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RESEARCH PAPER

Moss diversity distribution patterns and agglomerates of local floras in the Russian Far East

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ABSTRACT

Published materials on the mosses of the Russian Far East are summarized. Nine hundred and thirty species of mosses were revealed, and a bibliography is provided for each taxon. The distribution of each taxon within 39 spatial units (5×5 degrees latitude/longitude) is analyzed. The list for each square was regarded as the flora of minimal size involved in analysis. Analysis of interrelationships between each minimal flora has revealed seven floristic associations that correspond to the following territories: Beringian Chukotka, the continental part of Chukotka Autonomous District and continental part of Magadan Province, northern coast of the Sea of Okhotsk, Kamchatka and adjacent islands, Sakhalin and southern Kurils, Russian Manchuria, and the rest part of continental southern Russian Far East. Centers of moss species diversity are considered.

Keywords: Russian Far East, mosses, bryoflora, distribution patterns, diversity, conservation, phytogeography

РЕЗЮМЕ

Писаренко О.Ю., Бакалин В.А. Закономерности распространения разнообразия мхов и естественные агломераты локальных моховых флор на российском Дальнем Востоке. Проведена ревизия опубликованных материалов по мхам российского Дальнего Востока; общий список включает 930 видов. Приводится библиография. Составлена таблица распределения видов по 39 выделам территории размера (5×5 градусов широты/долготы). Сравнение списков видов мхов по «квадратам» выявило 7 флористических агломераций, соответствующих следующим территориям: Берингийская Чукотка, континентальные части Чукотки и Магаданской области, северное побережье Охотского моря, Камчатка и прилегающие острова, Сахалин и южные Курилы, южное Приморье, остальная часть юга Дальнего Востока. Рассмотрены центры видового разнообразия мхов. Выявлено, что 6 основных центров охватывают более 4/5 видового состава флоры мхов российского Дальнего Востока.

Ключевые слова: российский Дальний Восток, мхи, бриофлора, закономерности распространения, разнообразие, охрана, фитогеография

The examination of spatial patterns of taxonomic diversity and richness is a necessary stage for the conservation and sustainable use of biological resources. Moss species diversity in non-tropical Eurasia is higher in oceanic regions, whereas inland territories have poorer moss floras, with highest diversity occurring in the mountainous areas with high amounts of rainfall (Ignatov 1993, 2001). The Russian Far East covers more than 3 000 000 square kilometers in latitudinal span from 72°N to 42°30'N. Zonal communities in the area range from arctic tundra in the North to cool temperate forests in the South. The great variability in climate, landscapes and geology of the Russian Far East results in a taxonomically diverse flora, with many taxa occurring only here in the country. The Russian Far East houses ca. 80 % of the bryophyte taxonomic diversity of Russia; more than a quarter of species of the Far Eastern moss flora do not occur in Russia outside of it.

This paper continues the investigation on bryophyte distribution patterns in the Russian Far East. We follow the previous work on liverworts and hornworts (Bakalin 2013) but deal with the moss portion of the biota. The aims of the present work are: 1) to summarize published moss data for the Russian Far East, to attribute the data on plots of the area according to grid cells 5×5 degrees, to evaluate the state of knowledge of moss flora of the plots; 2) to consider moss taxonomic diversity 'hot spots' in the Russian Far East; and 3) to estimate latitudinal (~ zonal) patterns of the moss flora in the Russian Far East.

MATERIAL AND METHODS

This paper uses basically the same approaches for analysis of diversity distribution patterns as proposed for hepatics of the Russian Far East (Bakalin 2013). The studied area was divided into plots 5×5 degrees in latitude and longitude. These quasi-squares (further 'squares') are numbered with a general trend from northeast to south (Fig. 1). They vary in area from 112 243 km^2 (in latitudes 65–70°N) to 208 747 km^2 (in latitudes 45–50°N). Some of them are completely 'land' squares, whereas in some squares sea surface occupies more than 90 % of the area. Then the distribution of each moss species recognized in the Russian Far East through the set of squares was reviewed. In the

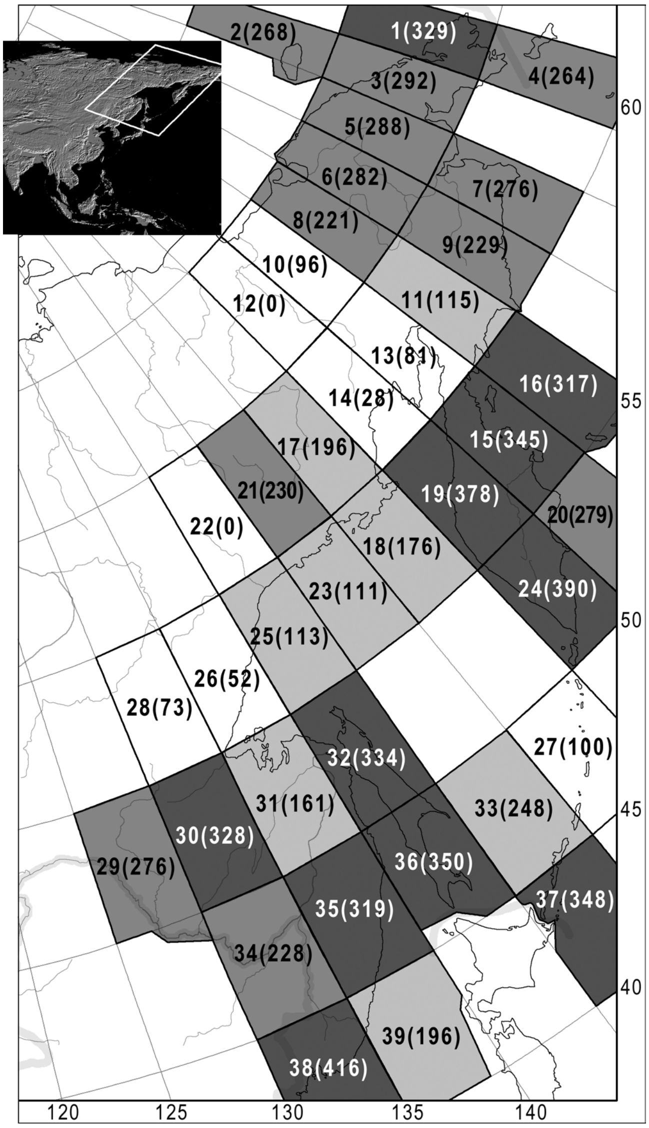

Figure 1 The subdivision of the territory into squares, their numeration and number of recorded moss species per square (in brackets)

case of comparatively small islands on a boundary of two squares moss data were ascribed as follows: Wrangel Island – square No. 2, Commander Islands – square No. 16, Iturup Island – square No. 33.

