercospora beticola*, *Erysiphe ehrenbergii*, *E. syringae-japonicae*, *Golovinomyces bolayi*, *Phytophthora infestans*, and *Pseudoperonospora cubensis* (Fig. 9). Of these, 83.3% were found on exotic plants (group A) and 16.7% on Siberian plants (group B), but they were not found on plants of group C. Naturalized species together with invasive species comprise 28 species, which constitutes 33.7% of the alien fraction. Fungi of the richest synanthropic group—Ia (random)—populate exotic and Siberian substrates in approximately equal proportions, and only a few northern ones. The maximum proportion of fungi (83–100%) on exotic plants include groups IIc (anthropophiles) and Ic (invasive), and the least (27–30%) are naturalized and anthropotolerant (groups Ib and IIb). The largest number of naturalized fungal species develop on Siberian plant species (Ib, 54.5%). A similar parameter was found for anthropotolerant fungi (IIb, 50%).

The largest number of alien fungi were collected on plants in greenhouses (24 species), followed by a group of plants used in urban landscaping (20 species) and on weeds (16 species) (Table 2). The maximum number of samples was collected from weeds (43) and greenhouse plants (32). The minimum species richness and number of samples were collected from plants used in garden landscaping (13 and 14, respectively). The Menhinick and Shannon diversity indices, as well as the number of specific fungal species, are highest for greenhouse plants, followed by a group of plants used in urban as well as garden landscaping.

The most invasive group is agricultural plants, mainly grown in garden associations: *Cercospora beticola* develops on beets, *Pseudoperonospora cubensis* on cucumbers, and *Phytophthora infestans* on potatoes and tomatoes (three species, accounting for 21.4% of the group of agricultural plants). Also, three invasive species of fungi were identified in urban landscaping (*Erysiphe ehrenbergii*, *E. syringae-japonicae*, and *Golovinomices bolayi*; 15%). Only one species (*P. cubensis*) is associated with greenhouse plants, and invasive species

**Table 2.** Species richness of fungi developing on five groups of synanthropic plants

| Plant groups | Number of species | Number of samples | Manning's index | Shannon index | Unique species |
|---|---|---|---|---|---|
| Plants in greenhouses | 24 | 32 | 4.3 | 3.11 | 18 |
| Urban greening | 20 | 28 | 3.8 | 2.88 | 16 |
| Weeds | 16 | 43 | 2.5 | 1.92 | 11 |
| Agricultural plants | 14 | 24 | 3.0 | 2.15 | 10 |
| Garden landscaping | 13 | 14 | 3.6 | 2.56 | 10 |

