



Climate continentality increases the *beta* diversity of macrofungal communities

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Manuscript received: 18.05.2020
Review completed: 14.10.2020
Accepted for publication: 30.10.2020
Published online: 03.11.2020

ABSTRACT

The data on changes in the diversity of the model group of fungi of the middle boreal subzone in Eurasia are summarized. From Finland to Yakutia, with increasing climate continentality, the α - and γ -diversity of fungal communities decreases, but the β -diversity increases 1.7–5 times, which indicates an increase in the spatial isolation of local fungal communities. Similar trends have been found for other high-latitude regions: tundra and forest-tundra.

Keywords: Eurasia, Siberia, biogeography, climate, clavarioid fungi, distribution, diversity, ecology

РЕЗЮМЕ

Ширяев А.Г. Континентальность климата увеличивает бета-разнообразие сообществ грибов. Обобщены данные по изменению разнообразия модельной группы грибов среднетаежной подзоны Евразии. От Финляндии до Якутии, с ростом континентальности климата снижается α - и γ -разнообразие сообществ грибов, а β -разнообразие возрастает в 1,7–5 раз, что свидетельствует об усилении пространственной изоляции локальных сообществ грибов. Аналогичные тренды установлены и для других высокоширотных регионов – тундровых и лесотундровых.

Ключевые слова: Евразия, Сибирь, биогеография, климат, распространение, разнообразие, клавариоидные грибы, экология

Studying the spatial trends of biodiversity at various scales in connection with the ongoing climate change and the growth of economic activity is one of the leading problems of biogeography and ecology (Lomolino et al. 2010). In connection with global changes, a new environmental protection methodology is developed that takes into account the dynamics of the spatial distribution of species (Mateo et al. 2016). However, such studies are carried out by the example of plants and animals, while the distribution of the Kingdom Fungi has been studied extremely poorly. Although it is common knowledge that macrofungi are considered as important natural resources in ecosystems owing to their major role in decomposition, nutrient cycling and mutualistic associations with other organisms.

Traditionally, the change in mycobiota diversity is studied by the example of two spatial gradients: latitudinal and altitudinal. Typically, with this approach, a clear decrease in inventory diversity is recorded in localities (α -diversity) and areas (γ -diversity) as one approaches the arctic or alpine borders of the forest (Mukhin 1993, Bocharnikov 2015). As regards the third-longitude gradient of climatic continentality, information is extremely scarce. At the same time, Eurasia is the largest continent, where changes in the continental climate, from oceanic to ultracontinental, are most prominently represented. Along the continental gradient, from the Atlantic and Pacific coasts to the direction of Yakutia and Transbaikalia, the severity of the climate increases, the edaphic parameters and structure of the vege-

tation change, the α - and γ -diversity of the bryo- and lichen flora of the zonal habitats, various fauna groups decrease (Ignatov 1993, Urbanavichus 2009, Mordkovich 2014).

A change in another important characteristic, β -diversity, which reflects the differentiation of species composition, has been studied very poorly. For many groups of vascular plants, the peak of β -diversity falls on equatorial latitudes, although for Northern Eurasia there are examples of growth of this parameter in the direction of the upper, arctic or arid borders of the forest zone, i.e., to ecotone zones of forest vegetation with tundra and steppe (Bocharnikov 2015). For cryptogams, with the prevailing β -diversity growth paradigm decreasing with latitude, more and more information has appeared in recent decades indicating that, for example, the β -diversity of the European moss floras grows northward (Mateo et al. 2016).

One of the problems of the low level of knowledge on the principles of the spatial distribution of macromycete diversity is that only about 10 % of the potential number of planet species have been identified at the moment, and many regions of the planet still remain mycological “blank spots”. A possible way out of this situation is to investigate the distribution of a well-studied, model group of macromycetes – clavarioid fungi (Basidiomycota). This group of fungi is one of the best studied in Russia and neighboring countries (Shiryayev 2014, 2018).

