Distribution pattern of seven *Polytrichum* species in the East European Plain and Eastern Fennoscandia

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ABSTRACT

Distribution of seven species of the genus *Polytrichum* (*P. commune*, *P. hyperboreum*, *P. jensenii*, *P. juniperinum*, *P. piliferum*, *P. strictum* and *P. swartzii*) on the territory of the East European Plain and Eastern Fennoscandia (EEPEF) was studied. For each species, model maps of distribution ranges were constructed and the causes that determine the pattern of species are considered. Distribution of most species correlates to a high degree with spatial changes in the amount of precipitation, relative humidity and monthly temperature averages during the vegetative season. However, *P. piliferum* is an exception to this rule, as its distribution is influenced not only by climate, but also by location of fluvioglacial deposits on the territory of EEPEF. Distribution range of *P. hyperboreum* and *P. jensenii* is mainly limited by Subarctic region (Tundra and Forest-Tundra), and this range looks diminishing.

Keywords: *Polytrichum*, kriging-method, distribution range, Biogeography, climatic optimum, arecological analysis, BIOCLIM

РЕЗЮМЕ

Попов С.Ю. Закономерности распространения семи видов рода *Polytrichum* на территории Восточно-Европейской равнины и восточной Фенноскандии. Изучено распространение семи видов рода *Polytrichum* (*P. commune*, *P. hyperboreum*, *P. jensenii*, *P. juniperinum*, *P. piliferum*, *P. strictum* и *P. swartzii*) на территории Восточно-Европейской равнины и Восточной Фенноскандии (ВЕРВФ). Для каждого вида построены модельные карты ареалов и рассмотрены причины, обуславливающие рисунок ареалов видов. Распространение большинства видов высоко коррелирует с изменением количества осадков, относительной влажности воздуха и среднемесячных температур вегетационного периода. Однако, *P. piliferum* является исключением из этого правила, поскольку его распространение обусловлено не только климатом, но распространением флювиогляциальных отложений на территории ВЕРВФ. Распространение *P. hyperboreum* и *P. jensenii* связано преимущественно с северными регионами – тундрой и лесотундрой, а их ареалы имеют рисунок сокращающихся.

Ключевые слова: *Polytrichum*, кригинг, ареал, биогеография, климатический оптимум, ареалогический анализ, BIOCLIM

At present, as the floras of most regions are very well studied and due to development of GIS, biogeography raises the question of establishing the boundaries of individual taxa and biogeographic regions on quantitative basis with the help of statistical methods (Mateo et al. 2011). At the present stage of the development of bryology, the bryophytes of various regions are well studied. Studies of local and regional bryofloras conducted by different researchers starting from the late 20th century produce almost complete inventory of the bryoflora on such a large territory as the East European Plain and Eastern Fennoscandia (EEPEF). Therefore, the task of generalizing these materials, of visualizing them on maps, and of establishing the biogeographical patterns of the species' distribution and the species' diversity is extremely topical. Spatial distribution of species depends on many factors. At the local (regional) level, it is determined by the habitat parameters (Clymo 1982, Maksimov 1982, Gignac & Vitt 1990, Gignac

et al. 1991, Hájková & Hájek 2007, Wojtun 2013, Popov & Fedosov 2017, Smagin et al. 2017 and many others). At a more global level (interregional and subcontinental, i.e. covering several natural zones), climate exerts the dominant influence on species' distribution (Woodward 1987) and the main climatic factors of species' distribution, i.e. monthly and annual temperature averages, precipitation, humidity and others, might be considered as leading (Gignac & Vitt 1990, Gignac et al. 1991, Melosik 2006, Séneca & Söderström 2008, Popov 2016).

Of course, these above mentioned two approaches have a different format, which is due to the fact that the scope of examination is different. Thus, at the local level one can study the biotopic distribution. While at the interregional level the biotopic distribution is invisible because of the smaller scale, and we consider the species' occurrence in the local floras of the region. At this case the species' distributional range is compiled from the set of local floras. Thus,

considering the distribution of the species in large areas on a smaller scale, we have to abandon the study of its biotopic distribution and the study of ecological factors affecting the species' coenotic distribution. In this case, we turn to arealogical analysis and to studying the biogeographical patterns of species' distribution. The traditional task of biogeography is to identify the boundaries of the species' ranges and to find patterns of species' distribution determined by geographical, biotic and climatic factors (Tolmachev 1974). In biogeography, the ecological aspect of the analysis of the species' distribution is most often associated with the concept of an ecological niche as it was defined by Grinnel (1917), i.e. the response of a species to spatial changes in environmental parameters. In contrast to the ecological niche as defined by Hutchinson (1965) (which is determined by the properties of species in the hyperspace of environmental factors, i.e. the species' own properties, and not these of the environment), the Grinnel's niche is attached to environmental parameters, which alteration determines the species' distribution. Therefore, comparing, for example, the climatic factors and the species' quantitative characteristics in a certain space, it is possible to identify the species' climatic optimum and pessimum. So far, the problem of analyzing the species' range has been mostly solved with vascular plants and animals, in order to establish the boundaries of natural zones and to map the species' diversity (Kurnaev 1973, Tolmachev 1974, Schmidt 1979, Danilenko & Rumyantsev 2000, Ignatov 1993, Kier et al. 2005, Krestov et al. 2006).

At present, the task of creating a species' distributional range is done with the help of computer simulation methods (Mateo et al. 2011). The model's verity and reliability depend on the choice of predictors and on the modeling method, scale, ways of interaction between environmental and geographic factors and the extrapolation method used.

The maximum entropy method is now increasingly used in mathematical modeling of species' ranges (Sergioa 2005, Phillips et al. 2006, Puzachenko et al. 2011, Mateo et al. 2013). This method allows building a model of species' ranges with the use of binary data (presence-absence). However, a model map based on binary data allows us only to estimate the boundaries of the range as a whole. The species' quantitative characteristics within the range (such as occurrence and abundance) can not be considered.

