

SEASONAL DYNAMICS OF SPOROPHORE FORMATION OF MYXOMYCETES IN POLISTOVO-LOVATSKAYA BOG SYSTEM (PSKOV AND NOVGOROD REGIONS, RUSSIA)

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Received 25 June, 2023; revised 21 October, 2023; accepted 28 December, 2023

We investigated the seasonality of myxomycete fruiting body formation under natural conditions in the field during four years in the Polistovo-Lovatskaya bog system (Northwestern Russia). It was shown that the species diversity of myxomycetes peaks in mid-summer and gradually decreases afterwards. The species composition of myxomycetes varies depending on the season. There were five phenological groups distinguished: summer, early autumn, late autumn, spring and species without pronounced periods of mass formation of fruiting bodies. It is shown the list of identifiable taxa may significantly vary in different years and there are widespread species that do not form sporophores every year. Thus, when conducting field studies, it is necessary to make observations over several years and throughout the entire snowless period.

Keywords: biodiversity, methodology of field work, phenology, population dynamics, slime molds

DOI: 10.31857/S0026364824030034, **EDN:** viytttd

INTRODUCTION

The myxomycetes are a relatively small group of soil protozoans currently attributed to the *Amoebozoa* clade (Adl et al., 2019). Their life cycle includes motile trophic, dormant and dispersal stages. Myxomycetes are a traditional object of study for mycologists, as they form sporocarps that resemble the fruiting bodies of some fungi and are well preserved in herbaria (Ronikier, Halamski, 2018). They inhabit almost all terrestrial ecosystems and are extremely abundant (Bailly et al., 2007; Urich et al., 2008) in soil and on many substrates of plant origin such as forest floor and tree bark. They influence the abundance of bacteria, yeasts, fungal spores and other microscopic organisms (Stephenson et al., 2011).

As a rule, it is challenging to assess the abundance of myxomycetes in a particular area. This is due to the fact that identification of myxomycete species by morphological characters is only possible at the dispersal stage represented by sporophores of diverse structure. The trophic stages, apparently more numerous, are usually located within the substrate (Shchepin et al., 2019). In most cases, they escape the eyes of researchers and are not suitable for identification of morphospecies

(Novozhilov et al., 2016). Myxomycetes can form sporophores during the entire snowless period that lasts from the end of March to the end of November in Central Russia. It is thought that the main factors influencing the sporophore formation in myxomycetes are temperature and humidity (Martin, Alexopoulos, 1969). As a result, many species exhibit pronounced peaks of sporophore formation (Schnittler, Novozhilov, 1996), whereas some species may massively sporulate once in several years for unknown reasons (Barsukova, 2001).

The seasonality of sporophore formation in myxomycetes varies across the world depending on the climate. In regions without snowy winters, the abundance and diversity of myxomycetes are higher in warm and moist seasons compared to cool and dry seasons (Stephenson et al., 2004b; Ko Ko et al., 2011). In the boreal zone, the periods of mass sporulation are thought to occur in early to mid-autumn (Eliasson, 1981; Vlasenko, Novozhilov, 2011; Gmoshinskiy, Matveev, 2016), when nights become cooler than in the relatively dry and warm beginning of summer, the dew falls abundantly, and the precipitation is usually high (Schnittler et al., 2022).

The Polistovo-Lovatskaya bog system is located in the west of the East European Plain. Research and nature conservation in this area are facilitated by the Polistovsky and Rdeysky nature reserves in the Pskov and Novgorod regions, respectively. The proximity of the Polistovo-Lovatskaya bog system to the warm Baltic Sea results in temperate continental climate with humid summers and warm winters with frequent thaws. In January, the average monthly temperature is -8.1°C and the average snow cover reaches 20–30 cm, but the snow completely disappears by mid-April, sometimes even in March. The average temperature of July is 17°C . The average annual precipitation is 685 mm, 40% of which falls in the summer months in the form of short showers with thunderstorms (Zavyalov, 2022). However, according to the recent data from the Kholmensk weather station collected from 2009 to 2021, the average precipitation has increased significantly and now amounts to 771 mm (Zavyalov, 2022). The microclimate of the bog system has a number of peculiarities. For example, due to the low thermal conductivity of peat, the bog surface heats more in summer and thaws slowly in spring so that individual blocks of ice can persist until mid-May. In the warm season, the bog vapors increase the air humidity. The high water holding capacity of bogs provides water inflow in dry years and drainage in rainy years (Reshetnikova et al., 2006).

The Polistovo-Lovatskaya bog system is part of the Lovat district of the Severodvinsko-Verkhnedneprovskaya subprovince of the North European taiga province (Aleksandrova, Yurkovskaya, 1989). Most of the forest areas in the bog and along its edges have been subjected to

anthropogenic pressure in the last centuries, the intensity of which has significantly decreased after World War II. Thus, a significant part of the forests is represented by young single-age stands, mostly spruce or mixed (with spruce, birch, aspen, alder, etc.). Small areas of coniferous-broadleaf forests are confined either to uplands or to well-drained areas along river valleys. The herb layer is dominated by taiga small herb species (Reshetnikova et al., 2007).

MATERIALS AND METHODS

Study area. Specimens of myxomycete sporophores were collected in the Polistovsky (from 2018 to 2021) and Rdeysky (in 2020 and 2021) state nature reserves and adjacent territories. The material was collected in trips of 7–10 days conducted 2–3 times per field season at different times of the year. A total of 8 expedition trips were made, during which 57 sample plots (Fig. 1) about 100×100 m in size were surveyed. The sampling effort was identical in all surveys within one expedition trip. A group of 2–3 people spent 60 min in the sample plots. Sporophore specimens were collected throughout the snowless period, from March to the end of October. In May, June and November, no surveys were made for technical reasons.

For convenience of data processing, all plots were grouped by location:

Vicinity of the Fryunino village, edge of the bog (R1): Loc. 1 ($N57.07747^{\circ}$, $E30.73317^{\circ}$): 30.09.2020, 14.07.2021; Loc. 2 ($N57.07580^{\circ}$, $E30.73447^{\circ}$): 30.09.2020, 14.07.2021; Loc. 3 ($N57.09136^{\circ}$, $E30.72548^{\circ}$): 01.10.2020, 12.07.2021; Loc. 4 ($N57.09343^{\circ}$, $E30.72402^{\circ}$): 01.10.2020, 12.07.2021; Loc. 5 ($N57.09311^{\circ}$, $E30.72947^{\circ}$): 01.10.2020; Loc. 6 ($N57.09219^{\circ}$, $E30.72915^{\circ}$):

