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EXPERIMENTAL ARTICLES

Community Structure of Yeast Fungi in Forest Biogeocenoses

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Abstract—The results of longterm studies of yeasts inhabiting soil, plant surfaces, and plant residues in typical subboreal forests of the European part of Russia are summarized. The cell number and species diversity of yeast communities in the array of substrates corresponding to succession stages in plant residue decomposition are shown to steadily decline. Each stage is characterized by its specific set of dominating species. The yeast diversity in forest biogeocenoses is shown to surpass that in other geographic zones. This manifests itself in a greater number of species occurring in similar arrays of substrates, in the absence of conspicuous dominants on the biogeocenotic level, and in a higher differentiation of the yeast population with respect to its habitat type. The forest yeast populations are also characterized by a high diversity of yeasts of ascomycetous affinity and of the anamorphic stages of *Taphrinales* and *Tremellales* and by the presence of typical pedobiont species (except *Lipomyces* spp.).

Key words: yeasts, forest, microbial communities, spatial succession array.

A new vertical stratification approach was developed over the last few decades at the Soil Biology Department, Moscow State University, to the study of natural microbial community structure. This approach looks at the change in the structure of microbial populations in the postulated spatial succession sequence corresponding to different biogeocenotic strata [1, 2]. It originated in studies of the vertical distribution pattern of yeast fungi in the plant–soil system [3]. Based on this approach, the taxonomic structure of yeast communities was studied in the most typical biogeocenoses of all major natural and geographic zones from polar deserts to the subtropics [4], and each was found to be characterized by its own pattern of yeast distribution over vertical strata. The least studied in this respect remained yeast communities of the taiga–forest zone. Meanwhile, significant changes had taken place in yeast taxonomy since the first and sole comprehensive survey of the yeast population in the forests of Central Russia [3]. Other zymologic studies of the forest belt were concerned mostly with characteristics of yeast communities in specific habitats: e.g., bore powder in bark beetle holes [5], ant hills [6], sap flows released by plants in spring [7], and soil [8]. Given all these factors, a broad comparative study of the yeast population of taiga–forest biogeocenoses employing the same approaches and methods as in the preceding surveys of other geographic zones [4] became topical.

This work sums up and generalizes a long series of studies of the yeast population structure in several forest types of Central Russia that employed the vertical stratification approach. Our major goal was quantitative synecologic analysis of the yeast population in forest biogeocenoses rather than compilation of an extensive taxonomic list of the occurring yeasts. A quantitative analysis of species cell numbers is not possible unless the group under study is clearly delineated. In our studies, this group traditionally consists of fungi able to form yeast colonies on acidified wort agar. For this reason, several widespread yeast groups such as *Lipomyces* spp. and many tremelloid yeasts are not considered since they require different media for isolation.

MATERIALS AND METHODS

Three types of biogeocenoses were selected for the study, representing the widespread forest variants found in the central region of the European part of Russia: bilberry spruce forest on podzolic soil, mixed herb birch forest on soddy-podzolic soil, and mixed herb alder forest on humus–gley soil. Each biogeocenosis type was represented by two sampling plots. The spruce forest plots were located in the Kashinskii and Nelidovskii regions of Tver oblast and the birch and alder plots, in the Shakhovskii region of Moscow oblast.

On each plot, several dozen samples were taken of different substrates that could be referred to one of the following types: live leaves and plant branches, dry but not yet fallen leaves and plant branches, fallen leaves and branches in various stages of decomposition, forest litter, and different soil horizons up to the depth of 40–50 cm. These substrates make up a natural sequence that corresponds to biogeocenotic strata or stages in plant residue decomposition and will be referred to in

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what follows as the spatial succession array. The samples were collected in 1993–1998 at the end of May and at the end of September.

Samples of succulent plant parts were analyzed within a day upon collection. Samples of dry parts of plants and samples of plant residues and soil were stored at a temperature of 0–5°C and analyzed within 2–3 weeks. The green plant parts were assayed in full; only a 2- to 3-mm surface layer was cut off for assay from trunks, large branches, and roots.