The most valuable procedure was to reveal the distribution of moss taxa through the Russian Far East – the information was then placed in the data matrix used for subsequent analyses. The matrix represents the table with the indication of the distribution of each revealed taxon within 38 squares (presence – 1, absence – 0). The database was based on published papers, with the most valuable placed into Table 1. Along with regional lists and notes on new records, the data from recent taxonomic revisions have been taken into account. The main revisions used are following: Brachytheciaceae (Ignatov et al. 2015, Ignatov & Milutina 2007ab, 2010, Huttunen et al. 2015), Polytrichaceae (Ivanova et al. 2005, 2014, 2015, Ivanova & Ignatov 2007); *Anacamptodon* (Czernyadjeva 2007), *Anoectangium* (Ignatova 2009), *Aongstroemia* (Drugova 2010), *Bryoerythrophyllum* (Fedosov & Ignatova 2008), *Coscinodon* (Ignatova et al. 2008), *Dichelyma* (Czernyadjeva & Ignatova 2013), *Dicranum* (Ignatova & Fedosov 2008, Tubanova et al. 2010, Tubanova & Ignatova 2011), *Didymodon* (Afonina & Ignatova 2007a, Afonina et al. 2010), *Encalypta* (Fedosov 2012a, 2012b, 2013), *Grimmia* (Ignatova & Munoz, 2004, Ignatova et al. 2016), *Hygrohypnum* (Czernyadjeva 2004), *Leptopterigynandrum* (Ignatov et al. 2012), *Lindbergia* (Ignatov et al. 2010), *Neckera* (Ignatov et al. 2009), Orthotrichum (Fedosov & Ignatova 2011), *Philonotis* (Koponen et al. 2012), *Pohlia* (Czernyadjeva 1999), *Pylaisiadelpha* (Afonina et al. 2007), *Schistidium* (Blom et al. 2006, Ignatova et al. 2010, Ignatova et al. 2016), *Scouleria* (Ignatova et al. 2015), *Sphagnum* (Maksimov 2007, Maksimov & Ignatova 2008, Lapshina & Maksimov 2014, Flatberg et al. 2016, Maksimov et al. 2016), *Stereodon* (Afonina 2004a, Afonina & Ignatova 2007b), *Syntrichia* (Afonina et al. 2014), *Thamnobryum* (Ignatova & Ignatov 2011).

All data were collected and sorted using the IBIS 6.2 software (Zverev 2007). The resulting table is available online in the electronic version of the paper (online appendix). Nomenclature of mosses follows to Ignatov et al. (2006) with some recent updates (www.arctoa.ru/Flora/).

The number of known species was evaluated for each square. The squares were sorted from not studied to well-studied and then the diversity 'hot spots' were found in the course of speculative analysis of the distribution of the taxa within the most taxonomically rich squares.

Species lists of all squares were regarded as the minimal flora involved in the analysis. The species lists for each 'minimal flora' were compared using cluster and detrended correspondence analysis to find interrelationships between minimal floras and to reveal natural flora associations. The dendrogram and ordination diagram were obtained with PAST 2.14 (Hammer et al. 2001).

RESULTS AND DISCUSSION

The compiled database (online appendix) includes 930 species distributed through 38 squares. The numbers of recorded species for each square are shown in Fig. 1 and 2.

The number of known species reflects 'exhaustiveness' in bryological studies for each square and varies drastically: from 0 to 416 species. On the other hand, the general regularities of taxonomic diversity distribution are sometimes obvious even from this undoubtedly incomplete matrix. For example, in humid regions of Northern Palearctic there is a general tendency of increasing species number in regional moss floras from North to South and in latitude range 80°N–40°N the number may increase by more than two times (Ignatov 2001). Previously we recognized 300–400 recorded taxa per unit as a confirmation of more or less comprehensive bryofloristic study there. Within 'northern' squares the same number could be somewhat less and reaches about 200–300 species per unit. A revealed taxonomic diversity of less than 100 species per square shows that the unit is undoubtedly poorly studied. These poorly studied squares are at the junction of Chukotskij Autonomous District, Magadan Province and Kamchatka Territory (Fig. 1, squares 10, 12, 13, 14), north of Khabarovsk Territory and Amur Province (Fig. 1, squares 22, 26, 28). The listed squares were excluded from subsequent analyses. A

