

Concerning the problem of integrated biogeographical analysis of different components of biotas

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Summary: The problem of integrated biogeographical analysis of different components of diverse biota is discussed. The floras of vascular plants and mosses as well as the biotas of lichens and myxomycetes from the Valdai and adjacent geographical provinces of the East European Plain are examined as model objects. We reveal the specifics of how the main parameters of floras and biotas change in terms of the longitudes and latitudes. The general level of richness, specificity and degree of similarity of the species composition in the analyzed components are determined at various levels, by climatic features, the differentiation of the plants based on the latitude and on geomorphology. The different structure of the longitudinal and latitudinal trends is defined by the features of biology and ecology of the taxonomical groups.

Keywords: biogeographical analysis, biota, flora, vascular plants, mosses, lichens, myxomycetes, level of species diversity of floras, differential species, specific component of floras and biotas, East European Plain, integrated analysis of various components of biodiversity

The basics of biogeographical analysis were developed mainly on vascular plant and vertebrate animal material (OCHIAI 1957; TOLMACHEV 1962, 1974; MALYSHEV 1975, 1992; SHMIDT 1980, 1984; KAFANOV & KUDRYASHOV 2000; PETROV 2005; MASHKIN 2006; CHERNOV 2008). The obtained results became the basis for creating floristic and faunistic zones of world's biota and large biogeographical entities (BARANOVA et al. 1971; TAKHTADJYAN 1978; YURTSEV 1991, 1992; GASTON 2000; MALYSHEV 2000, 2002; PETROV 2005; MASHKIN 2006). Currently, comparative floristics allow to reveal the patterns of territorial distribution of floras (YURTSEV 2000, 2004; KHITUN 2005; KHITUN et al. 2007). The idea of monitoring biodiversity at the level of local floras of vascular plants is going to be formed in Russia now. The possibilities of its practical use have already been determined (YURTSEV 1997, 2004; YURTSEV et al. 2001, 2002; POSPELOVA & POSPELOV 2005), and methods of mapping biodiversity have been developed (OGUREEVA & KOTOVA 2004). The spatial distribution of other biotas' components has its own specifics, which is determined by biological and ecological features of the representatives of various high level kingdoms and taxons. On the example of mosses it was shown that, unlike vascular plants, the main parameters of their floras depend chiefly on air humidity rather than on temperature (IGNATOV 1993, 2001). The first factor is also more important for lichens (JØRGENSEN 1983; GOWARD & AHTI 1992; URBANAVICHUS 1998, 2001, 2002). For some groups of organisms the zonal and sectorial features of the plant life and climate play a smaller role than the characteristics of specific ecotopes and ecological niches. Ecological niches can be rather versatile and many of them exist on large territories relatively regardless of the latitude and longitude. Among these groups are myxomycetes (NOVOZHILOV 1988, 2005a, b) and some microorganisms (MISHUTIN 1954; CHERNOV 1993, 1997, 2005; ZAVARZIN 1994; CHERNOV & MATVEEVA 2002). The development of the basics of biogeographical analysis on algae, lichens, liverworts, microscopic

fungi and other components of biota is limited by the insufficient knowledge of floras and biotas of a large number of systematic groups. The traditional separation of geographical elements is connected to specific difficulties which are due to biological and ecological features as well as specifics of the taxonomical evolution and sources of floras and biotas (OKSNER 1940–1942, 1944; MAKAREVICH 1968; TRASS 1970; SHLYAKOV 1975; KONDRATYUK 1987, 1988; URBANAVICHUS 2001; NOVOZHILOV 2005a,b).

At the end of the 20th century the problem of integrated biogeographical analysis on different components of biota has started to be discussed (PCHJELKIN 1991; IGNATOV 1993, 2001; CHERTOPRUD 2010). The particularities of the lichen coefficient LC (the ratio of lichens to vascular plants, or L:P-ratio) in different geographical regions worldwide and different areas of Russia are determined on the basis of an analysis of numerous quantitative estimations of lichen and vascular plant diversity (URBANAVICHUS 2009). High values of LC in Arctic regions are caused by adverse conditions for vascular plants, while low LC values in plain regions with arid climate are caused by adverse influences of bioclimatic conditions on the development of the lichen flora (URBANAVICHUS 2009). Number of fungal species : number of vascular plant species ratio is also used for the estimation of fungal diversity in different regions (SCHMIT et al. 2005). The development of integrated biogeographical analysis has a large implication on general biology. Knowledge about the trends of geographical distribution of various biota components will allow us to connect their biological, ecological and taxonomical evolution features with the characteristics of flora and biota creation. All of this will help us to understand the patterns which underlie biome formation, and the mechanisms of their stability and the preservation of their entirety (GASTON 2000). The development of the basics of integrated biogeographical analysis will help to solve the problem of complex biogeographical zoning (YURTSEV 2000). The results of integrated analysis are helpful in organizing multi-level monitoring and development of strategies for preserving biodiversity (BUKVAREVA & ALESCHENKO 2005). However, the lack of information about moss, algal, lichen and fungal floras of many territories prevents from conducting integrated analysis on these and many other components of biodiversity, which are traditionally the subject of florists' and biogeographers' studies. Complex studies of large areas, compiling of catalogues and summaries of various biota components (TSVELEV 2007; TCHESUNOV 2008) and the development of approaches, which allow to evaluate the level of the completeness of the revealed species composition (BARINOVA 2000; BARINOVA & ANISIMOVA 2004; BUKVAREVA & ALESCHENKO 2005; SHCHERBAKOV 2006), are all of current importance.

It is necessary to search for model territories of a large size, to analyze correctly different components and to reveal the floras' and biotas' main latitudinal and longitudinal trends of changing parameters and characteristics. The floras of mosses are more homogeneously and entirely studied (IGNATOV & IGNATOVA 2005; IGNATOV et al. 2006), while the floras of liverworts and lichen biotas need further investigations (POTEMKIN 2005; URBANAVICHUS 2006). Model territories with natural phytogeographic and physiographic boundaries are of special interest. The analysis of their floras and biotas may reveal very important gradients and tendencies of changes in biodiversity parameters. These could be explored later in more detail by using smaller territories that generally model the larger ones (SHMIDT 1984; SHCHERBAKOV 2006). The methodology of 'retrospective' evaluation of territorial distribution of various components of biodiversity needs further research. It is appropriate to enlarge the spectrum of factors being analyzed in integrated analysis of floras and biotas. Studies mainly look at the tendencies how the indexes of vascular plant floras change

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in terms of the latitudinal and longitudinal directions (TOLMACHEV 1974; MALYSHEV 1975, 1992; SHMIDT 1984). The nature of the main flora characteristics depending on geomorphological and landscape features of the territory is less studied (NOTOV et al. 2004, 2005b). The regional specificity of taxonomic differentiation and the separation of many systematic groups aren't represented entirely in taxonomical and genetic flora analysis. There are reasons to believe that species compositions in moss floras rely on lithological features and on the geomorphology of the territory more than floras of vascular plants do. Epilithic and epigeic species that are connected with various bare substrates play a significant role in their differentiation components (NOTOV et al. 2004). Some difficulties in recognizing the latitudinal geographical elements of mosses probably depend on the fact that the distribution of many species is relatively less influenced by physiographic factors reflecting the specifics of the latitudinal location of the territory. This is also true for lichens (PCHJELKIN 1991; URBANAVICHUS 1998, 2001, 2002; SONINA & MARKOVSKAYA 2005). In this sense, the systems of physiographical zoning may be of interest for the development of the basics of integrated analysis of various components of biodiversity.

