

DISTRIBUTION PATTERNS OF *SPHAGNUM* SECT. *ACUTIFOLIA* SPECIES IN THE  
EASTERN EUROPEAN PLAIN AND EASTERN FENNOSCANDIA

ЗАКОНОМЕРНОСТИ РАСПРОСТРАНЕНИЯ ВИДОВ СЕКЦИИ *ACUTIFOLIA* РОДА  
*SPHAGNUM* НА ТЕРРИТОРИИ ВОСТОЧНО-ЕВРОПЕЙСКОЙ РАВНИНЫ И  
ВОСТОЧНОЙ ФЕННОСКАНДИИ

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Abstract

Distribution of 11 species of *Sphagnum* from section *Acutifolia* in the East European Plain and Eastern Fennoscandia (EEPEF) is analysed. Area of each species was compiled using geostatistics methods. Within the range of each species, the abundance zones determined on a six-point scale are shown. Patterns of species distribution, depending on changes in climatic factors, were revealed with using the methods of multivariate analysis. A map of species richness for the studied territory is drawn up and regularities of changes in the number of growing species are determined, in connection with the change in climatic parameters. Eleven species of the section *Acutifolia* are divided in two groups by their distribution pattern. First group contains such species as *S. girgensohnii*, *S. russowii*, *S. capillifolium*, *S. warnstorffii*, *S. fuscum*, *S. rubellum*, and *S. fimbriatum*, widespread in EEPEF. They grow in all vegetation zones (except desert and semidesert zones) and have maximal abundance in the west of the territory, in boreal and hemiboreal zones. Second group includes *S. quinquefarium*, *S. subnitens*, *S. subfulvum*, and *S. molle*, the rarest species in EEPEF. These species are distributed in boreal and hemiboreal zones only around the Baltic Sea and have low abundance elsewhere. High moisture is necessary for high species abundance. For the group of widespread species, values of precipitation amount must be not less than 600 mm per year and relative humidity – not less than 60% during growing season through the zones of climatic optimum. In the zones of climatic pessimum it might be various, but not less than 450 mm and 50% respectively. For the group of rare species, annual precipitation must be not less than 600 mm and relative humidity during growing season – not less 70% through the whole range. In addition to the climatic factors, distribution of rare species is probably associated with areas of maximal distribution of peatlands and presence of glacial forms of relief within the zone of maximal spread of the Last Glaciation. In these regions maximal species diversity is also observed.

Резюме

Проведено исследование распространения 11 видов сфагновых мхов из секции *Acutifolia* на территории Восточно-Европейской равнины и Восточной Фенноскандии (ВЕРВФ). Составлены ареалы всех видов с применением методов геостатистики. В пределах ареала каждого вида показаны зоны встречаемости, определенные по шестибальной шкале. Посредством методов многомерного анализа выявлены закономерности распространения видов в зависимости от изменения климатических факторов. Составлена карта видовой богатства для изученной территории и определены закономерности изменения количества произрастающих видов в связи с изменением климатических показателей. По характеру рисунка ареалов 11 видов из секции *Acutifolia* можно разбить на две большие группы. Первая – это обычные на территории ВЕРВФ виды. С разным обилием они распространены повсеместно от зоны лесостепи до тундры. Зоны их максимального обилия приходятся на регионы с наибольшим количеством осадков, которые в силу закономерностей движения воздушных масс сосредоточены вокруг Балтийского моря. В эту группу входят *S. girgensohnii*, *S. russowii*, *S. capillifolium*, *S. warnstorffii*, *S. fuscum*, *S. rubellum* и *S. fimbriatum*. Вторая группа (*S. quinquefarium*, *S. subnitens*, *S. subfulvum*, *S. molle*) представлена достаточно редкими для территории ВЕРВФ видами. Эти виды в пределах своих ареалов не обладают высокой встречаемостью. Территория их распространения находится вокруг Балтийского моря. Помимо климатических факторов, распространение редких видов, возможно, связано с зоной максимального распространения болот и наличием ледниковых форм рельефа в пределах зоны максимального распространения последнего оледенения. В этих же регионах наблюдается и повышенное видовое разнообразие.

KEYWORDS: biogeography, ecology, ARCGIS, BIOCLIM

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## INTRODUCTION

This paper continues a study of the spatial patterning of the *Sphagnum* species distribution by climatic factors in the East European Plain. The previous paper dealt with the species of the section *Sphagnum* (Popov, 2016), while the present one addresses to the section *Acutifolia*. The study territory is somewhat expanded here so to cover the territory of Finland (Fig. 1). There are 11 species of the section *Acutifolia* in the study area, out of 17 in Europe (Hill *et al.*, 2006; Kyrkjeeide *et al.*, 2015).

The aim of present work is modeling of species distribution range according to the gradients of the climatic factors, an attempt to explain the limits of species range by correlation with climatic and other environmental factors (Tolmachev, 1962). The ecological aspect of the analysis of distribution range is related to the concept of ecological niche *sensu* Grinnell (1991). In contrast to the Hutchinson's ecological niche (Hutchinson, 1965), which is specified by the own species properties, the Grinnell's niche is determined by the environmental parameters. Thus, by correlation of climatic gradient with the quantitative spatial characteristics of species, we can obtain the climatic optimum and the pessimum of the species.

General patterns of climatic factors within the study area were described earlier (Popov, 2016). Patterns of variation of the selected climatic factors by BIOCLIM are shown in Fig. 2. The distribution of peatlands, which cover more than 10% in the study area, are shown in Fig. 3.

Eleven zones are stretching from north to south in the study area (Fig. 1). Tundra zone is characterized by a relatively low precipitation, but evaporation here is also low, which cause a high degree of paludification, thus bogs occupy over half of the whole territory or tundra zone in lowlands.

Peatlands are especially abundantly represented in the boreal forest zone, where about 80% of all peat resources occur (Boch & Mazing, 1979). A prolonged excess surface moisture in combination with a relatively warm summer favor the peat accumulation. The thickness of the peat deposits reaches 2–6 m, occasionally 10 m and more. Karelia, Kola Peninsula and Finland are the areas most rich in peatlands, where they occupy about 30% of the territory, with aapa-mires dominant north of 62°N (Boch & Mazing, 1979). A similarly high peatland abundance is in Polesye region: in Belarus, north-western Ukraine, and Bryansk Province of Russia); most of the basin of Pripyat' River is occupied by mires. The peatland area is declining southwards, becoming no more than 3–5% of the territory in forest-steppe zone.

In the East European Plain and Eastern Fennoscandia, the area of wide scale distribution of bogs in general coincides with the boundary of maximum distribution of the Last (Valdai) Glaciation and stretches to the fluvio-glacial landscapes formed southward of the Glacier. It includes Polesye (Belarus, Bryansk Province of Russia and Northern Ukraine), Meschera (big lowland between Mos-

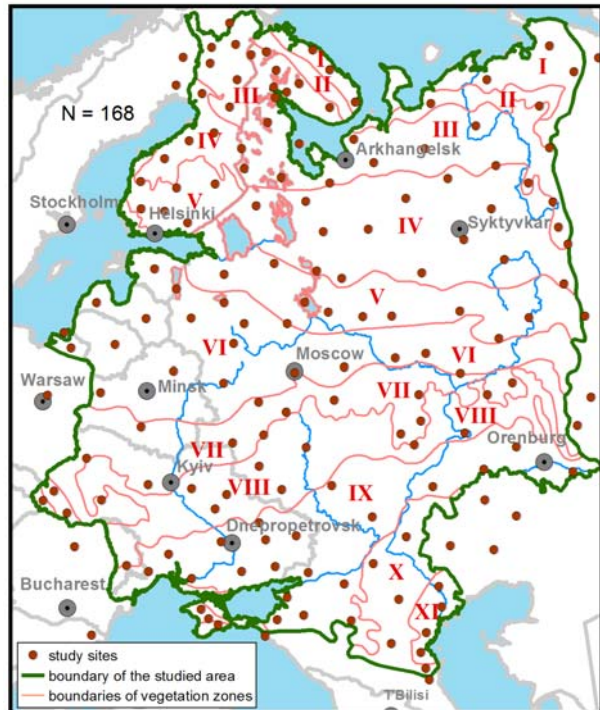


Fig. 1. Study area, showing localities involved in analysis and vegetation zones, following Kurnaev (1973) for the former USSR and Ahti *et al.* (1968) for Finland: I – tundra; II – forest-tundra; III – northern taiga; IV – middle taiga; V – southern taiga; VI – hemiboreal forests; VII – broadleaved forests; VIII – forest-steppe; IX – steppe; X – semidesert; XI – desert.

cow and Nizhniy Novgorod), and North-East of Russia (Komi Republic) (Fig. 2B). This boundary also corresponds to the boundary of the maximal spreading of bogs in the European part of the USSR established by Mazing *et al.* (1990).