Table 1. Main sources of bryoflora information by sectors of the territory

Sector No. as in Fig. 1	Bibliography
1	Afonina 2004b, Otnyukova et al. 2004, Zolotov & Afonina 2015, Flatberg et al. 2016
2	Afonina 2004b, Afonina 2006, Zolotov & Afonina 2015, Maksimov et al. 2016
3	Afonina 2004b, Maksimov & Ignatova 2008, Zolotov & Afonina 2015, Flatberg et al., 2016
4	Afonina 2004b, Flatberg et al. 2016, Maksimov & Ignatova 2008, Zolotov & Afonina 2015, Flatberg et al. 2016, Ignatova et al. 2016
5	Afonina 2004b, Afonina & Konstantinova 2008, Zolotov & Afonina 2015, Ignatova et al. 2016, Maksimov et al. 2016
6	Afonina 2004b, Afonina 2006, Afonina & Konstantinova 2008, Maksimov & Ignatova 2008, Flatberg et al. 2016
7	Kuzmina 2003, Afonina 2004b, Maksimov & Ignatova 2008, Flatberg et al. 2016
8	Afonina 2004b, Flatberg et al. 2016
9	Kuzmina 2000, Afonina 2004b, Kuzmina 2003, Maksimov & Ignatova 2008
10	Afonina 2004b
11	Kuzmina 2003, Afonina 2004b, Kuzmina et al. 2013, Beldiman & Kuzmina 2016
13	Kuzmina et al. 2012, Beldiman & Kuzmina 2016, Maksimov et al. 2016
14	Blagodatskikh 1984, Maksimov & Ignatova 2008
15	Czernyadjeva 2012, Kuzmina et al. 2013
16	Bakalin & Cherdantseva 2006b, 2008, Zolotov 2011, Fedosov et al. 2012
17	Blagodatskikh 1984, Cherdantseva & Bakalin 2011, Malashkina 2012a, Malashkina & Cherdantsava 2012, Chemeris & Mochalova 2015, Pisarenko 2015b
18	Blagodatskikh 1984, Chemeris & Mochalova 2015, Cherdantseva & Bakalin 2011, Pisarenko 2015b
19	Czernyadjeva & Ignatova 2008, Fedosov 2010, Czernyadjeva 2012
20	Czernyadjeva 2012, Fedosov & Kuzmina 2012
21	Blagodatskikh 1984, Afonina & Blagodatskikh 2006, Chemeris & Mochalova 2015, Pisarenko 2015abc, Maksimov et al. 2016
23	Blagodatskikh 1984, Chemeris & Mochalova 2015
24	Bakalin & Cherdantseva 2006a, Czernyadjeva 2012, Kuzmina et al. 2013, Ignatov et al. 2014, Maksimov et al. 2016
25	Lazarenko 1940, 1941ab, 1944, Maksimov & Ignatova 2008, Cherdantseva et al. 2009, Omelko et al. 2010
26	Lazarenko 1940, 1941 ab, 1944
27	Nyushko et al. 2008; Bakalin & 2009
28	Lazarenko 1940, 1941 ab, 1944
29	Lazarenko 1940, 1941 ab, 1944, Abramova & Abramov 1966, Abramova & Abramov 1977, Abramova & Petelin 1981, Abramova et al. 1987, Cherdantseva 1973, Duduv et al. 2015, Ignatova et al. 2016, Maksimov et al. 2016
30	Lazarenko 1940, 1941 ab, 1944, Abramova & Abramov 1977, Cherdantsava 1989, Cherdantsava et al. 1997, Ignatov et al. 2000, Maksimov & Ignatova 2008, Bezgodov & Ignatova 2013, Maksimov et al. 2016
31	Lindberg 1872, Lazarenko 1940, 1941, 1944, Abramova & Abramov 1966, Cherdantsava 1989, Cherdantsava & Gambaryan 1989, Yakovchenko et al. 2013
32	Lindberg 1872, Lazarenko 1940, 1941 ab, 1944, Maksimov & Ignatova 2008, Afonina 2009, Bakalin et al. 2012, Ignatova & Pisarenko 2013, Yakovchenko et al. 2013
33	Nyushko et al. 2008; Bakalin et al. 2009, Ignatova et al. 2016
34	Lindberg 1872, Lazarenko 1940, 1941ab, 1944, Abramova & Abramov 1977, Cherdantsava & Gambaryan 1986, Gambaryan & Cherdantsava 1998, Cherdantsava 2007ab, Cherdantsava et al. 2008, Maksimov & Kornyagina 2013
35	Kolesnikov 1938, Lazarenko 1940, 1941ab, 1944, Abramova & Abramov 1966, Bardunov & Cherdantsava 1982, Cherdantseva 2002, Cherdantseva et al. 2006, Cherdantsava et al. 2008, Bezgodov & Ignatova 2013, Ignatova et al. 2013, Maksimov et al. 2016
36	Lindberg 1872, Savich 1936, Kamimura 1939, Horikawa 1955, Abramova & Abramov 1966, Cherdantsava 1976, 2006, Bakalin et al. 2012
37	Bardunov & Cherdantsava 1984, 1987, Maksimov & Ignatova 2008, Bakalin et al. 2009, Ignatov & Ignatova 2009, Ignatov et al. 2014, Kuzmina et al. 2014, Ignatova et al. 2016, Koroteeva et al. 2016
38	Lazarenko 1940, 1941ab, 1944, Bardunov & Cherdantsava 1982, Cherdantsava 1989, Cherdantseva et al. 2006, Ignatov et al. 2007, Cherdantsava et al. 2008, Cherdantsava & Gorobets 2012, Malashkina 2012b, Cherdantseva et al. 2013, Ignatov et al. 2013
39	Bardunov & Cherdantsava 1982

value of a little bit more than 100 species per unit (Fig. 1, squares 11, 23, 25, 27) mean the square is poorly studied, but we included it in the analyses.

In total, 31 squares were considered in the analysis; 24 of them are properly studied (Fig. 1, dark and medium gray fill) and for the seven remaining squares moss diversity data are not as rich, though certainly not exhaustively known (Fig. 1, light gray fill).

'Hotspots' of moss diversity in the Russian Far East

As well as in the case of hepatics (Bakalin 2013), there were no direct relationships between the number of recorded species and the land area in the square, i.e. squares 'occupied' mostly by the sea are not distinctly poorer that completely 'land' squares. The most taxonomically rich squares are: squares 38 (416 species, south of Primorsky Territory), 24, 19, 15 (390, 378, 345 species, all in Kamchatka Penin-