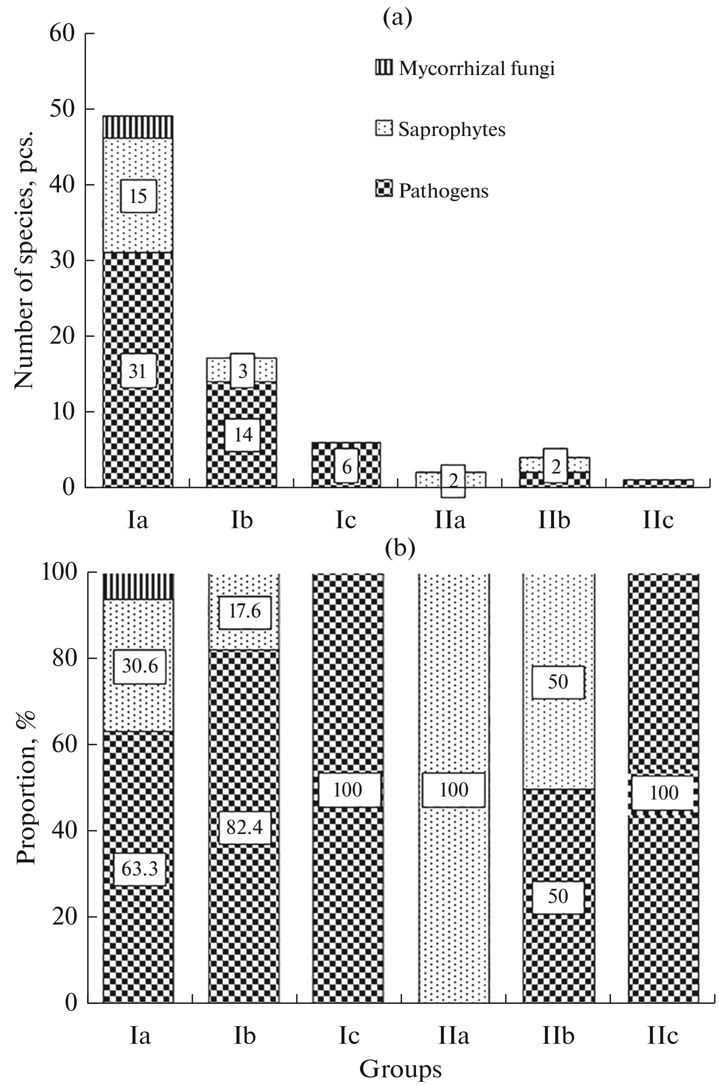


**Fig. 6.** Species richness (a) and proportion (b) of trophic groups forming six synanthropic groups of fungi in Norilsk.

of fungi have not been identified in garden landscaping or on weeds.

The species of fungi developing on weeds and agricultural plants form a single cluster, while another cluster is formed by two groups—mycocomplexes formed on plants used in urban and garden landscaping, as well as those found in greenhouses and on wooden structures (Fig. 10). Natural dark coniferous forests on Lake Lama (Shiryaev et al., 2025), located 100 km from Norilsk, form a separate cluster, the least similar to synanthropic groups of plants.

## DISCUSSION

From 1912 to 2024, 78 species of fungi were identified on alien plants in the Taymyrsky Dolgano-Nenetsky District of Krasnoyarsk krai. At present, this is the largest regional list of alien fungal species in the Russian Arctic. Thus, in the neighboring Yamalo-Nenets Autonomous Okrug (YNAO), 30 species are known (*Otchet*..., 1992; Karatygin et al., 1999; Shiryaev, 2006; Shiryaev et al., 2020; Tikhanovsky, 2021) and, in Murmansk oblast, 33 species (Shavrova, 1989; Karatygin et al., 1999; Ivanov and Milina, 2003; Isaeva and Khimich, 2011; Litvinova and Rak, 2017; Khimich et al., 2020; Khimich, 2022). The differences are related to the different levels of research in the regions.

In three regions, it is possible to compare data for only one well-studied group of fungi—aphyllophoraceae: 26 species of this group have been identified in Taymyr, 14 in the Yamalo-Nenets Autonomous Okrug, and 10 in Murmansk oblast. Mycobiota research in each region has lasted at least a century. A probable explanation for the fact that there is a smaller number of alien species of fungi in Murmansk oblast is that in