## METHODS

This work is based on the data of local bryofloras, which have been studied by different authors. References to these data were given in the previous paper (Popov, 2016). Some additional sources were used in the present paper, *i.e.*, Heikkilä & Lindholm, 1988; Maksimov, 1998; Smagin & Napreenko, 2003; Szurdoki & Odor, 2004; Petrova, 2008; Lain *et al.*, 2009; Vellak *et al.*, 2013; Lapshina *et al.*, 2016; Kozhin *et al.*, 2016; Belkina & Likhachev, 2016; Global Biodiversity Information Facility (GBIF) database (<http://www.gbif.org>). In total, data for 168 points (study sites) in East European Plain and Eastern Fennoscandia (EEPEF) were compiled (Fig. 1). On the basis of a layer of 168 points, continuous coverages with resolution 10 km per one pixel were made for each of 11 species, using the kriging method. Continuous coverages of species abundance in the territory of EEPEF were obtained as a result of approximating the values of 168 points to a regular network of pixels. The values of the points were assigned according to the numerical scale of species occurrence from 0 (absent) to 5 (common and abundant) (Popov, 2016, 2017). The verification of con-



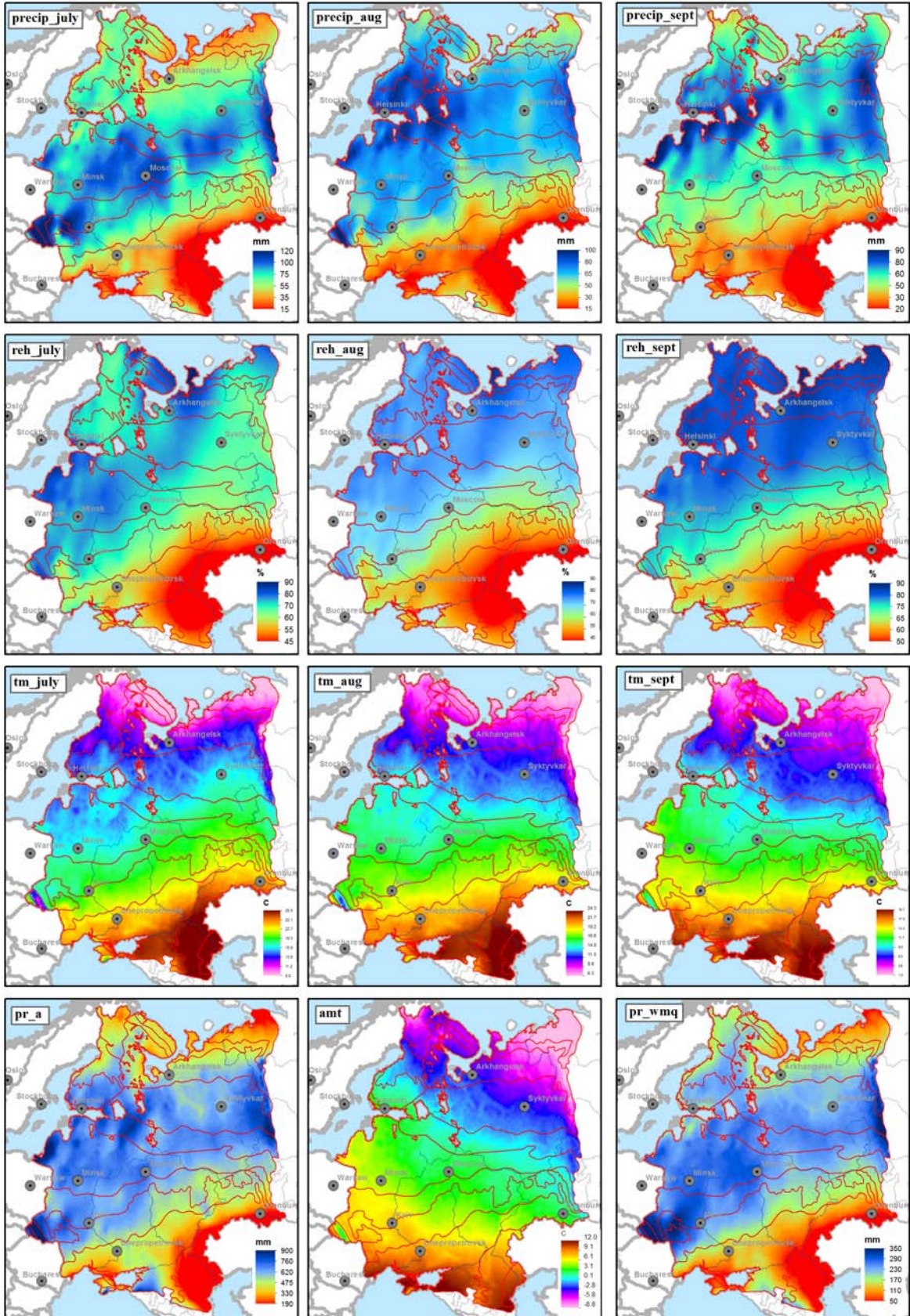


Fig. 2. Distribution of some important climatic variables on the territory of the EEPEF: precip – precipitation; reh – relative air humidity; tm – temperature by months; pr\_a – annual precipitation; amt – annual mean temperature; pr\_wmq – mean temperature of the warmest quarter of the year.



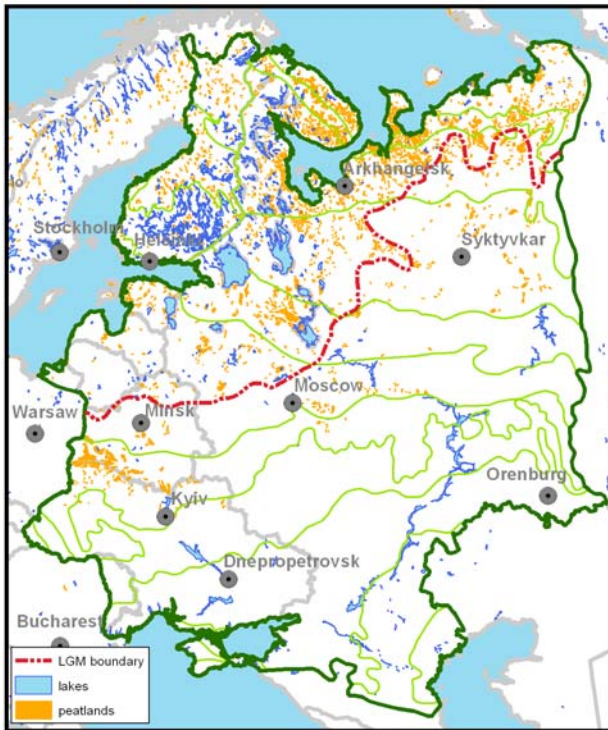


Fig. 3. Distribution of lakes and peatlands and the boundary of the Last Glacial Maximum (LGM). Boundary of LGM is given by Kvasov, 1974, lakes and peatlands by Lukicheva, 1964.

to 21.8°. The other above mentioned non-climatic factors were analyzed as qualitative.

For all climatic factors, altitude and slope continuous coverages were built. All coverages (11 species, number of species, 43 climatic factors and two relief characteristics) were combined into a single spatial coverage. This coverage was transformed into relational database consisting of 49557 rows (number of pixels) and 57 columns (11 species, number of species, 43 climatic factors, two relief characteristics) in ERDAS package. This database was used for correlation analysis in software Statistica 6.0. The operations by intersection of the vector layers and calculating of areas have been performed in ArcGis program.

## RESULTS

Correlation analyzes shows that the abundance of most species in general has the high association with values of precipitation, humidity and temperature in such months as August, September and October (Table 2). At the same time, different species have their own nuances. Distributional features of each species are given below.

*Sphagnum girgensohnii*. This is the most common species in the study area. Its range practically coincides with the boundaries of forest zone (Fig. 4). Comparison of the areas of its abundance zones shows that *S. girgensohnii* is common in more than 50.2% of the territory of the EEPEF, and total area of its range is 81.2% of the EEPEF area (Table 4). This species reaches the greatest abundance in the forest zone, somewhat declining northward, to tundra zone, but it remains a fairly common species there as well (Fig. 4). It totally disappears only in the south, in most xeric regions.

*Sphagnum girgensohnii* increases its occurrence according to the increase of precipitation amounts in August, September and October and the relative air humidity in all summer months (Table 2; Supplementary materials, Table I). The greatest abundance (zones **fr** and **com**, Fig. 4) is observed in areas with annual precipitation of at least 600 mm (in tundra zone – 445 mm), an average annual temperature no more than +2°C and not less than –3.7 °C (Figs. 6, 7; Supplementary materials, Table I). Comparison of the mean monthly temperatures of the summer and autumn months shows that in the zones of high abundance of this species the summer is relatively cool (Fig. 7; Supplementary materials, Table I, **tm06-tm10**, by the zones **fr** and **com**). The species is absent in regions with the mean annual temperature higher than +6 °C, temperatures in June, July and August higher than +20°C, relative humidity less than 60% in summer months, and annual precipitation less than 500 mm (Figs. 6, 7; Supplementary materials, Table I, **pr\_a**, **Amt**, **tm06-tm10**, in the **abs** zone).

tinuous covers was carried out by the cross-validation method in the SAGA GIS package (Savel'ev, 2012). The significance of coverages by the criterion of  $R^2$  are from 0.913 to 0.997 for 11 species. In addition, cover of number of species was built. The continuous coverages were transformed into integer ones by the method of "natural breaks" for creating maps of the species distribution range. Methods for creating distribution maps for the species of *Sphagnum* on the basis of a points layer are considered in detail in a previous paper (Popov, 2017) and in general these methods are considered in detail by Savel'ev (Savel'ev *et al.*, 2012), Lur'e (2010) and Dem'yanov & Savel'eva (2010)

Climatic variables were chosen for the analysis of their influence on the species distribution. These variables are proposed by the WORLDCLIM and BIOCLIM programs (BIOCLIM project, 2009; Hijmans *et al.*, 2005). In total, 43 climatic variables were included in the analysis (Table 1). Such variables as the relative humidity in January, February, March, November and December (reh01-03, reh11-12) were rejected, because they do not have biological significance.