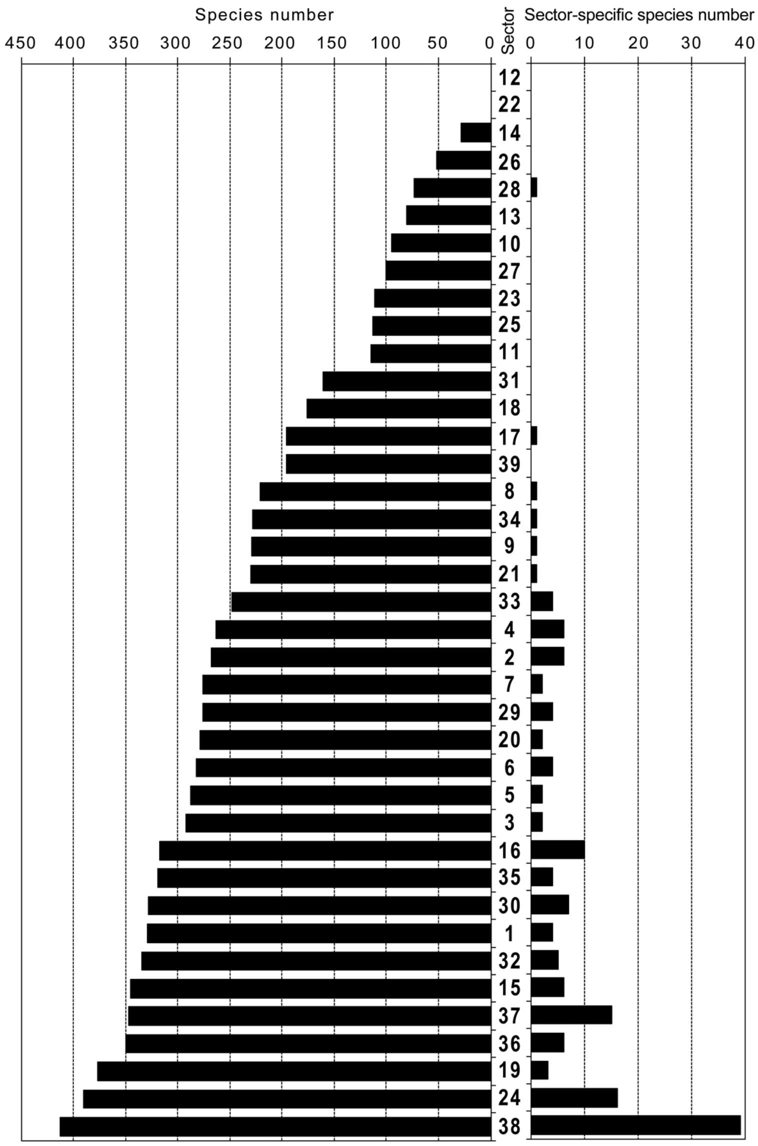

Figure 2 Number of recorded species (left) and number of square-specific species (right) by squares

sula), 37 (348 species, South Kurils), 32 and 36 (334 and 350 species, both mostly in Sakhalin Island), 30 (328 species, east of Amur Province), 1 (329 species, the east of Chukotka) and 16 (317 species, Commanders).

In fact the high diversity of the square is associated with different causes, which are considered below:

1. The taxonomic diversity in square 38 is mostly concentrated in the southern part of Sikhote-Alin and its southern spoors, where 351 moss species are recorded (Bardunov & Cherdantseva 1982; unpublished data), comprising 83 % of the total number of moss taxa of Primorsky Territory.

2. Kamchatka Peninsula is one of the best bryologically investigated areas in Russia and counts over 550 recorded species (Czernyadjeva 2005, 2012, Czernyadjeva & Ignatova 2008, Fedosov 2010, Fedosov & Kuzmina 2012, Fedosov & Ignatova 2012). Most of the diversity is housed in the central part of the Sredinnyj Mt. Range where 357 (65 %) of species are recorded. The best studied (and apparently richest) territory on the ridge is Bystrinsky Nature Park where 306 moss species have been recorded.

3. South Kurils is also an exceedingly taxonomically rich area, where 416 species have been recorded within area less than 8000 km^2. The latter number is not the final, and according to the recent studies the total number of taxa known in the area is close to 450 (unpublished data of Fedosov and Pisarenko).

4. Sakhalin Island has recently been well investigated (Bakalin et al. 2012, with several additions in Ignatova & Pisarenko 2013, Ivanova et al. 2014, Lapshina & Maksimov 2014). The highest diversity was observed in East Sakhalin Mountains, where 260 species (59 % of total island diversity) were recorded.

5. Bering Island is also one of the hot spots of taxonomic diversity of the Russian Far East. Although square 16 is in eleventh place in total ranging, the taxonomic diversity here is concentrated in the area less than 1/100 of the total square area; 312 taxa are recorded for the island.

6. Beringian Chukotka is characterized by high taxonomic diversity (391 species, Afonina 2004), with the most records coming from coastal areas.

The diversity centers are situated in approximately the same regions as those found in hepatics (Bakalin 2013). It should be noted however that these territories are among the best-studied areas in the Russian Far East. It seems in this case we have the complex process where the expectations of high diversity from researchers meet high taxonomic diversity in reality.

The six taxonomic diversity centers, as revealed above, include 778 taxa that comprise 83.7 % of the total diversity in the Russian Far East. Only one of them (Bering Island) belongs to a strictly protected area (Komandorsky Strict Nature Reserve), although the protection of the moss flora in other areas is also highly realized.

Spatial differentiation of the moss floras in the Russian Far East

Initially we were inclined to think the affinity between taxonomic compositions of various squares in the Russian Far East should be relatively high. This estimation was based on two facts: 1) the widely known ability of moss taxa to find 'micro-niches' in landscapes whose macro-climatic conditions may not be favorable to survival and 2) mostly mountainous relief of the area, which provides a wide range of local climatic conditions and thus the appropriate environments for arctic-alpine and oroboreal taxa, e.g., in the cool temperate zone. Surprisingly, the analysis showed that similarity is relatively low.

Two squares with no information on mosses were eliminated from the analysis. The remaining 37 squares only have

Table 2. Moss diversity and unique species of 39 designated squares and 7 square clusters of the Russian Far East

