DIATOMS OF PROTECTED AREAS OF NORTHEAST ASIA AS INDICATORS IN A GRADIENT OF GEOGRAPHICAL AND CLIMATIC FACTORS

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Northeast Asia is a vast region encompassing diverse natural and climatic zones, from arctic tundra to taiga, with much of it located within permafrost. This study of the regional diatom communities helped identify a number of important patterns and assess processes associated with past global climate change, as well as current climate trends and anthropogenic impacts. Protected Areas serve as natural laboratories for studying the response of biota to geographic and climatic conditions. Diatoms have long been recognised by experts as reliable bioindicators of the environment. However, such research in the regional Protected Areas remains insufficient. The main goal of our study was to assess the resilience of diatom communities across a broad gradient of geographical and climatic factors in Northeast Asia, using Protected Areas with the best-studied diatom floras as an example. Our studies were conducted in the Olyokma State Nature Reserve (Russia) as a model area in 2011 and 2024. Using scanning electron microscopy, we have increased the diatom species list of the Olyokma State Nature Reserve by 269 species. At most stations within the Olyokma State Nature Reserve, genera such as *Pinnularia*, *Eunotia*, and *Gomphonema* predominate in terms of the number of taxa; representatives of these three genera clearly play a key role in the studied flora. The intraspecific variability index Subspecies/Species for the water bodies of the Olyokma State Nature Reserve ranged from 1.00 to 1.06. Overall, 66% of diatom species in Olyokma State Nature Reserve are classified in one or more threat categories by IUCN; five diatom species are in the «Critically Endangered» category. Bioindication and statistical methods showed that the waters of the Olyokma State Nature Reserve correspond to natural water properties. Indicator characteristics demonstrate a significant response of diatom species composition to changes in salinity and pH. For a comparative analysis of our results, we selected 11 most well-studied diatom floras in Protected Areas of Northeast Asia using the Willis criteria. Comparative analysis revealed an increase in the number of taxa in coastal areas, which may be related to the ecotone effect occurring at the interface between continental and marine habitats. In Protected Areas without permafrost, with a milder climate and a longer open-water period, increased intraspecific variability and a specific number of species per unit area were observed. Patterns in the spatial distribution of diatoms were identified in 12 Protected Areas. Geography and the associated permafrost-climate interface play a significant role in shaping diatom communities in Protected Areas. The study is important for developing a framework for monitoring biodiversity in Protected Areas and climate change in the region.

Key words: bioindicators, climate, comparative floristics, diversity, ecology, IUCN, statistical mapping, threatened species

Introduction

Protected Areas are the basis of the surviving biosphere and serve as wildlife benchmarks against which to assess the scale of anthropogenic changes. Studying the Bacillariophyta diversity in Protected Areas is important not only for microflora inventory but also for ecology and conservation. Diatoms, as single-celled organisms that provide about a quarter of global primary production (Field et al., 1998; Tréguer et al., 2018), are an important component of continental aquatic ecosystems and ideal «sensors» of environmental health. Protected Areas serve as natural laboratories, where ecosystems develop with minimal anthropogenic impact. Studying of diatoms here allows us to establish background water quality indicators (Cantonati & Spitale, 2009). Analysis of diatom communities in Protected Areas helps to establish reference communities unaffected by anthropogenic impact. Many rare, endemic diatom or stenobiont species survive only in pristine water bodies of Protected Areas, which act as refugia. This has been demonstrated in the case of isolated high-altitude lakes, which have proven to be critical habitats for Red List diatom species (Ossyssek et al., 2022). Diatoms are extremely sensitive to water temperature and pH. Due to their short life cycle, they respond to climate change faster than other aquatic organisms (fish, vascular plants). In Protected Areas, where there is no direct pollution, the «noise» of anthropogenic factors is cut off, which makes it possible to see the net response of the biota to warming (Smol & Stoermer, 2010). Diatoms provide important ecosystem services; this was demonstrated by the example of how the structure of diatom communities in pristine locations ensures the stability of the entire aquatic ecosystem (Soininen, 2007). The study of diatoms in Protected Areas is the basis for the creation of databases for organising environmental monitoring, allowing us to evaluate the effectiveness of conservation measures, and also predict the consequences of climate change for the region's water resources.

Northeast Asia can be called the planet's «climate pendulum», where microalgal communities respond to the slightest changes in temperature and hydrochemistry. The region spans from the taiga to the Arctic tundra. The permafrost zone has a great impact on the stability of Northeast Asia's diatom communities. Permafrost degradation releases large quantities of organic matter and microelements into the water. The duration of ice cover is a critical factor. Warming leads to an earlier breakup of water bodies and an extended open water period, which inevitably impacts biodiversity and leads to biological invasions. The continental gradient and the proximity of specific habitats to the ocean coast can significantly influence aquatic communities within this region, contributing to the formation of ecotone zones and changing the importance of stenobionts (Barinova et al., 2023).

Studies of diatom communities in the region across a spatial gradient of climatic parameters and water chemistry have shown that water conductivity is the best indicator of environmental conditions, and a qualitative leap, or «turnover», i.e. a sharp change in community composition, occurs at the boundary of the forest-tundra and northern taiga (Pestryakova, 2008; Pestryakova et al., 2018). It was found that communities in lakes in the tundra zone are less diversified and more sensitive to warming. Palaeoecological studies have allowed us to establish the response of diatoms to glaciation and Holocene warming, and to determine how diatom communities have changed in response to modern warming since the beginning of the XX century (Biskaborn et al., 2023). The resilience of planktonic and benthic species to extreme Arctic ice conditions over a million years was assessed (Snyder et al., 2013). Current trends and anthropogenic influence on the community structure of the region are illustrated by the example of Lake Khamra, where a sharp shift occurred after 1970: planktonic species (*Discostella stelligera* (Cleve & Grunow) Houk & Klee) began to displace the common species of the genus *Aulacoseira* due to changes in the timing of ice melt (Stieg et al., 2025). Using the isotopic composition of diatom valves, researchers have been able to assess changes in precipitation and water balance in the region (Stieg et al., 2024).

Researchers have found that diatom communities in Northeast Asia exhibit a high «memory» of environmental changes. Although they are adapted to extremely low temperatures, current global warming is causing a process of «homogenisation» where unique arctic-alpine species are gradually being replaced by more common temperate species (Seastedt & Oldfather, 2021). However, bioindication studies of diatom communities across a gradient of geographical and climatic factors in Protected Areas across the vast region of Northeast Asia are still lacking.

The study of the diatom flora of Olyokma State Nature Reserve, which can be used as a model site, has so far been conducted only using light microscopy; there have been no studies using an electron microscope before our research. Moreover, only planktonic diatom communities have been studied, while periphyton communities have remained unexplored. The first algological material within the Olyokma State Nature Reserve was obtained by researchers on the River Olyokma and River Amga during the open water period from 1992 to 1995 (Vasilyeva et al., 1996, 1997, 1998; Rozhkova, 1996, 2001). In 2011, we obtained data on planktonic algae of the River Olyokma, on its section within the Olyokma State Nature Reserve (Gabyshev & Gabysheva, 2013). Based on the totality of these studies, 195 species and varieties were identified in the diatom flora of the Protected Area. The aim of our study was to obtain new data on the diatom flora of Olyokma State Nature Reserve and to assess the stability of diatom communities in a wide gradient of geographical and climatic factors of Northeast Asia using the example of 12 of the best-studied floras of Protected Areas.

Material and Methods

Description of the study area

The Olyokma State Nature Reserve is situated in Northeast Asia, in a zone of continuous permafrost, within the middle taiga subzone (Fig. 1). The climate is sharply continental, with significant annual temperature fluctuations. Minimal January temperatures are -60°C, maximal July temperatures are +34°C (Izyumenko, 1968). Stable snow cover lasts approximately 200 days. The open water period lasts 134 days.