Moreover, such non-climatic factors as vegetation zones, forestation of the EEPEF and coverage by lakes, bogs and swamps, historical factor (boundaries of the Last Glaciation cover) and relief characteristics have been analyzed (Fig. 3). Among these non-climatic characteristics, two quantitative variables were used, i.e., altitude and slope (altitude is a characteristic of the relief from WORLDCLIM data set; slope have been obtained on the basis of altitude coverage in ArcGis). On the territory of the EEPEF the range of altitudes varies from –33 m to 1661 m above sea level. The values of slopes vary from 0

Table 1. Variables from the database BIOCLIM used in analyses

Codes	Explanation
<b>tm 01-12</b>	Mean monthly temperature, °C (for each month: 01: January – 12: December)
<b>pr 01-12</b>	Monthly precipitation, mm (for each month)
<b>reh 04-10</b>	Relative humidity, % (for each month)
<b>pr_a</b>	Annual precipitation, mm
<b>amt</b>	Annual Mean Temperature
<b>pr_wtm</b>	Precipitation of Wettest Month
<b>pr_drm</b>	Precipitation of Driest Month
<b>pr_wtq</b>	Precipitation of Wettest Quarter
<b>pr_drq</b>	Precipitation of Driest Quarter
<b>pr_wmq</b>	Precipitation of Warmest Quarter
<b>pr_clq</b>	Precipitation of Coldest Quarter
<b>t_wtq</b>	Mean Temperature of Wettest Quarter
<b>t_drq</b>	Mean Temperature of Driest Quarter
<b>t_wmq</b>	Mean Temperature of Warmest Quarter
<b>t_clq</b>	Mean Temperature of Coldest Quarter

*Sphagnum russowii* and *S. capillifolium*. Like *S. girgensohnii*, these species are also widespread in the territory of the EEPEF. The patterns of their range and attitude in relation to the climatic factors are quite similar. The areas of their maximal abundance zones (**fr** and **com**) occupy about 50% of the total area of the EEPEF, and the entire range is more than 75% (Table 4). The range of these species lies in all vegetation zones, except for the desert and semi-desert ones (Fig. 4, Table 3). Their **fr**-zone covers almost the entire forest zone, and the maximum extent of their distribution reaches to the north and east of the Baltic sea (Fig. 4). In the tundra zone, *S. russowii* and *S. capillifolium* reduce their occurrence, but do not disappear at all.

In general, the abundance of these two species increases with the increase of precipitation in August–October and the annual amount of precipitation (Table 2). This may not be always the same if the mean values are considered, for example, the mean values of precipitation in **com**-zone in October is somewhat lower than in **fr**-zone at the same month (Fig. 6), because the spread of values in the latter is greater so it covers a much larger area and is located in several climatic zones.

These two species are also sensitive to high humidity in the summer and autumn months, showing a high positive correlation with the values of these factors (Table 2). A high negative correlation is observed between the values of occurrence and mean monthly temperatures in summer and autumn, as well as the average annual temperature (Table 2). The absolute values of climatic factors indicate that both species grow in regions with annual precipitation amount exceeding 450–460 mm and an average annual temperature less than +7°C (Fig. 6, 7; Supplementary materials, Table II, III). The optimum zones, i.e. areas of high occurrence, **fr(s)** and **com**, the annual precipitation exceeds 600 mm, relative humidity is in between 70–80%, and average annual temperature does not exceed +2°C. In northern subzones with high occurrence, **fr(n)**, the annual precipitation is lower at a

lower temperature (Fig. 6, 7; Supplementary materials, Table II, III). Monthly precipitation and air humidity increase from lower to higher abundance, being maximal in zones of highest species abundance. Monthly temperature, on the contrary, have a lowest values in the zones with highest species abundance.

Monthly precipitation and relative air humidity increase in absolute values, and the average monthly temperature falls from zones with low to high occurrence (Fig. 5, 6; Supplementary materials, Table II, III). The species are absent in regions with an average annual temperature above +7.7 °C, temperatures above +20°C in June, July and August, relative humidity less than 60% in summer months and an annual precipitation less than 450 mm (Fig. 6–7; Supplementary materials, Table I, **pr\_a**, **Amt**, **tm06-tm10**, in the **abs** zone)

*Sphagnum warnstorffii* has distribution that can be assumed as one of the most “northern” among the species of section *Acutifolia*. However the species distribution is probably caused not only by the climatic factors but likely corresponds to the numerous aapa-mires in Finland, Karelia and the Kola Peninsula (Kuznetsov, 1986; Elina *et al.*, 2010). At the same time, zone of the highest frequency of this species is not large, being only 7.4% of the total area of EEPEF (Table 4), though it grows in all vegetation zones, except for the desert and semi-desert ones (Fig.4; Table 4). The areas of their maximal abundance zones (**fr** and **com**) occupy about 35% of the total area of the EEPEF, and the entire range is 73.2% (Table 3).

Due to the confinedness of *S. warnstorffii* to aapa-bogs zone, the monthly absolute values of climatic factors do not change evenly by zones of abundance of this species (Fig. 6, 7; Supplementary materials, Table IV). However, correlation analysis shows that the abundance of *S. warnstorffii* increases along the moisture factors (**reh** and **pr**), namely the monthly precipitation and relative air humidity in August and September, and decreases according to increase monthly temperatures (Table 2). The average annual precipitation amount required for this species is at least 550 mm, and the average annual temperature is no more than +5°C. Relative humidity during the growing season should not be less than 60%, and the average monthly temperature is not higher than +20°C. In zones of maximal abundance of *S. warnstorffii*, the summer monthly temperatures are the lowest among the species of section *Acutifolia*: they do not exceed +13°C, and the humidity is the highest, 68% or more (Fig. 6, 7; Supplementary materials, Table IV).

*Sphagnum fuscum*. As well as for previous species, the abundance of *S. fuscum* increases in the regions with the greatest moisture in August–October (Table 2). However, it does not reach wide occurrence in any region. The maximum estimation of its occurrence, four (frequent), may depend on the species ecology: *Sphagnum fuscum* is predominantly a species of raised bogs (Boch & Kuzmina, 1985; Laine *et al.* 2009). In the northern

Table 2. 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. The statistically significant values are marked by asterisk. \*  $p < 0,05$ ; \*\*  $p < 0,01$ ; \*\*\*  $p < 0,001$