No. of square	Unique species per sector; number and list	Unique species for the cluster
Beringian Chukotka & Vrangel Island cluster		
1	**4:** *Bryum axel-blyttii*, *Oreas martiana*, *Orthotrichum laevigatum*, *Seligeria oelandica*	**19:** *Bryobrittonia longipes*, *Bryum calophyllum*, *B. mirabile*, *Bucklandiella afoninae*, *Campylium longicuspis*, *Didymodon johansenii*, *D. subandreaeoides*, *Encalypta mutica*, *Funaria polaris*, *Niphotrichum elongatum*, *Schistidium andreaeopsis*, *S. boreale*, *S. submuticum*, *Seligeria polaris*, *Sphagnum arcticum*, *S. olafii*, *Tayloria hornschuchii*, *Tortula laureri*, *Voitia hyperborea*
2	**6:** *Bryum nitidulum*, *Didymodon maximus*, *Pterygoneurum ovatum*, *Schistidium frisvollianum*, *S. grandirete*, *Tomentypnum falcifolium*	
3	**2:** *Drepanocladus latinervis*, *Schistidium venetum*	
4	**6:** *Amblyodon dealbatus*, *Didymodon leskeoides*, *Grimmia beringiensis*, *Plagiothecium undulatum*, *Pohlia torrentium*, *Sciuro-hypnum ornellanum*	
Rest of Chukotka & Continental part of Magadan Province cluster		
5	**2:** *Pterygoneurum lamellatum*, *Warnstorfia procera*	**4:** *Hamatocaulis lapponicus*, *Orthotrichum pellucidum*, *Scouleria rschewinii*, *Tortula acaulon*
6	**4:** *Pohlia sphagnicola*, *P. vexans*, *Polytrichastrum papillatum*, *Schistidium flexipile*	
7	**2:** *Orthotrichum pallens*, *Tayloria serrata*	
8	**1:** *Meesia hexasticha*	
9	**1:** *Pseudocalliergon angustifolium*	
11	**0**	
17	**1:** *Bryum longisetum*	
21	**1:** *Pohlia atropurpurea*	
Northern coast of the Okhotsk sea cluster		
18	**0**	**0**
23	**0**	
25	**0**	
Kamchatka Peninsula, Bering & Paramushir Islands cluster		
15	**6:** *Arctoa anderssonii*, *Bryum kunzei*, *Didymodon gaochienii*, *Grimmia fuscolutea*, *Pylaisia curviramea*, *Sciuro-hypnum dovrense*	**18:** *Bucklandiella vulcanicola*, *Dicranum spurium*, *Didymodon brachyphyllus*, *D. hedysariformis*, *Grimmia anomala*, *G. triformis*, *Hygrohypnella bestii*, *Kiaeria falcata*, *Lescuraea secunda*, *Pleuridium subulatum*, *Pohlia cardotii*, *P. obtusifolia*, *Sanionia orthothecioides*, *Schistidium dupretii*, *Sphagnum inexpectatum*, *Stereodon callichrous*, *Thuidium thermophilum*, *Tortula muralis*
16	**10:** *Brachythecium frigidum*, *Bucklandiella macounii*, *Claopodium bolanderi*, *Didymodon vinealis*, *Drepanocladus sordidus*, *Lescuraea baileyi*, *Lescuraea saviana*, *Rhytidiadelphus loreus*, *Sphagnum tescorum*, *Ulota phyllantha*	
19	**3:** *Didymodon maschalogenus*, *Encalypta microstoma*, *Tayloria splachnoides*	
20	**2:** *Pohlia viridis*, *Tetrodontium brownianum*	
24	**16:** *Brachydontium olympicum*, *B. trichodes*, *Bryum alpinum*, *B. mayrii*, *B. muehlenbeckii*, *B. violaceum*, *Campylopus atrovirens*, *C. umbellatus*, *Homalothecium lutescens*, *Loeskeobryum brevirostre*, *Niphotrichum barbuliodes*, *Ochyraea smithii*, *Plagiothecium platyphyllum*, *Sphagnum annulatum*, *Splachnum melanocaulon*, *Timmiella corniculata*	
Sakhalin & Kuril Islands cluster		
32	**5:** *Amblystegium minutissimum*, *Didymodon fallax*, *Fissidens neomagofukui*, *Orthotrichum furcatum*, *Platydictya fauriei*	**14:** *Brachythecium extremiorientale*, *Campylophyllum halleri*, *Dicranella curvipes*, *Dicranum hamulosum*, *Fissidens teysmannianus*, *Isothecium hakkodense*, *Mielichhoferia japonica*, *Mnium orientale*, *Neckera borealis*, *Pseudotaxiphyllum pohliaecarpum*, *Pylaisia obtusa*, *Sciuro-hypnum brotheri*, *Thuidium tamariscinum*, *Ulota japonica*
36	**6:** *Didymodon perobtusus*, *Palustriella decipiens*, *Rhynchostegium rotundifolium*, *Schistidium flaccidum*, *S. sinensiapocarpum*, *Sphagnum pungifolium*	
37	**15:** *Barbula indica* var. *kurilensis*, *Brotherella henonii*, *Campyliadelphus elodes*, *Campylium squarrosulum*, *Conardia compacta*, *Dicranum japonicum*, *D. setifolium*, *Didymodon tophaceus*, *Ditrichum rhynchostegium*, *Glossadelphus ogatae*, *Grimmia atrata*, *Hypnum fujiyamae*, *Plagiobryum hultenii*, *Stereodon dieckei*, *Thuidium glaucinoides*	
33	**4:** *Dichelyma japonicum*, *Fissidens nobilis*, *Philonotis marchica*, *Sphagnum subtile*	
27	**0**	
Amur Province, south of Khabarovsk Territory & north of Primorsky Territory cluster		
29	**4:** *Anomodon viticulosus*, *Entosthodon pulchellus*, *Fontinalis dalecarlica*, *Schistidium austrosibiricum*	**6:** *Brachythecium complanatum*, *Grimmia muehlenbeckii*, *Orthotrichum iwatsukii*, *O. striatum*, *Physcomitrium sphaericum*, *Pohlia lutescens*
30	**7:** *Actinothuidium hookeri*, *Cynodontium fallax*, *Dicranodontium asperulum*, *Grimmia unicolor*, *Hedwigia stellata*, *Lyellia crispa*, *Sphagnum auriculatum*	
31	**0**	
35	**4:** *Brachythecium dahuricum*, *Pylaisia steerei*, *Rhizomnium hattorii*, *Schistidium pruinosum*	
34	**1:** *Glyphomitrium warburgii*	
39	**0**	
South Primorsky Territory cluster		
38	**39:** *Anomodon abbreviatus*, *A. solovjovii*, *Archidium alternifolium*, *Brachythecium helminthcladum*, *Campylium radicale*, *Coscinodon pseudohartzii*, *Dicranoloma cylindrothecium*, *Didymodon cordatus*, *Entodon giraldii*, *E. rufescens*, *E. sullivantii*, *Entosthodon muhlenbergii*, *Ephemerum spinulosum*, *Fissidens hyalinus*, *Forsstroemia stricta*, *F. trichomitria*, *Haplohymenium longinerve*, *Homaliadelphus targionianus* var. *laevidentatus*, *Hyophila involuta*, *Lindbergia geniculata*, *Macromitrium hymenostomum*, *Meteorium buchananii*, *Miyabea fruticella*, *M. rotundifolia*, *Neckera goughiana*, *N. konoi*, *N. polyclada*, *Orthotrichum consobrinum*, *Physcomitrium eurystomum*, *Plagiothecium cordifolium*, *P. succulentum*, *Pylaisiadelpha tristoviridis*, *Rhizomnium parvulum*, *Schistidium elegantulum*, *Seligeria recurvata*, *Stereodon calcicola*, *Taxiphyllum alternans*, *Weissia planifolia*, *Weissia rutilans*	**0**