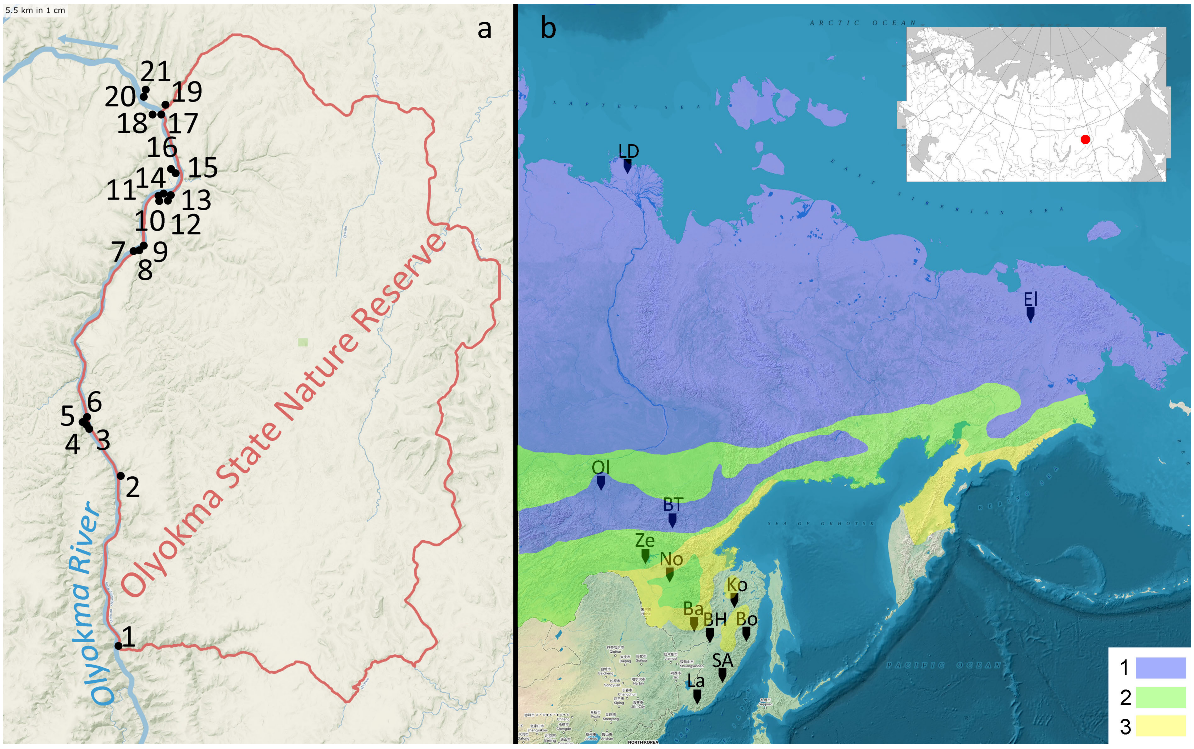

Fig. 1. Study area of Olyokma State Nature Reserve (a), with numbers of sampling stations. Designations: 1 – Mouth of River Tas-Haiko; 2 – Lake 7; 3 – Lake Podskalnoye; 4 – River Olyokma above the mouth of River Oryus-Miele; 5 – Mouth of River Oryus-Miele; 6 – River Olyokma below mouth of River Oryus-Miele; 7 – River Olyokma above mouth of River Krestyakh; 8 – Mouth of River Krestyakh; 9 – River Olyokma below mouth of River Krestyakh; 10 – Lake 4; 11 – Lake 3; 12 – Lake 1; 13 – Lake 2; 14 – River Olyokma; 15 – Lake Bolshoy Sordonokh; 16 – Pool 1; 17 – Swamp 1; 18 – Lake 5; 19 – Stream 1; 20 – Stream 2; 21 – Lake Mundunda. Northeast Asian Protected Areas and permafrost extent in Russia (b), including continuous (1), discontinuous (2), sporadic (3) permafrost. In the upper left corner is the map of Russia, where red dot indicates the Olyokma State Nature Reserve. Name codes of Protected Areas: Ze – Zeya State Nature Reserve; La – Lazovsky State Nature Reserve; SA – Sikhote-Alin State Nature Reserve; Bo – Botchinsky State Nature Reserve; BH – Bolshekhekhtsirsky State Nature Reserve; Ba – Bastak State Nature Reserve; Ko – Komsomolsky State Nature Reserve; No – Nora State Nature Reserve; BT – State Nature Sanctuary Bolshoye Toko; Ol – Olyokma State Nature Reserve; El – State Nature Sanctuary Elgygytgyn Lake; LD – Lena Delta State Nature Reserve.

The hydrographic network of Olyokma State Nature Reserve is a part of the River Lena basin and includes tributaries of the River Olyokma and the upper part of the River Amga basin. There are no large lakes, but there are numerous small water bodies, represented mostly by oxbow lakes located in river valleys.

Sampling

Sampling was carried out in the Olyokma State Nature Reserve from 30.06.2011 to 1.07.2011 and from 12.08.2024 to 18.08.2024. We surveyed various water bodies located in the River Olyokma floodplain on 21 stations, including several small oxbow lakes, a swamp, a pool on a salt lick, streams, and the River Olyokma itself (Table 1). Lake 5, Swamp 1, Stream 2, Pool 1, Lake Mundunda, and Lake Bolshoy Sordonokh are located within the buffer zone of the Protected Area; the remaining water bodies are located within its boundaries (Fig. 1a). The River Olyokma flows for 130 km through the Olyokma State Nature Reserve, and upstream, several mining operations are located on its banks. The selection of sampling sites along the River Olyokma channel, including the river course and its floodplain water bodies that connect with it during flood periods, was motivated by the need to assess the impact of anthropogenic factors on the aquatic ecosystems of the Protected Area. In addition, we used data obtained between 1992 and 1995 on the River Olyokma and River Amga sections located within the boundaries of Olyokma State Nature Reserve (stations 22, 23) (Vasilyeva et al., 1996, 1997, 1998; Rozhkova, 1996, 2001). Station numbers are ordered by increasing latitude (Table 1).

A total of 24 samples were collected, including plankton, biofilms, moss extracts, and stone scrapings (Table 1) in accordance with the methods generally accepted in algology (Abakumov, 1983). An Apstein net (SEFAR NITEX fabric, mesh size 15 µm) (Sefar Holding AG, Thal, Switzerland) was used to collect plankton and moss extracts. Biofilm was removed from the surface of the lake silt with a spatula, and stone scrapings were washed off with a brush. All samples were fixed with neutral formaldehyde solution and transported to the lab for analysis.

Northeast Asia is a vast region with diverse natural and climatic conditions, as well as varying degrees of anthropogenic impact on aquatic ecosystems, most of which are situated in the permafrost zone. Our study used data from 11 other Northeast Asian Protected Areas (NAPAs), which diatom flora has been best studied (Fig. 1b, Table 2). These NAPAs include areas in the Northeast part of Eurasia that are located on the meridional direction from south to north both within the permafrost zone (including continuous, discontinuous, and sporadic permafrost) and beyond.

Table 1. Information on the type of samples and sampling locations in the Olyokma State Nature Reserve in 1992–1995, 2011, and 2024

Station number	Name of water body	Sampling date	Number and type of sample	Altitude, m a.s.l.	Latitude, °N	Longitude, °E
1	River Mouth of Tas-Haiko	30.06.2011	1	220	58.17449	121.61271
2	Lake 7	17.08.2024	2	236	58.50153	121.62024
3	Lake Podskalnoye	17.08.2024	3, 3b	199	58.59180	121.50616
4	River Olyokma above the mouth of River Oryus-Miele	01.07.2011	4	199	58.59583	121.50170
5	Mouth of River Oryus-Miele	01.07.2011	5	195	58.60170	121.49432
6	River Olyokma below mouth of River Oryus-Miele	01.07.2011	6	194	58.61239	121.49639
7	River Olyokma above mouth of River Krestyakh	01.07.2011	7	180	58.92738	121.67821
8	Mouth of River Krestyakh	01.07.2011	8	175	58.92814	121.68592
9	River Olyokma below mouth of River Krestyakh	01.07.2011	9	215	58.93161	121.69260
10	Lake 4	13.08.2024	10	169	59.03040	121.76072
11	Lake 3	13.08.2024	11, 11b	170	59.03211	121.75743
12	Lake 1	12.08.2024	12, 12b	165	59.03387	121.78001
13	Lake 2	12.08.2024	13	164	59.03545	121.78547
14	River Olyokma	18.08.2024	14b	165	59.03722	121.77220
15	Lake Bolshoy Sordonokh	16.08.2024	15	168	59.07370	121.81822
16	Pool 1	16.08.2024	16b	168	59.07783	121.80769
17	Swamp 1	14.08.2024	17b	155	59.18480	121.76170
18	Lake 5	14.08.2024	18	155	59.18483	121.75874
19	Stream 1	14.08.2024	19b	200	59.19830	121.78297
20	Stream 2	14.08.2024	20b	157	59.21868	121.69631
21	Lake Mundunda	14.08.2024	21	162	59.21925	121.70235
22	River Olyokma (averaged data for 1992–1995)	n/a	n/a	n/a	n/a	n/a
23	River Amga (averaged data for 1992–1995)	n/a	n/a	n/a	n/a	n/a

Note: Sample type: number without letter index is a plankton sample, number and «b» index is a periphyton sample. «n/a» – data are not available.

Table 2. Data on Northeast Asian Protected Areas

Name code	Names of Protected Areas	Administrative district	Latitude, °N	Longitude, °E	References
Ze	Zeya State Nature Reserve	Amur Region	53.96278	127.37250	Medvedeva (2010a)
La	Lazovsky State Nature Reserve	Primorsky Krai	43.23333	133.40000	Goncharov et al. (2002), Medvedeva (2005)
SA	Sikhote-Alin State Nature Reserve	Primorsky Krai	45.03333	136.33333	Medvedeva (2001, 2016)
Bo	Botchinsky State Nature Reserve	Khabarovsky Krai	48.13639	139.22111	Medvedeva (2015)
BH	Bolshekhekhtsirsky State Nature Reserve	Khabarovsky Krai	48.20500	134.85889	Medvedeva (2019)
Ba	Bastak State Nature Reserve	Jewish Autonomous Okrug	48.94361	133.12028	Medvedeva & Savateev (2007), Savateev (2008), Savateev & Medvedeva (2008), Medvedeva (2024)
Ko	Komsomolsky State Nature Reserve	Khabarovsky Krai	50.81000	137.71917	Barinova & Medvedeva (1989)
No	Nora State Nature Reserve	Amur Region	52.50111	130.29250	Medvedeva (2010b)
BT	State Nature Sanctuary Bolshoye Toko	Yakutia	56.26667	130.53333	Barinova et al. (2025c)
Ol	Olyokma State Nature Reserve	Yakutia	58.65611	122.25778	Vasilyeva et al. (1996, 1997, 1998), Rozhkova (1996, 2001), Gabyshev & Gabysheva (2013), and present research
El	State Nature Sanctuary Elgygytgyn Lake	Chukotka	67.50000	172.00000	Kharitonov & Genkal (2012)
LD	Lena Delta State Nature Reserve	Yakutia	73.18111	125.31583	Barinova et al. (2023)

Diatom analysis

Diatom valves were freed from organic matter by cold combustion (Balonov, 1975). The suspension of cleaned valves was applied to a stage and dried at room temperature. Specimen preparation was carried out by sputter gold, using an Eiko IB 3 ion coater (Eiko Engineering, Ltd.; Hitachinaka, Japan). The material was examined under a JSM-6510LV scanning electron microscope (JEOL Ltd.; Tokyo, Japan). The preparations are stored in the collection of Sergey I. Genkal (Institute of Biology of Inland Waters of RAS, Russia). Algal abundance was assessed using a six-point frequency scale (Barinova, 2017a). For taxonomic identification of diatoms, reference books and individual articles were used (Krammer & Lange-Bertalot, 1986, 1988, 1991a,b; Lange-Bertalot & Moser, 1994; Krammer, 1997a,b, 2000, 2002, 2003; Lange-Bertalot & Genkal, 1999a,b; Reichardt, 1999; Lange-Bertalot, 2001; Werum & Lange-Bertalot, 2004; Levkov, 2009; Genkal et al., 2011; Lange-Bertalot et al., 2011, 2017; Kharitonov & Genkal, 2012; Levkov et al., 2013, 2016; Kulikovskiy et al., 2016; Beauger et al., 2022). Names of taxa were adopted in accordance with algaebase.org (Guiry & Guiry, 2026). Threatened species are designated based on the distribution data of well-studied diatoms in Central Europe (Hofmann et al., 2018) in comparison with the IUCN criteria (IUCN, 2012).

