Chapter

Species Distribution Patterns in Subgenus Cuspidata (Genus Sphagnum L.) on the East European Plain and Eastern Fennoscandia

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Abstract

The geographic range of 13 species from the subgenus Cuspidata in the East European Plain and Eastern Fennoscandia has been studied. Model maps for each species occurrence were constructed using geostatistics techniques (kriging method). Continuous coverages of 23 climatic factors were used in analysis also. We used dataset that proposed by authors of program WORLDCLIM. To learn how corresponding values of climatic factors and species occurrence correlation and cluster analysis were conducted. It was found that 7 of 13 species are widespread on the East European Plain and Eastern Fennoscandia, and 6 species have the restricted ranges. Values of occurrence of all species (except *Sphagnum lenense*) have a strong correlation with moisture factors (relative air humidity and sum of precipitation) in summer-autumn period. Such preferences allow them to grow successfully in Subarctic and Baltic regions, where high climatic humidity is observed. Restricted species are concentrated around the Baltic Sea and zones of the highest occurrence of widespread species are located at the same region. All species can be divided into four clusters according to its climatic preferences. Distribution of such species as *S. obtusum* seems to be strongly associated with two tongues of the Last Glacier, and this species seems to be a glacial relic.

Keywords: Sphagnum, Cuspidata, biogeography, BIOCLIM, distributional range, GIS, geostatistics, kriging method

1. Introduction

Sphagnum mosses are widely distributed plants in wet habitats. They are edificators in boggy forests and bogs in all plant zones. The ecology of species of the genus Sphagnum is now well studied, and environmental factors that play a leading role in the division of ecological space among Sphagnum species are well known [1–11]. Until now, however, the question about the division of geographical space by species remains open, especially due to the influence of climatic factors. There are two principal works on the biogeography of the genus Sphagnum [12, 13], which consider the geographical variability of species diversity of the genus in Western

Europe by methods of zonal statistics, that is, within the administrative boundaries of administrative states. In both cited works, the authors find the center of species diversity of the genus Sphagnum in the Scandinavian Peninsula. There does not seem to be any work that considers the distribution of species within its natural boundaries. Therefore, the present article is intended to fill this gap for the territory of the East European plain and Eastern Fennoscandia. As more than 50 species of Sphagnum grow in Europe [14], it is not possible to consider all of them in a single article due to lack of space. Therefore, in this chapter, we consider the distribution of species of the subgenus Cuspidata only, growing on the territory of the East European plain and Eastern Fennoscandia (EEPEF). In Europe (from the Atlantic to Urals), there are 17 species of the subgenus Cuspidata [14]. Only 14 species occur in the EEPEF. These are as follows: *Sphagnum angustifolium*, *S. annulatum*, *S. balticum*, *S. cuspidatum*, *S. fallax*, *S. flexuosum*, *S. jensenii*, *S. lenense*, *S. lindbergii*, *S. majus*, *S. obtusum*, *S. pulchrum*, *S. riparium*, and *S. tenellum*. Although some species are difficult to identify, these errors are easy to identify and correct by comparing bulk materials from different geographic locations. Moreover, a mathematical method for modeling maps, which is used in this work—the kriging method [15–20] serves as error protection. This method is widely used to build maps of temperature distribution in climatology, compiling digital elevation models in geodesy, etc. The advantages of this modeling method, compared to other ones currently used, are discussed in detail in previously published paper [21]. In bryology and biogeography, we use the kriging method for the first time. In short, the kriging method allows us to create model maps of the species distribution, which can reflect not only the boundaries of the species range as a whole, but also the species activity within the range. In addition, taking into account the weights of input points, values allow to cut off the noise while maintaining the overall trend of the distribution of the species. In the case of the study of mosses distribution, random incorrect definitions of species in some geographic points just appear as noise on a mathematical surface. All of the above is true for such species for which we have data set from the entire study area. Among the 14 species of the subgenus Cuspidata which is found in European Russia and adjacent countries, only one species does not satisfy this condition. This is *Sphagnum annulatum*. Since the valid description of this species was made relatively recently [22], and actually in Russian local floras, it "appears" around the late of 1990s, the definitions of this species cannot cover the entire study area (the database of local floras includes works, which were conducted since 1960s till 2017). In this connection, in the present work, 13 species of Sphagnum of the subgenus Cuspidata (from the list above), excluding *S. annulatum*, are analyzed.

The purpose of the present work is to simulate the ranges of species and study their distribution patterns, in connection with spatial changes of climatic factors in the EEPEF. In other words, it is completely within the competence of biogeography. The traditional task of biogeography is to identify the boundaries of the species ranges and find distribution patterns of the species due to geographic, biotic, and climatic factors. The ecological aspect of the species distribution analyzing in biogeography is most often associated with the concept of ecological niche in the understanding of Grinnell [23], that is, the attitude of a species to changes in environmental parameters. Unlike Hutchinson's ecological niche [24], which is determined by the properties of a species in the hyperspace of environmental factors (i.e., the ecological preferences of the species, rather than the environment), Grinell's niche is determined by environmental parameters. Changes of these parameters lead to changes of species environmental preferences. Therefore, studying the joint change of climatic factors and the numerical characteristics of the species in space, one can identify the climatic optimum and pessimum of the species.

2. Methods

To study the Sphagnum distribution on the EEPEF, 13 species were chosen, and the literature data with annotated lists of specific bryofloras from different regions (European part of the Russian Federation, the Baltic States, Ukraine, Belarus, and Moldova) were analyzed (**Figure 1**). Some dots have been chosen outside the study area (e.g., Romania, Poland, Kazakhstan, Cauacasus, and eastern mountainside of Ural) to correct possible errors of extrapolation at the boundaries [17, 20]. Earlier,