three species in common (*Aulacomnium palustre*, *Hylocomium splendens*, *Sanionia uncinata*). Further, if we were to eliminate from analysis six more squares where less than 100 species per square are known, only three more common species (*Ceratodon purpureus*, *Pogonatum dentatum*, *Polytrichum juniperinum*) will be added. This fact suggests drastic regional differentiation of the moss flora in the Russian Far East.

The opposite situation is the specificity of each square. About 1/6 of the species list (152 taxa) are known from only one square (Fig. 2, Table 2). The richest square flora bears the highest numbers of specific taxa. The number of specific taxa varies from 0 to 16, with the prominent exclusion of the very specific 'Manchurian' square (No. 38) that houses 40 species.

To find some statistically reliable relationships in the flora we have compared moss lists of all squares using detrended correspondence analysis (DCA) and cluster analysis (Ward's Method) (Figs. 3, 4). Both methods showed similar regularities (although 9 groups are separable by DCA, but 7 by cluster analysis). It is possible to recognize the following 'natural' groups according to moss flora similarity (cf. also Table 2):

- Beringian Chukotka & Wrangel Island – 37 specific taxa (squares 1–4, Fig. 4-A; Fig. 5-I);
- continental part of Chukotka Autonomous District and continental part of Magadan Province – 16 specific taxa (squares 5–9, 11, 17, 21, Fig. 4-B, C; Fig. 5-II);
- northern coast of the Okhotsk Sea – 0 specific taxa (squares 18, 23, 25, Fig. 4-D; Fig.5-III);
- Kamchatka Peninsula, Commanders and North Kurils – 55 specific taxa (squares 15, 16, 19, 20, 24, Fig. 4-E; Fig. 5-IV);
- Sakhalin and Kuril Islands (excluding North Kurils) – 44 specific taxa (squares 32, 36, 33, 37, Fig. 4-F, G; Fig. 5-V);
- Amur Province, South part of Khabarovsk Territory and North of Primorsky Territory – 22 specific taxa (squares 29–31, 34–35, Fig. 4-H, Fig.5-VI);
- south of Primorsky Territory – 40 specific taxa (square 38, Fig. 4-J, Fig. 5-VII).

The similarity between the moss cumulative floras (as defined above) is somewhat higher than between the squares themselves, although still remains relatively low. The clusters are defined due to two groups of species: (1) species, common for all squares of the cluster which unites them, and (2) species, peculiar for the cluster which separates it from other clusters.

The groups of species causing the separation of the described units are reflected in Fig. 5. The figure shows in graphical form the distribution types of mosses in the Russian Far East: strips show types of species occurrence by the clusters, thickness of a stripe correlates with the number of species.

The symbols a, b, c, e, f, g, h, j (Fig. 5) correspond to the letter symbols of the clusters (Fig. 3); the lists of taxa specific for the clusters are in Table 2. In addition the following categories are introduced into the comparison: n – taxa restricted to the northern half of the Russian Far East; k – taxa distributed everywhere with the exception of southern Primorye; l – everywhere except in the North (Wrangel Island, Chukotka & Magadan Province); m – taxa restricted to the southern half of the Russian Far East; z – taxa common for all clusters; x – taxa that have an indefinite (impossible to formalize) distribution.

Only 87 species are known in all seven clusters (Fig 5 – z). Those are boreal to arcto-boreal circumpolar species and are widespread in the Holarctic: *Abietinella abietina*, *Aulacomnium palustre*, *Brachythecium salebrosum*, *Bryoerythrophyllum recurvirostrum*, *Calliergon cordifolium*, *Calliergonella lindbergii*, *Ceratodon purpureus*, *Climacium dendroides*, *Dicranum majus*, *Distichium capillaceum*, *Eurhynchiastrum pulchellum*, *Hylocomium splendens*, *Hypnum cupressiforme*, *Mnium thomsonii*, *Niphotrichum canescens*, *Oncophorus wahlenbergii*, *Plagiomnium ellipticum*, *Polytrichum piliferum*, *P. strictum*, *Rhizomnium magnifolium*, *Sanionia uncinata*, *Sphagnum capillifolium*, *S. girgensohnii*, *Straminergon stramineum*, *Thuidium assimile*, *Warnstorfia exannulata*, etc.

If we were to eliminate cluster D (northern coast of the Okhotsk Sea) from the analysis, the number of the common species among the remaining clusters increases to 35 (Fig. 5 – w: *Bryum amblyodon*, *Anomobryum concinnatum*, *Brachythecium*

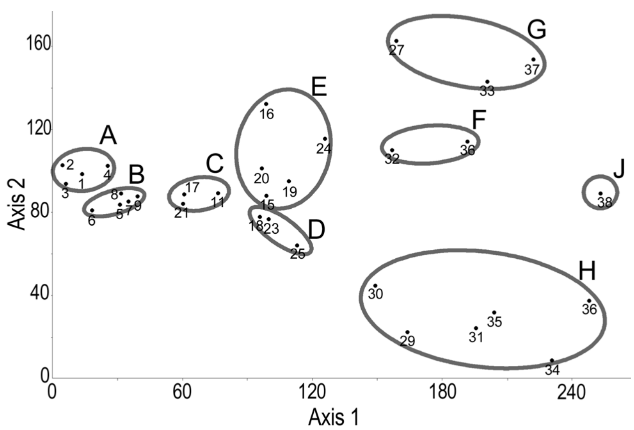

Figure 3 DCA ordination diagram of moss lists of the squares of the Russian Far East. The squares (numbered) group into some clusters (dotted lines with letters). (Squares with less than 100 species recorded are not included)