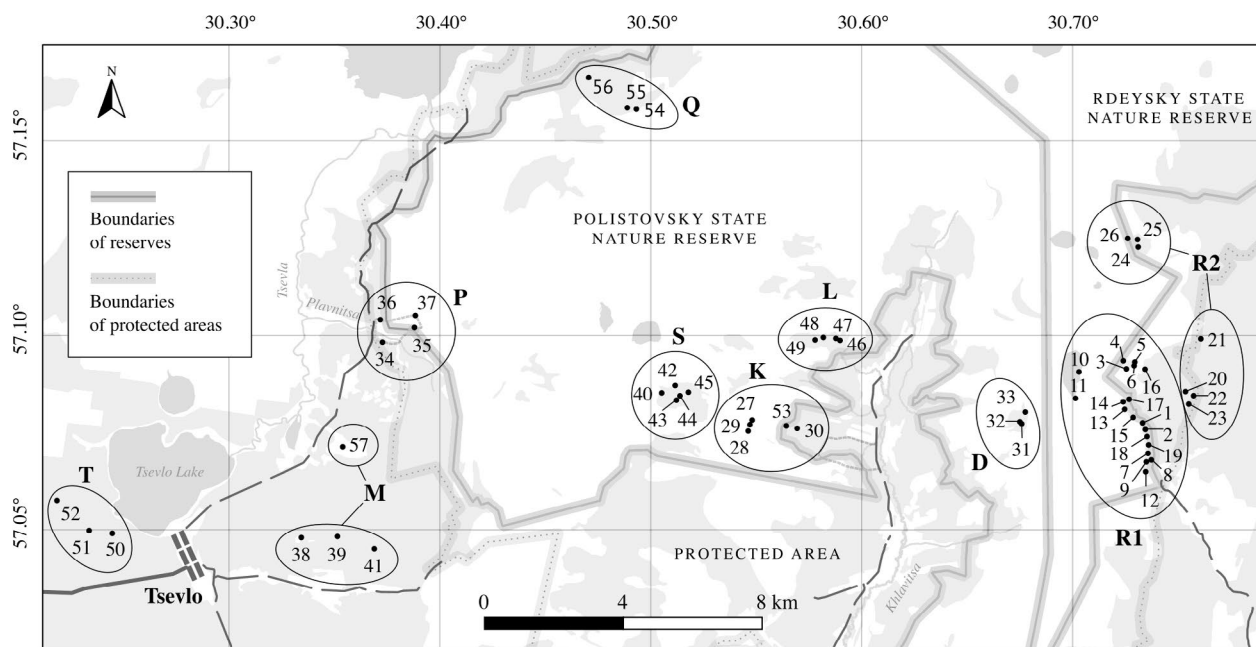


Fig. 1. Schematic map of study area. Points indicate 56 sampled plots.

01.10.2020, 12.07.2021; Loc. 7 (N57.06966°, E30.73573°): 02.10.2020, 19.07.2021; Loc. 8 (N57.06797°, E30.73731°): 02.10.2020, 19.07.2021; Loc. 9 (N57.06747°, E30.73497°): 02.10.2020, 19.07.2021; Loc. 10 (N57.09060°, E30.70301°): 03.10.2020; Loc. 11 (N57.08379°, E30.70135°): 03.10.2020. Loc. 12 (N57.06496°, E30.73463°): 03.10.2020, 19.07.2021; Loc. 13 (N57.08098°, E30.72466°): 04.10.2020, 13.07.2021; Loc. 14 (N57.08290°, E30.72396°): 04.10.2020, 13.07.2021; Loc. 15 (N57.07890°, E30.72867°): 04.10.2020, 13.07.2021; Loc. 16 (N57.09127°, E30.73434°): 12.07.2021; Loc. 17 (N57.08355°, E30.72676°): 13.07.2021; Loc. 18 (N57.07397°, E30.73525°): 14.07.2020; Loc. 19 (N57.07183°, E30.73602°): 14.07.2020.

Mixed forests on the edge of a bog near Fryunino village (R2): Loc. 20 (N57.08553°, E30.75351°): 17.07.2021; Loc. 21 (N57.09913°, E30.76080°): 17.07.2021; Loc. 22 (N57.08447°, E30.75736°): 17.07.2021; Loc. 23 (N57.08231°, E30.75506°): 17.07.2021; Loc. 24 (N57.12268°, E30.73109°): 18.07.2021; Loc. 25 (N57.12463°, E30.73076°): 18.07.2021; Loc. 26 (N57.12490°, E30.72612°): 18.07.2021.

Koroleva Borina Island (K): Loc. 27 (N57.078211°, E30.548037°): 28.08.2019, 27.07.2020, 19.10.2020, 25.03.2021, 13.07.2021; Loc. 28 (N57.075392°, E30.546172°): 28.08.2019, 27.07.2020, 19.10.2020, 25.03.2021, 13.07.2021; Loc. 29 (N57.077021°, E30.546965°): 28.08.2019, 27.07.2020, 19.10.2020, 25.03.2021, 13.07.2021; Loc. 30 (N57.076061°, E30.569385°): 28.08.2019, 27.07.2020, 19.10.2020, 25.03.2021, 13.07.2021; Loc. 53 (N57.076715°, E30.564218°): 25.03.2021.

Dubovets Island (D): Loc. 31 (N57.077252°, E30.675861°): 29.08.2019, 28.07.2020, 20.10.2020, 15.07.2021; Loc. 32 (N57.077772°, E30.674964°): 29.08.2019, 28.07.2020, 20.10.2020, 15.07.2021; Loc. 33 (N57.080269°, E30.677567°): 29.08.2019, 28.07.2020, 20.10.2020, 15.07.2021.

Plavnitskoe bog (P): Loc. 34 (N57.098263°, E30.372753°): 07.09.2018, 30.08.2019, 31.07.2020, 24.10.2020, 27.03.2021, 13.07.2021; Loc. 35 (N57.101996°, E30.387909°): 30.08.2019, 31.07.2020, 24.10.2020, 27.03.2021, 19.07.2021; Loc. 36 (N57.104007°, E30.371716°): 30.08.2019, 31.07.2020, 24.10.2020, 19.07.2021; Loc. 37 (N57.105113°, E30.388360°): 30.08.2019, 31.07.2020, 24.10.2020, 27.03.2021, 19.07.2021.

Vicinity of Mazurovo and Tereshikha localities (M): Loc. 39 (N57.048300°, E30.351386°): 31.08.2019, 01.08.2020, 18.07.2021; Loc. 38 (N57.048006°, E30.334258°): 08.09.2018, 31.08.2019, 01.08.2020, 23.10.2020, 18.07.2021; Loc. 41 (N57.045130°, E30.368872°): 04.09.2018, 31.08.2019, 01.08.2020, 23.10.2020, 18.07.2021; Loc. 57 (N57.071356°, E30.353906°): 11.09.2018.

Slepnoe locality (S): Loc. 40 (N57.085199°, E30.505156°): 02.09.2019, 29.07.2020, 21.10.2020, 14.07.2021; Loc. 42 (N57.087105°, E30.511542°): 02.09.2019, 29.07.2020, 21.10.2020, 14.07.2021; Loc. 43 (N57.083305°, E30.512137°): 03.09.2019, 29.07.2020, 22.10.2020, 14.07.2021; Loc. 44 (N57.084458°, E30.513806°): 10.09.2018, 03.09.2019, 29.07.2020, 22.10.2020, 14.07.2021; Loc. 45 (N57.085370°, E30.517817°): 10.09.2018, 03.09.2019, 29.07.2020, 21.10.2020, 14.07.2021.

Osinovy Island (L): Loc. 46 (N57.09871°, E30.58971°): 26.03.2021, 12.07.2021; Loc. 47 (N57.09922°, E30.58775°): 26.03.2021, 12.07.2021; Loc. 48 (N57.09948°, E30.58180°): 26.03.2021, 12.07.2021; Loc. 49 (N57.09883°, E30.57788°): 26.03.2021, 12.07.2021.

Forest by Tsevo Lake (T): Loc. 50 (N57.04909°, E30.24463°): 28.03.2021, 17.07.2021; Loc. 51 (N57.04981°, E30.23364°): 28.03.2021, 17.07.2021; Loc. 52 (N57.05754°, E30.21841°): 28.03.2021, 17.07.2021.

Polisto Lake vicinities, quarters 14–15 (Q): Loc. 54 (N57.158131°, E30.493145°): 5.09.2018; Loc. 55 (N57.158491°, E30.488823°): 5.09.2018; Loc. 56 (N57.166274°, E30.470525°): 6.09.2018.