The spatial distribution of the taxonomic and eco-morphological structure of the clavarioid fungi of the boreal

zone of Eurasia has been studied quite well (Shiryayev 2014). It has been found that the prevalence of widespread species in the tundra, taiga and steppe regions with an almost complete lack of narrow areal distinctions distinguishes the inland continental “plain” mycobiota from the oceanic one (Mukhin 1993, Shiryayev 2014). In general, according to the main taxonomic and ecological-geographical parameters, there is a very clear distinction between the mycobiota from the oceanic and continental zones. For example, in case of the clavarioid fungi of the Urals, β -diversity estimated by various methods reaches the maximum levels on the steppe and arctic borders of the forest zone, but this indicator is lower in the richest hemiboreal and broad-leaved forests (Shiryayev 2018).

The aim of the work is to characterize the changes in the β -diversity of clavarioid fungi communities along the gradient of the climatic continentality of Eurasia. We have tested the hypothesis that, as continentality increases, the fungal communities become more even in species composition. Thus, β -diversity is reduced.

MATERIAL AND METHODS

Climate continentality in Eurasia

The Siberian anticyclone controls weather conditions on the vast areas of Siberia and supports formation of continental climate in the inner part of northern Asia. The continental climate is characterized by sharp contrast between the summer and winter temperatures and strongly affects the distribution and development of vegetation and, respectively, nutrition of heterotrophs, their ontogenesis rhythms, and combinations of biota species. The continental gradient is expressed in all radial directions from the center of Siberian anticyclone activity, in Eastern Siberia. This study is focused on a gradient of continentality from the center of Eastern Siberia to the west to the Atlantic coast of Fennoscandia.

The farther from the center of the Siberian anticyclone to the west, the weaker its influence. Northern Atlantic cyclones soften the dry and cold continental air contributing to the formation of clouds, thaws and precipitation. The invasion of warm and moist air masses from the west is very common in Northern and Eastern Europe, not every year in the Urals, rarely in Western Siberia, but never in

Eastern Siberia. Due to the Siberian anticyclone the mean temperature of January changes from $-38,6^{\circ}\text{C}$ in Yakutsk to $+1,8^{\circ}\text{C}$ in Norway (Bodø). The absolute minimum temperature in the same direction decreases from $-64,4^{\circ}\text{C}$ to -15°C (Table 1). The difference of mean temperature of July over a distance of 7 thousand kilometers from Yakutia to Norway is only 5°C , but the degree day temperatures ($> 10^{\circ}\text{C}$) in those locations are 1050 to 2550°C respectively. Thus the Siberian anticyclone shortens the growth period of plants and, hence, heterotrophic organisms inside of the continent, to 68 days, while in Norway this parameter reaches 310 days (Fick & Hijmans 2017).

An integrated assessment of changes in climatic conditions from the interior of the continent to its oceanic margins is illustrated by distribution of the index of continentality. Here, we use the Conrad's continentality index (I_c), commonly used by different authors (Tuhkanen 1984, Talbot & Meades 2011):

$$I_c = 1.7A / \sin(\varphi + 100) - 14,$$

where, A – is an average annual temperature amplitude of the coldest (January) and warmest (July) months, φ – latitude. The index value is expressed as a percentage (%) of the maximum value and is displayed on Figure 1.

Study sites description

The middle boreal subzone has been studied along the way of the Atlantic transport of air masses, from the coast of the Gulf of Bothnia of the Baltic Sea (Oulu, Finland) to Yakutia (Yakutsk and Churapcha, Russia). The Atlantic vector was selected due to its greater length (6200 km)

Table 1. Climatic parameters along middle boreal subzone in Norway (Bodø) and Yakutia (Yakutsk).