	girgensohnii	russowii	capillifolium	warnstorfi	fuscum	fimbriatum	rubellum	molle	quinquefarium	subfulvum	subnitens	species number
pr01	-0.02*	-0.01**	-0.03***	-0.14***	-0.21***	-0.12***	-0.07***	0.11**	0***	0.07***	-0.03***	0***
pr02	-0.17***	-0.16***	-0.13***	-0.28***	-0.33***	-0.12***	-0.12***	0.11**	0.08***	-0.12***	0.04***	-0.06***
pr03	0.17***	0.20***	0.23***	0.05***	0.004**	0.14***	0.26***	0.34**	0.43***	0.1***	0.38***	0.31***
pr04	0.12***	0.10***	0.13***	-0.11***	-0.13***	-0.08***	0.11***	0.18**	0.27***	-0.1***	0.13***	0.16***
pr05	0.25***	0.18***	0.19***	-0.07***	-0.07***	-0.10***	0.13***	0.05*	0.25***	-0.17***	0.08***	0.16***
pr06	0.27***	0.21***	0.24***	0.003*	-0.02***	0.007*	0.18***	0.12**	0.30***	-0.12***	0.14***	0.25***
pr07	0.54***	0.48***	0.49***	0.24***	0.22***	0.27***	0.38***	0.19**	0.45***	0.07***	0.24***	0.50***
pr08	<b>0.79***</b>	<b>0.84***</b>	<b>0.84***</b>	<b>0.73***</b>	<b>0.69***</b>	<b>0.61***</b>	<b>0.78***</b>	0.37**	<b>0.75***</b>	0.47***	0.6***	<b>0.83***</b>
pr09	<b>0.83***</b>	<b>0.86***</b>	<b>0.81***</b>	<b>0.77***</b>	<b>0.74***</b>	<b>0.57***</b>	<b>0.79***</b>	0.27***	<b>0.57***</b>	0.45***	0.42***	<b>0.78***</b>
pr10	<b>0.77***</b>	<b>0.78***</b>	<b>0.70***</b>	<b>0.67***</b>	<b>0.64***</b>	0.45***	<b>0.65***</b>	0.11**	0.36***	0.39***	0.24***	<b>0.62***</b>
pr11	<b>0.58***</b>	<b>0.58***</b>	<b>0.55***</b>	0.36***	0.31***	0.35***	<b>0.51***</b>	0.31**	0.47***	0.35***	0.36***	<b>0.58***</b>
pr12	0.17***	0.14***	0.14*	-0.06***	-0.10***	0.01**	0.12***	0.21**	0.20***	0.05***	0.13***	0.18***
reh04	<b>0.64***</b>	<b>0.68***</b>	<b>0.71***</b>	<b>0.87***</b>	<b>0.87***</b>	<b>0.77***</b>	<b>0.76***</b>	0.24***	<b>0.60***</b>	0.35***	<b>0.52***</b>	<b>0.73***</b>
reh05	<b>0.47***</b>	<b>0.49***</b>	<b>0.54***</b>	<b>0.68***</b>	<b>0.7***</b>	<b>0.67***</b>	<b>0.63***</b>	0.25***	<b>0.57***</b>	0.19***	<b>0.52***</b>	<b>0.61***</b>
reh07	<b>0.64***</b>	<b>0.63***</b>	<b>0.67***</b>	<b>0.7***</b>	<b>0.71***</b>	<b>0.71***</b>	<b>0.72***</b>	0.32***	<b>0.63***</b>	0.21***	<b>0.56***</b>	<b>0.73***</b>
reh06	<b>0.47***</b>	<b>0.46***</b>	<b>0.52***</b>	<b>0.57***</b>	<b>0.6***</b>	<b>0.63***</b>	<b>0.62***</b>	0.29***	<b>0.56***</b>	0.09***	<b>0.50***</b>	<b>0.61***</b>
reh08	<b>0.74***</b>	<b>0.77***</b>	<b>0.78***</b>	<b>0.91***</b>	<b>0.93***</b>	<b>0.77***</b>	<b>0.81***</b>	0.24***	<b>0.58***</b>	0.39***	<b>0.52***</b>	<b>0.77***</b>
reh09	<b>0.77***</b>	<b>0.81***</b>	<b>0.82***</b>	<b>0.94***</b>	<b>0.95***</b>	<b>0.79***</b>	<b>0.82***</b>	0.23***	<b>0.56***</b>	0.44***	<b>0.50***</b>	<b>0.78***</b>
reh10	<b>0.80***</b>	<b>0.79***</b>	<b>0.78***</b>	<b>0.88***</b>	<b>0.91***</b>	<b>0.65***</b>	<b>0.76***</b>	0.08***	0.44***	0.35***	0.28***	<b>0.69***</b>
amt	<b>-0.63***</b>	<b>-0.62***</b>	<b>-0.58***</b>	<b>-0.78***</b>	<b>-0.8***</b>	<b>-0.51***</b>	<b>-0.51***</b>	0.11*	-0.17**	<b>-0.33***</b>	<b>-0.08***</b>	<b>-0.52***</b>
tm01	-0.45***	-0.40***	-0.35***	<b>-0.54***</b>	<b>-0.55***</b>	-0.24***	-0.29***	0.26***	0.11***	-0.16***	0.21***	-0.22***
tm02	-0.42***	-0.38***	-0.33***	<b>-0.54***</b>	<b>-0.55***</b>	-0.26***	-0.27***	0.24***	0.09***	-0.19***	0.18***	-0.21***
tm03	-0.47***	-0.45***	-0.41***	<b>-0.65***</b>	<b>-0.66***</b>	-0.4***	-0.36***	0.18***	-0.03***	-0.27***	0.04***	-0.32***
tm04	<b>-0.71***</b>	<b>-0.72***</b>	<b>-0.69***</b>	<b>-0.89***</b>	<b>-0.89***</b>	<b>-0.64***</b>	<b>-0.64***</b>	0.01*	-0.32***	-0.41***	-0.24***	<b>-0.61***</b>
tm05	<b>-0.75***</b>	<b>-0.76***</b>	<b>-0.75***</b>	<b>-0.92***</b>	<b>-0.93***</b>	<b>-0.70***</b>	<b>-0.7***</b>	-0.07**	-0.42***	-0.42***	-0.32***	<b>-0.69***</b>
tm06	<b>-0.76***</b>	<b>-0.77***</b>	<b>-0.77***</b>	<b>-0.94***</b>	<b>-0.95***</b>	<b>-0.73***</b>	<b>-0.73***</b>	-0.10**	-0.48***	-0.42***	-0.38***	<b>-0.72***</b>
tm07	<b>-0.75***</b>	<b>-0.77***</b>	<b>-0.79***</b>	<b>-0.94***</b>	<b>-0.95***</b>	<b>-0.79***</b>	<b>-0.77***</b>	-0.19**	-0.58***	-0.42***	-0.50***	<b>-0.77***</b>
tm08	<b>-0.75***</b>	<b>-0.76***</b>	<b>-0.75***</b>	<b>-0.92***</b>	<b>-0.93***</b>	<b>-0.70***</b>	<b>-0.69***</b>	-0.07**	-0.43***	-0.42***	-0.33***	<b>-0.69***</b>
tm09	<b>-0.74***</b>	<b>-0.73***</b>	<b>-0.71***</b>	<b>-0.88***</b>	<b>-0.90***</b>	<b>-0.64***</b>	<b>-0.63***</b>	0.02*	-0.33***	-0.39***	-0.23***	<b>-0.62***</b>
tm10	<b>-0.59***</b>	<b>-0.56***</b>	<b>-0.52***</b>	<b>-0.72***</b>	<b>-0.73***</b>	-0.45***	-0.44***	0.15**	-0.08***	-0.30***	0.02***	-0.41***
tm11	<b>-0.52***</b>	-0.48***	-0.43***	<b>-0.63***</b>	<b>-0.65***</b>	-0.35***	-0.35***	0.21**	0.01**	-0.24***	0.11***	-0.32***
tm12	-0.48***	-0.44***	-0.39***	<b>-0.58***</b>	<b>-0.59***</b>	-0.29***	-0.32***	0.23***	0.06***	-0.21***	0.15***	-0.27***
pr_a	<b>0.57***</b>	<b>0.57***</b>	<b>0.56***</b>	0.32***	0.28***	0.27***	<b>0.50***</b>	0.30***	<b>0.57***</b>	0.22***	0.36***	<b>0.57***</b>
pr_clq	0.04***	0.04***	0.05***	-0.14***	-0.19***	-0.07***	0.01**	0.20***	0.17***	0.06***	0.05***	0.08***
pr_drm	0.12***	0.15***	0.19***	0.02***	-0.03***	0.11***	0.16***	0.27***	0.35***	0.10***	0.22***	0.23***
pr_drq	0.08***	0.10***	0.13***	-0.07***	-0.12***	0.01**	0.12***	0.27***	0.31***	0.04***	0.17***	0.18***
pr_wmq	<b>0.55***</b>	<b>0.52***</b>	<b>0.54***</b>	0.31***	0.27***	0.28***	0.46***	0.26***	<b>0.56***</b>	0.12***	0.35***	<b>0.55***</b>
pr_wtm	<b>0.53***</b>	<b>0.52***</b>	<b>0.53***</b>	0.29***	0.26***	0.3***	0.46***	0.29***	<b>0.56***</b>	0.15***	0.35***	<b>0.55***</b>
pr_wtq	<b>0.57***</b>	<b>0.57***</b>	<b>0.58***</b>	0.36***	0.32***	0.33***	<b>0.53***</b>	0.32***	<b>0.63***</b>	0.18***	0.43***	<b>0.62***</b>
t_clq	<b>-0.43***</b>	-0.38***	-0.32***	-0.52***	<b>-0.53***</b>	-0.23***	-0.27***	0.25***	0.12***	-0.17***	0.21***	-0.2***
t_drq	<b>-0.57***</b>	<b>-0.53***</b>	<b>-0.51***</b>	<b>-0.64***</b>	<b>-0.68***</b>	-0.41***	-0.48***	0.14***	-0.13***	-0.11***	-0.02***	-0.41***
t_wmq	<b>-0.76***</b>	<b>-0.77***</b>	<b>-0.77***</b>	<b>-0.94***</b>	<b>-0.95***</b>	<b>-0.73***</b>	<b>-0.73***</b>	-0.10*	-0.48***	-0.42***	-0.39***	<b>-0.72***</b>
t_wtq	<b>-0.69***</b>	<b>-0.72***</b>	<b>-0.71***</b>	<b>-0.88***</b>	<b>-0.88***</b>	<b>-0.69***</b>	<b>-0.70***</b>	-0.12**	-0.49***	-0.44***	-0.43***	<b>-0.68***</b>
Non-climatic factors												
altitude	0.07***	0.02***	0.06***	0.02***	0.01*	0.002*	-0.08***	-0.08*	0.09***	-0.02***	0.01**	0.05***
slope	-0.05***	-0.06***	-0.06***	-0.02***	-0.03***	-0.07***	-0.12***	-0.11*	-0.06***	0.03***	-0.06***	-0.07***

regions of the EEPEF, it rarely occur in boggy forests, so its distribution may be underestimated. In the south of the forest zone, it occurs both in bogs and in boggy forests, but it is rare in all habitats. In general, its range

covers almost the entire forest zone (Fig. 4), and the southern boundary of zone of its maximal abundance almost coincides in its northern part with the boundary of zone of maximal distribution of bogs (Figs. 3, 4). To the north



Table 3. Mean values of climatic factors by zones of number of species (from 0 to 11)