Methods for collecting and identifying sporophores of myxomycetes. Sporophores were collected using standard methods (Wrigley de Basanta, Estrada-Torres, 2022; Novozhilov et al., 2022) described in our first works on the biota of the Polistovsky (Gmoshinskiy, Matveev, 2019) and Rdeysky nature reserves (Borzov et al., 2021). This work adopts the concept of morphospecies like most modern monographs (Martin, Alexopoulos, 1969; Novozhilov, 1993; Neubert et al., 1993, 1996, 2000; Ing, 1999; Poulain et al., 2011a, b; Stephenson, 2021). In the present work, the classic system based on the morphology of myxomycete sporophores (Lado, Eliasson, 2022) is used, and the names and authors of taxa are given according to the Nomenmyx information system (Lado, 2005–2023). Despite the fact that the genus *Ceratiomyxa* belongs to the class Ceratiomyxomycetes rather than Myxomycetes (Leontyev et al., 2019), we included its only representative, *Ceratiomyxa fruticulosa* (O.F. Müll.) T. Macbr. in order to compare our data with the results of previous studies (Vlasenko, Novozhilov, 2011; Matveev, Gmoshinskiy, 2016).

Statistical data processing. Species diversity was measured using the Hill numbers (Hill, 1973), a parametric family of metrics based on the inverse of the weighted power mean of relative species abundances: ${}^qD = (\sum_{i=1}^S p_i^q)^{1/(1-q)}$, where S is the number of species, p_i is the relative abundance of species i , and q is the order determining the sensitivity of the function to abundance.

Species richness (at order $q = 0$), the exponential Shannon index (at q tending to 1), and the inverse of the Simpson index (at $q = 2$) are special cases of the Hill numbers. Diversity continuous q -profile characterizes the species relative abundance distribution best: species richness has high sensitivity to rare species, Shannon diversity is balanced with respect to abundance, and Simpson diversity is most influenced by dominant species.

Since empirical diversity values strongly depend on the sample size, statistical estimation was used to make a more fair comparison of results. For asymptotic estimation of diversity, a method based on the slopes between neighboring points of the species accumulation curve was used (Chao, Jost, 2015).

A parametric family of metrics dependent on the order q was used to determine the completeness of detected species diversity (Chao et al., 2020). The theoretical formula ${}^qC = (\sum_{i \in \text{det}} p_i^q) / (\sum_{i=1}^S p_i^q)$ is equal to the ratio of the sums of abundances (raised to the power of q) for sampled species and all species present in the general population (natural community). Since quantitative data for the general population are most often unknown, a statistical estimate qC is used. In the special case of $q = 0$ it is equal to the

conventional measure of completeness, ${}^0C = S_{\text{obs}}/S_{\text{Chao1}}$ which is widely used in ecological studies of myxomycetes. It represents the ratio of detected species richness and its estimate, expressed according to the formula by A. Chao (Chao, 1984). When $q = 2$, the measure is equal to sample coverage ${}^1C = \sum_{i \in \text{det}} p_i$, first proposed by A. Turing (Good, 1953), which is interpreted as the proportion of individuals in the general population belonging to the species identified in the sample. The coverage estimate is equal to ${}^1C = 1 - (1/f_1)(A(1 - A)/(\sum_{x_i \geq 2} X_i(X_i - 1)/[n(n - 1)])$, where $A = 2f_1/[(n - 1)f_1 + 2f_2]$, n is the total number of count units, f_1 is the number of singletons (species represented by one count unit), f_2 is the number of species represented by two count units, X_i is the empirical absolute abundance of species i . This measure is less sensitive to sample size than 0C . In addition, it quantifies sample completeness when all specimens are treated equally, in contrast to the conventional measure (which disproportionally sensitive to rare species), and may therefore be preferable when interpreting the results (Chao et al., 2020).

The Sørensen similarity coefficient was used for pairwise comparison of species lists: $C_{\text{Sor}} = 2c/(a + b)$, where c is the number of common species for two biotas, a is the number of species in the first biota, b is the number of species in the second biota (Sørensen, 1948).

Calculations were performed in the statistical environment R4.2.1 (R Core Team, 2022). The diversity and completeness of the sample set were evaluated using the iNEXT.4step 1.0.1 package (Chao, Hu, 2023). The vegan 2.6.4 package was used for pairwise comparisons of periods using the Sørensen index and for non-metric multidimensional scaling (Oksanen et al., 2022).

RESULTS AND DISCUSSION

During 4 field seasons, 3394 specimens of myxomycete sporophores were collected, 3359 of which were identified to species level and are discussed below. A total of 162 species from 40 genera, 11 families and 6 orders were identified. For convenience, all results were summarized by decades of the survey months. However, for the most accurate interpretation of the results, it should be noted that sporophores of most species are able to persist in natural conditions for a long period of time (sometimes up to half a year).

The number of identified species varies considerably depending on the survey period (Table 1). The highest number of species (88) was identified during expeditions in Polistovsky nature reserve between 20–30 August 2019 and between 10–20 July 2021. In total, 104 species were identified during the expedition conducted in July 2021. This high diversity is due to the large number of sampling areas investigated and, as a consequence, a large sampling effort. At the same time, the summer of 2021 in the study area was characterized by very high air temperatures (up to 35 °C) combined with abundant heavy rainfall, which probably created favorable conditions for the formation of myxomycete sporophores. The ratio of the number of detected species to the Chao1 species richness estimator (a conventional measure of completeness) ranged from 68.5% for 10–20 July 2021 to 82.5% in July 2020 (Table 1), indicating that species diversity was sufficiently detected.

Thus, it can be concluded that for comparable sampling efforts, both the highest number of specimens and the highest number of taxa detected were observed during the summer months.

Table 1. Characteristics of myxomycete biota of the Polistovo-Lovatskaya bog system in different time periods

Decades		March–III (P)	July–II (P)	July–II (R)	July–III (P)	August–III (P)	September–I (P)	October–I (R)	October–III (P)	Total
Number of specimens		259	743	479	450	653	227	188	360	3359
Species richness		47	88	74	68	88	54	56	58	162
Number of species found during this period alone		6	9	4	3	13	3	9	7	
Estimate of species diversity	⁰ D	61	128.4	100.4	82.4	122.7	78.1	66.7	72.7	196.2
	¹ D	29.6	48.8	48.6	40.8	51.7	46	43.4	34.7	67.9
	² D	18.7	30.6	33.7	24.5	29	27.9	31	21.1	44.2
Sample completeness,%	⁰ C	77	68.5	73.7	82.5	71.7	71.7	80.9	79.8	82.6
	¹ C	94.2	96.4	95.2	96.2	96.2	89.4	93	95	98.9

Note. Roman numerals indicate decades in the corresponding months. The reserve where the material was collected is indicated in brackets: R – Rdeysky Nature State Reserve, P – Polistovsky Nature State Reserve.

It is important to note that the value of the Shannon diversity was significantly lower between 20–30 March and 20–30 October compared to other study periods (Table 1), indicating the presence of some medium-to-high abundance species in the biota, whereas the other species were much less frequent. The six most abundant species [*Trichia botrytis* s.l. (J.F. Gmel.) Pers., *Hemitrichia decipiens* (Pers.) García-Cunch., J.C. Zamora et Lado, *Metatrichia vesparia* (Batsch) Nann.-Bremek. ex G.W. Martin et Alexop., *Oligonema persimile* (P. Karst.) García-Cunch., J.C. Zamora et Lado, *T. varia* (Pers. ex J.F. Gmel.) Pers., and *Lycogala epidendrum* s.l. (L.) Fr.] accounted for 51.4% of the total number of finds. In other months, this share was much lower. Therefore, during the rest of the year, the Shannon diversity was much higher (Table 1). Similar patterns can be observed for Simpson's diversity. Its lowest values are observed between 20–30 March and between 20–30 October (18.7 and 21.1, respectively), while in other periods its values range from 24.5 to 33.7.