The samples were reduced to fragments, and three to four portions from each sample were treated in sterile water in a tissue microdisintegrator at 3000 rpm for 3 min. Depending on the nature of the substrate, a dilution was selected (1 : 10 to 1 : 100) in order to obtain tens to hundreds of yeast colonies per a dish. Each sample part was plated in three replications on wort agar with 40% lactate (4 ml/l). To suppress growth of mycelium fungi, the samples were incubated at a temperature close to 5°C for 2–4 weeks. Using a binocular magnifier, the grown yeast colonies were classified into different types based on their macromorphological features, and the relative abundances of the types were determined. Several colonies of each type were isolated in pure cultures that were identified based on their morphological and physiological characteristics using yeast manuals [9, 10]. For each sample, the total yeast population was determined in terms of colony-forming units per gram of substrate (CFU/g), and a list of identified species with their relative abundances was composed.

By studying a total of 550 plants, plant residues, and soil samples, we were able to quantitatively estimate the distribution of dominating species in terms of their occurrence frequency, calculated as the fraction of samples in which the given species was found. The observed differences in species abundances and other parameter values of the yeast community structure were tested for confidence by conventional statistical methods, including variance factor analysis and different nonparametric tests. The results addressed in the discussion are statistically significant at the level of 0.05.

RESULTS AND DISCUSSION

A total of 47 yeast species belonging to 20 genera were determined in the analyzed biogeocenoses on live plant parts, in plant residues, and in soil (Table 1). The highest diversity was shown by basidiomycetous yeasts (35 species), among which the largest number of species belonged to the anamorphic genera *Cryptococcus* (13 species) and *Rhodotorula* (9 species). Species of these genera are known to prevail in yeast populations in all types of biogeocenoses in all geographic zones. The taxonomic composition of the forest yeast population is characterized by a wide diversity of genera representing anamorphic stages of phytopathogenic fungi from the *Taphrinales* and *Tremellales* groups, the tele-

Table 1. Yeast species isolated from plants, plant residues, and soils in forest biogeocenoses

Species	Occurrence, %
Arxula adeninivorans (Middelhoven *et al.*) van der Walt *et al.*	0.6
Bulleromyces albus Boekhout et Fonseca	0.6
Candida membranaefaciens (Hansen) Hansen	1.3
C. oregonensis Phaff et do CarmoSousa	2.5
C. sake (Saito et Ota) van Uden et Buckley	0.6
C. schatavii (Kockova-Kratochvilova et Ondrusova) Yarrow et Meyer	1.3
Cryptococcus aerius (Saito) Nannizzi	1.3
C. albidus (Saito) Skinner	62.0
C. curvatus (Diddens et Lodder) Golubev	1.9
C. diffluens (Ruinen) von Arx et Weijman*	1.9
C. flavus (Saito) Phaff et Fell	2.5
C. humicola (Daszewska) Golubev	0.6
C. laurentii (Kufferath) Skinner	37.3
C. luteolus (Saito) Skinner	5.1
C. macerans (Frederiksen) Phaff et Fell	0.6
C. magnus (Lodder et Kregervan Rij) Baptist et Kurtzman	1.3
C. podzolicus (Bab'eva et Reshetova) Golubev	7.0
C. terreus di Menna	1.3
C. terricola Pedersen*	19.6
Cystofilobasidium bisporidii (Fell *et al.*) Oberwinkler et Bandoni	0.6
C. capitatum (Fell *et al.*) Oberwinkler et Bandoni	15.8
C. infirmo-miniatum (Fell *et al.*) Hamamoto *et al.*	0.6
Debaryomyces hansenii (Zopf) Lodder et Kreger-van Rij	2.5
Dioszegia hungarica Zsolt emend Takashima *et al.*	6.5
Hanseniaspora guilliermondii Pijper	1.9
Lalaria polystichi Moore	0.6
Leucosporidium scottii Fell *et al.*	10.1
Mastigomyces philippovii Imshenetskii et Kriss	1.3
Metschnikowia pulcherrima Pitt et Miller	4.4
M. reukaufii Pitt et Miller	2.5
Mrakia frigida (Fell *et al.*) Yamada et Komagata	0.6
Pichia angusta (Teunisson *et al.*) Kurtzman	0.6
P. wickerhamii (van der Walt) Kregervan Rij	1.3
Rhodotorula aurantiaca (Saito) Lodder	3.8
Rh. glutinis (Fresenius) Harrison	17.7
Rh. graminis di Menna	5.7
Rh. fujisanensis (Soneda) Johnson et Phaff	18.4
Rh. ingeniosa (di Menna) von Arx et Weijman	0.6
Rh. lactosa Hasegawa	1.9
Rh. minuta (Saito) Harrison	10.8
Rh. mucilaginosa (Jorgensen) Harrison	6.3
Rh. nothofagi (Ramirez et Gonzalez) Roeijmans *et al.*	1.9
Rhodosporidium toruloides Banno	1.3
Sporidiobolus johnsonii Nyland	0.6
Sporobolomyces roseus Kluyver et van Niel	39.2
Trichosporon pullulans (Lindner) Diddens et Lodder	5.7
Udeniomyces puniceus (Komagata & Nakase) Nakase & Takematsu	1.3