Data analysis

Data on the physicochemical composition of the water of the studied water bodies, used in the statistical analysis of this study, have been published previously by Gabysheva & Gabyshev (2023) and Barinova et al. (2025a) and represented in Electronic Supplement 1. Bioclimatic variables for statistical analysis were obtained from the worldclim.org portal (Fick & Hijmans, 2017; Zomer et al., 2022) and include data about precipitation, water temperature, wind speed and solar radiation in the mentioned geographical co-ordinates. The source of composite Dynamic Habitat Indices (DHI) based on the MODIS (Moderate Resolution Imaging Spectroradiometer) collection, also used in the statistical analysis, is the portal Spatial Analysis for Conservation and Sustainability by SILVIS LAB (Myneni et al., 2015).

For analysis of the completeness of diatom floras in NAPAs, we examined three classes of species – area relationship (SAR) models: (i) log-log models following the Arrhenius-Wilson-MacArthur formulation (Arrhenius, 1921; MacArthur & Wilson, 1963); (ii) semi-log models of the Gleason type (Gleason, 1922); and (iii) «direct models» describing the dependence of species richness on area without logarithmic transformation. For each class, we considered both a basic formulation, with NAPAs area as the sole predictor, and climatically extended versions, in which area was combined with an additional climate-related factor (Barinova et al., 2025b).

Bioindicator analysis was performed according to Barinova (2017b) with species-specific ecological preferences of revealed taxa (Barinova, 2025). The saprobity index S was calculated on the data and equation represented in Barinova (2025). Statistical maps were constructed with Statistica 12.0 program (StatSoft, USA). The network analysis in JASP (significant only) and correlation analysis was done on the botnet package in R Statistica package (Love et al., 2019). The BioDiversity Pro 2.0 program was used for Index Shannon H' and similarity calculation (McAleece et al., 1997). For the calculation of the average values of the species per genus index, the genus index and the species index was performed using Microsoft Excel.

The diatom flora of the Olyokma State Nature Reserve was shown to be relatively rich (Electronic Supplement 2), allowing us to analyse the degree of its endemism and clarify questions regarding threatened species. Research devoted to the study of diatom species under threat in Russia is currently scarce (e.g. Geltman, 2018a,b; Degteva et al., 2021). We used a well-established and regularly updated resource, Germany's Red Data Book of diatom species (Hofmann et al., 2018), as a basis for identifying potentially endangered species in the Olyokma State Nature Reserve.

Results

Taxonomic analysis of diatom community in the Olyokma State Nature Reserve

Using electron microscopy, a considerable diversity of diatoms (329 taxa; Electronic Supplement 2; Fig. 2) was identified for the first time in water bodies of the Olyokma State Nature Reserve in communities of 21 sampling stations (Fig. 1). This allowed us to expand the total floristic list of diatoms in the Protected Area, which, considering previously identified 151 diatom species mentioned for the station 22 and station 23, amounted to 420 taxa (Electronic Supplement 2). Hence, the species composition of diatoms in the Protected Area increased by 269 species. The number of species in the diatom flora of the Protected Area alone is now 420, and the number of genera is 81 (Electronic Supplement 3).

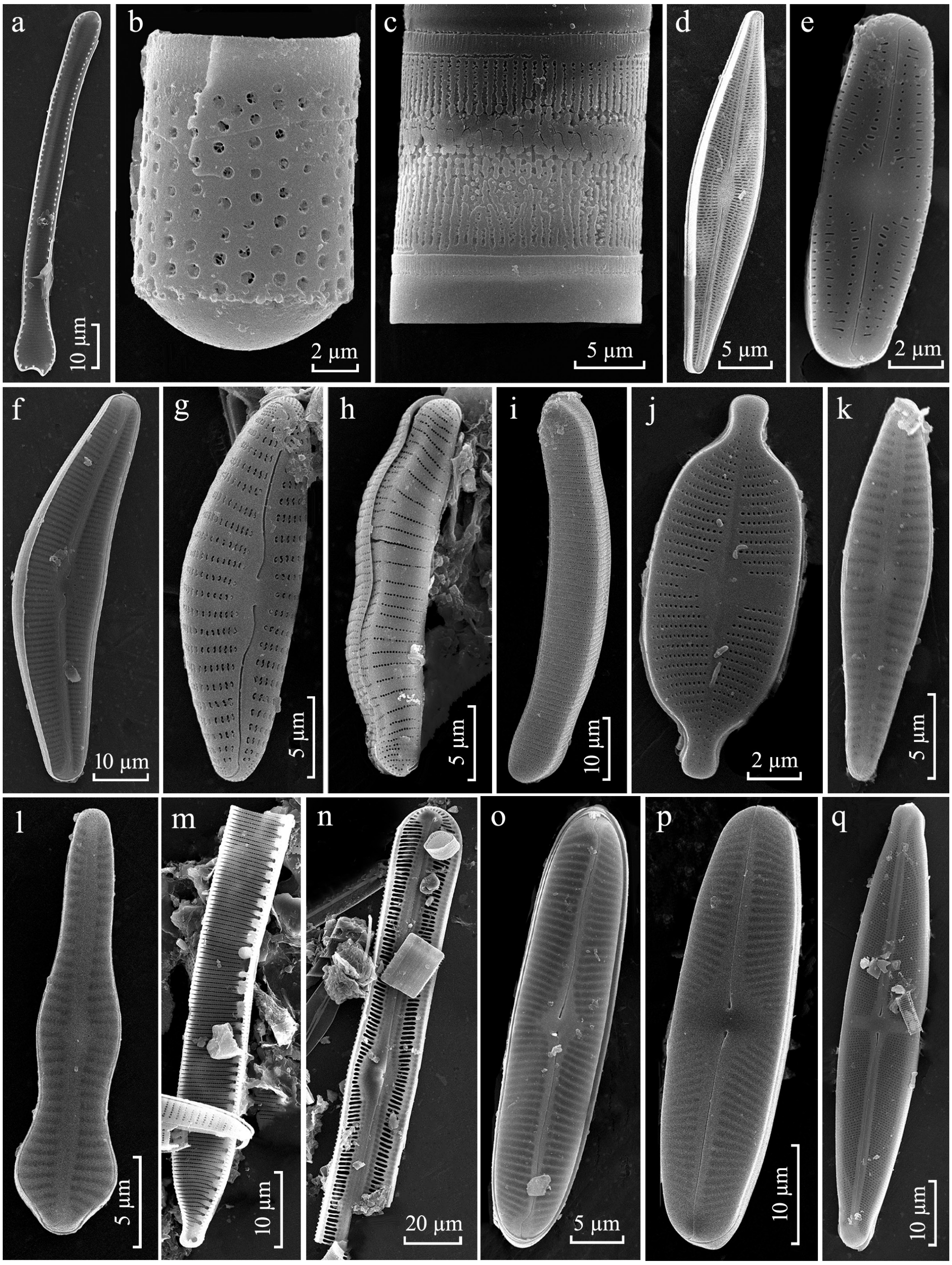

Fig. 2. Electron micrographs of diatoms of studied water bodies of Olyokma State Nature Reserve (Russia). Designations: a – *Actinella punctata* F.W.Lewis, b – *Aulacoseira crassipunctata* Krammer, c – *A. lacustris* (Grunow) Krammer, d – *Brachysira liliana* Lange-Bertalot, e – *Chamaepinnularia witkowskii* (Lange-Bertalot & Metzeltin) Kulikovskiy & Lange-Bertalot, f – *Cymbella cymbiformis* C.Agardh, g – *C. hustedtii* Krasske, h – *Eunotia circumborealis* Lange-Bertalot & Nörpel, i – *E. metamonodon* Lange-Bertalot, j – *Gogorevia exilis* (Kützing) Kulikovskiy & Kociolek, k – *Gomphonema jadwigae* Lange-Bertalot & E.Reichardt, l – *G. pseudacuminatum* Kulikovskiy, Kociolek & Solak, m – *Hantzschia abundans* Lange-Bertalot, n – *Pinnularia gentilis* (Donkin) Cleve, o – *P. isselana* Krammer, p – *P. neohalophila* Kulikovskiy, Genkal & Mikheeva, q – *Stauroneis subgracilis* Lange-Bertalot & Krammer.

According to a six-score frequency scale, the three most abundant plankton species in the studied water bodies were *Aulacoseira alpigena* (Grunow) Krammer, *A. italica* (Ehrenberg) Simonsen, and *A. valida* (Grunow) Krammer (scale score = 3); in periphyton, five species: *Didymosphenia geminata* (Lyngbye) Mart.Schmidt (scale score = 4) and *Aulacoseira valida*, *Navicula radiosa* Kützing, *Rhoicosphenia abbreviata* (C.Agardh) Lange-Bertalot, *Tabellaria flocculosa* (Roth) Kützing (scale score = 3; Electronic Supplement 2). Of all the species detected, more than half were found in plankton samples (241 taxa) collected at 16 stations and slightly fewer (214 taxa) in periphyton from eight stations.