Traditionally, different indexes and figures of similarity are used to analyze species composition (SHMIDT 1980, 1984). The Ochiai Index is a good tool to compare territories of different areas (OCHIAI 1957; MALYSHEV 2000, 2002; NOTOV et al. 2004).

Further search for parameters that characterize the specifics of florogenesis and the special features of regional differentiation of leading taxons is reasonable. In floristic works the following features have already been used: ratio between the number of species in Cyperaceae–Poaceae, Asteraceae–Poaceae, Asteraceae–Fabaceae (SHMIDT 1984; YURTSEV et al. 2001, 2002), Pottiaceae–Dicranaceae and the number of species *Cinclidotus* P. Beauv. (IGNATOV 2001). Diversity analyses of taxons with a wide distribution of apomixis deserve special attention. The number of microspecies in genera like *Hieracium* L., *Alchemilla* L., and *Rubus* L. of different basic floristic areas is rather different (MALYSHEV 1991, 2002; NOTOV et al. 2004). The composition of microspecies can contribute significantly to the data on floras specificity. That's why the agamous complexes on various territories also need further research. A critical revision of all the material is necessary.

At this stage, it is not always possible to connect all the floristic and biogeographic informations with the system of geobotanical and physiographic zoning, because many reports and summaries apply the administrative-territorial method. Fragments of various provinces are included within the boundaries of each administrative area. On the one hand, this complicates the systematization of data collected with the physiographic method, but on the other hand the inaccuracy of comparative analysis of floras of administrative regions is defined. Many regions include large fragments of two or three, and sometimes four or five provinces. Sometimes various physiographic countries cross the territories of regions. For example, a portion of the Saint Petersburg region is part of Fennoscandia, while the central and southern areas of this region are within the boundaries of the East European Plain.

In vascular plants it is sometimes difficult to identify unambiguously the florogenetic status of species and to assign it to indigenous or adventive. Further discussion is needed concerning the issue of choosing the zoning system that corresponds more with the goal of integrated analysis. The nature of geographical distribution of individual groups often depends on the features of geomorphology and lithology of the territory more than on the structure of vegetation. In this context, physiographic zoning has more opportunities than geobotanical zoning. In

the first case, not only the traits of latitudinal zonal vegetation and longitudinal climatic and landscape differentiation are taken into account. Azonal geological and, connected with them, geomorphological specifics of the territory are included. Although physiographic provinces have different areas (GVOZDETSKII & ZHUCHKOVA 1963; GVOZDETSKII 1968), their sizes are smaller than the sizes of phytocoria and phytogeographical regions (TAKHTADJAN 1978; FEDOROV 1979). Provinces are better matched in terms of area and they are uniform in source and landscape structure.

To develop the basics of integrated floristic analysis of various components of biodiversity it is necessary to search for large model territories. An important condition is a high level of floristic and biogeographical knowledge about the various biota components. This will make it possible to evaluate correctly the relative roles of factors that define specific characteristics of floras and biotas. The East European Plain can be a convenient territory for integrated analysis of moss and vascular plant floras as well as other biota components (NOTOV et al. 2004, 2005b). It is not uniform in geomorphology (ZHUCHKOVA & SHULGIN 1968). There are areas on the boundaries of natural zones and the habitats with extrazonal vegetation components are diverse. In the East European Plain many active migrations of various floral complexes took place. The large spread and a sufficient diversity in terms of physiography allow to distinguish groups of model regions. On their basis, it is possible to investigate the role of various physiographic factors and evaluate the regional specificity of taxonomic differentiation of systematic groups. The species composition of vascular plant and moss floras is sufficiently well identified within the East European Plain. Zonal and longitudinal trends of floras' parameters are clearly observed (NOTOV et al. 2004). Collection of material on lichens and myxomycetes is still in progress in different regions of Central and North-Western Russia (NOTOV et al. 2006, 2008; MUCHNIK et al. 2007, 2009a, b; ISTOMINA & LIKHACHEVA 2008; LEBEDEV 2008; BIAZROV 2009; and others).

We attempted to analyze the floras of vascular plants and leafy mosses of the Valdai and adjacent physiographic provinces (NOTOV et al. 2004, 2005b). We also started to generalize the data on lichens and myxomycetes (NOTOV et al. 2006; LEBEDEV 2008; NOTOV & LEBEDEV 2009). The species composition of vascular plant floras and mosses of six physiographic provinces have been identified. Among them are the West-Coast province (WCP), the Baltic province (BP), the Valdai province (VP), the Smolensk-Moscow province (SMP), the Mescherskaya province (MP) and the Upper-Volgian province (UVP). As a whole, the model region contains all of the Tver, Novgorod and Yaroslavl regions, a large part of Smolensk and Pskov regions, large fragments of Saint Petersburg, Moscow, Kostroma, Estonia, Latvia and Lithuania regions as well as some areas in Vologda, Ivanovsk and Kaluga regions (see Figs 1 and 2). In general, the analyzed territory is characterized by a large spread in both longitude and latitude. All of the provinces are within the forest zone (ZHUCHKOVA & SHULGIN 1968). They are different in continentality, structure of vegetation and geomorphological composition (ZHUCHKOVA & SHULGIN 1968). Most of them are within the southern taiga subzone. The zonal vegetation types are southern taiga and mixed coniferous–broadleaved (sub-taiga) forests. A zone of broadleaved forests is adjacent to its southern border. Small fragments of extrazonal vegetation such as meadow-steppe can be seen in valleys of large rivers. Only on the north of Upper-Volga regions there are semi-taiga forests. Most of the Smolensk-Moscow province is covered by coniferous–broadleaved (sub-taiga) forests, but there are some broadleaved forest formations in the south. The model territory is heterogeneous

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in terms of geomorphology. In VP and SMP there are a lot of habitats with a great diversity of microniches on which epilithophytic synusia are formed. WCP, MP, BP and UVP are mostly low plain territories with small-sized individual highlands and ridges. VP and SMP are elevated territories with a hilly landscape. Within the boundaries of the Valdai highlands the influence of the last Valdai glaciation is obvious: a dissected hill and ridge landscape prevails and a lot of glacial lakes of many different sizes and forms can be observed. Boulder deposits are common on the entire territory of the province. In SMP meadow landscapes with uncovered carbonate-bearing rocks create large and intricate complexes.

The sources of information on bryoflora and vascular plant floras were cited in previous publications, which also shed light on some results of preliminary analyses (NOTOV et al. 2004, 2005b). Adventive species were excluded from floristic lists of vascular plants. Additionally, we noted data on microspecies and some critical taxa which are not regarded as independent species by all researchers (NOTOV et al. 2004). The structure of the specific component of moss, vascular plant, lichen and myxomycete biotas has been revealed. The specific component includes differential species (occurring only within one province) and co-differential species (noted only in one or two provinces). The levels of species richness and volumes of the specific component of vascular plant and moss floras were brought to light (see Fig. 1). We also evaluated the level of similarity of their floras' species composition using the Ochiai index (NOTOV et al. 2004). Preliminary lists of lichens and myxomycetes were put together (NOTOV et al. 2006; LEBEDEV 2008), and the levels of their species richness and specificity of their biotas were revealed (see Fig. 2, Tab. 3).

Moss and vascular plant floras

Floras' level of species richness

All together 509 species of mosses and 1677 species of vascular plants were noted on the analyzed territory (if you include critical taxa and microspecies – 2801 species). The level of species richness in moss floras varies from 222 to 447 species, and in vascular plant floras it varies from 857 to 1203 species (see Tab. 1). In specific physiographic provinces there are 43.6% to 87.8% mosses and 51.1% to 71.7% vascular plants (see Tab. 1, Fig. 1).

