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Biodiversity of plasmodial slime moulds (Myxogastria): measurement and interpretation

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Summary

For myxomycetes the understanding of their diversity and of their ecological function remains underdeveloped. Various problems in recording myxomycetes and analysis of their diversity are discussed by the examples taken from tundra, boreal, and arid areas of Russia and Kazakhstan. Recent advances in inventory of some regions of these areas are summarised. A rapid technique of moist chamber cultures can be used to obtain quantitative estimates of myxomycete species diversity and species abundance. Substrate sampling and species isolation by the moist chamber technique are indispensable for myxomycete inventory, measurement of species richness, and species abundance. General principles for the analysis of myxomycete diversity are discussed.

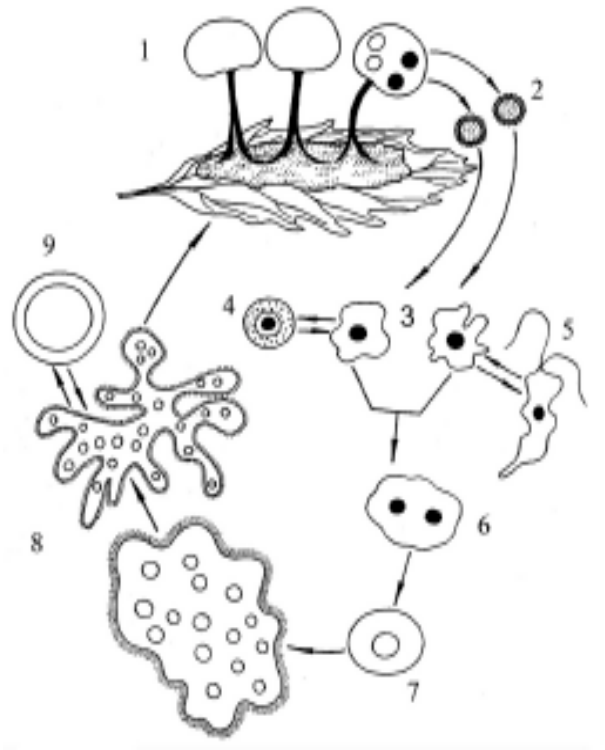
Key words: slime moulds, Mycetozoa, Myxomycetes, biodiversity, ecology, distribution, habitats

Introduction

General patterns of community structure of terrestrial macro-organisms (plants, animals, and macrofungi) are well known. Some mathematics methods are used for their studying, from which the most popular are the quantitative analysis of information diversity, species abundance, and estimation of similarity of communities (Whittaker, 1960, 1977; Chernov, 1975; Vasilevich, 1969; Pianka,1973; Pesenko, 1982; Magurran, 1988; Mukhin, 1993; Watling, 1994; Chernov and Matveeva, 1997). Similar research of micro-organisms remains very underdeveloped and has been limited, to a large extent, by methodical difficulties of their inventory (Chernov, 1997; Dobrovol'skaia et al., 1999). Considerable success here can be expected in the studies of separate groups that can be easily recorded and identified. One of them is plasmodial myxomycetes or "slime moulds" (Myxogastria).

Myxomycetes (plasmodial slime moulds), are a group of protista comprising about 1000 species (Mitchell, 2000). Myxomycetes in ecological terms are predators of bacteria, holding maintenance between bacterial and fungal decay (Madelin, 1984). The life cycle of myxomycetes includes two trophic stages: uninucleate myxoflagellates or amoebae, and a multi-nucleate plasmodium (Fig. 1). The entire plasmodium turns almost all into fruit bodies, called sporocarps (sporangia, aethalia, pseudoaethalia, or plasmodiocarps). The plasmodium is very mobile, covered only by a simple membrane, live mostly inside the substrate and can achieve macroscopic dimensions, clearly visible in the field in only one group (Physarales). The dispersal units are spores, which can be dispersed via air or insects. Various dormant stages (microcysts, sclerotia, and spores) may interrupt this cycle under harsh environmental conditions (Gray and Alexopoulos, 1968; Blackwell et al., 1984).

Unique among living organisms is the combination of single-cell stages living as true microorganisms (Feest, 1987) with sporocarps. Due to this feature the myxomycetes can be safely preserved as herbarium specimens. This peculiarity permits to accumulate data on occurrence, ecology and geography of myxomycetes into a comprehensive computer database, which will be electronically accessible to the scientific community over the Internet.



➢ **Fig. 1.** Schematic drawing of the general life cycle of the plasmodial slime moulds (myxomycetes). **1** – developing sporocarps and sporogenesis, **2** – germinating spore, **3** – myxamoeba, **4** – microcysts, **5** – swarm cell, **6, 7** – zygote formatting, **8** – plasmodium formatting and mature fan-shaped plasmodium, **9** – sclerotium (macrocysts).

These observations serve as a basis for additional research emphasising all forms of myxomycete diversity in the world, including qualitative composition, community diversity, adaptive types, and functional (ecological) groups.

Up to the present time, about 3000 (or probably more, due to under-representation of publications on biochemical aspects) papers focusing on myxomycetes inventory have been published. About 1200 of these are local or regional species lists, and about 400 describe new taxa (Schnittler and Mitchell, 2000).

Except in a very few arctic (Schinner, 1983; GØtzsche, 1984, 1989, 1990; Stephenson and Laursen, 1993, 1998; Novozhilov et al., 1998a, 1998b, 1999; Stephenson et al., 2000), temperate (Stephenson, 1988, 1989; Nannenga-Bremekamp, 1991; Ing, 1994), boreal (Schnittler and Novozhilov, 1996), desert (Blackwell and Gilbertson, 1980; Novozhilov and Goloubeva, 1986; Schnittler and Novozhilov, 1999; Schnittler, 2000), mediterranean (Lado, 1993, 1994), tropical (Alexopoulos, 1970; Alexopoulos and Saenz, 1975; Farr, 1976; Maimoni-Rodella and Gottsberger, 1980; Eliasson, 1991) communities, evaluation of species diversity is scarce and inventory is widely scattered. Russia, with its vast arctic, boreal territories, is not an exception in this respect.

In this paper we want to determine methodical approaches in study of myxomycete biodiversity and to discuss these methods on examples of diversity measurement in some local and regional myxomycete biotas of Russia and Kazakhstan.

Evaluation of α-diversity

For myxomycetes typically α-diversity indices are calculated using Shannon's formula (Shannon and Weaver 1963; Stephenson, 1988, 1989; Novozhilov et al., 1999). Species diversity (H′) = $- \sum P_i \log P_i$, where P_i is the relative abundance of a particular species (the proportion of the total number of individuals represented by species i). Maximum values for this diversity index are usually observed when there are many species with equal abundance. Values decrease with both a reduction in the number of species and an increase in abundance of a very few species. Species diversity (H′) is a function of both the number of species present (species richness) and the evenness with which individuals are distributed among these species (species equitability). Stephenson (1988) has calculated the equitability component (J′) using the formula suggested by Pielou (1975). $J' = H'/ H'_{max}$ where H'_{max} represents the maximum possible diversity for the number of species (S) present in the community (i.e., all of these species are equally abundant) and is calculated as $H'_{max} = \log S$.

Commonly employed α-diversity indices require an examination of at least three components: species richness (number of species), evenness (a gauge of how evenly the individuals are distributed among the samples), and abundance or the total number of organisms per sample (Magurran, 1988; Vasilevich, 1992a; Bills, 1995; Miller, 1995).

Measurement of species richness and species abundance

The estimation of myxomycete diversity has been limited by the difficulties in defining individuals. Myxomycetes refer to the group of organisms for which it is difficult to define a module unit in ecological research requiring evaluation of species abundance. Until the publication of a method for the enumeration of myxomycetes in soil (Feest and Madelin, 1985; Feest, 1987; Madelin, 1990), no data regarding the numbers of myxogastrid propagules in any substrate had been reported. In their papers, Feest and Madelin showed it was possible to obtain numerical data for soil using a unit (the plasmodium-forming unit, PFU) analogous to the clone-forming unit of dictyostelids used by Cavender (1989). Individual free-living plasmodium is physically discrete and functionally independent, that is the reason for describing plasmodia as individuals. Feest and Madelin (1985) used the presence or absence of plasmodia as an unambiguous indicator of the presence of myxomycetes

in the study sites. However, this method permits to estimate a total abundance of myxogastrids in the soil but is time-consuming and almost useless for estimation of abundance of separate species.