The highest number of diatom taxa was found at station 12 (Lake 1) and station 22 (River Olyokma, averaged data for 1992–1995) (Table 3). Among plankton samples based on 2024 data, the highest number of taxa was found at station 2 (Lake 7); among periphyton samples – station 12b (Lake 1) (Electronic Supplement 4). The smallest number of taxa was noted at station 11 (Lake 3), station 3 (Podskalnoye Lake), and station 17b (Swamp 1) (Electronic Supplement 4). The species-only number in the studied communities varied from nine at station 11 (Lake 3, plankton sample) to 104 at station 22 (River Olyokma, averaged data for 1992–1995). The average species per genus index ranged from 1.5 to 3.0 (averaged 1.4) and was the highest at station 12, where out of 38 genera only three included 39% number of taxa: *Pinnularia* (16 taxa), *Eunotia* (15 taxa) and *Gomphonema* (14 taxa). The index of intraspecific variability (taxon richness per species) ranged from 1.0 to 1.06 with a maximum value at station 22 and station 23 (Table 3). The saturation of revealed genera by species was calculated for each diatom community in the Protected Area and represented in Table 3 and shows that usually genera are 1–2 species rich, apart from the community of station 12, where were up to 3 taxa per genus. The infraspecific variability index calculated as number of taxa per species number (Subspecies / Species index) varied in low range and demonstrated a high specificity of revealed species (Table 3).

Station 12 (Lake 1) and station 22 (River Olyokma, averaged data for 1992–1995) also stand out in the distribution of the ten richest genera of diatoms in the Protected Area (Fig. 3a). At most stations, such genera as *Pinnularia*, *Eunotia*, and *Gomphonema* predominate in terms of the number of taxa; representatives of these three genera obviously play a crucial role in the Protected Area's flora (Fig. 3b). However, in the upper and lower parts of the River Olyokma valley, *Cymbella* species are of great importance. The genus *Navicula* is distinguished by many taxa at station 15, station 16, and station 23. The genus *Nitzschia* is present at station 16 and station 21. In the middle part of the River Olyokma valley, *Sellaphora* species have a great proportion (up to 20%).

Table 3. Distribution of diatom diversity data over sampling stations in the Olyokma State Nature Reserve in 1992–1995, 2011 and 2024

Station	Number of taxa	Genus	Species/Genus index	Species only	Subspecies / Species index
1	24	15	1.6	24	1.00
2	61	33	1.8	61	1.00
3	50	25	2.0	50	1.00
4	38	24	1.5	37	1.03
5	40	25	1.6	39	1.03
6	39	23	1.7	38	1.03
7	47	31	1.5	46	1.02
8	49	31	1.6	49	1.00
9	43	27	1.6	42	1.02
10	39	20	2.0	39	1.00
11	77	40	1.9	76	1.01
12	116	38	3.0	115	1.01
13	49	21	2.3	49	1.00
14	48	28	1.7	48	1.00
15	35	19	1.8	35	1.00
16	28	13	2.2	28	1.00
17	15	8	1.9	15	1.00
18	57	30	1.9	57	1.00
19	17	11	1.5	17	1.00
20	51	35	1.5	51	1.00
21	50	28	1.8	50	1.00
22	110	47	2.2	104	1.06
23	64	34	1.8	61	1.05

Note: Sampling station numbers refer to Table 1.

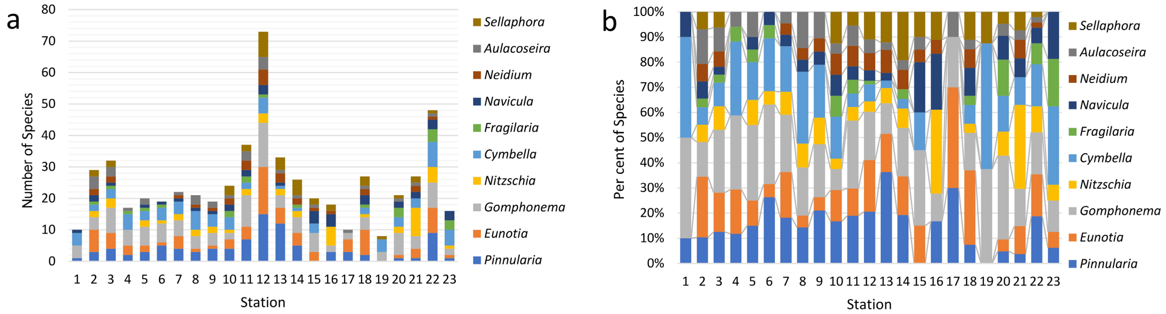

Fig. 3. Distribution of ten richest genera of diatoms on sampling stations in the Olyokma State Nature Reserve (Russia). Sampling station numbers refer to Table 1.

Bioindicators of diatom community

The ecological preferences of diatoms identified in the Olyokma State Nature Reserve are presented in Electronic Supplement 2 and Electronic Supplement 4. The distribution of indicator species by ecological preference is shown in Fig. 4. Species of benthic and planktonic-benthic habitats predominate (Fig. 4a). Species preferring moderate temperatures, as well as indicators of moderately aerated waters, find the best habitat conditions here (Fig. 4b,c). Low salinity indicators and indifferent species predominate (Fig. 4d). Water pH indicators demonstrate a predominance of alkaliphile and pH-indifferent groups (Fig. 4e). Organic pollution indicators according to the Watanabe classification allow us to characterise the studied water bodies as clean (Fig. 4f). Among nutritional indicators, autotrophs (ats and ate) strongly predominate (Fig. 4g). Trophic state indicators are distributed unevenly across groups, with two peaks observed in the oligotrophic and eutrophic (ot and e) groups, reflecting some impact on aquatic ecosystems, leading to increased trophic status in individual water bodies (Fig. 4h). The water quality was determined using the species-specific saprobity index S for classes 1–5: indicators of organic-free waters in class 2 and class 3 predominate (Fig. 4i). Detailed information on the distribution of indicator species in the Olyokma State Nature Reserve across ecological groups is presented in Electronic Supplement 4.

Environmental – biological variables relationships in the Olyokma State Nature Reserve

An analysis of the identified diatom diversity and their predominant groups of environmental preferences as dependent variables (Electronic Supplement 4) was conducted in comparison with hydrochemical data as independent variables (Electronic Supplement 1). Since the RDA method commonly used for such analysis showed insufficiently reliable results (eigenvalue = 0.654; $p = 0.44$), we conducted a correlation analysis of the same data and constructed a heatmap (Fig. 5).

Fig. 5 shows that the number of taxa has a highly significant correlation ($r = 0.56–0.94$; $p < 0.01$, $p < 0.001$) with the Shannon index and all other groups of bioindicators. A significant negative correlation was found between the water pH and TDS (total dissolved solids), calcium, carbonate, nitrate, and ammonium nitrogen concentrations (from $r = -0.58$ to $r = -0.78$; $p < 0.01$, $p < 0.001$) and a positive correlation with the number of indicators for slow-flowing (st-str), slightly alkaline waters (alf), with low salinity (i) ($r = 0.45–0.58$; $p < 0.05$, $p < 0.01$). The group of oligotrophic indicators has a positive correlation with the water temperature ($r = 0.466$; $p < 0.05$). Macroscale factors, such as bioclimatic variables and DHI (Electronic Supplement 5, Electronic Supplement 6) did not reveal a significant relationship with diatom communities in the Olyokma State Nature Reserve, given the relatively small area of its territory and, accordingly, the small gradient of climatic indicators.

As it was previously established (Gabysheva & Gabyshev, 2023; Barinova et al., 2025a), hydrochemical parameters of water, except for pH, increase along the river flow in the Protected Area. Therefore, we analysed the response of communities to increasing element concentrations. The saprobity index S was chosen as one of the indicators of trophic organic load. The community structure, species richness, and the dynamics of the saprobity index values were analysed for phytoplankton and phytoperiphyton samples, collected in the Protected Area. Fig. 6 shows that these parameters have opposite dynamics along the river flow. Thus, the trend lines show that phytoplankton communities tended to increase in the number of species and structural complexity (Shannon index), simultaneously with an increase in the saprobity index S values (Fig. 6a). Phytoperiphyton communities showed a smoother change in these parameters and a decrease against the background of increasing element concentrations in the water (Fig. 6b).

