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The local populations of the fungus *Schizophyllum commune* Fr. as drivers of its biodiversity

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Abstract

Changes that occur on the local level can explain the processes on the population level and, at the same time, are the driving force of species adaptation. This manuscript reports data about genetic diversities of the fungus *Schizophyllum commune* on the level of a local population. Objects of the study were dicarious cultures of *S. commune* collected from 38 basidiocarps grown on the territory of Holosiivskyi National Nature Park, Lysa Hora Regional Landscape Park and Feofaniya forest parcel (Ukraine). Results showed similarity of genetic variability of *S. commune* in different local populations. The heterozygote deficiency of some loci that was discovered might have resulted from new forms of allozymes that have not become widespread or due to small population sizes. The degree of differentiation of genes between local studied populations was moderate due to the high flow of genes. The absence of spatial structuration of genotypes is established, and the Mantel test showed a lack of interconnection between the genetic component and the geographical coordinates of the samples. It has been suggested that wind direction and terrain are the factors that influence the genetic structure of local populations.

Key words

Schizophyllum commune, gene drift, genetic structure, local populations, terrain

Introduction

Understanding the regularity of genetic diversity in fungi is a fundamental problem that is associated with the development of strategies for their preservation (Urbanelli et al. 2003). Longest genetic distances correspond to a subdivision of the Eastern and Western Hemisphere, within which the population's structure exists. For fungi species with the sex cycle and a big population size, genetic variation is very high, and most of the variations are observed within the population. In the last decades, using molecular markers has allowed to establish geographical limitation of gene flow for some fungi (Garbelotto et al. 1993; Hibbett et al. 1995; Kauserud and Schumacher 2003). Density and genetic diversity significantly vary for some fungi. It suggests that their dissemination is not limited only by the ability to spread the spore mass. The idea of global fungi distribution only by spores is not correct, and human intervention plays a significant role in fungi spreading (Fry et al. 1992; Maurice et al. 2014).

Schizophyllum commune is a xylotrophic cosmopolitan fungus. In most cases, it settles on dead wood and can be found on weakened live wood (Raper 1988).

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Its genetic variability allows discriminating substructures in common, widespread populations (James et al. 1999). The widespread growth of *S. commune* enables researchers to collect the required number of samples on the local population level. The use of *S. commune* as a model object in population studies will make it possible to find rare genotypes and identify factors that contribute to the isolation process with possible further interpolation of the results to other species. Very frequently, changes that occur on the local level can explain the processes on the level of population.

According to literature data, the stands of Holosiivskyi National Nature Park (HNNP), Lysa Hora Regional Landscape Park (LHRLP) and Feofaniya forest parcel (Ffp) were continuous forests in the 17th century (Netsvetov and Prokopuk 2016). The settlement of surrounding areas started in the second half of the 19th century and continued till the beginning of the 20th century. In the 1960s–1970s, boundaries of HNNP and Ffp were separated by a part of Great Ring Road. LHRLP was separated from HNNP by the overpass and developed living area. Based on this, at least for the last 50–60 years, the described region has not been a continuous forest because of anthropogenic factors, and therefore is an important object for population studies. The unique conditions of partial geographical isolation over a long period of time make it possible to research the possible genetic differentiation of the model fungus *S. commune*.

The study's goal was to establish genetic differentiation of local populations of the fungus *S. commune* in partially isolated areas with complex terrain.

Material and methods

Sample collection

Objects of the study were the dikaryotic cultures of *S. commune* collected from 38 basidiocarps grown on the territory of HNNP, LHRLP and Ffp in Ukraine (Fig. 1). Isolation of pure dikaryotic cultures was performed as follows: precleaned basidiocarp was cut into pieces 3 ´ 3 mm in size, which were transferred by a sterile mycological hook to 8% H_2O_2 solution and incubated for 1–2 min. The treated fragment was placed in a tube with potato agar, and, after the appearance of pure fungus mycelium, reinoculation on a pure nutrient media was performed. Monokaryotic cultures were obtained in aseptic conditions as previously described (Boiko 2018b).