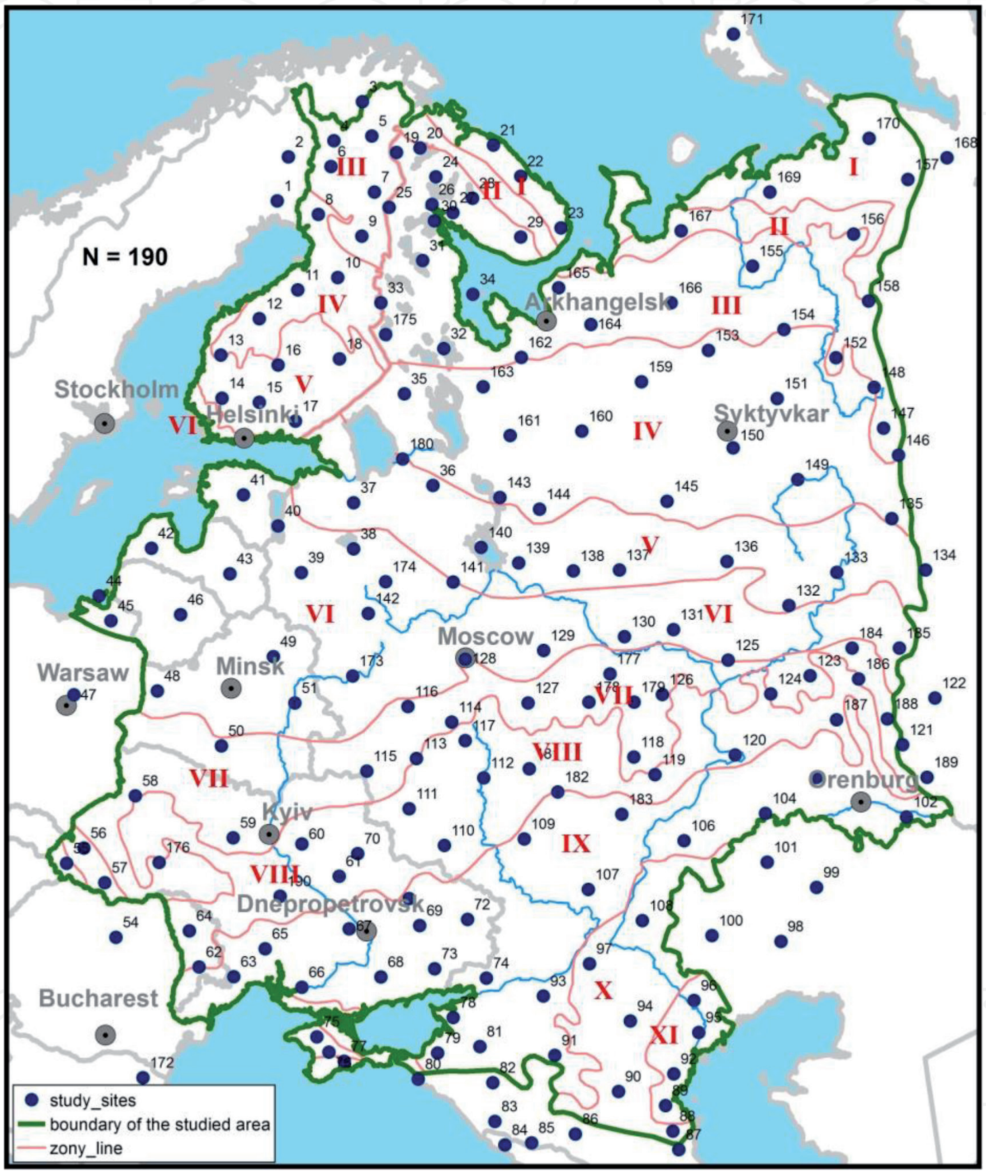
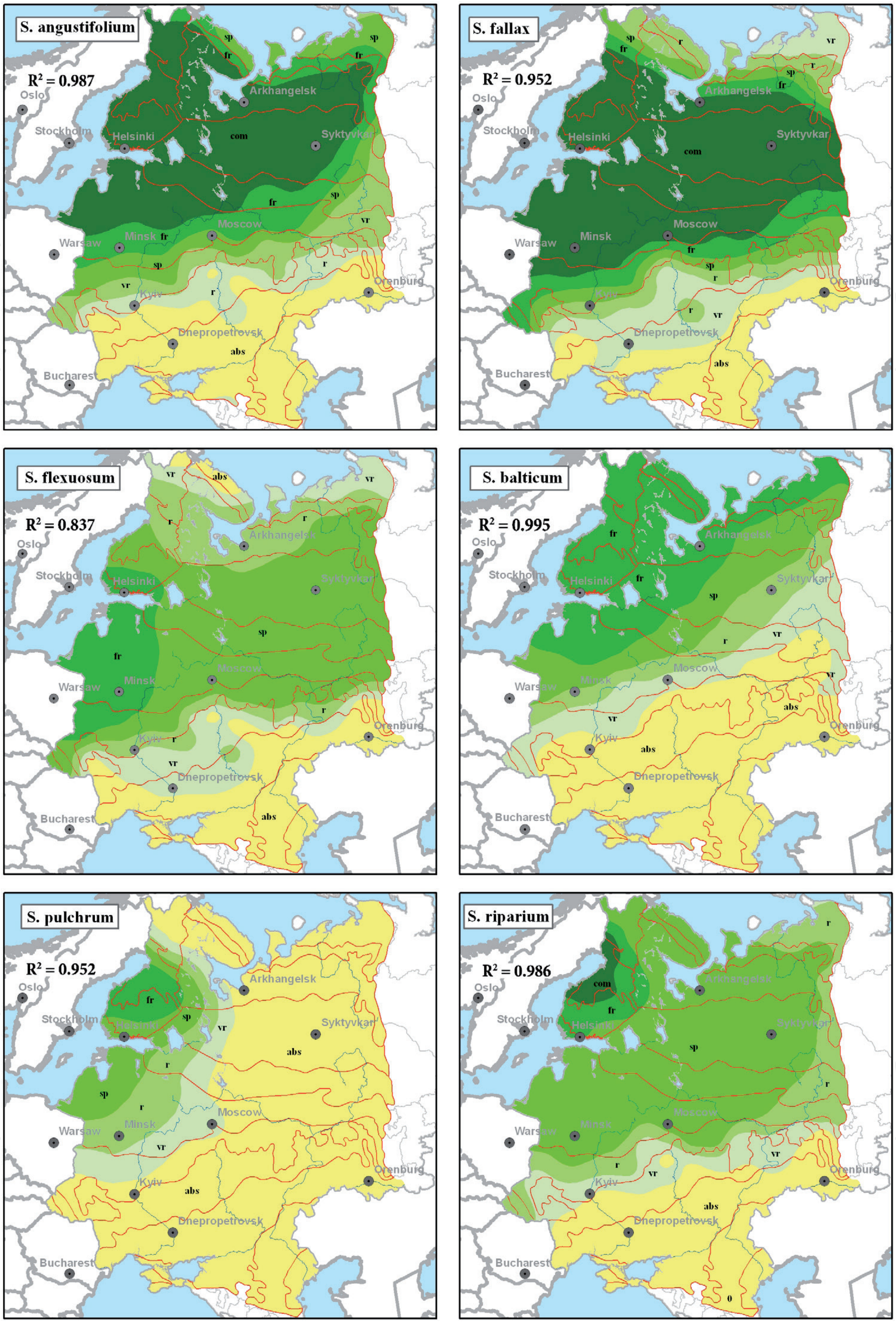
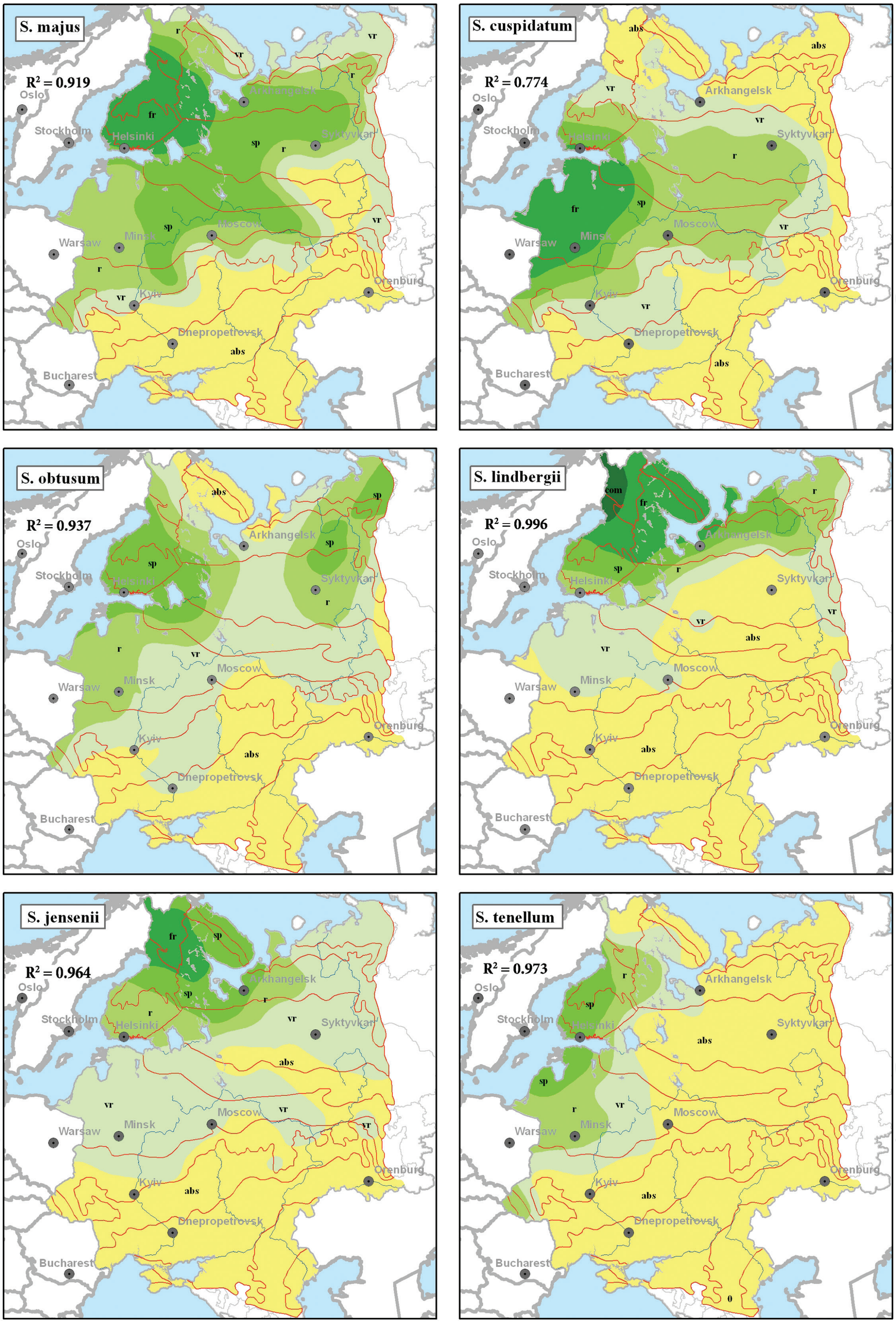


