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Scales and levels of vegetation cover heterogeneity in the Arctic

Nadya V. Matveyeva, St. Petersburg

Abstract. Heterogeneity on different levels and scales is typical for the arctic plant cover with its elements ranging from few square centimeters up to hundreds of square meters. Mosaics with large repetitive modules are usually described as mosaics composed of different associations. However with decreasing size of the modules, differentiation of mosaic of communities from mosaic communities with an inherent small-scale pattern becomes difficult. Various approaches to this problem are discussed with special reference to the frost-boils and polygonal mires. It is suggested, that vegetation with modules of about 1 m^2 or less can be described as a mosaic community.

1 Introduction

The detailed investigation of the horizontal structure of vegetation is always an actual topic because structure reflects the processes within a plant community. Consideration of horizontal vegetation structure is especially important when dealing with the many problems of vegetation mapping, but also classification, determination of biological productivity etc.
The subject of the present paper is the discussion of difficulties connected with the heterogeneity of vegetation cover with special focus on the tundra and polar desert zones and approaches to their typology.

2 Horizontal heterogeneity in vegetation studies

It is common knowledge that vegetation cover is heterogeneous on different scales. This is reflected by numerous studies with pictures of the horizontal structure of the sample plots on all scales up to the differentiation of large territories. There is a certain level of heterogeneity on each scale of mapping. The size of heterogeneity elements varies from few square centimeters and decimeters up to tens and even hundreds of square meters and kilometers.

A very particular problem of horizontal heterogeneity concerns the basal unit of vegetation that phytosociologists use: the phytocoenose or community. This fundamental unit is used widely in different countries and schools of vegetation science, thus with qualitative and quantitative differences in its delimitation. There are numerous definitions of phytocoenose both in Russian and Western references. A simple and short one is given in the "Dictionary of notions and terms of modern phytosociology" (MIRKIN et al. 1989: 199): "Phytocoenose (syn. of plant community, on Greek phyton – plant, koinos – common) is conditionally restricted and homogeneous (by eye) vegetation contour, a part of phytocoenotical continuum". What follows from this definition is that its authors believe that: 1) in spite of the continuum in plant cover it is possible to distinguish discrete units within it; 2) an inner homogeneity of such units is estimated in the field by eye; 3) phytocoenose and community are considered as synonyms. However there are no qualitative criteria of the homogeneity measure as well as the scale of the distinguished and described units including their size.

There were several periods of hot discussions in Russia (and other countries) in connection with the understanding and determination of a plant community. In the first third of the last century, when the famous discussion in botanical societies took place "What is the phytocoenose?", this problem was under permanent attention in the course of more than half of a century. Results were summarized several times (NITZENKO 1971, MIRKIN & ROSENBERG 1978, NORIN 1979, VASILEVICH 1983). In spite of the hot disputes, sharp assessments, and intransigence of opponents, less disagreements existed concerning how to chose and limit a phytocoenose in the field for making a relevé due to common sense and ecological intuition based upon the collective experience of phytosociologists.

Generally apparent homogeneity is considered as essential for a phytocoenose, however accurate quantitative criteria of the heterogeneity degree and scale of this natural phenomenon are still lacking (NITZENKO 1968) and thus a researcher often has no other choice than to decide subjectively what level of heterogeneity he would tolerated.

A Russian geobotanist P. D. YAROSHENKO (1950, 1961), who was deeply interested in the study of vegetation spatial structure, separated plant stands of different sizes as micro-, meso-, and macrostands and believed that the phytocoenose is a meso-stand of vegetation. Different spatial scales are also. reflected in the proposal of terms additional to phytocoenose as gregation, aggregation, synusia, microstand on one hand, and complex, ranges, series of phytocoenoses, on the other. However phytocoenose has the peculiar status in this range: it is the unit (!), lower of that are parts of unit and higher of that are sets of units.

In the last 20 years the intensity of emotions connected with the basic unit in phytosociological research cooled down and researchers have come to a certain consensus. At present, papers dealing with vegetation classification dominate in Russian phytosociology, and numerous relevés made on sample plots from 4 to 400 m^2 are becoming available. Just such sizes correspond to the concepts of phytocoenose as a community of meso-scale.

The phytocoenose has the outstanding status that it is the fundamental or basal unit of vegetation description.

