

## Research paper

# Landscape gradients in *Sphagnum* peatlands: Nutrients, trace elements and diversity of free-living mites (Arthropoda: Acari) along a 1600 km transect on the West Siberian Plain

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## ABSTRACT

The West Siberian Plain holds special ecological significance as the largest peatland region of the world, which is expected to be affected by the climate change. We analysed water chemistry, chemical composition of *Sphagnum* tissues (total C, total N, K, P, and a range of trace elements) and biodiversity (abundance, species richness, community composition) of free-living mites (Oribatida and Mesostigmata) in twelve *Sphagnum* peatlands along the 1600 km transect (54°46'N to 67°29'N) on the West Siberian Plain. Mites were classified into two functional groups – “limnic” (Oribatida species which inhabit aquatic habitats), and “terrestrial” (all other species).

The results showed a latitudinal productivity gradient, with a consistent increase in nutrient content of *Sphagnum* and water pH from North to South; the northern-most site had lowest N and highest C:N ratio, indicating potential N limitation. There was an increase in levels of Cr, Zn, Ni and Sr in the *Sphagnum* tissues in proportion to the abundance of lithophile Ti on the southern end of the transect; however, in absolute terms, the concentrations of these elements were low. The abundance patterns of terrestrial and limnic mites reflected increasing nutrient load in *Sphagnum* bogs from North to South, as well as increasingly xeric conditions. Latitude and nutrients (P and C:N ratio) together explained 67.2 % variability in community composition of Oribatida and Mesostigmata. We found no effect of latitude or productivity on species richness; the main driver for species richness appeared to be the local micro-topography, with dryer areas colonised by a wider range of species. Our data help to elucidate landscape-scale patterns of productivity and biodiversity in West Siberian peatlands and provide a checkpoint in the timeline of global change. As sensitive intrazonal ecosystems, peatlands can act as useful early warning systems, offering insights about the effects of human activities on a large scale.

## 1. Introduction

Latitudinal gradients in biodiversity represent one of the most well-documented patterns in ecology. Several mechanisms have been proposed to explain these gradients, including available area, evolutionary history, biotic interactions, energy supply, range sizes, stochastic processes, and others (e.g., Willig et al., 2003; Hillebrand, 2004; De Frenne et al., 2013; Kinlock et al., 2018; Zhang et al., 2022).

In phytogeography, latitudinal gradients manifest as bioclimatic zonation, representing broad zones of climate and vegetation (Box,

2016). In addition to theoretical interest, latitudinal gradients and bioclimatic zonation have been extensively used to assess and predict the impacts of climate change on species and communities, as they undergo range shifts in response to a warming climate (Parmesan, 1996; Fielding et al., 1999; Parmesan et al., 1999; Andrew and Hughes, 2004; Chen et al., 2011; Hanberry and Hansen, 2015; Cokola et al., 2020). This is expected to become an increasingly important issue as bioclimatic zones and species ranges are projected to shift in the future (Bonebrake et al., 2018; Niskanen et al., 2019; Anjos et al., 2021). However, documenting change requires data points in time, and for many regions of

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the world these data are missing or incomplete.

*Sphagnum*-dominated peatlands offer a unique model system to assess large-scale environmental patterns. Peatlands occupy extensive areas in boreal and subarctic regions of Europe, Siberia and North America and contribute significantly to long-term carbon storage (Gorham, 1991; Limpens et al., 2008; Yu, 2012; Rydin and Jeglum, 2013). Peat bogs can be considered as intrazonal ecosystems on a continental scale, as their unique environmental characteristics – high water level, low pH and low nutrients – set them apart from the typical regional patterns of bioclimatic zonation (Sieben, 2018). Instead, peat bogs form isolated habitat “islands”, which have their own ecological dynamics and biodiversity, and which remain relatively consistent across large geographical regions (Rydin and Jeglum, 2013). However, peatlands are still subject to large scale latitudinal gradients imposed by the overriding influence of temperature and sunlight on productivity and decomposition rates.