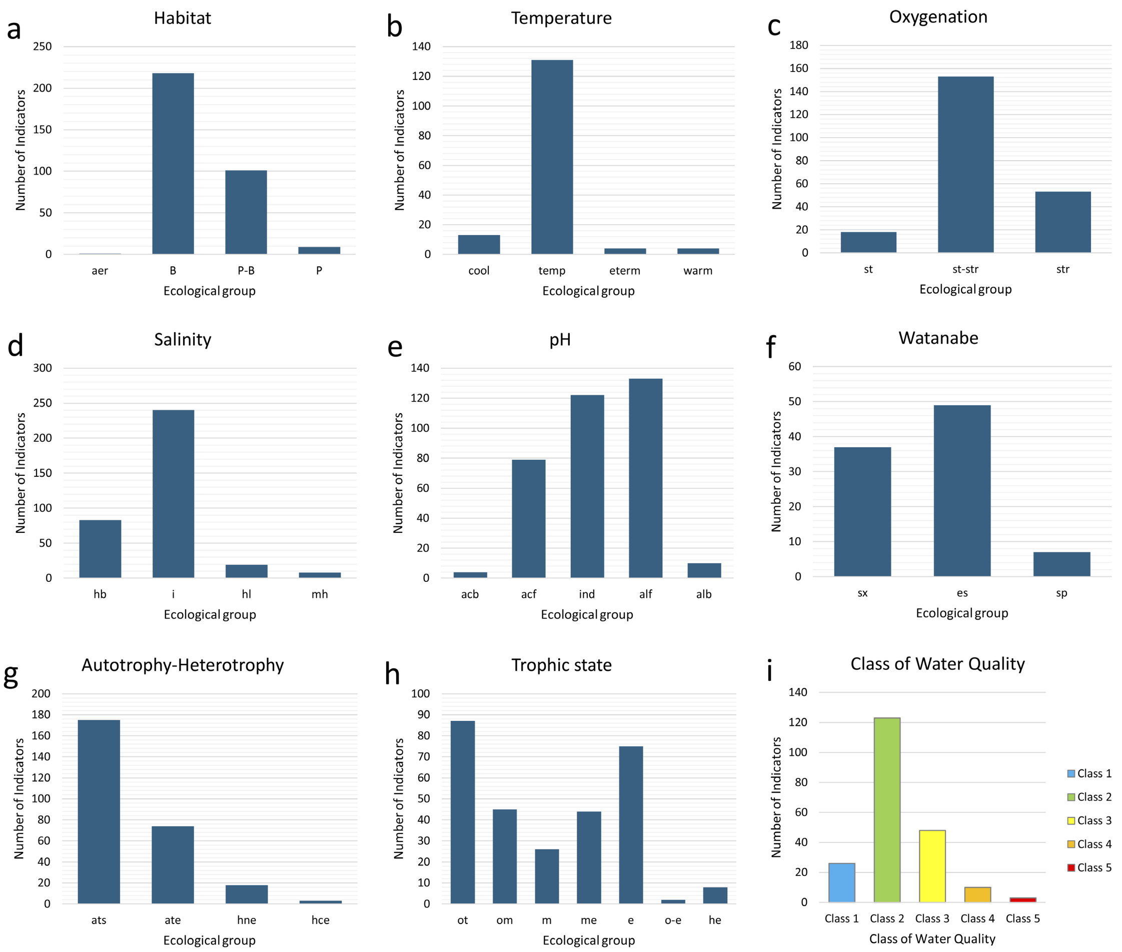

Fig. 4. Distribution of diatom bioindicators over the ecological groups in the Olyokma State Nature Reserve (Russia). Designations: Aquatic habitat preferences (Habitat): p – planktonic, p-b – planktonic-benthic, b – benthic, aer – aerophiles; Temperature preferences (Temperature): cool – cool-loving, temp – temperate temperature, eterm – eyrythermic, warm – warm-water; Rheophility (Oxygenation): st – Standing, st-str – Slow-streaming, str – Streaming; Salinity ecological groups (Salinity): hb – oligohalobes-halophobes, i – oligohalobes-indifferent, hl – halophiles; mh – mesohalobes; pH preferences groups (pH): alb – alkalibiontes; alf – alkaliphiles, ind – indifferent; acf – acidophiles; acb – acidobiontes; Organic pollution indicators groups (diatoms only according Watanabe): sx – Saproxen, es – Eurysaprob, sp – Saprophil; Groups of nitrogen uptake metabolism (Autotrophy-Heterotrophy): ats – Autotropic, ate – Autotrophic, hce – Obligately nitrogen-heterotrophic taxa, hne – Facultatively nitrogen-heterotrophic taxa; Groups of trophic state indicators: ot – Oligotraphentic, om – Oligo-mesotraphentic, m – Mesotraphentic, me – Meso-eutraphentic, e – Eutraphentic, o-e – Oligo-to Eutraphentic, he – Hyper-eutraphentic.

The similarity of the diatom community and the ecological preferences of its constituent species was calculated using Electronic Supplement 4 to identify the similarities between sites within the Protected Area that responded similarly to changes in environmental parameters. Fig. 7 shows that the taxonomic and ecological similarity at the stations was quite high, exceeding 70%. However, at the 75% level, two clusters can be seen, cluster 1 highlights station 17 and station 19, while Cluster 2 includes all the others. Stations 17 and station 19 are distinguished by the poorest periphyton communities (Fig. 3a, Fig. 6b) in a small swamp and a stream in the lower reaches of the River Olyokma.

To identify the importance of hydrological conditions for the survival of diatom communities in the Protected Area, a JASP Network plot (Fig. 8) was constructed based on data on species diversity, structure, ecological preferences, and saprobity indices (Electronic Supplement 4) for stations 1–21. The data were correlated by habitat type – river, lake, or swamp. Fig. 8 identifies two clusters. The first cluster includes only lotic habitats, while the second cluster contains all other lentic and weak-flow stations.

Diatom diversity and threatened categories of IUCN

The distribution of diatom species in the Olyokma State Nature Reserve by conservation category is shown in Fig. 9. Five species were classified as highly threatened: *Eunotia circumborealis* Lange-Bertalot & Nörpel (its electron micrograph can be found in Fig. 2), *E. faba* Ehrenberg, *E. serra* Ehrenberg, *Pinnularia nobilis* (Ehrenberg) Ehrenberg, and *Tetracyclus glans* (Ehrenberg) F.W.Mills. The photo table in Fig. 2 contains electron micrographs of the valves of several other rare diatoms, classified in the following IUCN categories: Endangered (*Brachysira liliana* Lange-Bertalot, *Cymbella cymbiformis* C.Agardh, and *Eunotia metamonodon* Lange-Bertalot), and Vulnerable (*Chamaepinnularia witkowskii* (Lange-Bertalot & Metzeltin) Kulikovskiy & Lange-Bertalot, *Cymbella hustedtii* Krasske, and *Pinnularia gentilis* (Donkin) Cleve).

Comparative floristics

Our analysis of the completeness of the study of diatom floras in NAPAs revealed that of the 14 floras analysed, only 12 satisfy the Willis criterion (Willis, 1922; Barinova, 2017b), while floras of the Vitimskiy State Nature Reserve and Kostyanoy Nos State Nature Reserve were excluded from analysis, since they do not satisfy Willis's criteria. These 12 floras were selected for comparative floristic analysis (Table 2, Fig. 10). As a result of our consolidation of data on diatom flora of the 12 best-studied NAPAs, the species list consisted of 1463 taxa (including 1319 species) (Electronic Supplement 7).

The total number of genera of the studied flora is 172 (Electronic Supplement 8) and varies in the studied NAPAs from 34 to 124; the index of genus saturation with species ranges from 2.1 to 4.9 (Table 4). In terms of the number of taxa, Lena Delta State Nature Reserve, Sikhote-Alin State Nature Reserve, State Nature Sanctuary Elgygytgyn Lake and Olyokma State Nature Reserve stand out (Table 4).

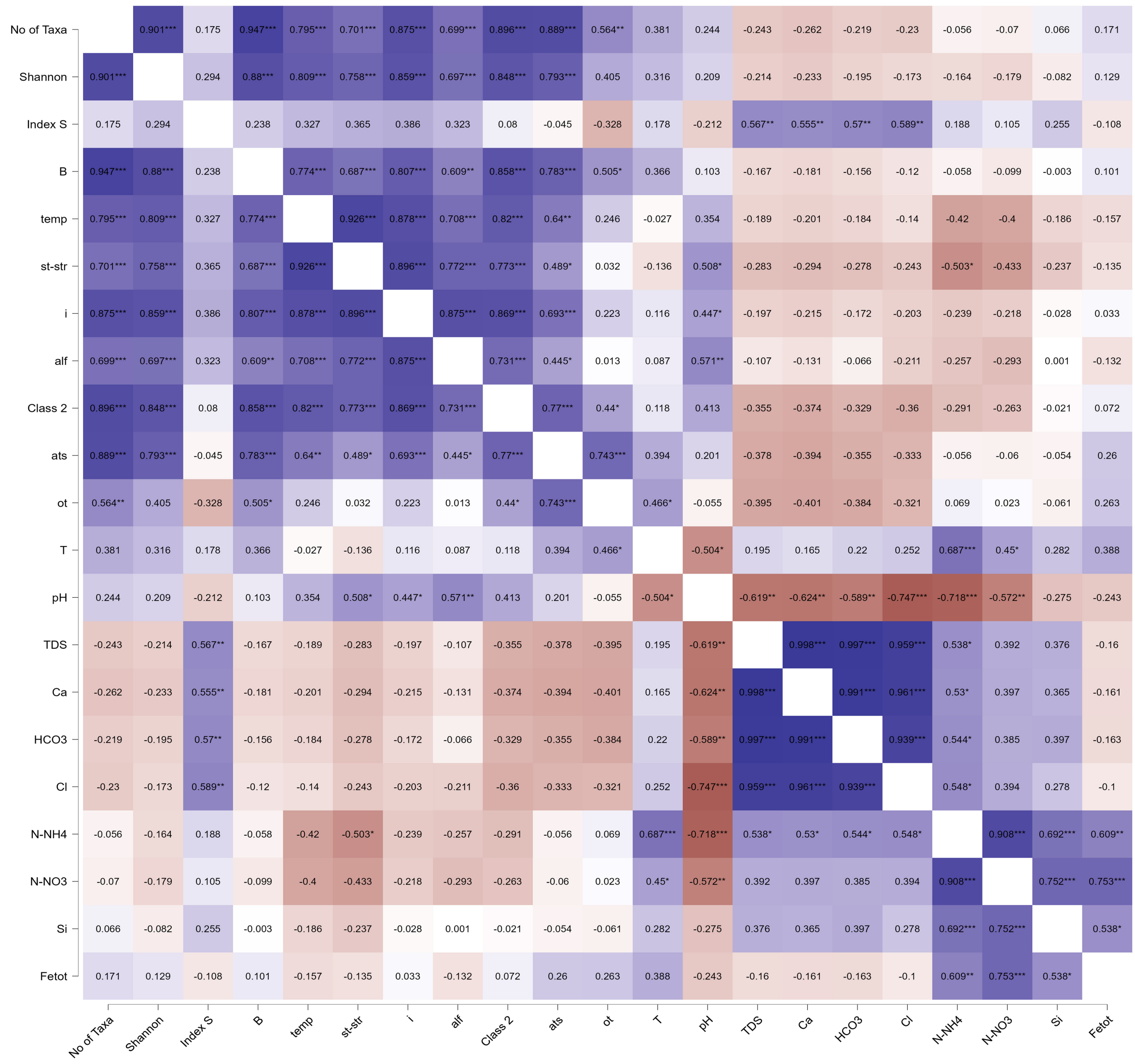

Fig. 5. The heatmap plot for biological and environmental variables relationships in the Olyokma State Nature Reserve (Russia). Abbreviation names and data of variables are in Electronic Supplement 1 and Electronic Supplement 4. Significance: * – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$.