Figure 1.
Study area, showing localities involved in analysis and vegetation zones: I—Tundra; II—Forest Tundra; III—Northern Taiga; IV—Middle Taiga; V—Southern Taiga; VI—Mixed forests; VII—Broadleaved forests; VIII—Forest Steppe; IX—Steppe; X—Semidesert; XI—Desert (boundaries of vegetation zones are given by [30, 31]. Study sites: 1–18—[32]; 19—[33]; 20—[34]; 21–23—[35]; 24—[33]; 25—[36]; 26—[33]; 27–29—[35]; 30—[37]; 31–32—[38]; 33—[39]; 34—[40]; 35—[41]; 36–39—[42]; 40—[43]; 41—[44]; 42–43—[45]; 44—[46]; 45—[32]; 46—[32, 47]; 47—[48]; 48–51—[49]; 52—[50]; 53—[51]; 54—[52]; 55–57—[53]; 58–59—[54]; 60–61—[55]; 62–64—[56]; 65–69—[27]; 70–72—[57]; 73–74—[58]; 75–77—[59]; 78–80—[60]; 81—[61]; 82—[62]; 83—[63]; 84—[64]; 85—[65]; 86—[66]; 87—[67]; 88—[68]; 89–92—[61]; 93–96—[69]; 97—[70]; 98–105—[71]; 106–108—[70]; 109–115—[57]; 116—[72]; 117—[73]; 118—[74]; 119—[75]; 120—[76]; 121—[77]; 122—[78]; 123–124—[79]; 125—[80]; 126—[81]; 127—[82]; 128—[83]; 129–130—[84]; 131—[85, 86]; 132—[87]; 133—[88]; 134—[89]; 135—[90]; 136—[91]; 137–138—[92]; 139–140—[93]; 141—[94]; 142—[95]; 143—[96]; 144—[97]; 145—[91]; 146—[98]; 147—[99]; 148—[100]; 149–158—[101]; 159–162—[40]; 163—[102]; 164–166—[103, 104]; 167—[105]; 168—[106, 107]; 169–171—[107, 108]; 172—[109]; 173—[110]; 174 —[94]; 175—[111]; 176—[112]; 177—[113]; 178—[114]; 179—[115]; 180—[116]; 181–182—[117]; 183—[75]; 184–188—[118]; 189—[77]; 190—[55].



the basic principles for creating model areas by geostatistics methods using the kriging method were printed, and the methodology for compiling model maps of species ranges was adapted to the goals of biogeography [20]. After literature data compilation, the occurrence of each species was estimated in ordinal six-point scale: 0—absent (**abs**), 1—very rare (1–2 records) (**vr**), 2—rare (3–7 records) (**r**), 3—sporadically (more than 7 records, but not everywhere) (**sp**), 4—frequent (usual species, but sometimes absent in suitable phytocoenosis) (**fr**), and 5—common



(usual and phytocenotically active species in the study area) (**com**). In the following text, these abbreviations will be used to denote areas of species occurrence. According to this scale, continuous coverages were constructed for each species using the kriging method [17] with a resolution of 10 km in 1 pixel. In total, a sample of 190 points (local floras) was used to create continuous coverages (**Figure 1**). Verification of continuous coverages was carried out by cross-validation method in the SAGA GIS software. The index of quality of cross-validation in geostatistics is

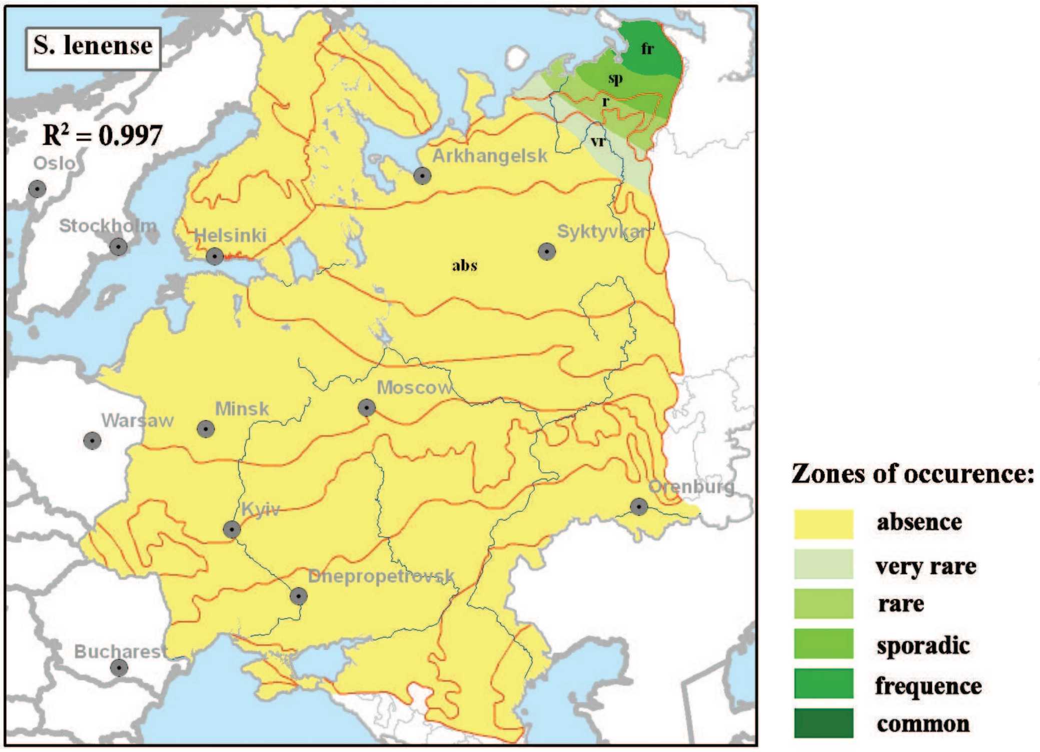


Figure 2.
Model ranges of 13 species of the subgenus Cuspidata (the red lines indicate the boundaries of vegetation zones). Zones of occurrence: ***abs****—species is absent;* ***vr****—very rare;* ***r****—rare;* ***sp****—sporadic;* ***fr****—frequent; and* ***com****—common. For each species on the maps is shown R^2.*

the coefficient of determination (R^2) [17]. The values of this indicator for continuous coverages of species under study are shown in **Figure 2**. Climatic optimum was determined for zones of frequent (**fr**) and common (**com**) occurrences.