Climatic factor	Number of species zones										Total mean		
	0	1	2	3	4	5	6	7	8	9		10	11
pr05	38.7	41.7	45.1	45.8	46.9	49.3	49.0	45.3	49.4	52.1	45.4	39.0	45.3
pr06	48.0	55.0	60.8	63.5	64.8	66.4	65.8	60.7	68.4	70.9	61.8	54.6	60.9
pr07	43.3	54.2	62.6	68.4	73.1	79.1	76.8	72.7	80.1	80.3	72.5	72.0	69.1
pr08	35.9	43.3	48.9	53.7	57.7	63.6	68.2	67.4	71.6	75.0	77.0	81.1	62.6
pr09	32.5	40.2	42.8	45.9	49.7	54.6	57.8	59.9	60.1	62.7	65.7	68.5	54.3
pr10	29.2	35.7	38.0	41.0	44.2	48.3	54.1	54.8	53.9	54.0	56.6	60.1	48.7
pr_a	417.3	489.9	539.6	559.1	572.4	598.7	591.6	567.7	611.0	631.2	607.1	621.8	560.5
reh05	56.5	56.0	58.2	58.3	58.4	59.5	63.4	67.2	66.6	68.3	68.7	67.1	63.5
reh06	57.5	59.7	62.3	63.2	63.9	65.1	67.5	68.1	68.8	70.7	69.7	67.8	65.8
reh07	56.3	60.4	63.6	65.4	66.9	68.7	71.5	71.8	72.7	74.2	73.9	72.9	68.7
reh08	56.5	59.6	62.8	65.1	67.1	70.0	74.7	76.8	76.8	77.6	78.4	78.9	71.6
reh09	61.6	64.2	66.9	68.9	70.8	73.7	79.1	81.6	81.2	81.8	82.9	84.0	76.1
reh10	73.1	75.0	76.4	77.8	79.2	81.6	85.5	88.5	86.5	85.8	86.7	86.8	83.3
amt	8.6	6.8	6.7	6.0	5.2	4.1	2.5	0.5	2.4	4.1	3.3	3.3	3.7
tm05	16.7	15.5	15.2	14.7	14.1	12.9	10.2	7.2	9.3	10.7	9.1	8.8	11.0
tm06	20.7	19.3	18.8	18.3	17.7	16.8	14.7	12.9	14.1	14.8	13.9	13.9	15.6
tm07	23.1	21.2	20.5	19.9	19.4	18.7	17.1	16.2	16.4	16.5	16.0	16.0	18.0
tm08	21.8	20.0	19.4	18.7	17.9	16.9	15.1	13.6	14.4	15.2	14.5	14.4	16.2
tm09	16.3	14.6	14.2	13.4	12.6	11.5	9.6	8.2	9.3	10.5	9.8	9.4	11.0
tm10	8.6	7.0	7.0	6.2	5.4	4.2	2.8	0.9	2.9	4.9	4.3	4.2	4.1

of the forest zone, this species does not reduce its abundance, continuing to be a frequent component of tundra mires, as well as mires in the north of the forest zone (Fig. 4). Total area of the range of *S. fuscum* is 71.9% of the total area of EEPEF and its northern zone (*fr*-zone) is almost 25% (Table 4), so it can be considered as wide-spread species with a tendency to northern distribution.

Correlation analysis shows that this species occurrence has a high positive correlation with the precipitation and air humidity of August-September and high negative dependence to mean temperature of these months. *Sphagnum fuscum* requires at least 500 mm precipitation per year and an average annual temperature not more than +7°C. In areas where it reaches maximal abundance, the annual rainfall is 500–650 mm, and the average annual temperature does not exceed +2.3°C (Fig. 6, 7; Supplementary materials, Table V). The rainfall maximum is observed in sporadic-zone. This can be explained by the fact that substantial part of frequent-zone is situated within the tundra zone, where precipitation is low, while the air humidity is high enough. Similarly to other species, *S. fuscum* needs at least 60% of humidity in summer months; it does not grow in areas with an average monthly temperature above +20°C, and in a zone of its maximal development summer is the coldest (Fig. 6, 7; Supplementary materials, Table V).

***Sphagnum fimbriatum*.** General distribution pattern of this species is not especially clear. It is only partly correlated to the climatic factors (Table 2). The *sp*-zone lies within the zone of the wide distribution of bogs, but since this species mostly grows in forests rather than in bogs (Boch & Kuzmina, 1985), it is difficult to find a satisfactory explanation of such distribution. Especially strange is the absence of *S. fimbriatum* in areas of maximal distribution of mires in the south of Arkhangelsk

Province and in Vologda Province (Fig. 4). This absence can not be totally accidental, as it has been recorded by different authors who worked in this region in different years (Churakova, 2002; Karmazina, 2013; Fillipov *et al.*, 2015; Smagin *et al.*, 2017). At the same time, *S. fimbriatum* is frequent in the same zone in Lake District of Finland (Fig. 4), where the humidity is higher due to the presence of water bodies (Alisov, 1956).

Similarly to the species described above, the abundance of *S. fimbriatum* increases in northwestern region of the EEPEF (Fig. 4). Although this species occurs in all vegetation zones except the deserts, covering 76.3% from the area of the EEPEF (Table 4), its area of *fr*-zone is only 6% of EEPEF.

Correlation analysis shows that *Sphagnum fimbriatum* is more sensitive to precipitation in August and September, than in other months. Moreover, it requires high air humidity: species is absent in areas with humidity lower than 64% and its zone of highest humidity lies in areas of humidity over 70–80% in summer months (Supplementary materials, Table VI). This species requires annual precipitation at least 500 mm and average annual temperature not higher than +6.9°C, while in the zone with frequent occurrence of this species it does not exceed +2.1°C. Mean annual temperature –0.2°C in the zone of sporadic occurrence of this species (Fig. 6, 7; Supplementary materials, Table VI) is explained by the fact that a largest part of this zone is situated in tundra zone, where *Sphagnum fimbriatum* occurs no less frequently than in the forest zone. Also, this species requires monthly temperature no more than +18.8°C (Fig. 6, 7; Supplementary materials, Table VI).

***Sphagnum rubellum*.** The abundance of this species increases from the southeast to the northwest and reaches its maximal value in the forest zone of Finland. Sim-

ilarly to other species, it increases in direct proportion to moisture factors and inversely proportional to temperature. However, there are nuances in distribution of this species. *Sphagnum rubellum* is an ecological counterpart of *S. fuscum*: unlike the latter, it grows almost exclusively in raised bogs throughout its range (Isoviita, 1970). Therefore, it is extremely rare in the central and eastern parts of the forest zone. The southern boundary of the zone of its rare occurrence (Fig. 5, zone **r**) coincides with the boundary of maximal distribution of bogs and the boundary of the Last Glaciation Maximum (LGM) (Fig. 3B). To the north and northwest from LGM, where raised bogs appear, it becomes more frequent. As Table 4 shows, *S. rubellum* has maximal distribution in the forest zone only, and it has partial areas of absence in all vegetation zones. This type of distribution fundamentally distinguishes *S. rubellum* from other species of section *Acutifolia*. Since the area of distribution of this species covers 59% of the territory of the EEPEF (Table 3), it can be called relatively widespread.

As correlation analysis shows, *S. rubellum* increases its abundance in regions with high precipitation and air humidity in summer-autumn period (Table 2). However monthly precipitation is distributed unevenly by zones of abundance (Fig. 6), likely because the distribution of this species is determined not only by climatic factors.

*Sphagnum rubellum* is the most cold-resistant species, because the average annual temperature within its range varies from +0.4 to +3.6°C. But, according to the requirements for moisture, it needs annual precipitation no less than 500–600 mm. This species requires no less than 64% humidity through all range and in zones with maximum abundance it should be 70–80%. In areas with monthly temperatures within the vegetation period above +17°C, this species does not occur (Fig. 6, 7; Supplementary materials, Table VII).

***Sphagnum subfulvum*, *S. subnitens*, *S. quinquefarium* and *S. molle*.** The distribution limits and zones of abundance of these species cross the boundaries of natural zones, thus their occurrence patterns do not have an explicit dependence on climatic factors (Table 2). These species are rare in the territory of the EEPEF, have low occurrence in the areas of their ranges, and the proportion of their whole areas relative to the whole area of the EEPEF is low and ranges from 29.6% (for *S. quinquefarium*) to 12.9% (for *S. molle*). The areas of maximal distribution of all four species are found in the taiga zone, except for *S. quinquefarium*, which occupies in addition a very small area in the zone of mixed forests (Table 4).

*S. subfulvum* is the most northern of these four species, as its southern limit in the study area is the north of zone of mixed forests (Fig. 5, Table 4). However, it has a quite distant refugium in the East of EEPEF, in the Perm Region (Kama River basin) (Fig. 5). Ranges of *S. subnitens* and *S. quinquefarium* include small areas of the forest-steppe zone in the south (Fig. 5, Table 4); the dis-

tribution range of *S. molle* is limited by the deciduous forest zone (Fig. 5, Table 4). In the north, three species, except for *S. molle*, reach the tundra zone. The area of *S. molle* is limited by the forest zone both in the north and in the south (Fig. 5, Table 4).

The analysis of the absolute values of climatic factors in the areas of abundance of these four species in question suggests that they need the same average annual precipitation as widespread species, *i.e.* not less than 550 mm, but they require a higher humidity in summer months, of no less than 65–70%. Mean annual and monthly mean temperatures for these species vary in a narrower range than for widely distributed species (Fig. 6, 7; Supplementary materials, Table VIII-XI).

**The number of species** of the section *Acutifolia* in the territory of the EEPEF varies unevenly (Fig. 5). Eight to eleven species occur in areas with an average annual precipitation of at least 600 mm and an amount of rainfall in the warm quarter of the year of at least 220 mm (Table 3). Apparently, this fact determines the submeridional direction of the boundaries of zones to at least the “eight-species” east boundary (Fig. 5). To the east of the “eight-species” zone, the “seven-species” zone covers almost the entire forest zone (Fig. 2A, 5). Within this zone, there is an area of “six-species” where *Sphagnum fimbriatum* is absent. To the south of the forest zone, gradual decrease in species diversity is observed down to the south of the steppe zone. This decrease is primarily caused by the increase of both mean annual temperature and temperature of the warmest quarter of the year (Table 3). Correlation analysis shows that the number of species in the territory of the EEPEF, as well as the abundance of species, increases in proportion to the increasing of the moisture content in the region and inversely proportional to the monthly temperatures of the vegetation period (Table 2).

