forests

MDPI

Article

Global Warming Favors the Development of a Rich and Heterogeneous Mycobiota on Alien Vines in a Boreal City under Continental Climate

Anton G. Shiryaev [1,*], Ivan V. Zmitrovich [2], Timur S. Bulgakov [3], Olga S. Shiryaeva [1] and Lyudmila M. Dorofeyeva [4]

1 Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences, 620144 Ekaterinburg, Russia; olga.s.shiryaeva@gmail.com
2 V.L. Komarov Botanical Institute, Russian Academy of Sciences, 197376 St. Petersburg, Russia; iv_zmitrovich@mail.ru
3 Federal Research Centre the Subtropical Scientific Centre, Russian Academy of Sciences, 354002 Sochi, Russia; fungi-on-don@yandex.ru
4 Institute Botanic Garden, Ural Branch of the Russian Academy of Sciences, 620144 Ekaterinburg, Russia; dorofeyeva.lm@gmail.com
* Correspondence: anton.g.shiryaev@gmail.com

Abstract: The species richness and composition of macro- and microfungi on vine species in the parks of Ekaterinburg City (the Ural macroregion, Russia) located in the southern boreal vegetation subzone in a continental climate was studied. The average annual air temperature has increased by 3.1 °C since the beginning of the 20th century; therefore, the conditions for the growth of vines have improved. These conditions include warmer winters and, consequently, less frost damage to perennial plants. Due to the warmer climate, the area of vines grown in the city has increased five times over half a century, and the yield of grapes has grown 3.7 times. The alien East Asian vines are the most dominate vine species cultivated, while European, North American, and native plant species, including archaeophytes, together only represent a handful of the species cultivated. At the same time, 65% of the area of woody vines in the city is covered by a North American species, namely *Parthenocissus quinquefolia*. An increase in the number of vine species, their biomass, and covered areas contributes to an increase in the number of fungal species growing on these vine species. In total, 81 species of phytopathogenic and 87 species of saprobic macro- and microfungi have been recorded during the century-long history of mycological research in Ekaterinburg City. Mycobiota of vines in Ekaterinburg City is biogeographically heterogeneous and 1.1–3.2 times richer in comparison with ones of the regions located on the northern limit of natural ranges of the vines. Recorded macrofungi (Basidiomycota) are predominantly present on native boreal species; however, some exotic tropical and subtropical East Asian fungal species (that have not ever been recorded on other substrates in the natural forests of the Urals and Siberia) are found here too. Recorded microfungi are highly specialized vine-associated species (mainly Ascomycota) that are widespread within the natural ranges of the vines and absent in the boreal zone of Eurasia: there are 63 vine-associated species (15 macro- and 48 microfungi) in Ekaterinburg that are not found in the Urals on other substrates. Many of these species have been recorded for the first time in this study, so we consider that they invaded Ekaterinburg City in the last 20 years, likely due to the warming climate observed over the last decades in the region. There are 19 and 32 species of phytopathogenic fungi collected in the families Cucurbitaceae and Vitaceae, respectively. During the past 40 years, the recorded fungal species richness has increased by 16% on Cucurbitaceae, as well as 37% on grapes. In this study, the distribution of vine-associated fungi, including phytopathogenic fungal species, from the nearest regions of ancient vine culture (Southern European Russia and the Caucasus, Central Asia, the south of the Russian Far East) to the boreal regions of the Urals were investigated. The increase in the range of these phytopathogenic fungal species can lead to significant economic losses to the regional agricultural sector.

Citation: Shiryaev, A.G.; Zmitrovich, I.V.; Bulgakov, T.S.; Shiryaeva, O.S.; Dorofeyeva, L.M. Global Warming Favors the Development of a Rich and Heterogeneous Mycobiota on Alien Vines in a Boreal City under Continental Climate. *Forests* **2022**, *13*, 323. https://doi.org/10.3390/f13020323

Academic Editors: Nadezhda Tchebakova and Sergey V. Verkhovets

Received: 25 January 2022
Accepted: 11 February 2022
Published: 16 February 2022

Keywords: climate change; disturbance; urban ecology; alien plants; biological resources; northern viticulture; plant pathogens; biogeography; fungal diversity; vitis; liana

1. Introduction

Vines (lianas) play an important role in modern cities, acting as the main elements of vertical urban landscapes, and help cultivate an optimal microclimatic environment [1,2]. Due to global warming, vines are becoming more commonly used in the cities of North Eurasia that exhibit ultra-continental climates, such as the macroregions of Ural and Siberia in Russia [3].

Vines are a very common plant life form in the tropical and subtropical regions of Earth, where a high amount of vegetation and biodiversity can be found as well as an overproduction of biomass and a deep differentiation of ecological niches. However, in continental regions of the Eurasian boreal zone, vines (especially woody vines) are rare and are largely considered as one of the most exotic plant life forms in Ural and Siberia [4]. There are only two native vine species in the Ural region: hop (*Humulus lupulus* L.) and Siberian clematis (*Atragene sibirica* L.). Other vine species, especially woody vines, are alien species growing exclusively as cultivated plants [4]. Thus, exotic vines grown in Ural and Siberia are not well adapted to the cold climates of these regions and are highly susceptible to frost damage, and often cannot restore died perennial parts (twigs and branches) after a very cold winter [1].

The alien vines currently grown in Ekaterinburg, one of the largest cities in the Urals (Northern Asia), largely comprises East Asian and European subtropical vine species [1,4]. The role of economically important edible vines of the families Vitaceae Juss. ex Bercht. & J. Presl and Cucurbitaceae Juss. is increasing in Ekaterinburg due to the gradual warming climate over the last few decades. The frontier of northern viticulture is shifting further to the north in Ural and Siberia, and a yield of cucurbitaceous crops and grapes is increasing in the regions too [1,2,5]. As a consequence of the climate warming, vine culture (primarily viticulture) is expanding further north in Ural and Siberia, and yields of cucurbitaceous crops and grapes are increasing in these macroregions [1,2,5].

The cultivation of vines in Ekaterinburg dates to the 18–19th centuries, when the city was developed as an administrative center for the mining industry in the Ural macroregion [6–9]. Top managers of local factories and mines of the city were inspired by the estates they often watched in Saint Petersburg and Moscow and tried to design their own local estates and gardens in a similar "European manner". This often resulted in the introduction and cultivation of many exotic ornamental plants (including some vines) in their local gardens. For example, the most popular vine—common grape vine (*Vitis vinifera* L.)—was introduced in Ural cities from the Southern European Russia (mainly from West Caucasus and Crimea). Several manors in the center of Ekaterinburg City had at least a 50-year history of vine cultivation by the beginning of the 20th century. However, the center of Ekaterinburg underwent an urban change in the 1940–1950s, with many old houses and estates being demolished and replaced by high-rise blocks, resulting in the destruction of those cultivated vines and vineyards.

Most popular edible herbal vines and cucurbitaceous crops, first of all the ridge cucumber (*Cucumis sativus* L.) and field pumpkin (*Cucurbita pepo* L.), were already being grown in open fields and in greenhouses across Ekaterinburg by the 18th century [6]. Other common herbaceous vines, such as climbing nightshade (*Solanum dulcamara* L.) and field bindweed (*Convolvulus arvensis* L.), were originally accidentally introduced into Ekaterinburg as weeds at the end of the 19th century [6]. Later, hedge false bindweed (*Calystegia sepium* (L.) R. Br.) and ground virgins bower (*Clematis recta* L.) were introduced too, and now they are the most common alien herbaceous vines in the modern Ekaterinburg [6]. In addition, the oldest thickets of native vines (hops and Siberian clematis) were preserved in old cemeteries, which have been around since the 19th century. For example, large thickets of hops are present at the Ivanovskoye cemetery, which has existed since 1810, and centennial thickets of hops and the Siberian clematis are preserved at the Mikhailovskoye cemetery, founded in 1865 [8].

Many alien woody vine species grow in Ekaterinburg along the walls of various buildings and in parks. The most common of these vines include European common grape (*Vitis vinifera*) and European ivy (*Hedera helix* L.), North American Virginia creeper, or five-leaved ivy (*Parthenocissus quinquefolia* (L.) Michx.), and several East Asian plant species: Amur grape (*Vitis amurensis* L.), Chinese magnolia-vine (*Schisandra chinensis* (Turcz.) Baill.), Variegated-leaf hardy kiwi (*Actinidia kolomikta* (Rupr. et Maxim.) Maxim.), Yellow honeysuckle (*Lonicera prolifera* (Kirchn.) Rehder), Chinese bittersweet (*Celastrus orbiculatus* Thunb.), Regel's Threewingnut (*Tripterygium regelii* Sprague et Takeda), and climbing hydrangea (*Hydrangea petiolaris* Siebold et Zucc.). The common grape and European ivy are often grown indoors.

Approximately 200–300 km south of Ekaterinburg, the grapes have been grown in large quantities for wine production in the last 50–80 years [1,5,9]. Due to warming climate in recent decades, some local farmers of Ekaterinburg and Sverdlovsk province have also started to produce wine [5]. At the same time, many vine-associated saprobic and phytopathogenic fungi were found on grapes in the city and its suburbs for the first time in the 2000–2010s [8,10].

We will test the hypothesis that alien vine species, cultivated far from their natural range, carry much less pathogenic fungi than they do inside their natural range.

The purpose of this study is to determine what fungal species are present on vines cultivated in Ekaterinburg City, and to determine the potential risk phytopathogenic fungi pose to the economically important groups of vines such as fruits and vegetable crops. Some related problems should be resolved: to study the dynamics of the climate in Ekaterinburg during the 20th to 21st centuries; to assess the species diversity and dynamics of vine productivity in Ekaterinburg over the last 40 years; to make a list of phytopathogenic fungi infecting Cucurbitaceae and Vitaceae plants and their dynamics over the last 40 years; to analyze the covered areas of studied plant species; and to investigate whether the "core species" of saprobic and phytopathogenic fungi is preserved on the vines outside their natural and traditional cultural ranges.

2. Materials and Methods

2.1. Climate of Ekaterinburg City

Ekaterinburg City (former Sverdlovsk City, capital of Sverdlovsk province) is situated in the south boreal subzone (56.825° N; 60.565° E; 280 m a.s.l.) in the Ural macroregion on the border of Europe and Asia (Figure 1). The city area covers 468 km^2, and the population is about 1.5 million people. The average annual temperature over the last ten years has varied in the range of 3.1–5.3 °C [11,12]. The local climate is considered continental, with sharp variability in weather conditions and clearly defined seasons. The average monthly temperature in July is 19.4 °C, the absolute daily maximum is 39.6 °C. The average monthly temperature in January is −14.3 °C, and the absolute daily minimum is −46.7 °C.

Figure 1. Map of Russia with Ekaterinburg City location.

The climate in Russia is warming twice as fast as the global one, and this climatic trend can is recorded in Ekaterinburg City too [12,13]. The local climate was relatively cold from the 1900s to the 1970s: the average annual temperatures varied in the range of −0.7–−3.3 °C (Figure 2A). Until the 1970s, regular long-term frosts (with temperatures below −35–−40 °C) were recorded in the city, with the absolute recorded minimum −46.7 °C. A steady climate warming has started since the late 1970s: frost periods have become shorter, the middle-winter frosts have eased, and during the latter 40 years, nowadays temperature in the city rarely drops below −30 °C. Over the last half-century, the coldest year (with the coldest winter) was 1969 (−0.7 °C), while the warmest year was 2020 (5.3 °C) [12]. Thus, the climatic regime of 2020 became similar to the cities of Central Russia at the end of the 20th century [12]. Over 100 years, the average winter temperature increased by 3.1 °C, and the average summer temperature—by 0.2 °C [12,13].