Mosses and vascular plants show a tendency to decrease in floras' species richness from west to east. The highest level of species richness was noted in regions near the Atlantic (see Tab. 1, Fig. 1). Significant differences in rate of floristic richness change between mosses and vascular plants have been established. If we analyze the relative level of moss floras diversity (i.e., the species richness of the province's flora in percents from the total number of species that have been noted on the territory including all of the analyzed provinces) we obtain the following characteristics: WCP – 87.8%, BP – 85.7, VP – 47.0, UVP – 43.6. For vascular plants the figures are different: WCP – 63.4%, BP – 71.7, VP – 51.1, UVP – 51.7 (see Tab. 1). The decrease in level of species richness from west to east can be seen better in moss floras. The differences between their quantitative characteristics are more concise (see Fig. 1). Moss floras near the Atlantic are more than twice as rich in number of species than the UVP flora. In the corresponding vascular plant floras similar characteristics differ only in 20%. At the same time, the proportions of the index changes are violated, due to the different sizes of the BP and VP territories, as well as to the possible marginal position of BP (it is on the border between floristic provinces).

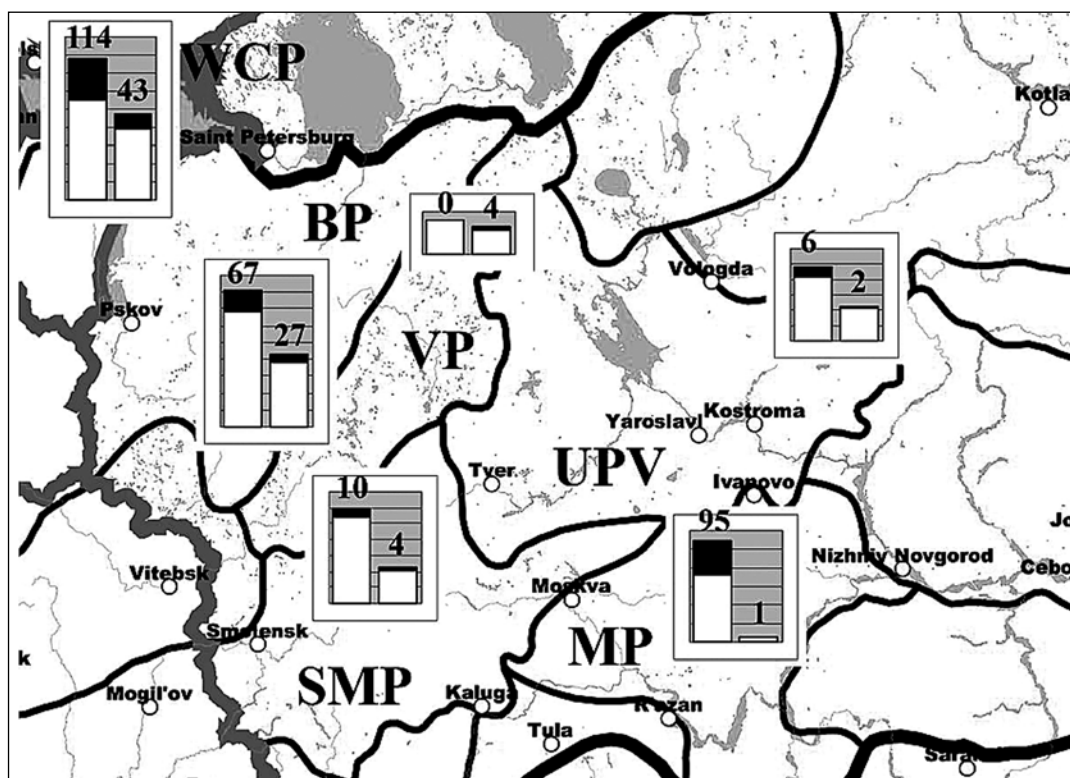


Figure 1. Species richness, specific and differential components of vascular plant floras (left columns) and mosses (right columns) in the Valdai and adjacent provinces. Black – specific component; numbers – differential species; thick black line – physiographic countries; medium black line – physiographic provinces; grey thick line – borders of the states.

In vascular plant floras there is a clear tendency of increase in the level of species richness in the north-south direction (VP – 857 species, SMP – 951, UVP – 867, MP – 1023) (see Tab. 1, Fig. 1). At the same time, the increase in the number of species for VP – SMP and UVP – MP is proportional (in the first case the total level of species diversity increases by 11%, in the second case by 18%). In bryofloras a similar tendency has been noted, but the differences in quantitative characteristics are less proportional (VP – 239, SMP – 291, UVP – 222, MP – 241, and correspondingly by 21% and 8.5%).

Level of floras' specificity

Mosses and vascular plants have shown a tendency to decrease the number of species in floras from west to east (see Fig. 3B, Tabs 1, 2). This tendency is sharper and clearer in mosses. In vascular plant floras, there is a significant increase of the number of species in floras from north to south (VP – 40 species, SMP – 109, UVP – 42, MP – 180) (see Tab. 1, Fig. 1). In moss floras, these indexes have shown macromosaic features (VP – 28, SMP – 42, UVP – 21, MP – 12) (see Fig. 3C). Decrease in unit weight of the differential component from west to east has been shown both in moss and vascular plant floras (see Fig. 3B). Changes in volume of the differential component from north to south in vascular plants and mosses is multi-directional (see Fig. 3B). Differences have been found in the ratio of unit weight between differential and co-differential species within the species component of moss and vascular plant floras. In vascular plant floras the differential species varies from 0% to 10.7%, and the co-differential species varies from 0% to 20.9%. In

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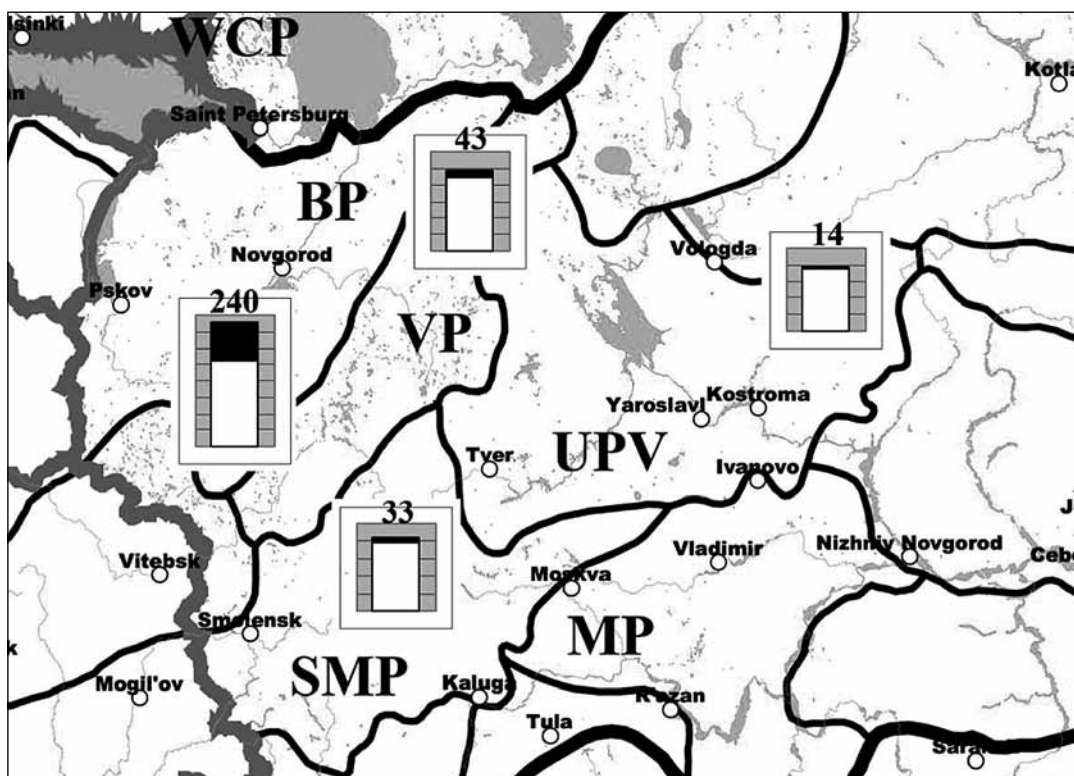


