

## **Spatial distribution of bryophyte species diversity in Eastern Europe**

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To assess the spatial distribution of bryophytes in Eastern Europe, more than 53,000 localities of 1296 species were analyzed in 397 squares of 100 x 100 km. The number of species within (or density) of one square varies from 591 (southwest of the Kola Peninsula to less than 50 (in arid steppe and semi-desert regions in the southern part of Eastern Europe and in some of arctic and north-taiga poorly studied territories). 8 centers of bryophytes species diversity have been identified in Eastern Europe: Kola Peninsula, South Karelian, Ural, Estonian, Smolensk-Moscow Upland, Carpathians, Black Sea, Caucasian, as well as 7 intermediate sub-centers: Arkhangelsky, Timansky, Narochansky, Volzhsko-Kamsky, South Ural, Belovezhsky, Kiev-Mozyrsky. Their characteristics and unique species for each centers are given. A structural model of the organization and interrelationships of bryofloras in Eastern Europe is proposed. The elevated mountain regions are the concentration of maximum diversity and refuge for many rare species of bryophytes in the region. The central connecting core of the system is the Smolensk-Moscow Upland. It is through this center, there is a connection between the western and eastern parts of the bryoflora of Eastern Europe. The most related element of the spatial structure of bryophytes in Eastern Europe is the Kyiv-Mozyr subcenter (5 ribs), through which the main migration of bryophytes from north to south and vice versa occurs. The Belovezhsky and Narochansky subcenters each have 4 ribs and also actively contribute to the migration process. Through the elevated areas of the Arkhangelsky and Timan subcenters, the Kola Peninsula and South Karelian regions are connected with the Urals. The most isolated in the region is the Caucasus, which maintains links with other centers through the Black Sea center.

*Key words: bryophytes, species diversity, Eastern Europe, spatial distribution*

Масловський О.М. (2020). **Просторовий розподіл видового різноманіття мохоподібних Східної Європи.** *Чорноморськ. бот. ж.* **16** (4): 323–332. doi: 10.32999/ksu1990553X/2020-16-4-5

Для оцінки просторового розподілу мохоподібних на території Східної Європи були проаналізовані більше 53 000 місцезнаходжень 1296 видів в 397 квадратах розміром 100 x 100 км. Кількість видів в межах (або щільність) одного квадрата варіює від 591 (південний захід Кольського півострова) до менш ніж 50 (в посушливих степових і напівпустельних регіонах в південній частині Східної Європи і ряду арктичних і північно-тайгових мало вивчених територій). Виділено 8 центрів видової різноманітності мохоподібних Східної Європи: Кольський, Південно-Карельський, Уральський, Естонський, Смоленсько-Московська височина, Карпати, Чорноморський, Кавказький, а також 7 проміжних субцентрів: Архангельський, Тіманський, Нарочанський, Волзько-Камський, Південно-Уральський, Біловезький, Київсько-Мозирський. Дана їх характеристика і наведені унікальні види. Запропоновано структурну модель організації та взаємозв'язків бріофлори Східної



Європи. Гірські райони є зосередженням максимальної різноманітності і притулком для багатьох рідкісних видів мохоподібних в регіоні. Центральним сполучним ядром системи є Смоленсько-Московська височина. Саме через цей центр біорізноманіття здійснюється зв'язок між західними і східними частинами бріофлори Східної Європи. Найбільш зв'язуючим елементом просторової структури бріофлори Східної Європи є Київсько-Мозирський субцентр (5 ребер), саме через нього здійснюється основна міграція бріофітов з півночі на південь і назад. Біловезький і Нарочанський субцентри мають по 4 ребра і також активно сприяють міграційному процесу. Через піднесені ділянки Архангельського та Тиманського субцентрів здійснюється зв'язок Кольського і Південно-Карельського регіонів з Уралом. Найбільш ізольованим в регіоні є Кавказ, який здійснює зв'язки з іншими центрами через Чорноморський центр.

*Ключові слова:* мохоподібні, видове різноманіття, Східна Європа, просторовий розподіл

МАСЛОВСКИЙ О.М. (2020). **Пространственное распределение видового разнообразия мохообразных Восточной Европы.** *Черноморск. бот. ж.*, **16** (4): 323–332. doi: 10.32999/ksu1990553X/2020-16-4-5