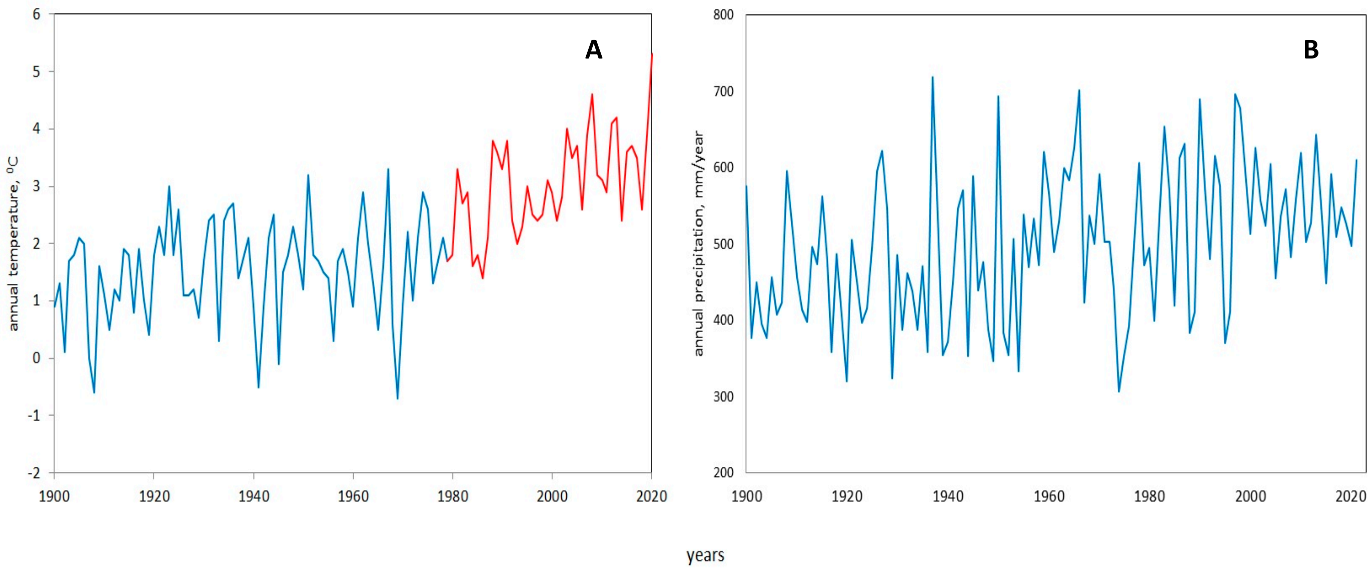

Figure 2. The 120-years-long dynamics of average annual temperature (**A**) and average annual precipitation (**B**) in Ekaterinburg City. For annual temperature data separated by two periods: blue—1900–1978 years, and red—1979–2020 years.

The frequency of last spring frosts in April–June is also important for thermophile plants. Until the 1970s, regular frosts down to −5 °C and snowfall 0.5 m deep were recorded in May–June every 4–6 years (Figure S1). However, such late frosts were not observed in the city in the 2010s (were registered only once in the last 20 years), although short snowfalls outside the city are still possible. Average annual precipitation in Ekaterinburg was 483 mm/year in the 1920s, and it has increased to 537 mm/year in the 2010s (Figure 2B). Thus, the average annual precipitation has slightly increased over the past century, with an average rate of 5.4 mm/10 years.

2.2. Systematic Review of Yield Dynamics and Assessment of Vines Covered Areas

The model plant was Amur grape, the cultivar "Amur breakthrough" (also known as "Potapenko-7"), which has grown here since 1961. The following method was used to estimate the annual yield dynamics: 10 model bushes for 8 years were observed and studied (1966, 1972, 1979, 1986, 1993, 2001, 2012, 2020). The length of each model plant was about six meters long with the same crown shape (E.V. Sinitsyn, pers. data). This grape cultivar was chosen for cultivation due to its high frost resistance, high yields, and high sugar content in the berries (23%).

In addition, we carried out an approximate assessment of the covered area dynamics of the most common woody vines in the last five decades (1920, 1950, 1970, 1990, 2010). The actual covered areas of vines were estimated during the collection of fungi in 2018–2019. The archive records and photographs of the Ekaterinburg Historical Museum and archive records of (1) ironworks founded in the 18–19th centuries, (2) cemeteries founded in the 19th century, (3) educational institutions built in the early and the middle of the 20th century, (4) arboreta that were planted in 1930–1940, as well as published scientific data, can approximately estimate the area of various vines in Ekaterinburg in 1921–2020.

2.3. Fungal Sampling

In the present research work, we studied fungi growing on stems, roots, leaves, and fruits of the outdoor vines collected in Ekaterinburg City and its suburbs by the authors as well as fungal specimens collected by earlier researchers in the three main periods (the names of the collectors are given): (I) 1913–1950: N.A. Naumov, Z.A. Demidova, F.A. Solovyov, S.I. Vanin, and A.S. Kazanskiy; (II) 1951–1990: Z.A. Demidova, N.T. Stepanova-Kartavenko, L.K. Kazantseva, A.V. Sirko, L.M. Mezentseva, and E.A. Shurova; (III) 1991–2021: A.G. Shiryaev, N.V. Ushakova, K.A. Fefelov, E.V. Bryndina, O.S. Shiryaeva, and L.M. Dorofeyeva [8,10,14,15]. The present research work does not include fungal species found in greenhouses only, as well as macrofungi that form fruiting bodies on the soil surface only.

Aphyllophoroid fungi, which predominates on some woody vines (up to 80–100% of all species), can be considered as the best-studied group among all recorded macrofungi on vines, whereas agaricoid, gasteroid, and heterobasidiomycetous fungi are represented by a smaller numbers of species and may be considered as still insufficiently known groups [8]. The fungi were recorded in 25 vine species in the last 100 years, but the present research only includes the 17 most fungal-rich plant species (on which more than five fungal species are recorded): *Actinidia kolomikta*, *Atragene sibirica*, *Calystegia sepium*, *Celastrus orbiculatus*, *Clematis recta*, *Convolvulus arvensis*, *Dioscorea caucasica*, *Hedera helix*, *Humulus lupulus*, *Hydrangea petiolaris*, *Lonicera prolifera*, *Menispermum dauricum*, *Parthenocissus quinquefolia*, *Schisandra chinensis*, *Tripterygium regelii*, *Vitis amurensis*, and *V. vinifera* (Figure S2).

We subdivided all studied vine species into three groups by their natural ranges to analyze the species richness of the associated fungi: (1) four European species (*Clematis recta*, *Dioscorea caucasica*, *Hedera helix*, and *Vitis vinifera*); (2) four Eurasian species, including two common native species (*Atragene sibirica* and *Humulus lupulus*), and archaeophytes that have been present in the city since its foundation (*Calystegia sepium* and *Convolvulus arvensis*); (3) nine "geographically distant" species from East Asia (*Actinidia kolomikta*, *Celastrus orbiculatus*, *Hydrangea petiolaris*, *Lonicera prolifera*, *Menispermum dauricum*, *Schisandra chinensis*, and *Tripterygium regelii*) and North America (*Parthenocissus quinquefolia*). East Asian and North American woody vines were analyzed together because North American vines are represented by a single species (*Parthenocissus quinquefolia*).

The fungal diversity was studied in the eleven perennial woody vine species: *Atragene sibirica*, *Actinidia kolomikta*, *Celastrus orbiculatus*, *Hedera helix*, *Hydrangea petiolaris*, *Lonicera prolifera*, *Parthenocissus quinquefolia*, *Schisandra chinensis*, and *Tripterygium regelii*, and in the six annual herbaceous vine species: *Calystegia sepium*, *Clematis recta*, *Convolvulus arvensis*, *Dioscorea caucasica*, *Humulus lupulus*, and *Menispermum dauricum*. Most attention was paid to phytopathogenic macro- and microfungi affecting crops of the two most economically important plant families, Cucurbitaceae and Vitaceae.

Living plants and their dead parts were examined for fruit bodies of macrofungi and/or plant disease signs caused by phytopathogenic fungi (leaf spots or mildews on leaves, shoot dieback or blight, trunk rot, fruit rot, and so on) and/or the presence of fungal generative structures (conidiomata and conidia, ascomata and ascospores, sporangia and sporangiospores, and others). Affected plant parts with phytopathogenic microfungi were collected and dried according to the traditional methods [15] and placed in paper envelopes. Fruiting bodies of macrofungi were collected on living and dead parts of plants according to the standard methods [8] and placed in paper bags. All specimens were labeled to provide complete information about the host plant, locality, date of collection, and collector [16,17]. Most of the fungal specimens were collected in summer and early autumn seasons (mainly in July, August, and September). The identification of ascomycetous microfungi was made by T.S. Bulgakov, the identification of basidiomycetous macrofungi—by A.G. Shiryaev, I.V. Zmitrovich, and O.S. Shiryaeva.

More than 1180 fungal specimens were examined during the present research. The collected fungal species were identified using light microscopes LEICA 2000 and Axio Imager A1. The collected specimens are deposited in Institute of Plant and Animal Ecology Herbarium (SVER) and V.L. Komarov Botanical Institute Herbarium (LE F). The fungal species nomenclature is given according to the open database Index Fungorum [18].

2.4. Data Analysis

The main static parameters (mean, SE, SD), box–whisker plots (using middle point—median, whisker value—min–max, and box value—percentiles (25–75%)), and 95% confidence intervals were calculated in Statistica 8.0. A Mann–Whitney U-test was used to compare the data series on the number of phytopathogens on stems and leaves of woody vines. The cluster analysis was performed using Statistica 8.0, using a matrix of Ward's method and 1-Pearson correlation coefficient.

3. Results

3.1. Dynamics of Grape Yield and Woody Vines Areas in Ekaterinburg City

The mean yield range of Amur grape (cultivar "Amur breakthrough", or "Potapenko-7") in Ekaterinburg suburbs was 4.7–6.4 kg per model bush during the 1960–1970s. Later, it increased to 13.1 kg in 1993, to 15.5 kg in 2001, to 20.6 kg in 2012, and to 23.9 kg in 2020. In 2020, there was a maximal harvest per one plant—28 kg (Figure 3). Thus, the mean yield was stably low during the 1960–1970s, and it had started to increase since 1979 ($F (5.52) = 61.703$, $p = 0.00001$). Consequently, the harvest of cultivar "Amur breakthrough" has grown significantly ($p < 0.001$) for 41 years (from 1979 to 2020): the average yield per plant increased 3.7 times, and the maximum yield per plant increased 2.8 times (from 10 to 28 kg).