Climatic parameters	Locations	
	Bodø	Yakutsk
mean annual temperature ($^{\circ}\text{C}$)	+4.6	-9.1
mean temperature in January ($^{\circ}\text{C}$)	+1.8	-38.6
minimum temperature ($^{\circ}\text{C}$)	-15	-64.4
degree days ($>10^{\circ}\text{C}$)	2550	1050
annual precipitation (mm/year)	1070	217
winter precipitation (mm)	315	27
number of days with snow	8	157
number of frost-free days	310	68

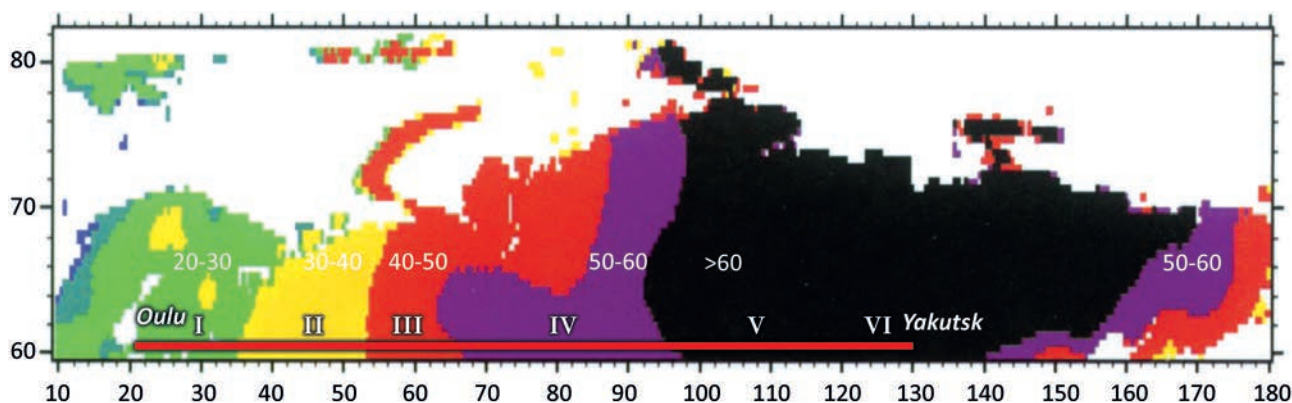


Figure 1 Conrad's index of continentality (0–100) and continentality sectors (I–VI, see explanation in the text) in the Eurasian North based on the 0.5° gridded monthly temperature data for the years 1991–1998). Red line is transect between Oulu and Yakutsk. Map is modified from Skre et al. 2002

compared with the Pacific (1100 km) and the prevalence of lowland territories, while the east of Yakutia is mostly represented by mountainous landscapes. The species richness of fungi was studied on a macroscale: in six sectors of continentality (approximately 100 000 km² each): I – maritime (Fennoscandia), II – subcontinental plain (Eastern Europe), III – subcontinental hills (Urals), IV – continental plain (Western Siberia), V – continental hills (Central Siberia), VI – ultracontinental (Eastern Siberia).

On the mesoscale, diversity was studied in 43 localities, each with an area of 100 km², nearly equally distributed in six continental sectors (Table 2). European sectors are smaller in area compared to Siberian ones. In this regard,

six to seven localities were studied in the European sectors, and eight in the Siberian sectors.

Temperature and humidity were estimated for four localities in each sector of continentality according to data from ten loggers (40 loggers in each sector) installed at the soil-litter contact in various sites in relief. Therefore, along the entire transect, we received data from a total of 240 loggers. In Table 1, the environmental parameters and the continentality index are calculated from the logger records.

The author develops the CLAVARIA WORD database, which includes information on the finds of clavarioid fungi in the world based on numerous personal collections, published data in the literature, herbarium materials from

Table 2 Longitudinal sectors, names, distribution and coordinates of 43 localities studied in the middle boreal zone of Eurasia (localities distributed along longitude)