*Sphagnum* peatlands have the characteristic micro-topography of hummocks and pools (hallows), which influences plant and invertebrate biodiversity as well as carbon sequestration patterns (Tahvanainen, 2004; Rydin and Jeglum, 2013; Spitzer and Danks, 2006; Hajkova and Hajek, 2007). Among the invertebrates abundant in peat bogs are mites (Arthropoda: Acari), which include high diversity of species across different trophic levels. Oribatid mites (Oribatida), primarily fungivores and microbivores but occasionally plant feeders and predators, are abundant and diverse in peatlands (e.g., Borcard and von Ballmoos, 1997; Starý, 2006; Seniczak, 2011; Seniczak et al., 2014, 2020; Lehmitz and Maraun, 2016; Minor et al., 2016). Predatory mesostigmatid mites (Mesostigmata) have been well studied in European peatlands, although community-level data are less common (Wisdom et al., 2011; Barreto et al., 2015; Markkula et al., 2019; Minor et al., 2022; Seniczak et al., 2022). The diversity patterns of free-living mites in *Sphagnum* bogs are influenced by the gradients of pH, nutrient availability and micro-topography (Donaldson, 1996; Minor et al., 2016, 2019; Seniczak et al., 2020). Experimental warming and/or fertilization of peatlands have been shown to induce shifts in species abundance and community assemblages of these animals (Markkula, 1982; Markkula et al., 2019; Barreto et al., 2021; Pettit et al., 2023).

Oribatida and Mesostigmata in *Sphagnum* bogs can be classified into two functional groups – aquatic, or “limnic” (Oribatida species from genera *Hydrozetes*, *Limnozetes*, *Tyrphonostrus* and *Trhypochthoniellus*, which inhabit aquatic habitats (Weigmann and Deichsel, 2006; Seniczak, 2011)), and “terrestrial” mites which prefer drier environments (all other Oribatida species and all Mesostigmata). Previous research on *Sphagnum* bogs found a significant increase of total Oribatida abundance from North to South, but no significant change in total species richness (Minor et al., 2016). At the bog level, the abundance and community structure of terrestrial Oribatida in hummocks correlated with productivity gradient, while for aquatic Oribatida in pools water table depth was the single most important predictor variable (Minor et al., 2019).

Systematic studies of peatlands across extensive latitudinal gradients are uncommon (e.g., Dorrepaal et al., 2005). At the same time, *Sphagnum* mosses within peat bogs have been extensively used as reliable bioindicators for monitoring both local and large-scale gradients in anthropogenic deposition of nutrients, trace elements and heavy metals (Harmens et al., 2004; Steinnes et al., 2011; Shotyky et al., 2016; Kempter et al., 2017). Concentrations of heavy metals, trace elements and other contaminants in *Sphagnum* tissue have been shown to closely reflect the atmospheric deposition rates (e.g., in dust and precipitation) (Berg and Steinnes, 1997; Gerdol et al., 2000).

Our study aimed to analyse environmental conditions (water pH, nutrients and trace elements in *Sphagnum* moss) and biodiversity (abundance, species richness and community assemblages) of oribatid and mesostigmatid mites in *Sphagnum* peat bogs along a large-scale latitudinal transect in the West Siberian plain. The West Siberian Plain (or West Siberian Lowland) is a large low-lying poorly drained region that lies between the Ural Mountains in the west, the Altai Mountains in

the south-east and the Yenisei River in the east. This area holds a special ecological significance: this is the largest peatland area of the world, with the total area of West Siberian peatlands estimated as 0.6–1.0 million km<sup>2</sup> (Kirpotin et al., 2009). This region holds 18–30 % of the area and 11–15 % of the peat carbon pool of all boreal and subarctic peatlands globally (Repo et al., 2007; Kirpotin et al., 2009). Climate models predict that Western Siberia temperatures will increase higher than the global average due to climate change, especially in the arctic and sub-arctic regions (IPCC, 2019; Niskanen et al., 2019), so we hope that this study will provide an important set of checkpoints in the timeline of global change.