The covered area of woody vines in the city was consistently low from the 1920s to the 1950s, varying slightly in the range from 38 to 65 m^2 (Figure 4). In the 1960s, due to the introduction of many East Asian alien species, the covered area of vines began to grow, reaching 516 m^2 in the 1970s, mainly due to the Vitaceae plants, whose area was 365 m^2 (Table S1). In the 2010s, the total covered area of vines increased to 2587 m^2, while the area of Vitaceae was 1958 m^2. The main growth in the covered area (among all woody vine species) was recorded for the Virginia creeper (*Parthenocissus quinquefolia*). This species was introduced in Ekaterinburg in the late 1950s only and was absent in the city in the 1920–1940s. However, the covered area of five-leaved ivy had reached 280 m^2 in the 1970s already, and in the 2010s it increased up to 1685 m^2, i.e., it currently comprises 65% of the total area of all woody vines in the city. Thus, nowadays, *Parthenocissus quinquefolia* is the most common vine species in the city. Among *Vitis* species, the largest area in the 2010s was covered by *Vitis amurensis* (195 m^2). The area covered by the plants of the Vitaceae family has grown 78 times over a 100-year period—from 25 to 1958 m^2, and the covered area percentage of Vitaceae plants among all woody vines has also grown steadily, increasing from 62% in 1920 to 76% in 2010 (Table S1).

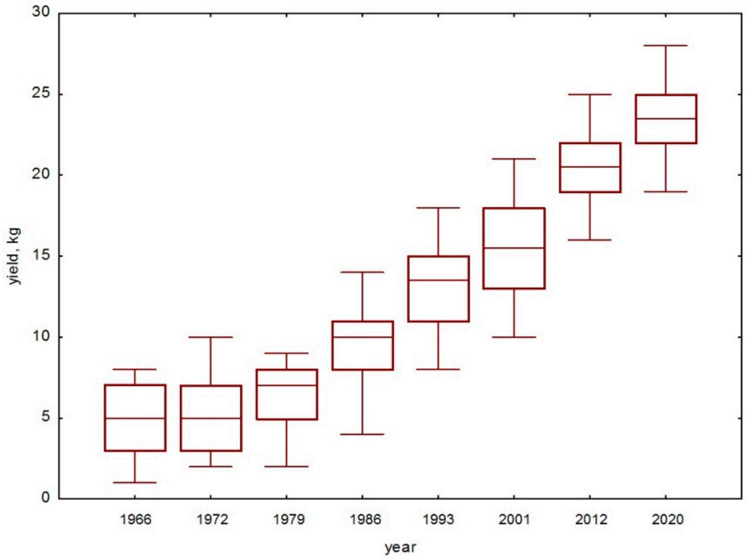

Figure 3. Box–whisker plots of the 55-year-long yield dynamic for the one model bush of Amur grape (cultivar "Amur breakthrough", or "Potapenko-7").

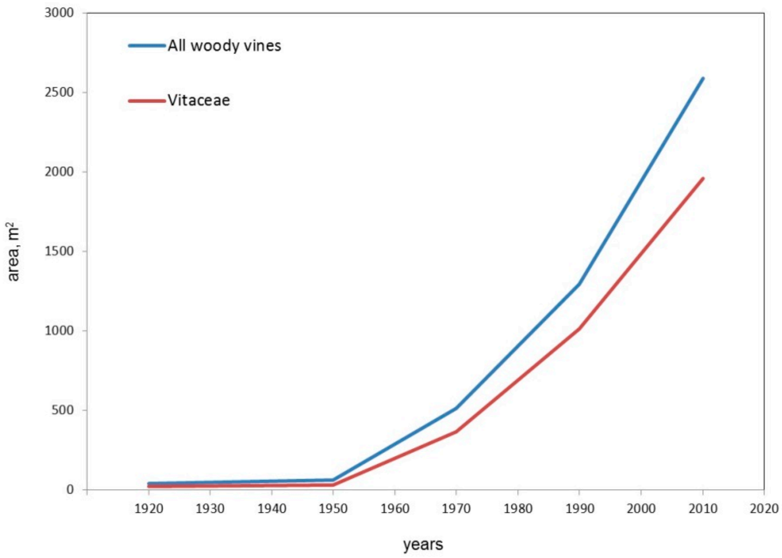

Figure 4. Schematic visualization of the 100-year-long dynamic of covered areas for all woody vines and for Vitaceae family only in Ekaterinburg City. Data correspond to the 1920s, 1950s, 1970s, 1990s, and 2010s.

3.2. Systematic Review of the Fungal Species Richness Revealed during the Last 100 Years

The number of identified macrofungal species on all vines increased from 4 to 15 from the 1920s to the 1940s (Figure 5A). During these years, common grape (*Vitis vinifera*) was the most common woody vine in Ekaterinburg City, while the most common herbaceous vine was common hop (*Humulus lupulus*). Common grape plantations (private vineyards) were destroyed in the 1950s, so there were no fungal specimens collected from grapes by the end of that decade, and all local vines were represented only by hops and Siberian clematis covering small areas in suburbs. Because any large woody vines were absent in Ekaterinburg in the 1950s, only corticioid and clavarioid vine-associated fungi were found at that time. In the late 1950s and early 1960s, East Asian frost-resistant vine species were introduced in the city. Beginning with the 1970s, these vine species—*Actinidia kolomikta*, *Schisandra chinensis*, and *Vitis amurensis*—had grown intensively, and dead woody parts infesting by poroid fungi (including phytopathogenic ones) appeared. The peak of regional fungal research fell in the same period—the 1970s, which can be considered as the most "fruitful" period for the local mycology in the 20th century in general, when 60 species were first found. As a result, the number of known vine-associated macrofungal species in Ekaterinburg increased from 36 to 67 (Figure 5A), i.e., doubled, compared to the previous decade. This period of active mycological research in the 1970s gave way to a decline in scientific activity in the 1980s.

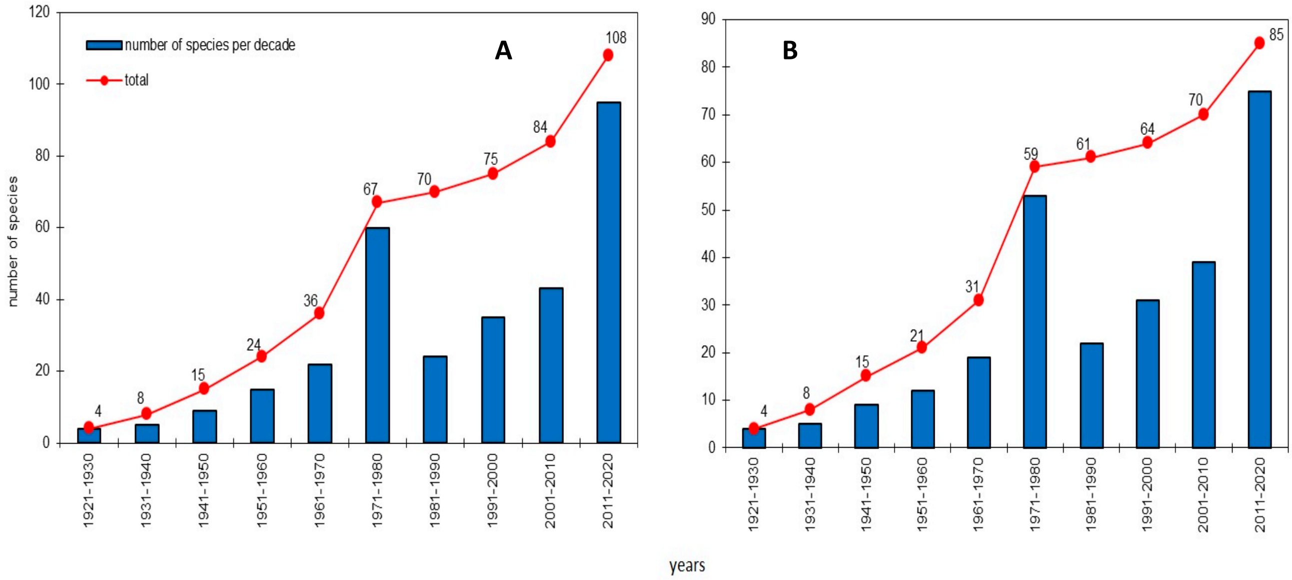

Figure 5. Dynamics and accumulation curve of species richness for macrofungi (**A**) and aphyllophoroid fungi single (**B**) on vines in Ekaterinburg for the ten last decades (since the 1920s to the 2010s).

The next period of active research in the 1990s was associated with the activities of the authors, which have continued in the 2000s. The second peak in the collection of macrofungi fell in the 2010s. As a result, the total number of recorded fungal species increased and reached 95 species. Thus, there were two main peaks (periods) of active scientific research on vine-associated fungi: the 1970s and the 2010s, which are separated by 40 years.

In total, 110 species have been found and identified during 100 years of studying the macrofungi diversity on vines in Ekaterinburg (Table S2). They can be subdivided into the following ecological groups: 87 saprobic, 5 symbiotic, and 18 phytopathogenic species. In addition, 63 species of microfungi were collected on living leaves, shoots, and twigs (Table S3). The dynamics of the species richness of aphyllophoroid fungi are similar to those for the entire macrofungi group (Figure 5B) and are determined mainly by aphyllophoroid fungi collected and identified on woody vines in the 1920s and all subsequent decades. The collecting of macrofungi also peaked in the 1970s and 2010s, when 53 and 75 species were recorded, respectively.

An average of 24.7 aphyllophoroid fungi species were recorded on the East Asian and North American vine species (Table S2). The average species richness of fungi among the 17 most fungal-rich vine species is statistically significantly higher for East Asian and

North American vine species (24.7 fungal species), whose natural habitats are the furthest from Ekaterinburg, than for geographically closer European and native Northern Eurasian vine species, whose average species richness are 9.7 and 8.9 fungal species, respectively (Figure 6A).

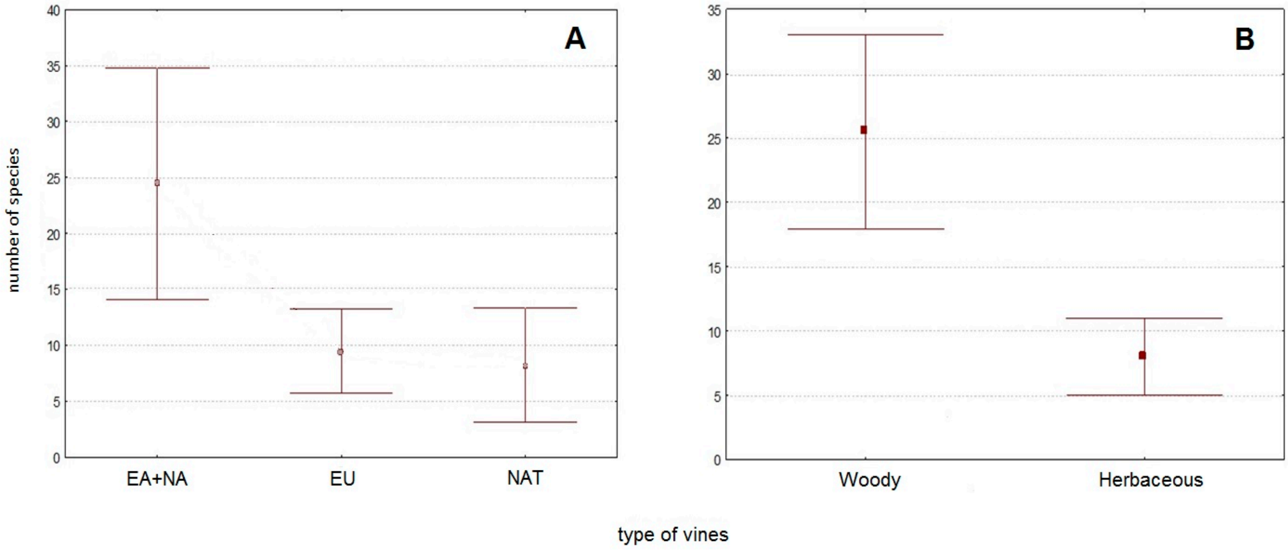

Figure 6. Comparison of species richness for macrofungi in Ekaterinburg City on different geographical groups of vines (**A**) and structural types (**B**). Means and 95% confidence intervals are given. Geographical range: EA + NA—East Asian and North American vines, EU—European, NAT—native (Eurasian), incl. archaeophytes; Structural type: Woody—woody vines, Herbaceous—herbaceous vines.