Pairwise comparisons were made between species lists obtained at different time periods using the Sørensen coefficient (using binary presence-absence data, i.e. without taking abundance into account). The highest similarity was observed between pairs of species lists obtained during the summer months (mid-July and late August) and late July and September ($C_{\text{Sor}} = 0.67$). In contrast, the greatest differences compared to the other periods were observed in the species lists identified in late March (Table 2).

Non-metric multidimensional scaling results confirm the differences in species composition and abundance (Fig. 2). Differences between the samples in mid-summer, late-summer, early-autumn and late autumn – spring periods are clearly expressed. The outlier in the Plavitskoe group of sample plots (point P) in September 2018 is explained by the fact that in this period only one plant

association from this group with a small sample of specimens, including some rare species, was investigated.

Differences are also observed at the level of the taxonomic structure of the biota. To make comparisons with results from other regions, specimens studied during one-decade period during different expeditions were combined together. In early spring and autumn, the greatest diversity (representation of orders by species) of the *Trichiales* order representatives can be detected in the field, while in the summer months there is a relative decrease in their abundance (Fig. 3). The greatest diversity and abundance of representatives of the order *Stemonitidales* is observed in mid-summer, and closer to the autumn their relative proportion in the biota gradually decreases. For representatives of the order *Physarales*, on the contrary, an increase in species diversity and abundance is observed in early autumn (Figs. 3). It is important to note the unusual biota structure revealed in the

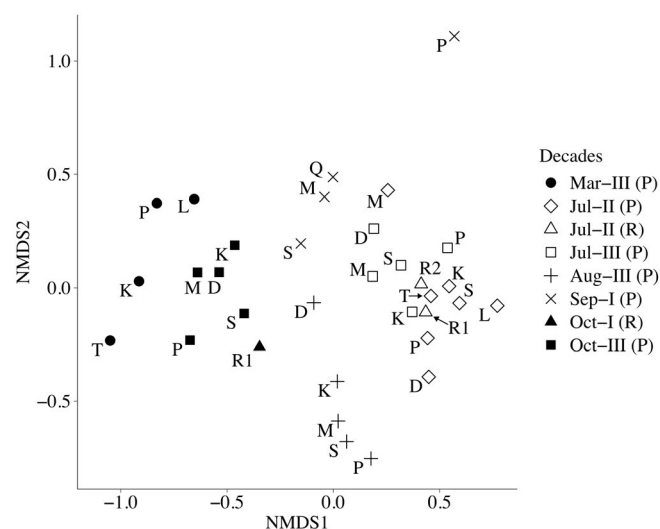


Fig. 2. Results of non-metric multidimensional scaling. Sample areas are grouped by geographical position (see materials and methods section).

Table 2. Values of the Sørensen coefficient for different periods of material collection

Collection periods	March–III (P)	July–II (P)	July–II (R)	July–III (P)	August–III (P)	September–I (P)	October–I (R)	October–III (P)
March–III (P)	1							
July–II (P)	0.46	1						
July–II (R)	0.51	0.72	1					
July–III (P)	0.52	0.68	0.66	1				
August–III (P)	0.52	0.64	0.62	0.62	1			
September–I (P)	0.53	0.55	0.55	0.67	0.56	1		
October–I (R)	0.52	0.50	0.48	0.58	0.56	0.6	1	
October–III (P)	0.59	0.53	0.56	0.59	0.60	0.55	0.58	1

Note. Roman numerals indicate decades of the corresponding months. The reserve where the material was collected is indicated in brackets: R – Rdeysky Nature State Reserve, P – Polistovsky Nature State Reserve.

second decade of July 2020. During this period, the greatest diversity was observed among representatives of the order *Cribrariales*, while the proportion of representatives of the order *Physarales* significantly decreased. The contribution of other orders remained at the same level.

Considering relative abundances of orders (representation by specimens) and the total number of specimens collected during the corresponding period, we can see that while in spring and autumn months *Trichiales* is the dominant order, in mid-summer there is a gradual decrease in their abundance (Fig. 3). In August, there was a simultaneous decrease in the abundance of the order *Cribrariales* and a significant increase in the representation of *Physarales*. Similar phenomena were observed when analyzing the seasonal differences in sporulation in the Moscow region (Matveev, Gmoshinskiy, 2016) and the Novosibirsk region (Vlasenko, Novozhilov, 2011). This fact may indicate different temperature and humidity optima for the formation of sporophores by representatives of these orders. However, it should be taken into account that in our study this phenomenon is well expressed only between 20–30 August. Thus, additional long-term observations on standardized plots are required to confirm this hypothesis.

No strong differences in the representation of myxomycetes substrate complexes between the collection periods were detected (Fig. 4). The observed outliers in some months are largely explained by the peculiarities of sampling and, presumably, by weather conditions. Additional studies are needed to fully explain the fluctuations in the ratio between substrate complexes and to establish the factors influencing the substrate confinement of myxomycetes and its expression in different phenological periods.

The core biota (species making up at least 3% of all observations) is formed by 9 species: *Physarum album* (Bull.) Chevall. (5.7%), *Arcyria cinerea* (Bull.) Pers.

(4.8%), *Lycogala epidendrum* s.l. (4.8%), *Stemonitis axifera* (Bull.) T. Macbr. (4.3%), *Metatrichia vesparia* (3.9%), *Trichia varia* (3.9%), *Hemitrichia decipiens* (3.6%), *A. affinis* Rostaf. (3.6%), and *Ceratiomyxa fruticulosa* (3%). However, depending on the season when the material was collected, the list of the core biota varied considerably. Fig. 5 and 6 shows the proportion of species in the biota during different phenological periods. All species diversity can be roughly divided into 5 categories:

1) Mid-summer species. Quite a large number of myxomycete species have relatively short periods of sporophore formation in mid-summer, when warm weather with high precipitation was observed in the years of research. Such species include *Arcyria cinerea* (Fig. 5, k), *Ceratiomyxa fruticulosa* (Fig. 5, j), *Cribraria cancellata* (Batsch) Nann.-Bremek. (Fig. 5, i), *Stemonitis axifera* (Fig. 5, f), *Stemonitopsis typhina* (F.H. Wigg.) Nann.-Bremek. (Fig. 5, h), *Stemonitopsis hyperopata* (Meyl.) Nann.-Bremek. (Fig. 5, g). For these species, we made similar observations on the seasonality of sporophore formation in the Moscow region (Matveev, Gmoshinskiy, 2016). In the Moscow region, these species begin massive sporulation in late May and reach their peak abundance in June and mid-July, with a significant decrease in the number of their findings afterwards.

2) Late summer-autumn species. This group includes *Hemitrichia calyculata* (Speg.) M.L. Farr (Fig. 6, c), *Physarum album* (Fig. 6, a), and *Oligonema favogineum* (Batsch) García-Cunch., J.C. Zamora et Lado (Fig. 6, g). Reaching the maximum in late August-early September, their abundance decreases strongly by October.