Для оценки пространственного распределения мохообразных на территории Восточной Европы были проанализированы более 53 000 местонахождений 1296 видов по 397 квадратам размером 100 x 100 км. Количество видов в пределах (или плотность) одного квадрата варьирует от 591 (юго-запад Кольского полуострова) до менее 50 (в засушливых степных и полупустынных регионах в южной части Восточной Европы и ряда арктических и северо-таежных слабоизученных территорий). Выделены 8 центров видового разнообразия мохообразных Восточной Европы: Кольский, Южно-Карельский, Уральский, Эстонский, Смоленско-Московская возвышенность, Карпаты, Черноморский, Кавказский, а также 7 промежуточных субцентров: Архангельский, Тиманский, Нарочанский, Волжско-Камский, Южно-Уральский, Беловежский, Киевско-Мозырский. Дана их характеристика и приведены уникальные виды. Предложена структурная модель организации и взаимосвязей бріофлор Восточной Европы. Возвышенные горные районы являются сосредоточением максимального разнообразия и убежищем для многих редких видов мохообразных в регионе. Центральным связующим ядром системы является Смоленско-Московская возвышенность. Именно через этот центр биоразнообразия осуществляется связь между западными и восточными частями бріофлоры Восточной Европы. Наиболее связанным элементом пространственной структуры бріофлор Восточной Европы является Киевско-Мозырский субцентр (5 ребер), именно через него осуществляется основная миграция бріофітов с севера на юг и обратно. Беловежский и Нарочанский субцентры имеют по 4 ребра и также активно способствуют миграционному процессу. Через возвышенные участки Архангельского, Тиманского субцентров осуществляется связь Кольского и Южно-Карельского регионов с Уралом. Наиболее изолированным в регионе является Кавказ, осуществляющий связи с другими центрами через Черноморский центр.

*Ключевые слова:* мохообразные, видовое разнообразие, Восточная Европа, пространственное распределение

Eastern Europe is a big region, on the territory of which various natural zones are represented: tundra, taiga, deciduous forests, steppes, semi-deserts and fragments of subtropics. The species diversity of various plant groups is represented here unevenly, which is due to the zonal aspect, physical and geographical conditions, ecological and anthropogenic factors, as well as the history of ecosystem formation. Thus, the spatial distribution of plant species richness in the region is the most important characteristic of biodiversity.

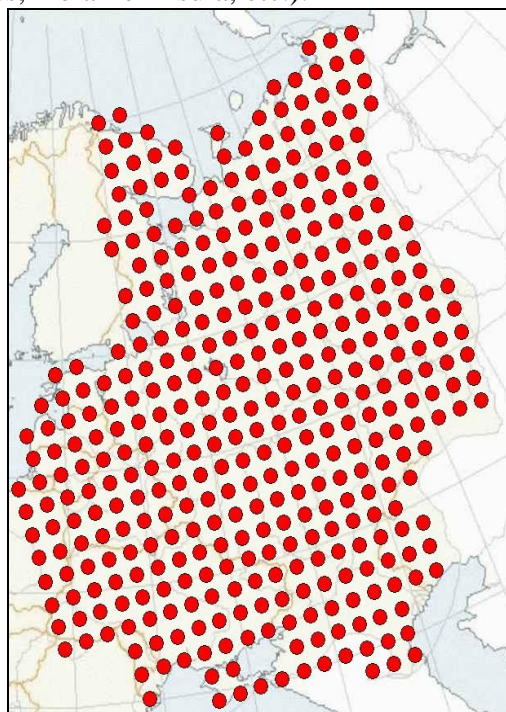
In addition, to study the history of the formation of floras of separate territories within the big region, their current state and prognosis of their development under conditions of increasing anthropogenic impact, it is necessary to consider them in a broader spatial aspect.

The territory often studied by florists is located in the place of contact of various natural zones and species of various origins take part in the flora. Therefore, it is advisable to consider the flora of a particular territory as part of the floristic system of a large region. This approach, substantiated by us [MASLOVSKY, 2002], seems to be justified also in connection with the peculiarities of the geographic distribution of bryophytes, their ecology and biology (a considerable extent of their ranges, the settlement of microeconiches, etc.), as well as the close phytogeographic connections of individual bryofloras. region. Thus, the object of our study was the spatial distribution of species biodiversity of bryophytes in Eastern Europe.

### **Materials and research methods**

To assess the spatial distribution of bryophytes on the territory of Eastern Europe, more than 80,000 localities of 1296 species were analyzed in 397 squares 100 x 100 km in size (Fig. 1); in fact, the density of distribution of the number of species per unit area (10,000 sq. km) was estimated. Bryophyte mapping was carried out as a result of processing of literature sources, herbarium materials and field studies, and on the basis of the basic system of geographical maps – the Universal Transverse Mercator (UTM), which is used for the publication of the Atlas Florae Europaeae for vascular plants [ATLAS .., 1972]. All records of bryophytes were used, including historical ones, but with critical recommendations from the authors of regional floras. Of course, using only recent collections would make it possible to study the current state of bryological species diversity and its dynamics, but this is a task for further separate investigations. We also define the geographical boundaries of Europe according to this publication, when only the northern part of the Caucasus is part of Europe. The mapping of Arctic islands may be a separate study and not included in the objectives of the work.

