

Spatial Distribution of Species Diversity of Clavarioid Mycobiota in West Siberia

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Abstract—The results of a 20-year study of the spatial distribution of clavarioid mycobiota in the West Siberian Plain (WSP) are discussed. The species structure has been studied on two scales: regional (an area of 100 000 km²) and local (100 km²). In the studied area, 121 species of clavarioid fungi are found. The patterns of spatial variability of species diversity on the plain are revealed. On the regional scale, the maximum species richness of fungi is observed in hemiboreal forests (104 species); on the local scale it ranges from the middle boreal to hemiboreal (54.3–54.5 species). With the increasing pessimality of the hydrothermal regime, the number of species decreases sharply on both scales in the direction of the tundra and steppes. The study of the distribution of diversity among the localities reveals changes not only along the latitudinal gradient, but also in the longitude sectors: in the forest zone, the richest localities are located on the western and eastern edges of the plain, while in the extensive marshy areas in the center the number of species is lower ($p < 0.05$). A map of the spatial distribution of species diversity for the local scale is constructed. The correspondence of the spatial distribution of the studied fungi group to a global latitudinal gradient is discussed. The main abiotic factors forming a variety of the studied group of fungi in the region are revealed.

Keywords: biogeography, longitudinal gradient, mapping, climate, forest tundra, fungal ecology, Basidiomycota

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INTRODUCTION

The identification of patterns of spatial differentiation of biological diversity on various scales and from various factors is one of the main problems of modern ecology and biogeography (Lomolino et al., 2010). The basic biogeographical rules and zoning are based on regularities in the distribution of flora and fauna objects, whereas representatives of the kingdom of fungi were not used for such constructions, despite the fact that fungi are not inferior to animals in regards to general species richness (Blackwell, 2011; Peterson and Soberon, 2018).

The inclusion of fungi in such studies is complicated by a number of factors, the main one being the fact that fungi are understudied at taxonomic and regional levels: only 5–10% of fungi from the potential wealth of the planet have been described, and many regions have not been explored (Mueller and Schmit, 2007). Nevertheless, the study of the spatial distribution of the diversity of individual fungi groups on a continental and global scale has been carried out for more than a century. Such groups include macromycetes—aphyllophoroid fungi, for which species richness in the Holarctic is higher in forest ecosystems than in the tundra and desert-steppe

regions. Is the number of fungi species everywhere in the forest zone equally high?

The species richness of fungi is considered based on the example of the model group—clavarioid fungi (Fungi, Basidiomycota)—one of the life forms in the composition of aphylophoroid fungi. Clavarioid are a phylogenetically heterogeneous group (Hibbett et al., 2007). They are characterized by significant fruiting bodies with a weight reaching 10 kg and a diameter of up to 60 cm. These fungi are distributed on all continents from polar glaciers and highlands to tropical deserts and equatorial rain forests. They play an important role in most terrestrial biomes, forming part of three main functional groups: saprotrophs, parasites, and symbionts, and, as a result, participate in key biospheric processes: the soil formation and cycling of basic nutrients (Shiryaev, 2014).

The study of the diversity of clavarioid in separate natural zones of Russia has been carried out for more than 20 years: it is shown that, from the tundra zone to the south, the number of species increases 27 times; the highest number of species is found in hemiboreal forests (Shiryaev, 2014). In general, forest zones/sub-zones are richer than treeless zones. This result is consistent with the spatial patterns of fungal distribution

in Europe (Kotiranta et al., 2009; GBIF, 2018). For the use of “localities” of 100000 km², the conclusion obtained for zonal mycobiotes (Shiryaev, 2007) remains the same, but specific features were revealed within the forest mycobiota: the richest were maritime hemiboreal regions, and territories located under ultracontinental climate were substantially poorer (Shiryaev, 2017, 2018).

The extension of our studies to the continental scale raised a new question: is the distribution of clavarioid fungi consistent with the global latitudinal gradient of diversity? Globally it was shown that the distribution of the diversity of all fungal groups on the planet, studied using genetic methods for analyzing soil samples (the so-called “hidden diversity”), is generally subjected to the rule of the latitudinal gradient; however, for different fungal groups, the trends and location of the maximums were different: the higher abundance of micromycetes was in low latitudes, whereas for some groups of macromycetes the peak of richness was at medium latitudes (Tedersoo et al., 2014; Peay et al., 2016). Recent studies conducted on a transect with a length of about 6300 km along 58° E from the tropical deserts of the Arabian Peninsula to the polar deserts of Novaya Zemlya Island in the Arctic Ocean demonstrated that the peak of clavarioid fungi species richness (116–129 species) for “localities” with an area of 100000 km² falls on the latitude range of 50°–60° N and the number of species was sharply reduced to the north and south. A similar result was obtained for localities of 100 km² in size: the richest localities (65.2–74.8) correspond to the latitude range of 50°–65° N, and the species richness in the polar and tropical deserts tends to zero, although the localities in the polar deserts turn out to be statistically significantly richer than tropical analogs (Shiryaev, 2018). These results indicate that the distribution of clavarioid fungi probably does not fully correspond to the general patterns of latitudinal gradient of species diversity. However, this question remains open, both for clavarioid and for other groups of macromycetes. On the studied transect, the increase of the taxonomic diversity of fungi did not follow the increase in thermal resources, and a strong positive correlation with the average annual precipitation was found (Shiryaev, 2018). It is possible that the spatial coverage of the territory and the scale of the considered data also affect the revealed regularities: for high latitudes of Eurasia, the dependence of the species abundance of clavarioid fungi on the average annual temperature for regional and local localities scales was found, and the significance of precipitation decreases with the increase of the studied grain size (Shiryaev, 2017). Thus, it is not yet clear on which climatic factors the diversity of the studied fungi group depends. Probably the answers to these questions will be found when the problem is investigated at various scales or in more regions of the planet.

The West Siberian Plain (WSP), having a well-defined latitudinal zonation and clear gradients of environmental factors, is a convenient polygon for studying the distribution of diversity. Earlier, for the territory of the WSP, the patterns of change in species richness were revealed for vascular plants and lichens (Malyshev, 1994; Sedel'nikov et al., 2008; Sedel'nikova, 2017). For aphyllorphic fungi, including clavarioid, despite the long history of studies of their diversity, the results of studies are limited (Mukhin, 1993; Shiryaev, 2008).

The goals of this study were (1) establishing a change in the species abundance of clavarioid fungi of the West Siberian Plain at various scales on a latitudinal gradient, (2) creating a map of the distribution of species diversity, and (3) establishing an association between the variety of fungi and abiotic factors.

MATERIALS AND METHODS

In this study, the boundaries of WSP correspond to a physical–geographical regionalization map of the USSR (1967). Species richness of clavarioid fungi was studied in nine latitudinal regions that correspond to the main natural zones/subzones; the area of each region averages an area of 100000 km². Within each region, 58 localities (an area of 100 km²), uniformly distributed in the range from 73° to 51° N, were studied over a length of 2400 km from the tundra zone to the steppes (Table 1).