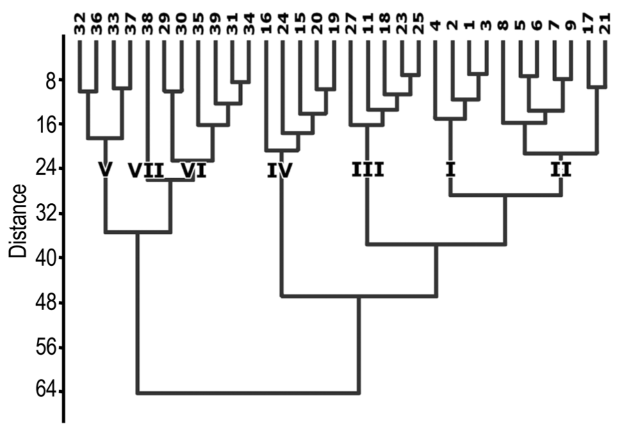

Figure 4 Dendrogram of similarity of moss lists of the squares of the Russian Far East (Ward's method). (Squares with less than 100 species recorded are not included)

erythrorrhizon, *Breidleria pratensis*, *Bryum cyclophyllum*, *B. elegans*, *B. pseudotriquetrum*, *Bucklandiella microcarpa*, *Cnestrum schistii*, *Dichodontium pellucidum*, *Dicranella schreberiana*, *Dicranum fuscescens*, *Drepanocladus polygamus*, *Encalypta ciliata*, *Entodon concinnus*, *Fissidens bryoides*, *F. osmundoides*, *Grimmia longirostris*, *Gymnostomum aeruginosum*, *Hamatocaulis vernicosus*, *Hymenostylium recurvirostrum*, *Neckera pennata*, *Ochyraea duriuscula*, *Oxystegus tenuirostris*, *Plagiomnium medium*, *Plagiopus oederianus*, *Platydictya jungermannioides*, *Polytrichum densifolium*, *Schistidium papillosum*, *Sciuro-hypnum plumosum*, *S. starkei*, *Sphagnum balticum*, *Stereodon bambergeri*, *S. subimponens*, *Trichostomum crispulum*). The lack of a given species in the area is possible to explain by an insufficient knowledge of local floras composing that cluster, but also by the peculiar and uniform hemiarctic climate and acidic rock dominance.

Naturally the distribution of many of taxa in the Far East is limited by its northern part. The latter group includes species specific for squares 1–9, 11, 17, 21 and corresponding clusters, there is the set of taxa that are not registered further south of Chukotka & Magadan Province (Fig. 5 – n: *Aulacomnium acuminatum*, *Cinclidium arcticum*, *Didymodon acutus*, *Distichium hagenii*, *Drepanocladus arcticus*, *Encalypta longicollis*, *Grimmia anodon*, *Leptopterigynandrum austro-alpinum*, *Mnium blyttii*, *Molendoa tenuinervis*, *Ochyraea mollis*, *Plagiothecium svalbardense*, *Pseudocalliergon brevifolium*, *Schistidium holmenianum*, *Splachnum vasculosum*, *Stegonia latifolia*, *S. pilifera*, *Tetraplodon pallidus*, *T. paradoxus*, *Timmia sibirica*, *Warnstorfia pseudosarmentosa*, etc.). Many of them have mainly arctic and hemiarctic areas of distribution.

On the contrary, the specificity of southern squares results from taxa of subtropical, or nearly so distribution (*Entodon giraldii*, *Forsstroemia trichomitria*, *Homaliadelphus targionianus*, *Hyophila involuta*, *Macromitrium hymenostomum*, *Meteorium buchananii*, *Miyabea fruticella*, *M. rotundifolia*, *Taxiphyllum alternans*, etc.; *cf.* Bardunov et al. 2008). In addition, there are the series of temperate taxa that do not occur in the boreal zone and northward and, therefore, cause the negative specificity of the northern group of clusters. Most of them are characterized by East Asian distribution (Fig 6 – m: *Anacamptodon latidens*, *Anomodon giraldii*, *A. thraustus*, *Bartramiopsis lescurii*, *Brachythecium auriculatum*, *B. buchananii*, *Claopodium pellucinerve*, *Codriophorus brevisetus*, *Dicranum hakkodense*, *D. pacificum*, *Echinophyllum sachalinense*, *Eurhynchiadelphus eustegius*, *Glyphomitrium humillimum*, *Leucodon pendulus*, *Okamuraea hakoniensis*, *Plagiomnium acutum*, *P. vesicatum*, *Pleuroziopsis ruthenica*, *Pogonatum contortum*, *P. japonicum*, *Pylaisiadelpha tenuirostris*, *Rauiella fujisana*, *Rhizomnium striatulum*, *Rhytidiadelphus japonicus*, *Rigodiadelphus robustus*, *Sciuro-hypnum uncinifolium*, *Tetraphis geniculata*, *Trachycystis flagellaris*, etc.).

Negative specificity is largest for the most southern square (and the same cluster) (Fig 5 – k: *Bartramia ithyphylla*, *Blindia acuta*, *Brachythecium cirrosum*, *Bryum weigelii*, *Buxbaumia aphylla*, *Calliergon richardsonii*, *Dicranella cerviculata*, *D. subulata*, *Dicranum elongatum*, *D. groenlandicum*, *Grimmia reflexidens*, *Helodium blandowii*, *Hygrohypnella polare*, *Hymenoloma crispulum*, *Isopterygiopsis pulchella*, *Leptobryum pyriforme*, *Loeskypnum badium*, *Myurella julacea*, *Niphotrichum ericoides*, *Oligotrichum hercynicum*, *Paludella squarrosa*, *Pohlia andrewsii*, *P. crudoides*, *P. wahlenbergii*, *Polytrichastrum sexangulare*, *Polytrichum jensenii*, *Pseudobryum cin-*