Field floristic research was carried out by the author on the territory of Belarus and in a number of regions of Eastern Europe (Lithuania, Carpathians, Crimea, Ural, Valdai and Smolensk-Moscow Uplands, Kola Peninsula, etc.).



**Fig. 1. Area of mapping and division into squares.**

More than 700 literary sources were processed. Among them, as generalizing publications of the bryoflora of the former USSR [IGNATOV, AFONINA, 1992; IGNATOV, AFONINA et al. 2006; KONSTANTINOV et al., 1992; SAVICH-LYUBITSKAYA, SMIRNOVA, 1970],

Belarus [RYKOVSKY, MASLOVSKY, 2004, 2009], Ukraine [BACHURINA, MELNICHUK, 1987-2003; BOIKO, 2002, 2008], Lithuania [JUKONIENE, 2003], Latvia [ABOLIN, 1965, 2001], Estonia [INGERPUU et al., 1998], Moldova [Simonov, 1978], Russia [IGNATOV, IGNATOVA, 2003, 2004; POTEKIN, SOFRONOVA, 2009; KONSTANTINOVA et al., 2009], many regional floras, Red Data Books. A list of the main part of the literature is presented in the book [MASLOVSKY, 2017].

Of course, a complete mapping of all known distribution sites of bryophytes in such a large territory as Eastern Europe is impossible, since the volume of bryological literature and concrete data is constantly growing rapidly. The concrete locations of some species were difficult to establish, although they were listed in the flora of certain regions.

The species composition and spatial distribution of bryophytes in the western part of Eastern Europe have been studied most fully, in our opinion, and, conversely, the eastern lowland arctic, taiga and steppe regions are less studied in the bryological sense. However, the general patterns of the spatial distribution of bryophytes in Eastern Europe are already more or less visible.

The materials were inputted in specialized databases, on the basis of which an electronic atlas of the distribution of bryophytes in Eastern Europe was created (Fig. 2).

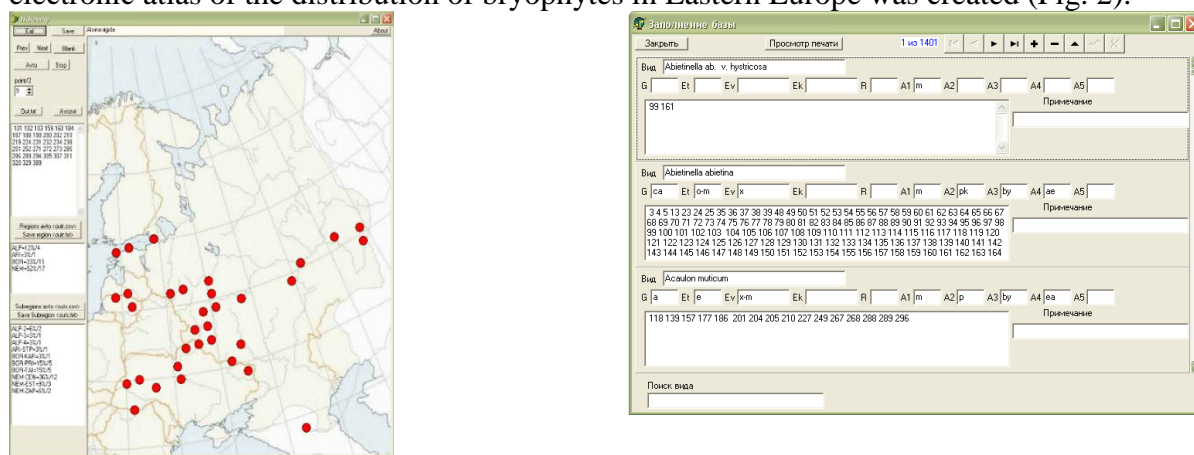


Fig. 2. Electronic atlas of the distribution of bryophytes in Eastern Europe.

The taxonomic species names of bryophytes are given mainly according to the general European summary [HODGETTS, 2015].

### The results

The number of species within one square varies from 591 (south-west of the Kola Peninsula to less than 50 (in arid steppe and semi-desert regions in the southern part of Eastern Europe and a number of Arctic and north-taiga poorly studied areas). For the latter, more detailed studies can to some extent change the data on the spatial distribution of bryophytes in the analyzed territory without changing the general nature of the patterns.

A general analysis of the distribution of the spatial bryophytes species diversity in Eastern Europe shows (Fig. 3) that the species diversity is mainly concentrated in the mountainous and upland regions of the Kola Peninsula, southern Karelia, the Urals, the coastal territories of Estonia (alvars), the Carpathians, Crimea and foothills Caucasus.