3) Autumn species. These are *Arcyria stipitata* (Schwein.) Lister. (Fig. 6, j), *Metatrichia floriformis* (Schwein.) Nann.-Bremek. (Fig. 6, h), and *Trichia varia* (Fig. 6, i). They are formed in early autumn and possess comparatively fragile sporophores, which are almost

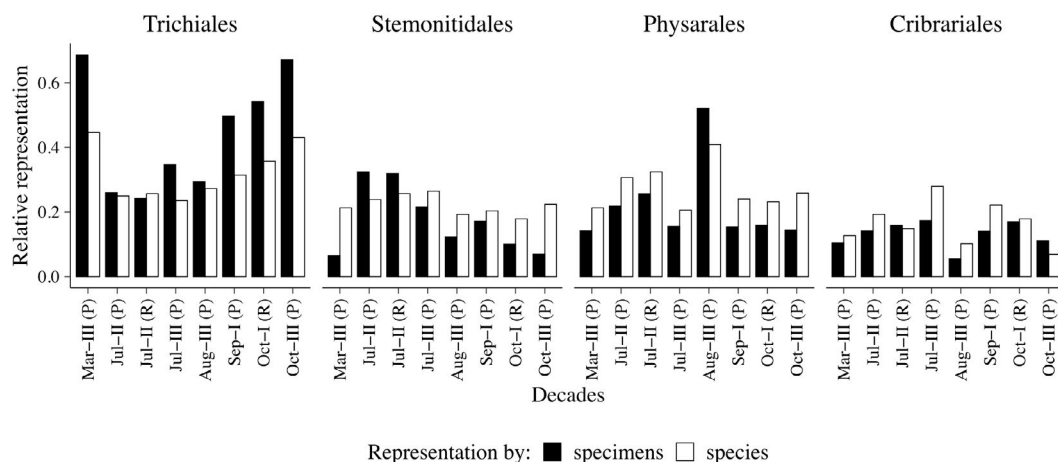


Fig. 3. Number of species (white bars) and specimens (black bars) belonging to different orders in % of the total number of specimens collected during the corresponding period.

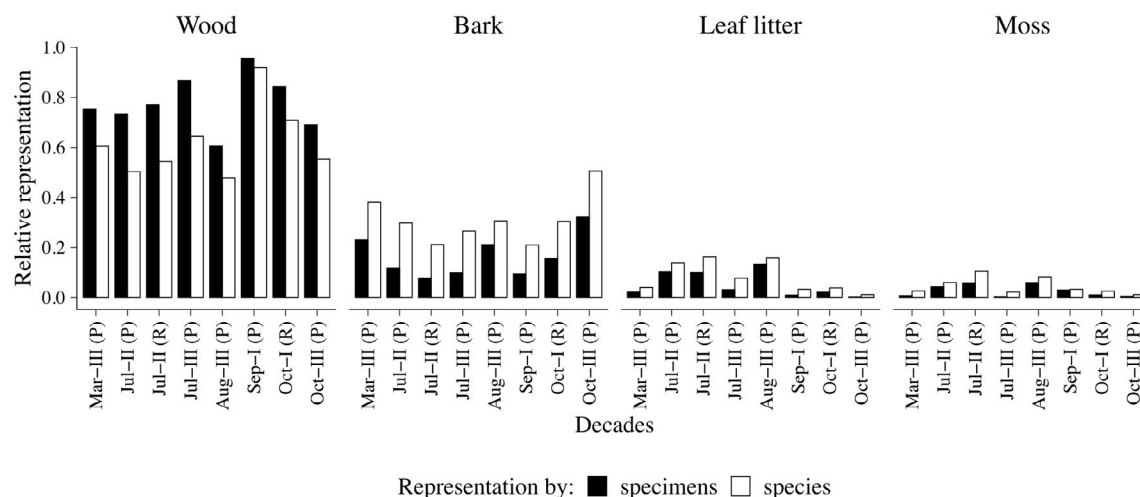


Fig. 4. Relative representation of substrate types (by specimens and by species of myxomycetes) in different periods of material collection. Due to specimen occurrences on mixed substrates, the sum of abundances can exceed 100% in some decades.

completely destroyed under snow. Therefore, their detection in spring months is quite rare.

4) Spring species. In the present study, this group includes *Oligonema persimile* (Fig. 5, c), *Trichia botrytis* s.l. (Fig. 5, b), *T. contorta* (Ditmar) Rostaf. (Fig. 5, a), *Licea variabilis* Schrad. (Fig. 5, d), and *Hemitrichia decipiens* (Fig. 6, l). Most likely, sporophores of these species are formed in late autumn and persist under snow during winter due to their relatively large colony size and dense peridium. This is supported by an increase in their abundance in the third decade of October. It should be noted that no species of the nivicolous group were found during the present study.

5) Species found throughout the entire growing season. This group includes *Lycogala epidendrum* s.l. (Fig. 6, k) and *Metatrichia vesparia* (Fig. 6, f). These species possess large and somewhat dense sporophores that do not collapse for a long time. Thus, their proportion among the identified taxa is always quite high. At the same time, this does not mean that these species do not have seasonality of sporulation. We did not record the degree of preservation of sporophores *in situ* because it is hard to assess objectively in many species and, therefore, could not draw conclusions about their age. In addition, it should be taken into account that *Lycogala epidendrum* s.l. is a complex of species (Leontyev et al., 2022, 2023), whose members may be characterized by individual seasonality of sporophore formation requiring additional research.

The study also revealed species that had strictly defined periods of mass formation of sporophores. For example, in the territory of the Polistovo-Lovatskaya bog system, mass development of *Badhamia lilacina* (Fr.) Rostaf. (Fig. 6, d) starts from around 20 August on the surface of *Sphagnum* and *Polytrichum* mosses in forest wetlands, where these mosses form a continuous cover

on the soil (Borzov, Gmoshinskiy, 2020). We observed a similar phenomenon in the Central Forest State Nature Reserve (Nelidovsky urban district, Tver Region). Due to the large size of sporophores, they can persist for a long time and can be found until the very end of the growing season, and sometimes even in the next year. However, we did not observe the formation of new sporophores of this species between 1–10 October as well as in spring or mid-summer. All specimens were heavily water-damaged and most likely persisted on the substrate for a long period of time.

Tatyana Nikolaevna Barsukova, in the course of long-term observations of myxomycete abundance at the Zvenigorod biological station of the Moscow State University, showed that some species can form sporophores once in several years (Barsukova, 2001). As one of the examples in her work, she cites *Leocarpus fragilis* (Dicks.) Rostaf. that forms sporophores once every 2–3 years in the Moscow region. According to our observations, this species can indeed massively form sporophores in some years, while in other years it could be almost completely absent from our collections. Thus, in August 2019, the proportion of specimens of this species was 9% of the total number, while among the collections made between 1–10 September 2018, the proportion of finds of this species was only 0.4% of the total number (Fig. 6, b).