Figure 1. The local populations of *Schizophyllum commune* (1 – Holosiivskyi National Nature Park, 2 – Lysa Hora Regional Landscape Park, 3 – Feofaniya forest parcel)

Incubation procedure

The obtained cultures were grown superficially on a liquid glucose-peptone nutrient medium of the following composition (g L^{-1}): glucose – 10.0, peptone – 3.0, K_2HPO_4 – 0.4, $MgSO_4 \times 7H_2O$ – 0.5, $ZnSO_4 \times 7H_2O$ – 0.001 and $CaCl_2$ – 0.05. The medium was poured into 100-mL Erlenmeyer's flasks by 25 mL. The starting pH level of the nutrient medium was 5.0, and cultures were cultivated at 28°C for 14–15 days.

Enzymatic profile

For histochemical studies, the mycelium was prepared in the following way: triple washed in distilled water, dried using vacuum filtration, homogenised in the Tris-citrate buffer and filtered. Protein concentration was determined spectrophotometrically using ULAB S131UV (Layne 1957). The amount of protein loaded into each well for electrophoresis ranged between 40 and 60 μg. Electrophoretic separation of intracellular proteins was

done in 7.5% and 11.25% polyacrylamide gel (PAAG) using tris-glycine buffer (pH 8.3). Polymorphic enzymatic systems (Boiko 2015, 2018a) were used as genetic markers for the fungus *S. commune* and included catalase (CAT) (EC 1.11.1.6), glutamic-oxaloacetic transaminase (GOT) (EC 2.6.1.1), a-amylase (AMY) (EC 3.2.1.1) and endo-1.3(4)-β-glucanase (EG) (EC 3.2.1.6) (Manchenko 2003). Gel documentation was done using AlphaImager 2200 (Alpha Innotech). The processing of electropherograms was done using TotalLab TL 120 software.

Statistical analysis

The genetic diversity of the population was characterised based on allele frequency, average number of alleles per locus (A), effective number of alleles (A_E), Shannon's diversity index (I), observed and expected heterozygosity (H_o and H_e), Wright's fixation index and an F-statistic (Nei 1978). For each locus, the Ewens–Watterson test for neutrality was performed to identify possible selection effects (10,000 imitations) (Manly 1985). Principal Coordinates Analysis (PCoA) is a multivariate technique that allows one to find and plot the major patterns within a multivariate dataset. PCoA is a process by which the major axes of variation are located within a multidimensional data set. For multidimensional data sets, each successive axis explains proportionately less of the total variation. The procedure is based on an algorithm published by Orloci (1978). All computations were done using the POPGENE32 and GenAlEx 6.5 software (Yeh and Boyle 1997; Peakall and Smouse 2006). Topographic maps were generated using QGIS 2.18 software.

Results

The locations of *S. commune* basidiocarp collection are separated from each other. The distance between HNNP (1) and Ffp (3), that is, between the nearest samples from both stands, was 0.7 ± 0.05 km, and the distance between HNNP (1) and LHRLP (2) was 1.2 ± 0.05 km. The genetic diversity of fungi is illustrated by indices that are calculated individually for each artificial local population and the general population (Tab. 1–3). For the HNNP population, locus *Eg2* was represented only by allele $Eg2^{100}$, and in LHRLP appeared allele $Eg2^{93}$ with the frequency 0.056 (Tab. 1).

Table 1. Frequency of *Schizophyllum commune* alleles in studied populations and in total.

Locus	Allele	HNNP (1)	LHRLP (2)	Ffp (3)	Total
Eg2	$Eg2^{102}$	0.000	0.000	0.385	0.132
	$Eg2^{100}$	1.000	0.944	0.615	0.855
	$Eg2^{93}$	0.000	0.056	0.000	0.013
Amy2	$Amy2^{110}$	0.156	0.111	0.000	0.092
	$Amy2^{107}$	0.000	0.056	0.115	0.053
	$Amy2^{100}$	0.813	0.667	0.846	0.789
	$Amy2^{95}$	0.031	0.167	0.038	0.066
Cat	Cat^{107}	0.000	0.000	0.077	0.026
	Cat^{100}	0.656	0.722	0.846	0.737
	Cat^{97}	0.188	0.222	0.038	0.145
	Cat^{86}	0.156	0.056	0.038	0.092
Got	Got^{100}	0.844	0.944	0.923	0.895
	Got^{84}	0.125	0.056	0.077	0.092
	Got^{null}	0.031	0.000	0.000	0.013