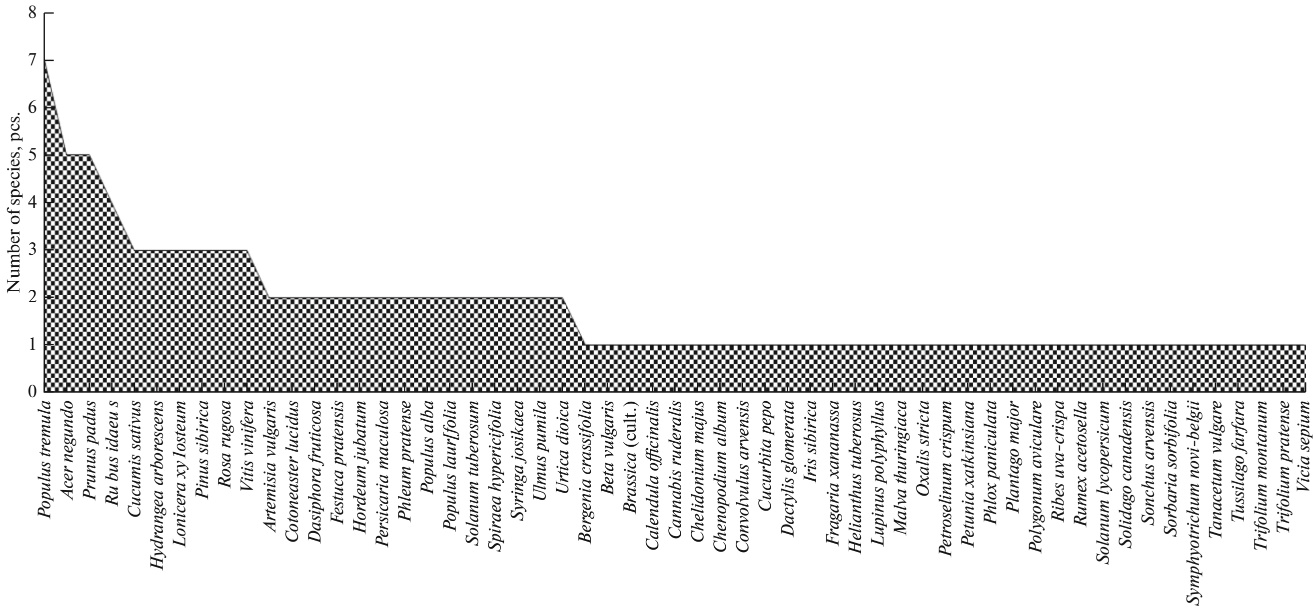


**Fig. 7.** Number of fungi species on 57 species of alien plants of Taymyr.

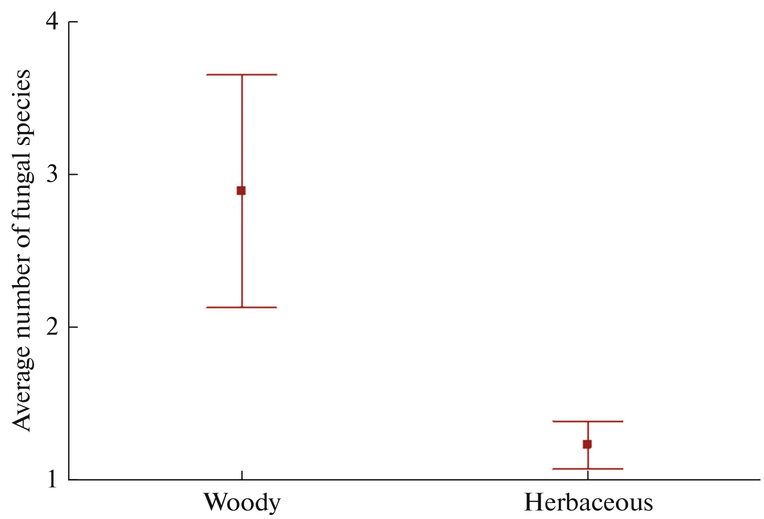


**Fig. 8.** Average number of fungal species (and 95% confidence interval) collected from alien woody and herbaceous plants of Taymyr.

Taymyr, bird cherry and aspen are alien substrates, while in Murmansk oblast they are native. Therefore, the specific fungi associated with these trees are alien to Taymyr and local for Murmansk oblast. The similarity between the mycocomplexes of the three regions is average ($I_{CS} = 0.58 \pm 0.11$). As a result, the increased rate of plant introduction may lead to homogenization of the northern aphyllophoran fungal biota.

For microscopic mycocomplexes, the similarity is lower, since all alien species in the north are associated with introduced plants. Therefore, the spectrum and species richness of mycobiota depend on the list of "exotic" plants imported for landscaping and gardening, weeds that have spread due to the import of hay, etc. An arbitrary set of plants is imported to various regions of the Arctic, which does not contribute to the homogenization of the species composition of synanthropic mycobiota.