Another commonly used method for compiling a species' range is dot mapping based on the herbarium data (for example, GBIF, Ivanov et al. 2017). This method has evident superiority in accuracy and reliability in installing the points, but it can not guarantee the completeness of coverage – simply because no territory sufficiently large can be explored in full, and certainty of data for those places, where herbarium specimens have not been collected, will always remain a question (Mateo et al. 2011). Moreover, this method is extremely time-consuming, and it takes a lot of time to identify the species' location points. As a rule, dot mapping gives us an objective picture of what we know about the species' distribution of, but not of the species' actual distribution. Such method of mapping can take dozens of years (Lahti & Lampinen 1999). However, despite

the limitations that the species' presence data have, actually the vast majority of studies are based on this type of data, since the data on the species' absence are simply lacking.

The simplest method for studying floristic diversity is Zonal Statistics (Ignatov 1993, Geffert et al. 2013, Pisarenko & Bakalin 2017). This method allows using statistical indicators (average, minimum, maximum, etc.) for individual regions already mapped. Thus, statistics for administrative regions or ecoregions can be used. It is clear that this method permits us only to identify general trends, without drawing natural boundaries of species' range. In addition, when using Zonal Statistics, one needs to recalculate the number of species per area – since the compared regions can vary in area quite widely (Arrhenius 1921).

There are also a large number of quantitative methods for creating spatial models for species or species' diversity that are based on multidimensional statistics. When creating such models, we choose climatic and non-climatic (relief, soil, etc.) factors as independent variables, and the presence / absence (or quantitative characteristics) of species or the number of species at the point studied – as depended ones (Phillips et al. 2006). Paradoxically, when generating models of species distribution by methods of multidimensional techniques, which result in a map, the spatial relationships between the points are not considered, since each point's coordinates are used exclusively to extract the values of independent variables at that point, without taking into account what is happening around. The fact is that the multidimensional statistics methods estimate the value of a particular point with no regard to the neighboring points' values. Possible spatial correlation between the independent variables is also not taken into account. Therefore, in my opinion, these methods are more suitable for creating maps of potential distribution (based on predictors' values) than for creating maps of the species' real distribution (based on an independent basis).

Whichever method of mapping is used, a critical evaluation of the data's reliability on individual locations has great importance. As a rule, one has to rely on a large amount of data available in the literature. Often one cannot be absolutely confident in the correctness of the species' definition.

Geostatistics can help us to overcome all these problems. Geostatistical methods are based on interpolation of quantitative data obtained during field studies in an irregular network of points, and transforming it into a regular grid of pixels. In other words, when an irregular network of values is turned into a regular one, the data fill all the points where measurements have not been made. This can be realized with the help of kriging-method (Demyanov & Savelieva 2010, Lurie 2010, Saveliev et al. 2012), which is based on regression equations, where the comparative weights of points (by distance from each other), correlations between points and variance are also considered. Among all methods of Geostatistics, the kriging-method is the most powerful, since it permits 1) to establish a general trend of the values' changes in space (deterministic variation), 2) to make visible autocorrelation, and 3) to cut off possible noises, and to compile on this basis a statistically significant coverage (Demyanov & Savelieva 2010, Lurie 2010, Saveliev

et al. 2012). Finally, methods of geostatistics (in contrast to the multivariate analysis) permit to consider spatial correlation between points based on their weights. Therefore, even when there are no data for a space between two points with known values, the kriging method permits to interpolate possible deviations from the general trend.

Currently, geostatistical methods are extensively used in such areas of science, as environmental science (air pollution maps), climatology and meteorology (temperature distribution maps, precipitation distribution, and so on), geodesy and cartography (Digital Elevation Model) (Demyanov & Saveliev 2010, Lurie 2010). However, these methods have not been used yet in biogeography to study the species' distribution. Perhaps this can be explained by the territories' insufficient exploration (a sufficient number of points is required to create a valid continuous coverage).

The East European Plain, with its vast lowland territory, can be used as a model area for studying regularities of the species' distribution caused by climatic variables. For the last 30–40 years a lot of local moss flora lists within this area have been published. Thus now it seems to be possible to compile maps of individual species' ranges based on this data. In addition, WORLDCLIM / BIOCLIM climate database (Hijmans et al. 2005) was made available to the public recently, and it provides suitable climatic data to study the species' spatial distribution patterns in the climatic context.

Previously, I have already analyzed the distribution of some species of the *Sphagnum* genus using geostatistics methods (Popov 2016). The methodology for creating model maps of species' ranges is adapted to the goals of biogeography (Popov 2017). For the present work, we have chosen as the objects of study seven species of the genus *Polytrichum*, related to sections *Polytrichum* and *Juniperina* (*Polytrichum commune*, *P. hyperboreum*, *P. jensenii*, *P. juniperinum*, *P. piliferum*, *P. strictum* и *P. swartzii*) (Ignatov 2017). The goal of this work is to compile and to visualize a distributional ranges model for these species and to analyze the patterns of their distribution. Since the scale we use is too small to regard the species' biotopic distribution, and only the species' presence in local floras and its occurrence over the territory is considered, the hypothesis that the climatic factors have primary influence on the species' distribution has been taken as the basic one. In addition, we also compared the patterns of the species' areas with the boundaries of natural zones (Ahti et al. 1968, Kurnaev 1973) and the contours of a landscape map (Isachenko 1988).

MATERIAL AND METHODS

In order to study distribution of species of the genus *Polytrichum* on the EEPEF, we analyzed publications, which contain annotated lists of local bryofloras in different regions (European part of the Russian Federation, the Baltic States, Belarus, Moldova, Ukraine and Finland). The annotated lists usually note the geographical coordinates of the area studied and of the species' occurrence. All these data were compiled into a relational database created with the help of MS Access. The moss collection points were superimposed on the EEPEF map following the geographic coordinates (see Fig. 1). The species' occurrence in diffe-

rent lists is estimated either by number of herbarium specimens of each species, or by number of records made by the collector, or by collector's general impression. Taking all this in account, for compiling our database, we assessed each species' occurrence by a six-point scale:

- 0 – species absent,
- 1 – 1–2 records (very rare),
- 2 – 3–7 records (rare),
- 3 – more than 7 records, but not everywhere (sporadic),
- 4 – frequent, but not always present in suitable habitats (frequent),
- 5 – common and always present in suitable habitats (common).