The following centers with the maximum species density on the territory of Eastern Europe can be distinguished (Tabl. 1):

Table 1.

Maximum species density in the centers of bryological species diversity (on 10000 square km) on the territory of Eastern Europe.

Centres	Maximum number of species
A – Kola Peninsula	591
B – South Karelian	370
C – Ural	480
D – Estonian	445
E – Smolensk-Moscow Upland	326
F – Carpathians	495
G – Black Sea.	429
H – Caucasian	361

**A – Kola Peninsula** (mainly south-western part). It is located at the junction of the Arctic, Alpine and Boreal regions, which determines the maximum species diversity of bryophytes per square – 591. Only in this center of species diversity are bryophytes found on the territory of Eastern Europe (within the study area): *Asterella lindenbergiana* Corda ex Nees) Lindb., *Barbilophozia rubescens* (M.Schust. & Damsh.) Kartt. & L.Soederstr., *Cephaloziella varians* (Gottsche) Steph., *Lophozia schusteriana* Schljakov, *Mesoptychia heterocolpos* var. *arctica* (S.W. Arnell) L. Söderstr. & Váňa, *Saccobasis polymorpha* (R.M.Schust.) Schljakov, *Scapania glaucocephala* (Taylor) Austin, *S. obscura* (Arnell & C.E.O.Jensen) Schiffn., *S. sphaerifera* H.Buch & Tuom., *S. spitsbergensis* (Lindb.) Muell.Frib., *Schistochilopsis grandiretis* (Lindb. ex Kaal.) Konstant., *Andreaea blyttii* Bruch et al., *Bryum bryoides* (R. Br.) Wijk & Margad, *B. lapponicum* Kaurin, nom. Illeg., *B. muehlenbeckii* Bruch & Schimp., *B. teres* Lindb., *Drepanocladus angustifolius* (Hedenäs) Hedenäs & C.Rosborg, *Encalypta brevipes* Schljak., *Gymnostomum boreale* Nyholm & Hedenäs, *Hygrohypnum smithii* (Sw.) Broth., *Oncophorus virens* var. *serratus* (Bruch & W. P. Schimper) Braithwaite, *Sanionia georgicouncinata* (Müll.Hal.) Ochyra & Hedenäs, *Schistidium subjulaceum* H.H.Blom, *S. tenerum* (J.E.Zetterst.) Nyholm, *Sciuro-hypnum dovrense* (Limpr.) Draper & Hedenäs, *Trematodon brevicollis* Hornsch., *Ulota phylantha* Brid.

**B – South Karelian.** Covers various parts of the boreal region. The combination of a variety of different taiga conditions, the presence of two large lakes (Ladoga and Onega) and the proximity of the Baltic, as well as small areas of alvars, cause a significant species diversity of bryophytes (326 in the east and 370 in the west per 10,000 km<sup>2</sup>). Only in this center of species diversity are found in Eastern Europe (within the study area): *Cephaloziella stellulifera* (Taylor ex Spruce) Schiffn., *Gymnomitrium obtusum* Lindb., *Climacium japonicum* Lindb., *Orthotrichum urnigerum* Myrin, *Schistidium canadense* (Dupr.) Ignatova & H.H. Blom.

**C – Ural** (central part of the Ural mountain range). Here, the number of species per square reaches 480. This diversity of mountain conditions, as well as the surrounding areas of the boreal regions and immoral. Only in this center of species diversity are found in Eastern Europe (within the study area): *Asterella saccata* (Wahlenb.) A. Evans, *Brachythecium buchananii* (Hook.) A. Jaeg., *Bryum sauteri* Bruch & Schimp., *Fontinalis hypnoides* var. *Duriaei* (Schimp.) Kindb., *Hylocomium splendens* var. *obtusifolium* Geh.) Paris, *Molendoa tenuinervis* Limpr., *Oligotrichum falcatum* Steere, *Orthotrichum pellucidum* Lindb., *Timmia sibirica* Lindb. & Arnell.