Our first objective was to determine the extent to which the bog environments (nutrients and trace elements) change with latitude. In relation to biodiversity patterns (abundance, species richness and community assemblages of mites in hummocks and pools), we expected that total abundance would increase North to South and/or will be linked to productivity (pH, N and/or P) gradient, provided that the latitudinal gradient and productivity gradient can be separated. We expected that species richness and community assemblages would show changes from North to South and/or be linked to productivity gradient. Finally, we expected that aquatic and terrestrial mites will show similar patterns in relation to productivity and latitude.

## 2. Methods

### 2.1. Study sites

The twelve investigated *Sphagnum* bogs are located along a latitudinal transect within the West Siberian plain between 54°46'N and 67°29'N. The transect represented a 200 km wide corridor; the total length of the transect was ca. 1600 km, the distance covered North to South was 1416 km and East to West 985 km (WGS 84) (Fig. 1). The distance between sampled *Sphagnum* bogs varied from 90 to 188 km from each other (on average about 120 km). The altitude ranged from 23 to 160 m a.s.l, with an increase from North to South. The *Sphagnum* bogs on the transect are situated within seven bioclimatic subzones (Yurkovskaya and Safronova, 2019), with a total of one to three bogs per subzone (Fig. 1).

The climate of the West Siberian Plain is continental; northern part of the plain is more influenced by the ocean, while the southern part is characterized by a more continental climate. Due to the significant extent of the research area from North to South, there are substantial differences in the climatic conditions along the transect, reflected in bioclimatic zonation. According to Köppen's climate classification (Peel et al., 2007), the climate of the West Siberian Plain is moderately cold with uniform precipitation throughout the year (Df). In the southern part of the transect, where three *Sphagnum* bogs were sampled, the climate is cold continental with warm summers (Dfb), while the rest of the transect lies within the cold continental climate with cold summers (Dfc).

### 2.2. Sampling and analysis

Samples were collected during the warm season of 2023 when plant communities were in a similar phenological stage, starting from the southern end of the transect. Sampling was limited to *Sphagnum*-dominated communities and *Sphagnum* mosses in each sample were identified to a species level. In each of the twelve sites (*Sphagnum* bogs) we collected 15 samples (ten from hummocks and five from pools), selecting areas dominated by *Sphagnum magellanicum* or, in its absence, species with similar environmental preferences. Ten samples from hummocks and five samples from pools (hallows) were used to stratify sampling effort based on relative number of Oribatida species in hummocks and pools (Minor et al., 2016, 2019). Samples were taken with a plastic cylinder (10 cm dia.) to 6 cm depth of live *Sphagnum*, including the capitulum and the length of stems. The distance between samples