The current species concept for myxomycetes is almost entirely a morphological one, based mostly on the characters of the sporocarps (Lister, 1925; Gray and Alexopoulos, 1968; Martin and Alexopoulos, 1969; Rammeloo, 1974; Eliasson, 1977; Nannenga-Bremekamp, 1991; Keller and Eliasson, 1992; Gilert, 1996; Keller and Braun, 1999; Mitchell, 2000; Novozhilov and Goodkov, 2000). In virtually, the presence or absence of a species in diversity analysis is dependent on the appearance of the sporocarps in the study site (transect, plot,) and substrate samples. Sporocarps can be used as the module units for estimation of species richness and species abundance because they are extractable, identifiable, and quantifiable.

An advantage of this approach is the easy way to collect specimens: the colonies of sporocarps can simply be dried, glued with the substrate in small boxes like matchboxes and stored like other herbarium collection. Eliasson (1981) and Stephenson (1988) considered a "collection" as one or more (colony) sporocarps originated from a single plasmodium. In these studies, the sporocarps were regarded as separate collections if the intervening distance was at least 30 cm.

For approximate estimation of species abundance and species productivity, a simple scale was proposed by Stephenson et al. (1993), based on the proportion of a species in the total number of records (collections of sporocarps) and dividing between R – rare (<0.5%); O – occasional (0.5–1.5%); C – common (1.5–3%); A – abundant (>3%).

Spore numbers probably is more accurate measure of resource allocation and species productivity (Morton et al., 1995). Recently, Schnittler (2000) proposed to measure the spore numbers for species cultivated in the moist chamber cultures. For each species recorded, the number of spores per sporocarp was estimated, using average sporocarp size, their shape (i.e. half-globose, globose, cylindrical) and spore diameters. The dimension of these values was confirmed by counting the spore numbers of a few selected sporocarps with a counting chamber (as used for determination of erythrocyte levels). However, this method evidently is laborious for mass-analysis of species abundance. Moreover, our knowledge about myxomycete space distribution still is scarce to understand the resolving possibility of this method. It is obvious that Stephenson's scale and the calculation of the spore numbers give us only an approximate estimation of the species abundance and permit to evaluate virtually only "frequency of species" (occurrence).

About 1–3 % of the species form rather large (cm-range) clustered fructifications called aethalia or pseudaethalia, the majority (60–80 %) of the species has colonies of fragile, single sporocarps in the mm-range, the remaining 20–40 % show minute fructifications less than 0.5 mm in size. The latter are usually not observed in the field. The percentage of these size-classes varies widely between climatic zones as well as between ecological groups, with a tendency to have more minute forms in harsh, especially dry, environments.

As an obvious consequence, in additional to the field collection substrate sampling and the moist chamber technique has usually applied for evaluation of α-diversity and the ecological analysis of myxomycete community structure (Härkönen, 1977; Stephenson, 1985, 1988; Novozhilov, 1988; Schnittler, 2000).

Moist chamber technique for assessing species richness and species abundance in substrata (microhabitats)

Myxomycetes live mostly very hidden, but are present in all habitats with decaying organic material, ranging from tropical rainforests over deserts up to the arctic tundra. Numerous research of myxomycete diversity in different microhabitats (substrata) show that species composition varies considerably on the certain types of substrata (e.g. on the bark of trees). However, the set of species that dominate in a certain sample of substrate (microhabitat) is rather limited. In every substrate sample usually 1–4 species comprise more than 30–50% of all group ("potential dominants"). With the help of moist chamber technique (Gilbert and Martin, 1933) these dominants are revealed rather easily and definitely, which gives an opportunity to carry out mass analysis and receive statistically true results. This simple method permits to evaluate α-diversity and abundance as "frequency of species" and determinate the "nucleus" of species diversity.

The respective moist chamber technique does not need sterile conditions and is easy to carry out. It requires nothing more than Petri dishes, filter or even toilette paper and a good dissecting microscope for checking. The cultures run up to 2 months, for coprophilous forms sometimes longer (up to 3–4 months). To reveal more ecological data with less effort, the following slight modifications are proposed:

- pooling of bark scales (about 3 to 8 scales of 1–2 cm size for one tree or shrub, only including the non-living layer, with sampling 5–10 trees from the same habitat (equal tree species, height, and light exposition);
- measuring of the pH in the moist chamber after 2–5 days, ideally with a solid state probe (substrata often show buffering capacity, therefore being stable for a longer period);
- optionally, for statistical evaluations the number of sporocarps in a moist chamber can be estimated.

For moist chambers, substrate pieces are densely placed on filter paper in Petri dishes (63.6 cm^2), with the pieces touching but not overlapping each other and with the outer side of bark uppermost. Cultures are watered

with distilled water adjusted to pH 7.0 and maintained up to 2 months under diffuse daylight and at room temperature (22–23 °C). At five times (days 2, 6, 11, 21 and 40 after start) the chambers are checked with a high-magnification dissecting microscope. Mature fructifications are boxed, and sporocarps of minute species are immediately preserved in polyvinyl lactophenol or glycerol gelatine, when calcareous structures are present in sporocarps.

It currently for all ecological analyses, one or more of the following measures are applied: (i) number of records per species, in this case the occurrence of one species in one moist chamber constitutes a collection (record), (ii) absolute abundance (number of sporocarps for one species in one moist chamber culture) and (iii) weighted abundance, calculated by dividing the absolute number of sporocarps recorded in a particular moist chamber through the mean value from all moist chambers with this species (Schnittler, 2000).

Consequently, the sum of all weighted abundances for all cultures with a species is equal to the number of records for this species.

Limitation of inventory studies and completeness of evaluation of species richness

The examples above demonstrate how many factors can influence on spatial distribution of myxomycetes in the biotope. The spatial distribution of myxomycetes is reflected in the species/sample number curve. At present time the problem "number species/area" is studied insufficiently for myxomycetes and invites further investigations.

Our experience shows that the completeness of the evaluation of species richness depends on the number of samples for moist chamber culture and from their distribution in the space. The sample plot 0.1 ha (1000 sq. m) is typically sufficient. The bootstrap analysis shows a steep increase in the mean cumulated number of recorded species over the first 50 samples putted in Petri dish. In virtually the curve "species/sample" shows that 30 substrate samples (60 square cm each) are typically sufficient to record all of the more common species.

According to the experience of the authors, a one-season project gives a comparable and fairly complete species list for an area, although annual shifts in the species abundance is known for many species as it was shown below. With recording all colonies and describing the microhabitats, in a wooded area of temperate or boreal zone an experienced collector can observe up to 50–70 developments during a field day (about 6 hours), occasionally much more if mass fructifications occur. For example with about 5 major vegetation types per area, and half a day for each, four field surveys of 3 to 4 days each give a fairly complete picture of the species inventory.

As in most protista, species determination is time-consuming and requires a good compound as well as a dissecting microscope. The moist chambers are the most time-consuming part, running up to 2 monthes and needing regularly checks from the 5th day on. About thirty minutes per one moist chamber culture have to be invested, considering also mounting of the often minute specimens on permanent slides. Although not very costly in terms of equipment, a well-done regional survey requires about 2–4 months of pure working time. In special environments, like arid areas, more time may be necessary due to the fact that almost all species have to be detected by moist chambers.

The majority of the species having large sporocarps (aethalium, plasmodiocarps) typically does not develop in the moist chamber culture. For this reason this technique can be used as only an additional method for evaluation of myxomycete diversity. The interpretation of moist chamber detection has to be done cautiously, because spores of species regularly not occurring in the region may be trapped and develop into fructifications. Colonies including numerous sporocarps, developing in a short time, point to a microcyst population (a dormant stage) occurring naturally.