The largest part of the area (25.1%) in the territory of the EEPEF belongs to the seven-species zone. Most part of this zone lies within the taiga and tundra zones. Areas of zones with other number of species are somewhat smaller. The nine-species zone lies entirely within the forest zone. 10th and 11th-species zones are completely located within the taiga zone (Fig. 5). Zones with a small number of species (1 to 2) are characteristic for broadleaved forests, forest-steppe and steppe zones. In the tundra zone, six to eight species of *Sphagnum* of the section *Acutifolia* grow.

#### DISCUSSION

Assuming that the species range should be limited not only by climatic factors, we tested the hypothesis that such factors as availability of lakes, bogs, forests, historical factor (LGM boundary) and relief may also affect the species distribution. Excluding the relief characteristics, all these factors are qualitative. Their influence may be verified by visual comparison of maps. Relief should be represented by two quantitative factors having



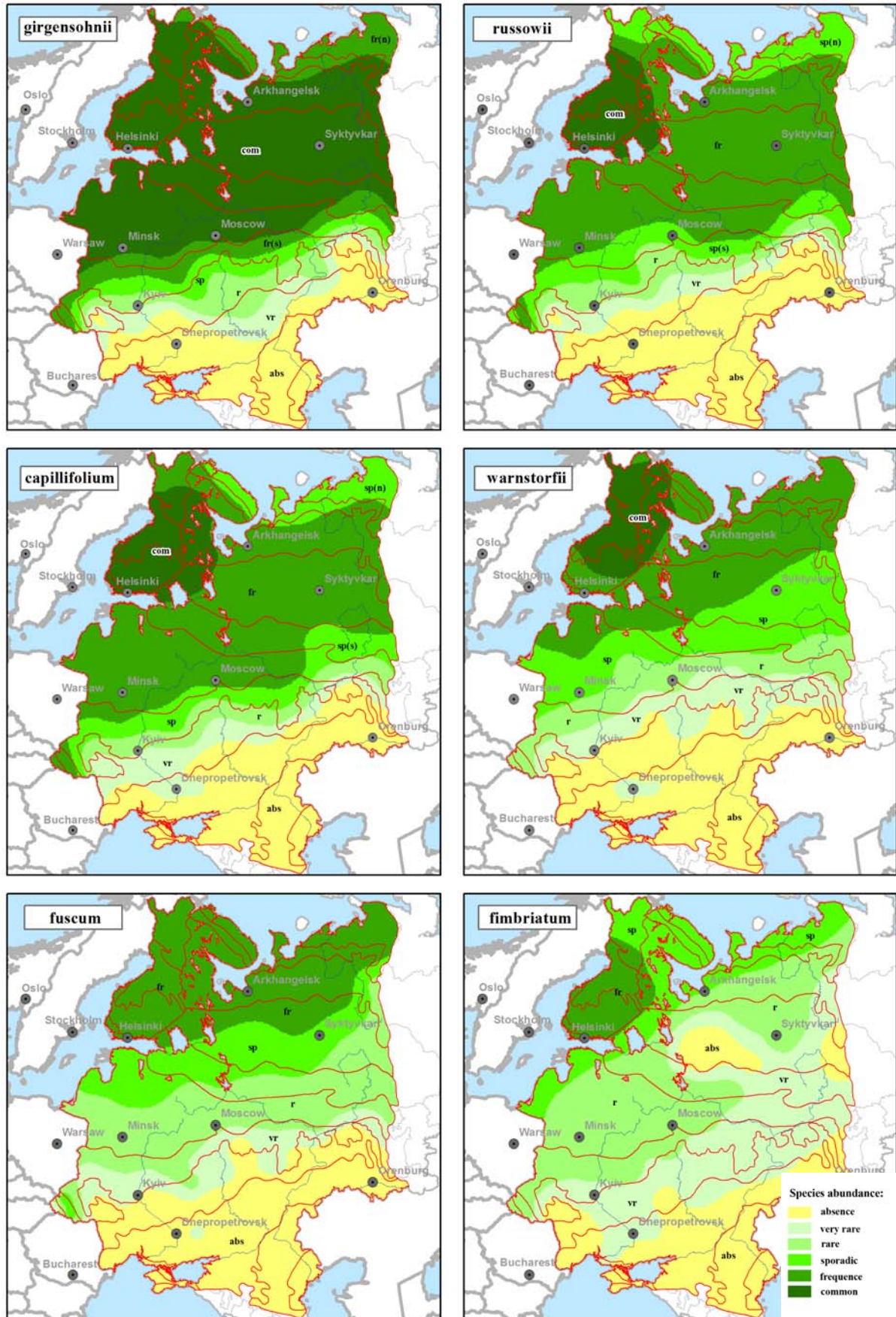


Fig. 4. Zones of abundance of species of *Sphagnum* sect. *Acutifolia* in the Eastern European Plain and Eastern Fennoscandia.



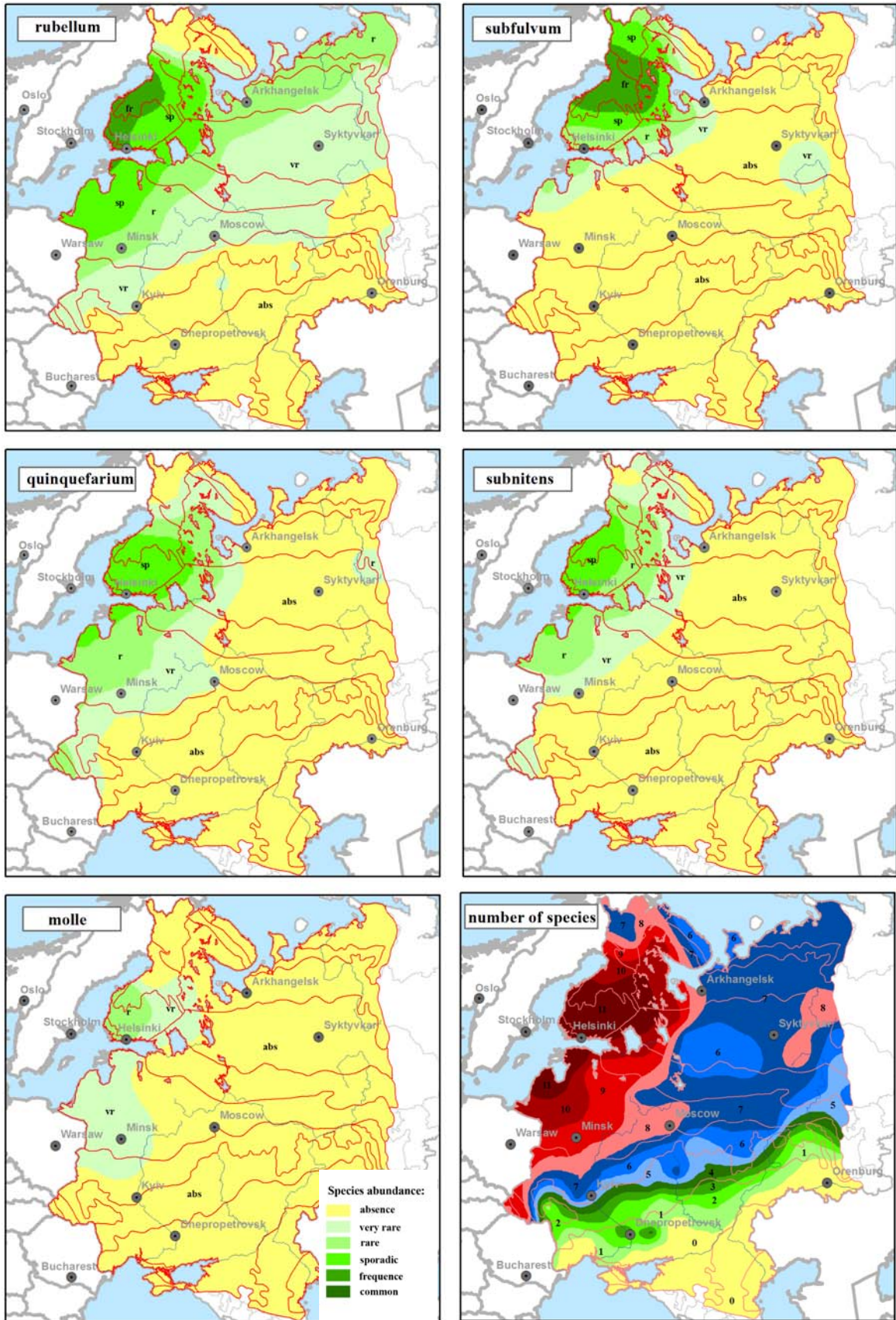


Fig. 5. Zones of abundance of species of *Sphagnum* sect. *Acutifolia* in the Eastern European Plain and Eastern Fennoscandia and zones of number of species.