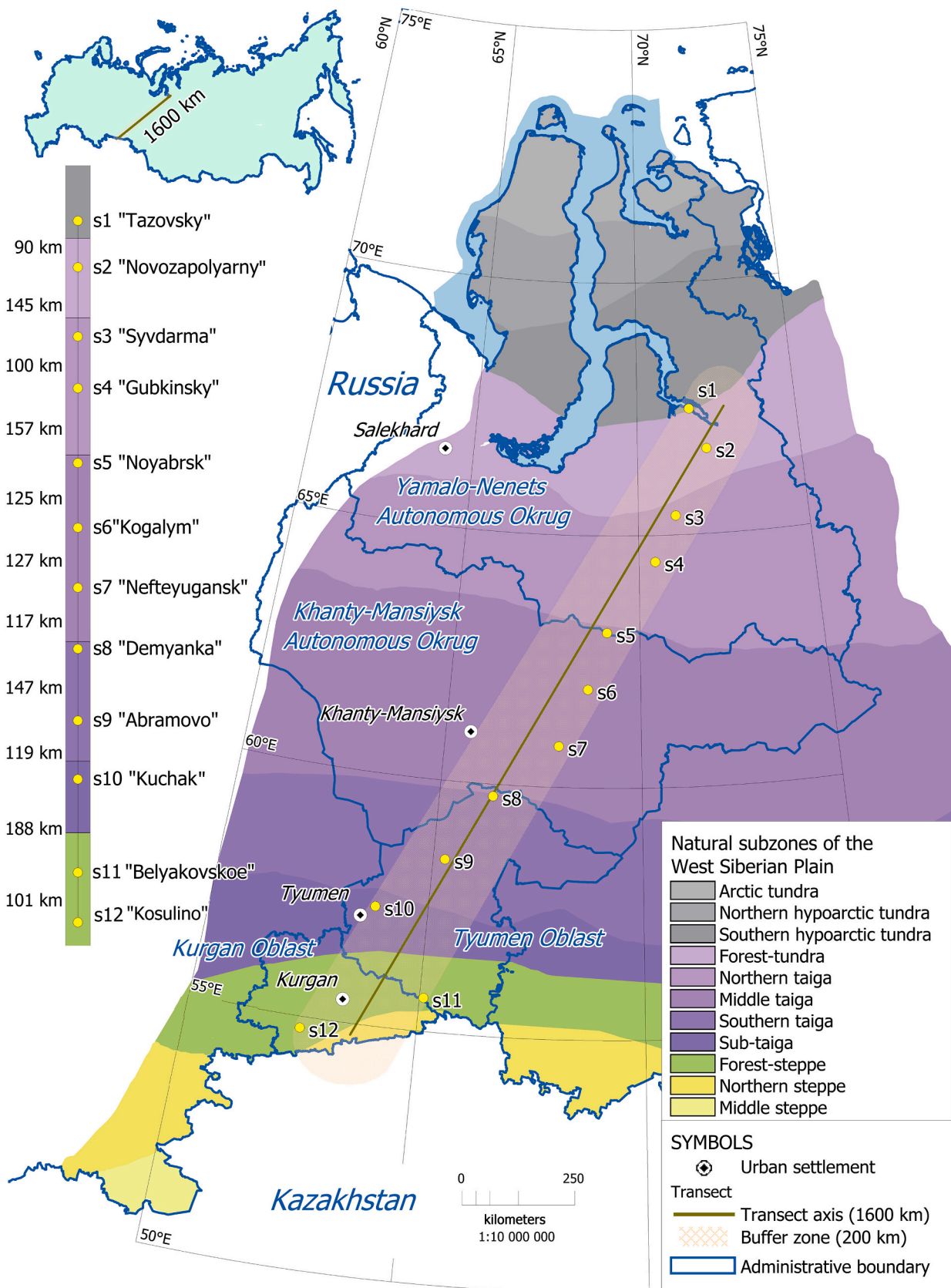


Fig. 1. Sampling transect in the West Siberian Plain, covering a range of bioclimatic subzones; sampled *Sphagnum* bogs are marked as yellow circles; see Supplementary Material S1 for full description of the sites. Bioclimatic subzones after Yurkovskaya and Safronova (2019).

usually ranged 40–80 m, in rare cases 10–15 m. A total of 180 samples were collected from twelve sites. Full description of sites (*Sphagnum* bogs) is provided in the Supplementary Material S1.

Variables recorded for each collected sample were: GPS coordinates; depth to water table; water pH; water mineralisation and electrical conductivity; *Sphagnum* species identity; abundance, species richness and community composition of oribatid and mesostigmatid mites. Each sample was assigned to one of the five qualitative productivity classes (“trophic class”) on the oligotrophic-eutrophic gradient based on plant community features within 1 m<sup>2</sup> radius (Rydin et al., 1999). Water electrical conductivity (μS/cm) and mineralisation (mg/L) was determined using MARK-603 portable conductivity meter (Vzor LLC, Russia). Water pH was measured using Hanna pH Checker (Hanna Instruments, Romania). Dry weight of each sample was determined after microarthropod extraction (see below) and complete drying of the substrate. Elevation and the total bog area were recorded at the site level.