Due to the intensification of oil and gas production, increased areas of settlements, roads, and economic impact on forests (cutting, plowing, etc.), local bioclimatic conditions on the plain change with time. We considered the actual state of mycobiota, i.e., those species that are able to form fruiting bodies “here and now” (realized diversity), under modern natural and climatic and anthropogenic conditions. Moreover, many species of clavarioid fungi are recognized indicators of intact ecosystems (Shiryaev, 2014).

Each latitudinal region was studied for about 20 years. The localities for the study were chosen arbitrarily and had the form of a square (10 × 10 km) or a circle (radius 5.6 km). Variations of the form were allowed, for example, a rectangle (20 × 5 km). Ideally, each location was studied 30 working days for 3 years (over the past 20 years) by different researchers. Some data were also borrowed from the published materials of various researchers; information from various databases and numerous herbals was used. The parameter “90% of the number of species” for the most studied locality was used as a unit of measure for estimating the minimal number of accounting units (collected samples, diary notes, photographs, etc.) detected in each locality. For tundra and taiga localities, it was necessary to collect a different number of accounting units (e.g., apply a different selective effort). For example, in the Payute region, the most well-studied

Table 1. Studied localities in the West Siberian Plain

Latitudinal region	No.	Name of locality	Geographical coordinates	Location
Arctic tundra (<i>n</i> = 2)	1	Bely-east	73°13' N, 71°32' E	Yamalo-Nenets AO, Yamal district, eastern part of Bely Island
	2	Bely-west	73°06' N, 70°03' E	Yamalo-Nenets AO, Yamalsky district, western part of Bely Island
Subarctic tundra (<i>n</i> = 3)	3	Bovanenkovo	70°27' N, 68°26' E	Yamalo-Nenets AO, Yamal district, vicinity of Bovanenkovo village
	4	Payuta	67°57' N, 68°33' E	Yamalo-Nenets AO, Yamalsky district, 178 km N of Salekhard city
Forest tundra (<i>n</i> = 4)	5	Nakhodka	67°19' N, 72°10' E	Yamalo-Nenets AO, Yamalsky district, vicinity of Nakhodka village
	6	Aksarka	66°30' N, 67°47' E	Yamalo-Nenets AO, Nadymy district, 52 km E of Salekhard city
	7	Nadym	65°32' N, 72°30' E	Yamalo-Nenets AO, Nadymy district, vicinity of Nadym city
	8	Yamsovei	65°31' N, 75°31' E	Yamalo-Nenets AO, Pyurovsky district, 81 km SW of Novy Urengoy city
North taiga (<i>n</i> = 4)	9	Pangody	65°53' N, 74°30' E	Yamalo-Nenets AO, Nadymy district, 98 km NE of Nadym city
	10	Yamgort	64°57' N, 64°21' E	Yamalo-Nenets AO, Shuryshkarsky district, vicinity of Yamgort village
	11	Soryum	64°07' N, 69°08' E	Khanty-Mansiysk AO, Beloyarsky, middle reaches of Sorum River
	12	Chatyl'nskoe	63°26' N, 80°59' E	Yamalo-Nenets AO, Krasnoselkupsky district, 257 km S of Krasnosel'kup village
Middle boreal (<i>n</i> = 8)	13	Lyantor	61°47' N, 71°43' E	Khanty-Mansiysk AO, Surgutsky district, vicinity of Lyantor village
	14	Oyus	60°53' N, 61°32' E	Sverdlovsk oblast, Ivdelsky district, 62 km SE of Ivdel city
	15	Pelymskii Tyuman	60°05' N, 62°58' E	Sverdlovsk oblast, Gagarinsky district, vicinity of Pelymskiy Tuman Lake
	16	Nyangan'	62°03' N, 65°32' E	Khanty-Mansiysk AO, Oktyabrsky district, vicinity of Nyagan city
	17	Khanty-Mansiysk	60°59' N, 69°03' E	Khanty-Mansiysk AO, vicinity of Khanty-Mansiysk city
	18	Uim	58°51' N, 71°07' E	Tyumen oblast, Uvatsky district, 164 km E of Tobolsk city
	19	Ust'-Tegusskoe	58°42' N, 73°57' E	Tyumen oblast, Uvatsky district, 318 km E of Tobolsk city
	20	Aleksandrovs-koe	60°25' N, 77°48' E	Tomsk oblast, Aleksandrovsky district, vicinity of Aleksandrovs-koe village
South taiga (<i>n</i> = 10)	21	Sabun	62°24' N, 81°42' E	Khanty-Mansiysk AO, Nizhnevartovsky district, Sibirskiye Uvaly Nature Park
	22	Bor	62°17' N, 89°07' E	Kranoyarsk krai, Turukhansky district, vicinity of Bor village
	23	Turinsk	58°09' N, 63°43' E	Sverdlovsk oblast, Turukhansky district, vicinity of Turinsk city
	24	Tobolsk	58°13' N, 68°31' E	Tyumen oblast, vicinity of Tobolsk city
	25	Abaul	57°48' N, 70°19' E	Tyumen oblast, Bagaisky district, 122 E of Tobolsk city
	26	Zapadno-ostninskoe	57°42' N, 79°01' E	Tomsk oblast, Parabelsky district, 36 km NE of Kedrovyy village
	27	Novyi Tevriz	59°08' N, 77°30' E	Tomsk oblast, Karasoksky district, vicinity of Novyi Tevriz village
	28	Kolpashevo	58°18' N, 83°05' E	Tomsk oblast, Kolpashevsky district, vicinity of Kolpashevo village
Hemiboreal (<i>n</i> = 10)	29	Tomsk	56°29' N, 84°39' E	Vicinity of Tomsk city
	30	Bely Yar	58°49' N, 84°47' E	Tomsk oblast, Beloyarsky district, vicinity of Bely Yar village
	31	Ulu-Yul	57°54' N, 86°38' E	Tomsk oblast, Pervomaisky district, vicinity of Zakharkovo village
	32	Irbitskoe	57°10' N, 62°17' E	Sverdlovsk oblast, Irbitsky district, vicinity of Irbitskoe Lake
	33	Talitsa	56°55' N, 63°40' E	Sverdlovsk oblast, Talitsky district, vicinity of Talitsa village
	34	Levashi	56°48' N, 65°29' E	Tyumen oblast, Tyumensky district, vicinity of Levashi village
	35	Novyi Tap	57°01' N, 67°44' E	Tyumen oblast, Urginsky district, 100 km NE of Yalutorovsk city
	36	Robruchi	56°33' N, 67°59' E	Tyumen oblast, Omutinsky district, 23 km NE of Omutinskoe village
	37	Bol'shoe Beloe	56°18' N, 81°47' E	Tomsk oblast, Bakcharsky district, 176 km E from Tomsk city
	38	Kolbasa	57°01' N, 76°40' E	Novosibirsk oblast, Kyshotvsky district, 54 km N from Kyshtovka village
39	Taiga	56°07' N, 85°34' E	Kemerovo oblast, Yashkinsky district, vicinity of Taiga city	
40	Bolotnoe	55°42' N, 84°14' E	Novosibirsk oblast, Bolotinsky district, vicinity of Bolotnoe village	
41	Lebedevo	54°55' N, 84°20' E	Novosibirsk oblast, Toguchinsky district, vicinity of Lebedevo village	

Table 1. (Contd.)