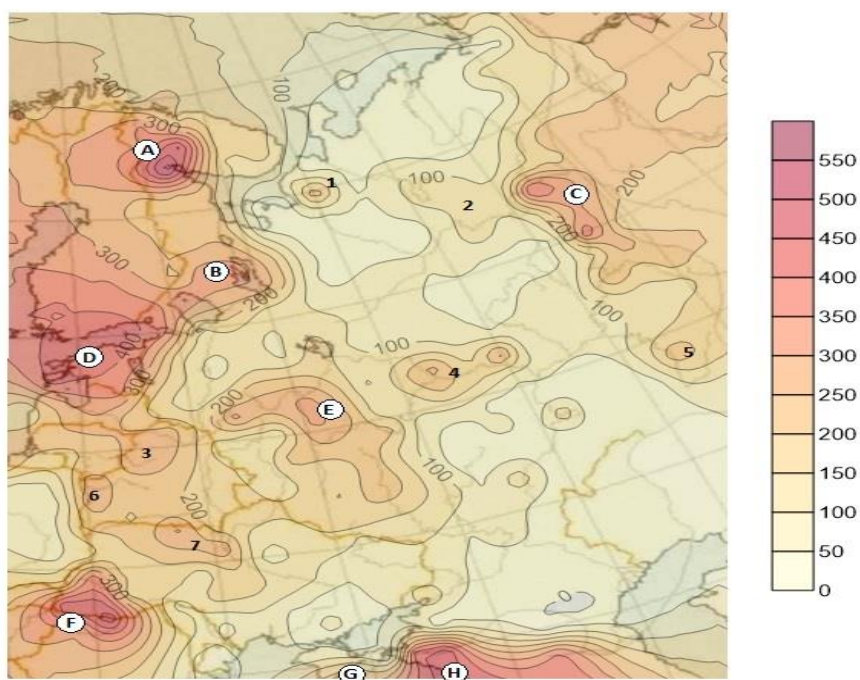


Fig. 3. Centers and sub-centers of species diversity of bryophytes of Eastern Europe: A – Kola Peninsula, B – South Karelian, C – Ural, D – Estonian, E – Smolensk-Moscow Upland, F – Carpathians, G – Black Sea, H – Caucasian, 1 – Arkhangelsky, 2 – Timansky, 3 – Narochansky, 4 – Volzhsko-Kamsky, 5 – South Ural, 6 – Belovezhsky, 7 – Kyiv-Mozyr.

**D – Estonian.** Located within the boreal region and adjacent to the Baltic Sea. The center of species diversity here is concentrated in the so-called alvars, formed by limestone, treeless landscapes, where a thin fertile alvar soil with a high calcium content is formed. Alvars are typical for the northern part of Estonia, including the island of Saaremaa. In addition to specific substrates, Atlantic climatic conditions are most pronounced here. The density of bryophyte species per square meter here reaches 445. Only in this center of species diversity are found on the territory of Eastern Europe (within the study area): *Cephaloziella elegans* (Heeg) Schiffn., *Mannia sibirica* (Muell.Frib.) Frye & L.Clark, *Riccia warnstorffii* Limpr. ex Warnst., *Archidium alternifolium* (Hedw.) Mitt., *Bryum blindii* Bruch & Schimp., *B. marratii* Wilson, *Hedwigia stellata* Hedenäs, *Microbryum floerkeanum* (Weber & D. Mohr) Schimper, *Orthotrichum rogeri* Brid., *O. rupestre* var. *sturmii* (Hoppe & Hornsch.) Jur., *Splachnum pensylvanicum* (Brid.) Grout ex H. A. Crum, *Thamnobryum subserratum* (Hook. ex Harv.) Nog. & Z. Iwats., *Tortella rigens* Alberts., *Zygodon stirtoni* Schimp. The Estonian center of species diversity borders in the east on the South Karelian one, and in the south it extends to the territory of Belarus (Narochansky subcenter).

**E – Smolensk-Moscow Upland,** including the northern part of the Central Russian Upland. It is located on the border of the boreal and nemoral (temperate) regions. The species diversity is up to 326 species per 10,000 km<sup>2</sup>. In the west, it partly extends to the territory of Belarus and passes into the Naroch sub-center. Specific bryophytes growing only here in Eastern Europe are practically absent (*Hypnum cupressiforme* var. *heseleri* (Ando & Higuchi) M.O.Hill., *Leucodon pendulus* Lindb.), but this center may have some importance in supporting biodiversity and species migration in the central part of Eastern Europe. Some of our thoughts on this will be discussed in more detail below.

**F – Carpathians.** It ranks second in species density (up to 495) in Eastern Europe. The high diversity, in addition to a wide range of varied mountain conditions, also determines

the climatic features and the proximity of the nemoral region. Only in this center of species diversity are found in Eastern Europe (within the study area): *Bucegia romanica* Radian, *Clevea spathysii* (Lindenb.) Muell.Frib., *Frullania jackii* Gottsche, *Gymnomitrium adustum* Nees emend. Limpr., *Metzgeria hamata* Lindb., *Porella baueri* (Schiffn.) C.E.O.Jensen, *Scapania Helvetica* Gottsche, *S. verrucosa* Heeg, *Bryoerythrophyllum alpigenum* (Vent.) P.C. Chen, *Campylopus gracilis* (Mitt.) A.Jaeger, *Campylostelium strictum* Solms, *C. saxicola* (F. Weber et D. Mohr) Bruch et Schimp., *Grimmia fuscolutea* Hook., *Homalia webbiana* Mont.) Schimp., *Isothecium holtii* Kindb., *Orthotrichum scanicum* Gronvall, *Plagiothecium neckeroideum* Schimp., *Tetradontium ovatum* (Funck) Schwägr., *Tortula canescens* Mont., *Ulota rehmannii* Jur., *Zygodon dentatus* (Limpr.) Kartt.