For Ffp, in addition to allele $Eg2^{100}$, allele $Eg2^{102}$ was observed with the frequency 0.385. For locus *Amy2,* four alleles were found; however, allele $Amy2^{107}$ was not detected in the HNNP population and allele $Amy2^{110}$ in the Ffp population. Despite being rare, allele $Amy2^{95}$ was found in all researched locations. For locus *Cat,* we observed striking differences in allele frequencies depending on the location. Specifically, allele Cat^{107} was found only in the fungi of Ffp. In addition, the frequency of Cat^{97} was relatively high in the HNNP and LHRLP populations (0.188 and 0.222, respectively), but significantly decreased in Ffp (0.038). Locus *Got* showed a relatively similar profile of allele frequencies in different populations, except that allele Got^{null} was observed only in the HNNP. Taking into account only dominant alleles, we observed a significant decrease in the frequencies of locus *Eg2* in the Ffp population (0.615), locus *Amy2* in the LHRLP population (0.667) and locus *Cat* in the HNNP population (0.656). In general, the rarest alleles were $Eg2^{93}$ and Got^{null} with a frequency of 0.013.

The average number of alleles per locus was from 2.5 (HNNP) to 2.75 (LHRLP and Ffp) (Table 2). The effective number of alleles, Shannon's diversity index and expected heterozygosity were not significantly oscillating in the studied populations. The difference

was bigger for observed heterozygosity. For all local populations, a lack of heterozygotes was observed; it was lowest in the Ffp, which is supported by H_o and F indexes. Of note, in the LHRLP population of *S. commune,* the lack of heterozygotes is insignificant and by all indexes of genetic variability has the highest rankings (Tab. 2).

Determination of the genetic distance between studied populations was conducted using F-statistic (Tab. 3). We found that a lack of heterozygotes was observed on the population level for some loci, and it can be a result of the inbreeding process (F_{is} = 0.323). It is highly influenced by *Eg2* and *Cat* loci. We previously reported similar results for *Eg2* locus on the territory of Ukraine (Boiko 2018b). Also, the uneven distribution of alleles for this locus is a characteristic feature of not only large territories, but also of local populations.

Table 2. Genetic variation of fungus *Schizophyllum commune* in local populations and in total

Local population	Locus	n	A	A_e	I	H_o	H_e	F
HNNP	*Eg2*	16	1.000	1.000	0.000	0.000	0.000	N/D
	Amy2	16	3.000	1.459	0.567	0.250	0.314	0.205
	Cat	16	3.000	2.040	0.880	0.313	0.510	0.387
	Got	16	3.000	1.373	0.512	0.250	0.271	0.079
	Average	16	2.500	1.468	0.490	0.203	0.274	0.224
LHRLP	*Eg2*	9	2.000	1.117	0.215	0.111	0.105	–0.059
	Amy2	9	4.000	2.051	0.974	0.556	0.512	–0.084
	Cat	9	3.000	1.742	0.730	0.222	0.426	0.478
	Got	9	2.000	1.117	0.215	0.111	0.105	–0.059
	Average	9	2.750	1.507	0.533	0.250	0.287	0.069
Ffp	*Eg2*	13	2.000	1.899	0.666	0.000	0.473	1.000
	Amy2	13	3.000	1.368	0.516	0.308	0.269	–0.143
	Cat	13	4.000	1.380	0.589	0.077	0.275	0.720
	Got	13	2.000	1.166	0.271	0.154	0.142	–0.083
	Average	13	2.750	1.453	0.511	0.135	0.290	0.374
Total		12.7	2.667	1.476	0.511	0.196	0.284	0.222

A – average number of alleles per locus; A_e – effective number of alleles;
I – Shannon's diversity index; observed (H_o) and expected (H_e) heterozygosity;
F – Wright's fixation index.