Latitudinal region	No.	Name of locality	Geographical coordinates	Location
Forest steppe (<i>n</i> = 7)	42	Bolshie Kharlushi	55°11' N, 60°59' E	Chelyabinsk oblast, Sosnovsky district, 15 km NW from Chelyabinsk city
	43	Krasny Oktyabr	55°36' N, 64°48' E	Kurgan oblast, Ketovsky district, 20 km NW from Kurgan city
	44	Medvezh'e	55°13' N, 68°00' E	Kurgan oblast, Petukhovskiy district, vicinity of Bol'shoe Medvezh'e Lake
	45	Tatarsk	55°15' N, 75°57' E	Novosibirsk oblast, Tatarskiy district, vicinity of Tatarsk village
	46	Malyshevo	54°59' N, 78°48' E	Novosibirsk oblast, Zdvinskiy district, vicinity of Malyshevo village
	47	Vysokaya Griva	53°56' N, 80°37' E	Altai krai, Pankrushikhinskiy district, vicinity of Pankrushikha village
	48	Akademgorodok	54°48' N, 83°08' E	Novosibirsk oblast, Akademgorodok of Novosibirsk city
Steppe (<i>n</i> = 10)	49	Kulevichi	53°07' N, 61°26' E	Chelyabinsk oblast, Varenkiy district, 53 km E of Kartaly city
	50	Nadezhdinka	53°43' N, 63°42' E	Kazakhstan, Kostanay oblast, 60 km N from Kostanay city, vicinity of Nadezhdinka village
	51	Dokuchaevka	51°35' N, 64°09' E	Kazakhstan, Kostanay oblast, 181 km S from Kostanay city, vicinity of Dokuchaevka village
	52	Uyaly	53°07' N, 69°32' E	Kazakhstan, Akmola oblast, 20 km S from Kokchetav city
	53	Stepnogorsk	52°22' N, 71°47' E	Kazakhstan, Akmola oblast, 142 km NE of Astana city, vicinity of Stepnogorsk city
	54	Tambovka	52°50' N, 70°33' E	Kazakhstan, Akmola oblast, 195 km N from Astana city
	55	Ul'kenkaroi	53°51' N, 71°46' E	Kazakhstan, Severo-Kazakhstan oblast, 199 km SE from Petropavlovsk
	56	Karasuk	53°39' N, 77°59' E	Novosibirsk oblast, Karasuk district, vicinity of Karasuk village
	57	Shcharbaky	52°32' N, 78°09' E	Kazakhstan, Pavlodar oblast, 77 km NE of Pavlodar city, vicinity of Shcharbaky village
	58	Aleisk	52°26' N, 82°41' E	Altai krai, vicinity of Aleisk city

The number of localities in the corresponding zone/subzone is in brackets.

locality in the subarctic tundra (Yamalo-Nenets AO, 67°57' N, 68°33' E), 19 species were identified, represented by 410 accounting units. In this case, 90% of 410 accounting units were 370 accounting units. Thus, at least 370 accounting units must be collected in each locality in the subarctic tundra. In the hemiboreal forests, the Talitsa locality (Sverdlovsk region, 56°55' N, 63°40' E) is the most fully studied, including 66 species represented by 820 accounting units, and 90% of this number is 740. Therefore, in the current study for hemiboreal regions, we use data on localities in which at least 740 accounting units are known. Localities that do not meet the above-listed parameters were excluded from this study. Localities corresponding mostly to intra- and extrazonal habitats, for example spruce forests (islands) in the tundra or pine forests (islands) in the steppe, were also excluded.

After compiling a basic list of fungi species for each locality, its verification was carried out. The following species were excluded from the list: (1) recently described as new to science, i.e., known only from locus classicus, or an extremely limited number of localities, although their distribution is potentially

much wider: *Ramaria cistophila*, *Ramariopsis robusta*, *Typhula suecica*, etc.; (2) with a discussion of taxonomic status: *Clavariadelphus borealis*, *Ramaria alticola*, *Pterula caricis-pendulae*, etc.; and (3) found only in intra- and extrazonal habitats but not detected on the plakor under zonal conditions.

The names of the species of fungi correspond to the data from the Internet portal IndexFungorum (<http://www.indexfungorum.org>; date of access to the resource February 14, 2018).

Over a 20-year period of research in the region, a lot of material, represented by 1173 clavarioid fungi samples deposited in the mycological collection of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg (SVER), was accumulated. About 13000 records (taken from field diaries, analysis of photographs and data published by other researchers, and online databases) concerning the detection of clavarioid fungi in the studied region were included in the CLAVARIA^{WORLD} database, which is compiled by the author and regularly updated with new data based on the analysis of all

Table 2. Bioclimatic characteristics of the West Siberian Plain

Parameter	Latitudinal region								
	1	2	3	4	5	6	7	8	9
Mean annual temperature, °C	−9.8	−8.5	−5.7	−2.9	−0.8	1.2	2.2	2.8	3.5
Mean temperature of the coldest month, °C	−24.6	−23.9	−23.2	−20.5	−18.9	−16.8	−16.0	−15.9	−14.5
Absolute minimal temperature, °C	−51.7	−50.5	−53.7	−52.6	−49.0	−50.0	−50.4	−46.4	−47.8
Mean sum of temperatures above 10°C	120	270	380	990	1460	1610	1750	1960	2320
Seasonality of temperatures, °C	31.7	33	38.0	37.8	37.3	35.7	33.8	35.1	35.4
Mean annual precipitation, mm	245	255	450	490	530	510	478	386	320
Area of permafrost, %	100	100	88	40	5	0	0	0	0
Area of saline soils, %	0	0	0	0	0	0	15	35	45
HTC	4.0	2.8	1.9	1.7	1.5	1.4	1.2	0.9	0.7

Here and after, (1) arctic tundra, (2) subarctic tundra, (3) forest tundra, (4) northern taiga, (5) middle boreal, (6) southern taiga, (7) hemiboreal, (8) forest steppe, and (9) steppe. HTC is the hydrothermal coefficient of Selyaninov.

possible material for clavarioid in the world. The database currently has about 79000 records.