Between 1–10 July 2021, mass development of *Valtolecarpus trechisporus* (Berk. ex Torrend) Gmoshinskiy, Prikhodko, Bortnikov, Shchepin et Novozh. (= *Symphytolecarpus trechisporus* (Berk. ex Torrend) Nann.-Bremek.) was observed. This species is quite rare. Earlier it was only recorded in the territory of the Republic of Karelia (Bortnikov et al., 2020). However, in the summer of 2021, its sporophores were massively formed in black alder and mixed forests. Notably, sporophores were

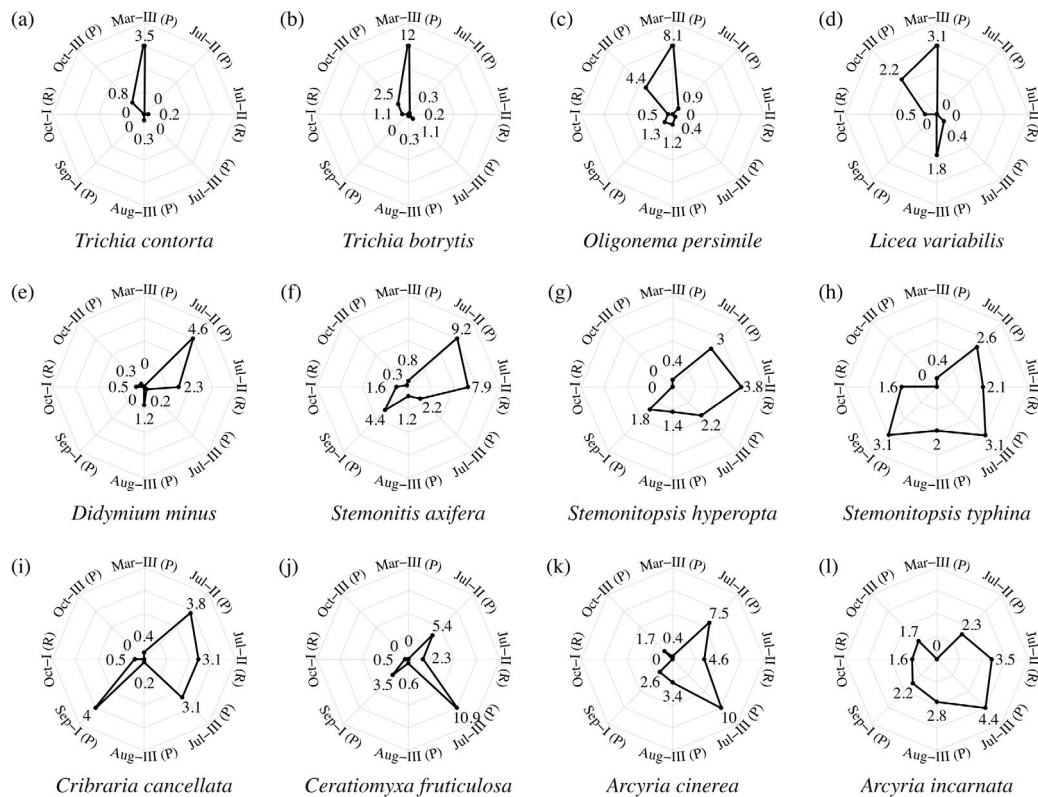


Fig. 5. Seasonality of sporophore formation for the most widespread species of myxomycetes from the Polistovo-Lovatskaya bog system (part 1).

formed so abundantly that it was impossible to count all large pseudoethalia in some sample plots. Thirty-seven specimens of this species were recorded in the database. A similar burst of this species was recorded by us in the same time period in the Central Forest state nature reserve 200 km east of the study area as well as in the Taldom district of the Moscow region (Gmoshinskiy V.I., unpublished). Thus, with an example of this species, we conclude that some species can stay in the trophic stage hidden in the substrate for a long period of time and form sporophores only under a combination of certain conditions.

We also noted sharp population increase of some species in certain time periods. For example, all seven finds of *Diderma tigrinum* (Schr.) Prihodko et al. were made in March. Apparently, the sporophores had persisted under snow since late autumn. In July 2021, sporophores of *Didymium proximum* Berk. et M.A. Curtis (26 specimens) were found on the surface of *Sphagnum* sp. along the edges of bogs, being the first records in the study area. Between 20–30 August, sporophores of *Didymium melanospermum* (Pers.) T. Macbr. were formed (31 specimens). Again, we have not recorded this species during other studies.

Thus, different species of myxomycetes have not only a certain seasonality of sporophore formation, but also

can form them not every year, which should be taken into account when planning field work.

CONCLUSION

The obtained results confirm the assumption that many species of myxomycetes have seasonal formation of sporophores. Despite the fact that the greatest diversity is found in the period from mid- to late summer, there are many species that form sporophores either in late autumn or early spring. For some of the most common species, periods of mass sporulation can be traced, while others, in contrast, can be found in the field throughout the entire snowless period. Some species of myxomycetes do not form sporophores every year. For these species, there are occasional bursts of abundance that are probably associated with weather conditions suitable for their sporulation. In the spring and autumn months, representatives of the order *Trichiales* take the lead in both abundance and diversity, while in summer their proportion is significantly reduced. Mass development of representatives of the order *Physarales* is observed from mid-summer to mid-autumn. Thus, a comprehensive research on the species diversity of myxomycetes in a particular territory requires long-term studies, which should be carried out in different phenological periods from snow melt to snow fall.

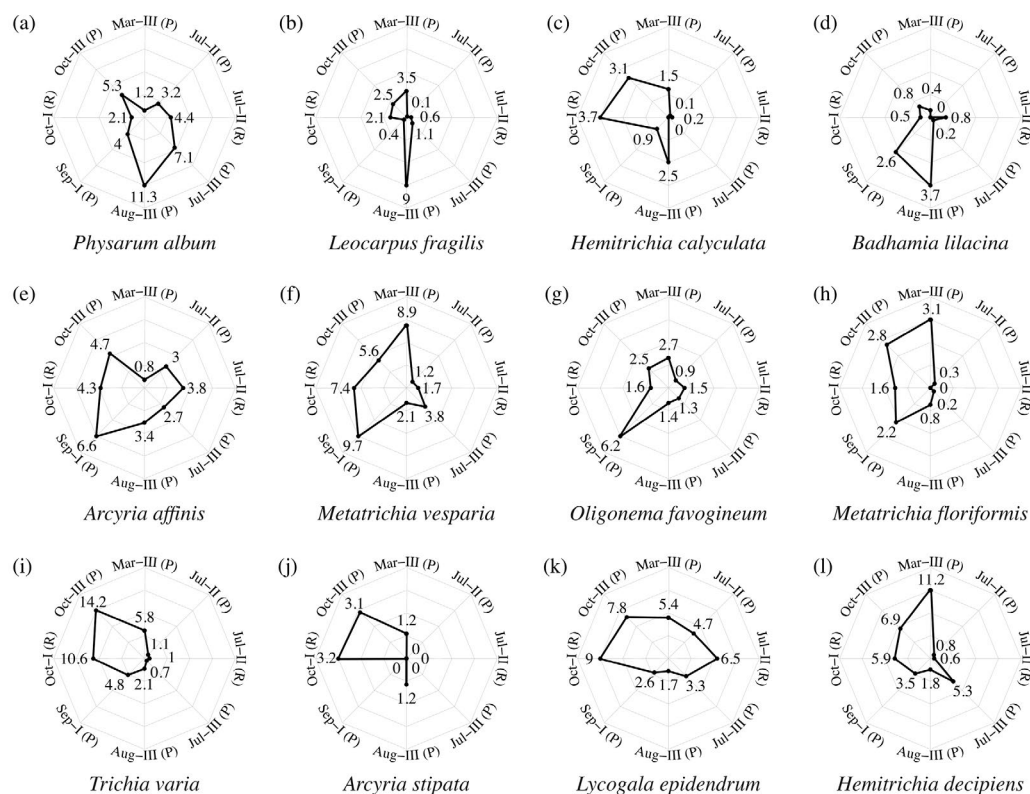


Fig. 6. Seasonality of sporophore formation for the most widespread species of myxomycetes from the Polistovo-Lovatskaya bog system (part 2).