Even though the premise of a community is homogeneity, almost no vegetation types without at least small mosaics in the spatial structure will exist. This inherent heterogeneity of the main classification unit is silently accepted.

All these considerations make clear, that the study of plant community structure is the background for the further understanding of the basic unit of vegetation science.

3 Heterogeneity in Arctic vegetation

It is out of my competence to review how the problem of identifying phytocoenoses, their structural parts and combining into territorial units on above-phytocoenose level is solved in other natural zones. But I testify that all the questions concerning heterogeneity in particular for typology and classification of units on all levels are still very actual for studies of Arctic vegetation.

From the very beginning of the study of arctic vegetation, the basic unit in Russia was and still is named as 'type of tundra' (or even 'tundra') that is used instead of terms community or phytocoenose. Within the Arctic, it seems not more difficult to recognize phytocoenoses than in any other biomes, at least than in the boreal.

However, perhaps the most striking feature of almost all arctic communities is a mosaic structure with the smallest elements measured by centimeters or few decimeters. Heterogeneity of substrate and vegetation is notably high on different scales due to permafrost and cryogenic processes. There are no large plants (edificators) that control all the territory within the phytocoenose (like trees in forests). This is one reason that the delimitation of phytocoenoses in tundra zone and the polar deserts, can be difficult.

A very typical arctic mosaic structure are frost-boils with modules of three elements of nanorelief (patches of (almost) bare ground, rims and troughs) and the corresponding plant cover repeatedly occurring in space along very short distances (Fig. 1). The number of such modules on a standard sample plot of 100 m^2 along the latitudinal gradient on Taymyr Peninsula (Siberia) changes northwards from approximately 20 in the southern part of the tundra zone up to 30-60 in the middle part, 90-150 in the northern part, and up to 400 in the polar desert (MATVEYEVA 1998). The elements differ in composition and structure of plant cover. In general, small bryophytes, epigeous lichens and single vascular plants form a scarce cover on the patches, mesophilous apocarpous mosses and fruticose lichens cover relatively dry rims, and hygrophilous pleurocarpous mosses and liverworts as well as foliose lichens fill the wet troughs. The majority of tundra researches consider frost-boil communities with the regular cyclic type of horizontal structure (MATVEYEVA 1988) as mosaic phytocoenoses, make relevés on the sample plots of 16, 25 or 100 m^2, thus joining the vegetation of the three elements in one association or community type. When necessary, according to a special aim, a separate list of species for each microstand can be made, their size and configuration be described, and their area proportions assessed.

However as the three elements differ considerably in habitat, physiognomy and floristic, other researchers refer to such small elements as independent associations (NORIN 1979, WALKER et al. 1994). The vegetation of non-sorted circles (about 0.5 m in diameter) within the *Eriophorum vaginatum* tussock tundra in Alaska for example has been described as a separate community of *Anthelia juratzkana-Juncus biglumis* (WALKER et al. 1994).

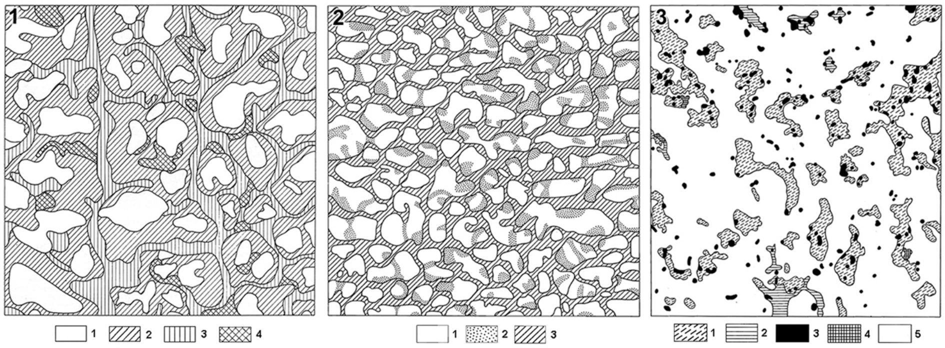


Fig. 1: Regular cyclic type of horizontal structure in frost-boil community of ass. *Carici arctisibiricae-Hylocomietum alaskani* MATVEYEVA 1994, southern tundra subzone, Kresty, Taymyr (after MATVEYEVA & ZANOKHA 1986, CHERNOV & MATVEYEVA 1997). Sample plot 10x10 m^2.
1: patches of bare ground at different successional stages with single vascular plants and small cushions of mosses and epigeous lichens; **2**: rims with *Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum, Carex ensifolia* ssp. *arctisibirica, Dryas punctata*; **3**: shallow troughs with *Tomentypnum nitens, Betula nana, Vaccinium uliginosum* ssp. *microphyllum*; **4**: deep troughs with *Tomentypnum nitens, Aulacomnium turgidum*.