Continuous coverages of climatic factors were used in analysis also. We used dataset that authors of WORLDCLIM program [25] propose. In total, 23 climatic variables were used. This is the following: annual mean of precipitation (**amt**), monthly temperature of April–October (**tm04–tm10**), annual precipitation (**pr_a**), monthly precipitation (**pr04–pr10**), and relative humidity (**reh04–reh10**) of April–October. We have chosen only months of growing season from dataset. Each coverage was composed in Azimuthal Equidistant Projection (Central Meridian 45°E, chief of the parallel 55°N). The coverages of climatic factors were combined with coverages of species occurrence to a single spatial database. This spatial database was converted into relative table, which contains 36 variables (23 climatic factors and 13 species occurrence) and 49,557 cases (number of pixels). This database was used for calculation of descriptive statistics and performing correlation and cluster analysis in software Statistica 10.0. Operation with creating and verification coverages was performed in SAGA software. The operations by intersection of the vector layers and calculating of areas were performed in software ArcGis 10.0. In more detail, all techniques were described in previous article [21].

3. Results

Model maps for 13 species are shown in **Figure 2**. The following species distribution patterns were found.

Sphagnum angustifolium. This species is widely distributed in the study area (**Figure 2**). The maximum score on the scale of occurrence is 5 (**com**). It grows in boggy forests and bogs. Its range is associated with the forest zone and tundra,

Zones	abs	vr	r	sp	fr	com	*Total*
Tundra			3.6	136.8	47.8	3.6	*191.8*
Forest Tundra			0.0	1.9	85.6	14.6	*102.1*
North Taiga			13.3	5.8	56.1	475.5	*550.7*
Middle Taiga			24.4	44.7	59.9	619.1	*748.0*
South Taiga		0.1	92.8	32.7	88.4	326.0	*540.0*
Mixed Forest		0.6	81.5	113.1	278.9	340.2	*814.3*
Broadleaves Forest	44.3	72.1	235.4	155.0	10.3		*517.2*
Forest Steppe	209.0	253.0	58.4	2.2			*522.7*
Steppe	659.1	49.5					*708.6*
Semidesert	204.8	0.0					*204.8*
Desert	54.9	0.0					*54.9*
Total, km^2	*1172.1*	*375.4*	*509.5*	*492.1*	*626.9*	*1778.9*	*4955.0*
Total, %	*23.7*	*7.6*	*10.3*	*9.9*	*12.7*	*35.9*	*100*

Table 1.
Areas (in 1000 km^2) covered by S. angustifolium by zones of its occurrence.

where such habitats are widespread. To the south of the forest zone, *S. angustifolium* decreases its abundance and completely disappears in the steppe or even in forest steppe in some places. Its occurrence increases in the northern and middle taiga. It grows in all vegetative zones from tundra to steppe (**Figure 2** and **Table 1**). The zone of its greatest occurrence (**com**) occupies 35.9% of the total area of the EEPEF. The zone of total absence is 23.7% (**Table 1**). Thus, the range of this species covers 76.3% of the total area of the EEPEF, therefore *S. angustifolium* can be considered here as a common and widespread species.

The southern boundary of the range of *S. angustifolium* (the southern boundary of **vr** zone) passes in sublatitudinal direction and is approximately parallel to the boundaries of natural zones. The border of the zone of maximum occurrence (**com**) passes diagonally to the meridians. In terms of biogeography, this is the zone of its climatic optimum. In the best way, the border of the **com** zone correlates with the boundary of the maximum occurrence of wetlands [26] and with isotherm of July +17°C and with maximal average values of air humidity in July–September.

Sphagnum fallax. This species is distributed from tundra to forest steppe zone (**Figure 2**). The maximum score on the scale of occurrence is 5 (**com**). In the south of the steppe zone, this species is absent, with the exception of its tongue with lower occurrence along Dnieper river, where it occurs on rare bogs, located on the river terraces [27]. It has maximal abundance (**com**) in the forest zone and occurs with a small abundance (**vr**) in the forest tundra and forest steppe, but here it is rare (**Table 2** and **Figure 2**). The zone of maximal occurrence of the species takes about a half area of the EEPEF (44.7%) (**Table 2**). This species is absent in 13.9% of the area only, that is, its range covers 86.1% of the EEPEF area. Thus, *S. fallax* is the most common and widespread species.

As well as *S. angustifolium*, *S. fallax* has similar climatic preferences. The boundaries of all zones of *S. fallax* are generally parallel to the boundaries of natural zones (**Figure 2**). Unlike *S. angustifolium*, *S. fallax* comes further south—its range reaches the Black Sea along the Dnieper. However, in the steppe zone, it is an extremely rare species. In the north of the EEPEF, *S. fallax* does not completely disappear, but becomes much more rare, in contrast to *S. angustifolium*, which is a fairly frequent species in the tundra (**Figure 2** and **Table 2**). The boundaries of all zones best correspond to region with the greatest average summer precipitation and air humidity, and the southern border of its range is generally well suited the isotherm of July of +21°C (southern boundary of the **vr** zone) and to +13°C in the north (southern boundary of the **r** zone) (**Figure 2**).

Sphagnum flexuosum. This species is distributed from tundra to the steppe zone (**Figure 2**). The maximum score on the scale of occurrence is 4 (**fr**). It reaches the highest occurrence (**fr**) to the west of the forest zone (**Figure 2**), but it occurs sporadically throughout almost the entire forest zone. Sporadic zone occupies most of the range of this species −41.2%—and extends from the northern taiga to the forest steppe (**Table 3**). In general, *S. flexuosum* covers 80.7% of the total area, and therefore this species, as well as two previous species, can be considered as widespread species in this area.

The boundaries of almost all zones of occurrence of this species run almost parallel to the boundaries of natural zones (**Figure 2**). The boundary of the zone **fr** passes in the submeridianal direction. This fact indicates that the optimum zone of *S. flexuosum* is limited by the factors of humidity and not by temperature. This zone is located in regions around the Baltic Sea, where relatively warm summers and the greatest amount of precipitation are observed [28]. In the south, the range of this species reaches to the northern steppes only and in the north—to the Arctic Ocean. True, in tundra, it is very rare. In the best way, the boundaries of all zones of occurrence (except for zone **fr**) correspond to the high average values of precipitation in July–September, and they have a weak correspondence with isotherms (**Table 3**).

Sphagnum balticum. The range of this species from north to south covers the area from the tundra zone to the zone of deciduous forests, and its occurrence does not exceed four on a six-point scale (**Figure 2**). In the southern Urals, it captures a small section of the forest steppe zone (**Table 4**). The maximum occurrence of *S. balticum* is observed in the tundra and in the north of the forest zone. Zone **fr** occupies about a quarter of the total area (25.6%) of the EEPEF (**Table 4**). The territory, where *S. balticum* is absent (**abs**), makes up 38.6% of the EEPEF, that is, the range of this species occupies 61.4% of total area. Therefore, *S. balticum* can also be called a relatively widespread species.