Most alien fungal species (69.2%) are taxa that are widespread in Siberian forests and have been able to expand their range northward thanks to alien host plants, while 30.8% of species are exotic, including 7.7% that are invasive throughout the Arctic and Siberia. In general, for a number of species of fungi, the primary ranges are located in America (*Erysiphe rus-*

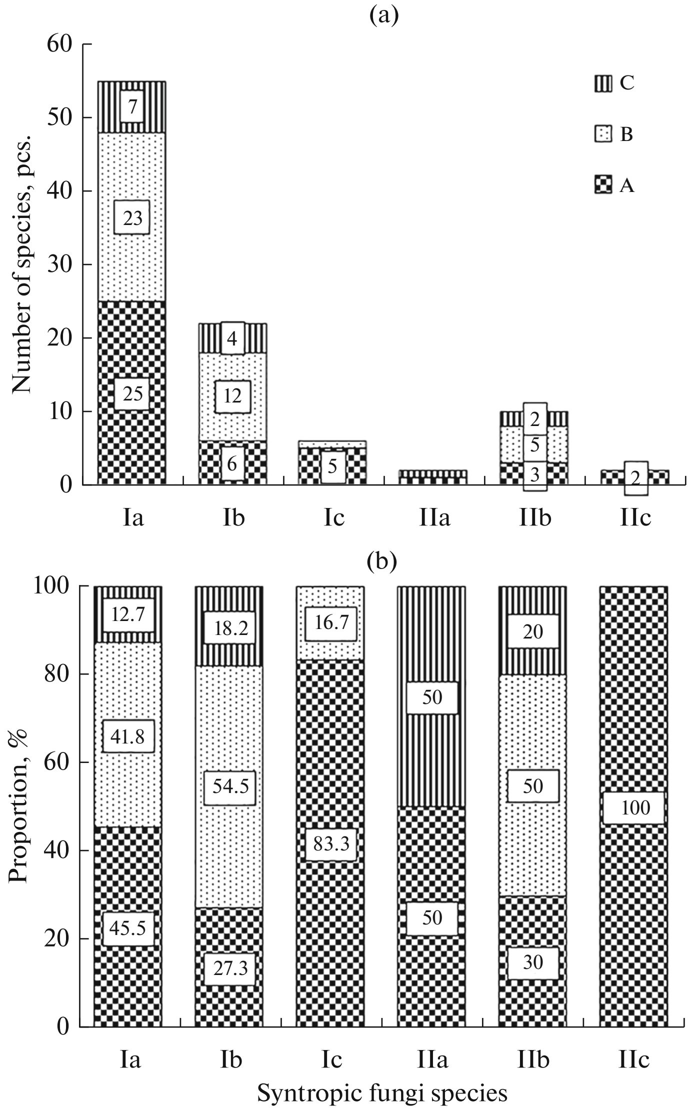


**Fig. 9.** Species richness (a) and ratio (b) of six synanthropic groups of fungi developing on alien plants of Taymyr.

*sellii*, *Golovinomyces asterum* var. *asterum*, *G. asterum* var. *solidaginis*, *G. latisporus*, *Phytophthora infestans*, etc.) and in East Asia and Europe (*Athelia rolfsii*, *Cercospora hydrangeae*, *Erysiphe ehrenbergii*, *E. macleayae*, *E. syringae-japonicae*, *Mutinus ravenelii*, *Peniophora limitata*, *Plasmopara viticola*, *Septoria petroselini*, *Serpula lacrymans*, *Rhizoctonia solani*, etc.) (Voglmayr et al., 2023).

By the start of the study in 2024, 11.5% of the fungal species from the current list were known in the region. It is possible that the sharp increase in the number of fungi collected in Taymyr can be explained by a targeted study in 2024. However, given that alien fungi were found only on alien plants, and also that a sharp increase in the number of alien plants in Norilsk has been observed since 2010, we have established a strong and positive correlation ($R^2$ = 0.96) between these parameters. At the same time, in the 1960s, four researchers studied alien mycobiota in Taymyr, one in the 1970s, one in the 1980s, three in the 1990s, two in the 2000s, two in the 2010s, and two in the 2020s. Thus, there is no correlation between the number of researchers and the identified fungal species in each decade ($r_{SP} = 0.63$, $p = 0.13$). It is worth noting that, in the Yamalo-Nenets Autonomous Okrug (Priuralsky District), a sharp increase in the number of alien fungi has been recorded since the second half of the 2010s, although this region can be characterized as one of the most studied in the Arctic (Shiryaev, 2006, 2017, 2018; Shiryaev et al., 2019, 2020).