No	Locality	Distribution	Coordinates
Sector I FENNOSCANDIA			
1	Oulu	Finland, Northern Ostrobothnia, surrounds of Oulu town	64°55'N 25°38'E
2	Hiidenportti	Finland, Kainuu, Hiidenportti National Park and its surrounds	63°52'N 29°00'E
3	Tolvoyarvi	Karelia Republic, Suoyarvi area, surrounds of Tolvoyarvi village, western shores of Tolvoyarvi lake	62°17'N 31°27'E
4	Kolatselga	Karelia Republic, Pryazhinsky area, surrounds of Kolatselga village	61°40'N 32°13'E
5	Veshkelitsa	Karelia Republic, Pryazhinsky area, surrounds of Veshkelitsa village	61°55'N 32°48'E
6	Kivach	Karelia Republic, Kivach Nature Reserve	62°15'N 33°59'E
Sector II EASTERN EUROPE			
7	Sheleksa	Arkhangelsk Region, Plesetsk area, surrounds of Sheleksa village	62°51'N 40°22'E
8	Ukhmenga	Arkhangelsk Region, Verkhnetoemski area, surrounds of Ukhmenga village	62°26'N 45°20'E
9	Vasilyevskoye	Arkhangelsk Region, Kotlas area, surrounds of Vasilyevskoye village	60°55'N 46°19'E
10	Fominski	Arkhangelsk Region, Vilegodski area, surrounds of Fominski village	61°16'N 48°44'E
11	Chukhlam	Komi Republic, Sysola area, surrounds of Chukhlam village	61°11'N 50°10'E
12	Keross	Perm Region, Gainy area, surrounds of Keross village	60°45'N 52°52'E
13	Pil'va	Perm Region, Cherdyn' area, surrounds of Pil'va village	60°50'N 55°52'E
Sector III URAL			
14	Kvarkush	Perm Region, Krasnovishersk area, eastern slope of Kvarkush Plateau	60°07'N 58°46'E
15	Ljaga	Komi Republic, Pechoro-Ilych Nature Reserve, surrounds of Ljaga cordon	62°28'N 58°58'E
16	Molebny Kamen'	Sverdlovsk Region, Ivdel area, eastern slope of Molebny Kamen' mountain	61°14'N 59°20'E
17	Konzhakovski Kamen'	Sverdlovsk Region, Karpinsk area, southern slope of Konzhakovski Kamen' mountain	59°36'N 59°15'E
18	Denezhkin Kamen'	Komi Republic, Severouralsk area, Denezhkin Kamen' Nature Reserve	60°26'N 59°29'E
19	Kumba	Sverdlovsk Region, Severouralsk area, southern slope of Kumba mountain	60°08'N 59°39'E
Sector IV WESTERN SIBERIA			
20	Ous	Sverdlovsk Region, Ivdel area, 62 km NE of Ivdel town	60°53'N 61°32'E
21	Pelymski Tuman	Sverdlovsk Region, Gari area, surrounds of Pelymski Tuman lake	60°05'N 62°58'E
22	Njagan'	Khanty-Mansi Autonomous District, Oktyabrsk area, surrounds of Njagan' town	62°03'N 65°32'E
23	Khanty-Mansiysk	Khanty-Mansi Autonomous District, surrounds of Khanty-Mansiysk town	60°59'N 69°03'E
24	Uim	Tyumen Region, Uvat area, 164 km E of Tobolsk town, surrounds of Uim village	58°51'N 71°07'E
25	Alexandrovskoye	Tomsk Region, Alexandrovskoye area, surrounds of Alexandrovskoye village	60°25'N 77°48'E
26	Sibirskiye Uvaly	Khanty-Mansi Autonomous District, Nizhnevartovsk area, Nature park "Sibirskiye Uvaly"	62°24'N 81°42'E
27	Bor	Krasnoyarsk Territory, Turukhansk area, surrounds of Bor village	62°17'N 89°07'E
Sector V CENTRAL SIBERIA			
28	Mirnoye	Krasnoyarsk Territory, Turukhansk area, Central-Siberian Nature Reserve, surrounds of Mirnoye village	62°14'N 89°12'E
29	Stolbovoy	Krasnoyarsk Territory, Evenkia, Central-Siberian Nature Reserve, surrounds of Stolbovoy cordon	62°07'N 91°30'E
30	Severo-Yeniseisk	Krasnoyarsk Territory, Severo-Yeniseisk area, surrounds of Severo-Yeniseisk town	60°23'N 93°02'E
31	Velmo	Krasnoyarsk Territory, Evenkia, surrounds of Velmo meteor station	60°51'N 94°02'E
32	Baikit	Krasnoyarsk Territory, Evenkia, surrounds of Baikit village	61°39'N 96°18'E
33	Vanavara	Krasnoyarsk Territory, Evenkia, Tungusky Nature Reserve	60°23'N 102°17'E
34	Strelka-Chunya	Krasnoyarsk Territory, Evenkia, surrounds of Strelka-Chunya village	61°44'N 102°49'E
35	Yerbogachen	Irkutsk Region, Yerbogachen area, surrounds of Yerbogachen village	61°18'N 108°02'E
Sector VI EASTERN SIBERIA			
36	Mirnyi	Yakutia Republic, Mirny area, surrounds of Mirny town	62°30'N 113°58'E
37	Suntar	Yakutia Republic, Suntar area, surrounds of Suntar village	62°13'N 117°41'E
38	Namana	Yakutia Republic, Olekma area, 25 km N of Olekminsk Balagannakh village	61°54'N 120°18'E
39	Biryuk	Yakutia Republic, Olekma area, 15 km N of Biryuk village	60°17'N 120°32'E
40	Kysyl-Syr	Yakutia Republic, Vilyu area, 20 km NW of Kysyl-Syr village	63°57'N 122°21'E
41	Buotoma	Yakutia Republic, Khangalas area, Lenskiye Stolby National Park	61°15'N 128°47'E
42	Yakutsk	Yakutia Republic, surrounds of Yakutsk town	62°00'N 129°41'E
43	Churapcha	Yakutia Republic, Churapcha area, surrounds of Churapcha village	62°01'N 132°28'E