Fig. 2: Regular cyclic type of horizontal structure in lichen-*Salix polaris*-moss polygonal community, arctic tundra subzone, Maria Pronchishcheva Bay, Taymyr (after MATVEYEVA 1979, CHERNOV & MATVEYEVA 1997). Sample plot 10x10 m^2.
1: patches of bare ground; **2**: single vascular plants and crusts of epigeous lichens; **3**: troughs with *Salix polaris*, lichens and mosses (*Hylocomium splendens* var. *alaskanum, Aulacomnium turgidum* and *Tomentypnum nitens*).

Fig. 3: Sporadically spotted type of horizontal structure in a *Dryas punctata* heath on a fell-field, arctic tundra subzone, Maria Pronchishcheva Bay, Taymyr (after MATVEYEVA 1979, CHERNOV & MATVEYEVA 1997). Sample plot 10x10 m^2.
1: *Dryas punctata*; **2**: *Salix polaris*; **3**: *Novosieversia glacialis*; **4**: moss turf of *Dicranum elongatum* and *Polytrichum strictum*; **5**: fell-fields with fruticose lichens.

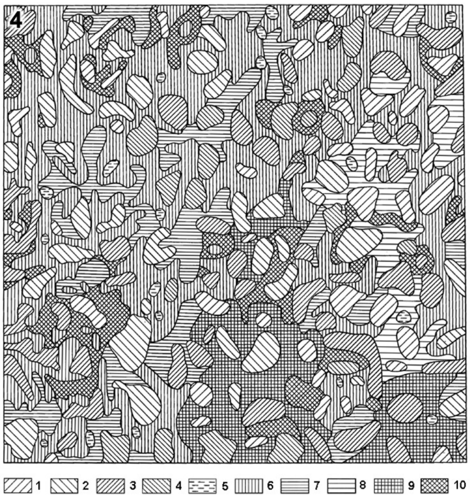
So, such mosaic structures can be considered both as a complex of phytocoenoses or as a mosaic community (MATVEYEVA 1998). In my opinion to solve this dispute is possible on conciliating rather than on evidential background. Principle of analogy may be useful in that kind of discussion. Besides frost-boils with a trinomial regular cycle structure type there are many other arctic communities like polygonal lichen-*Salix polaris*-moss communities with a net-like system of narrow (less than 10 cm) cracks filled by mosses and almost bare patches with single vascular plants in the northernmost part of the tundra zone (Fig. 2), dryad stands with the very small (0.5 m in diameter) polygons and narrow cracks (1-2 cm) on sands or with small isolated cushions or mats on stone deposits (Fig. 3), as well as complete cover with the mosaic that reflects differences in nanorelief (small hummocks and narrow troughs) in the southern tundra, that are usually described as a single unit in classification procedure. Long-term practice of making relevés in tundra phytocoenoses has convinced me to consider a heterogeneous stand with the size of elements less than 1 m^2 (or less than the area occupied and controlled by a specimen of a vascular plant, including its root system) as a single unit and classify it at the association rank. In this case, the elements of the inner mosaic would be microstands, and their composition can be recorded separately but classified at another level, say as microassociations. Such approach is supported by the size of sample plots used by phytosociologists, where essential attributes of phytocoenose, in its commonly accepted sense, entirely manifest themselves. If to use another concept, more than 100 phytocoenoses have to be distinguished within the standard sample plot of 100 m^2. At that it will be necessary to revise the concept of minimal area and the whole procedure of making relevés.

In the case when we want to get an impression of the separate elements of the mosaic in frost-boil stands, without recording many small-scale plots, we a-priory decide how many units and consequently associations will there be within the sample plot of a standard size (25 or 100 m^2). We put all species found on patches of bare ground in one list, although there is often visible differentiation in species assembling not only between the patches but also within. The same is being done for the plant cover on rims and in troughs. In case of small-hummocks, stands with two visible and well distinguished elements of nanorelief (hummocks 10-12 cm height and 15-30 cm in diameter) and troughs (15-20 cm in wide) only two separate list of species would be recorded. Each of these lists would be referred to as a separate "association".