Table 3. Parameters of *Schizophyllum commune* populations structure according to F-statistic

Locus	F_{is}	F_{it}	F_{st}	N_m
Eg2	0.808	0.855	0.244	0.773
Amy2	–0.016	0.028	0.043	5.546
Cat	0.495	0.515	0.039	6.091
Got	0.007	0.023	0.017	14.710
Average	0.323	0.355	0.086	6.780

Importantly, the same *S. commune* cultures showed a balanced level of heterozygotes at *Amy2 and Got* loci on the population level (F_{is} was –0.016 and 0.007, respectively), which excluded the significant influence of the inbreeding process. Therefore, the lack of heterozygotes at the mentioned loci can be a result of new and rare allozymes or a small population size.

In the aggregate sample of populations, a single basidiocarp revealed a lack of heterozygotes on 35.5%. The degree of differentiation of genes between experimental populations relative to the frequencies of alleles (F_{st}) was average and indicated that 91.4% of the entire genetic diversity can be found within each population. This is the evidence for a certain genetic separation among the studied populations. Among the polymorphic loci, the greatest contribution to the interpopulation component of variability was made by the locus *Eg2* (F_{st} = 0.244). The data we obtained indicates a relatively high gene flow among local populations (N_m = 6.78), and a significant contribution to this index was made by the *Got* locus. Low genetic diversity and high gene flow are observed in populations that are supported by the spread of spores.

Many factors lead to a disturbance of equilibrium in nature (Maurice 2014). In the *S. commune* populations, for each enzyme system, we determined the actual distribution of genotypes to the expected by Hardy–Weinberg principle. For the loci *Eg2* (Ffp) and *Cat* (HNNP and Ffp), the Hardy–Weinberg equation was violated, which indicates that they are influenced by factors that cause deviation of

allele frequencies. The possible reasons are aforementioned.

Calculation of genetic distance according to Nei and cluster analysis (UPGMA algorithm) allowed us to determine the isolation of Ffp (3) from HNNP (1) and LHRLP (2). The geographical distance between Ffp (3) and HNNP (1) is almost twofold less than between HNNP (1) and LHRLP (2). PCoA, which shows the interconnection of samples by genetic material, determined isolation of the Ffp cultures (Fig. 2). Of note, this exact population of Ffp makes the greatest contribution to the diversity of the first main coordinate.

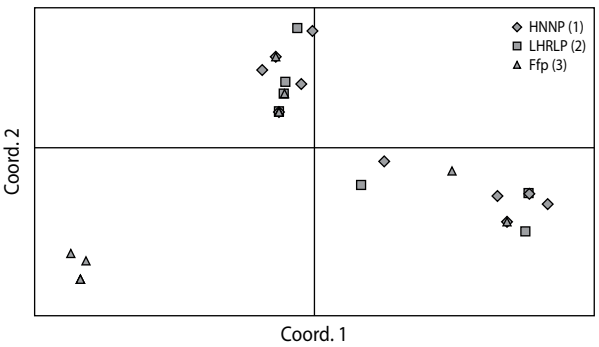

Figure 2. The position of *S. commune* cultures from locations in the space of the first two principal coordinates

Ewens–Watterson test on neutrality for each locus showed that the frequency of alleles at all loci was selectively neutral and the F values were within 95% of the expected value (Tab. 4). Spatial structure is an important characteristic for a particular population and is a result of the interaction among many components. To determine the geographical isolation of the studied populations, the Mantel test was conducted. As a result, it can be reasonably argued that the null hypothesis was true (R^2 = 0.0016); there was no interconnection between the genetic component and the geographical coordinates of the studied samples.

Table 4 Ewens-Watterson test on neutrality for *S. commune* loci

Locus	n	k	Obs. F	SE*	L95*	U95*
Eg2	76	3	0.7490	0.0309	0.3653	0.9484
Amy2	76	4	0.6389	0.0278	0.3044	0.8985
Cat	76	4	0.5731	0.0277	0.3051	0.8985
Got	76	3	0.8092	0.0310	0.3653	0.9484

Obs. F – sum of squares of observed allele frequencies; SE – standard error; L95 and U95 – lower and upper limits of 95% confidence interval; * denotes statistics calculated for 100000 simulations.