The average species richness of macrofungi on woody vine species is 3.3 times higher than that for herbaceous vine species (25.2 vs. 7.7 species) (Figure 6B). Thus, woody vines have statistically significantly higher fungal diversity than herbaceous ones: F (1.14) = 16.047, p = 0.0013. In addition, these conclusions are confirmed by the fact that 95% confidence intervals for the species richness of the compared groups do not overlap.

The comparison of the lists of macrofungi found and identified over the last 100 years indicates that the vine species have united into two basic clusters: woody and herbaceous vine species (Figure 7). The first subcluster includes woody vine species of the Vitaceae family (*Vitis amurensis*, *V. vinifera*, and *Parthenocissus quinquefolia*), and the second subcluster includes the woody vine species of other plant families and genera: *Actinidia*, *Hedera*, *Lonicera*, *Schisandra*, etc. The herbaceous vine species can be grouped into two subclusters too: (1) the alien vine species (e.g., *Clematis recta*, *Dioscorea caucasica*, and *Menispermum dauricum*), including the weeds (*Calystegia sepium* and *Convolvulus arvensis*); (2) the native vine species (*Atragene sibirica* and *Humulus lupulus*).

The aphyllophoroid fungi have the widest possible range of vines substrates among recorded macrofungi. For example, *Typhula micans* was recorded on the largest number of vine species (16 host plant species), as well as some other macrofungi: *T. setipes* (14 host plant species), *Xylodon sambuci* (13), *Typhula crassipes* (13), *T. culmigena* (12), *T. juncea* (10), *Pterulicium gracile* (11), *Bjerkandera adusta* (9), *Irpex lacteus* (9), *Peniophora cinerea* (9), *Cylindrobasidium evolvens* (8), *Schizophyllum commune* (7). The agaricoid, gasteroid, and heterobasidiomycetous fungi were recorded on one or two vine species only. All these species are common native species at the Urals and Siberia.

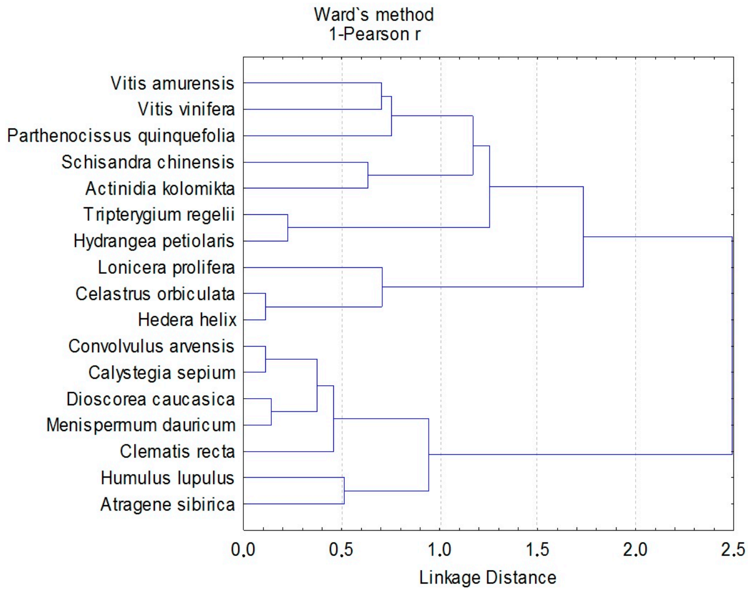

Figure 7. Correlation of macrofungi species composition for the 17 most fungal-rich vine species in Ekaterinburg City.

In contrast, we found some thermophilous fungi on a large number of woody vine species, also nonnative species for the region—they are not recorded in the wild nature at a distance of 2000–5000 km from Ekaterinburg City. For example, *Hydnophlebia chrysorhiza* are species known only in the south of the Far East of Russia (the nearest finds). This species was also recorded in East Asia (Japan, South Korea), the Himalayas (India), tropical Africa (Cameroon), the eastern United States, southeastern Canada, and South America (Brazil, Venezuela); moreover, this fungus is a candidate for inclusion in the international Red Book (http://iucn.ekoo.se/iucn/species_view/332100/) (accessed on 20 November 2021). The nearest recorded locations for the *Tomentella olivascens* are in deciduous forests of Europe (France, the Carpathians in Ukraine, the Caucasus in Russia), East Asia (the Kuril Islands and Primorsky province of Russia), and North America (USA). *Radulomyces rickii* was also collected for the first time in the Ural macroregion; this fungus is known in deciduous and tropical regions of East Asia (Japan), Africa (Ethiopia), Europe (Great Britain, France, the Netherlands, Italy, southern Scandinavia, western Russia), North America (USA), Australia, and New Zealand. There are collections of this species in Siberia (Tomsk Region) in 1931 (https://www.gbif.org/occurrence/3043183453) (accessed on 20 November 2021). *Steccherinum bourdotii* was collected for the first time in Ekaterinburg. This species is known from mixed coniferous–deciduous forests in the tropics; it was found in Asia (India), Europe (from southern Scandinavia to the Iberian Peninsula, western Russia), Africa (Uganda), and North America (USA). There is a single find in Siberia (https://www.gbif.org/occurrence/2309708470) (accessed on 20 November 2021). In addition, we found *Crustomyces expallens*, which is common in deciduous forests of Manchuria (China), Europe (Great Britain and from southern Scandinavia to the Alps), North America, and the European part of Russia; its nearest record is in the Altai Mountains (https://www.gbif.org/species/2550290) (accessed on 20 November 2021). *Gloeohypochnicium analogum* is the next first-time-collected species in the Urals; it was found in East Asia (China and Primorsky province of Russia), Africa (Malawi), New Zealand, North America (USA, Canada), Europe (from the south of Scandinavia to the Mediterranean) (https://www.gbif.org/species/2544664) (accessed on 20 November 2021). For *Lilaceophlebia* cf. *ochraceofulva,* the center of the natural range lies in deciduous forests of Europe (from southern Scandinavia to the Mediterranean) and North America (USA, Canada) (https://www.gbif.org/species/2545063) (accessed on 20 November 2021). The record of the cosmopolitan poroid fungus *Cerioporus scutellatus* (https://www.gbif.org/species/2547190) (accessed on 20 November 2021) on hardy kiwi is extremely interesting because this species is treated as arcto-alpine, associated with deadwood of *Alnus fruticosa* and *A. viridis* in Europe, Ural, and Siberia. We have two specimens of this species collected in hardy kiwi at 5000–6000 km distance from Ekaterinburg, in East Asia (Jilin province in China and Sakhalin province in Russia) (H. Kotiranta, pers. comm. and A. Shiryaev, unpubl. data). The full list of first-found species is much longer and includes many other macro- and microfungal species: *Elsinoe ampelina*, *Erysiphe necator*, *Eutypa scabrosa*, *Mycoacia uda*, *Phaeomoniella chlamydospora*, *Ramularia schisandrae*, *Taeniolina scripta*, etc.

3.3. Fungal Groups' Tendencies during the Last 40 Years

The distribution of fungal species richness in the three main biogeographic groups of macrofungi recorded in the 1970s and 2010s is similar ($p < 0.01$) to that for the entire study period (Figure 6A). However, the result for the 2010s show that the vine-associated fungal species richness in vine species originated from the most distant regions (East Asia and North America) is 3.5 times higher than in European and native vine Northern Eurasian species (16.4 species vs. 5.0 and 4.7) (Figure 8). East Asian and North American vines have also higher fungal diversity than European and native Northern Eurasian ones in the 1970s (the average numbers of species were 7.7 vs. 1.7 and 3.3). However, the average number of fungal species recorded on East Asian and North American vines has increased from 7.7 to 16.4 (U = 7, z = −2.57, $p = 0.009$) in the last 40 years, while the fungal diversity for European and native (Eurasian) vines did not change significantly ($p = 0.58$ and 0.66, respectively), remaining stably low. Among the native vine species, the most fungal-rich is hops, on which seven and five fungal species, respectively, were identified in two compared periods.

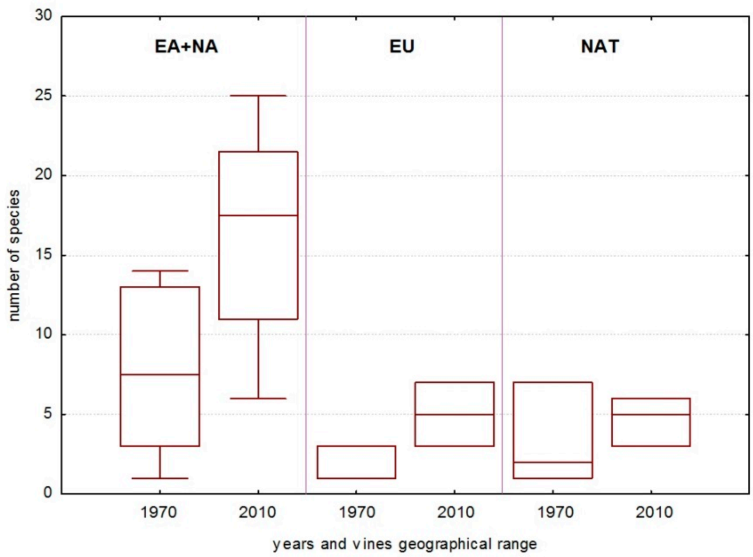

Figure 8. Box–whisker graph of 40-year-long dynamics of aphyllophoroid fungi species richness at three geographical range groups of vine species. EA + NA—East-Asian and North American vine species; EU—European; NAT—native.

The number of aphyllophoroid fungi on woody vine species has significantly increased in the last 40 years (F (1.25) = 11.05, $p = 0.002$): the average species richness has doubled, from 6.6 to 13.7 species (Figure 9). On the other hand, the number of fungal species on herbaceous vine species does not differ significantly between 40 years ago and now (F (1.13) = 1.41, $p = 0.256$), so the average species richness has changed insignificantly, from 3.3 to 4.6 species.

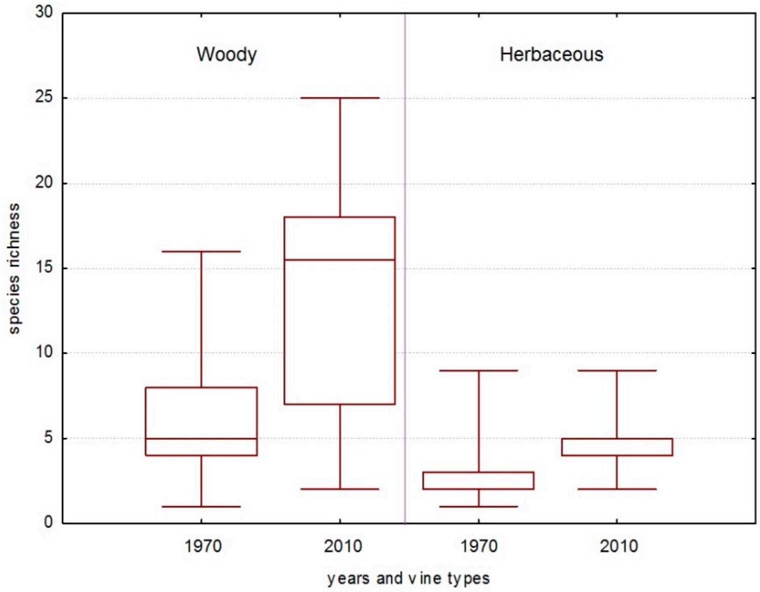

Figure 9. Box–whisker graph of 40-year-long dynamics of aphyllophoroid fungi species richness on woody and herbaceous vine species.