Figure 2. Species richness and number of differential species of lichen biotas of the Valdai and adjacent provinces: Black – differential component; all other symbols as in Fig. 1.

moss floras these indexes change from 0.4% to 9.6% and from 0% to 37.4% correspondingly. These differences are especially clear in floras near the Atlantic (in WCP the differential species of moss comprise 22.1% of the total number of specific species, while differential species of vascular plants comprise 40.9% of specific species; in BP – 14.2% and 19.7% correspondingly). The most contrasting indexes can be seen in MP (8.3% and 52.8%). Mosses on the analyzed territory lack endemic species (see Tab. 2). A relatively smaller volume of the differential component and lack of endemics point to the tendency noted earlier: the majority of bryophytes has larger ranges than vascular plants (IGNATOV 1993, 2001).

Analyses of geographical spectra of moss and vascular plant floras have shown that the central Atlantic-European and steppe–forest-steppe (arid) fractions have a larger differentiating importance (Fig. 3). In vascular plant floras the percentage of steppe and forest-steppe species changes accordingly: VP – 1.2%, SMP – 7.6%, UVP – 2.9%, MP – 12.8% (Fig. 3). Moss floras also show a change in arid species, but the differences are less contrasting (VP – 0.4%, SMP – 2.1%, UVP – 0.5%, MP – 1.7%). The rate of change of steppe, forest-steppe and arid fractions of vascular plants is larger than of mosses (see Fig. 3). The indexes of the unit weight of arid species in moss floras are more disproportionate (see Fig. 3). Both in moss and vascular plant floras there is a pattern of decreasing of Central European and Atlantic-European species from west to east. In moss floras the unit weight of this fraction changes more gradually. In vascular plants the differences are more noticeable and disproportionate (Fig. 3). Changes of differentiating fractions in moss and vascular plant floras happen differently (Fig. 3D). In moss floras the specificity of

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Table 1. Level of species richness and volume of specific components of moss and vascular plant floras in the Valdai and adjacent provinces. WCP – West-Coast province, BP – the Baltic province, VP – the Valdai province, SMP – the Smolensk-Moscow province, UVP – the Upper-Volgian province, MP – the Mescherskaya province. Numerical data including agamic complexes and critical taxa are in parentheses. Numbers in the bottom half of the cells are the percentages of the total number of species that have been noted in the analyzed territory.

Flora	Vascular plants			Mosses		
	Total number of species	Differential species	Specific component	Total number of species	Differential species	Specific component
WCP	1064 (1478) 63.4 (52.8)	114 (241)	279 (646)	447 87.8	43	195
BP	1203 (1641) 71.7 (58.6)	67 (161)	340 (718)	436 85.7	27	190
VP	857 (1037) 51.1 (37.0)	0 (2)	40 (130)	239 47.0	4	28
SMP	951 (1080) 57.0 (38.6)	10 (18)	109 (136)	291 57.2	4	42
UVP	867 (972) 51.7 (34.7)	6 (11)	42 (66)	222 43.6	2	21
MP	1023 (1107) 61.0 (39.5)	95 (108)	180 (206)	241 47.3	1	12

geographical structure is largely defined by the Atlantic-European fraction, while in moss floras it is defined by the forest-steppe–steppe fraction. Differences in the structure of geographical spectra of vascular plant and moss floras can be seen more clearly if individual physiographic zones within different provinces are analyzed (NOTOV et al. 2005a).

The established tendencies of change in geographical structures of floras can be seen more distinctly in quality analysis of the specific component (Fig. 3). In moss floras the percentage of specific species with Atlantic connections changes more proportionally than in vascular plant floras (Fig. 3). In vascular plant floras of UVP there are virtually no specific species with Atlantic connections, but East European and Siberian species appear. Among differential species of UVP there are some Euro-Siberian plants (*Cacalia hastata* L., *Calamagrostis obtusata* Trin., *Schizanthus callosa* (Turcz. ex Griseb.) Ohwi, *Anemonoides altaica* (C. A. Mey.) Holub). The change gradient of the percentage of arid species in moss floras (VP – 0 differential and 0 co-differential species, SMP – 1 and 4, UVP – 0 and 0, MP – 1 and 3, correspondingly) is less obvious than the change gradient of the increase of steppe and forest-steppe species in vascular plants (VP – 0 and 2, SMP – 4 and 44, UVP – 0 and 7, MP – 65 and 41) (see Tab. 2).

The indexes of species richness and the level of vascular plant floras specificity change significantly if we include the diversity of microspecies and critical taxa (see Tabs 1 and 2, Fig. 3). The

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Table 2. Characteristics of the specific component of vascular plant and moss floras in the Valdai and adjacent provinces. E – European or mostly European; CE – Atlantic-European and mostly Central-European; EN – endemics; S, A – steppe and forest-steppe or arid.

Flora	Total number of species	E	CE	EN	S, A
Vascular plants					
WCP	279(646)	122(380)	11(330)	4(70)	9(11)
BP	340(718)	130(341)	92(285)	5(38)	57(58)
VP	40(130)	4(20)	3(15)	0(4)	2(2)
SMP	109(136)	18(32)	7(12)	2(7)	48(48)
UVP	42(66)	7(17)	2(8)	1(4)	7(7)
MP	180(206)	32(44)	4(10)	6(15)	106(106)
Mosses					
WCP	195	58	49	0	13
BP	190	49	45	0	12
VP	28	5	7	0	0
SMP	42	8	3	0	6
UVP	21	3	2	0	0
MP	12	1	0	0	4

relative level of floras' representativeness decreases due to the increase of the total level of floristic richness of the territory and more local distribution of specific microspecies. The percentage of differential species and the volume of the specific component increase significantly in floras near the Atlantic. The relative values of these indexes are even higher than the corresponding qualitative characteristics of moss floras (Fig. 3B). In some cases, for example, on the VP-SMP stretch, gradients that characterize the unit weight of the specific component gain an opposite direction. The tendency to increase the volume of specific species in near-Atlantic regions has been shown for almost all agamic complexes. It is especially clear in *Hieracium* L., *Taraxacum* Wigg., *Ranunculus* L. (NOROV et al. 2004). The characteristics of geographic distribution of agamic microspecies in *Alchemilla* L. is different. In this genus, we can see a pattern of increase in the number of differential species and group volume from west to east (NOROV et al. 2004). In the Baltic as well as in Scandinavia, there are few differential species of *Alchemilla*. Also, the majority of common agamic species in Europe are probably naturalized foreign plants, which be classified now as archaeophytes. The geographic originality of floras near the Atlantic increases significantly due to the inclusion of agamic microspecies (Fig. 3D). There is a change in proportions of percentages of the Central-Atlantic-European and forest-steppe–steppe fractions. In regions near the Atlantic, the percentage of the first fraction increases, while in more continental areas the percentage of the second decreases. In general, the inclusion of microspecies increases the sharpness of longitudinal trends on the area adjacent to the Atlantic regions.

