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Spatial diversity of clavarioid mycota (Basidiomycota) at the forest-tundra ecotone

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ABSTRACT

The article studies the change of clavarioid mycota species richness along the longitudinal gradient of climatic continentality in the forest tundra ecotone of Eurasia and the results are discussed for continental and regional levels using the basic climatic variables. It was found that species richness declines, both continentally and regionally, with climate continentality increasing. The Fennoscandian sector situated in the mild maritime climate is the richest, whereas Yakutia, with an ultracontinental harsh climate is the poorest. Strong positive correlations were found between species richness and mean annual temperature and precipitation. On the other hand, spatial turnover of species, or beta diversity, has a negative correlation with the macroclimatic gradient. There are European sectors, where clavarioid mycota associating with the birch and pine-spruce open woodlands have high similarity with their boreal variants, whereas in Siberian sectors, east of the Yenisei River, where mycota is associated with larch and cedar elfin bushes, the similarities are more akin to tundra variants. At the continental scale, there is no reliable relationship between mycota diversity with the flora richness and soil pH, but the permafrost thickness is significantly correlated with the studied levels of the clavarioid mycota diversity.

1. Introduction

Arctic areas are among the most vulnerable habitats and are exposed to some of the greatest changes that are occurring due to current global climate change. Over the past 15 years, abundant data have demonstrated both “greening of the Arctic” and significant changes within the forest-tundra ecotone (FTE) (Hofgaard, Harper, & Golubeva, 2012; Walker et al., 2012; Yurtsev et al., 2004). The selection of groups of organisms, which may act as “models” for monitoring changes in high-latitude biota, will contribute to a more qualitative assessment of these climate changes. Such studies have already been conducted for various groups of plants and animals (Gaston, 2000), but fungi were not included, mainly due to the limitations of our knowledge on their distribution. However, over the past decade, there has been increased interest in global trends for fungal biodiversity (Peay, Kennedy, & Talbot, 2016; Tedersoo et al., 2014), and a lot of fresh information has been generated from the Arctic regions (e.g., Shiryaev, 2013a, 2015a; Zmitrovich & Ezhov, 2015). The study of FTE mycota over the course of the last century (Dahlberg et al., 2013) has permitted the accumulation, for some fungal groups, of data on spatial differentiation, and how this is affected by anthropogenic impact and climate change (Mukhin, 1993; Shiryaev, 2014).

Aphyllophoroid fungi (Basidiomycota) are an important group of wood and litter decomposers in Northern Eurasia. Corticioid and poroid fungi are the richest life forms of aphyllophoroids in the nemoral and boreal forests, while in the high-latitude treeless regions the woody substrates they require are absent. In such habitats, clavarioid fungi is one of the richest groups of aphyllophoroids, more suited to the conditions of the Eurasian Arctic (Shiryaev & Mukhin, 2010; Shiryaev, 2012), as most species produce basidiomes on soil and different types of litter. Moreover, only species of clavarioid life-form can produce basidiomata in both the native conditions of the arctic deserts and in the Eurasian High Arctic (Shiryaev, 2014, 2015a). Of aphyllophoroid fungi, the clavarioids are the most adaptable to withstand the coldest areas of the temperate global gradient. The genera *Typhula* and *Multiclavula*, with sclerotioid and basidiolichen life strategies, respectively, are the most adaptive of all aphyllophoroids to the harsh conditions of the High Arctic. In general, clavarioid species richness is relatively high, based on studies in the forest zone of Northern Eurasia, where they are recognized as good indicators of anthropogenic disturbance and climate change (Shiryaev, 2014).

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In general, clavarioid fungi (the so-called coral-fungi and club-fungi) spread on all continents, from the polar deserts and alpine glaciers to the tropical deserts and equatorial rain forests. This group contains about 660 described species (Index fungorum, 2017). They are macromycetes, characterized by bright, large-sized visible basidiomes, reaching 20 kg and 0.6 m in diameter (species of the genus *Sparassis*), which can be preserved for a long time in herbaria. Clavarioids combine three major functional groups of fungi: parasites, saprotrophs and symbionts (including mycorrhizal and "basidiolichens"), thereby participating in the key processes of the biosphere (e.g., soil formation and nutrient cycling), and are basic species of primary succession, as well as pathology. Clavarioid fungi are phylogenetically polyphyletic group (Hibbett et al., 2007). There are 38 genera (the richest are *Ramaria*, *Typhula*, *Clavaria*) of Agaricomycetes with clavarioid-form basidiomes worldwide (Shiryaev, 2014). Several genera also have clavarioid-like basidiomes, but genera *Tremellodendropsis* and *Calocera* are heterobasidioid fungi. Such taxa were excluded from this study.

The spatial variation of fungal diversity is traditionally carried out on latitudinal or altitudinal gradient, while longitudinal gradients of continentality, although exhibiting clear patterns of change, are rarely used in mycogeographical studies. Our studies reveal that in the forest zone of Northern Eurasia, latitudinal and longitudinal changes in species richness and eco-morphological structure of clavarioid mycota are relatively similar (Shiryaev, 2014). These results demonstrate that clavariod fungi could be a convenient model group for the study of spatial differentiation of mycota.