For 40 years, the largest number of fungal species was found on woody vine species that cover the largest areas in the city (1970s: r = 0.84, p = 0.0002 vs. 2010s: r = 0.64, p = 0.003) (Figure 10A). During the 2010s, the largest number of macrofungi was known on *Parthenocissus quinquefolia*—26 species were found over an area of 1685 m^2 (Table S1), 19 species—on *Actinidia kolomikta* were recorded from an area of 210 m^2, and 16 species—on *Vitis amurensis* from an area of 195 m^2. For comparison, only 22 macrofungal species were recorded in the 1970s on *Parthenocissus quinquefolia* from an area of 280 m^2, 14 species—on *Actinidia kolomikta* from an area of 45 m^2, 13 species—on *Schisandra chinensis* from an area of 40 m^2, and 13 species—on *Vitis amurensis* from an area of 70 m^2 (Figure 10B).

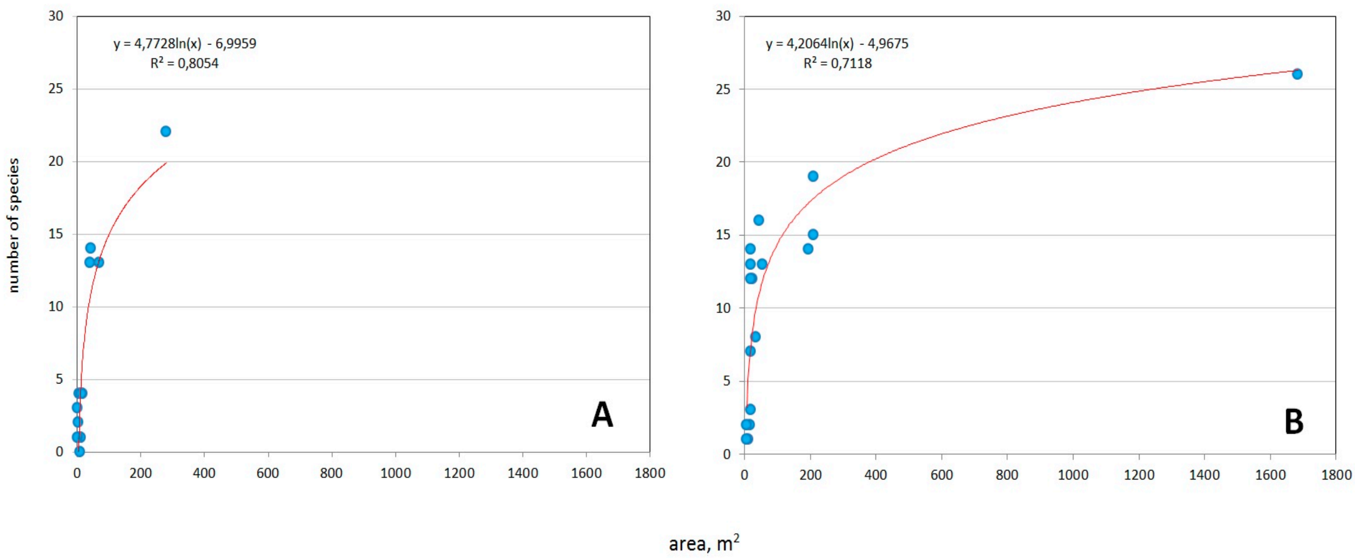

Figure 10. The correlations between the macrofungal species richness at each woody vine species and the covered area (**A**) in 1970s (n = 14), and (**B**) in 2010s (n = 17).

The morphological structure of the recorded macrofungi has been transformed in the last 40 years (Figure 11A). In the 1970s, East Asian and North American vine species had young and thin branches and twigs, on which mainly saprobic poroid and agaricoid macrofungi formed their basidiomas. The bio- and mortal masses, as well as the area of the vines, have increased significantly in the 2010s. The number of poroid (from 11 to 20 species) and corticioid (from 33 to 43 species) macrofungi increased most significantly, while the number of clavarioid species remained almost the same (Figure 11A). Consequently, the proportion of recorded poroids increased. The species richness of saprobic fungal species has almost doubled after 40 years, while the number of phytopathogenic fungi has increased by a third only (Figure 11B).

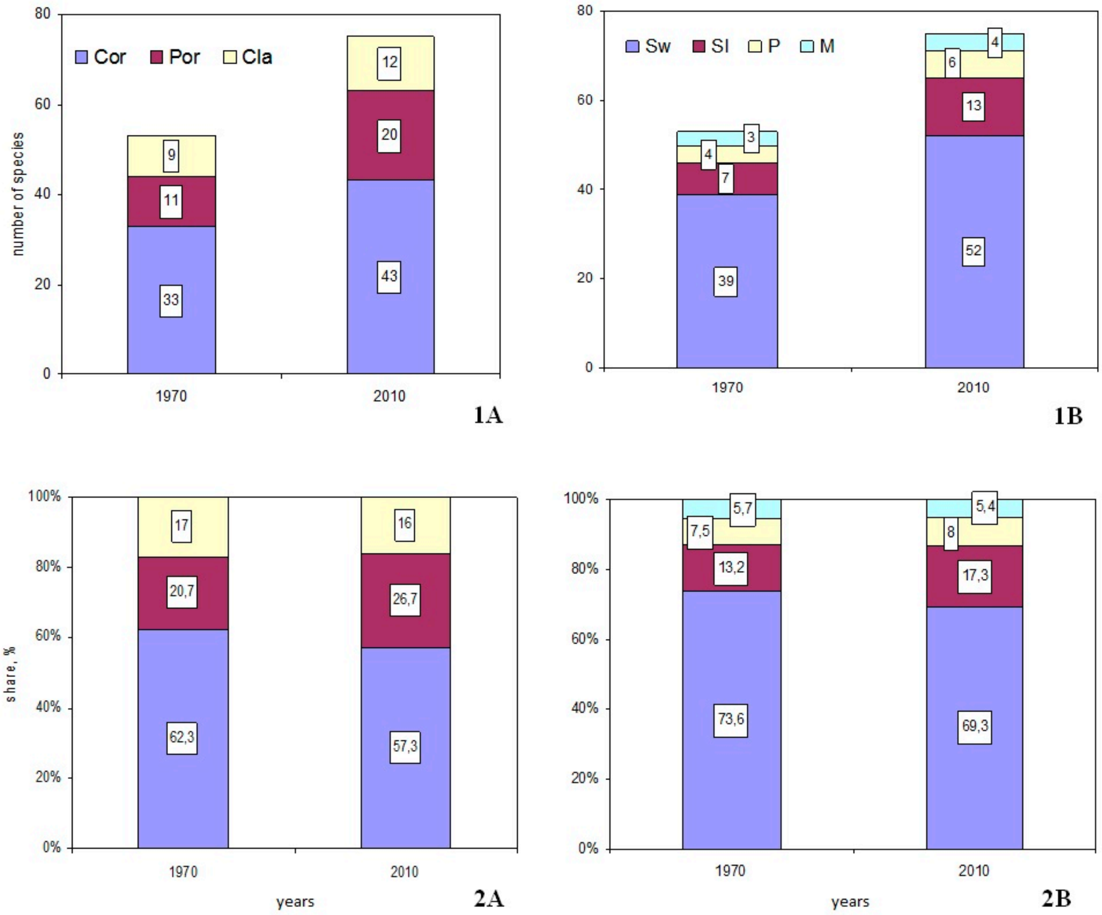

Figure 11. 40-year-long dynamics of morphological form and ecological strategy groups of aphyllophoroid fungi on the vine species. **1**—number of species, **2**—percentage (%); **A**—morphological form, **B**—ecological strategy. Morphological forms: Cor—corticioid, Por—poroid, Cla—clavarioid; ecological strategies: Sw—saprobes on wood, Sl—saprobes on litter, P—phytopathogens, M—mycorrhizal fungi.

3.4. Phytopathogenic Fungi on Edible Vines

The edible vine species of Cucurbitaceae and Vitaceae plant families cover the largest areas among plantations of the economically significant groups of vines in Ekaterinburg City (Table 1). They have the longest history of cultivation in the city: for example, the pumpkin (*Cucurbita* spp.) has been cultivated here since the beginning of the 18th century and the grapes (*Vitis* spp.)—since the middle of the 19th century. The covered area of Vitaceae plants in Ekaterinburg has increased five times (Figure 4; Table S1), and the covered area of Cucurbitaceae plants—about three times, since the 1970s (A.L. Manilova, pers. data).

Table 1. The species list of phytopathogenic fungi recorded in Cucurbitaceae and Vitaceae plants in Ekaterinburg City.

Cucurbitaceae	**Vitaceae**
Macrofungi	
Ceratobasidium cornigerum	***Armillaria borealis***
Rhizoctonia solani	*Athelia rolfsii*
Typhula micans	*Ceratobasidium cornigerum*
Typhula culmigena	***Fomitiporia punctata***
	Ganoderma applanatum
	Irpex lacteus
	Inonotus hispidus
	Phanerochaete velutina
	Phellinopsis conchata
	Pholiota limonella
	Pleurotus pulmonarius
	Schizophyllum commune
	Stereum hirsutum
Microfungi	
Alternaria alternata	*Alternaria alternata*
Alternaria cucumerina	*Aureobasidium pullulans*
Botrytis cinerea	*Botrytis cinerea*
Cladosporium cucumerinum	***Colletotrichum parthenocissicola***
Colletotrichum orbiculare	***Colletotrichum quinquefoliae***
Fusarium oxysporum	*Coniella diplodiella*
Golovinomyces tabaci	*Diplodia seriata*
Podosphaera xanthi	***Elsinoe ampelina***
Pseudoperonospora cubensis	*Erysiphe necator*
Pythium aphanidermatum	***Eutypa scabrosa***
Septoria cucurbitacearum	*Fusarium oxysporum*
Sclerotinia sclerotiorum	*Globisporangium debaryanum*
Stagonosporopsis cucurbitacearum	*Nectria cinnabarina*
Verticillium alboatrum	***Phaeomoniella chlamydospora***
Verticillium dahliae	*Phyllosticta ampelicida*
	Plasmopara viticola
	Pseudocercospora vitis
	Ramularia vitis
	Verticillium glaucum

Note: ***in bold***—the fungal species were not known on these substrates in the 1970s but were collected in the 2010s. *Fumago vagans* s. l. was excluded from the list as an unclear and not plant parasitic species. This fungus was recorded on the plants of the both families in the 1970s and 2010s.