Similarity of species compositions

Indexes that characterize the similarity level of floras' species composition (the Ochiai index) are different in mosses and vascular plants (NOTOV et al. 2004). The composition of vascular plant floras with the exception of microspecies diversity is similar. The floras of SMP, UVP and VP are the most similar ones. The biggest differences have been found between MP and WCP (the Ochiai index is 0.67).

Moss floras clearly fall into two groups (NOTOV et al. 2004). One of them combines floras near the Atlantic (WCP and BP), while the other one combines the continental floras. Connections between these two groups are weak. In comparison to vascular plant floras, the connections within these groups are also weak. The maximum similarity is between WCP and BP (0.88). The minimal similarity can be seen between WCP and UVP. If we include the diversity of microspecies the vascular plant floras also make two correlational groups. The maximum similarity is between SMP and UVP (0.86), and the minimum similarity is between MP and WCP (0.60).

The features of connections in moss and vascular plant floras in geomorphologically similar provinces (VP, SMP and UVP) show some differences (NOTOV et al. 2004). In mosses, the floras of VP and SMP are more similar. The index value (0.81) is close to the maximum level for moss floras. At the same time, floras of provinces that have the biggest length of common boundary (VP and UVP) are characterized by a lesser similarity than SMP and VP (0.76). In vascular plants, the similarity between VP and UVP floras reaches the maximum value (0.92), while the floras of SMP and VP are less similar.

Specificities of moss and vascular plant floras

Within the analyzed territory and based on the main qualitative characteristics (floristic richness, relative level of floras' species richness, percentage of differential species, unit weight of the specific component, proportions of participation of differential fractions of geographic elements) longitudinal trends in moss floras are clearer and more acute than in vascular plant floras. Changes in parameters are more proportional. Latitudinal trends in moss floras are less clearly seen if they are compared with vascular plant floras. The gradients are less sharp. Some of them have an opposite direction from the vascular plant floras (for example, percentage of differential species in floras) or are not revealed due to macromosaic features (for example, volume of specific component). Comparing geographical spectra of moss and vascular plant floras we found a difference in the balance of fraction unit weight having a differential importance. The features of the geographic structure of moss floras is defined more by the Atlantic-European fraction, while the features of vascular plant floras are defined by steppe and forest-steppe fractions (Fig. 3D). These distinctions are due to the difference in how longitudinal and latitudinal physiographic gradients influence the spatial distribution of the diversity of mosses and vascular plants. The geographical distribution of mosses, unlike that of vascular plants, depends largely on the characteristics of the water conditions of the territory but less on temperature. Inclusion of the diversity of microspecies of vascular plants strengthens the longitudinal floristic trends, and in some cases 'shades' the latitudinal tendencies (for example, the decrease of the volume of the specific component in the VP – SMP area) (Fig. 3C).

Manifestation of macromosaic features within the changes in qualitative characteristics of moss and vascular plant floras depends on different factors. On the WCP – BP and VP – UVP areas the

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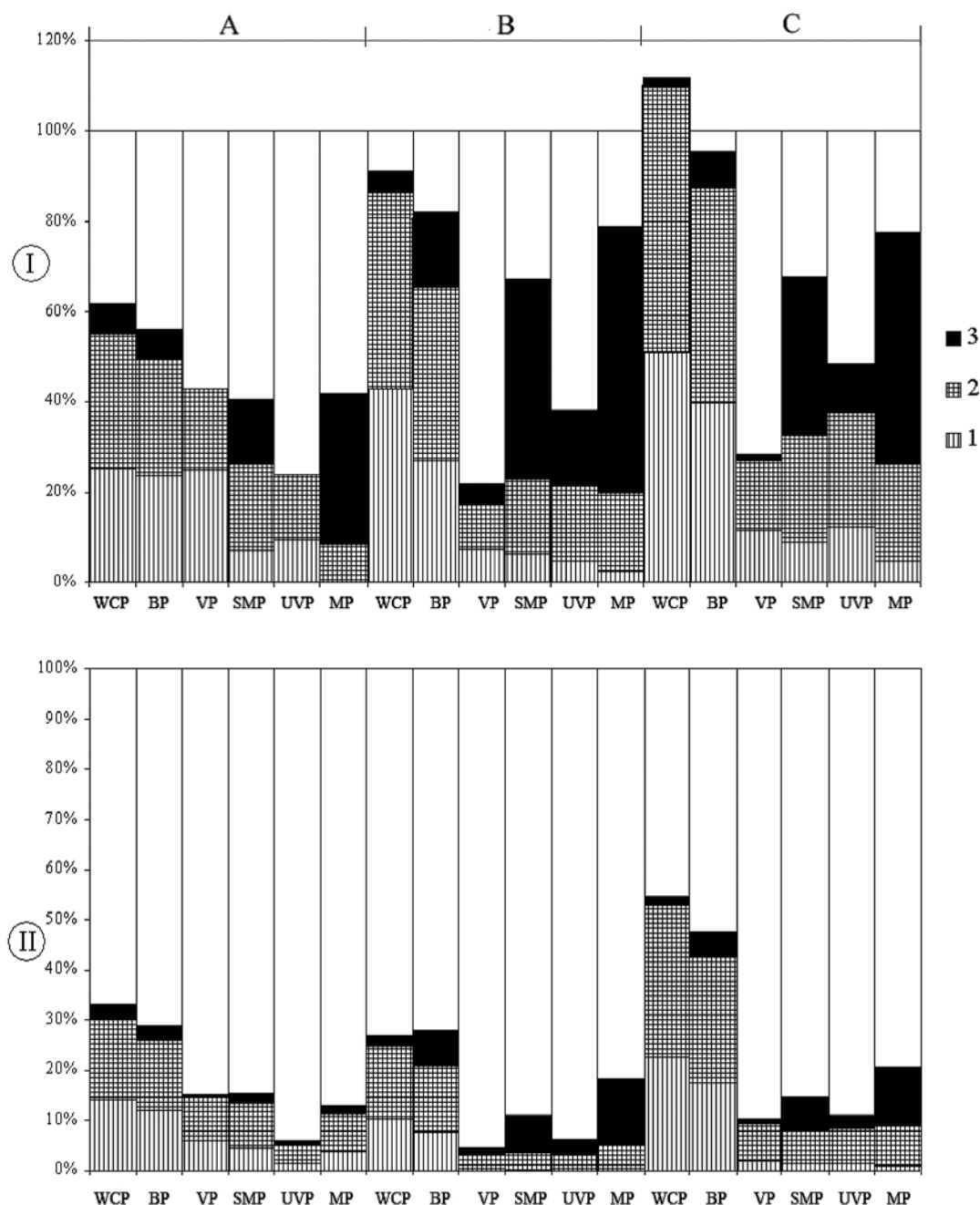


Figure 3. Percentage of some fractions of geographical elements in florae (II) and in the specific component of florae (I): A – mosses; B – vascular plants; C – vascular plants with the inclusion of microspecies; 1 – mostly Central European and Atlantic European species; 2 – European species; 3 – steppe and forest-steppe or arid species; all other symbols as in Tab. 1.

‘masking’ of directive changes of some parameters in vascular plant florae (relative level of florae’ species richness, percentages of differential species, relative volume of the specific component) (see Fig. 1, Tab. 1) can be connected with the different sizes of provinces. In case of BP, it can also be connected with the possible boundary of phytochoria on the province’s territory.