Considering that the distance between populations is relatively small, we conducted the spatial structure analysis, which establishes the correlation of the genotypes' diffusion in space (Fig. 3).

Except for the locus *Eg*, no correlations were detected. A positive probabilistic correlation was observed within 0.049–0.056 interval and negative probabilistic correlation within 0.028–0.035 interval. The absence of a general correlogram trend may indicate an accidental peak. Considering that the positive correlation found mainly concerns cultures from HNNP and LHRLP, and that HNNP is represented only by the allele $Eg2^{100}$, we think this is exactly the reason for this maximum.

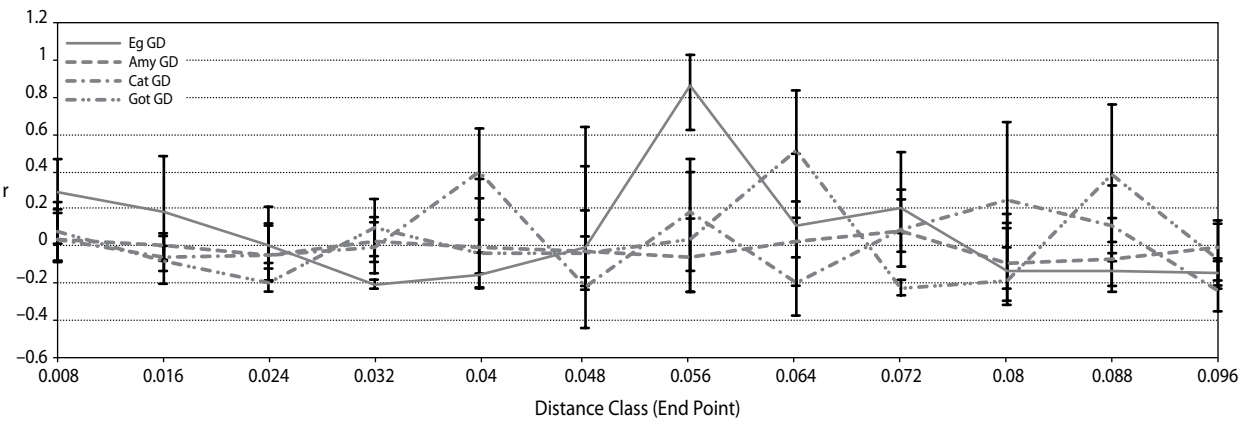

Figure 3. Correlograms of different *S. commune* loci

A similar trend was observed with a probabilistic negative correlation for basidiocarps from HNNP and Ffp. Based on this, it can be argued that no genotype structure was observed at the studied locations.

Discussion

In our research, we considered three artificial local populations. The critical question arising is: what will we observe if this is a single population? Applying UPGMA analysis to allele frequencies data, experimental cultures were divided into three clusters (Fig. 4). The first cluster, the most distant, was solely formed by fungi from the Ffp; the second cluster was formed by cultures from the HNNP (67%), LHRLP (22%) and Ffp (11%); and fungi forming the third cluster were from the HNNP (43%) and the other two locations (28.5% each). Of course, due to migration and drift of genes, there was no clear separation of genotypes by growth area, especially at small distances, but certain isolation of cultures was observed.

Cross-breeding system and gene flow are the main factors that determine the genetic structure of fungal populations. Considering that *S. commune* has a tetrapolar cross-breeding system that greatly prevents inbreeding (James et al. 1999), the main contributor to the population's local genetic profile is the process of gene migration and drift. The genetic drift effect is greatest in small populations and lowest in largest populations.

For fungi, the basis for these processes is the dissemination of spores. Light spores of fungi can travel considerable distances and are at high altitudes, which indicates a high power of migration processes. The distance of spore dissemination is a controversial issue and depends on many components. According to some au-