We express our special gratitude to the managers and staff of the Polistovsky state nature reserve and the Rdeysky state nature reserve and personally to N.P. Korablev, V.V. Krolikov, N.A. Zavyalov, S. Yu. Igosheva, as well as to the inspectors of the conservation department of the reserves who provided transport accessibility and safety during the fieldwork. Field work by V.I. Gmshinskiy was supported by the Polistovsky nature reserve (FEA project № 1-22-66-3). Identification of specimens was supported by the grant from the Ministry of Science and Higher Education of the Russian Federation (№ 075-15-2021-1396).

The work of the third author was supported by the state task "Taxonomic, ecological and structural-functional diversity of fungi and fungus-like protists", 12401310-0829-3 (Komarov Botanical Institute RAS)

REFERENCES

- Adl S.M., Bass D., Lane C.E. et al. Revisions to the classification, nomenclature and diversity of *Eukaryotes*. J. Eukaryot. Microbiol. 2019. V. 66 (1). P. 4–119. <https://doi.org/10.1111/jeu.12691>
- Alexandrova V.D., Yurkovskaya T.K. Geobotanical zoning of the Non-Black Earth Region of the European part of the RSFSR. L., Nauka, 1989 (in Russ.).
- Bailly J., Fraissinet-Tachet L., Verner M.C. et al. Soil eukaryotic functional diversity, a metatranscriptomic approach. ISME J. 2007. V. 1. P. 632–642. <https://doi.org/10.1038/ismej.2007.68>
- Barsukova T.N. Ecological and biological features of myxomycetes of Zvenigorod Biological Station. Trudy Zvenigorodskoy biologicheskoy stantsii. 2001. V. 3. P. 90–91 (in Russ.).
- Bortnikov F.M., Matveev A.V., Gmshinskiy V.I. et al. Myxomycetes of Russia: a history of research and a checklist of species. Karstenia. 2020. V. 58 (2). P. 316–373. <https://doi.org/10.29203/ka.2020.502>
- Borзов N.I., Bortnikov F.M., Matveev A.V., Gmshinskiy V.I. First data on plasmodial slime moulds (*Myxomycetes* = *Myxogastrea*) of Rdeysky Nature Reserve (Novgorod Region, Russia). Novosti Sist. Nizsh. Rast. 2021. V. 55 (2). P. 361–377. <https://doi.org/10.31111/nsnr/2021.55.2.361>
- Borзов N.I., Gmshinskiy V.I. *Badhamia lilacina*: rare or poorly studied species? Polistovskaya pravda. 2020. V. 4(28). P. 7–9 (in Russ.).
- Chao A. Non-parametric estimation of the classes in a population. Scand. J. Stat. 1984. Vol. 11. P. 265–270.
- Chao A., Hu K. iNEXT4steps: four steps of INTERpolation and EXTrapolation analysis. R package version 1.0.1. 2023 (дата обращения: 26.08.2023).
- Chao A., Jost L. Estimating diversity and entropy profiles via discovery rates of new species. Methods Ecol. Evol. 2015.

- V. 6 (8). P. 873–882.
<https://doi.org/10.1111/2041-210X.12349>
- Chao A., Kubota Y., Zelený D. et al. Quantifying sample completeness and comparing diversities among assemblages. *Ecol. Res.* 2020. V. 35 (2). P. 292–314.
<https://doi.org/10.1111/1440-1703.12102>
- Eliasson U.H. Patterns of occurrence of myxomycetes in a spruce forest in South Sweden. *Holarc. Ecol.* 1981. V. 4. P. 20–31.
<https://doi.org/10.1111/j.1600-0587.1981.tb00976.x>
- Gmoshinskiy V.I., Matveev A.V. First data on *Myxomycetes* of Polistovsky Nature Reserve (Pskov Region). *Novosti Sist. Nizsh. Rast.* 2019. V. 53 (2). P. 279–290.
<https://doi.org/10.31111/nsnr/2019.53.2.279>
- Gmoshinskiy V.I., Matveev A.V. Seasonal dynamics of sporophore formation in myxomycetes of Moscow and Moscow Region. *Mikologiya i fitopatologiya.* 2016. V. 50 (3). P. 139–147.
- Good I.J. The population frequencies of species and the estimation of population parameters. *Biometrika.* 1953. V. 40 (3/4). P. 237–264.
<https://doi.org/10.1093/biomet/40.3-4.237>
- Hill M.O. Diversity and evenness: A unifying notation and its consequences. *Ecology.* 1973. V. 54 (2). P. 427–432.
<https://doi.org/10.2307/1934352>
- Ing B. The myxomycetes of Britain and Ireland. London, The Richmond Publishing Co. Ltd., 1999.
- Ko Ko T.W., Stephenson S.L., Hyde K.D., Lumyong S. Influence of seasonality on the occurrence of myxomycetes. *Chiang Mai Journal of Science.* 2011. V. 38. P. 71–84.
- Lado C. 2005–2023. An online nomenclatural information system of *Eumycetozoa*. <http://www.nomen.eumycetozoa.com>. Accessed 15.05.2023.
- Lado C., Eliasson U. Taxonomy and systematics: current knowledge and approaches on the taxonomic treatment of *Myxomycetes*: updated version. In: C. Rojas, S. L. Stephenson (eds.). *Myxomycetes: biology, systematics, biogeography, and ecology.* 2nd edition. Academic Press, L., 2022. P. 269–324.
<https://doi.org/10.1016/B978-0-12-824281-0.00005-1>
- Leontyev D., Buttgerit M., Kochergina A. et al. Two independent genetic markers support separation of the myxomycete *Lycogala epidendrum* into numerous biological species. *Mycologia.* 2022. V. 115 (2). P. 1–12.
<https://doi.org/10.1080/00275514.2022.2133526>
- Leontyev D., Ishchenko Y., Schnittler M. Fifteen new species from the myxomycete genus *Lycogala*. *Mycologia.* 2023. V. 115 (4). P. 1–37.
<https://doi.org/10.1080/00275514.2023.2199109>
- Leontyev D.V., Schnittler M., Stephenson S.L. et al. Towards a phylogenetic classification of the *Myxomycetes*. *Phytotaxa.* 2019. V. 399 (3). P. 209–238.
<https://doi.org/10.11646/phytotaxa.399.3.5>
- Martin G.W., Alexopoulos C.J. The *Myxomycetes*. University of Iowa Press, Iowa, 1969.
- Neubert H., Nowotny W., Baumann K. Die Myxomyceten Deutschlands und des angrenzenden Alpenraumes unter besonderer Berücksichtigung Österreichs. Bd 1: *Echinosteliales, Liceales, Trichiales.* Gomaringen. Karlheinz Baumann Verlag, 1993.
- Neubert H., Nowotny W., Baumann K. Die Myxomyceten Deutschlands und des angrenzenden Alpenraumes unter besonderer Berücksichtigung Österreichs. Bd 2: *Physarales.* Gomaringen. Karlheinz Baumann-Verlag, 1995.
- Neubert H., Nowotny W., Baumann K. Die Myxomyceten Deutschlands und des angrenzenden Alpenraumes unter besonderer Berücksichtigung Österreichs. Bd 3: *Stemonitales.* Gomaringen. Karlheinz Baumann Verlag, 2000.
- Novozhilov Yu.K., Rollins A.W., Shchepin O.N. et al. Ecology and distribution of myxomycetes. In: C. Rojas, S. L. Stephenson (eds.). *Myxomycetes: biology, systematics, biogeography, and ecology.* 2nd Edition. Academic Press, L., 2022. P. 325–376.
<https://doi.org/10.1016/B978-0-12-824281-0.00010-5>
- Novozhilov Yu.K., Malysheva V.F., Malysheva Ye.F. et al. Hidden diversity of fungi and fungus-like protists in natural ecosystems: problems and prospects. *Biosfera.* 2016. V. 8 (2). P. 202–215 (in Russ.).
<https://doi.org/10.24855/biosfera.v8i2.244>
- Novozhilov Yu.K. Definitorium Fungorum Rossiae. Issue 1. Class Myxomycetes. Nauka, SPb., 1993 (in Russ.).
- Oksanen J., Simpson G., Blanchet F. et al. Vegan: Community Ecology Package. R package version 2.6-4, <https://CRAN.R-project.org/package=vegan>. 2022. Accessed: 26.08.2023.
- Poulain M., Meyer M., Bozonnet J. Les *Myxomycetes*. Tome 1. Sévriér, Fédération mycologique et botanique Dauphiné-Savoie, 2011a.
- Poulain M., Meyer M., Bozonnet J. Les *Myxomycetes*. Tome 2. Planches. Sévriér, Fédération mycologique et botanique Dauphiné-Savoie, 2011b.
- R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>. 2022. Accessed: 26.08.2023.
- Reshetnikova N.M., Korolkova E.O., Novikova T.A. Vascular plants of the Polistovsky Nature Reserve. Moscow, Komissia RAN po sokhraneniю biologicheskogo raznoobrazia i IPEE RAN, 2006 (in Russ.).
- Reshetnikova N.M., Korolkova K.O., Zueva N.V. Vascular plants of the Rdeysky Nature Reserve. Moscow, 2007 (in Russ.).
- Ronikier A., Halamski A.T. Is *Myxomycetes (Amoebozoa)* a truly ambiregnal group? A major issue in protist nomenclature. *Protist.* 2018. V. 169 (4). P. 484–493.
<https://doi.org/10.1016/j.protis.2018.05.002>
- Schnittler M., Dagamac N.H.A., Woyzichowski J. et al. Biogeographical patterns in myxomycetes. In: C. Rojas, S.L. Stephenson (eds.). *Myxomycetes: biology, systematics, biogeography, and ecology.* 2nd edn. Academic Press, L., 2022. P. 377–416.
- Schnittler M., Novozhilov Y.K. The myxomycetes of boreal woodlands in Russian northern Karelia: a preliminary report. *Karstenia.* 1996. V. 36. P. 19–40.
<https://doi.org/10.29203/ka.1996.316>
- Shchepin O.N., Schnittler M., Erastova D.A. et al. Community of dark-spored myxomycetes in ground litter and soil of taiga