* Although these species are not to be found in the manual [10], they refer to well-defined phenotypic groups with clear-cut ecological preferences.

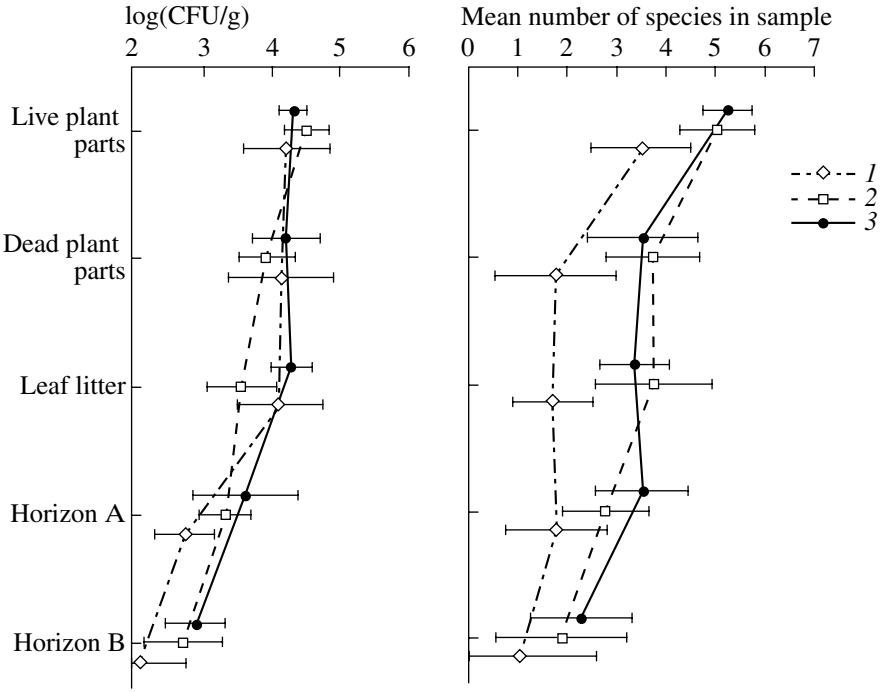

Fig. 1. Variation of the total cell number and species diversity of yeast groupings across the spatial succession array in (*1*) spruce, (*2*) birch, and (*3*) alder forests.

omorphs of which are able to form fruiting bodies, mostly on dead wood. The composition is also characterized by a relatively high occurrence of yeast species of ascomycetous affinity, primarily of the genera *Candida* and *Pichia*.

As previously noted, the assayed substrates make up a fairly natural succession corresponding to the vertical stratification of the biogeocenoses, or to succession stages in plant residue decomposition. In decaying, plant residues constitute increasingly extreme habitats for yeasts, which are typical saccharolytic microorganisms. This fact is reflected in the yeast community structure.

In all biogeocenoses studied, the total yeast population density declined regularly across the spatial succession array from 10^4–10^5 CFU/g on live plant parts to 10^2 CFU/g in soil horizons (Fig. 1). A similar decline was observed with all other species diversity indicators of yeast communities. The mean number of species found in a single substrate sample also decreased from five to six in green parts of plants to two in mineral soil horizons. The domination of a single species becomes more salient across the spatial succession array. The differentiating diversity also declines steadily, meaning that individual groupings become increasingly similar in their species structure.