Zones	abs	vr	r	sp	fr	com	*Total*
Tundra		117.3	73.0	1.5	0.0	0.0	*191.8*
Forest Tundra		2.4	76.8	22.1	0.8	0.0	*102.1*
North Taiga			67.1	118.6	126.4	238.6	*550.7*
Middle Taiga					2.5	745.5	*748.0*
South Taiga				0.5	85.0	454.5	*540.0*
Mixed Forest				36.5	70.1	707.7	*814.3*
Broadleaves Forest	10.5	20.4	58.6	151.4	208.2	68.2	*517.2*
Forest Steppe	30.9	220.5	170.8	89.1	11.3		*522.7*
Steppe	390.6	289.3	28.4	0.2			*708.6*
Semidesert	202.5	2.2					*204.8*
Desert	54.9						*54.9*
Total, km^2	*689.4*	*652.2*	*474.6*	*420.0*	*504.2*	*2214.5*	*4955.0*
Total, %	*13.9*	*13.2*	*9.6*	*8.5*	*10.2*	*44.7*	*100*

Table 2.
Areas (in 1000 km^2) covered by S. fallax by zones of its occurrence.

Zones	abs	vr	r	sp	fr	*Total*
Tundra	25.3	112.9	41.6	12.0		*191.8*
Forest Tundra	8.9	18.5	66.5	8.2		*102.1*
North Taiga	12.1	61.7	320.8	156.1		*550.7*
Middle Taiga			78.9	669.1		*748.0*
South Taiga			1.8	461.0	77.2	*540.0*
Mixed Forest		0.4	6.5	435.0	372.4	*814.3*
Broadleaves Forest	35.6	27.4	119.1	261.7	73.3	*517.2*
Forest Steppe	92.9	270.9	118.5	38.5	1.8	*522.7*
Steppe	524.0	174.7	9.9			*708.6*
Semidesert	204.8					*204.8*
Desert	54.9					*54.9*
Total, km^2	*958.5*	*666.5*	*763.8*	*2041.5*	*524.7*	*4955.0*
Total, %	*19.3*	*13.5*	*15.4*	*41.2*	*10.6*	*100.0*

Table 3.
Areas (in 1000 km^2) covered by S. flexuosum by zones of its occurrence.

Zones	abs	vr	r	sp	fr	*Total*
Tundra			5.8	33.6	152.3	*191.8*
Forest Tundra				23.3	78.8	*102.1*
North Taiga		21.3	28.9	147.6	353.0	*550.7*
Middle Taiga		124.2	161.2	198.5	264.0	*748.0*
South Taiga	57.1	110.7	74.9	77.4	219.9	*540.0*
Mixed Forest	92.7	187.2	139.4	195.4	199.6	*814.3*
Broadleaves Forest	294.2	194.3	27.6	1.1		*517.2*
Forest Steppe	504.4	18.3				*522.7*
Steppe	705.2	3.4				*708.6*
Semidesert	204.8					*204.8*
Desert	54.9					*54.9*
Total, km^2	*1913.2*	*659.5*	*437.7*	*676.8*	*1267.8*	*4955.0*
Total, %	*38.6*	*13.3*	*8.8*	*13.7*	*25.6*	*100*

Table 4.
Areas (in 1000 km^2) covered by S. balticum by zones of its occurrence.

The boundaries of the range of *S. balticum* as a whole and the boundaries of zones of occurrence within the range are oblique with respect to the borders of natural zones and show a clear tendency toward concentration around the Baltic Sea (**Figure 2**). The boundary of the zone of maximal occurrence (**fr**) lies parallel and entirely within the zone of maximum distribution of the Valdai glaciation [29]. The boundary of the zone of sporadic occurrence (**sp**) generally coincides with the zone of maximal distribution of wetlands [26]. This is not surprising if we recall that *S. balticum* is predominantly a boggy (and not forest) species, especially in the north [9–11]. Thus, it can be assumed that the distribution of *S. balticum* in the northern parts of its range, where it occurs most often, in addition to climatic factors, is influenced by the historical conditions and landscape features of the territory. The influence of climatic factors, however, also occurs, since the southern border of the **sp** zone roughly corresponds to the isotherm of July +17°C. In the best way, the boundaries of the zones of occurrence correspond to the monthly precipitation and relative humidity of air in August–September.

Sphagnum riparium. It is rather widely distributed in the EEPEF (**Figure 2**); however, in most of the area, it occurs sporadically. The **sp** zone occupies about half of the investigated area (45.8%) (**Table 5**). The maximal occurrence zone reaches in Finland and Sweden (**Figure 2**), which is connected, in my opinion, with the greater prevalence of suitable habitats in these countries, such as aapa-bogs. In general, the *S. riparium* range covers 74.7% of the EEPEF, so this species can be considered widespread in this area.

In the west, the boundary of the **sp** zone more or less coincides with the isotherm of July +17°C. In the east—in the Ural Mountains—any correspondence to climatic factors is not detected. The decrease of the occurrence of *S. riparium* in Urals seems to be due to the lack of suitable habitats.

Sphagnum majus and *S. cuspidatum*. Both species, as well as *S. riparium*, are widely distributed throughout the EEPEF, but with a small abundance. The peak of their coenotic activity is observed in western regions, where they grow jointly or separately in the flooded hollows of oligotrophic or mesotrophic bogs. Apparently, their lower occurrence in the east is related to the difference in the composition of the bog complexes of the Western European and East European bogs. Although the ranges of both species are largely similar, *S. majus* is more northern than *S. cuspidatum*. Area of *S. majus* covers 66.8% and *S. cuspidatum*—59.7% (**Tables 6** and **7**) from total area. The boundaries of the zones of occurrence of both species are weakly related to the isolines of any climatic factors, except zone **fr**. This zone (for both species) lies within the region with the highest humidity and precipitation in August–September.

Sphagnum jensenii. The boundary of the range of this species has a fancy pattern. In general, it occupies 56.1% of the total area (**Table 8**). It is most prevalent in Fennoscandia and in Russian North (**Figure 2**). Throughout its range, *S. jensenii*

Zones	abs	vr	r	sp	fr	com	*Total*
Tundra		2.1	128.3	61.3			*191.8*
Forest Tundra			13.3	88.8			*102.1*
North Taiga			40.4	444.1	60.0	6.2	*550.7*
Middle Taiga			49.4	592.6	41.5	64.5	*748.0*
South Taiga			110.8	323.3	90.1	15.8	*540.0*
Mixed Forest		6.5	128.5	672.7	6.7		*814.3*
Broadleaves Forest	34.6	205.9	190.9	85.7			*517.2*
Forest Steppe	279.5	228.3	14.9				*522.7*
Steppe	699.8	8.8	0.0				*708.6*
Semidesert	204.8	0.0					*204.8*
Desert	54.9						*54.9*
Total, km^2	1273.5	451.5	676.5	2268.6	198.3	86.6	*4955.0*
Total, %	*25.7*	*9.1*	*13.7*	*45.8*	*4.0*	*1.7*	*100*

Table 5.
Areas (in 1000 km^2) covered by S. riparium by zones of its occurrence.

Zones	abs	vr	r	sp	fr	*Total*
Tundra		180.9	10.8	0.0	0.0	*191.8*
Forest Tundra		49.6	52.1	0.4	0.0	*102.1*
North Taiga		60.4	200.7	193.1	96.6	*550.7*
Middle Taiga	62.3	107.4	98.9	332.3	147.1	*748.0*
South Taiga	104.3	53.2	39.4	207.6	135.4	*540.0*
Mixed Forest	31.0	73.1	401.0	304.5	4.7	*814.3*
Broadleaves Forest	93.4	174.1	227.5	22.2		*517.2*
Forest Steppe	384.5	127.8	10.4			*522.7*
Steppe	708.6					*708.6*
Semidesert	204.8					*204.8*
Desert	54.9					*54.9*
Total, km^2	*1643.7*	*826.5*	*1040.7*	*1060.1*	*383.9*	*4955.0*
Total, %	*33.2*	*16.7*	*21.0*	*21.4*	*7.7*	*100.0*

Table 6.
Areas (in 1000 km^2) covered by S. majus by zones of its occurrence.