In Taymyr, 12.4% of the species of aphyllophoral fungi are alien (Table 1). It is worth noting that, in the well-studied Sverdlovsk oblast, the proportion of the alien fraction is similar—11.3% (Shiryaev et al., 2010,

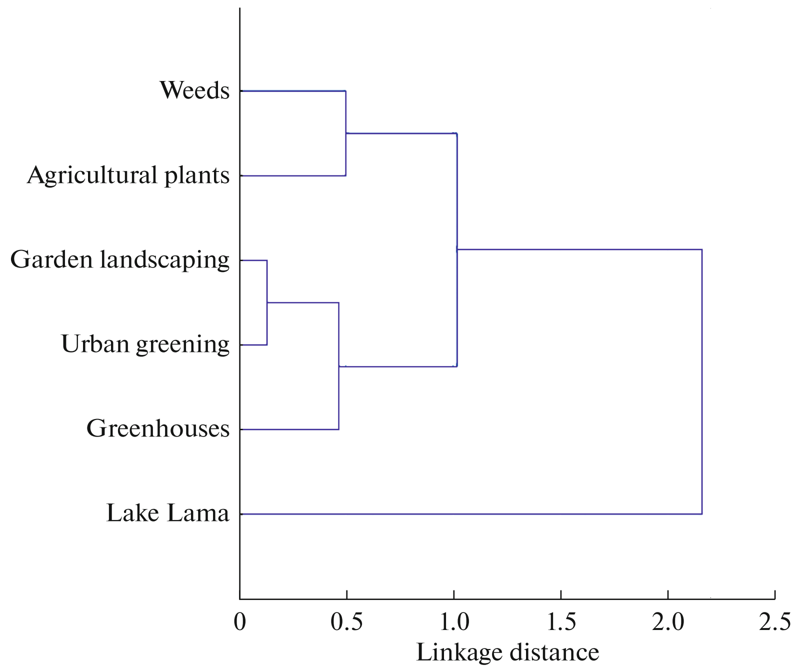


**Fig. 10.** Similarity of mycocomplexes developing on five groups of plant substrates in the city of Norilsk. Data are compared with the old-growth northern taiga forest massif on Lake Lama.

2024). In general, from north to south of Taymyr, a downward trend in this parameter was identified: in the Arctic deserts 28%, in the tundra 16%, and in the forest tundra 13%, while in the northern taiga it was only 10%. For two life forms, poroid and corticioid fungi, the proportion of alien species in Taymyr is 8.4 and 12.8%, while in Sverdlovsk oblast it is 7.7% and 13.8%, respectively. In Taymyr, the proportion of alien species on wood is 9.6%, on litter 7.3%, and on soil 5.4%. For macroscopic fungi, it is still problematic to draw conclusions about the latitudinal or longitudinal dynamics of the proportion of the alien fraction. In contrast to our results, for alien flora, minimum parameters were found in the Siberian sectors with an increase in the direction of Fennoscandia, as well as an increase in the proportion of alien species with a decrease in latitude (Morozova and Tishkov, 2021).

In Taymyr, 59.4% of powdery mildew fungi species are alien. In Sverdlovsk oblast, the proportion of alien species is lower, 38% (Budimirov, 2023; Budimirov and Shiryaev, 2024). On woody plants of Taymyr, 71.4% of powdery mildew fungi species are alien and, on herbaceous plants 56%, while in Sverdlovsk oblast these parameters are lower: 53.5 and 19.5%, respectively. These results seem unexpected given the prevailing paradigm about the small number (and proportion) of alien species in the Arctic (Morozova and Tishkov, 2021). A likely explanation for such high parameters in Taymyr is the rapid increase in the number of introduced plants in Norilsk. Many of the introduced species have been grown in the region for many years, and a specific mycobiota associated with specific plants has formed on them. However, the number of native host plants in the north is low. Consequently, the number of alien host plants exceeds the number of native ones. This factor determines the unexpectedly high diversity of alien fungi in the Taymyrsky Dolgano-Nenetsky District.