The map of distribution of fungal species richness was constructed based of an interpolation of the initial data on fungal diversity by the kriging method, one of the nonlinear algorithms in the Surfer 10 GIS system with a resolution of 0.1° latitude per 0.1° longitude. A similar method was used for determining the spatial structure of the flora of Eastern Europe (Morozova, 2008). For visualizing fungi diversity, a step between lines of ten species was selected.

For determining the relationship between the diversity of mycobiota and abiotic factors, basic bioclimatic indicators were used: average annual temperature; seasonality of temperature change, represented as the temperature difference of the warmest and coldest months; sum of active temperatures above 10°, and average annual amount of precipitation (Table 2). Climatic indicators were taken from the WorldClim database (Fick and Hijmans, 2017) with additions from climate-base.ru (query October 22, 2017) for some weather stations.

The Hydrothermal Coefficient of Selyaninov (HTC), defined as $HTC = R \times 10 / \Sigma t$, where R is the sum of precipitation in millimeters for a period with temperatures above +10°C and Σt is the sum of temperatures in degrees for the same period, was calculated. For each region, the average sum of active temperatures above 10°C was established. The area of ever-frozen and saline soils is given according to the study (*National Atlas...*, 2011).

Traditionally, in mycology, two levels of inventory diversity are studied: γ diversity and α diversity. The γ variety is the number of species in the latitudinal region; α diversity is estimated as the mean number of species at local points (localities) studied within the corresponding latitudinal region. Differential diversity (β diversity) is rarely considered in the study of myco-

biota. In this study, β diversity was estimated using Whittaker's index as the ratio of gamma and alpha diversity ($\gamma/\alpha-1$); the coefficient of variation (CV) for the mean number of species in the localities and the mean value of Jacquard similarity index (J) were also calculated. For additional estimates of β diversity, the standard deviation (SD) for the number of species in the localities and the magnitude of the change in species richness estimated as the difference between species richness of the poorest and the richest localities within the latitudinal region (D_{RPL}) were used.

An assessment of the dependence of species richness on climate was carried out using the nonparametric Spearman correlation coefficient (r_s). The significance of the differences in the values of the species richness between the localities was estimated using the Mann–Whitney U-test, with the Bonferroni correction for multiple comparisons. The similarity between localities was studied by cluster analysis using STATISTICA 8.0 software (StatSoft, 2008) with Ward's method and Euclidean distance. Accumulation curves for observed fungi species richness were plotted using EstimateS Win 9.10 (Colwell and Elsensohn, 2014).

RESULTS

During 80 years of research within WSP, 126 species of clavarioid fungi have been identified (Shiryaev, 2014), out of which 124 species (actual realized diversity) representing 18.5% of the global wealth of the group were collected over the past 20 years. For the neighboring territories, 166 species in Urals and 101 species for Middle Siberia are known (Shiryaev, 2014). Out of 124 species able to form fruiting bodies under actual climatic and anthropogenic conditions of the plain, 121 species (96%) were identified within 58 localities and 9 latitudinal regions. The number of

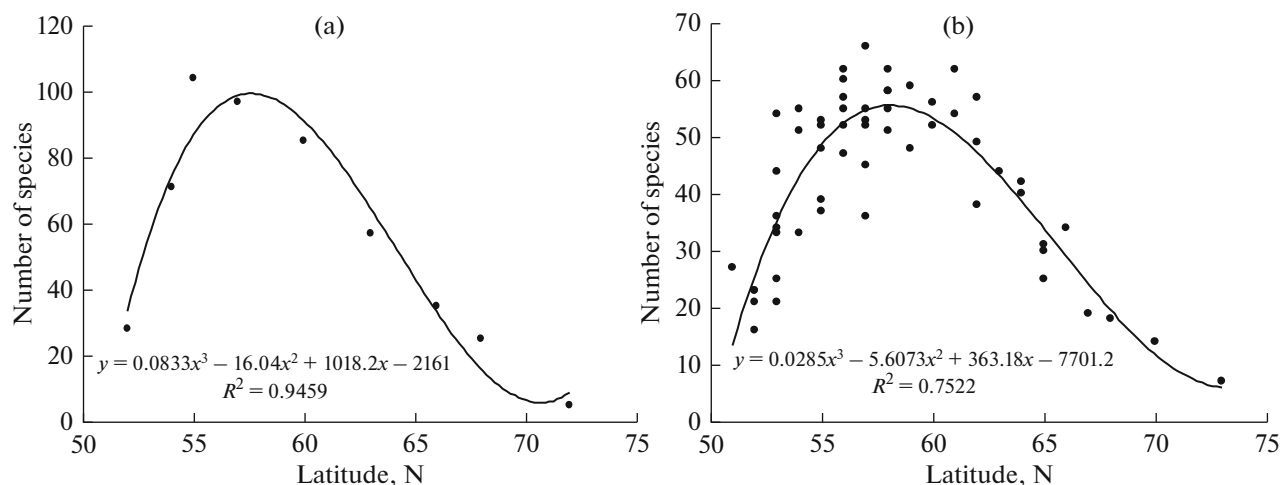


Fig. 1. Change in species richness with latitude (a) for latitudinal regions and (b) for localities.

species in the latitudinal regions varies from 6 to 104 and in the localities from 4 to 66.

The lowest number of species was detected in the Arctic tundra (6); the highest number of species (104) was noted in hemiboreal latitudinal region, to the south of which species richness was reduced to 52 species in the steppe region. The geographic center of hemiboreal region corresponds to 55° N; the species diversity decreased towards the north and south of it (Fig. 1a). A similar trend but with some differences was detected for the localities in general: the peak of richness (more than 60 species/locality) was between 61° and 56° N, i.e., corresponded not to a single natural zone, but to a range from the middle boreal to the hemiboreal. In both cases, the distribution of species diversity was described in the best way by a third-order polynomial equation (Fig. 1b).

In the Payuta tundra locality and in Talitsa middle boreal locality, the accumulation curve comes to the

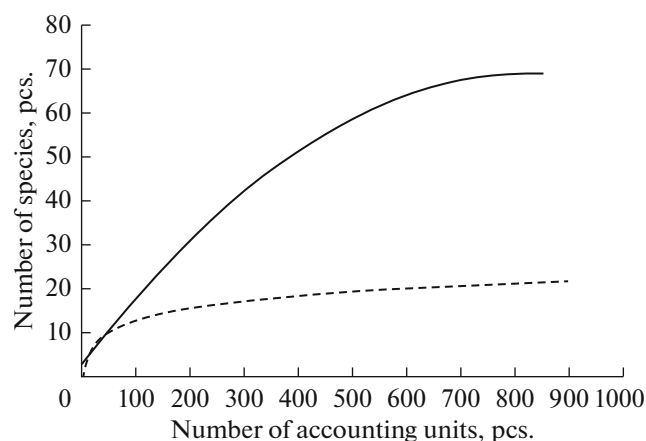


Fig. 2. Jackknife 1 accumulation curve of species richness of clavarioid fungi in the subarctic tundra; the Payuta locality (dotted line) and hemiboreal Talitsa locality (line).

plateau at indices of 21.2 and 69.4 species, respectively. Thus, at the moment, the species richness in the most studied locations is 89.6 and 95.1% of the potentially possible (Fig. 2).