In total, 81 species of phytopathogenic fungi were recorded on living vines during the last 100 years (Table S3), including 49 species found on the host plants of Cucurbitaceae and Vitaceae families (Table 1). Among them, 32 species were found in Vitaceae, including 13 species of macrofungi (*Armillaria borealis*, *Fomitoporia punctata*, *Stereum hirsutum*, and others) and 19 species of microfungi (*Erysiphe necator*, *Phyllosticta ampelicida*, *Pseudocercospora* *vitis*, and others) (Table 1). In addition, 19 species of phytopathogenic fungi were recorded in Cucurbitaceae plants, including four species of macrofungi (*Ceratobasidium cornigerum*, *Typhula micans*, and *T. culmigena*) and 15 species of microfungi (*Cladosporium cucumerinum*, *Golovinomyces tabaci*, *Septoria cucurbitacearum*, and others).

In the 1910–1970s, 16 species of phytopathogenic fungi were already known in Cucurbitaceae plants (84% of all species known in 2010s), while the phytopathogenic fungi in Vitaceae plants were represented by 20 species (63%) (Figure 12). The number of recorded macrofungi in Cucurbitaceae crops has increased by 25% in the last 40 years, while the number of recorded microfungi has increased by 20% in the same period. Some phytopathogenic fungi—*Colletotrichum orbiculare*, *Septoria cucurbitacearum*, and *Typhula culmigena*—were collected for the first time in Ekaterinburg in 2010s. The number of macrofungi recorded in Vitaceae plants has increased by 38% in the last 40 years, while the number of microfungi has increased by 33%. Compared to the 1970s, species such as *Armillaria borealis*, *Fomitiporia punctata*, *Phaeomoniella chlamydospora*, and some others have been found for the first time.

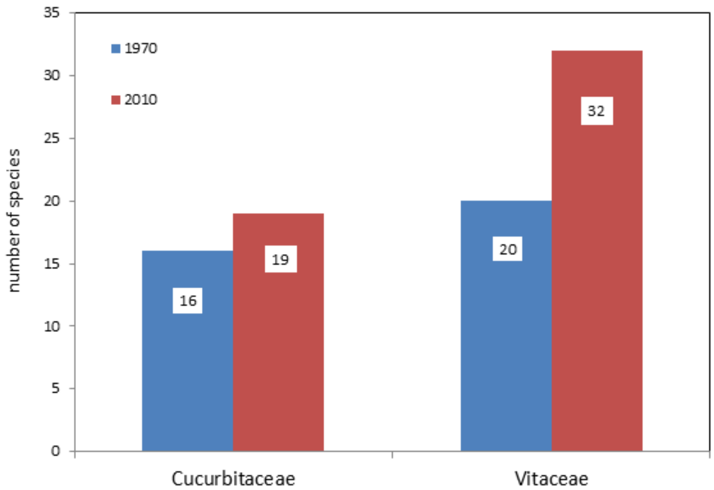

Figure 12. 40-year-long dynamic of phytopathogenic fungi richness on Cucurbitaceae and Vitaceae plant families.

4. Discussion

The climate of Ekaterinburg in the 1920–1940s was too cold for the development of many vine species in the 1920–1940s: the average annual temperatures varied in the range of −0.6 . . . −2.9 °C, and winters were extremely severe: frosts reached up to −40 °C and lasted more than one month. Only few woody vine species (*Vitis vinifera* and its hybrids) were grown in small numbers in such climatic conditions—mainly as ornamental plants, as they were regularly damaged by frost and produced low yields. Almost all grapes and old vineyards were destroyed in the 1950s due to the city center development.

Botanical and natural resource research in the 1940–1950s in the Russian Far East made it possible to find and introduce many East Asian vine species that are much more frost-resistant than the South European ones [2]. Based on *Vitis amurensis*, some new frost-resistant cultivars were bred in those years [5], and soon they gained popularity in Russia. The extensive introduction of such grape cultivars began in the boreal regions of the Russian Far East, Siberia, and Ural in the late 1950s [3], including Ekaterinburg in the late 1950s and early 1960s. At the same time, from the early 1960s, East Asian and North American woody vines were introduced in wide culture in boreal cities of Russia: *Actinidia kolomikta*, *Schizandra chinensis*, *Hydrangea petiolaris*, *Parthenocissus quinquefolia,* and many others. Thus, despite the closer location of European vineyards to Ekaterinburg, the current species diversity of exotic (mainly East Asian) vines in the city is 2.5 times higher compared with the species diversity of native and European ones due to the low number of the latter in the flora of the Urals and Siberia, as well as better winter hardiness of the East Asian species introduced from the Russian Far East [3,5,19–21].

The average annual temperature in the city has increased from 2.3 °C in the 1970s to 4.7 °C in the 2010s; at the same time, the average monthly temperature in January has increased from −18.3 to −14.5 °C, and the average duration of frosts below −30 °C has decreased from 22 to 11 days per year during the same 40-year period [11]. Consequently, the city climate has become more favorable for the alien vine species, which now are less frostbitten in cold winters and therefore can reach larger sizes and older age. The species diversity of cultivated vines has also increased: the number of vine species in the open field has increased 2.4 times in the last 40 years. The average grape yield has grown 3.7 times, and the covered area of woody vines has grown five times. The growth in productivity and area of grapes strongly positively correlates with the average annual temperature ($p = 0.0001$). The warming climate causes the increasing of the diversity of woody vine species as well as the covered area, and these processes lead to an increase in biomass of vines (which is the main substrate for phytopathogenic fungi) and accumulation of wood debris (which is the main substrate for wood-destroying fungi). Therefore, climate warming is the main reason for the local increase in the diversity of fungi associated with the vine species [22,23].

4.1. General Results of 100-Year-Long Monitoring

In modern time, 110 species of macrofungi were recorded on vines in Ekaterinburg City. This seems to be a significant number for a considerably small area of 468 km^2 located 2000–5000 km from the northern frontier of distribution of woody vines in Europe and Central and East Asia. For example, regional and local lists of fungi known on vines include not more than 20–30 species in the lands of ancient viticulture, such as Primorsky and Sakhalin provinces (Russia), Manchuria (Northern China), Uzbekistan, southeastern Kazakhstan, Caucasus, Crimea, and some Mediterranean countries [24–33].

Such relatively high fungal diversity in vines in Ekaterinburg City can be explained by a critical study of the substrate, i.e., high selective effort, as well as by a high species diversity of introduced vine species cultivated together in a relatively small area. The local climate is unfavorable for the vine species, which grow in conditions that are far beyond their ecological optimum and, therefore, they have weakened vitality. As is well known, stressed and depressed plants become more susceptible to weak and opportunistic pathogens, especially native macrofungal species. This can explain the high number (18 species) of phytopathogenic macrofungi recorded on the studied vines.

The review of 100-year-long research works shows that the average species number of macrofungi recorded on the most “geographically distant” East Asian and North American vine species is 3.3–3.5 times higher than on the European and the native ones (Figures 6 and 8). This fact allows us to compare the data on the East Asian vines of Ekaterinburg with any similar data, for example, with ones for Primorsky province (the Russian Far East), where only 34 macrofungal species on all vine species were recorded [33–35]. As we can see, the number of macrofungal species in Ekaterinburg is three times higher than in Primorsky province, despite the fact that the latter area is three orders of magnitude larger than the first one (165,900 vs. 468 km^2). The total number of phytopathogenic macrofungi in Ekaterinburg City is 18 species, whereas only 14 species were recorded in Primorsky province. Moreover, 81 species of phytopathogenic macro- and microfungi were found on all vine species in Ekaterinburg, whereas only 79 species are recorded in vines in the much larger Primorsky province [33–37]. However, this result mostly indicates the incompleteness of current data on the mycobiota of Primorsky province.

The comparison of fungal species richness of vine species indicates that, for example, 38 species of macrofungi were collected on the East Asian *Actinidia kolomikta* in Ekaterinburg [8], and only 17 species were recorded on the same plant in Primorsky province [37]. The number of known phytopathogenic microfungi on the same plant in Ekaterinburg is six, whereas in Primorsky province—five species [33–37]. *Vitis amurensis* demonstrates a similar pattern: 36 species of macrofungi, including eight pathogenic ones, were collected on this plant species in Ekaterinburg, and only 17 species (including seven phytopathogenic ones) are known in Primorsky province [37].

The mycobiota of vine species in Ekaterinburg City is not only unexpectedly rich but also is biogeographically heterogeneous (Section 3.3), including both boreal and cosmopolitan species, as well as many tropical and subtropical East Asian and European species. At least 15 species of macrofungi and 48 species of microfungi have been found exclusively on alien vines in Ekaterinburg City and Sverdlovsk province.

The overwhelming majority of the East Asian and North American vines were initially introduced in Ekaterinburg in the form of seeds that were germinated and grown in seedlings in greenhouses. Therefore, we can suppose that alien phytopathogenic microfungi have been introduced via infested seeds. Quite likely, the fungi first spread on host plants in greenhouses, and then in outdoor plantings in Ekaterinburg City and Sverdlovsk province. The spreading of highly specialized phytopathogenic microfungi with windborne spores over thousands of kilometers seems less likely, excluding rust and smut fungi [38,39], but these taxa were not recorded on the vines in Ekaterinburg City.

On the other hand, the main pathway for the spreading of wood-inhabiting macrofungi is wind-mediated spore dispersion [38], and for this reason, many macrofungi have very wide or cosmopolitan ranges. Such species prevail among the vine-associated macrofungi in our research, especially common tropical and subtropical East Asian and European saprobic macrofungi: *Crustomyces expallens*, *Gloeohypochnicium analogum*, *Hydnophlebia chrysorhiza*, *Lilaceophlebia* cf. *ochraceofulva*, *Mycoacia uda*, *Steccherinum bourdotii*, and *Tomentella olivascens*. Obviously, these species have entered Ekaterinburg in the 2010s, most likely as a consequence of global warming, which has accelerated the growth of vines and thereby led to the sufficient accumulation of live and mortal biomass—the substrates for saprobic and phytopathogenic fungi. Thus, the alien vine species retained only a weak biogeographical specificity for macrofungi. However, microfungi show a different pattern: highly host-plant-specialized fungal taxa predominate.

4.2. Dynamics of the Model Groups during the Last 40 Years

The number of macrofungal species known on woody vines in Ekaterinburg has increased by 37% in the last 40 years: from 60 species in the 1970s to 95 species in the 2010s. At the same time, the number of known fungal species on herbaceous vines has increased much less (p = 0.256), and the average species richness has changed insignificantly, from 3.3 to 4.6 species (Figure 8). Contrariwise, the average number of known species on woody vines has increased significantly (by 52%), from 6.6 to 13.7 species, while the covered area of woody vine species in the city has increased five times in the 40 years, and the covered area of herbaceous vine species—about three times.

Apparently, such a high revealed fungal diversity is not only the result of our high selective effort, but also the consequence of the increase in the biomass of host plants—woody vines—due to climate warming. The “overgrowing” of woody vines (such as grapes) also leads to the accumulation of a large amount of mortal mass, especially considering that sanitary pruning of dry twigs and branches in some unkempt gardens and vineyards has not been performed since the 1990s. Therefore, many overgrown woody vines (grapes, hardy kiwi, and magnolia vine) have been in the unkempt state for over 20 years. We found the largest number of fungi on lignified debris in abandoned vine thickets. Only a few species of fungi were found in stands where dead plant parts were regularly pruned and removed. For example, 10 phytopathogenic and 27 saprobic fungal species were found on an Amur grape vine in an abandoned garden (A.G. Shiryaev, E.V. Sinitsyn, pers. data), while only five phytopathogenic and eight saprobic fungal species have been recorded on a similar Amur grape vine in a same area in a neighboring garden. In the latter-mentioned garden, the trellis was being annually cleaned—all dead parts of grapevine were being annually pruned and removed during the last 20 years (the recorded yields are presented on Figure 4).