Over more than a century of research, rapid dynamics of the species composition of alien fungi has been established ($I_{cs}$ = 0.15). Initial results indicate high variability in the lists of alien fungi, as well as plants. In Taymyr, 81% of fungal species are found no more than twice, after which they disappear when the resource is exhausted. Therefore, many species collected in the 1960s–1980s are no longer found. Consequently, the mycobiota formed on alien plants (substrates) in the Arctic/Subarctic is represented, to a large extent, by random species. Only a third of the species have become naturalized. Like in other high-latitude regions, pathogens of some plants used in horticulture can be called naturalized in Taymyr: *Athelia rolfsii*, *Phytophthora infestans*, *Rhizoctonia fusispora*, *R. solani*, *Schizophyllum commune*, *Typhula ishikariensis*, and *Xylodon detriticus*. For example, of the alien aphyllophoran fungi, 28.2% of species (7 out of 26) have naturalized in Taymyr, which is similar to the Yamalo-Nenets Autonomous Okrug (30.7%) and Murmansk oblast (25.3%).

**The importance of native and alien flora.** The result established in Taymyr confirms the previously obtained conclusion that in Arctic regions 95–100% of alien fungi species develop on alien plants (substrates) (Shiryaev et al., 2020). This once again demonstrates that, in order to more fully identify alien fungi, it is necessary to fully study the entire diversity of alien plants in the northern regions.

The rate of warming and growth of economic activity suggests that the number of alien plants in Taymyr may be greater than the known 54 species (Pospelova and Pospelov, 2023). For example, in the neighboring Yamalo-Nenets Autonomous Okrug, this parameter is at least 224 species (Pismarkina et al., 2022). During our research, 57 species of alien plants were identified, some of which are being reported for the first time in Taymyr: *Acer negundo*, *Cannabis ruderalis*, *Rubus idaeus*, etc. Fungi were collected on eight species of alien plants included in the Black Book of Siberian Flora (2016): *Acer negundo*, *Fragaria* × *ananassa*, *Helianthus tuberosus*, *Hordeum jubatum*, *Lupinus polyphyllus*, *Senecio vulgaris*, *Solidago canadensis*, and *Ulmus pumila*, as well as on three (*Rosa rugosa*, *Sorbaria sorbifolia*, and *Symphyotrichum novi-belgii*) recommended for inclusion in the reprint of the book.

Discoveries of new alien species are important, given that the results and studies of the long-term dynamics of the natural vegetation cover of the tundra and forest tundra of Taymyr indicate the absence of reliable changes in the species richness of vascular plants (Pospelova and Pospelov, 2016; Matveyeva, 2017; Matveyeva et al., 2024).

The appearance and increase in the number of alien species of fungi is a marker of natural and climatic changes in the Arctic. Fungi, at least macroscopic ones, generally do not develop on introduced or weedy plants in the first year. They need time during which the plant will increase its phytomass or even naturalize. Almost all the fungi we identified were collected on plants that have been growing in Norilsk conditions for at least 3 years. The older the plant population, the more types of fungi can develop on it. The older the wooden structure, the more wood destroyers will be found on it. A 3-year period, the average period required for the first appearance of a new species of alien fungus on an introduced plant, was also previously identified for the Yamal-Nenets Autonomous Okrug (Shiryaev et al., 2020).

In the northern regions, North American species of microscopic fungi develop on North American plants, and the corresponding microscopic fungi coevolutionarily associated with them develop on East Asian and European plants ($r_{SP}$ = 0.78–0.93, $p < 0.01$). In taiga, broadleaf, and steppe regions, the strong positive relationship weakens ($p \leq 0.05$). Perhaps this is due not only to more comfortable natural and climatic factors, but also to the long period of time that has passed since the introduction of plants. It is worth noting that a similar trend was not identified for macroscopic fungi (Shiryaev et al., 2020). As the results of this study show, exotic plants, especially woody ones, have a high proportion of local or taiga Siberian species.