Mites from moss samples were extracted in modified Berlese funnels until fully dry (at least 10 days). Adult Oribatida and Mesostigmata were counted and identified to a species level. Juvenile stages and Uropodina were excluded. Prior to analysis, mite abundance counts were normalized by dry weight of their *Sphagnum* samples. Mites were divided into two functional groups – aquatic Oribatida (species of *Hydrozetes*, *Limnozetes*, *Tyrphonothrus* and *Trhypochthoniellus*) and terrestrial mites (all other Oribatida species and all Mesostigmata).

The chemical composition of *Sphagnum* was determined in five samples per site, following mite extraction, in three samples from hummocks and two from pools. Samples for chemical analysis were maximally distant from each other. A total of 60 samples from twelve *Sphagnum* bogs were analysed. Measurements were conducted using XRD Analyzer Tracer 5 g (Bruker, USA). The factory calibration provided by Bruker, Mudrock 2 Air, designed for soil analysis, was employed for measurements. This calibration is capable of determining concentrations of 31 elements: Na, Mg, Al, Si, P, S, Cl, K, Ca, Ti, V, Cr, Mn, Fe, Co, Ni, Cu, Zn, Ga, As, Se, Rb, Sr, Y, Zr, Nb, Mo, Ba, Pb, Th, U. Sample preparation and measurements were carried out in accordance with the regulatory standard (GOST 33850-2016, 2016).

Total C and total N content of *Sphagnum* moss were measured using Unicube analyser (Elementar, GmbH). The moss samples were dried for 48 h at 105°C to a constant weight and homogenised. Nutrient content (C, N) was analysed in triplicate, using 4–6 mg subsamples. Prior to each measurement the analyser was calibrated using sulfanilamide (C41.68 %; H4.04%; N8.05%; S18.47 %). Measurements were converted to % dry weight.

### 2.3. Statistical analysis

A multicollinearity analysis (SAS 9.4, proc. reg and proc. corr) was done to check simple correlations and variance inflation factors for environmental variables. Plot trophic class (an ordinal variable) was represented by a numerical dummy variable. Among plot-level variables, water mineralisation and electric conductivity were highly correlated ( $r = 0.96$ ,  $p < 0.001$ ) with variance inflation factor  $> 10$ ; as a result, conductivity variable was dropped and only water mineralisation was used in the subsequent analysis. Other variables were not strongly collinear (variance inflation factor  $< 2.0$ ).

Principal component analysis (PCA) was used to explore patterns in biodiversity and environmental variables (depth to water table, water pH, water mineralisation, latitude) in all samples from sites.

The generalized linear regressions (SAS 9.4 proc glimmix) were used to analyse (1) effect of micro-topography (depth to water table) on total species richness, abundance of terrestrial mites and abundance of limnic Oribatida; (2) effects of latitude and productivity variables (water pH, water mineralisation) on total species richness and on abundance of terrestrial mites and limnic Oribatida; distributions used in the models were chosen based on fit criteria. Site (bog) was included as a random effect in the models to account for the nested structure of the data with

multiple samples within each bog.

To identify chemical elements with significant influence on total species richness, abundance of terrestrial mites and abundance of limnic Oribatida, we used stepwise generalized linear regressions (SAS 9.4 proc hpgenselect) on the chemistry data subset.

Principal coordinates analysis (PCOA) with Bray-Curtis similarity as separation measure was used to explore patterns in community composition of Oribatida and Mesostigmata across sites (using combined species lists). Species with less than four individuals across all sites were excluded from the community analysis. Distance decay in community similarity between all sites was quantified using a matrix of pairwise Bray-Curtis similarities in site-level community composition and a matrix of pairwise geodesic distances (km) between sites, calculated from coordinate pairs. OLS linear regression was used to test the significance of distance decay.

The distance-based linear modelling (DistLM) in PRIMER 7 (Clarke et al., 2014) was used to test which variables best explain site-level community assemblages of Oribatida and Mesostigmata. Significance level  $\alpha = 0.05$  was used for all statistical tests.