Data on the occurrence were taken from the articles of different authors, cited in the caption to Fig. 1. In addition, in order to correct old and erroneous data, the latest issue of *Moss flora of Russia* (Ignatov 2017) and the Global Biodiversity Information Facility (<http://www.gbif.org/>) were used, as these sources provide information on availability of herbarium material for each species in different regions of EEPEF.

According to the scale described above, continuous coverage for each species was established using the kriging method (Demyanov & Savelyeva 2010) with a resolution of 10 km per 1 pixel. Validation of continuous coverage was carried out by cross-validation method with the SAGA GIS software. Geostatistics uses the coefficient of determination (R^2) as the index of cross-validation quality (Demyanov & Savelyeva 2010). The values of this indicator for continuous coverage of all species studied vary from 0.972 to 0.995 (Fig. 3 and 4). Methods of geostatistics used for creating and verifying continuous coverage, have already been described in literature (Demyanov & Savelyeva 2010, Savelyev et al. 2012). Methods for creating maps of the moss species' distribution based on a point layer were described in details in a previous publication (Popov 2017). In total, a sample of 177 points was used to create continuous coverage (see Fig. 1).

To analyze the dependence of the species' distribution on climatic factors, the variables recommended for studying distribution of biological objects within the programs WORLDCLIM and BIOCLIM (BIOCLIM project 2009) were chosen. A total of 43 climatic variables were included in the analysis (see Table 1). The authors of the WORLDCLIM program calculated these variables having compiled information from the world network of meteorological stations (Hijmans et al. 2005). For each variable of the BIOCLIM database, continuous grid coverages with a resolution of 10 km per 1 pixel were created.

Continuous coverages of the species' occurrence were rearranged in the ArcGis program with the help of the “natural breaks” method (Lurie 2010, Popov 2013) into integer ones for mapping species' distribution. In addition, the species' distribution was compared with the boundaries of vegetation zones, which in the present work are given after Ahti et al. 1968, Kurnayev 1973 (see Fig. 1).

Each GRID coverage was composed in Azimuthal Equidistant Projection (central meridian 45°E, chief parallel – 55°N). In total there were compiled 43 grid coverages for BIOCLIM data, and 8 – for the occurrence of

Figure 1 Study area, showing localities involved in analysis and vegetation zones: I – Tundra; II – Forest-Tundra; III – Northern Taiga; IV – Middle Taiga; V – southern taiga; VI – Hemiboreal Forests; VII – Broadleaved Forests; VIII – Forest-Steppe; IX – Steppe; X – Semidesert; XI – Desert. Study sites: 1–18 – Söderström 1998; 19 – Belkina & Likhachev 2004; 20 – Likhachev & Belkina 1999; 21–23 – Shlyakov & Konstantinova 1982; 24 – Belkina & Likhachev 2010; 25 – Drugova et al. 2017; 26 – Belkina & Likhachev 1997; 27–29 – Shlyakov & Konstantinova 1982; 30 – Bogdanova 1981; 31–32 – Abramov & Volkova 1998; 33 – Boichuk 2001; 34 – Churakova 2002; 35 – Boichuk 2002; 36–39 – Kurbatova 2002; 40 – Andreeva & Filip'eva 2005; 41 – Vellak et al. 2015; 42–43 – Abolin 1968; 44 – Dolnik & Napreenko 2007; 45 – Söderström 1998; 46 – Strazdiņa et al. 2011; Söderström 1998; 47 – Stebel 2012; 48–51 – Rykovsky & Maslovsky 2009; 52 – Dite et al. 2007; 53 – Papp et al. 2010; 54 – Erzberger et al. 2012; 55–57 – Zerov & Partyka 1975; 58–59 – Lazarenko 1955; 60–61 – Gapon 1997; 62–64 – Simonov 1978; 65–69 – Boiko 2009; 70–72 – Popova 2002; 73–74 – Sereda & Ignatov 2008; 75–77 – Partyka 2005; 78–80 – Ignatova et al. 2005; 81 – Doroshina 2011; 82 – Akatova & Ignatova 2015; 83 – Akatova 2002; 84 – Doroshina 2015; 85 – Ignatova et al. 2008; 86 – Kharzinov et al. 2004; 87 – Abakarova et al. 2015; 88 – Ignatov et al. 2010; 89–92 – Doroshina 2011; 93–96 – Suragina et al. 2002; 97 – Suragina 2001; 98–105 – Spirina & Zolotov 2004; 106–108 – Suragina 2001; 109–115 – Popova 2002; 116 – Teleganova 2008; 117 – Popova et al. 2015; 118 – Serebryakova 2009; 119 – Doroshina-Ukrainskaya 1999; 120 – Popov 2000; 121 – Zolotov & Baisheva 2003; 122 – Baisheva et al. 2015; 123–124 – Ariskina 1978; 125 – Ignatov et al. 2005; 126 – Popov et al. 2001; 127 – Volosnova et al. 2000; 128 – Ignatov et al. 2011; 129–130 – Popov et al. 2004; 131 – Czernjadjeva 2001a; Czernjadjeva et al. 2013; 132 – Rubtsova 2005; 133 – Bezgodov 2002; 134 – Dyachenko et al. 1996; 135 – Ignatova et al. 1995; 136 – Zheleznova 2014; 137–138 – Fedosov & Popov 2004; 139–140 – Volkova et al. 1994; 141 – Notov et al. 2002; 142 – Ignatov et al. 1998; 143 – Karnazina 2013; 144 – Filippov & Boichuk 2015; 145 – Zheleznova 2014; 146 – Djachenko & Djachenko 2010; 147 – Ignatova et al. 1996; 148 – Zheleznova & Shubina 1997; 149–158 – Zheleznova 1994; 159–162 – Churakova 2002; 163 – Boichuk et al. 2002; 164–166 – Ignatov et al. 2008; Popov & Buryanina 2012; 167 – Zheleznova & Shubina 2015; 168 – Czernjadjeva 1994; Czernjadjeva 2001b; 169–171 – Afonina & Czernjadjeva 1995; Czernjadjeva 2001b; 172 – Natcheva & Ganeva 2005; 173 – Ignatov & Ignatova 2003; 174 – Notov et al. 2002; 175 – Maksimov et al. 2009; 176 – Bolyukh 1995; 177 – Shestakova 2005

selected species and species number. All of them were combined into a single spatial coverage. This coverage was transformed into relation database consisting of 49 557 rows (number of pixels) and 51 columns (7 species, 1 species number and 43 climatic factors) in ERDAS package. This database was subjected to correlation analysis with software Statistica 6.0. Creation and verification of coverages were performed with SAGA software. The intersection of the vector layers and calculation of areas were performed with ArcGIS program.