Botanical data indicate that, in the 20th–21st centuries, rapid dynamics of alien plant species was observed in Taymyr (Pospelova and Pospelov, 2023). Many plant species that are “accidentally” introduced to the north disappear within 1–4 years, and the fungi associated with them disappear with them. The minimal similarity coefficients between individual decades and two main periods of mycobiota studies in the region support this conclusion. It is likely that, with climate warming and increased economic activity, the likelihood of alien plants surviving in the north will increase.

For certain groups of synanthropic plants (weeds used in urban and garden landscaping, etc.), only a few species of fungi are common. There is not a single species that was found in all six studied groups of synanthropic plants. In landscaping and greenhouses, local and alien species of fungi develop on woody plants, but only alien species develop on herbaceous plants in gardens and greenhouses.

In the last 20 years, there has been a massive, uncontrolled import of woody and herbaceous plants by private individuals into garden associations in Taymyr, which probably explains the maximum number and proportion of invasive fungi found on agricultural plants. The largest number of naturalized species have also been identified here. A similar trend was noted in the Yamal-Nenets Autonomous Okrug and a number of forest regions of the country (Bulgakov, 2024; Shiryaev et al., 2024). In northern cities, a similar problem is common to plants used in urban landscaping. Various woody plants are delivered to Norilsk in tubs with a closed root system, where a large number of alien species of fungi may be hidden. This is one of the main routes of penetration to the north of not only microscopic, but also macroscopic invasive fungi. The massive import of wooden building materials from the south of Krasnoyarsk krai to the north over the course of a century also contributes to the penetration of invasive fungi into Taymyr, as well as a large number of species of fungi that have already naturalized in the region. For comparison, in populated areas of Arctic Yakutia, invasive species of fungi have not been found, which is largely explained by the almost complete absence of the introduction of alien plant species, and only local species of fungi have been collected on wooden structures (Kotiranta and Mukhin, 2000; Shiryaev and Mikhaleva, 2013).

**Routes of introduction of alien fungi.** Despite the fact that Norilsk is located far in the north, far from railways and roads, which are traditionally considered vectors of invasions (*Chernaya Kniga*..., 2016; Tomoshevich, 2019; Morozova and Tishkov, 2021; Tomoshevich et al., 2023), the region has quite high transport accessibility. Norilsk is the largest Arctic industrial hub in Russia, with more than a century of history of economic development. The most important transport artery of the region is the Yenisei River, along which ships and barges deliver cargo from the south of

Siberia. The Trans-Siberian Railway passes through Krasnoyarsk, transporting goods and building materials across Eurasia, and a wide range of goods are then delivered north along the Yenisei. Another important transport corridor is the Northern Sea Route, along which cargo is delivered from Murmansk and Arkhangelsk. The third way is air communication with numerous cities of the country located in forest regions, as well as steppe and subtropical ones.

Starting in the 1920s and 1930s, hay, feed, and soil were imported for state farms, which led to the penetration of many alien plants and fungi into the north. Plants with soil were brought to the greenhouses from Krasnoyarsk, Novosibirsk, and Alma-Ata, resulting in a high probability of alien fungi being imported. Perhaps *Mutinus ravenelii* was brought in this way in the 1980s. Currently, local residents and entrepreneurs independently order seeds and seedlings for landscaping and garden plots, which contributes to the emergence of new “southern” plants—substrates for the development of alien mycobiota. Vast territories of sparsely populated taiga stretch between the settlements of the south of Krasnoyarsk krai, where alien fungi develop on various plant substrates, and up to Taymyr. Here the local population uses a minimal set of alien plants, mainly herbaceous ones. Therefore, it is unlikely that most species of alien fungi (developing on greenhouse plants and weeds used in landscaping) will spread to Taymyr to the north along the Yenisei River through small villages.