The rather low level of species richness of VP floras and its low specificity may also be the result of a more limited migration flow and steppe and forest-steppe species. With the inclusion of the diversity of microspecies in the VP – SMP area, the vascular plant trend's opposite direction can be explained by the taxonomical differentiation and settling of large agamic complexes. Within VP, there is a whole range of Scandinavian and Atlantic European microspecies from *Hieracium*, *Taraxacum*, and *Ranunculus*, which do not exist in SMP. The cases of macromosaic features of moss floras' characteristics (the opposite direction of change gradients of the specific component's percentage on the VP – SMP stretch (see Fig. 3C)) can be explained by the geomorphological features of the territory. In SMP, there are many landscapes with various microniches, which are occupied by calcareous epilithophytic plants. The same factors also define the differences between levels of similarity of species composition of moss and vascular plant floras in VP, SMP and UVP. The territories of all the studied provinces have rather large areas (98.3 km² on average) and are characterized by heterogeneity of landscape and geomorphological structures. If we analyze the parameters of specific moss floras of territories that are more homogeneous in geomorphology and landscape, macromosaic features may become more evident (NOTOV et al. 2005a).

Thus, within the boundaries of the Valdai and adjacent physiographic provinces zonal tendencies of changes in the common level of species richness and level of flora's specificity are shown up more clearly in vascular plants than in mosses. Specificities of bryofloras are defined by the longitudinal placement of the territory. The level of vascular plant floras' originality in the longitudinal direction increases if we include agamic complexes. Geomorphologic features of the territory have certain influence on the main characteristics of moss floras.

Lichen biotas

Currently, a detailed comparative analysis of lichen biotas is not possible, because many regions of Russia have different levels of exploration (NOTOV et al. 2006; URBANAVICHUS 2006). Preliminary lists of lichens of BP, VP, UVP, SMP and WCP have been compiled on the basis of research literature (252 sources which have been cited in the previous report (NOTOV et al. 2006)) and herbarium material. Regions of Central Russia which fall into the territories of these provinces were surveyed by NOTOV et al. (2006). Lists of provinces have been significantly enlarged due to new publications (TITOV 2006; KUZNETSOVA et al. 2007; MUCHNIK et al. 2007, 2009a, b; NOTOV et al. 2008; ERASTOVA et al. 2009; NOTOV et al. 2010). New studies of Saint Petersburg, Yaroslavl, Tver and Moscow regions raised knowledge to a relatively comparable level.

On the territory including all noted provinces 952 species of lichens and lichenophilic fungi have been registered until now. It is impossible to evaluate the level of species richness of the biotas of each province, because in Baltic countries it was not always possible to relate data on lichens with physiographic zoning. Due to this, a preliminary analysis of biotas of only four provinces was made (BP, VP, UVP and SMP). In BP, 761 species were registered, in SMP – 425, in VP – 490 and in UVP – 387 (see Tab. 3). This difference in level of species richness can be explained by the tendency of lichen biotas to decrease in diversity along the gradient of increase in level of continentality (see Fig. 2). The changes in indexes are similar to bryophytes. Further studies of lichens will allow a more accurate characterization of this trend, with the inclusion of the West-Coast province. Within one latitudinal interval it is characteristic of provinces with a higher level of species richness to have large highlands as well as larger distributions of landscapes

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Table 3. Level of species richness and number of differential species in lichen and myxomycete biotas of the Valdai and adjacent provinces. Below the underlined number of species are the percentages of the total number of species that have been marked on the analyzed territory.

Biota	Lichens		Myxomycetes	
	Total number of species	Differential species	Total number of species	Differential species
BP	<u>761</u> 86.6	240	<u>154</u> 75.5	32
VP	<u>490</u> 55.8	43	<u>63</u> 30.9	2
SMP	<u>425</u> 48,4	33	<u>150</u> 73,5	28
UVP	<u>387</u> 44,1	14	<u>109</u> 53,5	6

with openings of native bedrocks and scatterings of boulders (VP and SMP). The structures of taxonomical spectra of biotas in individual provinces and of the territory in general are mostly similar and reflect typical features of boreal zone floras (Norov et al. 2006).

In all provinces, there are 260 species. The level of specificity of species composition at the current stage of lichen biotas' investigation can be characterized as follows. Only in BP 240 species were registered, in VP – 43, in SMP – 33 and in UVP – 14 (Tab. 3, Fig. 2). To obtain more accurate data about the level of specificity of lichen biotas, special studies of many groups of crustose lichens are necessary. Microlichens and lichenophilic fungi have not yet been studied enough in many regions of Central Russia. In well-studied biotas microlichens are roughly twice as large in number as macrolichens (URBANAVICHUS 2006). Common lists of model territories may be significantly enlarged with a more detailed analysis of material about *Arthopyrenia* A. Massal., *Buellia* De Not., *Calicium* Pers., *Caloplaca* Th. Fr., *Chaenothecopsis* Vain., *Lepraria* Ach., *Micarea* Fr., *Pertusaria* DC., *Rinodina* (Ach.) S. Gray, *Usnea* Dill. ex Adans., *Verrucaria* Schrad. Lists of lichens of individual regions may be enlarged by studies on the diversity of *Arthonia* Ach., *Bacidia* DeNot., *Bryoria* Brodo et D. Hawksw., *Collema* F. H. Wigg., *Lecania* A. Massal., *Lecanora* Ach., *Opegrapha* Ach. Today only in one or just a few regions members of *Arthopyreniaceae* W. R. Watson, *Catillariaceae* Hafellner, *Mycoblastaceae* Hafellner, *Pannariaceae* Tuck., *Pilocarpaceae* Zahlbr., *Pyrenulaceae* Rabench., *Thelenellaceae* H. Mayrhofer, *Thrombiaceae* Poelt ex. J. C. David et D. Hawksw., *Trichothelliaceae* (Müll. Arg.) Bitter et F. Schill. have been registered.

Among the differential and specific species, there are lichens representing different geographical elements. Zonal connections in the distribution of lichens as well as in mosses is not clear-cut. The majority of the noted arctoalpine species on the territory of the Valdai Highlands and in coastal regions occur rather far south. Only a few arctoalpine species have been noted exclusively in the most northern areas of the territory (*Arctoparmelia centrifuga* (L.) Hale and *Flavocetraria nivalis* (L.) Kärnefeld et Thell). Among the arid species, *Caloplaca lactea* (A. Massal.) Zahlbr. was registered only at the southern border of the model territory.

Among the specific species of BP lichens with an oceanic-like or sub-oceanic-like character of distribution clearly stand out: *Dimerella lutea* (Dicks.) Trevis., *Hypotrachyna revoluta* (Flörke) Hale, *Lecidella laureri* (Hepp) Körb., *Leptogium palmatum* (Huds.) Mont., *Maronea constans* (Nyl.) Hepp, *Peltigera membranacea* (Ach.) Nyl., *Pertusaria flavida* (DC.) J.R. Laundon, *Punctelia subrudecta* (Nyl.) Krog, *Pyrenula nitidella* (Flörke ex Schaer.) Müll. Arg. (NOTOV et al. 2006). Longitudinal gradients can also be seen in the different activity levels and frequency of occurrence of some sub-oceanic species on the analyzed territory. Among them, there are *Acrocordia cavata* (Ach.) R.C. Harris, *Anaptychia rucinata* (With.) J.R. Laundon, *Cetrelia olivetorum* (Nyl.) W.L. Culb. et C.F. Culb., *Collema nigrescens* (Huds.) DC., *Heterodermia speciosa* (Wulfen) Trevis., *Lobaria pulmonaria* (L.) Hoffm., *Menegazzia terebrata* (Hoffm.) A. Massal., *Pertusaria hemisphaerica* (Florke) Erichsen, *Phaeographis dendricta* (Ach.) Mull. Arg., *Pyrenula nitida* (Weigel) Ach., *Sphinctrina anglica* Nyl., *Thelotrema lepadinum* (Ach.) Ach. They are common in regions near oceans, but they are rare in sub-continental and continental regions (NOTOV et al. 2006).