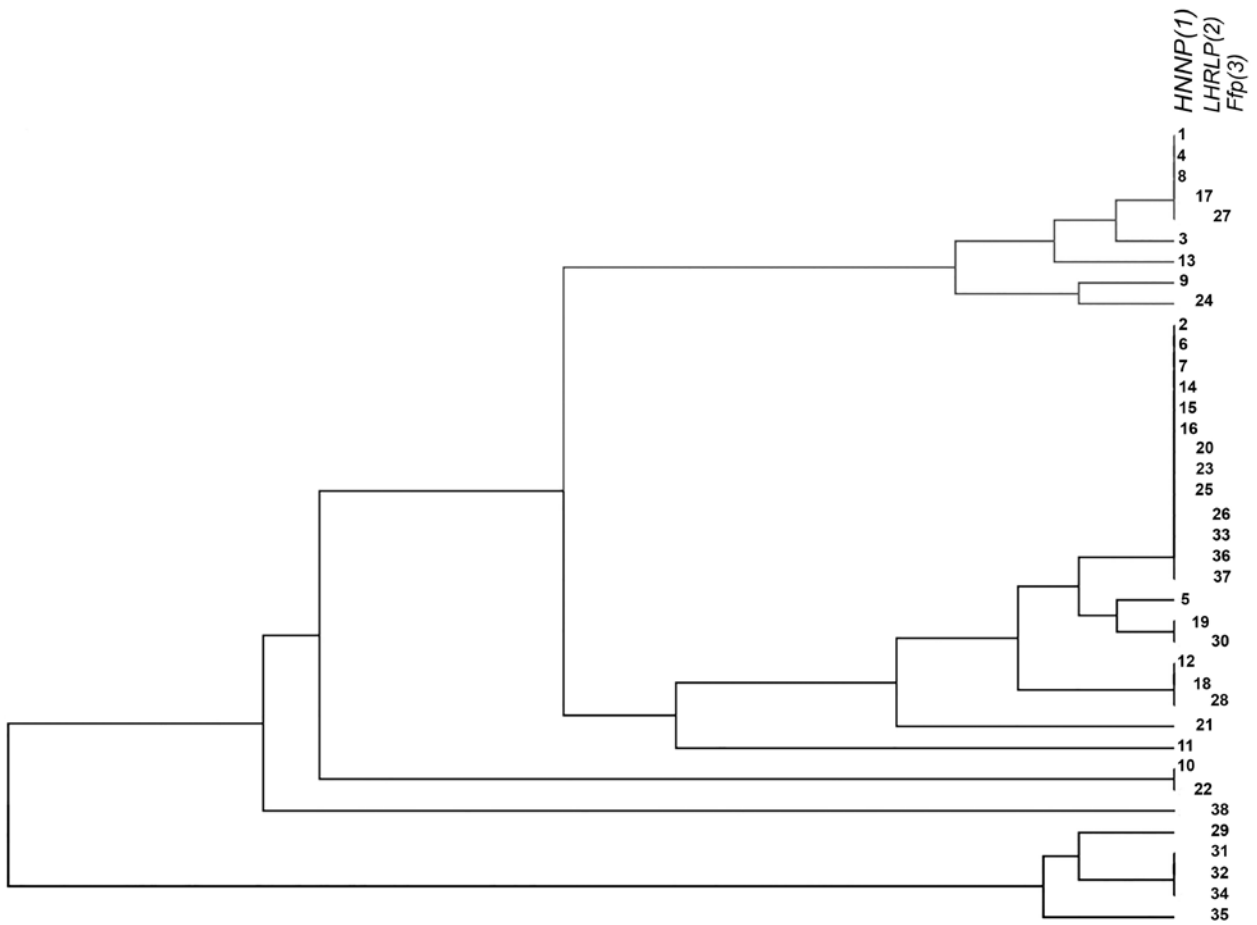

Figure 4. UPGMA dendrogram of the genetic similarity of cultures of *S. commune* (1–37 dikaryotic culture)