Zones	abs	vr	r	sp	fr	*Total*
Tundra	191.8					*191.8*
Forest Tundra	102.1					*102.1*
North Taiga	405.8	144.3	0.7			*550.7*
Middle Taiga	83.7	265.7	396.6	2.0		*748.0*
South Taiga	26.1	68.1	307.7	99.5	38.6	*540.0*
Mixed Forest	26.4	67.4	253.8	106.3	360.4	*814.3*
Broadleaves Forest	90.5	131.0	209.1	63.5	23.1	*517.2*
Forest Steppe	184.2	310.0	25.4	3.2		*522.7*
Steppe	627.0	81.6				*708.6*
Semidesert	204.8					*204.8*
Desert	54.9					*54.9*
Total, km^2	*1997.0*	*1068.1*	*1193.3*	*274.5*	*422.2*	*4955.0*
Total, %	*40.3*	*21.6*	*24.1*	*5.5*	*8.5*	*100*

Table 7.
Areas (in 1000 km^2) covered by S. cuspidatum by zones of its occurrence.

practically does not change its environmental preferences—it grows everywhere in the wet hollows of oligotrophic bogs. However, on the territory of the Russian Plain, such bogs are not rare, but wet hollows are usually occupied mainly by *S. majus*. Therefore, it cannot be said that *S. jensenii* is extremely rare due to the lack of habitats in the central and eastern parts of the range. At the same time, it cannot be said that the boundaries of the zones of occurrence are associated with isolines of climatic factors. This type of range appears to be shrinking.

Sphagnum obtusum. The maximum score on the scale of occurrence for this species is 3 (sporadically). In other words, this species does not have an optimum in the study area. At the same time, the **sp** zone "goes" to EEPEF with two tongues—from

Zones	abs	vr	r	sp	fr	*Total*
Tundra		139.7	13.8	38.2		*191.8*
Forest Tundra		55.1	9.2	37.5	0.3	*102.1*
North Taiga		179.4	76.0	154.1	141.2	*550.7*
Middle Taiga	104.7	411.9	126.8	82.0	22.7	*748.0*
South Taiga	181.6	220.3	134.0	4.1		*540.0*
Mixed Forest	111.0	696.7	6.7			*814.3*
Broadleaves Forest	310.0	207.2				*517.2*
Forest Steppe	501.8	20.9				*522.7*
Steppe	708.6					*708.6*
Semidesert	204.8					*204.8*
Desert	54.9					*54.9*
Total, km^2	*2177.2*	*1931.2*	*366.5*	*315.8*	*164.3*	*4955.0*
Total, %	*43.9*	*39.0*	*7.4*	*6.4*	*3.3*	*100.0*

Table 8.
Areas (in 1000 km^2) covered by S. jensenii by zones of its abundance.

Zones	abs	vr	r	sp	*Total*
Tundra	52.0	19.7	68.5	51.5	*191.8*
Forest Tundra	42.8	18.8	24.8	15.7	*102.1*
North Taiga	108.0	175.1	198.4	69.2	*550.7*
Middle Taiga	12.2	267.0	286.3	182.5	*748.0*
South Taiga	23.0	268.6	62.5	185.9	*540.0*
Mixed Forest	42.8	432.2	309.7	29.6	*814.3*
Broadleaves Forest	180.5	274.3	62.3		*517.2*
Forest Steppe	289.6	233.1			*522.7*
Steppe	656.3	52.3			*708.6*
Semidesert	204.8				*204.8*
Desert	54.9				*54.9*
Total, km^2	*1666.9*	*1741.1*	*1012.6*	*534.3*	*4955.0*
Total, %	*33.6*	*35.1*	*20.4*	*10.8*	*100.0*

Table 9.
Areas (in 1000 km^2) covered by S. obtusum by zones of its occurrence.

Finland and Polar Urals. This is very similar to the tongues of the last glacier [29]. This is a suggestion that this species is a glacial relic. In general, the area of this species is 66.4% of the total area of the EEPEF (**Table 9**). This species does not change its ecology when geographic areas changing—everywhere it grows on quagmire along the shores of lakes or in hollows of transitional bogs and rich fens. Therefore, in our opinion, the range of this species can also be called shrinking.

Sphagnum lindbergii. This species is quite rare on the Russian Plain. Judging by the pattern of its range—it is rather Scandinavian. The area of its range is less than half of the total area (38.7%) (**Table 10**). Therefore, this species should be considered as a species with a restricted range for the EEPEF territory. The zone of

Zones	abs	vr	r	sp	fr	com	*Total*
Tundra		26.5	99.7	16.6	49.1		*191.8*
Forest Tundra		0.4	27.8	36.1	37.9		*102.1*
North Taiga	0.3	63.8	120.6	118.5	208.7	38.8	*550.7*
Middle Taiga	371.1	190.7	48.4	59.2	63.1	15.5	*748.0*
South Taiga	293.7	104.7	61.6	70.4	9.6		*540.0*
Mixed Forest	372.5	435.1	6.7				*814.3*
Broadleaves Forest	509.4	7.7					*517.2*
Forest Steppe	522.7						*522.7*
Steppe	708.6						*708.6*
Semidesert	204.8						*204.8*
Desert	54.9						*54.9*
Total, km^2	*3037.9*	*829.0*	*364.8*	*300.7*	*368.3*	*54.3*	*4955.0*
Total, %	*61.3*	*16.7*	*7.4*	*6.1*	*7.4*	*1.1*	*100.0*

Table 10.
Areas (in 1000 km^2) covered by S. lindbergii by zones of its occurrence.

Zones	abs	vr	r	sp	fr	*Total*
Tundra	191.8					*191.8*
Forest Tundra	102.1					*102.1*
North Taiga	412.7	51.7	46.0	35.5	4.8	*550.7*
Middle Taiga	532.4	46.3	41.2	50.8	77.3	*748.0*
South Taiga	300.9	42.0	52.4	66.8	77.8	*540.0*
Mixed Forest	232.7	170.8	228.8	182.1		*814.3*
Broadleaves Forest	386.2	124.3	6.6			*517.2*
Forest Steppe	522.5	0.2				*522.7*
Steppe	708.6					*708.6*
Semidesert	204.8					*204.8*
Desert	54.9					*54.9*
Total, km^2	*3649.5*	*435.4*	*374.9*	*335.2*	*160.0*	*4955.0*
Total, %	*73.7*	*8.8*	*7.6*	*6.8*	*3.2*	*100.0*

Table 11.
Areas (in 1000 km^2) covered by S. pulchrum by zones of its abundance.

its maximal distribution occurs in subarctic regions, where an air humidity is high during the growing season (**Table 11**).

Sphagnum pulchrum and *S. tenellum*. These two species go to the EEPEF from Western Europe and Scandinavia. In the investigated area, they have a restricted range. Thus, the area occupied by *S. pulchrum* is only 26.3% and by *S. tenellum*—24.7% of the total EEPEF area (**Tables 11** and **12**).