Both indices of inventory diversity (α and γ diversity) increased from the tundra to the middle boreal and hemiboreal (from 6 and 4.5 to 104 and 54.5, respectively), but to the south their level decreased toward steppes (Table 3). The values of the mean number of species and medians in the localities were close: in hemiboreal, for example, the mean number of species was 54.3, and the median was 54.8 (Fig. 3). The differentiating variety, estimated by various methods, also increased to the south. For example, the Whittaker's index was 0.33 in the tundra and increased threefold to a maximum of 0.91 in hemiboreal, but then decreased to 0.13 in the steppes. The mean Jacquard coefficient (J) was maximal in tundra 0.80, decreasing to 0.53–0.58 in hemiboreal, which also indicated the increase in differentiating diversity. On the other hand, the coefficient of variation of the average number of species in the locality (CV) in the tundra was 11.0, increasing in the southern direction, reaching a maximum in the steppes (25.2). Other indices of β diversity (SD and D_{RPL}) also indicate the highest diversity in the hemiboreal region. SD had a minimal value in the tundra (0.7) and maximal in the hemiboreal (8.4), the ratio between the poorest and richest locality in the tundra was 20%, and hemiboreal was 45%.

DISCUSSION

Correspondence of diversity distribution and the latitudinal gradient. On the territory of WSP, the highest γ diversity of clavarioid fungi was noted in the hemiboreal region; it decreased in the direction to the north and south (Table 3, Fig. 1a). A similar result was obtained for the neighboring longitudinal transect,

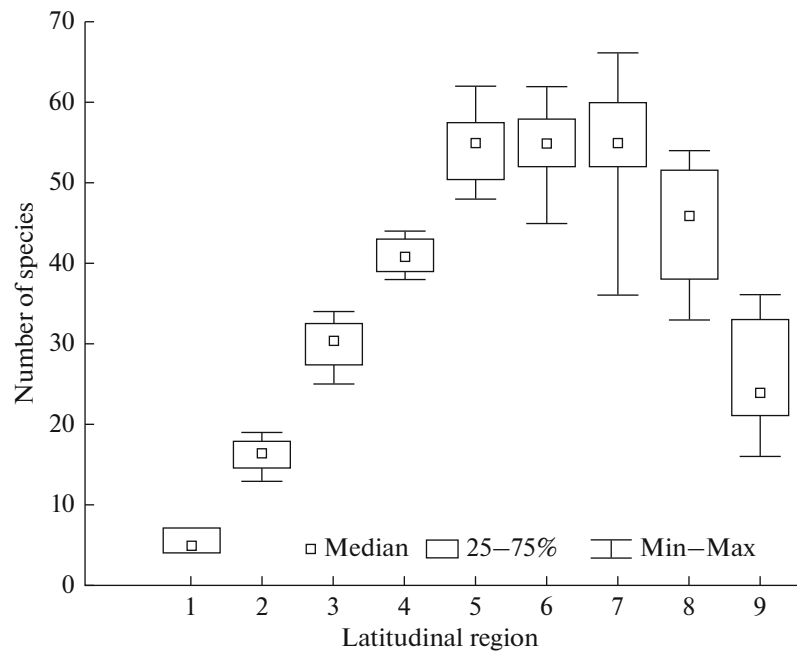


Fig. 3. Species diversity of clavarioid fungi of nine latitudinal regions of the West Siberian Plain.

occupying 6500 km from the islands of Novaya Zemlya (75° N) and Polar Urals along 58° E. through Central Asia and Iran to the tropical deserts of the Arabian Peninsula (20° N), where the peak of species richness was in the southern taiga and hemiboreal (53°–60° N), while the desert-steppe regions are extremely poor (Shiryaev, 2018).

The change in α diversity had a similar tendency: in localities, species richness increased with a decrease in latitude to the middle, southern taiga, and hemiboreal (56°–61° N), and decreased to the south, towards the steppes (Fig. 3). On the longitude transect Novaya Zemlya–Ural–Arabian Peninsula, the peak of richness

was on a similar range of latitudes from 50° to 65° N, and in the desert-steppe regions of Central Asia and in tropical deserts the number of species decreased almost to zero (Shiryaev, 2018). Thus, the trends of changes with the latitude of both indices of the inventory diversity did not correspond to the generally accepted latitudinal gradient of species richness ($p > 0.05$).

The differentiating variety varies in the same way as the inventory: the peak of β diversity was in the hemiboreal region, and β diversity decreased towards steppes. Only one index, the coefficient of variation, increased from the tundra to the steppes (Table 3).

Table 3. Indices of diversity of biota of clavarioid fungi in the latitudinal regions of the West Siberian Plain

Index	Latitudinal region								
	1	2	3	4	5	6	7	8	9
γ diversity	6	26	35	57	85	97	104	71	29
α diversity	4.5	18.7	30	41	54.5	54.4	54.3	44.7	25.9
Maximum	5	19	34	44	62	62	66	54	36
Minimum	4	14	25	38	48	45	36	33	16
Whittaker's index	0.33	0.39	0.17	0.39	0.56	0.78	0.91	0.59	0.13
SD	0.7	2.1	3.7	2.6	4.7	5.0	8.4	7.7	6.5
CV	11.7	11.0	12.4	6.3	8.7	9.2	15.4	17.3	25.2
Drpl (%)	20.0	24.0	26.7	13.6	22.6	27.4	45.4	38.9	37.5
Mean Jacquard index	0.80	0.54	0.73	0.71	0.69	0.62	0.58	0.56	0.53
Number of localities	2	3	4	4	8	10	10	7	10

Maximum is the maximal number of species in the locality; minimum is the minimal number of species.

Mapping species diversity. According to the species composition, the localities studied within the WSP can be divided into two basic clusters; the first one can be called tundra-steppe and the second one subboreal (Fig. 4). The first cluster includes localities from the tundra, forest-tundra, north-taiga and steppe regions, while the second cluster includes southern taiga and hemiboreal. Forest-steppe localities are present in both clusters. The highest similarity was found between neighboring localities or localities with the similar bioclimatic conditions. It can be said that the tundra-steppe cluster combines localities with low species richness, whereas subboreal cluster includes localities with high species richness.