Each stage in the spatial succession is characterized by its own set of species that can be found to predominate in individual yeast groupings (Table 2). In all types of forests, the species prevailing on aboveground plant parts were *Cryptococcus laurentii, Sporobolomyces roseus*, and *Rhodotorula glutinis.* In decaying plant residues, the most typical were the yeastlike fungi *Trichosporon pullulans* and *Cystofilobasidium capitatum.* In upper and, especially, deeper soil horizons, the most typical yeast population representatives were *Cryptococcus terricola* and *C. podzolicus.* It should be stressed that the variation of the yeast community species structure in the spatial succession array is directional. The cell number of most of the predominant species either gradually declines (*Cryptococcus laurentii* and *Sporobolomyces roseus*) or increases (*Cryptococcus terricola* and *C. podzolicus*) in the course of plant residue decomposition. The similarity with the original epiphytic communities gradually decreases. All these facts suggest that the community variation in the array follows the gradient of a single limiting factor, which, in our case, is most probably the concentration of readily available nutrients.

It follows that, in all the biogeocenoses studied, yeast communities in each spatial succession stage had their own distinguishing features. Below, these will be considered in greater detail.

Live plant parts. Green leaves and unlignified branches of vascular plants, as well as live parts of moss, constitute the most favorable habitats for most yeast species. In such habitats, the yeast fungi cell number (up to 10^6 CFU/g) and diversity reach their maximum values. From each sample of live plant parts, on average, five yeast species belonging to at least three genera were isolated. In all, as many as 41 yeast species were found in samples of these substrates, constituting

Table 2. Domination probability (%) of the yeast species* whose cell number reliably ($p < 0.05$) changes across the spatial succession array (averaged over all biogeocenoses studied)

Species	Live parts	Dead parts	Leaf litter	Upper horizons	Lower horizons
C. albidus	37	44	51		
C. laurentii	21	18	13		
R. glutinis	8				
M. pulcherrima	6				
S. roseus	5				
M. reukaufii	3				
Candida spp.	3				
L. scottii	10	15	4		
C. luteolus		7			
R. fujisanensis	3	8	4		
C. capitatum	4	8	15	10	
T. pullulans			9	20	
C. terricola				60	81
C. podzolicus			4	10	19

* The fraction of the samples assayed in which the given species was found to dominate (accounting for more than 30% of all grown colonies).

80% of the total number of species determined in forest biogeocenoses. The most widely occurring on live leaves were representatives of the genera *Rhodotorula, Sporobolomyces*, and *Cryptococcus*, the predominant species being *Sporobolomyces roseus* (occurrence frequency, 82%), *Cryptococcus laurentii* (68%), *R. minuta* (18%), and *R. mucilaginosa* (14%).

The cell number of different phylogenetic groups of yeast fungi varied with the taxonomic affiliation and ecological properties of host plants. The most trustworthy distinctions were observed in comparing epiphytic yeast communities occurring on leaves of plants that belong to different ecological groups. The cell number and the diversity of yeast fungi on spruce needles and on leaves of xerophytic half-shrubs (*Vaccinium*) were reliably lower than on leaves of mesophytic herbaceous plants and deciduous trees. The largest yeast populations were observed on the surface of hydrophytic plants such as *Oxalis acetosella* and on live parts of ground-surface mosses. Such an effect was previously observed when comparing populations of epiphytic yeasts on leaves of spring ephemerals and xerophytes in subtropical deserts [11]. The fact that populations of epiphytic yeasts on leaves of xerophytic plants are notably sparser can, apparently, be explained by such plants having a thicker cuticle that limits the release of exudates serving as the main nutrient for epiphytic yeasts [12]. Among live aboveground parts of plants, least populated were those in the process of lignification, specifically, young branches of shrubs and trees. This fact can also be explained by a lower exudation compared to that on leaves.

The distribution of some eurybiontic yeast species reliably reveals their affinity to specific plant groups. Thus, the typically epiphytic species *Sporobolomyces roseus* was almost never found on mosses, whereas on needles of coniferous trees and on leaves of herbaceous and ligneous plants its occurrence frequency was above 80%. The most significant distinctive feature of yeast groupings in moss-covered sod is a high cell number of *Leucosporidium scottii.* These are psychrophilic yeasts that fail to grow at temperatures over 25°C, and this can probably explain their wide distribution in the near-ground moss stratum, where temperature variations are largely smoothed out.