RESULTS AND DISCUSSION

The general patterns of the spatial variation of climatic factors in the study area were set out by us earlier (Popov 2016). In brief, they consist in the fact that the western regions during the growing season are characterized by a much greater amount of precipitation than the central and eastern ones, which is due to the patterns of movement of Atlantic cyclones from west to east. As a result, such regions as the west of Ukraine and Belarus, the Baltic States, the North-West of Russia, Karelia and Finland are the most humid, especially during the autumn-summer period, i. e. in August–October. The distribution of summer temperatures is associated with zonal patterns of distribution of the solar insolation. In addition, humidification of some regions is increased due to the presence of large bodies of water (Alisov 1956) (see Fig. 2).

Table 1. Variables used in the analysis from the database BIOCLIM

Codes	Explanations
tm 01-12	Monthly temperature, °C (January to December)
pr 01-12	Monthly precipitation, mm (January to December)
reh 04-10	Relative humidity, % (April to October)
pr_a	Annual precipitation, mm
amt	Annual Mean Temperature
pr_wtm	Precipitation of Wettest Month
pr_drm	Precipitation of Driest Month
pr_wtq	Precipitation of Wettest Quarter
pr_drq	Precipitation of Driest Quarter
pr_wmq	Precipitation of Warmest Quarter
pr_clq	Precipitation of Coldest Quarter
t_wtq	Mean Temperature of Wettest Quarter
t_drq	Mean Temperature of Driest Quarter
t_wmq	Mean Temperature of Warmest Quarter
t_clq	Mean Temperature of Coldest Quarter

Figure 2 The distribution of the most important climatic variables on the territory of the East European Plain and Eastern Fennoscandia: **precip_july...sept** – summ of precipitation of August–September; **reh_july...sept** – relation humidity of August–September. **tm_july...sept** – monthly temperature of August–September; **pr_a** – annual precipitation; **amt** – mean annual precipitation; **pr_wmq** – precipitation of Warmest Quarter. The red lines show the boundaries of the vegetation zones

The model maps of the distribution ranges for the species studied are shown on Fig. 3.

***Polytrichum commune*.** The results of modeling this species' range show that the species is widely distributed in the territory of EEPEF. It grows in all vegetation zones (see Fig. 3, Table 2). The maximum occurrence (**com**) is observed in the Forest zone and in the Tundra and Forest-Tundra zones of Polar Urals (Fig. 3). Area of the **com** zone makes more than half of the total area of EEPEF – 52.2 % (see Table 2). To the north and to the south of the Forest zone, the occurrence of *P. commune* is gradually decreasing (see Fig. 3, Table 2). This species becomes rare and very rare in the south starting with the Steppe zone. In Forest-Steppe and Broad-Leaved Forests zones its abundance varies from **vr** to **fr**. Summarily, this species' area covers 94.3 % of the total area of EEPEF (see Table 2).

***Polytrichum strictum*.** This species' area covers all the vegetation zones, except the Desert zone (see Fig. 3, Table 3). The species has the highest occurrence in the Tundra and Forest-Tundra zones – and not in the Forest zone, as *P. commune*. Area of the **com** zone is small – only 6.3 % of the total area of EEPEF. This is due to the fact that Tundra and Forest-Tundra zones cover rather a small part of the territory of EEPEF (see Table 3). However, *P. strictum* is also quite frequent in the Forest zone. Area of the zone **fr** of this species makes 55.5 % of the total area of EEPEF. The **fr** and **com** zones together make 61.8 % of the total

area (see Table 3). *P. strictum* gradually disappears from the cover to the south of the Forest zone (see Fig. 3, Table 3). In the Steppe and the Semidesert zones this species is rare or very rare. In different regions in the southern part of the Forest zone and in the Forest-Steppe, its abundance varies from **vr** to **fr** (see Table 3). Summarily, the *P. strictum* area occupies 81.2 % of the total area of EEPEF.

***Polytrichum juniperinum*.** This species occurs in all vegetation zones, but does not reach high occurrence (**com**) anywhere. However, from the Tundra, throughout the Forest zone and even slightly to the south, this species occurs quite often (**fr**) (Fig. 3, Table 4). In the zones of Deciduous forests, Forest-Steppe and Steppe, the abundance of *P. juniperinum* varies from **r** to **fr**. In the Steppe, Semidesert and Desert zones – very rare (see Table 4). Summarily, area occupied by the range of this species makes 98.6 % of the total area of EEPEF.

***Polytrichum piliferum*.** Distributed in all vegetation zones, except the Desert zone (see Fig. 3, Table 5). It does not reach status of widespread (**com**) in any region, but is a common species (**fr**) in four regions (Fig. 3) for reasons that will be discussed below. About half of the area of EEPEF (48.9 %) is the zone of sporadic distribution (**sp**) of *P. piliferum*. In general, area of this species' range makes 97.0 % of the total area studied (see Table 5).