various world herbaria. As of 01.04.2020, this base included more than 84,000 units accumulated worldwide.

Study sites description

Since the early 1990s, the Institute of Plant and Animal Ecology UB RAS (Ekaterinburg) in cooperation with other institutions of Russia and the World conduct annual mycological studies in Siberia as part of the International TRANS-Siberian mycological expedition (Shiryaev & Kotiranta 2015). Over a 30-years period, the middle boreal mycobiota has been studied best of all. But Siberia is vast and it is still problematic to visit each of its districts. Therefore, we developed a methodology for studying the spatial structure of mycobiota.

In general, the basic idea of approach was in unification of conditions of the material collection at each study site: the same number of collecting days (30), within the same total time period (within a period of the recent 20 years every study site is surveyed 3 times), the same area (100 km²). This gives a fairly clear picture of contemporary status of mycobiota. Therefore, it is possible to find how the actual diversity of fungi responds to the current climatic conditions. During the period of 20 years, dry and wet periods occurred repeatedly, and different fungi species responded to the wet periods by fruiting. Studies during the 3 years within 20 years time period increased a chance to catch the fruiting of the most species. This made possible to reveal the actual diversity of fungi under the current environmental and climatic conditions in particular locality nearly in full. The key points of the approach are described below:

1. Localities (area of 100 km²) for the study were chosen randomly and had the shape of a square (10×10 km), or a circle (radius 5.6 km). Variations of shape were allowed, for example, a rectangle (20×5 km). Ideally, each locality was explored for 30 days by one researcher in 3 visits in different years during the past 20 years. Also, analysis involved all published to date data, information from various databases and herbaria. The network of routes in each locality was laid out in such a way as to cover the entire variety of typical biotopes in the zonal habitats typical to the region (consequently, localities with strong human impact and prevailing intra-zonal biotopes were excluded).

At the next step, the data were analysed for completeness, and some localities were excluded from analysis by the following criteria: 1) if the number of samples collected on the site was not less than 90 % of the number of samples collected in the most well-studied study site in each continental sector; 2) if the largest area of study site was belonging to zonal habitat; 3) if the study site was not strongly affected by human activity. Localities not relevant to the above parameters are excluded from this study.