Dead plant parts were represented by dead but not fallen leaves, by branches of vascular plants, and by dead parts of moss. The essential difference of these substrates from live plant parts is the absence of exudates with a relatively high concentration of readily utilizable compounds. Therefore, for saccharolytic yeasts, dead plant parts constitute a less favorable environment, and this is manifest in the structure of the inhabiting yeast communities. The overall cell number (on average, 10^4 CFU/g) and diversity of yeasts here are somewhat lower than on live leaves, and, on average, three to four species of yeast fungi were isolated from each sample. The species most frequently occurring in dry leaf samples were *Cryptococcus albidus, C. laurentii*, and *Sporobolomyces roseus*, i.e., the same epiphytic yeasts that dominate on live plant parts. At the same time, typical saprobiontic and pedobiontic species such as *Trichosporon pullulans* and *Cryptococcus terricola* were also found on dead parts. The latter species is currently regarded as a synonym for *C. albidus* but differs from it in having the ability to form large lipid globules and in its affinity to soil and ground strata. There are some data suggesting that the type

Table 3. The strength of influence of the factors type of biogeocenosis (spruce, birch, or alder forest) and type of substrate (live leaves, dead leaves, leaf litter, horizon A, and horizon B) on the yeast community structure parameters: Fisher's criterion values yielded by two-factor variance analysis

Parameter	Biogeocenosis type	Substrate type
Total cell number	–	17.8
Number of species in the sample	6.6	8.6
Species structure (multivariate analysis)	1.3	1.9
Cryptococcus laurentii	6.8	10.7
Cryptococcus podzolicus	4.6	5.3
Cryptococcus terricola	21.3	10.8
Cystofilobasidium capitatum	8.9	3.5
Sporobolomyces roseus	–	7.3
Trichosporon pullulans	–	3.7

strains of *C. albidus* and *C. terricola* differ significantly in their rDNA nucleotide sequences, and it was argued that the latter strain might represent a species of its own [10].

The cell number and diversity of yeast fungi on dead moss parts were also lower than on live moss. Yeast populations on this substrate seldom exceeded 10^3 CFU/g. We found 14 species here, the most frequent of which were *Cryptococcus albidus* and *Leucosporidium scottii* (occurring in 90 and 50% of samples, respectively).

The sparsest yeast groupings were found on dry lignified branches of trees and dwarf shrubs. The population of yeast fungi on these substrates did not normally exceed 10^3 CFU/g.

Plant residues and leaf litter. The yeast population in fresh plant residues (fallen leaves and small branches that still mostly preserve their anatomy) does not differ much in its size and taxonomic structure from that of yeast groupings on dead plant parts above ground. The number of yeast fungi in these substrates varied between 10^3 and 10^5 CFU/g and, on average, was not lower than on dry leaves. The species diversity in these substrates, however, was markedly lower. The mean number of species observed in each sample did not exceed three. As in aboveground parts of plants, the most abundant were the eurybiontic yeasts *Cryptococcus albidus* and *C. laurentii*, determined in roughly 70% of samples. At the same time, the typically epiphytic species *Sporobolomyces roseus* occurred in plant residues notably less frequently and was isolated from only 17% of the corresponding samples. Very rarely found in plant residues were pigmented species of the genus *Rhodotorula*. This also applied to ascosporous yeasts from the genera *Debaryomyces, Metschnikowia*, and *Pichia* and anamorphic yeasts *Candida* spp., which were quite common on aboveground and, especially, live plant parts.

The yeast population structure undergoes significant changes in the deeper forest litter layers, specifically, the fermentation layer (F) and the humus-rich layer (H). The mean yeast population in these layers was as low as 10^3 CFU/g, and its taxonomic structure differed substantially from that found on the aboveground parts of plants. Even though the dominating species in leaf litter were the same typical eurybiontic *Cryptococcus albidus* and *C. laurentii*, the subdominants were represented by *Trichosporon pullulans* and *Cystofilobasidium capitatum*, which were hardly ever determined on plant leaves and in fresh plant residues. The typical soil species *Cryptococcus terricola* was also found in 10% of assayed leaf litter samples.