***Polytrichum hyperboreum*.** This species occurs only in the Forest and the Tundra zones, though not everywhere

Table 2. Zones of abundance of *P. commune* by the vegetation zones, km²

Zones	Frequency						Total	Percent of zones from total
	abs	vr	r	sp	fr	com		
Tundra	.	.	.	45640.8	127773.4	18344.0	191758.2	3.9
Forest-Tundra	.	.	.	.	32857.8	69234.1	102091.9	2.1
North Taiga	.	.	.	.	13464.8	537262.9	550727.7	11.1
Middle Taiga	.	.	.	.	26056.1	721963.5	748019.6	15.1
South Taiga	.	.	.	27837.8	60211.7	451924.3	539973.8	10.9
Mixed Forest	.	.	.	60038.7	53549.1	700736.5	814324.3	16.4
Broadleaves Forest	6876.6	9558.3	96964.7	142404.7	176101.8	85244.3	517150.5	10.4
Forest-Steppe	15938.7	120876.1	264708.6	108052.3	13127.1	.	522702.9	10.5
Steppe	93930.3	516889.0	97763.5	.	.	.	708582.7	14.3
Semidesert	112602.2	84781.5	7376.2	.	.	.	204760.0	4.1
Desert	54859.7	4.1	.	.	.	.	54863.8	1.1
Total	284207.5	732109.0	466813.0	383974.4	503141.8	2584709.6	4954955.4	100.0
Percent of zones from total	5.7	14.8	9.4	7.7	10.2	52.2	100.0	

Table 3. Zones of abundance of *P. strictum* by the vegetation zones, km²

Zones	Frequency						Total	Percent of zones from total
	abs	vr	r	sp	fr	com		
Tundra	.	.	.	.	16133.0	175625.2	191758.2	3.9
Forest-Tundra	.	.	.	.	38746.2	63345.7	102091.9	2.1
North Taiga	.	.	.	.	476885.4	73842.3	550727.7	11.1
Middle Taiga	.	.	.	.	748019.4	0.2	748019.6	15.1
South Taiga	.	.	.	2873.9	537099.9	.	539973.8	10.9
Mixed Forest	.	.	23.8	48797.3	765503.2	.	814324.3	16.4
Broadleaves Forest	9232.4	25763.8	81202.7	239879.1	161072.5	.	517150.5	10.4
Forest-Steppe	95471.2	125261.1	209851.1	84758.6	7360.9	.	522702.9	10.5
Steppe	566124.9	114985.9	27471.9	.	.	.	708582.7	14.3
Semidesert	203871.1	888.9	.	.	.	.	204760.0	4.1
Desert	54863.8	.	.	.	.	.	54863.8	1.1
Total	929563.3	266899.7	318549.6	376308.9	2750820.5	312813.4	4954955.4	100.0
Percent of zones from total	18.8	5.4	6.4	7.6	55.5	6.3	100.0

Figure 3 The model maps of seven species of the genus *Polytrichum*. Zones of abundance are given in green color gradient. Abbreviations for zones: *abs* – absence; *vr* – very rare; *r* – rare; *sp* – sporadic; *fr* – frequent; *com* – common or widespread. Red lines – boundaries of vegetation zones. For each species on the maps is shown an index of significance of the coverages crossvalidation – R^2

even in these regions (see Fig. 3, Table 6). It is not widespread anywhere, but in the Tundra it is characterized by frequent occurrence (*fr*). In general, this species' range occupies only 18.2 % of the total area of EEPEF.

***Polytrichum jensenii*.** This species is found in many vegetation zones, from the Forest-Steppe to the Tundra (see Fig. 3, Table 7), but reaches high occurrence nowhere. Sporadically occurs only in the northern part of its range, and the *sp* zone makes only 3.2 % of its total area (see Table 7). Further to the south it becomes very rare. The *vr* zone makes the largest part of the range's area (19.2 %), and this sharply distinguishes this species' range from previous ones. In general, the *P. jensenii* area makes 27.3 % of the total area of EEPEF.

***Polytrichum swartzii*.** It is very unevenly distributed from the Forest-Steppe to the Tundra zones, being very rare in most places (see Fig. 3, Table 8). Within this species'

range, one can distinguish the zones of very rare (*vr*) and rare (*r*) occurrence. Area of zone *vr* is about 3 times larger than that of the zone *r*. The entire range of this species makes 31.6 % of the total area of EEPEF.

Fig. 3 shows that four species: *P. commune*, *P. strictum*, *P. piliferum* and *P. juniperinum*, are spread widely throughout the territory of EEPEF and are quite abundant in most of the territory. Three other species: *P. hyperboreum*, *P. jensenii* and *P. swartzii*, occupy a smaller area, mainly in the northern regions, and have low occurrence. They are restricted species on the territory of EEPEF.

P. commune, *P. strictum* and *P. juniperinum* have the maximum occurrence in the Forest and the Tundra zones (see Fig. 3), which best correlates with the relative humidity indicators for August and September in the territory of EEPEF (Fig. 2). This is confirmed by a visual comparison of the corresponding maps (Fig. 2 and 3), and by the maximal po-

Table 4. Zones of abundance of *P. juniperinum* by the vegetation zones, km²

Zones	Frequency					Total	Percent of zones from total
	abs	vr	r	sp	fr		
Tundra	.	.	.	.	191758.2	191758.2	3.9
Forest-Tundra	.	.	.	.	102091.9	102091.9	2.1
North Taiga	.	.	.	.	550727.7	550727.7	11.1
Middle Taiga	.	.	.	.	748019.6	748019.6	15.1
South Taiga	.	.	.	.	539973.8	539973.8	10.9
Mixed Forest	.	.	.	.	814324.3	814324.3	16.4
Broadleaves Forest	.	.	3444.2	122087.2	391619.1	517150.5	10.4
Forest-Steppe	.	.	5939.4	435747.1	81016.4	522702.9	10.5
Steppe	2809.6	77382.7	200208.1	427502.8	679.5	708582.7	14.3
Semidesert	22826.2	78760.7	59885.0	43288.1	.	204760.0	4.1
Desert	41611.7	12432.1	820.0	.	.	54863.8	1.1
Total	67247.5	168575.6	270296.7	1028625.2	3420210.5	4954955.4	100.0
Percent of zones from total	1.4	3.4	5.5	20.8	69.0	100.0	