The morphological structure of macrofungal communities has been transformed in the last 40 years too. The majority of East Asian and North American woody vine species were introduced in the city in the early 1960s, so in those years they had only young and thin branches and twigs, on which only saprobic species with small basidiomata (mainly corticioid and clavarioid) could grow. Their mortal mass (branches and twigs thickness) had much increased by the end of the 1970s, when the vines were 15–18 years old. In this regard, the poroid and agaricoid macrofungi with larger basidiomata, including perennial phytopathogenic poroid species, began to grow on them. The morphological structure of macrofungal community changed in the 2010s (40 years later) as a result of increasing of the areas covered by vines, their age, and the bio- and mortal mass. The number of poroid and corticioid macrofungi has increased more than others, while the number of clavarioid species remained almost the same. Consequently, the proportion of poroids increased, while the proportion of corticioids decreased. The number of recorded saprobes on wood and litter also increased: the species richness of these two groups almost doubled, while the number of phytopathogenic fungi increased by a third only. These results indicate that the data were received correctly in the 1970s, and this fact makes it possible to compare them with the data for the 2010s. Moreover, not only has the number of aphyllophoroid phytopathogens increased after 40 years, but agaricoid fungi causing trunk rots of woody vines have also appeared [8].

4.3. Pathogenic Fungi on Alien Edible Vines

The frontier of viticulture is shifting to the north as the climate in the Urals and Siberia warms [5]. At the beginning of the 20th century, the grapes were grown as edible plants only in the south of the Ural macroregion (for example, in Orenburg city, 51–53° N, 500 km south of Ekaterinburg). However, the zone of home viticulture has expanded 250 km to the north in the middle of the 20th century (to the latitude of Ufa City, 54° N), and has reached Ekaterinburg (56° N) in the early 21st century [5].

For 150 years of grape cultivation in Ekaterinburg, 32 species of phytopathogenic fungi were recorded on the Vitaceae plants (*Parthenocissus* and *Vitis* species), including 13 macrofungal species (Table 1). Some of them, for example, *Fomitiporia punctata*, *Inonotus hispidus*, *Phellinopsis conchata*, *Pleurotus pulmonarius*, *Stereum hirsutum*, *Armillaria*, and *Pholiota* species, are common plant pathogens within the natural and cultural ranges of grapes [40]. However, 19 species of recorded phytopathogenic microfungi (*Coniella diplodiella*, *Erysiphe necator*, *Phyllosticta ampelicida*, *Pseudocercospora vitis*, and others) are widespread common species within the natural and cultural ranges of grapes, but these fungi were never found in natural boreal plant communities in Ural and Siberia. The number of known phytopathogenic fungal species in Vitaceae plants has increased by a third in the last 40 years, while the covered area of Vitaceae plants has increased in five times (Table S1). Therefore, the current ratio of phytopathogenic micro- and macrofungi is 60 to 40%. Moreover, all phytopathogenic macrofungi found in Vitaceae plants are native species growing on native deciduous trees, but all phytopathogenic microfungi are alien species and mainly highly specialized plant parasites of Vitaceae plants—common within their modern ranges but never recorded on native plants in the Ural macroregion.

More than 400 species of fungi associated with Vitaceae plants are known in the world, of which at least 70 species are recorded in Europe as plant pathogens [40,41]. Dozens of species of phytopathogenic fungi growing on the twigs and leaves of Vitaceae plants are also known in the geographically close regions of long-term viticulture—mountain foothills of Central Asia, Southern European Russia, and South Caucasus [42]. For example, 29 microfungal species (97%) and only one macrofungal species (3%) are known now as grape pathogens in the arid subtropical climate of Uzbekistan, in the desert zone of Central Asia ([43,44]; Y. Gafforov, pers. comm.). Similarly, 50 species of fungi are known on grapes in the semiarid temperate climate of Rostov province (Southern European Russia, steppe zone of Eastern Europe) ([45]; T. Bulgakov, pers. comm.), including 45 microfungal species (90%) and only five macrofungal species (10%). Thus, we can state that the percentage and the significance of phytopathogenic macrofungi on grapes increases (from 3 to 40%) from dry subtropics (Central Asia) to the semihumid boreal zone (the Urals and Siberia) parallel to a decrease in the average annual temperature and an increase in precipitation from south to the north.

Higher relative air humidity (rains in the warm seasons and snowfalls in winters) in Ekaterinburg City is the main climatic factor that could explain the greater number and proportion of macrofungal species in Ekaterinburg in comparison with other mentioned regions of ancient grape culture. In the boreal zone, the macrofungi often grow on root collars near wet soil surface, or on trunk at low height above the ground (at the level of snow in a winter season), or in frost cracks in the middle part of the vine trunk. Thus, analyzing the species richness and morphological spectrum of phytopathogenic micro- and macrofungi for the three compared regions with a relatively close level of knowledge of phytopathogenic grape fungi, we obtained an interesting result that requires further research and interpretation.

The other economically important vine species in Ekaterinburg are plants of Cucurbitaceae family (mainly pumpkins and cucumbers), which have been cultivated here for 300 years. The species composition of cultivated Cucurbitaceae formed a long time ago and does not change in modern time; therefore, the species composition of associated phytopathogenic fungi stabilized many decades ago and remains the same nowadays. Therefore, 84% of all recorded fungal phytopathogens in Cucurbitaceae plants were already known in Ekaterinburg 40 years ago (for example, *Cladosporium cucumerinum*, *Golovinomyces tabaci*, *Podosphaera xanthii,* and others). However, *Rhizoctonia solani* was not recorded in Sverdlovsk province as pathogen of these plants until the late 1950s, but by then it had started to affect Cucurbitaceae plants regularly. Some species, such as *Typhula culmigena*, *Septoria cucurbitacearum*, and *Verticillium alboatrum,* were not previously recorded in Ekaterinburg either. We should note the recent appearance of *Colletotrichum orbiculare* causing the anthracnose of cucumbers and pumpkins, which has become a common species now wherever the host plants cultivate. As in the case of Vitaceae, highly specialized phytopathogenic microfungi of Cucurbitaceae are mostly alien species for the region, but all recorded macrofungi are native species.

The list of known phytopathogenic fungi on annual Cucurbitaceae plants has increased by only 16% in the last 40 years, but the list of fungal pathogens in Vitaceae plants has increased much more (by 37%) during the same period, and many new wood-inhabiting macrofungi affecting old grape twigs, branches, and trunk were first found in Ekaterinburg in the 2010s. We assume that this is the result of aging of grape plants and the accumulation of mortal plant mass, mainly wood. Thus, the recorded 32 species of phytopathogenic fungi in Vitaceae plants and 19 ones in Cucurbitaceae plants are relatively large numbers for an area of 468 km^2, located far beyond the natural ranges of the host plants. Such results can be explained by the high level of selective effort as well as the pessimal conditions for the growth of the vines. Such a large number of recorded wound phytopathogens can be considered as evidence of a weakened state of vines, which have regularly been damaged by frost in cold winters. We must also take into account the long history of the host plants' cultivation in the region, which should inevitably lead to an increase in trophic connections between native fungi and alien plants as substrates for fungi.

The species composition of phytopathogenic fungi recorded on both plant families in Ekaterinburg is more constant and similar to the one in their natural and cultural ranges than the species composition of saprobic fungi. We attribute this to the closer and more specific trophic connection between phytopathogenic fungi and their host plants (especially for obligate plant parasites); more so, a similar pattern is shown for other regions of the planet [46,47].

5. Conclusions

Based on the results of this study, specific morphological features of the vines (i.e., special adaptations that help to maintain orthotropic growth of shoots) do not significantly affect their colonization by fungi. The main factor predetermining the presence and growth of wood-destroying fungi is a specific substrate—lignified tissues and organs of host plants (trunks, branches, and twigs of woody vines)—while the presence of living plant parenchyma is the main factor predetermining the presence and growth of phytopathogenic microfungi that infect nonlignified tissues and organs of host plants.

The macrofungal species recorded on woody vine species in Ekaterinburg include both native and widespread (often cosmopolitan) taxa, although some nonnative (alien) species are also present (mostly East Asian subtropical and tropical species). Contrarily, the recorded microfungal species are mainly highly host-specialized phytopathogens (growing mainly on leaves and other nonlignified plant parts), and they mostly can be considered as alien species strictly associated with genera and families of host plants in their natural ranges.

The number of phytopathogenic fungal species recorded on herbaceous vines (including Cucurbitaceae) has not increased significantly over the past 40 years. This fact can be explained by the long history of their cultivation in Ekaterinburg, starting from the 18th–19th centuries: the mycobiota of the herbaceous vines had time to form and stabilize over this time, in contrast with the mycobiota of woody vines.

The situation is quite different with woody vines: the warming climate contributes to an increase in their species diversity, covered area and age, thickness of trunks and branches, and also leads to an increase in the mass of wood and lignified debris, which are the main substrates for vine-associated macrofungi. Due to these factors, the number of recorded phytopathogenic macrofungal species has grown by a third in the last 40 years. Previously absent macrofungi with large basidiomata (perennial poroids) have now appeared, although saprobic macrofungi with small annual basidiomata (corticioids) are still predominant.

The total number of vine-associated macrofungal species is 1.1–3.2 times higher in Ekaterinburg compared to the regions located along the northern border of the natural ranges of many considered woody vine species, while the species diversity and composition of recorded phytopathogenic fungi are similar to the species diversity and composition typical for well-studied regions—the nearest regions of ancient culture of the studied vine species (the Mediterranean, the south of the European Russia and the Caucasus, Central Asia, the south of the Russian Far East and Northern China). Consequently, the results of this study demonstrate that the tested hypothesis that poor fungal species diversity on alien vine species (cultivated far away from their natural ranges) has not been confirmed, or it needs to be corrected. However, the main reason for this may be poor knowledge of the mycobiota of the vine species in some European and Central and East Asian regions near the northern border of the natural and traditional cultural ranges of the woody vine species. Nevertheless, we can state that the current expansion of many vine-associated fungal species (including phytopathogenic ones) occurs simultaneously with the expansion of vine culture zone to the north in the Ural macroregion, caused by the current climate warming. This process will undoubtedly lead to significant economic losses for the regional agriculture.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13020323/s1, Figure S1. June snowfall in Ekaterinburg city in 1973 and 1967. Figure S2. 17 most fungal-rich vines in Ekaterinburg city (on which more than 5 species of fungi are recorded). Table S1. 100-years long covered area (m^2) dynamic of woody vines in Ekaterinburg city. Table S2. The checklist of macrofungi collected on vines in Ekaterinburg (incl. subdivision in morphological and ecological groups) with a small addition. Table S3. The checklist of pathogenic micro- and macrofungi collected on live vines in Ekaterinburg.

Author Contributions: A.G.S.: Conceptualization, methodology, investigation, formal analysis, data curation, writing—original draft, writing—review and editing, project administration, funding acquisition. I.V.Z.: Methodology, formal analysis, writing—review and editing. T.S.B.: Methodology, formal analysis, investigation, conceptualization, writing—review and editing. O.S.S.: Formal

analysis, investigation, visualization, writing—review and editing. L.M.D.: Investigation, writing—review and editing. All authors have read and agreed to the published version of the manuscript.

Funding: The research was carried out with the financial support of Russian Science Foundation (project No. 22-26-00228).

Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available due to privacy.