Localities within the latitudinal regions were not homogeneous either in species composition or in number of species. Among the middle boreal localities, which mainly belong to the tundra-steppe cluster, two localities (Khanty-Mansiysk and Bor) were classified as a subboreal group, where southern taiga, hemiboreal, and forest-steppe localities were dominant. Some southern taiga (Abaul, Zapadno-Ostanskoe, and New Tevri), hemiboreal (New Tap, Robrouchi, Bolshoe Beloe, and Kolbasa) and forest-steppe (Medvezh'e, Tatarsk, and Malyshevo) localities were classified as being part of the tundra-steppe cluster. This result can be described as unexpected, due to the fact that no similar confusion of localities was observed on the neighboring Novaya Zemlya–Ural–Arabian Peninsula longitude transect (Shiryayev, 2018). Such inversion of some zonal localities may be associated with the peculiarities of the natural conditions of the central part of WSP, characterized by large areas of marshes, alternating with low-yield and unproductive forests on acid peaty soils. Localities in this part of the plain were much poorer than their forest counterparts (there are no more than 50 species/locality in them), and they were dominated by widespread species (65%) that are common in tundra, steppe, and marsh ecosystems from the genus *Typhula* (Shiryayev and Mukhin, 2010). The share of specific tundra-steppe or, in general, southern species, in these localities was extremely low (less than 10%). For subboreal localities, the share of ubiquitous species was also significant (35%), but there was also a significant proportion of specific taiga and nemoral species (about 50%) from the genera *Clavaria*, *Ramaria*, *Ramariopsis* etc., which explains the specificity of forest localities. Nemoral–boreal species, as a rule, do not occur in marshy areas or in tundra or steppe biotopes.

Cartographic visualization of the above result confirms our assumption. In the center of the plain, the localities in areas with the predominance of swampy terrain were not characterized by high species richness (less than 50 species/locality), and, when approaching the Ural mountains and the Central Siberian plateau, the forest cover of the territory increases, and here the species richness in the localities is more than 60 species (Fig. 5). In some regions of Urals, the Central

Siberian Plateau, and in the Altai-Sayan Mountains, there were localities where more than 70 species were identified and more than 80 are known in two localities of the Southern Urals. It can be stated that, in the central part of the WSP, there is a territory poor in clavarioid fungi. The level of species diversity revealed here corresponds to the forest-tundra and steppe regions of the European part of the country (Fig. 5).

Distribution of the fungi species richness along the southern border of the forest (in the forest-steppe and hemiboreal), which in the territory of European Russia and the Urals, characterized by one of the highest indicators of species diversity of clavarioid fungi, is of great interest (Shiryayev, 2018). On the WSP, localities in similar latitudinal regions were located along a line corresponding to the level of 40 species/locality. This was a low level of species richness, which in size corresponds to the middle boreal, and some localities from this line were even similar in terms of species richness with the forest tundra (Tatarsk, Bolshoe Beloe, Kolbasa), which is not typical for the western regions in relation to the plains. Such indices can probably be explained by the local bioclimatic conditions of the localities and by the prevalence of habitats with marshy or saline soils in them. In the European part of the country, a line of 40 species/locality predominantly corresponds to the northern (arctic) and southern (steppe) border of the forest, while a similar line on the territory of the WSP corresponds to the northern boundary of the middle taiga and the middle part of the southern taiga. The giant “break” of diversity in the central part of the forest zone supplements the above picture. In general, at the level of localities, mycobiota of the plain was significantly poorer ($p < 0.01$) when compared to the mountain environment: Ural, the Central Siberian Plateau, and the Altai-Sayan Region, which can probably be considered the leading role of the geographic diversity factor.

An analysis of distribution maps of the species richness of other groups of cryptogamous organisms such as bryophytes and lichens reveals a similar “compression” of the plain from the north and south, and a decrease in the level of diversity within the forest zone in the southeastern part of the region in Vasyugansk bogs area was demonstrated for lichen flora (Ignatov, 1993; Urbanavichyus, 2011).

Thus, the apparent simplicity and comprehensibility of the distribution of the species richness of clavarioid fungi from north to south on the territory of the WSP is more complicated than the mean data presented in the tables above.

Association of the fungi diversity with bioclimatic parameters. As was established in this study, the distribution of clavarioid fungi of the plain (and neighboring regions) does not correspond to the well-known latitudinal gradient of diversity. It is widely known that even the first researchers (Forster and Humboldt) associated the existence of this gradient with the