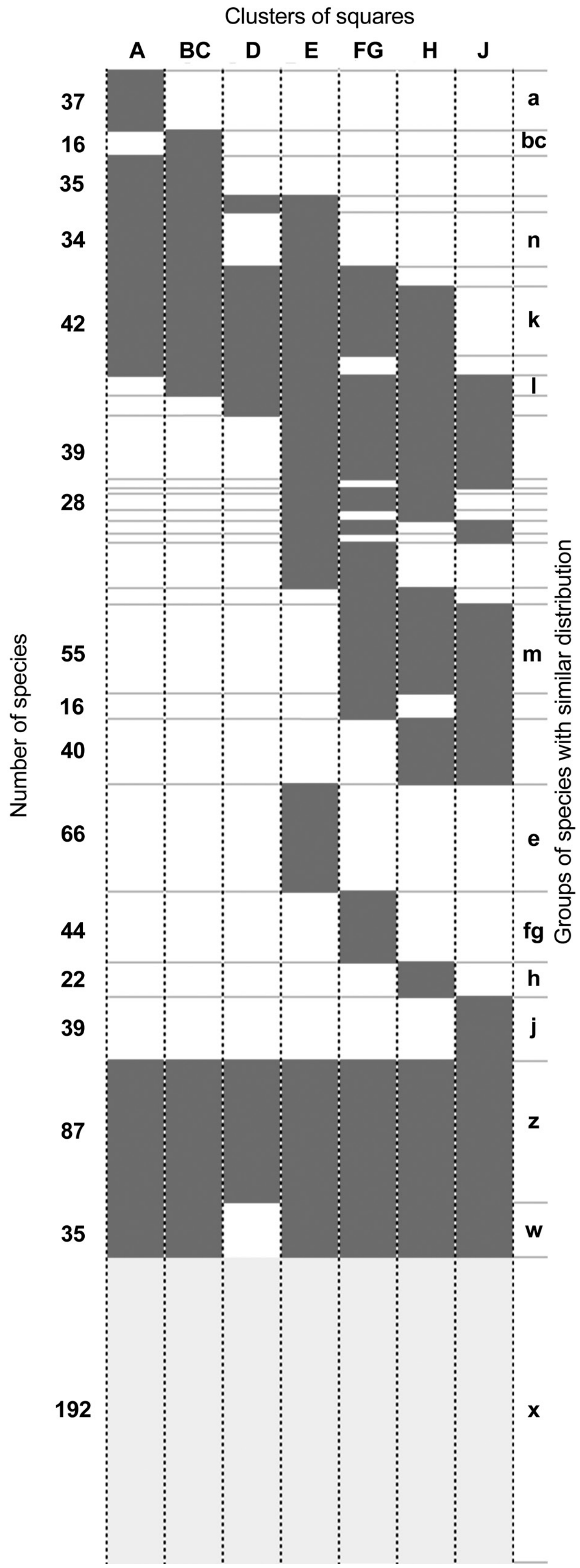

Figure 5 Graphical image of the table of moss species occurrence by clusters, which is sorted by peculiarity of species distribution. Capital letters mark clusters of squares according to Fig. 3. Gray strips show types of species occurrence by the clusters; thickness of a stripe correlates with the number of species; the numbers are given at left. Lowercase letters at right are groups of species with similar distribution by the clusters discussed in the text

clidioides, *Pseudoleskeella nervosa*, *Rhizomnium pseudopunctatum*, *Scorpidium revolvens*, *Sphagnum compactum*, *S. lindbergii*, *S. riparium*, *S. russowii*, *S. teres*, *S. warnstorfii*, *Splachnum rubrum*, *Tomentypnum nitens*, *Tortula hoppeana*, *Warnstorfia fluitans*, etc.). Many of them have mainly arctic-alpine distributions and are quite common northward. The relatively low elevations of the mountains in the southern flank of the continental Russian Far East does not permit them to survive.

The peculiar position of Kamchatka and adjacent islands should be noted. The cluster is the southern limit for many 'northern' species and at the same time it is the northern limit for numerous 'southern' taxa (Fig. 5). This character places Kamchatka 'between' boreal and Hemiarctic biomes. The latter circumstance, along with several species of the disjunctive distribution, results in outstanding taxonomical richness of the region.

Despite the difference in the approaches and used methods, the general traits of the subdivision of the Russian Far East according to moss flora similarity are the same as the regionalization developed for hepatics (Bakalin 2010). The Beringian and continental North-East Asia regions are well separated both for mosses and hepatics. The North Okhotsk region is not separated in hepatic flora analysis, and that could be a result of almost a complete lack of information on the hepatic flora in the southern portion of Magadan Province some years ago (the main researches on Magadan Province hepatics were carried out after 2010). Most parts of Kamchatka and adjacent islands are also separated both in mosses and hepatics. The same for the Manchurian part of the southern Far East. The continental part of the boreal Far East is also well defined in the hepatic analysis (although being divided there into two units, related to mostly boreal and mostly hemiboreal formations of the flora). At the same time relatively strong differences were observed in moss and hepatic regionalization of the 'insular' part of the southern Far East. For example, the hepatic flora of the southern Kurils is rather noticeably different from that of Sakhalin Island, whereas the moss floras of both the South Kurils and Sakhalin are rather similar. Whether it reflects more 'moisture-depending' nature of hepatics in comparison with mosses, or results from other reasons, cannot be evidently identified here.

CONCLUSIONS

1. The Russian Far East moss flora has outstanding value in Russia in the terms of environmental research and conservation purposes. Nine hundred and thirty taxa were recorded for the territory as of September 2016.

2. The maximal taxonomic diversity of the mosses within the Russian Far East is observed in the Bystrinsky Nature Park in the Kamchatka Peninsula, East-Sakhalin Mountains, Iturup Island in the Kurils, Bering Island in the Commanders, eastern coast of Beringian Chukotka and southern flank of Sikhote-Alin Range. These areas are among the most exhaustively studied bryologically in respect to the territories in the Russian Far East. In total 778 species were recorded in these 'hot spots' for taxonomic diversity that comprises 83.7 % of the total flora of the land. Among the localities listed, only one (Bering Island) is under protection by Federal law, whereas the conservation of bryophytes in other 'hot spots' should be among the crucial issues needed in proper management.

3. Seven territorial units are distinguishable according to moss flora similarity: Beringian Chukotka, continental part of Northeast Asia, northern coast of the Sea of Okhotsk, Kamchatka and adjacent islands, Sakhalin and southern Kurils, Russian Manchuria and the rest of continental South Far East. Noticeably, this subdivision is quite similar to that developed for hepatics in the area treated.

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