**G – Black Sea.** It includes the mountainous part of the southern Crimea and the western spurs of the Caucasus Mountains on the Black Sea coast. It is characterized by a subtropical climate. It grows from 220 species in the Crimea to 429 in the south of the Krasnodar region and Abkhazia. Only in this center of species diversity are bryophytes found on the territory of Eastern Europe (within its limits): *Calypogeia fissa* (L.) Raddi, *Cephaloziella turneri* (Hook.) Muell.Frib., *Frullania parvistipula* Steph., *Jubula hutchinsiae* subsp. *javanica* (Steph.) Verd., *Mesoptychia turbinata* (Raddi) L. Söderstr. & Váňa, *Scapania aspera* M.Bernet & Bernet, *Southbya tophacea* (Spruce) Spruce, *Targionia hypophylla* L., *Bryum gemmiparum* De Not., *Cinclidotus riparius* (Host ex Brid.) Arn., *Cryphaeae heteromalla* (Hedw.) D.Mohr, *Fissidens rivularis* (Spruce) Schimp., *Habrodon perpusillus* (De Not.) Lindb., *Homalothecium aureum* (Spruce) H. Rob., *Leptodon smithii* (Hedw.) F.Weber & D.Mohr, *Neckera menziesii* Drumm, *Plasteurhynchium meridionale* (Bruch et al.) M.Fleisch., *Tortella flavovirens* (Bruch) Broth.

**H – Caucasian.** It includes the foothills and the mountainous part of the Caucasus within Eastern Europe. The density of species here reaches 361. In fact, this center is only a small part of the specific bryoflora of the Greater Caucasus. Only in this center of species diversity are found in Eastern Europe (within the study area): *Lophozia lantratoviae* Bakalin, *Nardia compressa* (Hook.) Gray, *Andreaea heinemannii* Hampe & Müll.Hal., *Bryoerythrophyllum rubrum* (Jur. ex Geh.) P.C. Chen, *Bryum caucasicum* (Schimp. ex Broth.) C.J.Cox & Hedd., *Didymodon asperifolius* Mitt.) H.A.Crum et al., *D. perobtusus* Broth., *Entodon challengerii* (Par.) Card., *Entosthodon handelii* (Schiffn.) Laz., *Eurhynchiadelphus eustegius* (Besch.) Ignatov & Huttunen, *Hilpertia velenovskyi* (Schiffner) R.H.Zander, *Indusiella thianschanica* Broth. & Müll.Hal., *Jaffueliobryum latifolium* (Lindb. et Arnell) Thér., *Leptodontium flexifolium* (Dicks.) Hampe, *Lindbergia brachyptera* (Mitt.) Kindb., *L. dagestanica* Ignatova & Ignatov, *L. grandiretis* (Lindb. ex Broth.) Ignatov & Ignatova, *Molendoa schliephackei* (Limpr. ex Schlieph.) R. H. Zander, *Oreas martiana* (Hoppe & Hornsch.) Brid., *Orthotrichum callistomum* Fisch.-Oost. ex Bruch et al., *O. vladikavkanum* Venturi, *Oxyrrhynchium pumilum* (Wilson) Loeske, *Philonotis rigida* Brid., *Pogonatum inflexum* (Lindb.) Sande Lac., *P. neesii* (Müll.Hal.) Dozy, *Schistidium marginale* H.H. Blom, Bedn.-Ochyra & Ochyra, *S. obscurum* H.H. Blom, Köckinger & Ignatova, *S. sinensiacarpum* (Müll. Hal.) Ochyra, *S. subflaccidum* (Kindb.) H.H.Blom, *S. succulentum* Ignatova & H.H. Blom, *Syntrichia pseudohandelii* (J.Fröhl.) S.Agnew & Vondr., *S. papillosissima* (Copp.) Loeske, *Thamnobryum neckeroides* (Hook.) E.Lawton, *Tortula systylia* (Schimp.) Lindb., *T. transcaspica* Broth., *Trichostomum connivens* (Lindb. ex Broth.) Paris.

In addition to the above-described main centers of bryophyte species diversity, additional sub-centers can be distinguished in Eastern Europe. They are the following:

**1. Arkhangelsky**, bordering from the northwest on the Kola Peninsula. Possibly increased species diversity (254 species per square), among other features, is also associated with a more thorough study of the territory.