One explanation for the penetration of alien plant and fungal species into the north can be found in the following example. In the center of Norilsk on the lawn in the soil clod, in which the *Pinus sibirica* grows, a 3-year-old *Acer negundo* plant was found. The tub with cedar was brought by barge from Krasnoyarsk in 2020. The tub was kept in a heated greenhouse for one winter, and in 2021 the cedar with soil was planted in open ground. Consequently, the cedar and maple have already survived three winters in the open ground. It is worth noting that in this same greenhouse, whose owners ordered plants from Krasnoyarsk, several *A. negundo* have also been identified at present in tubs with *Prunus padus* and *Populus laurifolia*. Their seeds fell into the soil in Krasnoyarsk, where a nursery grew the corresponding woody plants for sale, and then they were transported north by barge.

We have no evidence that alien fungi were brought to Taymyr through tourism. Also, fungi were not detected on plants dispersed from the crop. In the work (Pospelova and Pospelov, 2023), *Elymus trachycaulus* (Link) Gould et Shinners, *Festuca pratensis*, *Dactylis glomerata* L., and *Iris setosa* Pall. ex Link are indicated among dispersing plants. We have collected fungi on *F. pratensis*, but only within the city lawns, where these grasses are purposefully planted as lawn mixtures. We also found a fungus on an iris, but it was *I. sibirica*, specially purchased, brought and planted in a garden plot, where it has grown for six years.

**Probability of survival of alien fungi.** The anthropogenic mycobiota of Norilsk is a fragile, unformed structure, which can very quickly, within 1 to 3 years, change its species composition by 60–70%. Without human support, no more than 20–30% of the Norilsk anthropogenic mycobiota species will be able to survive for 10 years or more: these are fungi associated with naturalized plants (*Chenopodium album*, *Populus tremula*, *Tanacetum vulgare*, and others.). For example, late blight of potatoes and septoria of parsley have been known since the 1980s. State farm workers sent infected plant samples for identification to the All-Union Institute of Plant Growing (*Otchet*..., 1992). However, many species of fungi found in greenhouses probably have no chance of naturalizing. This applies to fungi that specialize in developing on grapes, hydrangeas, and other exotic substrates that do not have close relatives in the northern flora.

With warming and an increase in the spectrum of local flora, some species of fungi will move from the status of alien to local, and local anthropophobic to anthropotolerant, from accidental to naturalized, and the latter to invasive. This is already observed in the forest zone of the country (Shiryaev et al., 2020; Bulgakov, 2024), as well as in Murmansk oblast, where the climate is milder and the range of local flora is wider compared to the Siberian regions.

## CONCLUSIONS

The results of the study of the species richness of the mycobiota of alien plants in Taymyr have been summarized. The analysis of the information made it possible to trace the history of the identification of the species composition of mycobiota, the influence of the dynamics of the number of introduced plant species on various aspects of the formation, and the possible future of alien fungi in the Arctic. It has been shown that the introduction and spread of alien species are local and mostly associated with settlements and industrial centers. The main vectors for the introduction of alien species are the movement of transport, people, and associated objects during economic and agricultural development of territories. Along the latitude-zonal gradient of the Russian Arctic, a negative correlation was found between the proportion of alien fungi and plants, which undoubtedly requires further research into this issue. Data on the impact that global warming has on the invasion of alien plant species and associated fungi also remains to be investigated. There is a rapid turnover in the species composition of alien fungi, which reflects the extreme nature of high-latitude natural and climatic conditions, but a third of alien fungi species have already become naturalized, and some have become invasive.

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## AUTHOR CONTRIBUTION

A.G. Shiryaev was responsible for the idea and methodology; collected and processed material; analyzed data; and wrote, reviewed, and edited the manuscript. A.S. Budimirov collected and processed material; analyzed data; and wrote, reviewed, and edited the manuscript. O.S. Shiryaeva processed material and wrote, reviewed, and edited the manuscript.

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## 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 conflict of interest.

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