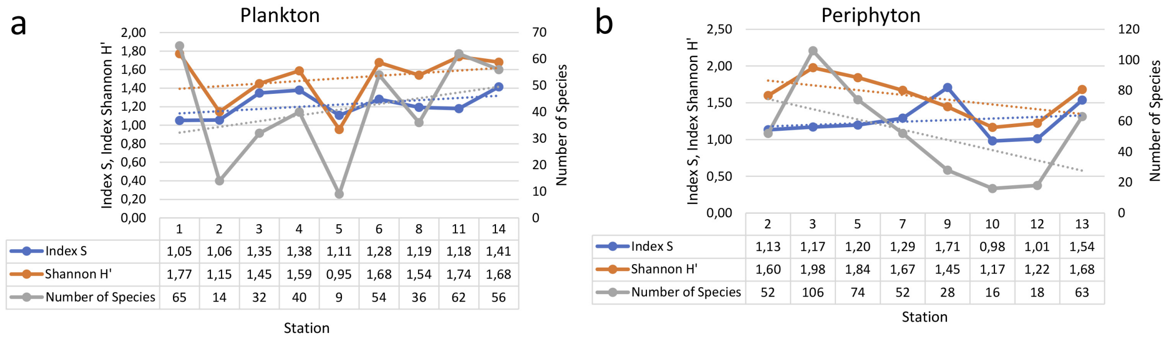

Fig. 6. Distribution of the major diversity variables of diatom communities in phytoplankton (a) and phytoperiphyton (b) over sampling stations in the Olyokma State Nature Reserve. Index S is the calculated saprobity index S for each station community; Shannon H' is the calculated Shannon index for each station community; the number of species is the number of revealed species in the station community. Sampling station numbers refer to Table 1.

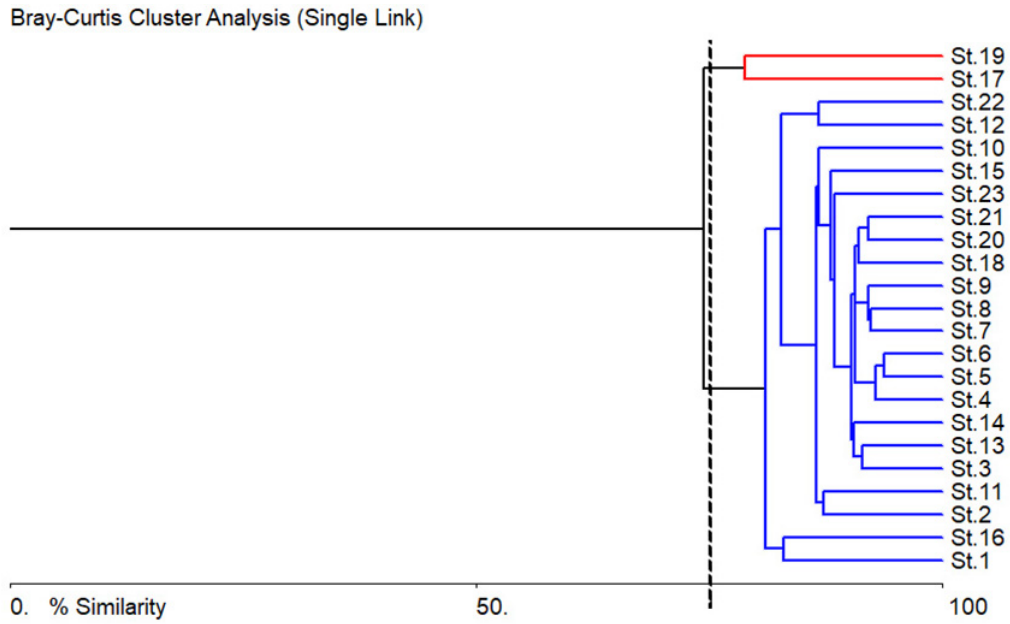

Fig. 7. Bray-Curtis similarity tree of diatom community and ecological preferences in habitats of the Olyokma State Nature Reserve (Russia). The black dashed line marks 75% similarity. The blue lines mark cluster 1. The red lines mark cluster 2. Sampling station numbers refer to Table 1.

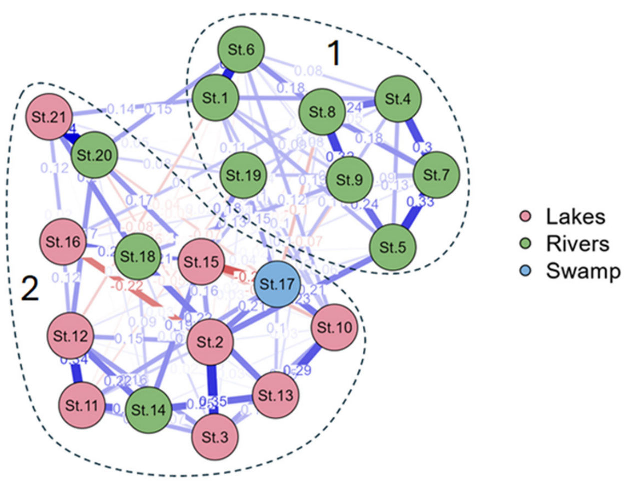

Fig. 8. JASP Network plot of similarity of diatom species and their ecological preferences in the Olyokma State Nature Reserve (Russia). The line thickness reflects the correlation value. Blue lines are the positive correlation; red lines are the negative correlation. Clusters are outlined by dashed lines and numbered. Sampling station numbers refer to Table 1.

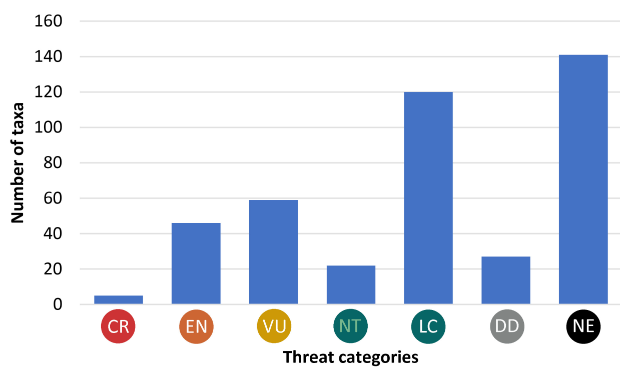

Fig. 9. Number of diatom taxa in each of the IUCN Red List categories in the Olyokma State Nature Reserve (Russia). Designations of threat categories: CR – Critically Endangered, EN – Endangered, VU – Vulnerable, NT – Near Threatened, LC – Least Concern, DD – Data Deficient, NE – Not Established.