- forest (Nizhne-Svirskiy Reserve, Russia) revealed by DNA metabarcoding. *Fungal Ecol.* 2019. Vol. 39. P. 80–93. <https://doi.org/10.1016/j.funeco.2018.11.006>
- Sørensen T. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *K. Dansk. Vidensk. Selsk. Skr.* 1948. Bd 5 (4). P. 1–34.
- Stephenson S.L. Secretive slime moulds. *Myxomycetes of Australia*. Melbourne, ABRIS. CSIRO Publishing, Canberra, 2021.
- Stephenson S.L., Fiore-Donno A.M., Schnittler M. *Myxomycetes in soil*. *Soil Biol. Biochem.* 2011. V. 43 (11). P. 2237–2242. <https://doi.org/10.1016/j.soilbio.2011.07.007>
- Stephenson S.L., Schnittler M., Lado C. et al. Studies of Neotropical mycetozoans. *Syst. Geogr. Plants.* 2004. V. 74. P. 87–108.
- Urich T., Lanzén A., Q.J., Huson D.H. et al. Simultaneous assessment of soil microbial community structure and function through analysis of the meta-transcriptome. *PLOS One*. 2008. V. 3 (6). e2527. <https://doi.org/10.1371/journal.pone.0002527>
- Vlasenko A.V., Novozhilov Yu.K. Phenological features of myxomycetes in the pine forests on the right bank part of the Upper Ob river. *Rastitelnyi mir aziatskoy Rossii*. 2011. V. 2(2). P. 3–8 (in Russ.).
- Wrigley de Basanta D., Estrada-Torres A. Techniques for recording and isolating myxomycetes: updated. In: C. Rojas, S.L. Stephenson (eds). *Myxomycetes: biology, systematics, biogeography, and ecology*. 2nd edn. Academic Press, L., 2022. P. 417–452. <https://doi.org/10.1016/B978-0-12-824281-0.00015-4>
- Zavyalov N.A. Weather. *Letopis prirody gosudarstvennogo prirodnogo zapovednika "Rdeyskiy"*. Rdeyskiy zapovednik, Kholm, 2022 (in Russ.).
- Александрова В.Д., Юрковская Т.К. (Alexandrova, Yurkovskaya) Геоботаническое районирование Нечерноземья европейской части РСФСР. Л.: Наука, 1989. 59 с.
- Барсукова Т.Н. (Barsukova) Эколого-биологические особенности миксомицетов Звенигородской биологической станции // Труды Звенигородской биологической станции. 2001. Т. 3. С. 90–91.
- Борзов Н.И., Гмошинский В.И. (Borzov, Gmoshinskiy) *Badhamia lilacina*: редкий или малоизученный вид? // Полистовская правда. 2020. № 4 (28). С. 7–9.
- Власенко А.В., Новожилов Ю.К. (Vlasenko, Novozhilov) Фенологические особенности миксомицетов сосновых лесов правобережной части верхнего Приобья // Растительный мир Азиатской России. 2011. № 2 (2). С. 3–8.
- Завьялов Н.А. (Zavyalov) Погода / Летопись природы государственного природного заповедника "Рдейский". Холм: Рдейский государственный заповедник. 2022. 341 с.
- Новожилов Ю.К. (Novozhilov) Определитель грибов России. Отдел Слизевика. Вып. 1. Класс Миксомицеты. СПб.: Наука. 1993. 288 с.
- Новожилов Ю.К., Малышева В.Ф., Малышева Е.Ф. и др. (Novozhilov et al.) Скрытое разнообразие грибов и грибоподобных протистов в природных экосистемах: проблемы и перспективы // Биосфера. 2016. Т. 8 (2). С. 202–215.
- Решетникова Н.М., Королькова Е.О., Новикова Т.А. (Reshetnikova et al.) Сосудистые растения заповедника "Полистовский". М.: Комиссия РАН по сохранению биологического разнообразия и ИПЭЭ РАН. 2006. 98 с.
- Решетникова Н.М., Королькова К.О., Зуева Н.В. (Reshetnikova et al.) Сосудистые растения Рдейского заповедника. М.: Комиссия РАН по сохранению биологического разнообразия. 2007. 89 с.

Сезонность формирования спороношений миксомицетов (*Myxomycetes*) Полистово-Ловатской болотной системы (Псковская и Новгородская области, Россия)

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Представлены результаты четырех лет наблюдений за сезонностью формирования спороношений миксомицетов, выполненных на территории Полистово-Ловатской болотной системы. Показано, что наибольшее видовое разнообразие миксомицетов наблюдается в середине лета, после чего оно постепенно снижается. Видовой состав миксомицетов изменяется в зависимости от времени года. Выделены 5 фенологических групп: весенние, летние, раннеосенние, позднеосенние и виды без ярко выраженных периодов массового формирования спороношений. Показано, что в разные годы перечень выявляемых таксонов может значительно отличаться и существуют широко распространенные виды, которые формируют спороношения не каждый год. Таким образом, при проведении исследований в полевых условиях, необходимо планировать их в течение нескольких лет, а выезды осуществлять на протяжении всего бесснежного периода.

Ключевые слова: биоразнообразие, динамика численности, методология полевых исследований, слизевика, фенология.