2. After the compilation, the potential list of species for each locality was verified. The following entries were excluded from the list: 1) recently described species 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, such as *Ramaria cistophila*, *Ramariopsis robusta*, *Typhula suecica*; 2) species with debatable taxonomic status: *Ramaria altaica*, *Pternula caricis-pendulae*; 3)

species found in intra- and extrazonal habitats, but not on the zonal habitats under zonal conditions; 4) found only in the anthropogenic habitats and/or on the alien plants.

Thus, the aim was not to complete list of species at the national or regional level, but to make the lists of localities studied comparable in terms of climatic controls of mycobiota. However, the lists of species of fungi identified for localities (excluding the species unsuitable for analysis) comprised 85–100 % of mycobiota at regional level: 85 % for the Republic of Yakutia, 91 % for the Komi Republic, 94 % for Khanty-Mansi Autonomous District, and 100 % for the Republic of Karelia.

The results of mycobiota inventory for individual localities were published (Shiryaev 2004, Shiryaev & Agafonova 2009, Kotiranta & Shiryaev 2015, Shiryaev & Kotiranta 2015, Shiryaev & Kudashova 2015, Shiryaev & Muzika 2015, Shiryaev & Ruokolainen 2017). The list of fungal species for each locality is presented in Table 3. The names of species and authors of taxa are given according to the IndexFungorum database (2020).

Study sites description

β -diversity was characterized using four parameters:

1) Whittaker index ($\beta_w = \gamma / \alpha - 1$) (Magurran 1988);
2) the average similarity for the species richness of fungi between all localities in each sector (Jacquard index, J) (Magurran 1988);

3) the speed of reaching the plateau of cumulative curves describing an increase in the number of species with an increase in the number of accounting units / individuals (the curves were approximated by the Michaelis-Menten (1913) equation, non-linear estimation), the rate constant is interpreted as the number of accounting units / individuals revealing half of all species of territory, i.e., the higher it is, the greater the β -diversity (CMM) (Trubina & Vorobeichik 2012);

4) species-area relationship, estimated as the specific species richness representing the bilogarithmic form of the “species-area” relationship (constant Z from the Arrhenius (1921) equation).

The calculations are performed in the program EstimateS 10.2.

RESULTS AND DISCUSSION

The climate continentality index increases from the maritime Fennoscandian climate to the ultracontinental Yakutian along the studied middle boreal transect (Table 4). In the maritime climate of Fennoscandia, the Conrad's continental index averages 24 %, while in the ultracontinental climate, it reaches 88 %. The range of parameters within these continental sectors increases 2.5 times (from 19 % to 51 %). Moreover, the maximum and minimum indicators differ almost 6 times (from 17 % to 100 %). With an increase in the climate continentality, the mean annual temperature decreases. In study sites located in the maritime Fennoscandian climate, the mean annual temperature is +3.5°C, but in the ultracontinental climate – only -7.2°C, i.e., 10.7°C lower. It is equally important that the range of values between the minimum and maximum temperatures increases: in the maritime climate, the range is 33.9°C, and

Table 4 Distribution parameters of clavarioid fungi communities in the six sectors of climatic continentality of middle boreal subzone. Ic – continentality index; T – temperature; RH – relative humidity; D – distance between localities; γ -diversity – total number of species; α -diversity – average number of species in localities; β_w – Whittaker index; SD – standard deviation; CV – variation coefficient; LV – differences between the richest and poorest locality; J – Jaccard index; R – linear correlation coefficient between J and D (* – $p < 0.01$; ns – $p > 0.05$); C_{MM} – Michaelis-Menten equation (\pm standard error); Z – Arrhenius equation; N disappeared / appeared – number of species when moving to the next sector. All are mean parameters; in parentheses – minimum-maximum.