Ecological groups of myxomycetes and distribution of myxomycetes in biotope

The role of the biotope and microhabitat (substrate) are considerable factors that influence the myxomycete distribution. Literature and our data show that the following 4 substrate types are the most different from each other as the myxomycetes environment and have different adaptive ecological groups of myxomycetes:

1. *Lignicolous myxomycetes* (on coarse decaying wood debris of all stages and sizes): the largest group, including 30–70 % of the total species number, with a higher proportion in temperate and boreal zones; 70–80 % of these slime moulds have macroscopical size (mm-range), relatively easy to collect, moist chambers technique works not for all species; often sharply defined sporulation peaks for certain species especially in temperate zones, here mid-summer to late autumn (Eliasson and Strid, 1976).
2. *Corticolous myxomycetes* (inhabiting the bark of living trees and shrubs): 20–40, up to 80 % (in deserts) of the total species number; almost all minute forms, making moist chamber technique indispensable which gives good and stable results in this group; can be studied throughout the year (Gilbert and Martin, 1933; Keller and Brooks, 1976, 1977; Härkönen, 1977, 1978; Schnittler and Novozhilov, 1999).
3. *Soil and litter species* (living in the upper soil layer and fructificating on all kinds of herbaceous or other small-sized plant refuse): 20–70 % of the species to expect, mainly Physarales, with much higher proportion in the tropics; mostly of macroscopic size but difficult to find in the field, for smaller forms moist chamber techniques works reasonable; often pronounced sporulation peaks in temperate zone

mid-summer to early autumn (Keller and Brooks, 1971; Härkönen, 1981)

4. *Coprohilous myxomycetes* (on dung of herbivores mammals and birds): a small group with only a few specialised species typically in higher abundance in arid areas, on dung with basic pH; moist chambers running up to 4 months are necessary for detection; seldom found in the field, but detectable throughout the year by moist chamber method (Eliasson and Lundqvist, 1979; Cox, 1981; Eliasson and Keller, 1999).

Some species are hardly related to concrete substrate group. These species associated with rather specific habitats and their distribution strongly depends from microclimate conditions in habitats.

Bryophilous or moss-inhabiting myxomycetes (associated with mosses, but more probably with slime algae, on wood or rocks provided with trickling water in humid ravines). This group includes less than 5 %, mostly macroscopic forms, temperate and boreal zones preferentially with sporulation peak in late autumn, and can be collected in the field only, moist chamber techniques almost always fails to work. Typically small forms (e.g. *Barbeyella minutissima*, *Colloderma oculatum*) have to be collected with lenses or dissecting microscops in the field.

Nivicolous myxomycetes (on plant refuse near the melting snow, preferentially in higher mountains with high snow cover in winter). Almost all nivicolous species are more or less conspicuous, and easy to collected for an experienced worker (Neubert et al., 1995). They occur very locally but often with mass fructifications with sporulation peak near snow melting. For nivicolous myxomycetes the relationship of the percentage of solid precipitation to monthly averages of air temperature and humidity is a very important factor (Kowalski, 1975).

The moist chamber technique gives insufficient results for briophilous and nivicolous species.

Estimation of β-diversity and niche breadth (NB)

It is known that one of the approach of β-diversity study is the estimation of species composition along the gradient of environment and comparison of species composition of different communities and habitats (Wittaker, 1960; MacArthur, 1965; Wilson, Mohler, 1983; Vasilevich, 1992b). Since the discovering of the right microhabitat is the key for the stable detection of the species, this could become the most important tool for enhancing our knowledge about biodiversity of myxomycetes. With the aim to gather as much as possible data about microhabitat a standardised, modular-build description system was used (Schnittler et al., 1996).

For example estimation of niche breadth (NB) on the basis of moist chamber data was carried out in the research of myxomycetes of upland forests of south-western Virginia (Stephenson, 1988) and Kazakh deserts (Schnittler 2000). Values for NB were calculated using the formula $NB = 1/s\ \Sigma P_{ij}^{\ 2}$, where s is the number of states for the environmental (microhabitat) parameter defining a niche dimension, and P_{ij} the proportion of species *i* associated with state *j* divided by the total abundance of species *i* across all states (Feinsinger et al., 1981). As abundance measures, either records or total abundances were used. In both cases, values range from 1/s (all individuals of one species are associated with one resource state) to 1.0 (equal numbers of individuals are associated with each resource state). In the same manner, niche overlap (NO) was computed, using the symmetrical index $NO_{ik} = \Sigma P_{ij} P_{ik}/\mathrm{sqrt}(\Sigma P_{ij}^{\ 2})\ (\Sigma P_{ik}^{\ 2})$, with P_{ij} and P_{ik} as the proportions of the *i*th resource state by the *j*th and *k*th species, respectively (Levins, 1968; Pianka 1973). Values for niche overlap range from 0 to 1 too.

For analysis of myxomycete associations, the Cole (1949) index of interspecific association and its standard error was computed. It is based on a 2 x 2 contingency table for presence and absence of a pair of species in one moist chamber, ranging from –1 (the species never occur together) to 1 (the species occur always together). With a chi-square test the significance level of deviations between observed association frequencies and those expected by chance was determined.

Inherent problems in estimating species diversity: seasonality and features of microhabitats

Numerous studies of myxomycetes have shown that there are often dramatic shifts in the appearance of sporocarps from the fall to the spring in boreal and temperate areas. The inventory of nivicolous species is a good example of this shift. Until recently, nivicolous species were not found in Russia. Intensive studies in the Khibine mountains in spring (Novozhilov and Schnittler, 1997) showed that this ecological group is abundant in this area. This region provides good conditions for cryophilous-nivicole litter myxomycetes. This ecological group can be separated into two subgroups, based on phenology and habitat requirements. The first subgroup contains the 'true' nivicolous species: *Diacheopsis effusa*, *Diderma niveum*, the *Lepidoderma*, and *Lamproderma* species (with the exception of *Lamproderma sauteri*). According to Schinner (1981, 1983), their habitat requirements can be characterized as follows: open ground, a more or less thick layer of herbaceous plant refuse, high snow cover in winter (may be for providing a dormant period, or simply for protection from hard frosts), and an exposition, providing enough water from the melting snow to keep the substrate wet over 2–3 weeks, relatively high daily temperatures (for plasmodium growth), alternating with lower night temperatures (possibly for inducing fructification). These habitats occur only very locally in the Khibine mountains, because conditions like open ground, heavy snow pack in winter and plants providing much herbaceous biomass are somewhat contradictory. Only a short time after snow

melting the ground is open and able to warm up during the day. Then the plants shoot very quickly and form a dense cover shadowing the ground. Therefore, the developing window for these species is small, in the Khibine Mountains probably the second half of June. We were already slightly too late and did not found fresh sporocarps of the above-mentioned species. From the slopes around the Kirovsk Botanical Garden obviously the best place was the avalanche gutter described above, wet enough for tall perennials and with high snow cover hindering tree growth.

Surprisingly, also in the plains of the valley grounds species of this group were found, especially on places with high umbellifers. The reason may be frequent changes of weather in the area. Probably the man-made meadows can serve as a secondary facultative habitat.

The second group of species is more cryophilous, growing predominantly in summer under cool and wet conditions on litter, especially in shady woodland. *Physarum cinereum*, *Didymium deplanatum* and *D. dubium*, perhaps *Trichia alpina* and *Lamproderma sauteri*, can be placed here. Their ecological requirements may be summarised as: shady ground, high moisture over a longer period (about two months) a more or less thick layer of herbaceous plant refuse.

Such habitats are common in the valleys of the Khibine mountains, also indicated by the abundance of *Physarum cinereum*. Hollow, collapsed previous year's stems of *Cicerbita alpina* or *Cirsium heterophyllum* form the most important substrate. The microclimate is moist and cold; here we found fresh sporocarps during the investigation time (July), especially of *Physarum cinereum* and *Lamproderma sauteri*.

Somewhat different are the microhabitats of two species. *Trichia alpina* was found predominantly on shaded leafy litter (especially rowan) between small boulders. Another exception was *Lamproderma sauteri*, preferring moss layers on rocks and boulders with running water. An extreme example was a place in the alpine tundra, a stony depression on a NO-exposed slope. On the ground floor there was a two meter pack of big granite stones; their sides were covered with mosses, mainly the arctic-alpine liverwort *Gymnomitrium concinnatum* (Lightf.) Corda. Under the stones runs water from a nearby snowfield. *Lamproderma sauteri* seems to be the most cryophilous species, which does not need higher temperature in any phase of its development. Also the other growth places were very shady, often almost hidden, e.g. moss-covered rocks under tree roots.