Sphagnum lenense. This species is widespread in Siberia and goes to the EEPEF from the Polar Urals. Also, this is a species with a restricted range. The area of its range is only 5.1% of the total area (**Table 13**). In the tundra and forest tundra, it grows on the hummocks of raised bogs. Under the conditions of the Russian plain, in forest zone, such habitats are usually occupied by *Sphagnum fuscum*. The

Zones	abs	vr	r	sp	*Total*
Tundra	191.8				*191.8*
Forest Tundra	96.5	5.5			*102.1*
North Taiga	341.1	131.5	78.2		*550.7*
Middle Taiga	617.6	26.2	50.3	54.0	*748.0*
South Taiga	335.1	52.8	73.4	78.7	*540.0*
Mixed Forest	282.1	215.8	234.0	82.4	*814.3*
Broadleaves Forest	383.0	112.9	21.2		*517.2*
Forest Steppe	515.1	7.6			*522.7*
Steppe	708.6				*708.6*
Semidesert	204.8				*204.8*
Desert	54.9				*54.9*
Total, km^2	*3730.5*	*552.2*	*457.1*	*215.1*	*4955.0*
Total, %	*75.3*	*11.1*	*9.2*	*4.3*	*100.0*

Table 12.
Areas (in 1000 km^2) covered by S. tenellum by zones of its occurrence.

Zones	abs	vr	r	sp	fr	*Total*
Tundra	51.3	13.6	29.7	50.4	46.8	*191.8*
Forest Tundra	56.4	15.5	20.9	9.4		*102.1*
North Taiga	484.6	53.2	13.0			*550.7*
Middle Taiga	748.0					*748.0*
South Taiga	540.0					*540.0*
Mixed Forest	814.3					*814.3*
Broadleaves Forest	517.2					*517.2*
Forest Steppe	522.7					*522.7*
Steppe	708.6					*708.6*
Semidesert	204.8					*204.8*
Desert	54.9					*54.9*
Total, km^2	*4702.6*	*82.2*	*63.6*	*59.8*	*46.8*	*4955.0*
Total, %	*94.9*	*1.7*	*1.3*	*1.2*	*0.9*	*100.0*

Table 13.
Areas (in 1000 km^2) covered by S. lenense by zones of its occurrence.

southern boundary of the **sp** zone approximately corresponds to the isotherm of annual mean temperature of −4°C and an annual precipitation amount of 500 mm.

4. Discussion

If we consider the model maps of species, constructed according to the value of occurrence, as their geographical range in the territory of the EEPEF, then the areas of occurrence identified on it indicate areas where mosses have optimal and pessimal conditions. Results show that almost all species have an optimal area in the regions around the Baltic Sea or in the subarctic, where the wettest conditions are observed in the EEPEF. If we express the values of the moisture factors necessary for the successful distribution of species, in absolute values, they look as follows: annual precipitation is not less than 550 mm and relative humidity is not less than 60–70%.

A total of 7 species of 13 are widespread in the study area. These are *S. angustifolium*, *S. fallax*, *S. flexuosum*, *S. balticum*, *S. riparium*, *S. majus*, and *S. cuspidatum*. All of them play an important phytocenotic role in wetlands. Restricted species have western distribution. And only *S. lenense* comes to the north of the European part of Russia from the east. Some of the restricted species, such as *S. obtusum* and *S. tenellum*, do not have an optimum in the EEPEF. This suggests that they come here only at the edge of the range, and the center of their distribution is outside the EEPEF. Abovementioned seven species are characterized by the largest phytocenotic significance in wetland communities. If we compare their ranges (**Figure 2**), it is clear that they overlap significantly, but, nevertheless, each species is characterized by its own characteristics. The *S. flexuosum* area pattern is the most different from the others. This species is practically absent in the tundra and reduces its abundance to the north and south of the forest zone. At the same time, it cannot be called the most "southern" of all seven species, since the range of *S. fallax*, for example, goes even further south than *S. flexuosum* (**Figure 2**). At the same time, *S. fallax* is able to grow in the tundra, that is, far north than *S. flexuosum*. Although *S. flexuosum* grows throughout the entire EEPEF forest zone, it is obvious that its western regions are under heavy rainfall conditions. The range of *S. angustifolium* in the southern part is similar to the pattern of the ranges of *S. fallax* and *S. flexuosum*. In the north, *S. angustifolium* comes much farther into the tundra and can be found there quite often, unlike the last two (**Figure 2**). The most northern species, perhaps, can be called *S. balticum*. On the southern limit of its range, it is limited to the southern boundary of the forest zone, and in the north, it is widely represented in taiga and in tundra. The orientation of the boundaries of its range is parallel to the boundary of the last glaciation and the zone of maximal spread of wetlands (and not the boundaries of natural zones). Such orientation of boundaries indicates that its distribution in the EEPEF is caused not only by climate parameters but also by the landscape structures that formed on the plain as they recede the glacier. This equally applies to *S. riparium*.

As correlation analysis shows (**Table 14**), the occurrence in the local floras of all species of the subgenus Cuspidata, except for *S. lenense*, *S. pulchrum*, and *S. tenellum*, has a high positive relationship with the rainfall of August (**pr08**), September (**pr09**), and October (**pr10**) (**Table 2**). According to WorldClim data [25], the maximum humidity in the EEPEF is observed in the west of forest zone and tundra zone during the summer-autumn season and sharply decreases in values starting from the south of the forest steppe zone, which is associated with an increase in monthly and average annual temperatures. Therefore, in the south, species of the subgenus Cuspidata quickly reduce their abundance, completely disappearing in the south of the steppe zone, or even further north (**Figure 2**). This is associated with high negative correlation coefficients between the values of occurrence and monthly temperatures (**tm**) of the vegetation period (**Table 14**). In the north, in the tundra, the occurrence of many species decreases, but not as sharply as at the southern limit of distribution. Apparently, despite the cold summer, they still find enough moisture here to grow successfully.

The cluster analysis conducted for 13 species of the subgenus Cuspidata by the values of 23 climatic factors shows that the studied species are divided into four clusters according to their climatic preferences (**Figure 3**). **First cluster:** *S. lenense*; **second cluster:** *S. tenellum*, *S. pulchrum*, and *S. lindbergii*; **third cluster:** *S. jensenii*, *S. obtusum*, *S. majus*, *S. cuspidatum*, and *S. balticum*; and **fourth cluster:** *S. fallax*, *S. flexuosum*, *S. angustifolium*, and *S. riparium*. It is interesting to note that within these groups, there is a similarity in environmental preferences also. So the species

Factor	ang	fal	flex	balt	cusp	jens	lenens
amt	**−0.65**	−0.47	−0.28	**−0.62**	0.08	**−0.66**	**−0.50**
pr04	0.05	0.30	0.41	−0.08	**0.54**	−0.08	−0.20
pr05	0.11	0.39	0.43	−0.06	**0.52**	−0.07	−0.21
pr06	0.15	0.43	**0.50**	0.00	**0.61**	0.02	−0.19
pr07	0.40	**0.65**	**0.69**	0.22	**0.71**	0.23	−0.17
pr08	**0.79**	**0.81**	**0.72**	**0.72**	**0.62**	**0.70**	−0.08
pr09	**0.80**	**0.80**	**0.74**	**0.71**	**0.50**	**0.69**	0.01
pr10	**0.77**	**0.78**	**0.67**	**0.59**	0.47	**0.58**	−0.10
pr_a	0.47	**0.69**	**0.73**	0.33	**0.72**	0.30	−0.20
reh04	**0.75**	0.48	0.39	**0.84**	0.19	**0.79**	0.25
reh05	**0.57**	0.32	0.30	**0.72**	0.17	**0.65**	0.24
reh06	**0.54**	0.43	0.45	**0.65**	0.44	**0.56**	0.15
reh07	**0.71**	**0.61**	**0.59**	**0.77**	**0.54**	**0.69**	0.05
reh08	**0.83**	**0.61**	**0.50**	**0.90**	0.30	**0.84**	0.17
reh09	**0.85**	**0.64**	**0.49**	**0.90**	0.28	**0.86**	0.16
reh10	**0.83**	**0.66**	**0.50**	**0.80**	0.22	**0.78**	0.19
tm04	**−0.75**	**−0.54**	−0.36	**−0.75**	−0.02	**−0.77**	−0.41
tm05	**−0.79**	**−0.58**	−0.42	**−0.81**	−0.09	**−0.82**	**−0.51**
tm06	**−0.81**	**−0.59**	−0.43	**−0.85**	−0.13	**−0.83**	**−0.51**
tm07	**−0.82**	**−0.59**	−0.45	**−0.89**	−0.19	**−0.86**	**−0.51**
tm08	**−0.79**	**−0.59**	−0.42	**−0.82**	−0.10	**−0.82**	**−0.50**
tm09	**−0.76**	**−0.57**	−0.38	**−0.75**	−0.05	**−0.78**	−0.40
tm10	**−0.59**	−0.44	−0.25	**−0.54**	0.11	**−0.59**	−0.20