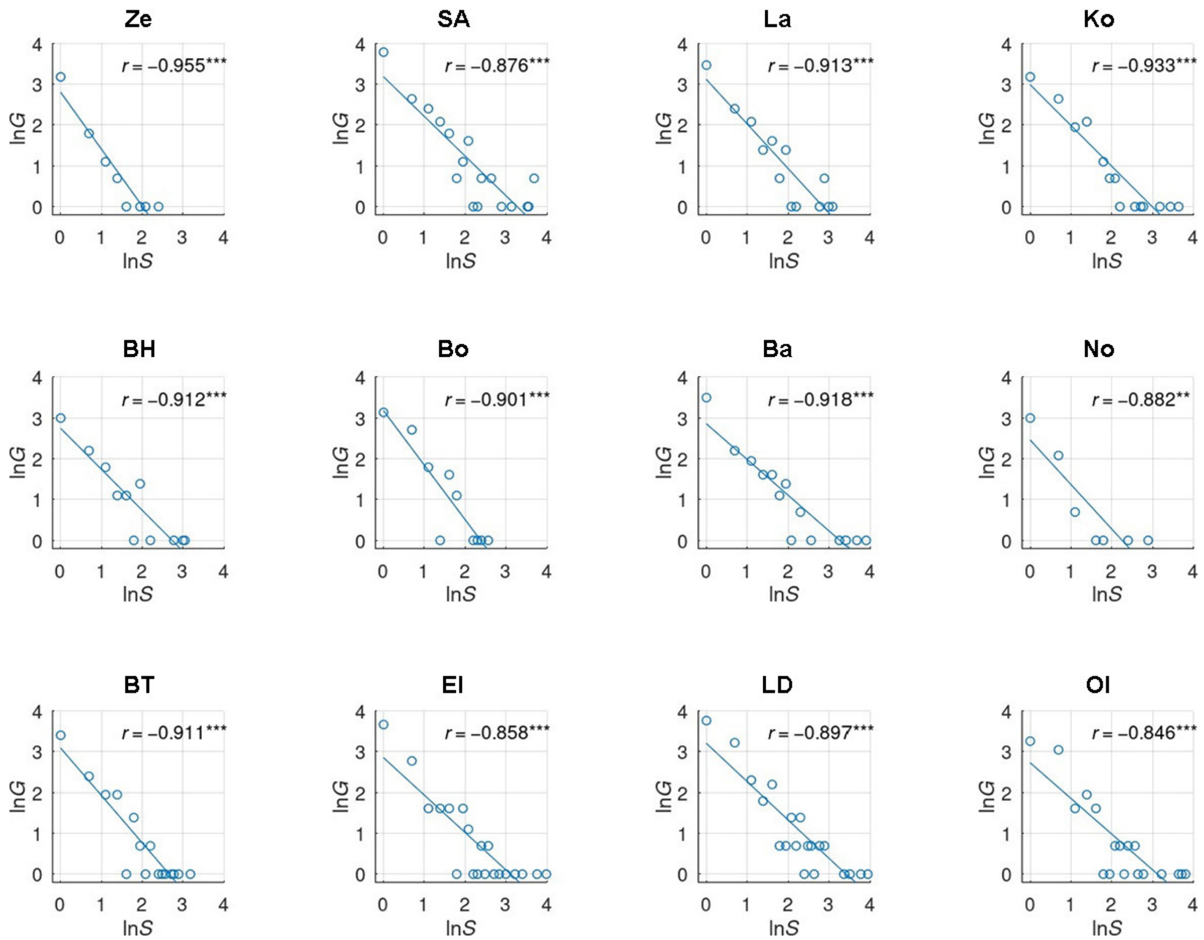

Fig. 10. Pearson correlation coefficients between the log-transformed number of genera (lnG) and the log-transformed number of species they contain (lnS), for the diatom floras of the studied Northeast Asia Protected Areas. Significance: ** – $p < 0.01$, *** – $p < 0.001$. Name codes of Protected Areas refer to Table 2.

Table 4. Biodiversity data on diatom algae in 12 Northeast Asian Protected Areas

Codes of Protected Area names	Ze	SA	La	Ko	BH	Bo	Ba	No	BT	El	LD	Ol
Number of taxa	84	498	270	299	183	161	348	82	279	479	664	420
Genus	39	105	73	68	50	57	74	34	73	95	124	81
Species/Genus	2.1	4.2	3.5	3.9	3.4	2.7	4.3	2.4	3.5	4.9	4.9	4.9
Species only	82	442	257	262	172	155	321	81	254	463	612	400
Subspecies/Species	1.02	1.13	1.05	1.14	1.06	1.04	1.08	1.01	1.10	1.03	1.08	1.05
Area, km^2	994	4016	1210	644	455	2674	1271	2112	2608	1400	14330	8500
Subspecies/Area	0.08	0.12	0.22	0.46	0.40	0.06	0.27	0.04	0.11	0.34	0.05	0.05
Cluster	2	1	2	1	2	2	1	2	1	1	1	1

Note. Cluster names refer to Fig. 11. Name codes of Protected Areas refer to Table 2.

To assess the exploration level of the diatom floras on 12 Protected Areas (Electronic Supplement 7), we tested the extent to which the observed distribution of genera by the number of taxa they contain fit the theoretical expectation established for well-explored biota (Barinova, 2017b). We found that Pearson correlation coefficients between the log-transformed number of species and the log-transformed number of genera were significantly negative for all 12 examined NAPAs (from r = -0.846 in Olyokma State Nature Reserve to r = -0.955 in Zeya State Nature Reserve; Fig. 10). These strong negative linear relationships suggest a sufficient level of floristic exploration across the studied NAPAs, which is a prerequisite for reliable further analysis.

Comparative analysis of 12 NAPAs biodiversity data (Table 4) and climatic variables (Electronic Supplement 9, Electronic Supplement 10) shows that the area of the NAPAs emerged as a significant predictor in Gleason-type semi-log models and in direct-relationship models, but not in Arrhenius-Wilson-MacArthur models. Specifically, in the basic Gleason model, the area was significant ($p = 0.031$), with a moderate overall fit ($R^2 = 0.387$). In the direct-relationship model, the effect of the area was stronger (p = 0.011), and the model explained a larger proportion of variance (R^2 = 0.490). The inclusion of climatic predictors did not improve the performance of Gleason-type models. In contrast, direct-relationship models were substantially improved by incorporating latitude. In this case, both area and latitude remained significant (p = 0.001 and p = 0.030, respectively), and the overall fit increased markedly (R^2 = 0.706, p = 0.004). Notably, both predictors exhibited positive effects, such that species richness tended to increase with larger NAPAs area and with higher latitude.

In addition to SAR models, we evaluated models that excluded the area altogether and relied exclusively on climatic predictors. Among these, Bio 15 (Precipitation Seasonality) provided the best performance, explaining approximately 54% of the variation in species richness (p = 0.007). A slightly weaker, yet still strong, performance was observed for Bio 5 (Max Temperature of Warmest Month), Bio 8 (Mean Temperature of Wettest Quarter), and Bio 10 (Mean Temperature of Warmest Quarter), each explaining about 45–46% of the variation (p = 0.015–0.017).

A JASP Network plot of comparative diatom algae floristics in the 12 NAPAs (Fig. 11), conducted for the administrative units where the compared floras are located, showed that the entire diatom species composition (1463 taxa) forms two clusters. Cluster 1 unites floras of northern territories, while cluster 2 includes more southern areas. An analysis of the distribution of species richness of the floras of the 12 NAPAs is reflected on the statistical maps in Fig. 12. It was noted that the species diversity is higher in coastal Protected Areas (Fig. 1, Fig. 12a). The index of intraspecific variability is higher in areas without permafrost (Fig. 1, Fig. 12b), and the specific number of species per unit area is also higher in non-permafrost Protected Areas (Table 4).

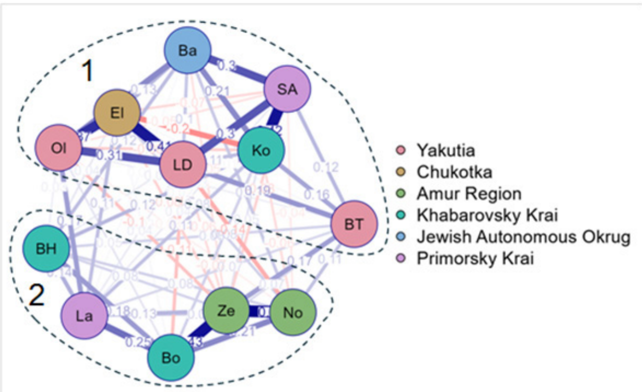

Fig. 11. JASP Network plot of comparative floristics of diatom algae in 12 Northeast Asian Protected Areas. The line thickness reflects the correlation value. Blue lines are the positive correlation; red lines are the negative correlation. Clusters are outlined by dashed lines and numbered. Name codes of Protected Areas refer to Table 2.

Discussion

After consolidation of old, previously published data on the diatom flora of the Olyokma State Nature Reserve (Vasilyeva et al., 1996, 1997, 1998; Rozhkova, 1996, 2001; Gabyshev & Gabysheva, 2013) and new data obtained in this study, the list of diatoms in the Protected Area includes 420 taxa. The calculation of the Willis criterion also indicates a sufficiently high degree of study of the diatom flora of this territory and the possibility of using these data for taxonomic and bioindication analysis.

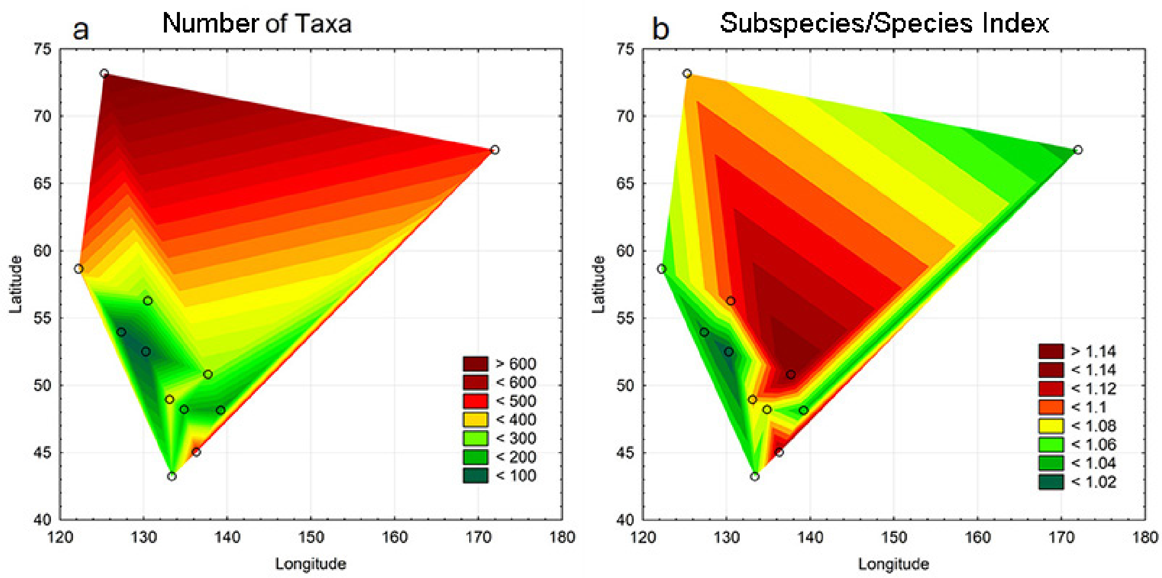

Fig. 12. Statistical map of distribution of diatom algae taxa number (a) and index of intraspecific variability (b) in 12 Northeast Asian Protected Areas over GIS co-ordinates (Table 2).