However as associations are usually described or identified from tables with ~10 relevés of the same association, this method appears vulnerable for the description of associations.

A methodical research on Tareya IPB field station (Taymyr, Siberia) purposely to assess the variety of species abundance and composition of micro-units, showed that it was possible to distinguish 12 units of vegetation (8 for hummocks and 4 for troughs), while in southern tundra subzone 10 units (5 and 5) were recognized with similar cover (Fig. 4) (MATVEYEVA et al. 1973, MATVEYEVA & ZANOKHA 1986, see also CHERNOV & MATVEYEVA 1997, MATVEYEVA & CHERNOV 2000). Usually two or three different micro-units could be distinguished within the sample plot in non-sorted circle stand; however, in a similar study in the arctic tundra subzone in the vicinity of Maria Pronchitscheva Bay (Taymyr), we distinguished 6 types (2 on the polygon surface and 4 in troughs) (MATVEYEVA 1979, MATVEYEVA & CHERNOV 2000). Without any doubts these small-scale variations are very important in arctic landscapes. There is only the consideration of the scale of these differences.

In practice the majority of associations known at present from the arctic Eurasia, Svalbard, Greenland, Canada, and Alaska are reflect by sample plots from 4 to 100 m^2. Especially in the Arctic almost no vegetation type without any mosaic in the spatial structure will be found, but often of even smaller extension than in the case of frost-boils. Several of the small-scale communities are dominated by bryophytes and/or lichens and for cryptogams an independent synsystem already exist. Cryptogam microcommunities are usually recorded in plots sized 0.3x0.3 m^2 to 0.5x0.5 cm^2 (e.g. PAUS 1997, BÜLTMANN 2005) or even smaller (NIMIS 1981). The micro-associations can be described with the same methods as associations: with proper table work. This approach would do justice to clear ecological differences between the small-scale elements. But however the workload increases strongly.



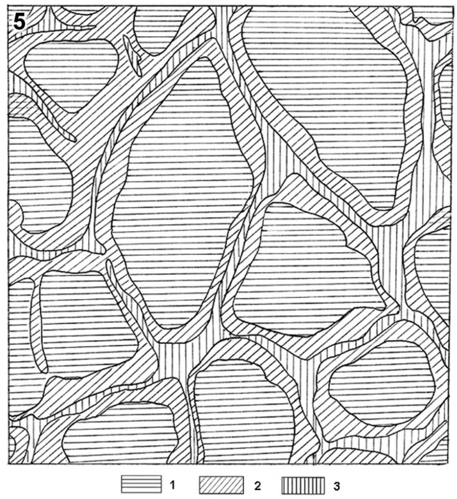


Fig. 4: Irregular mosaic structural type in a *Dicranum elongatum-Betula nana-Carex ensifolia* ssp. *arctisibirica* hummocky community, southern tundra subzone, Kresty, Taymyr (after MATVEYEVA & ZANOKHA 1986; CHERNOV & MATVEYEVA 1997).

Microstands on hummocks (1-5): **1**: *Ptilidium ciliare, Dicranum* spp.*, Aulacomnium turgidum, Vaccinium vitis idaea* ssp. *minus, Cassiope tetragona, Dryas punctata;* **2**: *Ptilidium ciliare, Dicranum* spp., *Aulacomnium turgidum, Betula nana, Salix reptans;* **3**: *Ptilidium ciliare, Dicranum* spp.*, Aulacomnium turgidum, Vaccinium vitis-idaea* ssp. *minus, V. uliginosum* spp. *microphyllum, Ledum decumbens, Betula nana;* **4**: *Aulacomnium turgidum, Dicranum* spp.*, Ptilidium ciliare, Vaccinium uliginosum* spp. *microphyllum, Ledum decumbens, Betula nana, Carex ensifolia* ssp. *arctisibirica;* **5**: *Dicranum elongatum, Sphenolobus minutus, Tritomaria quinquedentata*. Microstands in troughs (6-10): **6**: *Tomentypnum nitens, Aulacomnium turgidum, Carex ensifolia* ssp. *arctisibirica;* **7**: *Aulacomnium turgidum, Dicranum* spp.*, Betula nana;* **8**: *Ptilidium ciliare, Dicranum* spp.*, Aulacomnium turgidum, Vaccinium uliginosum* spp. *microphyllum, Ledum decumbens, Cassiope tetragona;* **9**: *Ptilidium ciliare, Aulacomnium turgidum, Dicranum* spp., *Carex ensifolia* ssp. *arctisibirica, Betula nana, Salix reptans;* **10**: *Tomentypnum nitens, Ptilidium ciliare*.