A shift in species composition and diversity can also occur from year to year. For example the effects of seasonality was the occurrence of *Colloderma oculatum* in moss communities on rocks on Srednii island of Keret Archipelago in the White Sea (Schnittler and Novozhilov, 1996). There are frequent vertical steps in the granite rocks on the island, which separate the damp woodlands from the dry pine-lichen community. If water trickles over for a long period of time, a thin cover of liverworts and blue-green algae is formed, especially under big cushions of mosses. During the summer 1993, these moss and liverworts layers provided a very good microhabitat for *Colloderma oculatum* and *Lepidoderma tigrinum*, especially in eastern exposure on very thin (less than 0.5 cm), slimy layers of liverworts, covered with a water film. This microhabitat is found at 1–3 m height on rocks that are provided with trickling water. The huge colonies, especially of *Colloderma oculatum*, suggest that moss layers are a normal microhabitat. The communities are nevertheless unstable, and in the exceptionally warm summer of 1994, when there was no trickling water, only dry scraps of dead liverworts were found on these rocks.

Other example of a shift in species composition in inventory studies is *Barbeyella minutissima*. The minute myxomycete *Barbeyella minutissima*, described by Meylan (1914) from the Swiss Jura Mountains, was long thought to be exceedingly rare. Stephenson and Studlar (1985) considered *Barbeyella* as strongly bryophilous. The pattern of occurrence during the year shows that in southern regions *Barbeyella* fruits in the winter, whereas in more northern regions the fructification peak occurs in September to early October (eastern North America) or mid-October (Germany). Observation in the Northern Ammergauer Alps (Schnittler and Novozhilov, 1998; Schnittler et al., 2000) provide evidence that *Barbeyella* can develop at temperatures between 0 and 10 °C. These collections were made after a first period of frost in the year, followed by a couple of warmer autumn days. Only the most cool and shady parts of the narrow ravines investigated in this study harboured *Barbeyella*. Observations and collections made in a narrow and cool valley system appear to add yet another aspect to the ecology of this myxomycete – the association with unicellular algae, which form a slime layer providing continuous moisture as well as a microenvironment suitable for microbial growth. In five of seven collections of *Barbeyella*, algae were clearly visible, forming a thin, slimy layer on the wood surface.

General principles for analyses of myxomycete diversity

1) Size and comparability of the area. To provide data comparable with those on other regions, study areas should be of minimal size, but include all major vegetation types of a region. In general, the simplest way to representative data might be to choose only a certain number of areas limited in size, e.g. in National Parks, reservations or near biological station of Universities which can be surveyed for a period of years within other activities and by local people.
2) Thoroughness of investigation. To provide the full species inventory, a systematic survey of all suitable microhabitats should be carried out, together with

extensive substrate sampling. Substrate sampling and detection by the moist chamber method is indispensable. Checklists of myxomycetes should be considered incomplete unless the list includes a systematic examination of diversity by moist chamber indirect isolation method.

3) Repeated survey. To ensure the recording of all phenological groups, more than one field survey in a year is recommended. Four surveys are optimal (spring, midsummer, early and late autumn).
4) Ecological niches. To reveal the microhabitat requirements of the species, as much as possible data about the microhabitat should be gathered besides collecting of specimens of substrata for moist chamber cultures (see above).

As shown for the commoner species, primarily substrate features, with pH, texture of bark, and probably water retention as the most important factors determinate ecological niches.

The practical examples of estimation and measurement of local and regional species diversity

The foregoing methodical approaches and general principles of inventory studies of myxomycetes were used in study of myxomycete biota of Russia and in some neighbouring countries.

According to our database, 326 species are reported from this area. The main biomes studied are: tundra and forest-tundra (Yamal peninsula, Taimyr peninsula), taiga or boreal coniferous forests (Tver' province, Leningrad province, Karelia, Kola Peninsula, Altai Krai, and Ural Mountains), deciduous temperate forests (Northern Caucase, Krasnodarskii Krai, and Vladivostok province), mediterranean xerophilic forests "shibliak" (Crimea peninsula), forest steppe and steppe (Voronezh and Volgograd provinces), and desert (Volgograd, Astrakhan' provinces, Kalmykia, and Mangyshlak peninsula in Kazakhstan). Some study areas where the most comprehensive and intensive of ecological studies of Myxomycetes have been carried out are shown on the Fig. 2. and summarised in tables 1, 2.

In the myxomycete biotas of different natural zones of Russia there are different sets of main ecological groups. For example in extreme conditions of high-latitude and arid regions not only the reduction of species numbers takes place but also the simplification and elimination of some groups (for example lignicolous K-strategs with large phaneroplasmodium of Physarales, (see table 1). Corticolous myxomycetes adapted to the life in the bark of trees and bushes reflect the climate conditions to a greater extent than the habitants of litter, dung, and decayed wood. In spite of their wide distribution, certain groups of myxomycetes have areas of mass reproduction. The structure of desert corticolous myxomycetes is the simplest one. The *Echinostelium*, *Licea*, and *Perichaena* dominate here. In the steppe and forest steppe, there dominate *Echinostelium minutum*, *Macbrideola cornea*. In temperate deciduous forests, there dominate *Macbrideola cornea*, *Cribraria violacea*, *Physarum decipiens*, and *Licea operculata*. *Arcyria pomiformis*, *Macbrideola cornea*, *M. synsporus*, *Echinostelium colliculosum*, and *Licea kleistobolus* dominate in Crimea "shibliak" communities. Considerable differences between southern taiga and northern taiga are not observed. *E. minutum*, *Paradiacheopsis fimbriata*, *Licea parasitica*, and *L. minima* dominate here.

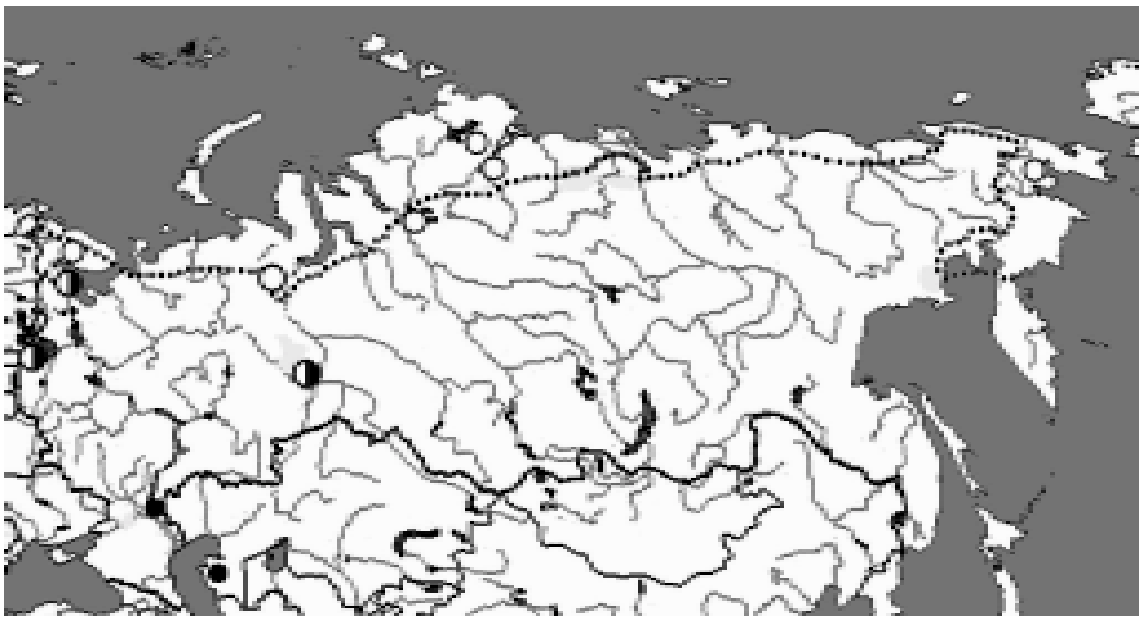


Fig. 2. Location map showing the main collecting areas for plasmodial slime moulds in Russia and Kazakhstan. A dotted line indicates the northern limit of boreal forests according to Word Atlas "Resources and Environment" (1998). White circles indicate the collecting areas in tundra and forest tundra biomes, half-black ones – boreal forest (taiga) biomes, black ones – desert and steppe biomes.

Table 1. Occurrence of myxomycetes in tundra, boreal, and desert zones of Russia and Kazakhstan.