**2. Timansky.** Covers the Timan Ridge and Northern Uvaly. These are elevated areas in the north taiga region. They are characterized by an increased species diversity in comparison with the surrounding territories and are associated with the Ural center.

**3. Narochansky** (Narochansko-Berezinsky). It is located in the north of Belarus and covers the boreal region. The species diversity here reaches 276 species per 10,000 km<sup>2</sup>. In the north-west it borders on the Estonian center and in the north-east on the Smolensk-Moscow Upland.

**4. Volzhsko-Kamsky.** It is characterized by a relatively increased species diversity (up to 300) compared to the surrounding territories due to the fact that it covers a nemoral region and borders on the boreal-taiga one.

**5. South Ural.** It is located at the junction of 3 regions: Alpine, Nemoral and Arid. The number of species here reaches 292.

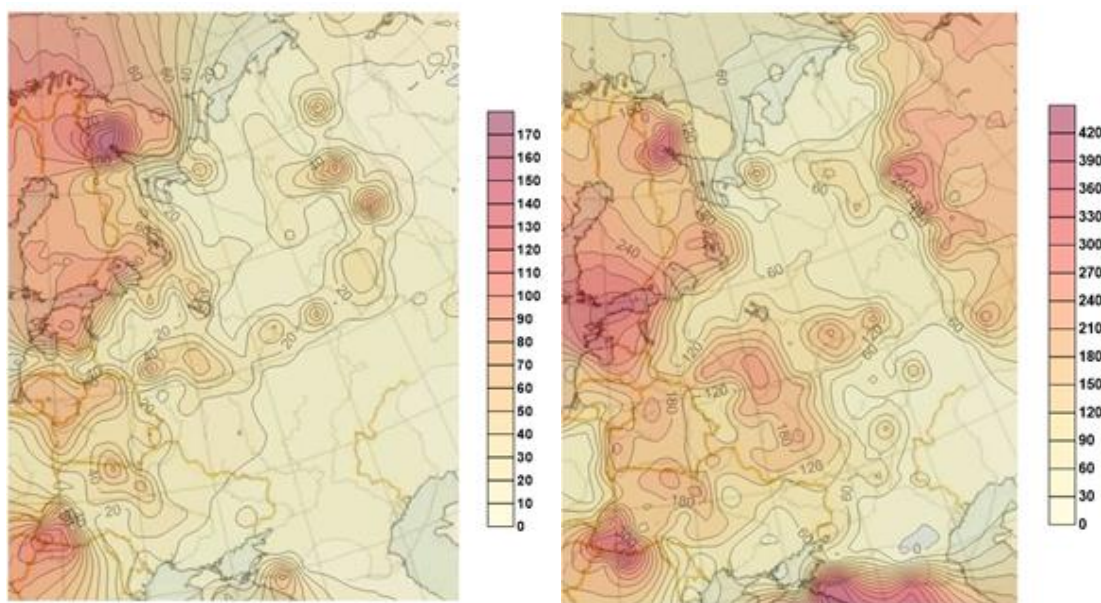
**6. Belovezhsky** (Grodno-Belovezhsky). It is located in the western part of the nemoral region and the species density here reaches 300. Probably continues on the territory of Eastern Poland.

**7. Kyiv-Mozyr.** It is located in the middle of the Polesie lowland on two low elevations above sea level, but with a significant relative difference in elevation, which creates additional favorable conditions for the growth of bryophytes. The number of species per square here reaches 311.

To the south, the species biodiversity of bryophytes noticeably decreases in the arid region, increasing only on the spurs of the Caucasus and Crimean mountains.

The species diversity of bryophytes in Eastern Europe has its own characteristics in various taxonomic groups (Fig. 4).

If the species diversity of mosses in general repeats the general diversity of bryophytes on the territory of Eastern Europe, then the diversity of liverworts and anthocerotes, due to their biological and ecological characteristics, has its own specificity. Most of the species and their localities of the latter are concentrated in the western part of the study area. The distribution of liverworts and anthocerotes on the Kola Peninsula is significant in area, and their diversity is also more clearly expressed in the nemoral region. However, they are almost completely absent in the arid region, southeast of 53 degrees east latitude and 37 degrees longitude, and in the arid northeastern foothills of the Caucasus.



**Fig. 4.** Species diversity (number of species in squares) of bryophytes in Eastern Europe: A – liverworts and anthocerotes, B – mosses.