Fig. 5: Regular structural type of vegetation cover in a polygonal mire, typical tundra subzone, Tareya, Taymyr (after MATVEYEVA et al. 1973, CHERNOV & MATVEYEVA 1997). Sample plot 60x60 m^2.

1: Saturated center of polygon with relatively homogeneous sedge-cotton-grass-moss plant cover; **2**: rim with irregular mosaic structure; **3**: saturated trough with relatively homogeneous sedge-moss vegetation.

Therefore as basic units for vegetation mapping and for the assessment of the topo-sequence changes within the landscape, the mosaic plant communities, which are distributed repeatedly and regularly across the landscape and are well distinguishable and recognizable, are used, while the small-scale approach gives detailed background for ecological studies with focus on species interactions and on populations.

Alternative approach prevents the direct comparison between the small-scale units and numerous classification units available for tundra vegetation. Considering smaller or larger plot size is not a question of who is wrong and who is right, as the methods depend on the aim. The trouble is that phenomena of a different scale are named by one and the same term. But for description of associations, it should be kept in mind, that apparent homogeneity of plots is the premise for this fundamental unit.

Similar to the discussed frost-boils, regular cyclic structures are known for polygonal mires (Fig. 5), which are also characteristic for the Arctic. However, the pattern of this phenomenon is on a much larger scale. Classical polygonal mires are a combination of tetragons with the length of their sides of 10-15 m, rims of 1 m in width and about 0.5 m height, troughs of 0.5-1 m in width with their bottom level lower than that of tetragon. The homogeneous (but only at the first glance) hygrophilous sedge-cotton-grass-moss vegetation is typical for tetragons with stagnant and troughs with running water, while the mosaic dwarf-shrub-lichen-moss vegetation similar to mesic tundra by composition and structure is common on the rims. The sizes of each element of this type of heterogeneity are comparable with the standard sample plots used for mosaic mesic tundra stands, although to use an accustomed square plot is possible only for the tetragons. For both other elements normally a narrow stripe of the same width and length as the element of microrelief and its vegetation is used. We made records separately for each element and their vegetation is considered as a different syntaxon (association). But because of the feeling that it will be not enough to record species for only one tetragon, rim or trough, we added information of several apparent similar elements to the list. Again this process of making a "relevé" was preceded by a decision that vegetation of all studied tetragons (consequently rims and troughs) within the whole sometimes huge depression with thousands of such units will be referred to as one syntaxon. Based upon field experience, of both my own as well as of colleagues, I can say that methodically the process of evaluating a relevé made like this is vulnerable because the list of species includes the information from more that one plot of each element. Unfortunately we usually do not have the time in the field for the alternative making of about 10 separate relevés for each element, though this would be very desirable.

Polygonal arctic mires are a classical example of a complex of phytocoenoses. There are different approaches to their classification and typology, e.g. by size, configuration, proportion of element squares (e. g. polygonal-rim, polygonal, tetragonal, 3-5 (and more)-unit mires that are used in Russian tundra references, when all attention is paid to horizontal structure). Principally it is possible, to combine the associations into the territorial unit of sigma-association rank. However well elaborated data for such complexes are still absent for the Arctic territory.

The type of horizontal structure of frost-boil stands and polygonal mires is similar: regularly repeating modules with 3-elements. The main, possibly the only difference, is the size of the elements: decimeters in the first case (Fig. 6A) and meters in the second (Fig. 6B). The result is that while on a 100 m^2 sample plot from tens to hundreds of modules can be found for frost-boils, there is not enough space for even one module of polygonal mire. The small size of modules might support the consideration of frost-boil tundra as a mosaic stand belonging to one association, and consider polygonal mires as a complex of stands of different associations within a sigma-association.