Parameter	Climate continentality sector					
	I	II	III	IV	V	VI
Ic. %	24 (17–36)	35 (30–53)	49 (37–62)	62 (48–79)	72 (50–87)	88 (49–100)
T. °C	3.5	2.2	0.5	-1.1	-4.0	-7.2
T max./min. °C	23.4 / -10.5	27.4 / -19.6	29.8 / -25.1	30.5 / -29.8	32.9 / -35.7	34.5 / -40.0
RH. %	83 (62–100)	77 (56–100)	80 (45–100)	77 (48–100)	70 (42–98)	66 (29–97)
area LK. km ²	600	700	600	800	800	800
D	189 (83–580)	353 (81–850)	140 (35–321)	542 (120–1518)	399 (44–874)	316 (58–769)
γ -diversity	97	90	95	81	72	59
α -diversity	65.3 (59–74)	60.7 (57–66)	68.0 (62–74)	56.1 (45–62)	49.2 (42–60)	27.5 (18–45)
β_w	0.48	0.48	0.39	0.44	0.46	1.14
SD	5.3	3.9	4.4	4.0	5.6	8.5
CV. %	8.3	6.1	6.5	7.1	11.4	30.9
LV. %	25.4	15.8	19.3	15.4	42.8	138.9
J	0.61 (0.69–0.55)	0.65 (0.73–0.59)	0.59 (0.69–0.51)	0.69 (0.79–0.55)	0.54 (0.64–0.40)	0.30 (0.46–0.20)
R	-0.38*	-0.35*	-0.30*	-0.31*	-0.25*	-0.02 ^{ns}
C_{MM}	238 \pm 19	257 \pm 25	252 \pm 28	244 \pm 32	289 \pm 40	398 \pm 56
Z	0.10 (0.08–0.12)	0.08 (0.06–0.10)	0.10 (0.08–0.12)	0.07 (0.06–0.09)	0.11 (0.08–0.13)	0.15 (0.13–0.18)
N disappeared		8	1	15	10	14
N appeared		1	6	1	1	1

mate (Kivach), while in the poorest one, located in the ultracontinental sector (Churapcha), 4.1 times less species are identified (18). Between European sectors of continentality (I–III), with a maritime and subcontinental climates, the diversity of clavarioid fungi does not change significantly (74–57 species: the difference is 1.3 times only). Moreover, the α -diversity within the Siberian continentality sectors (IV–VI) varies in a much wider range (from 18 to 62 species: the difference is 3.5 times). The border of a sharp separation of the species richness level for local fungal communities is located between the Urals and Western Siberia (Fig. 2). Therefore, results of the above multiscale studies of mycobiota showed that, as continentality increases, the number of species decreases for both scales, but the rate of decline is different. Thus, the γ -diversity is reduced 1.6 times (from 97 to 59 species), and the α -diversity drops 2.4 times (from 65.3 to 27.5 species), that indicates a high spatial unevenness of the process of species elimination at different spatial scales, namely, a faster decrease in species richness at the meso- compared to the macro-level.

Since γ -diversity decreases more slowly compared to α -diversity, the Whittaker's index in the ultracontinental sector is almost 3 times higher than in the maritime sector. The average similarity of species composition in Fennoscandia is 1.7–3.5 times lower than in Yakutia, and individual species richness increases 1.8–3.0 times, which also indicates a significant increase in β -diversity. The number of species in ultracontinental localities varies within a very wide range, therefore, differences between localities reach a maximum of 139 %, which is almost an order of magnitude higher compared to European sectors (15–25 %). Also in Yakutia, the coefficient of variation reaches maximum values (31 %) being 5 times more than its European counterparts. These examples indicate an extremely high spatial unevenness of the process of species extinction. The level of differences in the rate of cumulative

curve output on the plateau is similar: in the ultracontinental sector, half of all species require a 1.7–2.5 times higher selective effort to be applied than in the marine sector, which is characterized by optimal climatic conditions.