The situation with diatoms in the Red Data Books of Russia is quite specific. At the federal level (Geltman, 2024), diatoms are currently not represented. The main list includes mainly macroscopic algae (charophytes, brown algae, red algae). Diatom species are absent from the federal lists, which is usually explained by their microscopic size and the difficulty of identification. However, diatoms are actively included in regional Red Data Books. In the regions, especially where there are unique aquatic ecosystems, the situation is different. In total, 12 species are listed in the Red Data Book of St. Petersburg (Geltman, 2018b) and the Red Data Book of Leningrad Region (Geltman, 2018a), namely *Achnanthidium daonense* (Lange-Bert.) Lange-Bert., O. Monnier & L. Ector, *Gomphoneis clevei* (Fricke) Gil, *Brachysira serians* (Bréb.) Round & D.G. Mann, *Neidium binode* (Ehrenb.) Hustedt, *Pinnularia streptoraphe* Cleve, *Fistulifera pelliculosa* (Bréb. ex Kütz.) Lange-Bert., *Acanthoceras zachariasii* (Brun) Simonsen, *Ellerbeckia arenaria* (G. Moore ex Ralfs) R.M. Crawford, *Diatoma hiemalis* (Roth) Heiberg, *D. mesodon* (Ehrenb.) Kütz., *Hannaea arcus* (Ehrenb.) R.M. Patrick, *Fragilaria magocsyi* Lacsny. Diatoms are most widely represented in Central Europe, with several hundred species (Hofmann et al., 2018). Overall, 279 of the 420 diatom species in the Olyokma State Nature Reserve are classified into one or more threat categories (66%), highlighting the fundamental role of the Protected Area as key habitats for the conservation of threatened diatom species.

The response of diatom community diversity to environmental parameters in the Olyokma State Nature Reserve was determined using bioindication and statistical methods. The composition of the indicators was found to characterise waters of the Protected Area as consistent with natural parameters. As previously noted, electrical conductivity, pH, temperature, nitrates, and nitrites are the most effective factors determining the composition of the diatom community (Taurozzi et al., 2024). The saprobity index S, which reflects not only pollution, which is not a concern in the Protected Area, but also the state of the ecosystem as a whole, is also included in the list of indicators for monitoring in clean waters (Bere, 2016).

The analysis showed that the hydrological regime influences the composition of communities (Fig. 8), with processes occurring differently in plankton and periphyton (Fig. 6) (Ma et al., 2023). Periphyton communities are recommended for continued monitoring (Vilmi et al., 2016). They are less sensitive to stochastic processes but reflect the local state of the environment, for assessing aquatic ecology and interregional algal biomonitoring. This study also notes that benthic diatoms are the best indicators of river bioassessment, even during flood periods, when the reservoir is unstable under the influence of extreme climatic conditions. This is important for maintaining the balance of biota and the environment in Protected Areas. The hydrological factor is also important for understanding the connections between the river continuum and the adjacent lakes of the narrow River Olyokma valley within the Protected Area (Schofield et al., 2018). Periphyton of lentic water bodies, which abound in the northern part of the Protected Area, are located in the outer river channels, not permanently connected to the main channel but typically fed by alluvial soil (Alexander et al., 2018) and, therefore, subject to impacts affecting the entire Protected Area. Therefore, when monitoring the Protected Area, it is most productive to observe the development of periphyton communities, regardless of the type of aquatic habitat.

The observed increased number of taxa in coastal Protected Areas may be related to the ecotone zone effect, which occurs at the boundary of continental and marine habitats, as Barinova et al. (2023) previously observed when studying diatom communities in the Lena Delta State Nature Reserve (Russia). Statistically confirmed formation of two different cores, south and north, suggests that geography and the associated permafrost climatic boundary play a significant role in shaping the communities of NAPAs.

The increase in intraspecific variability in areas without permafrost reflects the influence of milder climatic conditions, when the role of intraspecific competition for resources decreases. The milder climate and longer open water period of non-permafrost Protected Areas have a beneficial effect on the increase in the specific number of species per unit area (Bogatov & Nikulina, 2010). However, at genus level (the number of genera and the richness of genera with species), the influence of climate is not evident. As previously noted, indices of intraspecific variability are associated with the latitude of the flora (Barinova, 2011), as well as with the altitude of the habitat (Şahin & Barınova, 2022). The results of statistical mapping of diversity indices revealed not only an ecotone effect (Fig. 12a) but also the influence of geographically (altitude) and climate-related (permafrost) environmental factors (Fig. 12b). Bioclimatic variables and DHI have a weak relationship with diatom communities in the Olyokma State Nature Reserve, but on the scale of Northeast Asia, correlations by both area and latitude remained significant, and climate predictors such as solar radiation in April, Bio 5 (Max Temperature of Warmest Month), Bio 8 (Mean Temperature of Wettest Quarter), Bio 10 (Mean Temperature of Warmest Quarter), and Bio 15 (Precipitation Seasonality) showed a significant effect on the variability of diatom species richness. Global warming modelling has revealed a trend showing that over the past 100 years, the Earth's temperature has increased by approximately 0.5 K (Beltrami & Bourlon, 2004). Since plants and animals migrate to higher altitude habitats and poles as temperatures rise (Pauli & Halloy, 2019), the trends in diatom community diversity identified in our data can serve as predictors for climate change monitoring, and solar radiation, temperature, and precipitation, which have significant influence on diversity, can be monitored in Protected Areas.

Conclusions

In 2011 and 2024, scanning electron microscopy analysis revealed a high diversity of diatoms (329 taxa) on 21 stations within the Olyokma State Nature Reserve. The diatom flora in the Protected Area counts now 420 taxa in total. Our study concluded that the Olyokma State Nature Reserve water bodies located along the River Olyokma are not affected by anthropogenic impacts of mining operations located upstream in the River Olyokma basin. Conservation measures implemented within the Protected Area should be considered effective. Two-thirds of the diatom species in the Olyokma State Nature Reserve are categorised by the IUCN, demonstrating the invaluable contribution of the Protected Area system to the conservation of threatened diatom species. Using spatial statistical mapping, RDA, and JASP methods, we identified the most important climatic (permafrost, temperature, and precipitation) and hydrochemical (pH and ammonium) factors associated with the geographical location of habitats that influence the composition of diatoms in Northeast Asia. We hypothesise that the results of this study can be used to create a database of diatom biodiversity as indicators of change in pristine areas and as critical sensors for monitoring the climate change.

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Supporting Information

Additional data for the paper by Gabyshev et al. (2026) may be found in the **Supporting Information**.

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ДИАТОМОВЫЕ ВОДОРОСЛИ ЗАПОВЕДНЫХ ТЕРРИТОРИЙ СЕВЕРО-ВОСТОКА АЗИИ КАК БИОИНДИКАТОРЫ В ГРАДИЕНТЕ ГЕОГРАФИЧЕСКИХ И КЛИМАТИЧЕСКИХ ФАКТОРОВ

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Северо-Восточная Азия – обширный регион, охватывающий разнообразные природно-климатические зоны, от арктической тундры до тайги, значительная часть которого расположена в зоне многолетней мерзлоты. Исследования сообществ диатомей региона позволили выявить ряд важных закономерностей, и оценить процессы, связанные с глобальными климатическими изменениями, происходившими здесь в прошлом, а также современные климатические тренды и антропогенное влияние. Особо охраняемые природные территории (далее – ООПТ), являются «природными лабораториями» для изучения реакции биоты на географические и климатические факторы. Диатомовые водоросли давно признаны экспертами в качестве надежных биоиндикаторов состояния окружающей среды. Однако подобных исследований на ООПТ по-прежнему недостаточно. Главная цель нашего исследования заключалась в оценке устойчивости сообществ диатомовых водорослей в широком диапазоне географических и климатических факторов Северо-Восточной Азии, используя в качестве примера ООПТ с наиболее изученными флорами диатомовых водорослей. Наши собственные исследования проводились в государственном природном заповеднике «Олекминский» в качестве модельной территории. С помощью сканирующей электронной микроскопии, видовой состав диатомовых водорослей государственного природного заповедника «Олекминский» был нами расширен на 269 видов. На большинстве станций наблюдений на территории государственного природного заповедника «Олекминский» по таксономическому составу преобладают такие роды, как *Pinnularia*, *Eunotia* и *Gomphonema*; представители этих трех родов явно играют ключевую роль в изучаемой флоре. Индекс внутривидовой изменчивости subspecies/species для водоемов Олекминского заповедника варьировался от 1.00 до 1.06. В целом, 66% видов диатомовых водорослей государственного природного заповедника «Олекминский» классифицируются МСОП в одной или нескольких категориях угрозы. Пять видов диатомовых водорослей находятся в категории «Находящиеся под критической угрозой исчезновения». Биоиндикация и статистические методы позволили определить, что воды государственного природного заповедника «Олекминский» соответствуют природным показателям. Характеристики индикаторов демонстрируют значительную реакцию видового состава диатомовых водорослей на изменения солености и pH. Для сравнительного анализа с полученными нами результатами, мы отобрали 11 хорошо изученных охраняемых диатомовых флор Северо-Восточной Азии, используя критерий Виллиса. Сравнительный анализ выявил увеличение числа таксонов на приморских территориях, что может быть связано с экотонным эффектом, возникающим близ границы континентальных и морских местообитаний. На ООПТ с более мягким климатом и более длительным вегетационным периодом, где отсутствует многолетняя мерзлота, отмечалось увеличение внутривидовой изменчивости и, следовательно, снижение внутривидовой конкуренции за ресурсы, а также увеличение удельного числа видов на единицу площади. Были выявлены закономерности пространственного распределения диатомовых водорослей на 12 ООПТ Северо-Восточной Азии. Особенности географического положения, многолетняя мерзлота и климатические условия играют значительную роль в формировании структуры сообществ диатомовых водорослей на ООПТ. Данное исследование важно для разработки системы мониторинга биоразнообразия на ООПТ в условиях глобальных климатических изменений в регионе.

Ключевые слова: биоиндикаторы, климат, МСОП, разнообразие, сравнительная флористика, статистическое картографирование, угрожаемый вид, экология