The main goal of this work is to estimate the diversity of clavarioid mycota in longitudinal sectors of Eurasian FTE and to establish the basic bioclimatic parameters by which it is determined. Additional questions addressed were whether clavarioid mycota in the FTE were more similar to those present in the taiga or the tundra.

2. Materials and methods

2.1. Investigated area and bioclimatic parameters in the longitudinal sectors of the Eurasian forest-tundra

The FTE at the north of Eurasia stretches from the Atlantic to Pacific oceans shores (Ermakov & Bohn, 2011; Walker et al., 2005). In Europe it is situated at about 70° N (northern Norway) and crosses Eurasia to Pacific areas (at 60° N, northern Kamchatka), traversing about 6670 km.

The climate of the FTE is characterized by great changes in the longitudinal direction, in particular in the areas with the oceanic and ultracontinental climate (Rivas-Martinez, Rivas Saenz, & Penas, 2011), for example between Arctic parts of Fennoscandia and Yakutia. The subarctic part of Yakutia has the lowest temperature in the northern hemisphere (−71 °C), causing this area to be named "the pole of cold", being the coldest permanently inhabited area of the world. Here also exists the highest difference between the maximum and minimum temperatures (about 107 °C) (Stepanova, 1958). These parameters reflect the most continental climate on the Earth (Borisov, 1959). Climatic continentality measured as Conrad's index of continentality (Oliver, 2005), reflects the difference between the mean annual temperature of the hottest (July) and coldest month (February) with correction to latitude. This index has a maximal parameter (100%) in the most inner continental part, to zero level in the hyperoceanic climate. In the Eurasian FTE, this parameter ranges from 72% in the Northern Yakutia to 14% in Fennoscandia.

An increasing index of continentality reflects the combination of climatic factors (Borisov, 1959), like the decrease in mean annual temperature and precipitation, lowest temperature and thickness of permafrost, which leads to a change in the type of vegetation (Table 1): from the closed mixed forests of conifers (*Pinus* and *Picea*) and broad-leaved trees (*Betula*) with humid climate in the maritime climate of Fennoscandia to the open *Larix* and *Pinus pumila* (Pall.) Regel bushes with cryo-semiarid climate, with tundra-steppe looking mesoxerophilous grasslands in ultracontinental Yakutia (Ermakov & Bohn, 2011). The lowest level of precipitation for the ultracontinental climate is in forest-tundra, which is similar to the steppe and temperate/tropical semideserts, as well as the lowest level of air humidity (69%). Variation in mean annual temperature and precipitation also increases with continentality. Such big climatic changes allow us to divide the FTE into 7 longitudinal sectors (Fig. 1).

2.2. Sample collection

There are 2 scales used in this study of spatial structure of clavarioid mycota: longitudinal sectors by 100,000 km^2 (mean size), and localities (100 km^2) distributed inside the same sectors. There are 37 localities studied inside the 7 longitudinal sectors (Supplementary Table S1): 6 localities are in the Atlantic (Fennoscandia) and Pacific Ocean sector (Chukotka) and 5 in each of the continental sectors (Kanin-Pechora, the Urals, Yamal-Gydan, Taimyr, Yakutia) (Fig. 1). Fungal species found only on the human-modified territories were excluded from this work. There is some information on species richness for localities and longitudinal sectors in the following articles: Shiryaev (2006, 2008, 2009, 2011, 2013a, 2013b, 2013c, 2014), Kotiranta and Shiryaev (2013), Shiryaev and Mikhaleva (2013).

Each longitudinal sector was studied for at least 15 years. In localities, in the ideal case, specimens were sampled during 3 years by different collectors. We used the parameter of 90% of species richness from the best studied locality as a measure to estimate the lowest level for the number of collection records needed from each locality. For example, from the best studied locality of Fennoscandia (Russia, Murmansk province, Pechenga area, Santajarvi, 69°30′N, 31°20′E), there are 47 species (Supplementary Table S2) represented by 450 collection records (specimens, photos and notes in diaries), 90% of this species richness is 42.3 species and accordingly based on the species richness rarefaction curve (Fig. 2), at least 239 records needed to be collected per locality for this sector of continentality. This parameter applies to the sector situated in the mild climate of the Eurasian FTE, because of the warming impact of the Gulfstream, but for the harsh ultracontinental climate of Yakutia (Ust'-Yana area, locality Ust'-Kuyga, 70°00′N, 135°36′E) also, at least 308 records were necessary to be collected in Yakutia, but this number represents only 25.2 species. For comparison, at least 30 collection records were needed from the arctic deserts and 210 from the southern shrub tundra (Shiryaev, 2015a).

2.3. Data analysis

Results were obtained using programs STATISTICA 8.0 (StatSoft, 2008) and EstimateS 9.10 (Colwell & Elsensohn, 2014). A non-parametric Mann-Whitney *U* test was used to detect significant differences in the number of species in localities distributed by different longitudinal sectors. There is Spearman's rank correlation coefficient (r_s) measured for study correlation between species richness and bioclimatic and soil-type parameters.

Several taxonomic parameters were estimated, e.g., total number of species in each longitudinal sector (γ-diversity); number of species within a locality; mean number of species per locality (α-diversity). The degree of changes in species composition along