Table 4. Areas (in km<sup>2</sup>) covered by species of sect. *Acutifolia* by zones of their abundance and areas of zones with numer of species (0 to 11)

Zones	abs	vr	r	sp	fr	com	Total	abs	vr	r	sp	fr	com	Total						
Tundra					174	18	192					173	19	192						
Forest-Tundra	<i>S. girgensohnii</i>								<i>S. capillifolium</i>											
Forest-Tundra					56	46	102					56	46	102						
North Taiga					29	522	551					16	396	138	551					
Middle Taiga						748	748					0.5	603	144	748					
South Taiga				3	67	469	540				0.5	116	288	135	540					
Hemiboreal Forest		0.6	16	45	94	658	814			7	63	72	663	10	814					
Broadleaves Forest	38	41	86	138	189	25	517	34	65	121	215	83		517						
Forest-Steppe	111	135	181	92	3		523	134	241	132	16			523						
Steppe	522	145	42				709	639	69					709						
Semidesert	205						205	205						205						
Desert	55						55	55						55						
Total area, km <sup>2</sup>	930	322	325	279	612	2487	4955	1067	381	317	664	2099	427	4955						
Total area, %	18.8	6.5	6.6	5.6	12.3	50.2	100	21.5	7.7	6.4	13.4	42.4	8.6	100						
Zones	abs	vr	r	sp	fr	com	Total	abs	vr	r	sp	fr	com	Total						
Tundra					174	18	192					187	5	192						
Forest-Tundra	<i>S. russowii</i>								<i>S. warnstorffii</i>											
Forest-Tundra					61	41	102					92	10	102						
North Taiga					66	428	57	551				32	329	190	551					
Middle Taiga						609	139	748				309	342	97	748					
South Taiga					52	353	135	540		0.1	90	221	165	65	540					
Hemiboreal Forest		4	50	176	574	10	814		64	335	284	132		814						
Broadleaves Forest	40	65	179	192	42		517	68	319	116	14			517						
Forest-Steppe	200	209	107	6			523	332	183	7				523						
Steppe	701	8					709	665	43					709						
Semidesert	205						205	205						205						
Desert	55						55	55						55						
Total area, km <sup>2</sup>	1200	286	336	727	2065	340	4955	1326	609	548	859	1246	366	4955						
Total area, %	24.2	5.8	6.8	14.7	41.7	6.9	100	26.8	12.3	11.1	17.3	25.2	7.4	100						
abs	vr	r	sp	fr	Total	abs	vr	r	sp	fr	Total	abs	vr	r	sp	fr	Total			
	1	11	179	192		5	36	151	192		36	27	129				192			
		0.7	101	102			22	80	102		28	16	58				102			
	33	25	492	551		13	36	195	251	56	551	86	151	248	65		551			
	122	308	318	748		169	215	224	35	104	748	14	493	104	81	55	748			
	0.04	252	153	135	540	21	199	174	20	125	540	97	224	64	107	48	540			
	39	585	180	10	814	4	150	558	92	10	814	61	375	160	204	13	814			
	95	242	177	3	517	52	233	232	0.1		517	261	232	24			517			
	336	175	11		523	106	398	20			523	482	40				523			
	700	8			709	550	158				709	709					709			
	205		<i>S. fuscum</i>			205	202	3	<i>S. fimbriatum</i>			205	205	<i>S. rubellum</i>			205			
	55				55	55					55	55					55			
	1391	464	1182	682	1235	4955	1172	1398	1460	629	296	4955	2034	1559	787	458	117	4955		
	28.1	9.4	23.9	13.8	24.9	100	23.7	28.2	29.5	12.7	6.0	100	41.0	31.5	15.9	9.2	2.4	100		
abs	vr	r	sp	fr	Total	abs	vr	r	sp	Total	abs	vr	r	sp	Total					
179	10	3			192	181	11			192	187	5			192					
83	9	10	0.01		102	81	21			102	84	18			102					
276	33	51	116	75	551	320	155	76		551	332	127	77	14	551					
437	157	46	18	89	748	550	67	66	65	748	503	96	75	74	748					
361	50	58	54	17	540	302	86	62	89	540	297	51	61	131	540					
709	72	33	0.1		814	479	161	150	24	814	259	281	230	44	814					
517					517	484	33			517	405	97	15		517					
523					523	521	2			523	488	35			523					
709					709	709				709	709				709					
205			<i>S. subfulvum</i>			205	205		<i>S. subnitens</i>			205	205	<i>S. quinquefarium</i>			205			
55					55	55				55	55				55					
4053	330	202	189	182	4955	3887	536	354	178	4955	3487	709	459	264	4955					
81.8	6.7	4.1	3.8	3.7	100	78.4	10.8	7.2	3.6	100.0	70.4	14.3	9.3	5.3	100					
Zones	abs	vr	r	Total	Zones of number of species	Total														
					0	1	2	3	4	5	6	7	8	9	10	11	Total			
Tundra				192							40	150	2				192			
Forest-Tundra				102							8	81	12				102			
North Taiga				551							11	275	106	54	78	27	551			
Middle Taiga				748						12	176	267	109	30	64	89	748			
South Taiga				540						31	88	174	25	64	28	130	540			
Hemiboreal Forest				814				0.1	21	46	13	182	157	197	122	76	814			
Broadleaves Forest				517				13	5	30	30	25	76	134	110	65	28	0	0	517
Forest-Steppe				523				14	59	105	91	101	95	52	5					523
Steppe				709				370	198	100	37	4								709
Semidesert				205				200	5											205
Desert				55				55	0											55
Total area, km <sup>2</sup>	4316	541	98	4955	Total area, km <sup>2</sup>	651	267	236	158	151	261	524	1245	475	373	292	322	4955		
87.1	10.9	2.0	100	Total area, %	13.1	5.4	4.8	3.2	3.0	5.3	10.6	25.1	9.6	7.5	5.9	6.5	100			



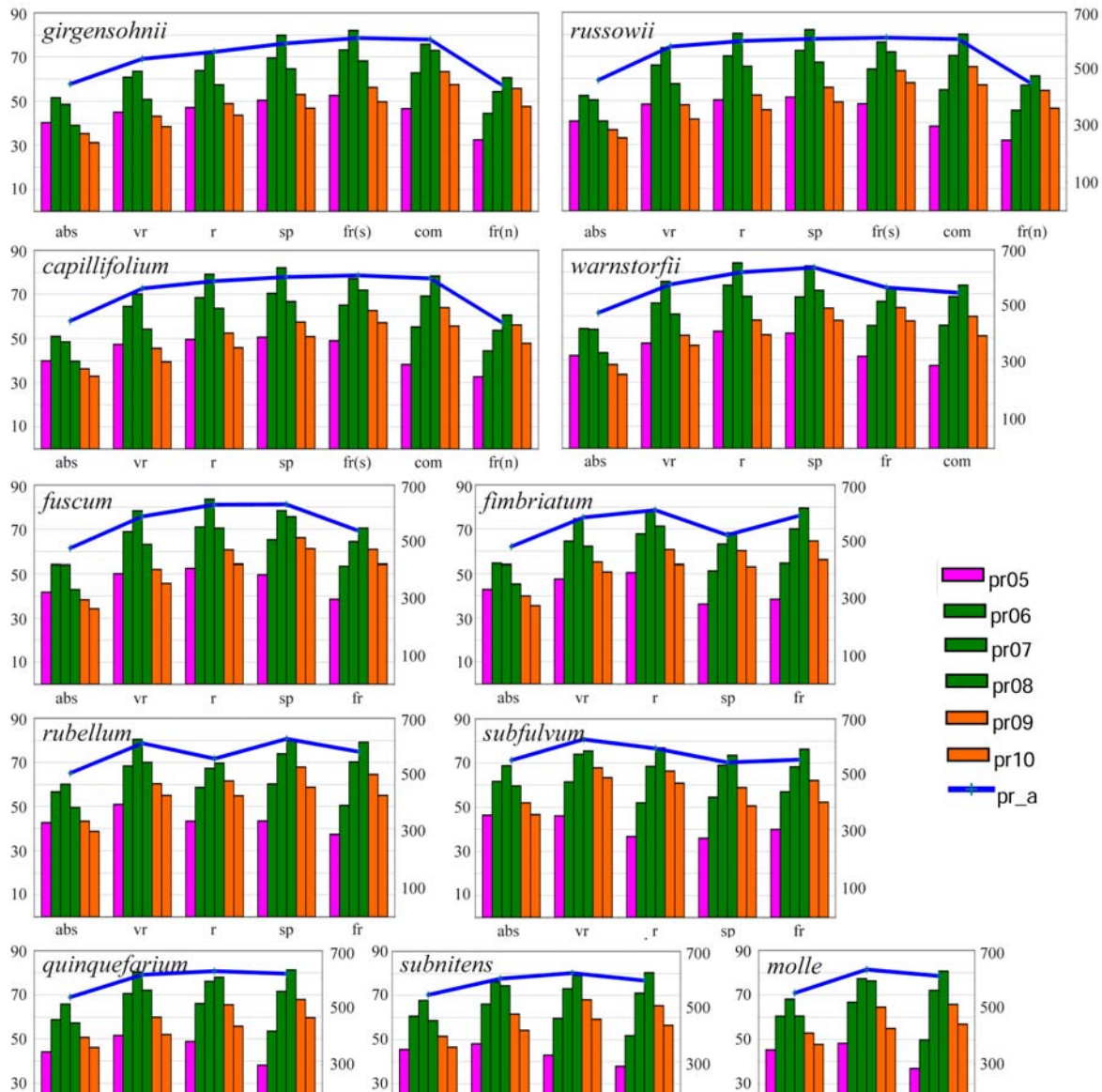


Fig. 6. The values of the climatic variables (see Table 1 for abbreviations) for the zones of abundance (shown in Figs. 4-5). Blue line indicates annual precipitation, with scale on the right; bars shows precipitation by selected periods, their scales are on the left.

biological significance: altitude and slope. In Western Europe, where mountains occupy a significant territory, altitude is one of the important factors that determine distribution of *Sphagnum* (Séneca & Söderström, 2008; Melosik, 2006), while in Eastern Europe Sphagna grow mainly in lowlands (Boch & Mazing, 1979). Correlation analysis between these two factors and species abundance demonstrated no correlation (Table 2). This is not surprising, because the scale of obtained maps is smaller than possible resolution, when it is possible to identify patterns of altitude distribution of species. In essence, used resolution allows “seeing” only the species composition, but not the altitude or biotopic distribution of the species. These problems can be resolved by using the “maximum entropy” method on a larger scale in more local areas (Sérgio *et al.*, 2007; Phillips *et al.*, 2008; Dudov, 2016).