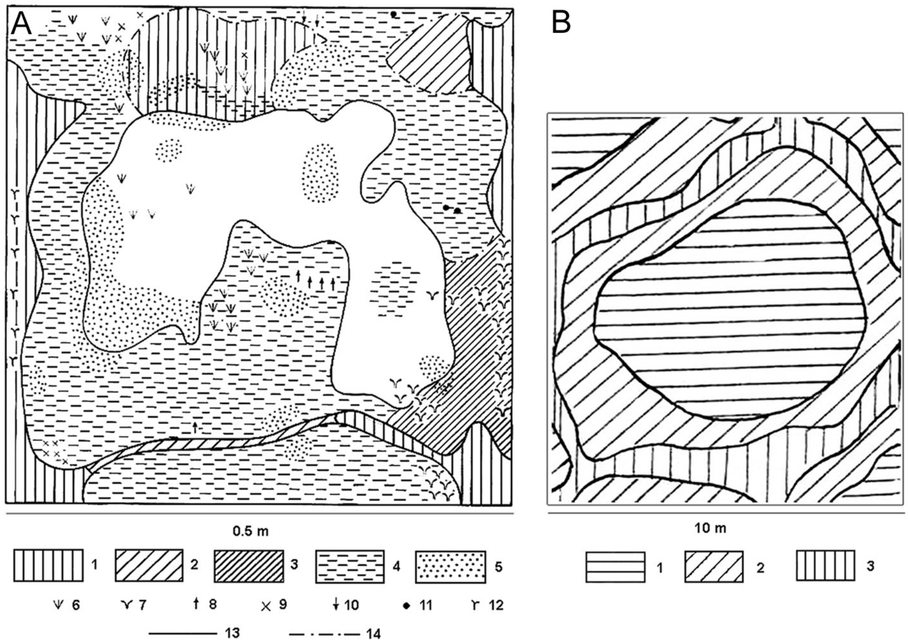


Fig. 6: Regular structural type of vegetation cover **A**: in *Dryas punctata* small-polygon heath (sample plot of 0.5x0.5 m^2) and **B**: in a polygonal mire (sample plot 10x10 m^2).

4 The concept of association in polar deserts

There is another problem that I want to discuss in this context. What to do and how to analyze and classify the extremely scarce (1-5 %) vegetation which is common within the polar desert zone. The scarcity of vegetation particularly in zonal positions on mesic habitats is one of the diagnostic features to distinguish a special type of vegetation and speak about a separate zone distinct of the tundra one (ALEKSANDROVA 1971, 1983). For such scarce plant cover Aleksandrova did not want to use the word "association" because she did not see any kind of associations between species in particular vascular plants, as often they make no influence on each other and even their roots do not have contact. She suggested the term "comitatsia" (coming from Latin comitur - accompany) instead of "association" for the basal unit of classification. Following this concept she suggested an independent parallel system of classification for polar desert scarce cover where the following terms were used*:* instead of phytocoenose nanocomplex (scarce net-like pattern of vegetation) and open stand (aggregations and semiaggregations) and instead of association consequently type of nanocomplex (named by capital letters A, B, C and D), and comitatsia and subcomitatsia (named after main species with detailed description of environment). I think however, that the term association can be applied in polar deserts, as the phytosociological use does not imply interconnection, but only stand groups similar in composition and structure (see definition by MIRKIN et al. (1989) in chapter 2). I believe there is no axiomatic difference when distinguishing and describing vegetation in polar deserts and other natural zones. The communities and syntaxa in the polar desert are not casual or unstable combination of species. On the contrary, these assemblages show regular patters in space and are well recognizable visually; they have stable and repeatable floristic compositions and structures and can be related to distinct habitats. The scarcity of plant cover itself is not a sufficient background to separate such sites of all other plant word. It is not rational to create a separate classification system with different names of hierarchical units for the cover of different closeness. Additionally, often the plant cover is not as scarce as it appears, but cryptogamic species take over, sometimes as "soil crusts" with typical, though difficult to distinguish combinations of algae, cyanobacteria, bryophytes and lichens.

There are more problems in this field of arctic ecology and vegetation science than is possible to discuss in this short message. But my aim is to direct attention towards the Arctic and to stress that there is a lot of work to do in the field of phytosociology in the Arctic.

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(* = in Russian; ** = with English summary)

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Address of the author

Dr. Nadya V. Matveyeva
Komarov Botanical Institute
Russian Academy of Science
Prof. Popov Str. 2
197376 Saint Petersburg
Russia
e-mail: nadyam@NM10185.spb.edu