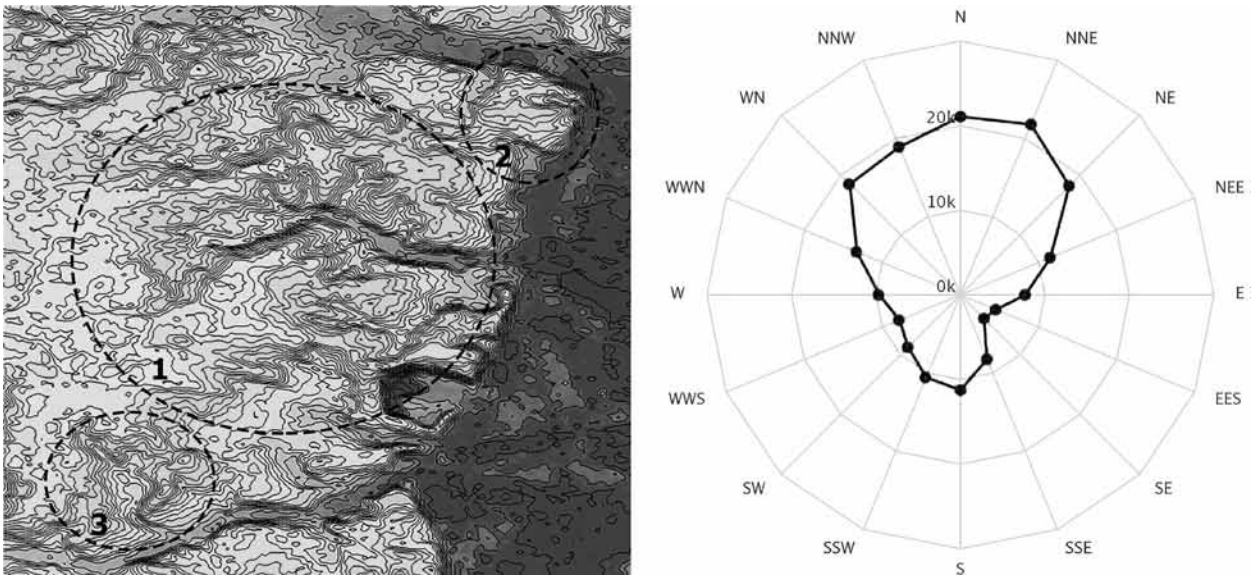

Figure 5. Topography of the landscape and repetition of the wind direction* in the explored territories

*Boris Sreznevsky Central Geophysical Observatory data for April–October 2016

thors, up to 95% of spores are concentrated at a distance of up to 1 m from the fruit body (Reddi 1976; Galante et al. 2011). Other groups argue that the percentage of spores in the air as well as the covered distances are much higher (Norros et al. 2012; Hallenberg and Küffer 2001; Viljanen-Rollinson et al. 2007). Importantly, there is a common view that wind is the main, essential factor for disseminating spores (Kuparinen et al. 2007; Dam 2013). According to Andrew et al., temperatures and precipitation are positively correlated with fungal richness (Andrew et al. 2019).

In addition, in our opinion, relief is a factor that affects the direction and force of airflow and forms a hydration regime necessary for the normal growth and formation of basidiocarps. We tried to correlate these two factors to our local populations (Fig. 5).

Relief topography suggests that the HNNP (1) forms a hill between two other local populations and the wind direction from April to October (which is the optimal period for the formation of basidiocarps) is more favourable to disseminate spores in the direction LHRLP (2) → HNNP (1) → Ffp (3), rather than in the opposite direction. Taking into account that the altitude of the HNNP is the highest, effective 'capturing' of spores takes place from the LHRLP, and at the same time, the probability of their dissemination to the Ffp decreases (difference in altitude 28 m).

On comparing our data with similar results obtained for the steppe zone of Ukraine, it was noticed that the level of gene differentiation was smaller there and the gene flow conceded, although distances between populations were much higher (Boiko 2015). This may support our assumption of the effect of terrain topography on the genotype of the local population. It is possible that for such topography, ravine plays the role of 'traps' for rare alleles, which, due to drift, can lead to their disappearance or increase their fraction.

Conclusions

Our results show the similarity of genetic variability of *S. commune* in different local populations. The heterozygote deficiency of some loci that was discovered may have resulted from new forms of allozymes that have not become widespread or due to small population sizes. In the aggregate sample of populations, a single basidiocarp revealed a lack of heterozygotes on 35.5%. The degree of differentiation of genes between local studied populations was moderate due to the high flow of genes. The absence of spatial structuration of genotypes is established, and the Mantel test showed a lack of interconnection between the genetic component and

the geographical coordinates of the samples. The direction of wind and terrain are the factors that influence the genetic structure of local populations.

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