Table 5. Zones of abundance of *P. piliferum* by the vegetation zones, km²

Zones	Frequency					Total	Percent of zones from total
	abs	vr	r	sp	fr		
Tundra	.	.	11928.8	115124.8	64704.6	191758.2	3.9
Forest-Tundra	.	.	.	62283.8	39808.1	102091.9	2.1
North Taiga	.	.	.	314498.9	236228.8	550727.7	11.1
Middle Taiga	.	.	106806.2	381747.9	259465.5	748019.6	15.1
South Taiga	.	.	84120.3	340075.0	115778.5	539973.8	10.9
Mixed Forest	.	.	43686.8	389794.9	380842.6	814324.3	16.4
Broadleaves Forest	.	15418.4	38501.5	237666.7	225563.8	517150.5	10.4
Forest-Steppe	.	7707.9	103432.6	396646.4	14916.1	522702.9	10.5
Steppe	14071.1	224015.1	283466.3	187030.2	.	708582.7	14.3
Semidesert	78928.4	85850.5	39981.1	.	.	204760.0	4.1
Desert	54863.8	.	.	.	.	54863.8	1.1
Total	147863.3	332991.8	711923.6	2424868.6	1337308.1	4954955.4	100.0
Percent of zones from total	3.0	6.7	14.4	48.9	27.0	100.0	

Table 6. Zones of abundance of *P. hyperboreum* by the vegetation zones, km²

Zones	Frequency					Total	Percent of zones from total
	abs	vr	r	sp	fr		
Tundra	.	.	11727.1	62189.1	117842.0	191758.2	3.9
Forest-Tundra	.	2820.2	41805.1	55769.9	1696.8	102091.9	2.1
North Taiga	150580.2	221641.8	151531.3	26974.4	.	550727.7	11.1
Middle Taiga	632908.6	114426.3	684.7	.	.	748019.6	15.1
South Taiga	453163.5	86810.3	.	.	.	539973.8	10.9
Mixed Forest	806760.3	7564.0	.	.	.	814324.3	16.4
Broadleaves Forest	517150.5	.	.	.	.	517150.5	10.4
Forest-Steppe	522702.9	.	.	.	.	522702.9	10.5
Steppe	708582.7	.	.	.	.	708582.7	14.3
Semidesert	204760.0	.	.	.	.	204760.0	4.1
Desert	54863.8	.	.	.	.	54863.8	1.1
Total	4051472.5	433262.6	205748.2	144933.4	119538.8	4954955.4	100.0
Percent of zones from total	81.8	8.7	4.2	2.9	2.4	100.0	

sitive correlation coefficient between these indicators and the species' occurrence (see Table 9). At the same time, the ranges of these three species have some differences.

P. commune has the highest occurrence (valued 5 by our scale) in the Forest zone. Here it is found in the maximal number of biotopes, and is quite a common and widespread species. Fig. 3 shows that the boundaries of the *com* zone of this species coincide with the northern and southern boundaries of the Forest zone. Further to the south, it becomes rarer, but does not disappear from the cover completely. Its habitats here are associated with small individual bogs and humidoherbaceous habitats of the Steppe and the

Forest-Steppe zones. It is completely absent only in the Pontic and the Caspian lowlands, where higher temperatures are combined with low humidity and low precipitation (see Fig. 2; Alisov 1956). In addition to air humidity, *P. commune* is also quite sensitive to the amount of precipitation during the autumn-summer period (see Table 9) in the Forest zone. However, in the Tundra zone summer falls mainly on July. At this time, the amount of precipitation here is quite small. This is why this species' occurrence apparently falls to the north of the Forest zone, where summer precipitation also decreases (see Fig. 2). Still, the abundance of *P. commune* does not decrease there so sharply as to the south of the

Table 7. Zones of abundance of *P. jensenii* by the vegetation zones, km²

Zones	Frequency				Total	Percent of zones from total
	abs	vr	r	sp		
Tundra	.	14011.8	43154.7	134591.7	191758.2	3.9
Forest-Tundra	.	10534.9	69903.5	21653.5	102091.9	2.1
North Taiga	119735.2	295435.7	133136.8	2420.0	550727.7	11.1
Middle Taiga	594413.4	153478.9	127.3	.	748019.6	15.1
South Taiga	290791.8	249182.0	.	.	539973.8	10.9
Mixed Forest	684535.7	129788.6	.	.	814324.3	16.4
Broadleaves Forest	440345.8	76804.7	.	.	517150.5	10.4
Forest-Steppe	502243.5	20459.4	.	.	522702.9	10.5
Steppe	708582.7	.	.	.	708582.7	14.3
Semidesert	204760.0	.	.	.	204760	4.1
Desert	54863.8	.	.	.	54863.8	1.1
Total	3600271.8	949696.1	246322.3	158665.2	4954955.4	100.0
Percent of zones from total	72.7	19.2	5.0	3.2	100.0	

Table 8. Zones of abundance of *P. swartzii* by the vegetation zones, km²

Zones	Frequency			Total	Percent of zones from total
	abs	vr	r		
Tundra	.	191758.2	.	191758.2	3.9
Forest-Tundra	7.5	102084.4	.	102091.9	2.1
North Taiga	219035.1	253968.1	77724.5	550727.7	11.1
Middle Taiga	492559.6	101695.0	153765.0	748019.6	15.1
South Taiga	221549.5	143775.5	174648.8	539973.8	10.9
Mixed Forest	547383.0	265812.8	1128.5	814324.3	16.4
Broadleaves Forest	425186.8	91963.7	.	517150.5	10.4
Forest-Steppe	515776.6	6926.3	.	522702.9	10.5
Steppe	708582.7	.	.	708582.7	14.3
Semidesert	204760.0	.	.	204760.0	4.1
Desert	54863.8	.	.	54863.8	1.1
Total	3389704.5	1157984.1	407266.8	4954955.4	100.0
Percent of zones from total	68.4	23.4	8.2	100.0	

Forest zone, as in the Tundra high air humidity in the summer is retained due to low temperatures.

As for *P. strictum*, this species, on the contrary, increases its abundance to the north of the Forest zone. In the south its range disappears in the north of the Steppe zone, that is significantly further north than the range of *P. commune*. Table 9 shows that this species is more sensitive to air humidity than to the amount of precipitation. Apparently, this is due to the peculiarities of its ecology. Unlike *P. commune*, *P. strictum* is more stenotopic. In the Forest zone, it prefers oligotrophic boggy forests on peaty soils and bogs, and is lesser common on the sands. In the Tundra, where both peaty tundra soils and high air humidity are present, this species finds its optimal conditions for existence.