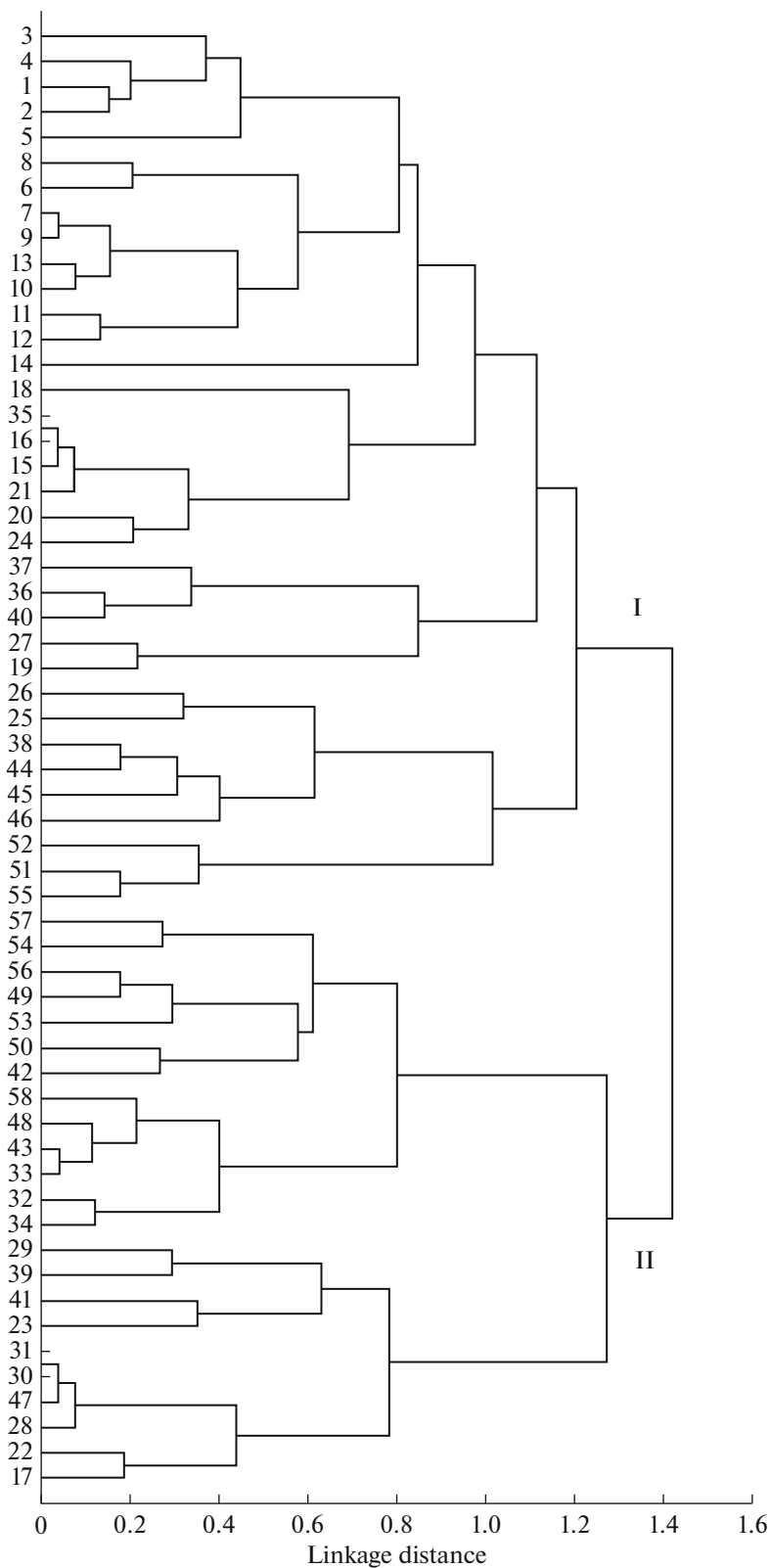


Fig. 4. Similarity of species composition of 58 localities of clavarioid fungi on the West Siberian Plain. Locality numbers correspond to Table I.

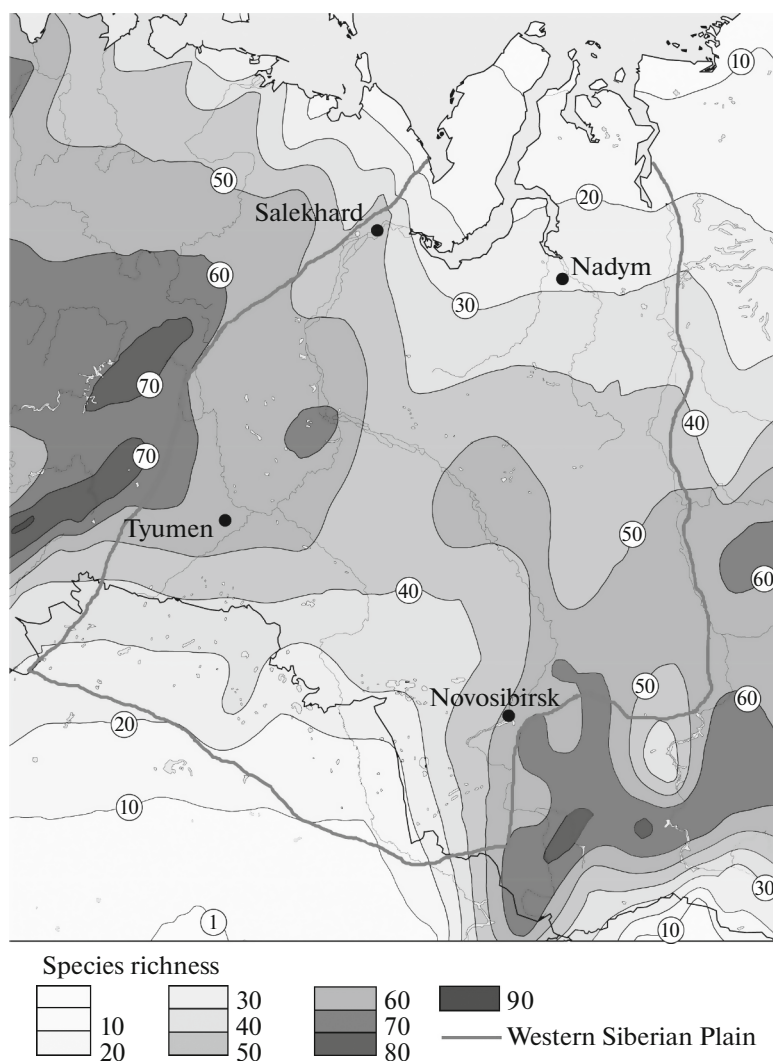


Fig. 5. Distribution of species diversity of clavarioid fungi of the West Siberian Plain.

uneven distribution of heat over the Earth's surface (Lomolino et al., 2010). However, for clavarioid fungi, the significant dependence of the number of species in the latitudinal regions and localities with the mean annual temperature ($r_s = 0.55$, $p > 0.12$ and $r_s = 0.48$, $p > 0.05$, respectively) was not detected (Table 4). For the neighboring transect Novaya Zemlya–Ural–Arabian Peninsula, an association of diversity with temperature ($p > 0.01$) on both scales was not detected either (Shiryayev, 2018). It should be noted that, for the group of lichenized fungi of the WSP (Sedel'nikova, 2017), a strong negative correlation with the average annual temperature ($r_s = -0.77$, $p = 0.01$) was established; i.e., the species diversity of this group decreases with the increase in thermal resources. The species diversity of the latitudinal regions and locality of the plain of clavarioid fungi depends only on the average precipitation level ($r_s = 0.82$, $p < 0.001$ and $r_s = 0.92$, $p < 0.001$) and the area occupied by permafrost $r_s = -0.72$, $p < 0.001$ and $r_s = -0.64$, $p < 0.05$).

In this study it was already indicated that marshy and saline soils are extremely poor in clavarioid fungi. Separately for these soils, no connection with a variety of fungi was established on either scale ($p > 0.05$), but the consideration of these factors together (permafrost + salinity) provides a statistically significant correlation ($r_s = -0.93$, $p < 0.0001$ and $r_s = -0.96$, $p < 0.0001$). The correlation of this factor with some indices of differentiating diversity was also noted: significant values were obtained for Whittaker's index ($r_s = -0.73$, $p < 0.05$) and the standard deviation ($r_s = -0.66$, $p < 0.05$).

The mean annual temperature affects the differentiating diversity: the positive correlation with the standard deviation ($r_s = 0.91$, $p < 0.0001$), the difference between the poor and rich locality ($r_s = 0.83$, $p < 0.0001$), and the mean Jaccard index ($r_s = -0.92$, $p < 0.0001$) was noted. For other temperature indices, a correlation with these two indices of differentiating diversity was also revealed, whereas no connection was

Table 4. Correlation of the species diversity of clavarioid fungi and bioclimatic factors of the West Siberian Plain