We see, therefore, that the yeast population of the forest leaf litter is characterized by cohabiting of typical epiphytes, pedobionts, and leaf litter species proper. Representatives of the epiphytic microflora continually make their way into the leaf litter with plant residues, whereas soil species are brought in as a result of activities of soil animals. At the same time, given the high abundance of epiphytic and soil species, their active proliferation in leaf litter may well take place.

Mineral soil horizons. The obtained evidence on the structure of yeast groupings formed in the subsurface and, particularly, deeper layers of the soils studied suggests that soil is the least favorable environment for yeast fungi. The mean cell number of yeasts in the upper horizons of the assayed soils immediately under the leaf litter amounted to 10^3 CFU/g. In all types of soils studied, the yeast population declined steadily across the profile and, at a depth of more than 15 cm, normally reached the sensitivity limit of the employed plating method (10^2 CFU/g). In contrast to vegetative substrates, yeasts were not always found in all soil samples. Their mean occurrence in organogenic horizons was close to 70% and did not exceed 50% in the illuvial horizon. At a depth of more than 20–25 cm, yeast fungi were virtually never determined in platings on wort agar, although it is well known that they are represented in these horizons by abundant populations of lipomycetes [13], which cannot be accounted for on rich media.

In all, 20 yeast species were found in soils of forest biogeocenoses. Most of these species occurred sporadically. They included typical saprobionts (*Cystofilobasidium capitatum* and *Trichosporon pullulans*) and also typical epiphytic species (*Cryptococcus laurentii, Sporobolomyces roseus, Rhodotorula glutinis*, and *R. mucilaginosa*). Only two yeast species—*Cryptococcus terricola* (total occurrence in soil, 60%) and *C. podzolicus* (16%)—were isolated from all soil substrates. In soil, their occurrence was higher than in the aboveground stratum, and in the mineral horizons, higher than in the leaf litter.

An interesting feature of the upper soil horizons is the constant presence of ascomycetous yeasts, which were identified to include *Candida intermedia,*