The occurrence of *P. juniperinum* does not exceed the grade frequent. It is rather monotonously distributed throughout the whole territory. Like *P. strictum*, it is quite stenotopic, but is found both on peat soils and on dry sands. Therefore, to the south of the Forest zone, where there are no boggy forests and only valley and karst bogs are present, it can grow on the forest litter in pine and birch picks. The air humidity here is lower than in the Forest zone, and this reduces the species' abundance. This species completely disappears from the cover only in the Desert zone – in the Caspian region (see Fig. 3).

A gradual decrease in the occurrence of the three described above species to the south of the Forest zone can

be explained, in addition to changes in humidity, by higher summer temperatures – the species' occurrence has a high negative correlation coefficient with the monthly temperature averages of the vegetative season (see Table 9).

P. piliferum has an unique range pattern, which differs from those of other species. The maximum value of this species' occurrence on the territory of EEPEF is 4. It occurs with this frequency in four regions (see Fig. 3). Maximal distribution of this species correlates not with the climatic factors, but with distribution of the fluvio-glacial deposits of the Last Glacial Maximum (Isachenko 1988), which fully conforms to the ecological preferences of this species: *P. piliferum* prefers to grow mainly on dry sands, where it is found in large quantities in lichen pine forests. However, in general occurrence of *P. piliferum* gradually diminishes to the south of the Forest zone, just like it is with other species (see Fig. 3). This fact is better explained by the change in climatic factors than by the landscape's peculiarities. High correlation coefficients of the species' occurrence and the precipitation and temperatures of the vegetative season make it evident (see Table 9). There is a zone of rare occurrence (*r*) in the center of this species' range – in the Middle and the Southern Taiga (Vologda and Kirov Regions). Apparently, this is due to the lack of suitable habitats on sandy soils. Moraine ridges of the Valdai and the Moscow glaciations coincide in this region (Isachenko 1988), and they are composed of fairly rich morainic loams.

Table 9. The Spearman correlation coefficient between the values of climatic factors and species abundance and number of species (number_sp). Bold highlighted values of $r > 0.5$ in absolute value. All values are statistically significant at $p < 0.05$

Climatic factor	Species name							Number of species
	<i>P. commune</i>	<i>P. strictum</i>	<i>P. juniperinum</i>	<i>P. piliferum</i>	<i>P. hyperboreum</i>	<i>P. jensenii</i>	<i>P. swartzii</i>	
pr01	-0.01	-0.17	-0.07	0.02	-0.20	-0.21	-0.17	-0.15
pr02	-0.13	-0.32	-0.20	0.05	-0.28	-0.29	-0.23	-0.27
pr03	0.23	-0.02	0.07	0.26	-0.29	-0.33	0.02	-0.08
pr04	0.17	-0.06	0.10	0.19	-0.34	-0.34	-0.21	-0.16
pr05	0.27	0.06	0.19	0.22	-0.31	-0.25	-0.20	-0.08
pr06	0.31	0.11	0.27	0.25	-0.29	-0.23	-0.12	-0.02
pr07	0.56	0.37	0.51	0.47	-0.15	-0.03	0.16	0.29
pr08	0.78	0.62	0.69	0.59	0.10	0.11	0.56	0.58
pr09	0.80	0.71	0.76	0.57	0.20	0.25	0.57	0.65
pr10	0.75	0.64	0.71	0.45	0.10	0.20	0.50	0.55
pr11	0.56	0.31	0.44	0.43	-0.16	-0.11	0.31	0.25
pr12	0.19	-0.07	0.03	0.16	-0.29	-0.25	-0.03	-0.11
pr_a	0.58	0.35	0.49	0.45	-0.12	-0.08	0.17	0.27
reh04	0.64	0.75	0.63	0.55	0.41	0.40	0.67	0.71
reh05	0.58	0.61	0.57	0.44	0.34	0.29	0.58	0.52
reh06	0.51	0.60	0.52	0.46	0.17	0.17	0.53	0.55
reh07	0.67	0.71	0.65	0.53	0.16	0.19	0.54	0.56
reh08	0.73	0.83	0.71	0.53	0.40	0.41	0.70	0.75
reh09	0.75	0.84	0.72	0.56	0.41	0.43	0.73	0.78
reh10	0.77	0.83	0.74	0.57	0.39	0.44	0.64	0.76
amt	-0.59	-0.75	-0.66	-0.38	-0.50	-0.51	-0.57	-0.75
tm01	-0.41	-0.55	-0.50	-0.23	-0.40	-0.41	-0.33	-0.55
tm02	-0.38	-0.54	-0.47	-0.22	-0.45	-0.43	-0.35	-0.56
tm03	-0.44	-0.61	-0.52	-0.27	-0.50	-0.48	-0.48	-0.66
tm04	-0.67	-0.82	-0.71	-0.45	-0.51	-0.51	-0.47	-0.81
tm05	-0.72	-0.86	-0.75	-0.50	-0.51	-0.50	-0.43	-0.82
tm06	-0.73	-0.86	-0.75	-0.53	-0.59	-0.58	-0.49	-0.82
tm07	-0.74	-0.85	-0.73	-0.56	-0.67	-0.65	-0.54	-0.82
tm08	-0.72	-0.86	-0.75	-0.50	-0.51	-0.59	-0.58	-0.83
tm09	-0.70	-0.84	-0.74	-0.48	-0.50	-0.51	-0.54	-0.82
tm10	-0.55	-0.71	-0.62	-0.35	-0.49	-0.50	-0.51	-0.72
tm11	-0.48	-0.64	-0.57	-0.29	-0.46	-0.47	-0.42	-0.65
tm12	-0.44	-0.59	-0.53	-0.26	-0.43	-0.44	-0.37	-0.60
pr_clq	0.04	-0.15	-0.05	0.11	-0.17	-0.17	-0.16	-0.10
pr_drm	0.14	-0.05	0.02	0.26	-0.12	-0.17	-0.08	-0.01
pr_drq	0.11	-0.10	0.02	0.20	-0.19	-0.22	-0.15	-0.09
pr_wmq	0.58	0.37	0.52	0.47	-0.12	-0.08	0.16	0.28
pr_wtm	0.55	0.36	0.49	0.48	-0.13	-0.05	0.22	0.30
pr_wtq	0.60	0.40	0.53	0.49	-0.09	-0.06	0.22	0.31
t_clq	-0.39	-0.54	-0.48	-0.22	-0.41	-0.41	-0.32	-0.54
t_drq	-0.55	-0.66	-0.61	-0.37	-0.35	-0.41	-0.50	-0.63
t_wmq	-0.73	-0.86	-0.75	-0.52	-0.49	-0.47	-0.70	-0.82
t_wtq	-0.66	-0.78	-0.66	-0.45	-0.45	-0.41	-0.66	-0.74