(Explain remarks: the number before a slash indicates the total of all specimens collected in the field, whereas the number after a slash indicates the total of all specimens obtained from moist chambers; abbreviations used for the study areas are: KM = Khibine Mountains, PU = Polar Ural, PP = Plateau Putorana, TP = Taimyr Peninsula, CH = Chukchi Peninsula, RK = Russian northern Karelia, LE = Leningrad province, SV = Sverdlovsk province, VO = Volgograd province, KZ = Mangyshlak Peninsula; study areas are situated in: tundra zone and forest tundra, (KM, PU, PP, TP, CH); boreal zone, taiga (RK, LE, SV); steppe and cold desert zones, intrazonal vegetation in riparian and wash woodlands (VO); central and southern desert, desert vegetation on the eastern shore of the Caspean Sea in the Mangyshlak Peninsula (KZ); widely distributed species (recorded from more than 4 study areas) are listed in bold; species with records from nivicolous situations are indicated with an asterisk).

Myxomycetes	KM	PU	PP	TP	CH	RK	LE	SV	VO	KZ
Amaurochaeta atra							**3/–**	**2/–**		
Arcyodes incarnata							**4/–**			
Arcyodes incarnata	**1/–**			**–/1**	**1/1**				**2/–**	
Arcyria cinerea	**1/5**	**–/13**	**1/19**	**–/23**	**2/12**	**–/9**	**58/7**	**12/2**	**21/–**	
Arcyria denudata			**–/1**	**–/1**		**1/–**	**8/–**	**1/–**	**10/–**	
Arcyria ferruginea						**1/–**	**1/–**	**6/–**		
Arcyria helvetica								**1/–**		
Arcyria incarnata		**1/1**	**1/5**	**1/9**	**2/7**	**11/1**	**5/–**	**33/1**	**23/–**	
Arcyria insignis							**1/–**	**1/–**	**2/–**	
Arcyria magna						**1/–**				
Arcyria minuta										**–/1**
Arcyria obvelata	**–/1**		**1/1**			**3/–**	**5/–**	**9/–**	**9/–**	
Arcyria oerstedtii									**1/–**	
Arcyria pomiformis	**1/–**		**–/1**	**–/2**	**1/1**	**5/–**	**3/–**	**47/6**	**9/–**	
Arcyria stipata							**1/–**	**5/–**		
Badhamia affinis							**1/–**			
Badhamia capsulifera							**4/–**		**1/–**	
Badhamia panicea						**1/–**	**1/–**		**3/–**	
Badhamia foliicola						**1/–**	**1/–**		**1/–**	
Badhamia macrocarpa							**3/–**	**3/–**	**1/–**	
Badhamia obovata							**1/–**			
Badhamia populina						**1/–**				
Badhamia utricularis							**5/–**	**3/–**		
Brefeldia maxima							**1/–**			
Calomyxa metallica		**–/3**		**–/1**	**–/3**	**1/–**		**2/–**		
Ceratiomyxa fruticulosa	**3/–**	**–/1**	**2/3**	**1/–**	**3/–**	**3/–**	**10/–**	**34/–**	**9/–**	
Clastoderma debaryanum						**2/–**	**1/–**	**7/–**		
Colloderma oculatum						**13/–**	**1/–**			
Comatricha* cf. *rigidereta								**1/–**		
Comatricha dictyospora						**1/–**				
Comatricha elegans						**9/–**	**1/–**	**7/–**		
Comatricha irregularis								**8/–**		
Comatricha laxa		**–/1**	**–/1**		**1/1**	**9/–**	**2/–**	**13/–**	**1/–**	
Comatricha longa							**2/–**			
Comatricha nigra	**2/1**	**2/3**	**4/7**	**1/35**	**2/10**	**12/2**	**9/–**	**60/1**	**15/–**	
Comatricha pulchella				**–/1**			**4/–**	**7/–**	**4/–**	**–/6**
Comatricha tenerrima							**1/–**	**1/–**		
Comatricha typhoides					**2/1**	**4/–**	**8/–**	**8/–**	**2/–**	
Craterium aureum								**1/–**	**1/–**	
Craterium leucocephalum		**2/–**		**–/1**		**6/–**	**5/–**	**1/–**	**11/–**	
Craterium minutum							**3/–**			
Cribraria argillacea						**7/–**	**5/–**	**6/–**	**2/–**	

Table 1. Continuation

Cribraria aurantiaca	**1/–**				**7/–**	**6/–**	**5/–**	**3/–**	
Cribraria* cf. *atrofusca				**–/1**					
Cribraria intricata							**2/–**		
Cribraria languescens							**3/–**	**2/–**	
Cribraria macrocarpa						**2/–**	**3/–**		
Cribraria microcarpa				**–/4**	**8/–**				
Cribraria minutissima					**2/–**				
Cribraria piriformis						**1/–**	**1/–**		
Cribraria piriformis						**1/–**			
Cribraria purpurea					**3/–**	**3/–**	**5/–**		
Cribraria rufa					**2/–**	**2/–**	**21/–**		
Cribraria splendens					**1/–**	**4/–**	**3/–**		
Cribraria tenella						**1/–**	**1/–**	**1/–**	
Cribraria violacea				**–/4**			**3/–**	**1/–**	
Cribraria vulgaris				**–/1**	**4/–**		**1/–**		
Diachea leucopodia						**2/–**		**1/–**	
Diachea splendens						**1/–**			
***Diacheopsis effusa* ***	**1/–**								
***Diacheopsis* sp. A**					**1/–**				
***Diacheopsis* sp. B**								**1/–**	
Dianema corticatum					**8/–**			**1/–**	
Dictydiaethalium plumbeum		**1/–**			**2/–**		**1/–**		
Dictydium cancellatum	**1/–**				**2/–**	**10/–**	**23/–**	**12/–**	
Diderma asteroides					**1/–**				
Diderma* cf. *simplex							**1/–**		
Diderma deplanatum	**2/–**					**2/–**			
Diderma floriforme						**1/–**			
Diderma globosum					**11/–**	**3/–**			
Diderma hemisphaericum						**3/–**			
Diderma montanum						**2/–**			
***Diderma niveum* ***	**1/–**				**1/–**	**2/–**			
Diderma radiatum				**1/–**	**1/–**	**6/–**	**2/–**	**8/–**	
Diderma sauteri							**1/–**		
***Diderma* sp. A**									
Diderma spumarioides							**1/–**		
Diderma trevelyani						**6/–**	**2/–**		
***Didymium anellus* agg.**							**1/–**		**–/24**
Didymium annulisporum									**–/1**
Didymium clavus		**3/1**			**1/–**		**3/–**	**2/–**	**1/–**
Didymium crustaceum					**–/1**		**3/–**		**7/–**
Didymium difforme	**–/1**			**–/1**	**1/1**	**4/1**	**4/–**	**4/–**		**–/12**
***Didymium dubium* ***	**3/–**		**4/1**	**–/2**		**1/1**	**2/–**		**1/–**
Didymium iridis								**1/–**	
Didymium melanospermum		**–/2**		**–/1**	**–/1**	**6/–**	**4/–**	**4/–**	**2/–**
Didymium minus								**3/–**	**4/–**
Didymium nigripes					**2/–**	**2/–**	**5/–**	**3/–**	**1/–**
Didymium squamulosum				**–/2**		**3/–**	**6/–**		**21/–**	**8/3**
Echinostelium arboreum									**–/16**
Echinostelium brooksii			**–/1**	**–/7**					
Echinostelium colliculosum									**–/45**
Echinostelium minutum	**–/5**	**–/10**	**–/15**	**–/45**	**–/21**	**–/6**	**–/4**	**1/22**		**–/3**
Enerthema papillatum		**–/4**	**–/1**	**1/4**	**1/1**	**9/2**	**7/–**	**39/–**	**1/–**	