Geomorphological features have a significant influence on the characteristics of species distribution and on the level of species richness of floras. The distribution of a number of lichens is clearly connected with the territory of the Valdai Highlands. The relative levels of species richness and the specificity of the lichen biotas on this territory is higher than the analogous indexes for moss and vascular plant floras. On the territory of the Valdai highlands, lichens have a more complete representation of arctoalpine and montane species than mosses. Connections with Fennoscandia can be seen clearly due to a wide distribution of boulders and deep ravines with streams and rocky bottoms. In the Valdai province, various arctoalpine species (*Bellemerea cupreoatra* (Nyl.) Clauzade, *Cetraria odontella* (Ach.) Ach., *Lecidea plana* (J. Lahm.) Nyl., *Porpidia speirea* (Ach.) Kremp., *Protoparmelia badia* (Hoffm.) Hafellner, *Stereocaulon alpinum* Laurer) and montane species (*Acarospora sinopica* (Wahlenb. in Ach.) Korb., *Aspicilia gibbosa* (Ach.) Korb., *A. laevata* (Ach.) Arnold, *Dermatocarpon luridum* (With.) J.R. Laundon, *D. rivulorum* (Arnold) Dalla Torre et Sarnth., *Lecanora cenisia* Ach., *Lecidea lithophila* (Ach.) Ach., *Melanelia sorediata* (Ach.) Goward et Ahti, *Parmelia fraudans* (Nyl.) Nyl., *Rhizocarpon disporum* (Nageli ex Hepp.) Müll. Arg., *R. hochstetteri* (Korb.) Vain., *Stereocaulon saxatile* H. Magn., *Thelidium minutulum* Korb., *T. zwackhii* (Hepp) A. Massal., *Umbilicaria hyperborea* (Ach.) Hoffm., *U. polyphylla* (L.) Baumg., *U. torrefacta* (Lightf.) Schrad.) have been noted (NOTOV et al. 2006).

The specificity of biotas conditioned by geomorphological features is especially clear in territories, which are more limited in area. For example, within the Tver region in the Valdai Highlands a mass distribution of many epilithophytic species can be seen. Among them, there are *Acarospora fuscata* (Schrad.) Th. Fr., *Aspicilia cinerea* (L.) Körb., *Lecanora cenisia* Ach., *Protoparmeliopsis muralis* (Schreb.) M. Choisy, *Rhizocarpon eupetraeum* (Nyl.) Arnold, and *Xanthoparmelia conspersa* (Ach.) Hale. *Melanelia sorediata* (Ach.) Goward et Ahti can be seen regularly in the Valdai Highlands (NOTOV et al. 2006). Currently, this species has been registered in all physiographic regions of the Tver sector of the Valdai Highlands as well as in the far south-west of the region. In the Saint Petersburg region a major part of the locations of this species is on the Fennoscandian territory. Singular occurrences beyond its area are confined to the Vepsian and Tikhvin Highlands (one location in the Saint Petersburg region and three locations in the Novgorod region) (NOTOV et al. 2006).

Myxomycete biotas

Myxomycete biotas of the analyzed physiographic provinces are characterized by various levels of exploration (NOVOZHILOV 2005b; LEBEDEV 2008). VP has the least number of materials (LEBEDEV et al. 2008). Apparently, the species composition of UVP has not yet been fully identified. Due to this, the data on the levels of species richness and biotas' specificity (Tab. 3) are preliminary. The identified differences are closely connected with patchy knowledge of the territory. The best studied provinces (SMP and BP) have little differences in the level of species richness (Tab. 3).

At the current stage of analysis of myxomycetes, the data on differential and co-differential species give evidence for a higher level of distinctiveness of SMP biota (see Tab. 4). Only two differential species (*Physarum serpula* and *Symphytocarpus impexus*) have been found in VP. Each of them has been noted only in one location: marsh area in the Eremkovsky forest district in the Udomel'skij region (LEBEDEV et al. 2008). An affiliation of these species with a specific geographical element has not been established yet (NOVOZHILOV 2005b). It is possible that *Symphytocarpus impexus* and other species of these genus may be found with a more detailed examination of large marsh areas in UVP and other provinces.

Six differential species have been noted in UVP. Many of them are rare within this province. For four species (*Didymium iridis*, *Licea biforis*, *Physarum citrinum* and *P. famintzinii*) the located whereabouts are confined within the northern border of their areals in European Russia.

The significant distinctiveness of SMP biota is explained by a wider distribution of valley landscapes with exposures of carbonate-bearing rock. Many species occurring only in SMP are obligatory or facultative calciphytes (Tab. 4). An especially wide representation of calciphylic myxomycetes can be seen in the Rzhev-Staritsa Volga region with more complicated complexes of valley landscapes and emersions of carbonate-bearing rocks. An abundance of microniches has been noted here, characterized by high humidity in the stream and river shores as well as in ravines, which are all habitats of myxomycetes. The obtained data give evidence to the fact that zonal and sector features of the territory and the specificity of vegetation have a smaller significance for myxomycetes than the characteristics of microniches.

Among the co-differential species noted in VP and SMP, there is a group of 'relict' mountainous-taiga cryotolerant myxomycetes of the arctic-boreal-alpine element of the subarctic-mountainous gap (e.g., *Colloderma oculatum*, *Lepidoderma tigrinum*, *Barbeyella minutissima*, as well as members of *Cribraria* Pers.). These species are rather often associated with liverworts.

Some co-differential species registered in UVP and SMP (e.g., *Licea tenera* and *Physarum psitacinum*) can be found on the northern border of their areals in European Russia. The remaining species are members of the boreal-nemoral group. Probably some of them can be found in VP after a more detailed investigation of the territory.

Marsh areas of the Tver region need a special analysis. Four species of the *Symphytocarpus* Ing. et Nann.-Brem. have been registered there. They are rare in Russia, and they can mostly be found in the marshes of the taiga zone.

In general, the spectra of geographical elements of biotas of well-investigated provinces are typical for the taiga zone and they are characterized by a low specificity (see Fig. 4). An insignificant

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Table 4. Some differential and co-differential species of myxomycetes of the Valdai and adjacent physiographic provinces (LEBEDEV 2008, with changes). GE – geographical element; Ca²⁺ – obligatory or facultative calciphytes; bn – boreo-nemoral, n – nemoral.