Regardless of the assessment method, as continentality increases, β -diversity grows by 1.7–5 times. Some localities in Yakutia have a Jaccard similarity index of only 0.20, despite the small distances between them. The correlation of the similarity index with the distance between the localities weakens as climate continentality grows, and in the ultra-

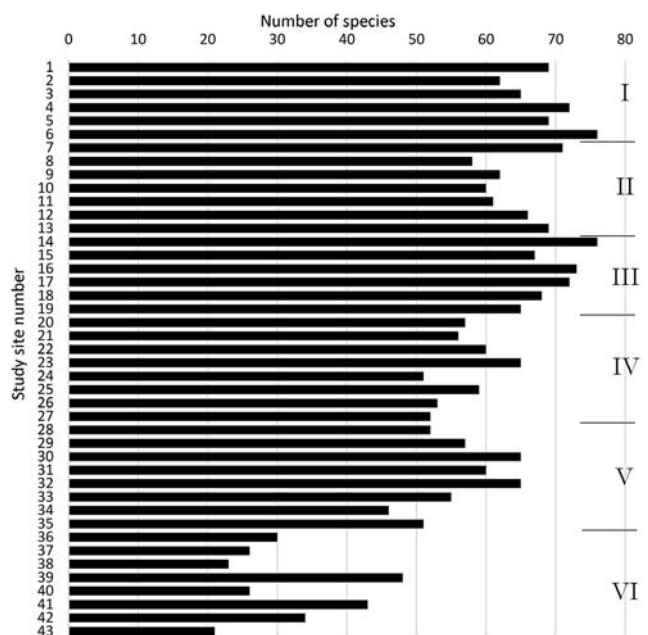


Figure 2 Species richness of clavarioid mycobiota in the 43 studied localities in the middle boreal subzone of Eurasia. Number of localities (1–43) and longitudinal sectors (I–VI) according Table 2. Localities are distributed along the increasing continental climate

continental sector, it is completely absent, which confirms the mosaic nature of the mycobiota transformation and indicates an increase in the spatial isolation of local fungal communities.

The growth of climate continentality and heterogeneity of the environment play a key role in the formation of fungi diversity in ultracontinental Yakutia. It would seem that the ultracontinental East Siberian cryosemiaride climate (Nazimova & Polikarpov 1996), with the widespread distribution of permafrost, boggy, and saline soils, with a wide spread of steppe landscapes, and a significant lack of rain moisture, should not support the existence of rich mycobiota. Nevertheless, on the hills, the soil warms up enough, which leads to thawing of permafrost, and the released moisture contributes to the development of a variety of rich boreal vegetation and mycobiota. Thus, within the cryosemiarid landscapes of Yakutia, extremely depleted areas unsuitable for the development of clavarioid fungi are adjacent to, and interspersed with relatively rich biotopes that ensure the existence of a wide range of species, although their number is reduced compared to the “optimal” conditions. This is confirmed by the fact that on the Prilensky Plateau of Central Yakutia, there are a number of localities (Buotoma, Biryuk), in which the level of species richness corresponds to the average richness of localities of Middle Siberia including the most heat-sufficient ones. Therefore, even in extreme conditions, some individuals are preserved in the “fragments” of suitable habitats, where, for various reasons, the conditions remain relatively favorable. A similar trend was found in tundra and forest-tundra zones, where the growth of β -diversity is 1.3–3.1 times (Shiryayev 2017, 2018). This growth of β -diversity due to increasing spatial heterogeneity of environmental conditions occurs in other gradients, for example, latitudinal, altitude, and also when industrial pollution increases (Mukhin 1993, Trubina & Vorobeichik 2012, Ordynets et al. 2018).

CONCLUSIONS

The initial hypothesis about the homogenization of the species composition of clavarioid fungi in the continental gradient was not confirmed: the rigidity and heterogeneity of the environmental conditions of the ultracontinental sector causes a decrease in the α - and γ -diversity of the fungal communities, but the β -diversity increases, which can be interpreted as differentiation of the fungal communities. These results indicate that an increase in the harshness of conditions in the ultracontinental Yakutian sector leads to a sharp increase in the spatial isolation of local fungal communities on the mesoscale and almost complete loss of mycobiota integrity for clavarioid fungi on a macroscale.

ACKNOWLEDGEMENTS

We thank the Russian Foundation for Basic Research (project № 18-05-00398 A) for financial supported.

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