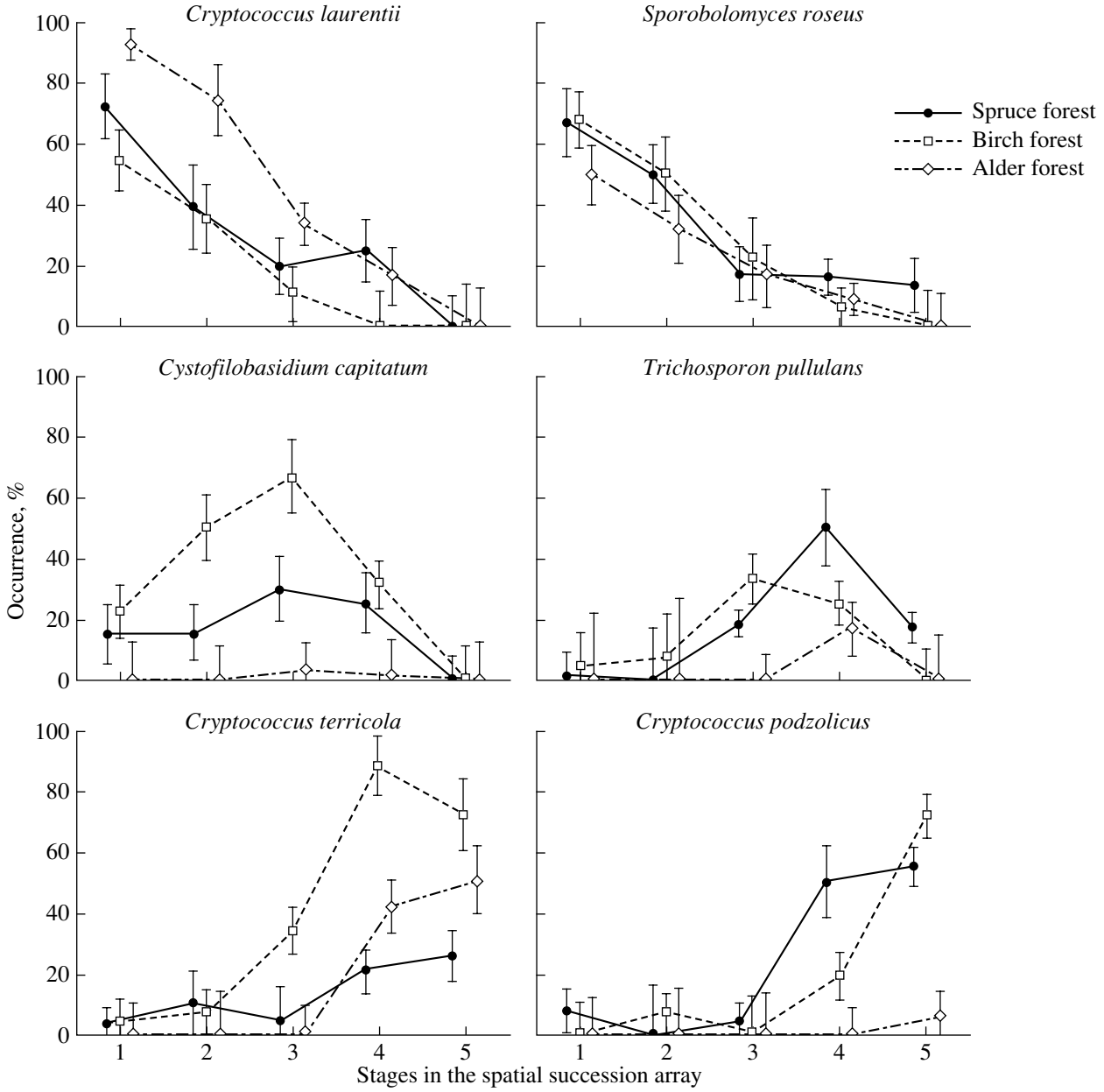

Fig. 2. Variation of relative abundance of dominating yeast species across the spatial succession array for different forest types. The substrate types in the array are (1) live plant leaves, (2) dead leaves, (3) leaf litter, (4) horizon A, and (5) horizon B.

C. membranaefaciens, Debaryomyces hansenii, and *Hanseniaspora guilliermondii.*

Biogeocenotic variations. The previously discussed features of yeast communities were found with all types of forests studied. At the same time, we were able to identify some distinctions in the structure of yeast populations in different forest biogeocenoses. By considering similar arrays of substrates in different biogeocenoses, we could use the full power of variance factor analysis and quantitatively estimate the effects of such factors as the type of substrate and the type of biogeocenosis on different characteristics of yeast communities. Our analysis showed (Table 3) that all parameters of the yeast fungi community structure did not depend in a similar manner upon these factors. For example, the total yeast cell number was determined by the substrate type, whereas the impact of the biogeocenosis type on this variable was not statistically significant. At the same time, the taxonomic diversity indicators (e.g., the mean number of taxa found in a sample) and the relative abundance of several predominant species were found to depend both on the position of the yeast grouping in the spatial succession array and on the biogeocenosis type (Fig. 2). There are also some species whose cell number is determined by the substrate type alone irrespective of the type of forest it

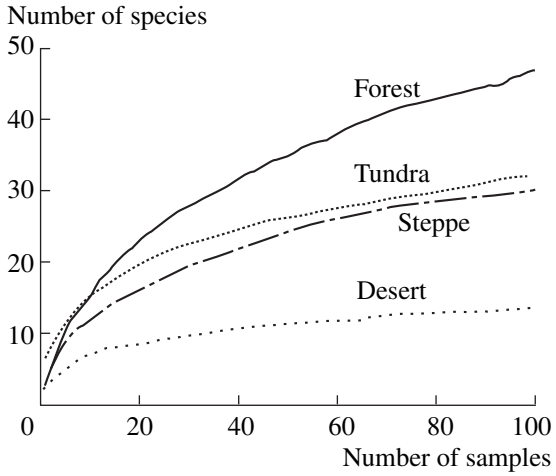

Fig. 3. Cumulative numbers of isolated species for different geographic zones. The curves were obtained by multiple random re-sorting of soil, plant, and plant residue samples (taken in roughly equal proportions) and calculation of the mean number of species found in the given number of samples.