Factor	lindb	maj	obtus	pulch	rip	tenell
amt	**−0.57**	−0.49	**−0.51**	0.02	**−0.59**	0.03
pr04	−0.21	0.12	0.19	0.27	0.02	0.15
pr05	−0.22	0.15	0.14	0.19	0.12	0.09
pr06	−0.16	0.23	0.19	0.28	0.18	0.18
pr07	0.02	0.43	0.40	0.41	0.45	0.26
pr08	**0.53**	**0.79**	**0.76**	**0.66**	**0.74**	**0.50**
pr09	**0.53**	**0.70**	**0.79**	0.43	**0.76**	0.34
pr10	0.37	**0.62**	**0.65**	0.28	**0.72**	0.16
pr_a	0.13	0.48	**0.52**	0.48	0.47	0.35
reh04	**0.75**	**0.69**	**0.69**	0.44	**0.69**	0.34
reh05	**0.63**	**0.55**	**0.53**	0.42	**0.52**	0.37
reh06	0.48	**0.56**	0.49	**0.51**	**0.51**	0.38
reh07	**0.56**	**0.70**	**0.60**	**0.58**	**0.67**	0.44
reh08	**0.75**	**0.75**	**0.72**	0.44	**0.77**	0.34
reh09	**0.76**	**0.78**	**0.75**	0.43	**0.81**	0.32
reh10	**0.66**	**0.72**	**0.73**	0.26	**0.75**	0.17
tm04	**−0.68**	**−0.61**	**−0.62**	−0.13	**−0.69**	−0.10

tm05	**−0.72**	**−0.65**	**−0.67**	−0.21	**−0.73**	−0.17
tm06	**−0.74**	**−0.69**	**−0.69**	−0.27	**−0.75**	−0.22
tm07	**−0.79**	**−0.73**	**−0.70**	−0.40	**−0.77**	−0.32
tm08	**−0.72**	**−0.66**	**−0.66**	−0.23	**−0.74**	−0.18
tm09	**−0.67**	**−0.62**	**−0.61**	−0.14	**−0.71**	−0.10
tm10	**−0.50**	−0.42	−0.46	0.10	**−0.54**	0.09

Values of r >0.5 in absolute value are highlighted in bold. All values are statistically significant at p < 0.05.
Note: Climatic factors: ***amt****—annual amount of precipitation;* ***pr01–pr12****—monthly amount of precipitation in January–December;* ***pr_a****—annual precipitation average;* ***reh4-reh10****—relative humidity in April–October; and* ***tm04–tm10****—monthly temperature average in April–October.*

Table 14.
The Spearmen correlation coefficient between the values of climatic factors and species abundance.

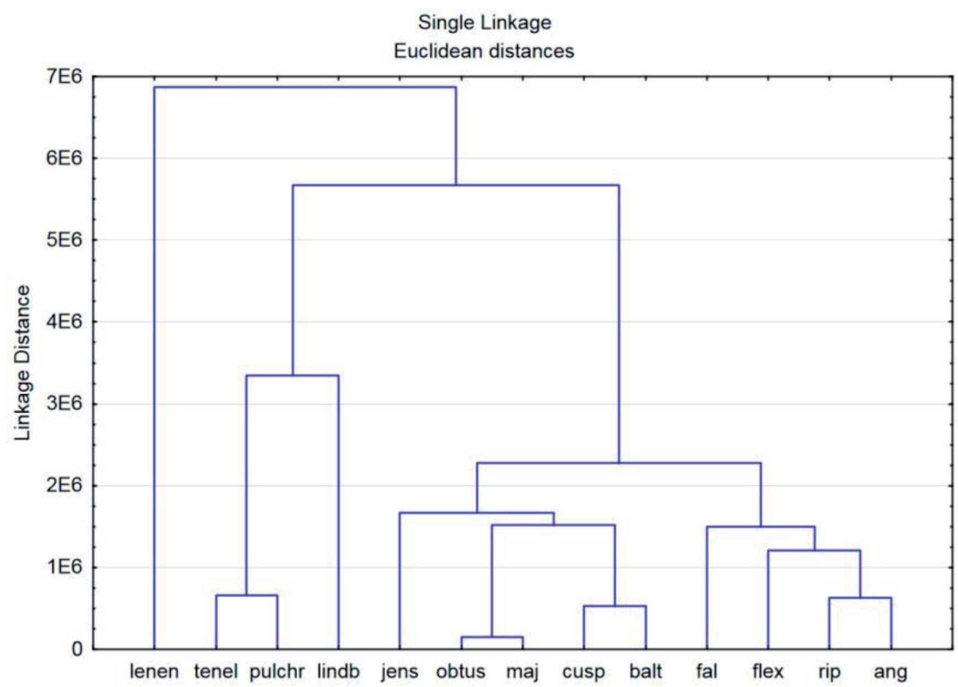


Figure 3.
Tree diagram of 13 species by 23 climatic factors.

belonging to the 4th cluster grow mainly in the carpets of mesotrophic or oligotrophic bogs and boggy forests; the species belonging to the third cluster are most often found in heavily flooded hollows of bogs and fens; the species belonging to the second cluster grow in less flooded hollows of bogs. The *S. lenense* stands apart, which is found in the studied territory on hummocks in the boggy tundra. It seems to us that the similarity in the species relation to the conditions of watering of the habitat and climate is not accidental. The fact is that the amount of precipitation determines the hydrological regime in peat, and the humidity of the air affects the safety of the growing point during the dry season in the middle of summer.

5. Conclusion

Comparing the distribution ranges of 13 species of the subgenus Cuspidata in the EEPEF shows that there are as well as widespread and restricted species. The widespread species are as follows: *S. angustifolium*, *S. fallax*, *S. flexuosum*, *S. balticum*, *S. riparium*, *S. majus*, and *S. cuspidatum*. The restricted ones are *S. pulchrum*, *S. obtusum*, *S. jensenii*, *S. tenellum*, *S. lindbergii*, and *S. lenense*. Widespread species are common in wetland communities through entire area of the EEPEF in forest zone and tundra (except *S. cuspidatum*, which is absent in tundra). Restricted species (except *S. lenense*) have western trend in its ranges. Maximum activity (optimum) of these species depends on moisture factors (humidity and precipitations), and southern boundaries are limited by temperature. The only *S. lenense* is eastern (Siberian) species. It mainly occurs in tundras and one can see a middle dependence of its distribution on the temperature factors (**Table 14**).

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