Parameter	γ diversity	α diversity	Whittaker's index	SD	CV	Drpl, %	J
Mean annual temperature, °C	0.55	0.48	0.42	0.91****	0.57	0.83***	-0.92****
Mean temperature of the coldest month, °C	0.55	0.48	0.28	0.91****	0.57	0.83***	-0.91****
Absolute minimal temperature, °C	0.33	0.4	0.32	0.67*	0.22	0.5	-0.81***
The mean sum of temperatures above 10°C	0.55	0.48	0.28	0.92***	0.57	0.83***	-0.9****
Seasonality of temperatures, °C	0.32	0.45	-0.15	0.08	-0.06	0.1	0.17
Mean annual precipitation, mm	0.82***	0.92****	0.52	0.35	-0.4	-0.01	-0.03
Permafrost, %	-0.72***	-0.64*	-0.48	-0.93****	-0.41	-0.78**	0.82***
Saline soils, %	0.14	0.1	0.1	0.76**	0.84***	0.82***	-0.84****
HTC	-0.55	-0.48	-0.28	-0.92****	-0.57	-0.83***	0.9****
Permafrost + salinity, %	-0.93****	-0.96****	-0.73 *	-0.66 *	0.21	-0.27	-0.40

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and **** $p < 0.0001$.

established with the average annual precipitation level (Table 4). The area occupied by permafrost correlates with the standard deviation ($r_s = -0.93$, $p < 0.0001$), the difference between the poor and rich locality ($r_s = -0.78$, $p < 0.01$), and the mean Jacquard index ($r_s = 0.82$, $p < 0.001$). For the standard deviation and the coefficient of variation, a strong positive correlation with the area of saline lands was established ($r_s = 0.76$, $p < 0.01$ and $r_s = 0.82$, $p < 0.001$), respectively. The hydrothermal coefficient showed a positive correlation with the standard deviation ($r_s = -0.92$, $p < 0.0001$), the difference between the poor and rich locality ($r_s = -0.83$, $p < 0.001$), and the mean Jacquard index ($r_s = -0.90$, $p < 0.0001$).

No reliable correlation with any diversity index was revealed only for one factor investigated in this study—the seasonality of temperatures.

For determining the association of β diversity with environmental factors, other methods are often used, for example, the Michaelis–Menten equation interpreted as a rate constant for reaching a plateau by the number of accounting units, for which half of all species are identified (i.e., the higher it is, the higher β diversity is) from the possible predicted maximum (Gotelli and Chao, 2013; Shiryayev, 2017). For the Payuta tundra locality, the presence of 21.2 species in the locality on the accumulation curve was predicted (Fig. 2) by this method and 50% of this species richness (10.6 species) was achieved by processing 71 accounting units; for the hemiboreal Talitsa locality, 223 accounting units should be collected for the identification of 34.7 species (half of the 69.4 species). Consequently, the β diversity in hemiboreal is more than 3 times higher than in the tundra.

On the WSP territory, the change in species diversity for the latitudinal regions and localities to the south of hemiboreal definitely reflects the specificity

of the studied region, where arid steppes are represented in the south, and beyond the plain there are deserts characterized by extremely pessimal climatic conditions for clavarioid fungi. In the steppes, with an extremely low level of precipitation and the presence of large areas with saline soils, the species richness of clavarioid fungi declines to the tundra level. Under such conditions, they are able to form basidiomata exclusively in intra- and extrazonal and anthropogenically altered habitats, where fresh water is available; on stony mountain slopes near a stream with a temporary current of water; or on slopes where dew condenses. At the same latitudes, in the more western regions (in the Urals and in European Russia) and in the eastern regions (in Altai and in the Sayan Mountains), there are mesophilic mixed forests rich in fungi. The leading role of the precipitation level in comparison with the temperature indices for explaining the regularities of mycobiota diversity was noted in other studies (Tedersoo et al., 2014; Peay et al., 2016). Also, the higher importance of precipitation compared with the temperature within Northern Eurasia was indicated for other groups of cryptogamous organisms—mosses and lichens (Ignatov, 1992; Urbanavichyus, 2011).

CONCLUSIONS

Which regions of the planet are the richest in the number of species of biota and what is the reason for this? These questions have long been of interest of mankind. The results of this study in the WSP, one of the world's largest plains, demonstrated that, for the model group of macromycetes—clavarioid fungi—the richest latitudinal regions (104 species) correspond to a latitude range of 55°–60° N, e.g., hemiboreal forests, while the regions located to the south and north—subarctic tundra and steppes—are characterized by a lower species richness (26 and 29 species, respectively). The average number of species in the localities

also has a peak in a near latitude range, but with a wider amplitude of 50°–65° N (54.3–54.5), from the middle boreal to hemiboreal, and reduced to a minimum in treeless regions—tundra and steppes (18.7 and 25.9 species, respectively). Thus, the magnitude of the effect is stable with a change in the scale of the study. Consequently, for both scales, the distribution of the number of species does not correspond to the latitudinal gradient (Wallace's rule) in the classical sense, detected for many groups of living organisms.

The level of mycobiota species richness on the whole WSP territory and its separate latitudinal regions occupies an intermediate position between the Urals and Middle Siberia, which can be explained by an increase in the continentality of the climate. On a local scale, the mycobiota of the WSP is poorer than the neighboring mountain territories: the Urals, the Central Siberian Plateau, and the Altai-Sayan Mountains region.

For both studied scales, the linear positive dependence of the species richness of fungi on the amount of average annual precipitation was established. No dependence on the mean annual temperature was observed: for the latitudinal regions, the maximal number of fungi species corresponds to temperatures from +1.2 to +2.2°C, while for localities the range is somewhat wider (from –0.8 to +2.2°C), but with a further increase in temperature the species richness significantly reduced, reaching a minimal level in the most heat-supplied part of the region. Similar results were obtained for the Urals region (Shiryaev, 2018).

One distinctive feature of the WSP from the neighboring ones is the huge gap of diversity (less than 50 species/locality) passing from north to the south through the entire middle part of the forest zone of the plain. Inside this corridor, the species richness in the localities corresponds to indices of forest tundra and forest steppe. At the same time, in the European part of the country, a similar level of species richness is characteristic for the localities of the arctic and steppe forest borders. Localities in the western and eastern parts of the plain, near the Urals and the Central Siberian plateau, respectively, are much richer (more than 50 and even 60–70 species) of their analogues studied in the marshy center of the plain.

However, the result obtained for the WSP on both scales probably demonstrates not a change in diversity with latitude, but the limiting rule under extreme conditions, which is characterized by a general trend—a reduction in species richness with increased pessimal conditions (with a decrease in temperature and humidity), which probably confirms the ideas of Yu.I. Chernov (2008) about the block structure of biota and the prosperity of some groups of organisms with a decreased positions of others. Similar conclusions were obtained for the longitudinal transect Novaya Zemlay—Urals—Arabian Peninsula. Further research involving more groups of fungi will confirm or dis-

prove this assumption. However, different groups of fungi—macromycetes are probably characterized by different principles of latitudinal distribution. Indirect confirmation of this assumption is a result of the study of one of the well-studied mycological groups—lichenized fungi, for which a negative correlation of species diversity in the WSP territory with an average annual temperature was established; i.e., we can say that the species richness of this group increases with the increase in latitude—the trend of change in species richness opposite to that of the latitudinal gradient.

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