On the contrary, distribution of the climatic factor values is in a good agreement with the distribution of species. Correlation analysis of the species occurrence and values of climatic factors in the territory of the EE-PEF demonstrates that most species have a high correlation with the amount of precipitation in August, September and October (Table 2). As it was shown earlier (Popov, 2016), the highest amount of precipitation in these months is observed in the Baltic countries, North-West of Russia and Finland. In the same areas, the highest occurrence of *Sphagnum* is also observed (Figs. 4, 5). Therefore, it can be stated that the amount of precipitation in summer-autumn period determines the maximal abundance of the species of section *Acutifolia*. Since the peak of vegetative activity of *Sphagnum* takes place at this period (Grabovik, 1994; Grabovik & Antipin, 1982, 2015), it is reasonable that they are the most common in

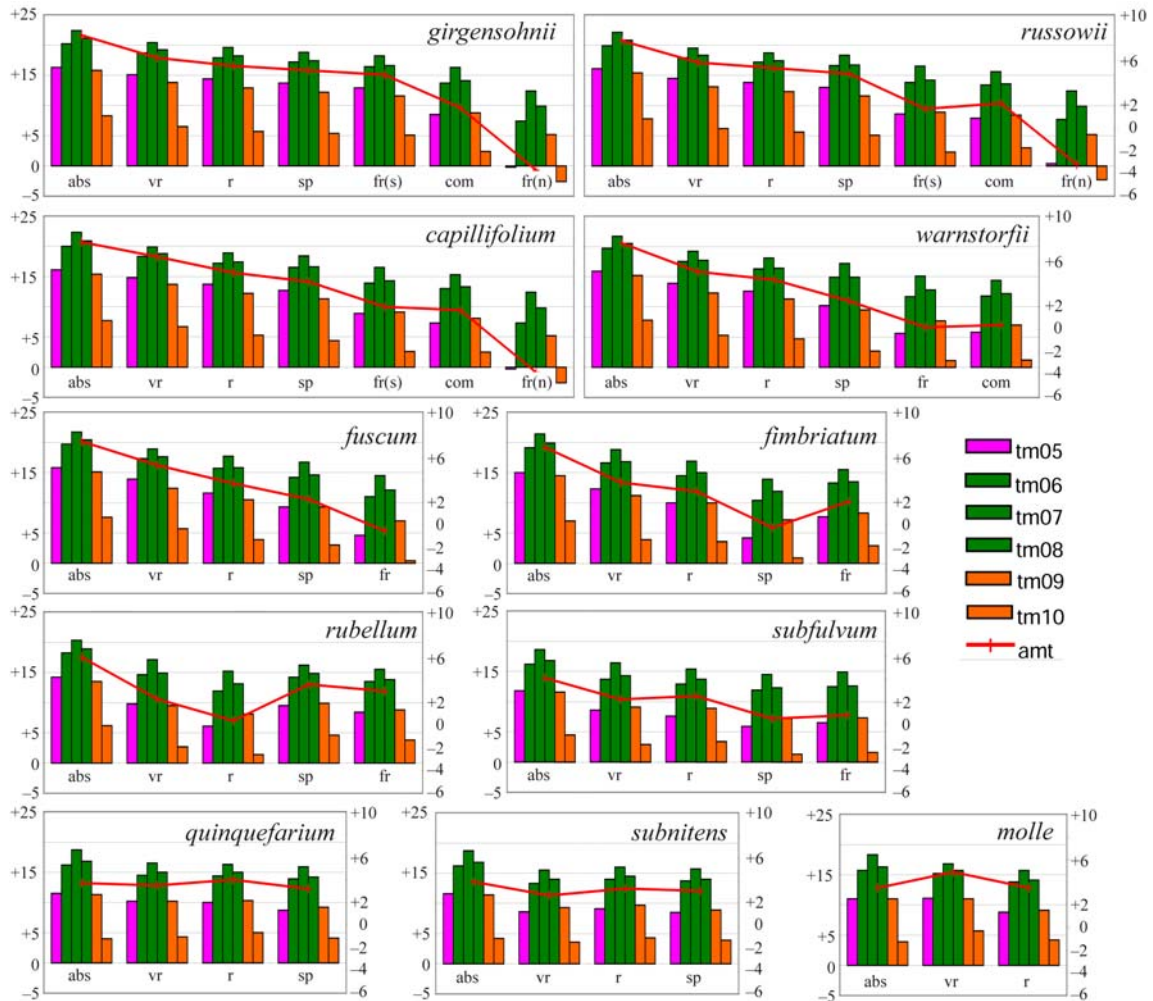


Fig. 7. The values of the climatic variables (see Table 1 for abbreviations) for the zones of abundance (shown in Figs. 4–5). Red line indicates annual mean temperature, with scale on the right; bars shows monthly temperature by selected periods, their scales are on the left.

the region with increased precipitation amount. Additionally, high relative humidity at warm months influences to the distribution of species of section *Acutifolia* (Table 2). Thus, it can be stated that studied species have climatic optimum in region with high precipitation amount and high relative humidity, *i.e.* in Baltic Sea region. Submeridional direction of the boundaries of the species optimum zones confirms this statement.

The boundaries of zones with a low abundance of species, *i.e.* zones of their climatic pessimum, may have a sublatitudinal direction. In this case, they are parallel to the boundaries of vegetation zones, which are defined for vascular plants by the temperature gradient (Ahti *et al.*, 1968; Kurnaev, 1973). However, only some species of the section have such spatial pattern (Fig. 4), *i.e.* *S. girgensohnii*, *S. capillifolium*, *S. russowii*, *S. warnstorffii*, *S. fimbriatum*, and *S. fuscum*. These species have a wide distribution in the territory of the EEPEF and a high phytocoenotic significance in plant communities, typical for each species. Correlation analysis shows that these species have a high negative correlation with the

monthly temperatures of the warm period (Table 2). Such pattern has been found by other authors too, who demonstrated that peat mosses decreased their growth and net-production as a result of high evapotranspiration, when temperature values became too high (Skre & Oechel, 1981; Weltzin *et al.*, 2001; Gerdol *et al.*, 2007). This fact shows that the growth of *Sphagnum* becomes limited by increasing of temperature; there are must be upper and lower temperature limits, beyond which they do not occur.

Four rare species of the section *Acutifolia*, *S. subfulvum*, *S. subnitens*, *S. molle* and *S. quinquefarium* have distribution limits not paralleled to the boundaries of the vegetation zones (Fig. 5). These species are rare in the territory of the EEPEF; their distribution is confined to the Baltic Sea region, *i.e.* to the region with maximal moisture in the autumn-summer period and where numerous lakes and bogs are situated. There is no strong relationship between the occurrence of these species and the values of climatic factors, but, there is an obvious correlation with such factors as humidity and precipita-

tion (Table 2). So, their distribution is more influenced by landscape factors than climatic ones. The areas of all four listed species lie within the zone of maximal distribution of bogs and zone of the Valdai Glaciation (Fig. 2), where glacial forms of relief and numerous lakes are prevailing.

Distributional patterns of species from section *Acutifolia* are very similar to ones of section *Sphagnum* species (Popov, 2016). As well as widespread species of section *Sphagnum* (*S. magellanicum*, *S. centrale*, *S. palustre*, *S. papillosum*), the widespread species of section *Acutifolia* (*S. girgensohnii*, *S. capillifolium*, *S. russowii*, *S. warnstorffii*, *S. fimbriatum*, and *S. fuscum*) have the boundaries of a whole range parallel to boundaries of vegetation zones. Rarest species of both sections have submeridional boundaries only and their areas of distribution are concentrated around the Baltic sea only and these species have low abundance elsewhere throughout their areas.

The number of species of the section *Acutifolia* grows simultaneously in a particular regions; it depends on the amount of precipitation and the average annual temperatures in these regions. Species of the section *Acutifolia* are absent in areas where annual temperature exceeds +7°C and precipitation is less than 450 mm. Regions with the maximal number of species – from 7 to 11 – are concentrated around the Baltic Sea, and their boundaries have submeridional direction. The boundaries of zones with small species richness (from 1 to 6) have sublatitudinal direction, parallel to the boundaries of vegetation zones. As well as in case of section *Sphagnum* (Popov, 2016) maximum species diversity of section *Acutifolia* is observed in Baltic Sea region. Therefore, the factor causing the increase of the species diversity is the amount of precipitation and relative humidity of air, and the factor limiting the distribution of species is temperature.

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