Species	GE	Ca ²⁺	VP	UVP	SMP
<i>Physarum serpula</i> Morgan	?	+	+		
<i>Symphytocarpus impexus</i> Ing et Nann.-Brem.	?		+		
<i>Didymium iridis</i> (Ditmar) Fr.	bn	+		+	
<i>Licea biforis</i> Morgan	bn			+	
<i>Lycogala conicum</i> Pers.	n			+	
<i>Physarum citrinum</i> Schum.	?	+		+	
<i>P. famintzinii</i> Rost.	bn	+		+	
<i>Symphytocarpus flaccidus</i> (Lister) Nann.-Brem.	n			+	
<i>Badhamia nitens</i> Berk.	?	+			+
<i>B. panicea</i> (Fr.) Rost. in Fuckel	bn	+			+
<i>Brefeldia maxima</i> (Fr.) Rost. in Fuckel	n				+
<i>Diderma alpinum</i> Meylan	?	+			+
<i>D. globosum</i> Pers.	bn	+			+
<i>D. hemisphaericum</i> (Bull.) Hornem.	bn	+			+
<i>D. niveum</i> (Rost.) Macbride	bn	+			+
<i>D. ochraceum</i> Hoffm.	?	+			+
<i>D. radiatum</i> (L.) Morgan	bn	+			+
<i>D. testaceum</i> (Schr.) Pers.	bn	+			+
<i>Didymium minus</i> (Lister) Morgan	bn	+			+
<i>D. serpula</i> Fr.	bn	+			+
<i>Physarum bivalve</i> Pers.	bn	+			+
<i>P. compressum</i> Alb. et Schw.	bn	+			+
<i>P. confertum</i> Macbride	bn	+			+
<i>P. decipiens</i> Curt.	bn	+			+
<i>P. dictyospermum</i> Lister et G. Lister	?	+			+
<i>P. galbeum</i> Wingate	?	+			+
<i>P. gyrosum</i> Rost.	bn	+			+
<i>P. murinum</i> Lister	?	+			+
<i>P. nudum</i> Macbride in Peck et Gilb.	bn	+			+
<i>P. oblatum</i> Macbride	bn	+			+
<i>P. pezizoideum</i> (Jungh.) Pav. et Lag.	n	+			+
<i>P. pusillum</i> (Berk.) G. Lister	bn	+			+
<i>P. rubiginosum</i> Fr.	bn	+			+
<i>P. stellatum</i> (Masse) G. W. Martin	?	+			+
<i>P. tenerum</i> Rex	bn	+			+
<i>P. vernum</i> Somm. in Frees.	bn	+			+
<i>Colloderma oculatum</i> (Lipp.) G. Lister	bn		+		+
<i>Cribraria purpurea</i> Schr.	bn		+		+
<i>C. splendens</i> (Schr.) Pers.	bn		+		+
<i>Lepidoderma tigrinum</i> (Schr.) Rost.	bn		+		+
<i>Physarum leucopus</i> Link	bn	+	+		+
<i>Licea tenera</i> Jahn	bn			+	+
<i>L. variabilis</i> Schr.	bn			+	+
<i>Lindbladia tubulina</i> Fr.	bn			+	+
<i>Lycogala exiguum</i> Morgan	bn			+	+
<i>L. flavofuscum</i> (Ehr.) Rost. in Fuckel	bn			+	+
<i>Physarum conglomeratum</i> (Fr.) Rost.	bn	+		+	+
<i>P. didermoides</i> (Pers.) Rost.	bn	+		+	+
<i>P. flavicomum</i> Berk.	bn	+		+	+
<i>P. globuliferum</i> (Bull.) Pers.	bn	+		+	+
<i>P. polycephalum</i> Schw.	?	+		+	+
<i>P. psitacinum</i> Ditmar in Sturm	bn	+		+	+
<i>Reticularia splendens</i> Morgan	bn			+	+
<i>Stemonitis flavogenita</i> E. Jahn	bn			+	+
<i>S. pallida</i> Wing. in Macbride	bn			+	+
<i>S. smithii</i> Macbride	bn			+	+
<i>Stemonitopsis typhina</i> (F. H. Wigg.) Nann.-Brem.	bn			+	+
<i>Symphytocarpus amaurochaetoides</i> Nann.-Brem.	?			+	+
<i>S. confluens</i> (Cooke et Ellis) Ing. et Nann.	bn			+	+

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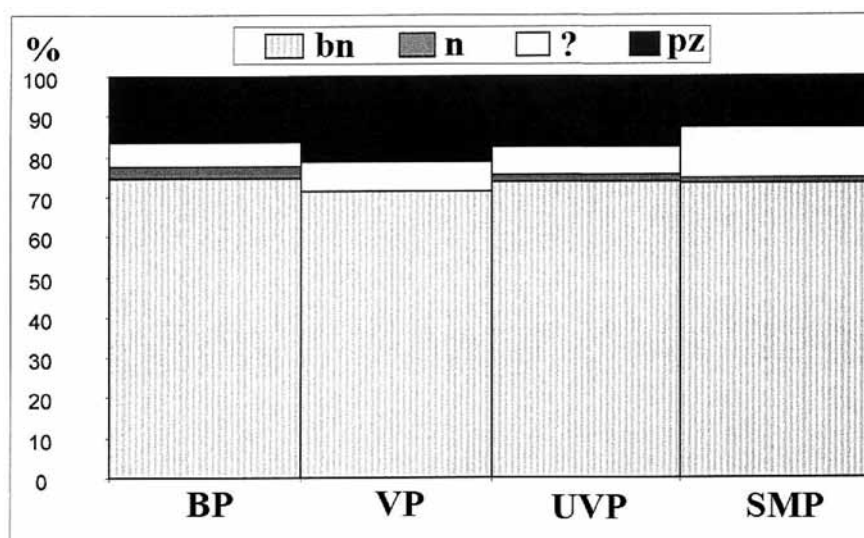


Figure 4. The spectrum of geographical elements of myxomycete biotas in the Valdai and adjacent physiographic provinces (LEBEDEV 2008, with changes): bn – boreal-nemoral, n – nemoral, pz – plurizonal.

increase in the percentage of boreal-nemoral species in the VP-UVP-SMP group, as well as somewhat of an increase of the role of polyzonal species can be seen. The percentage of the first group in BP is smaller than in VP and UVP. Apparently, the change of the degree of continentality has an insignificant influence on the geographical structure of the myxomycete biotas within the forest zone. This is also supported by the composition of the spectrum of noted geographical element groups (NOVOZHILOV 2005b). Myxomycetes are a biota component whose geographical distribution of its diversity is mainly influenced by the characteristics of specific microniches. Latitudinal and longitudinal trends are poorly expressed.

Conclusion

Thus, for further development of integrated biogeographical analysis of various biota components the realization of programs on complex studies of model territories of large sizes are necessary. The East European Plain may be used as such a model territory, because various phytogeographical zones, geomorphological areas and provinces are present. It is logical to use physiographic zoning together with an integrated analysis of various components. Nowadays, it is relevant to search for characteristics, figures and indexes which allow to compare different biotas. It is also logical to find out how the ascertained trends depend on the features of latitudinal climate differentiation and vegetation, specifics of geomorphology, and characteristics of confinement of various taxonomical groups to phytocoenoses and microniches. In the preliminary analysis of material, a large importance is attributed to the revealing of geographical specifics of differential and co-differential species.

Within the Valdai and adjacent physiographic provinces, zonal tendencies of change in species richness as well as degrees of flora specificity can be seen more clearly in vascular plants than in mosses. Specifics of bryofloras are mainly defined by the longitudinal location of the territory. The degree of originality of vascular plant floras in the longitudinal direction increases with the inclusion of the agamic complexes of *Hieracium* and *Taraxacum*.

Zonal tendencies in the changes of diversity parameters of lichen biotas as well as mosses of the Valdai and adjacent physiographic provinces can be seen less clearly than longitudinal trends which are due to the increase of continentality. Levels of diversity and specificity of moss floras and lichen biotas are somewhat dependent on geomorphological features of the territory. Floras and biotas of provinces with large highlands, exposures of bedrock and scatterings of boulders are characterized by a higher level of diversity and specificity.

It seems that geographical distribution of myxomycete diversity is less influenced by longitudinal and latitudinal features of the territory than the distribution of vascular plants, mosses and lichens. The degree of diversity of myxomycetes is largely dependent on the width of distribution of specific microniches. Richer biotas occur in physiographic regions and provinces where various habitats with exposures of carbonate-bearing rocks are usual.

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