occurs in. These species include the typically epiphytic *Sporobolomyces roseus* and also *Trichosporon pullulans*, which mostly occurs in leaf litter. However, the cell number of most dominants not only depended on the type of substrate but also varied with the forest types. For example, the typical pedobiont *Cryptococcus terricola* abounded in deciduous forest soils but was not often isolated from spruce forest soils, while the typical leaf litter species *Cystofilobasidium capitatum* and *Trichosporon pullulans* were rare in alder forests and common in spruce and birch forests. The mean figures of yeast community diversity in all alder substrates were lower than in biogeocenoses of other types (Fig. 1). This can, apparently, be explained by alder exudates containing a mixture of phenol compounds that hinder the development of epiphytic yeasts [14]. The low cell number of most common yeast species in the humus–gley soil under alder can be explained by relatively high pH values. It follows that the characteristics of yeast communities in forest biogeocenoses are determined not only by their substrate position in the spatial succession chain but also by the forest type. The nature of the latter dependence, however, can hardly be explained at present.

This work made use of the same approach as a number of previous studies carried out at the Soil Biology Department that examined the structure of yeast populations in biogeocenoses of different geographic and climatic zones. Detailed investigations of the density and the species structure of the yeast communities in soil and vegetative substrates were previously undertaken in tundra, steppe, and desert zones [11, 15, 16]. In these works, the most typical biogeocenoses for each region were identified and a large number of samples of different substrates was assayed, representing the same spatial succession stages as in our study. By comparing these data, we were able to conclude that the most complex and diverse yeast fungi groupings are formed in the forest belt as compared to biogeocenoses in other climatic zones (Fig. 3). In regions of climatic pessimums (Arctic tundras and subtropical deserts), a very large share of the yeast population is accounted for by representatives of asporogenous capsule yeasts from the genera *Cryptococcus* and *Rhodotorula* and a very small share belongs to yeasts of ascomycetous affinity [11, 15]. The species diversity of the yeast population in forests is significantly higher primarily because of a higher cell number of ascomycetous yeasts, represented by both teleomorphic (*Debaryomyces, Metschnikowia, Hanseniaspora*, and *Pichia*) and anamorphic (*Candida, Arxula, Blastobotrys*, and *Mastigomyces*) genera. In addition, in forest biogeocenoses, we also observed the widest diversity of genera of dimorphic fungi with a yeast phase, which are not traditionally referred to yeasts (e.g., *Tremella, Lalaria*, and *Microstroma*). Many of them are phytopathogenic in their perfect stage and are closely associated with certain plant species.

It was shown in previous studies of yeast populations in tundra [15] and subtropical deserts [11] that yeast communities in these natural zones, considered at the biogeocenotic level, are subject to the phenomenon of superdomination, which means that one or a small group of species prevail conspicuously not only in substrates of a certain type but also in the biogeocenosis at large, irrespective of its type. In Arctic and typical tundras, such species are *Cryptococcus gilvescens* in the soil stratum and *C. laurentii* in the aboveground stratum. In subtropical deserts, substrates of all types are manifestly dominated by *Cryptococcus diffluens*. Such indisputably dominating species are not found in the forest biogeocenoses studied in this work. The line separating the species with peak and intermediate occurrences is much more blurred here, and rank distributions of relative abundances have a much flatter nature.

To sum up, the yeast population of Russia's forest belt is characterized by a much wider species diversity than other environmental zones. This conclusion is attested to by the larger number of species and genera found in similar arrays of substrates, by the absence of salient predominating species on the biogeocenotic level, and by higher differentiation of the yeast population with regard to the habitat type. The yeast population of forests is characterized by a wide species diversity of the genera representing anamorphic stages of *Taphrinales* and *Tremellales* and by a larger diversity of ascomycetous affinity yeasts than in other natural zones. An important feature of yeast populations inhabiting forest soil is the constant presence not only of *Lipomyces* spp. but also of other typical pedobionts—*Cryptococcus terricola* and *C. podzolicus*—the cell number of which in mineral soil horizons is reliably higher than in other substrate types.

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