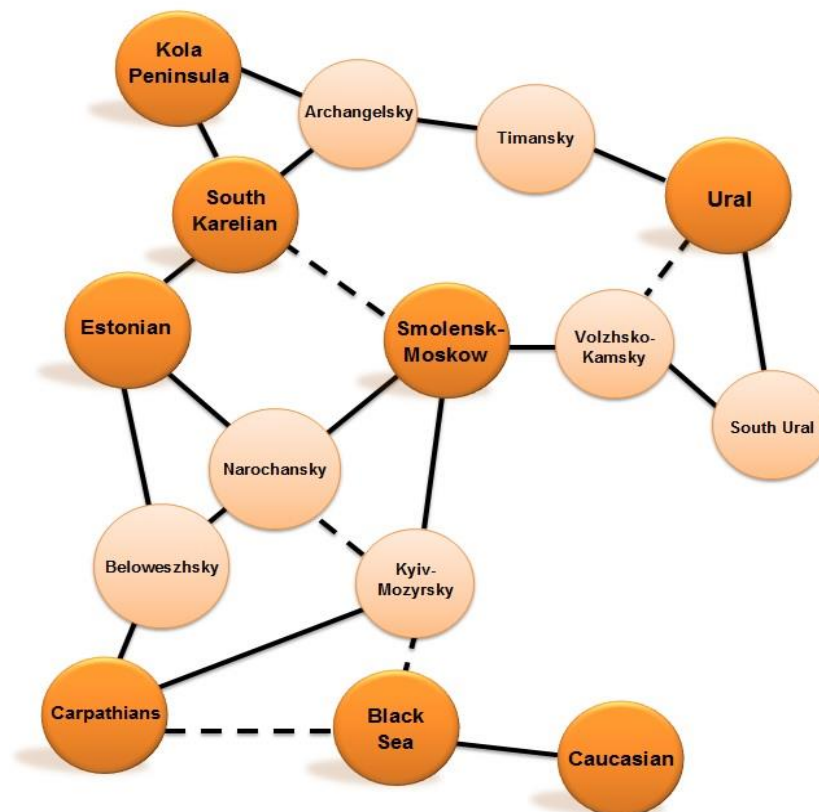


### Discussion

The centers of species diversity described above form a spatial structure, which can serve as a model for the basis of the structural organization of bryophytes in Eastern Europe (Fig. 5). It is the elevated mountainous regions that are the concentration of maximum diversity and refuge for many rare species in the region. Undoubtedly, one of the most important biological features of bryophytes is the long-distance transport of spores, which ensures their migration and the possibility of growing in similar mountain ecological conditions in remote areas. This is why we are seeing increased biodiversity in mountain centers. However, these possibilities are not endless with increasing distance and mountain ranges in Eastern Europe are located along the edges of this region. In the central part there are only small hills with rugged relief and the presence of boulders to the north of the border of the last glaciations. Here many mountain species may find some small opportunities for settlement and further transit into the mountain ranges. It is such a territory that the Smolensk-Moscow Upland is, where the biodiversity of bryophytes is not as great as in mountainous regions, but it is objectively higher than in the surrounding lowlands. A similar picture is observed at the local level in Belarus, where biodiversity in upland areas (3 – Narochansky, 6 – Belovezhsky (northern part), 7 – Kyiv-Mozyr) is higher than in the lowlands. At the same time, there remains a controversial issue that requires additional research, how great is the role of these territories in the migration of species and in ensuring the connectivity of mountain biodiversity centers in Eastern Europe.

Nevertheless, one can theoretically try to present a preliminary model scheme for the basis of the structural organization of bryophytes in Eastern Europe with possible channels for a higher migration of species from adjacent territories.

In terms of mathematical graph theory, the Smolensk-Moscow Upland is located at the center of the model. In theory, there could be a link between the western and eastern parts of the bryoflora of Eastern Europe. Also, one of the most related element of the spatial structure



**Fig. 5. Preliminary theoretical structural model of organization and interconnections of bryofloras in Eastern Europe.**

of bryoflora in Eastern Europe is the Kyiv-Mozyr subcenter (4 ribs), it is through it that the main migration of bryophytes from north to south and from south to north occurs. Belovezhsky and Narochansky subcenters have 4 ribs and also actively contribute to the migration process. Through the elevated areas of the Arkhangelsky and Timan sub-centers, the Kola Peninsula and South Karelian centers are connected with the Urals. The most isolated in the region is the Caucasus, which maintains links with other centers through the Black Sea center and Crimea.

Of course, this model is clearly of a preliminary theoretical character and does not pretend to be completely reliable, but it can serve as a scheme, a basis for further biogeographic and floristic studies.

In general, the obtained data are consistent with the results of previous similar studies [IGNATOV, 1993] on the species diversity of bryophytes obtained in the approximation to area of 100,000 km<sup>2</sup>. Our research provides a more detailed picture of the spatial distribution in the central part of the region, especially in the zone of deciduous forests.

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