Acknowledgments: We would like to thank the anonymous reviewers for their comments on an earlier version of the manuscript. We are deeply grateful to the staff of the Botanical Garden UB RAS O.A. Kiseleva and E.N. Minogina. We very much appreciate N.G. Erokhin for valuable advice on the history of Ekaterinburg City, as well as the staff of the Ekaterinburg History Museum. We are deeply grateful to E.V. Sinitsyn for providing personal data on grape yield. We thank Yu. Gafforov for personal data on the list of fungal species collected on grapes in Uzbekistan. The authors are grateful to K. Lynn and M. Bradshaw for their help in improving English text. We are deeply appreciative of the constructive comments from the editor and anonymous reviewers.

Conflicts of Interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

1. Dorofeyeva, L.M.; Mamaev, S.A. Introduction of the Far Eastern woody lianas in the Middle Ural and the prospects of their use. In *Plants in a Monsoon Climate*; Materials of the International Conference Dedicated to the 50th Anniversary of the Botanical Garden; Institute of the Far Eastern Branch of the Russian Academy of Sciences: Vladivostok, Russian, 1998; pp. 171–172. (In Russian)
2. Mamaev, S.A. *70th Anniversary of the Botanical Garden of the Ural Branch, Russian Academy of Sciences*; Ekaterinburg Publishing: Ekaterinburg, Russia, 2006. (In Russian)
3. Vlasenko, V.E.; Dorofeyeva, L.M.; Yakovleva, S.V.; Semkina, L.A. Green plantations in the dendroparks of Ekaterinburg City. *Bull. Samara Sci. Cent. RAS* **2010**, *10*, 1376–1378. (In Russian)
4. Dorofeyeva, L.M. Lianas collection from the Botanical Garden and its science-practice utilization. Northern Asia Plant Diversity 2021. *BIO Web Conf.* **2021**, *38*, 25. [CrossRef]
5. Nemytov, A.Y. *Shatilov's Grape*; Chelyabinsk Printing House: Chelyabinsk, Russia, 2016. (In Russian)
6. Govorukhin, V.S. *Flora of the Urals. Key Book of Plants Grow on the Urals and Hills from the Shores of KARA Sea till the Southern Treeline*; Sredural Press: Sverdlovsk, Russia, 1937. (In Russian)
7. Tretyakova, A.S.; Kulikov, P.V. Adventitious component of the flora of Sverdlovsk region: Dynamics of the species. *Bull Udmurt. Univ. Biol. Earth Sci.* **2013**, *4*, 184–188.
8. Shiryaev, A.G.; Zmitrovich, I.V.; Shiryaeva, O.S. Species richness of Agaricomycetes on hedge vines in Ekaterinburg City (Russia). *Mycol. Phytopathol.* **2021**, *55*, 340–352. [CrossRef]
9. Troshin, L.P. *Native Grapes in Russia*; Kuban University: Krasnodar, Russia, 2012.
10. Bulgakov, T.S.; Shiryaev, A.G. New finds of phyllotrophic plant pathogenic microfungi in Ekaterinburg and its suburbs. *Mycol. Phytopathol.* **2021**, *55*, 405–410. [CrossRef]
11. Fick, S.E.; Hijmans, R.J. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Clim.* **2017**, *37*, 4302–4315. [CrossRef]
12. RIHMI-WDC. *Federal Service for Hydrometeorology and Environmental Monitoring*; RIHMI-WDC: Obninsk, Russia, 2021. Available online: https://www.meteo.ru (accessed on 17 August 2021).
13. Leskinen, P.; Lindner, M.; Verkerk, P.J.; Nabuurs, G.-J.; Van Brusselen, J.; Kulikova, E.; Hassegawa, M.; Lerink, B. (Eds.) *Russian Forests and Climate Change*; What Science Can Tell Us 11; European Forest Institute: Joensuu, Finland, 2020. [CrossRef]
14. Demidova, Z.A. Diseases overview of cultivated and wild plants in the Ural region. *Bull. Uraloblzu.* **1925**, *10*, 9–20. (In Russian)
15. Stepanova, N.T.; Sirko, A.V. Flora of acomycetous and imperfect fungi of the Ural. Spore plants of the Ural. *Proc. Inst. Plant Anim. Ecol.* **1970**, *70*, 3–52. (In Russian)
16. Blagoveshchenskaya, E.Y. *Phytopathogenic Micromycetes: Educational Keybook*; URSS Press: Moscow, Russia, 2015. (In Russian)
17. Bondartsev, A.S.; Singer, R.A. A guide to collecting higher basidiomycetes for scientific study. *Proc. Bot. Inst. AS USSR* **1950**, *2*, 499–572. (In Russian)
18. Index Fungorum, CABI, Kew. 2021. Available online: http://www.indexfungorum.org/names/names.asp (accessed on 29 July 2021).
19. Shiryaev, A.; Kotiranta, H.; Mukhin, V.A.; Stavishenko, I. *Aphyllophoroid Fungi of Sverdlovsk Region, Russia. Biodiversity, Distribution, Ecology and the IUCN Threat Categories*; Goshchitskiy Publisher: Ekaterinburg, Russia, 2010.
20. Stepanova-Kartavenko, N.T. *Aphyllophoroid Fungi of the Ural*; UFAS USSR: Sverdlovsk, Russia, 1967. (In Russian)
21. Stepanova, N.T. Ecogeographical Analysis of Aphyllophoroid Fungi of the Ural. Ph.D. Thesis, Institute UFAS USSR, Sverdlovsk, Russian, 1971. (In Russian).
22. Shiryaeva, O.S. New records of Agaricoid fungi from Sverdlovsk region, Russia. *Botanica* **2018**, *24*, 150–161. [CrossRef]

23. Shiryaev, A.G.; Mukhin, V.A.; Kotiranta, H.; Stavishenko, I.V.; Arefyev, S.P.; Safonov, M.A.; Kodolapov, D.A. Biodiversity of aphyllophoroid fungi of the Ural. In *Biological Diversity of the Urals's Plant World and Adjacent Territories*; Mukhin, V.A., Ed.; Institute of Plant and Animal Ecology: Ekaterinburg, Russia, 2012; pp. 311–313. (In Russian)
24. Bondartseva, M.A. *Keybook to Fungi of Russia. Aphyllophorales*; Nauka: St. Pteresburg, Russia, 1998; Volume 2. (In Russian)
25. Ryvarden, L.; Melo, I. *Poroid Fungi of Europe*; Fungiflora: Oslo, Norway, 2014.
26. Bernicchia, A. A checklist of corticioid, polyporoid and clavarioid fungi (Basidiomycotina) from the Emilia-Romagna region, Italy. *Sydowia* **2001**, *53*, 1–33.
27. Bernicchia, A.; Gorjon, S.P. *Fungi Europaei: Corticiaceae s.l.*; Edizioni Candusso: Origgio, Italy, 2010; Volume 12.
28. Fischer, M.; Gonzalez, V. An annotated checklist of European basidiomycetes related to white rot of grapevine (*Vitis vinifera*). *Phytopathol. Mediterr.* **2015**, *54*, 281–298. [CrossRef]
29. Karadelev, M.; Rusevska, K.; Kost, G.W.; Kopanja, D.M. Checklist of macrofungal species from the phylum Basidiomycota of the Republic of Macedonia. *Acta Musei Maced. Sci. Nat.* **1995**, *21*, 23–112.
30. Isikov, V.P. *Systematic Catalogue of Fungi on Woody Plants in Crimea*; Arial Press: Simferopol, Russia, 2019.
31. Bernicchia, A.; Marchisio, V.F.; Padovan, F.; Perini, C.; Ripa, C. *Checklist of Italian Fungi. Basidiomycota*; Onofri, S., Ed.; Commission on Fungi of the Organization for the Phyto-Taxonomic Investigation of the Mediterranean Area: Sassari, Italy, 2005.
32. Tura, D.; Zmitrovich, I.V.; Wasser, S.P.; Nevo, E. Checklist of Hymenomycetes (Aphyllophorales s.l.) and Heterobasidiomycetes in Israel. *Mycobiology* **2010**, *38*, 256–273. [CrossRef] [PubMed]
33. Sarkina, I.S.; Mironova, L.P. Annotated list of basidiomycetous and ascomycetous macrofungi in the Karadag Nature Reserve. *Sci. Note Nat. Res. Martyan Penins.* **2015**, *6*, 297–327.
34. Ablakatova, A.A. *Mycoflora and Basic Fungal Disease of Fruit and Berry Crops at South of the Russian Far East*; Nauka: Moscow, Russia, 1965. (In Russian)
35. Azbukina, Z.M. (Ed.) *Flora, Vegetation and Mycobiota of Ussury Nature Reserve*; Dalnauka: Vladivostok, Russia, 2006. (In Russian)
36. Egorova, L.N. (Ed.) *Flora, Mycobiota and Vegetation of Lazovsky Nature Reserve*; Russkiy Ostrov Publishing: Vladivostok, Russia, 2002. (In Russian)
37. Pavlyuk, N.A. Plant's Mycobiota of the Botanical Garden Far East Branch RAS. Ph.D. Thesis, Far East Branch RAS, Vladivostok, Russia, 2009. (In Russian).
38. Golan, J.J.; Pringle, A. Long-distance dispersal of fungi. *Microbiol. Spectr.* **2017**, *5*, 1–24. [CrossRef] [PubMed]
39. Ingold, C.T. *Dispersal in Fungi*; Clarendon Press: Oxford, UK, 1953.
40. Jayawardena, R.S.; Purahong, W.; Zhang, W.; Wubet, T.; Li, X.; Liu, M.; Zhao, W.; Hyde, K.D.; Liu, J.; Yan, J. Biodiversity of fungi on *Vitis vinifera* L. revealed by traditional and high-resolution culture-independent approaches. *Fungal Divers.* **2018**, *90*, 1–84. [CrossRef]
41. Popushoy, I.S.; Marzhina, L.A. *Fungal Diseases of Grapevine*; Shtiintsa: Kishinev, Moldova, 1989. (In Russian)
42. Khokhryakov, M.K.; Dobrozrakova, T.L.; Stepanov, K.M.; Letova, M.F. *Guidebook of Plant Diseases*, 3rd ed.; Lan Press: Saint-Petersburg, Russia, 2003. (In Russian)
43. Gafforov, Y.S. A preliminary checklist of Ascomycetous microfungi from southern Uzbekistan. *Mycosphere* **2017**, *8*, 660–696. [CrossRef]
44. Gaponenko, N.I. *Survey of the Fungi of Bukhara*; Akademy of Science of Uzbek SSR Publ.: Tashkent, Uzbekistan, 1965. (In Russian)
45. Burdinskaya, V.F.; Poymanov, V.E.; Tolokova, R.P. *Diseases and Pests of Grapevine and Their Control*; Potapenko, Y.I., Ed.; VNIIViV Press: Novocherkassk, Russia, 2009. (In Russian)
46. Collado, E.; Bonet, J.A.; Camarero, J.J.; Egli, S.; Peter, M.; Salo, K.; Martínez-Peña, F.; Ohenoja, E.; Martín-Pinto, P.; Primicia, I.; et al. Mushroom productivity trends in relation to tree growth and climate across different European forest biomes. *Sci. Total Environ.* **2019**, *689*, 602–615. [CrossRef] [PubMed]
47. Nnadi, N.E.; Carter, D.A. Climate change and the emergence of fungal pathogens. *PLoS Pathog.* **2021**, *17*, e1009503. [CrossRef] [PubMed]