Table 1. Continuation

Enteridium intermedium							1/–			
Enteridium lycoperdon					1/–	1/–	2/–	3/–	1/–	
Enteridium oliviaceum					1/–					
Enteridium splendens var. ***juranum***			3/–			1/–	1/–	2/–	1/–	
Fuligo cinerea							1/–		1/–	–/2
Fuligo leviderma						1/–				
Fuligo septica						3/–	12/–	23/–		
Hemitrichia abietina				1/1				1/–		
Hemitrichia clavata	2/–					1/–	7/–	12/–	1/–	
Hemitrichia intorta							1/–			
Hemitrichia karstenii									1/–	
Hemitrichia serpula							4/–	1/–		
Lamproderma arcyrioides*	5/–				2/–		3/–			
Lamproderma arcyrionema						3/–	4/–	7/–	6/–	
Lamproderma carestiae*	1/–									
Lamproderma columbinum						7/–	5/–			
Lamproderma fuscatum*	1/–									
Lamproderma qulielmae						2/–				
Lamproderma sauteri*	12/–		3/–			10/–				
Lamproderma scintillans							2/–		2/–	
Leocarpus fragilis	1/–	2/–		–/1	3/2	2/–	7/–	6/–		
Lepidoderma aggregatum*	3/–									
Lepidoderma carestianum*					3/–		1/–			
Lepidoderma granuliferum*	4/–									
Lepidoderma tigrinum						2/–	3/–			
Licea biforis								1/–		–/1
Licea castanea						1/–	1/–			
Licea* cf. *belmontiana		–/3	–/4	–/6						
Licea denudescens										–/2
Licea kleistobolus		–/1		–/6	–/1	–/4	–/2			–/21
Licea marginata							1/–			
Licea minima	2/–	–/3	–/4	–/19	–/3	13/1	–/5	6/8		
Licea operculata		–/9			–/1		–/2			
Licea parasitica		–/10			–/3	–/1	–/3			
Licea pusilla							–/1			
***Licea* sp. A**					–/1					
***Licea* sp. B**										–/1
Licea testudinacea			–/5	–/15				–/1		
Licea variabilis		–/1				6/–	–/4	2/–		
Lindbladia tubulina						2/–	2/–			
Lycogala epidendrum	1/–	2/–	2/–	2/–	4/–	4/–	11/–	17/–	12/–	
Lycogala exiguum							1/–			
Lycogala flavofuscum							3/–		1/–	
Macbrideola cornea		–/2		–/3		–/2	1/–	–/1		
Macbrideola oblonga										–/25
Metatrichia floriformis							1/–			
Metatrichia vesparium							6/–	21/–	5/–	
Mucilago crustacea		1/–		1/–	13/–		7/–		11/–	
Oligonema flavidum							1/–		6/–	
Oligonema fulvum										
Oligonema schweinitzii							1/–		1/–	

Table 1. Continuation

Paradiacheopsis cribrata				**–/2**				**–/2**		**–/4**
Paradiacheopsis fimbriata		**–/6**		**–/20**	**–/3**	**–/3**	**–/3**	**3/36**		
Paradiacheopsis solitaria						**–/1**	**–/1**	**–/1**		
Perichaena chrysosperma		**–/2**	**–/1**	**–/5**	**–/3**	**–/5**	**–/2**		**3/–**	
Perichaena corticalis						**1/2**	**3/–**	**6/–**	**1/–**	**–/15**
Perichaena depressa				**–/2**	**1/3**		**1/–**	**1/–**		**–/3**
Perichaena liceoides					**–/2**					**–/1**
Perichaena minor						**–/2**		**–/1**		
Perichaena taimyriensis				**–/2**						
Perichaena vermicularis			**1/–**	**–/4**			**1/–**		**4/–**	**–/42**
Perichena quadrata									**1/–**	
Physarum alpinum*							**1/–**	**1/–**		
Physarum auriscalpium						**1/–**	**1/–**			
Physarum bitectum						**3/–**	**3/–**			
Physarum bivalve	**–/2**		**–/1**	**–/6**	**–/11**	**2/–**	**5/–**		**2/–**	
Physarum* cf. *carneum						**1/–**				
Physarum* cf. *confertum										**–/6**
Physarum conglomeratum							**3/–**	**1/–**	**2/–**	
Physarum leucopus						**1/–**	**3/–**	**10/–**		
Physarum* cf. *nudum			**–/1**	**–/4**			**/1**			
Physarum cinereum	**16/–**		**1/–**		**2/1**	**2/–**	**7/–**		**2/–**	**–/1**
Physarum citrinum								**1/–**		
Physarum compressum							**5/–**			
Physarum contextum						**9/–**	**3/–**			
Physarum decipiens						**–/4**	**1/–**	**–/1**		**–/1**
Physarum didermoides							**1/–**			**–/1**
Physarum famintzinii										
Physarum flavicomum							**1/–**		**1/–**	
Physarum globuliferum						**2/–**	**1/–**	**5/–**		
Physarum leucophaeum	**1/–**	**–/1**				**4/3**	**9/–**	**4/–**	**8/–**	
Physarum notabile							**1/–**	**3/–**	**1/–**	**2/82**
Physarum nutans		**2/3**	**–/1**	**2/2**	**3/6**	**7/–**	**12/–**	**70/–**	**10/–**	
Physarum oblatum		**–/2**		**–/2**	**–/2**	**2/4**	**1/–**	**1/–**		
Physarum pezizoideum							**1/–**		**6/–**	
Physarum psitacinum								**2/–**		
Physarum pulcherrimum							**1/–**			
Physarum pulcherripes								**8/–**		
Physarum rubiginosum							**1/–**			
Physarum serpula							**1/–**	**1/–**		
***Physarum* sp. A**		**–/2**								
Physarum straminipes								**6/–**	**7/–**	
Physarum sulphureum							**3/–**			
Physarum tenerum							**1/–**			
Physarum vernum							**1/–**	**1/–**		
Physarum virescens	**1/–**					**1/–**	**4/–**		**3/–**	
Physarum viride	**2/–**	**1/–**		**–/1**	**2/–**	**14/1**	**7/–**	**12/–**	**3/–**	
Protophysarum phloiogenum										**–/3**
Prototrichia metallica				**–/4**	**1/–**		**1/–**	**1/–**		
Stemonitis axifera	**–/1**	**3/–**	**2/–**		**2/1**	**5/1**	**9/–**	**16/–**	**16/–**	
Stemonitis fusca		**1/–**			**1/–**	**4/2**	**4/–**	**27/–**	**12/–**	
Stemonitis herbatica								**1/–**		
Stemonitis hyperopta	**1/–**					**3/–**		**4/–**	**3/–**	

Table 1. Continuation

Stemonitis nigrescens						**1/–**	**1/–**		**1/–**	
Stemonitis pallida							**2/–**			
Stemonitis smithii	**1/–**		**1/–**				**4/–**	**6/–**	**1/–**	
***Stemonitis* sp.**		**–/1**								
Stemonitis splendens							**2/–**		**19/–**	
Stemonitis virginiensis	**–/1**					**–/1**	**1/–**			**–/1**
Stemonitopsis microspora								**1/–**		
Stemonitopsis subcaespitosa			**–/2**							
Symphytocarpus confluens						**2/–**	**1/–**			
Symphytocarpus flaccidus						**2/1**		**2/–**		
Trichia alpina *	**18/1**						**1/–**			
Trichia botrytis	**6/–**	**–/2**		**–/2**	**1/1**	**4/–**	**4/–**	**19/–**		
Trichia contorta	**2/–**					**4/–**	**5/–**	**6/–**	**1/–**	
Trichia decipiens	**1/–**			**1/–**	**2/–**	**16/–**	**10/–**	**20/–**	**1/–**	
Trichia erecta	**1/–**									
Trichia favoginea	**1/–**					**4/–**	**6/–**	**12/–**	**1/–**	
Trichia floriformis							**1/–**	**2/–**		
Trichia lutescens		**–/2**		**–/2**	**–/1**	**1/–**		**7/–**		
Trichia munda		**–/10**	**–/1**	**–/5**	**–/5**					
Trichia scabra							**3/–**	**7/–**	**2/–**	
Trichia subfusca						**1/–**		**1/–**		
Trichia varia			**1/–**	**3/1**	**3/–**	**5/–**	**9/–**	**14/–**	**1/–**	
Tubifera ferruginosa	**1/–**					**1/–**	**10/–**	**19/–**	**3/–**	
Tubifera* cf. *microsperma								**2/–**		

In general, the myxomycete biota of the tundra zone of the Polar Ural, the Taimyr Peninsula, and the Chukchi Peninsula can be considered as impoverished biota of the northern taiga subzone. In extreme conditions (tundra, and desert ecosystems) the amount of species decreases and some species disappear. At the same time occurrence of *Echinostelium minutum* and *Licea minima* is not only lower but in some habitats in tundra (on bark of *Dushekia fruticosa*) and desert (on bark of *Artemisia*) is rather high. Thus, probably in this case the inverse dependence between population density and species richness in extremal conditions is obvious.