Unlike all other species, *P. juniperinum* and *P. piliferum* penetrate furthest to the south. However, *P. juniperinum* occupies larger areas in the Desert and Semi-Desert zones in the Caspian region. Apparently, this is due to a broader coenotic amplitude of *P. juniperinum*, as compared to *P. piliferum*: the latter grows mainly on sands, while *P. juniperinum* is able to grow on clay substrates.

P. hyperboreum and *P. jensenii* prevail mainly in the north of EEPEF. To the south, they are distributed only along the Tundras of the Ural Mountains (see Fig. 3). The pattern of their range shows that these species are hypoarctic ones. Among the climatic factors, the annual and monthly temperature averages have a significant effect on their distribution (see Table 9). *P. swartzii* also has rather low occurrence in its distribution areas (see Fig. 3). However, it can not be called hypoarctic, since its distribution maximum is located to the south of the Taiga zone (in Finland and Karelia), and is limited to the region with maximal precipitation and humidity (Fig. 2, Table 9). Although this species is distributed mostly throughout the tundra zone, its range stretches like a tongue-shaped band to the center of European Russia (see

Fig. 3). In my opinion, this may be due to anthropogenic factors, since this species prefers disturbed habitats (e.g. burns, cuttings, pits, etc.), at least in the south of the Forest zone. In any case, the ranges of these three species look reducing, because 1) they occupy rather a small part of EEPEF, and 2) total area of zones of their rare occurrence is notably larger than that of the zones of higher occurrence.

If we continue to study distribution of the species' ranges of the genus *Polytrichum* to the west of the study area, we can see that *P. hyperboreum*, *P. jensenii* and *P. swartzii* are common in the mountains of Sweden and Norway, in Svalbard and in Greenland (Söderström 1998, Goldberg 2003). These three species are absent in the continental part of Western Europe and in Great Britain. So, in Europe the borders of their ranges project most far southwards on the territory of EEPEF. Four species: *P. commune*, *P. juniperinum*, *P. piliferum* and *P. strictum*, are widespread throughout Europe, including Southern and Western Europe, Scandinavia, Svalbard, and Great Britain (Casas 1991, Hill et al. 2006, Sabovljević et al. 2008, Atherton et al. 2010). In Southern Europe, *P. juniperinum* is found most frequently, and *P. stric-*

tum is quite rare. But the latter, unlike *P. juniperinum*, increases its occurrence in Scandinavia, Svalbard and Greenland. *P. commune* and *P. piliferum* are more or less evenly distributed throughout Western Europe, still *P. piliferum* may be absent in some places – for example, in the Alps, where there are no sandy soils (Privitera et al. 2010). *P. piliferum* also goes much further into Southern Europe than *P. commune*. All these facts are fully consistent with the patterns of species' distribution that we have established for the territory of EEPEF. In Siberia, *P. commune*, *P. strictum*, *P. juniperinum* and *P. piliferum* occur throughout all the territory, and their occurrence patterns seem to be similar with those for EEPEF. *P. hyperboreum* and *P. jensenii* pass through the North of Siberia and go down further to the south in the Far East. *P. swartzii* grows in the Northern Siberia, and occurs in some localities in Southern Siberia (Ignatov 2017).

As it is seen from Tables 2–8, the species with high occurrence (*P. commune*, *P. strictum*, *P. juniperinum*, *P. piliferum*) are also widely spread. For these species, the area of high occurrence zones is several times larger than that of the low occurrence zone. The boundaries of their ranges generally coincide with the boundaries of vegetation zones and the isotherms of July and August (see Fig. 2 and 3). Apparently, the temperature is a limiting factor for these species, and the decreasing occurrence of these species nearer to the southern and northern limits of their distribution range fully conforms to the rule of tolerance of Shelford (1931). The inverse ratio is observed for the rare species (*P. hyperboreum*, *P. jensenii*, *P. swartzii*): the area of very low occurrence zones is several times larger than that of higher occurrence zones. Moreover, such species do not have a continuous distribution range on the territory of EEPEF. As it was already mentioned, their distribution is mainly limited by the Tundra zone.

Map of species' diversity taken on the basis of individual species distribution (Fig. 4), shows that on the north and north-east of studying area pattern of the species number

decreasing is too similar to the spatial pattern of July-temperature decreasing (Fig. 4). In other parts of the EEPEF patterns of species diversity look uneven, that is most likely due to the combining effects of climatic, landscape and random factors. As correlation analysis shows distribution of species number through the territory depends in general mostly on temperatures and humidity than on precipitation (Table 9).

CONCLUSION

Seven species of the genus *Polytrichum* can be divided into two groups according to the pattern of their distribution on EEPEF: 1) widespread species (*P. commune*, *P. strictum*, *P. juniperinum*, *P. piliferum*) and 2) restricted species (*P. hyperboreum*, *P. jensenii*, *P. swartzii*). Species of the first group find their climatic optimum mostly in the Forest zone, while species of the second group find it mostly in the Tundra zone. The distribution boundary of *Polytrichum juniperinum* extends most far to the south, as this species requires lesser moisture than others. Distribution range of *P. piliferum* is determined not only by climatic parameters, but also by distribution of fluvio-glacial deposits on EEPEF. Distribution of widespread species from the first group follows the spread of forests in the southern part of EEPEF. Distribution of species of the second group is mainly limited to Subarctic regions and their ranges look reducing.

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Figure 4 Map of species number distribution (areas with corresponding species numbers are given in color; numbers on the map are the number of species)

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