Due to the poor knowledge about myxomycete distribution we should be careful in making conclusions about their geography. The majority of species in Russia have polyzonal areas but some species show high abundance and mass distribution in separate climatic zones (tables 1, 2). There are arct-alpine species (numerous nivicolous species e.g. *Lamproderma*, *Diderma*, etc.), arct-boreal (e.g. *T. munda)*, boreal (*Trichia varia*), and desert-steppe species *(Echinostelium colliculosum*). The overall high degree of similarity between the biotas of the 10 study areas (expressed as coefficient of community indices in table 3) certainly suggests that most species of myxomycetes have high dispersal capabilities. Exceptional was western Kazakhstan, with extremely severe arid climatic conditions. The extreme fluctuations in air humidity favour species with a short development time or those able to survive repeated desiccation during development in desert areas (Schnittler and Novozhilov, 1999).

In the tundra, myxomycetes are represented mainly by multizonal and even cosmopolitan species. Many boreal species are widely distributed within the northern taiga and can be found also in forest-tundra and tundra vegetation (table 1). However, only *Echinostelium minutum* (2 collections), *Didymium dubium* (2), *Craterium leucocephalum* (1), *Licea minima* (1), and *L. testudinacea* (1) were recorded for typical tundra.

In general, the species richness of myxomycetes decreases northwards. In the Taimyr Peninsula (Fig. 3) results of moist chamber cultures obtained for all substrate types are demonstrated this trend (table 4). Due to the patchy nature of the vegetation, collections from one geographical locality may be assigned to more than one subzone. The Shannon diversity index for the taiga (H' = 1.31) is slightly higher than the value for the forest-tundra (H' = 1.28), whereas the value for the tundra is much lower (H' = 0.99). However, this pattern differs among particular ecological groups. For example, the mean value of the number of wood-inhabiting species per moist chamber culture decreases from 3.54 in the taiga to 1.66 and 1.13 in the forest-tundra and tundra, respectively. This correlates with a decrease in species richness and diversity. Corticolous myxomycetes exhibit similar patterns. In contrast, litter-inhabiting myxomycetes exhibit a higher diversity in forest-tundra (H' = 1.01) and tundra (H' =

Table 2. Summary data for specimens of myxomycetes collected in the field and from moist chambers (abbreviated as 'MC') for the ten study areas of Russia and Kazakhstan.

(Explain remarks: since more than one myxomycete species may occur in a given moist chamber, the number of specimens obtained from a set of moist chambers for a single study area is usually higher than the total number of positive moist chambers. Exceptions may occur in study areas where many moist chambers were prepared with litter, because these moist chambers often have high proportions of plasmodia that cannot be induced to fruit. These non-fruiting plasmodia remain unidentified and are not considered in the numbers of specimens from moist chambers. Moist chamber data could not be reconstructed for Karelia, Leningrad, Volgograd, and Sverdlovsk provinces, and are therefore not included in the totals given in the last column. ND – no data; abbreviations for study areas are the same as those used in Table 1).

Study area	KM	PU	PP	TP	CH	RK	LE	SV	VO	KZ	Total
Wood: MC positive	**3**	**9**	**10**	**56**	**14**	**ND**	**ND**	**ND**	**ND**	**ND**	**92**
MC prepared	**7**	**11**	**14**	**83**	**22**						**137**
% positive	***43***	***82***	***71***	***67***	***64***						***67***
Bark: MC positive	**9**	**32**	**17**	**37**	**27**	**ND**	**ND**	**ND**	**ND**	**72**	**194**
MC prepared	**71**	**37**	**19**	**61**	**32**					**81**	**301**
% positive	***13***	***86***	***89***	***61***	***84***					***89***	***64***
Litter: MC positive	**5**	**13**	**3**	**20**	**19**	**ND**	**ND**	**ND**	**ND**	**29**	**89**
MC prepared	**32**	**19**	**14**	**49**	**31**					**35**	**180**
% positive	***16***	***68***	***21***	***41***	***61***					***83***	***50***
Dung: MC positive	**1**	**4**	**1**	**6**	**9**	**ND**	**ND**	**ND**	**ND**	**16**	**37**
MC prepared	**13**	**6**	**5**	**25**	**12**					**30**	**91**
% positive	***8***	***67***	***20***	***24***	***75***					***53***	***41***
Total: MC positive	**18**	**58**	**31**	**119**	**69**	**ND**	**ND**	**ND**	**ND**	**117**	**412**
MC prepared	**123**	**73**	**52**	**218**	**97**	**ND**	**ND**	**ND**	**ND**	**146**	**709**
% positive	***15***	***80***	***60***	***55***	***71***	***ND***	***ND***	***ND***	***ND***	***80***	***59***
Specimens collected in the field	**101**	**22**	**27**	**14**	**68**	**341**	**493**	**821**	**352**	**10**	**2249**
Specimens from mc	**18**	**101**	**76**	**249**	**111**	**56**	**35**	**82**	**ND**	**323**	**1051**
Number of species	**40**	**35**	**29**	**48**	**48**	**96**	**148**	**105**	**77**	**27**	**222**
Number of genera	**20**	**19**	**15**	**22**	**23**	**33**	**40**	**32**	**25**	**12**	**42**
Species/genus ratio	**2.0**	**1.8**	**1.9**	**2.1**	**2.0**	**2.9**	**3.7**	**3.3**	**3.0**	**2.3**	**5.3**

0.90) than in the taiga (H '= 0.58). Myxomycetes cultured from dung in the taiga subzone occurred too sporadically to indicate any distribution trends.

However, zonal limits of myxomycete distribution are relative. Presumably, differences among myxomycete assemblages in taiga, forest-tundra, and tundra are more the result of differences in the abundance of shared species than actual differences in species composition.

Obviously, the main factors for the decrease in the number of myxomycete species in desert and arctic regions are unfavourable hydro-temperature conditions and the reduced range and extent of available microhabitats (α-diversity). For example as shown for the common species in the desert regions of Kazakhstan, ecological niches are determinated primarily by substratum features, with pH, texture and probably water retention as the most important factors (Schnittler, 2000). The CCA (canonical correspondence analysis), mean values for niche states restricted to the microhabitat (pH, substratum type) were lower than for climatic parameters (light, wind). This may express difficulties in estimating the latter parameters for a very small space, but more probably it reflects the generally higher importance of microhabitat features in comparison to habitat-describing parameters for myxomycetes. Regarding the generally low utilization of space (also in the most productive moist chambers not all substratum pieces had myxomycete colonies), a low niche overlap in already one dimension seems to allow the coexistence of two species.

The majority of species found in the boreal zone belongs to the group of xylophils and occurs in association with wood and bark debris (Eliasson, 1981; Schnittler and

Table 3. Pairwise comparisons of myxomycete biotas among the 10 study areas.

(Explain remarks: both coefficient of community indices (upper right) and numbers of species shared in common (lower left) are given; abbreviations for study areas are the same as those in Table 1.)

	KM	PU	PP	TP	CH	RK	LE	SV	VO	KZ
KM		**0,29**	**0,41**	**0,34**	**0,41**	**0,40**	**0,33**	**0,32**	**0,39**	**0,12**
PU	**11**		**0,44**	**0,58**	**0,67**	**0,38**	**0,38**	**0,36**	**0,29**	**0,06**
PP	**14**	**15**		**0,55**	**0,44**	**0,34**	**0,26**	**0,27**	**0,36**	**0,11**
TP	**15**	**24**	**21**		**0,63**	**0,43**	**0,35**	**0,42**	**0,30**	**0,21**
CH	**18**	**28**	**17**	**30**		**0,46**	**0,28**	**0,38**	**0,40**	**0,16**
RK	**27**	**25**	**21**	**31**	**33**		**0,62**	**0,58**	**0,47**	**0,10**
LE	**31**	**29**	**23**	**34**	**41**	**76**		**0,57**	**0,56**	**0,16**
SV	**23**	**25**	**18**	**32**	**29**	**58**	**72**		**0,49**	**0,14**
VO	**23**	**16**	**19**	**19**	**25**	**41**	**63**	**45**		**0,12**
KZ	**4**	**2**	**3**	**8**	**6**	**8**	**14**	**9**	**6**	

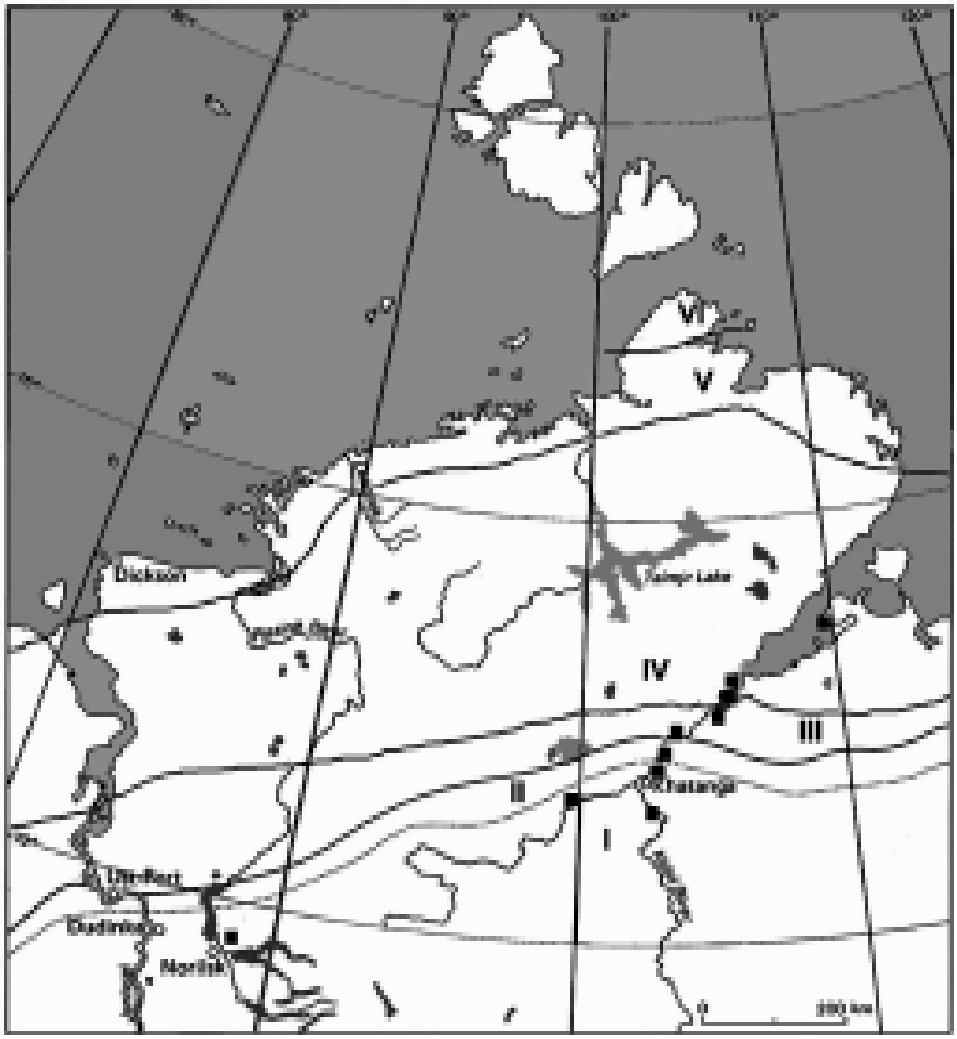


Fig. 3. Map of the Taimyr Peninsula showing the location of the ten study sites (black rectangles). A dotted line shows the northern boundary of the light larch taiga, whereas solid black lines indicate the boundaries of the tundra subzones: I- northern taiga; II – forest-tundra; III – southern tundra; IV – typical tundra; V – arctic tundra; VI – polar desert (according to Chernov and Matveyeva, 1997).

Table 4. Results obtained from moist chamber cultures prepared with substratum samples collected in the vegetation subzones of the Taimyr Peninsula.

Vegetation Subzones	Number of moist chamber cultures	Positive moist chamber cultures (% of total)	Number of collections	Number of species	Average yield (species per moist chamber) Mean ± SE	Shannon diversity index (H´)
I Taiga	**55**	**45 (82)**	**122**	**32**	**2.19 ± 0.26**	**1.31**
Wood (w)	**24**	**21 (88)**	**79**	**28**	**3.54 ± 0.48**	**1.26**
Litter (l)	**7**	**3 (43)**	**5**	**4**	**0.71 ± 0.40**	**0.58**
Bark (b)	**21**	**18 (86)**	**37**	**16**	**1.76 ± 0.23**	**1.06**
Dung (d)	**3**	**1 (33)**	**1**	**1**	**0.33 ± 0.33**	**0**
II Forest tundra	**110**	**54 (49)**	**119**	**36**	**1.08 ± 0.12**	**1.28**
Wood (w)	**34**	**21 (62)**	**54**	**22**	**1.66 ± 0.27**	**1.24**
Bark (b)	**34**	**19 (56)**	**39**	**15**	**1.15 ± 0.21**	**0.94**
Litter (l)	**25**	**8 (32)**	**19**	**13**	**0.76 ± 0.28**	**1.01**
Dung (d)	**17**	**4 (24)**	**7**	**5**	**0.41 ± 0.15**	**0.67**
III-IV Tundra	**105**	**51 (49)**	**90**	**22**	**0.84 ± 0.10**	**0.99**
Wood (w)	**39**	**22 (56)**	**45**	**15**	**1.13 ± 0.21**	**0.98**
Bark (b)	**25**	**14 (56)**	**26**	**8**	**1.04 ± 0.20**	**0.76**
Litter (l)	**31**	**12 (39)**	**16**	**9**	**0.52 ± 0.14**	**0.90**
Dung (d)	**10**	**2 (20)**	**3**	**2**	**0.30 ± 0.21**	**0.28**
All subzones	**270**	**145 (54)**	**331**	**48**	**1.22 ± 0.09**	**1.32**
Wood (w)	**97**	**64 (66)**	**178**	**37**	**1.82 ± 0.19**	**1.29**
Bark (b)	**80**	**51 (64)**	**102**	**21**	**1.27 ± 0.13**	**1.03**
Litter (l)	**63**	**23 (37)**	**40**	**16**	**0.63 ± 0.13**	**1.05**
Dung (d)	**30**	**7 (23)**	**11**	**8**	**0.32 ± 0.11**	**0.88**

Novozhilov, 1996). The xylophilic species diversity in forest-tundra and tundra considerably decreases compared to the boreal (taiga) zone, but the abundance of some species remains rather high (Novozhilov et al., 1998a, 1998b). For example, towards the tundra zone in the Taimyr Peninsula xylophilic species may penetrate into woodless territories inhabiting the tiny branchlets of shrubs in bush "islands" communities. Small dead and dying twigs of shrubs (*Salix* spp. and *Duschekia*) with exfoliating bark represent a rather suitable substrate for some species. When very moist, such bark easily becomes exfoliated, forming numerous small gaps or "shelters" between wood and bark. These "shelters" play a role of natural moist chambers, where the plasmodium can survive under unfavorable conditions.

Conclusion

In summary it may be said that myxomycetes with their vagility, relatively short life cycle and high ecological adaptation demonstrate the same patterns of distribution (constant structure of communities within certain biomes, reduction of adaptive complexes and decrease of species diversity in extreme conditions) as plants and animals. Our research and literature data show that some species have rather limited distribution connected with certain climatic zones and habitats. Nevertheless, these patterns are seen only at the scale of whole natural climatic zones and large ecosystems (biomes) characterised by similar vegetation, fauna, and climate when different groups of habitats are studied. At the present level of knowledge, further comparative investigations in other regions of Russia, especially steppe and desert biomes, are necessary to explore the whole richness of biotic diversity of myxomycetes and reveal their world-wide distribution patterns. Using of standardised sampling procedures and the introduction of a systematic program for surveying small representative areas ("concrete biota") throughout the large territory of Russia would rise our knowledge on myxomycete biodiversity to a new level with reasonable efforts.

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