## 3. Results

### 3.1. Environmental gradients

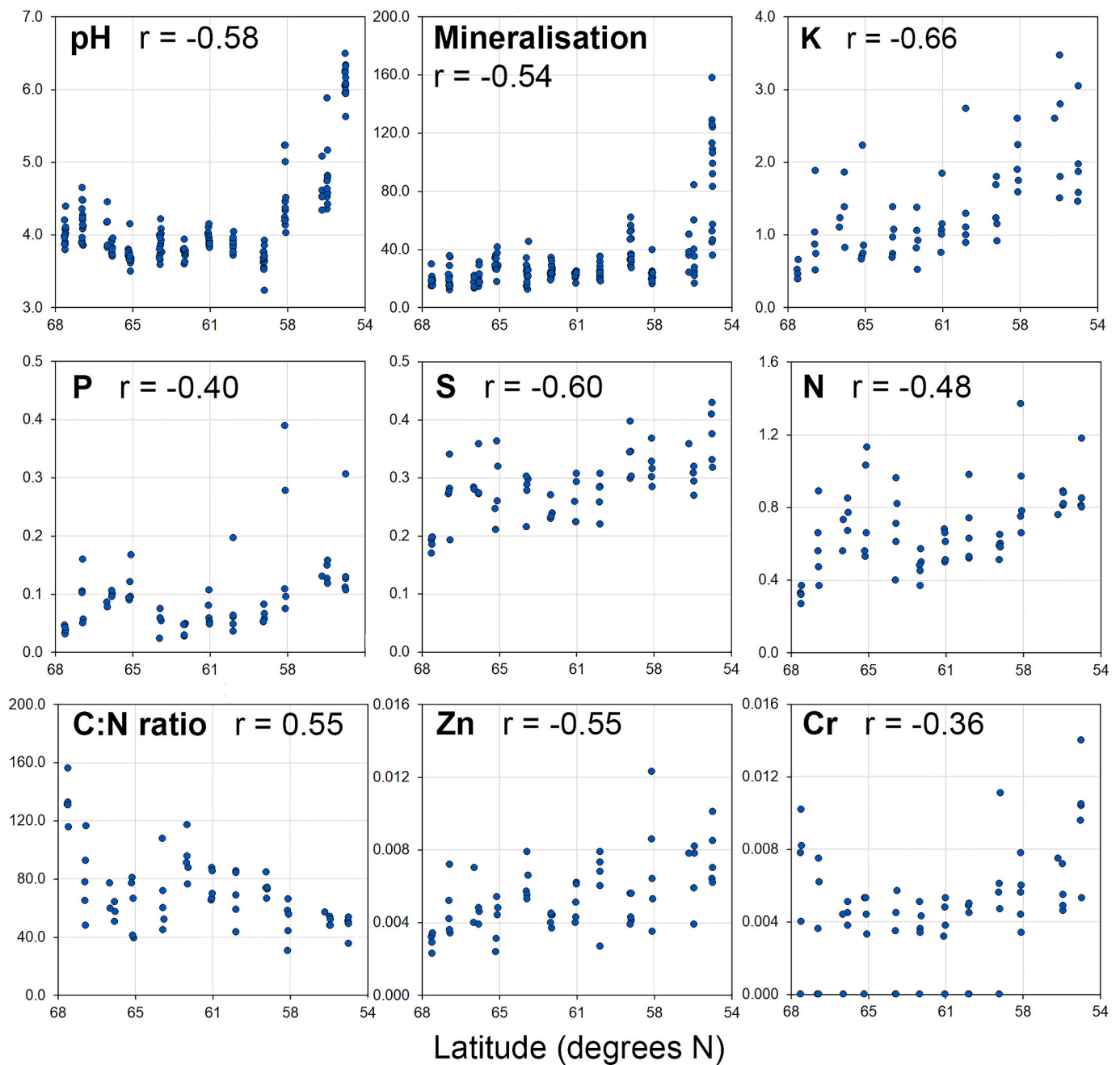
Clear latitudinal gradients were present on the transect. Water pH, water mineralisation, major nutrients (N, P, K) and C:N ratio were correlated with latitude and all increased North to South, except C:N ratio which decreased North to South (Fig. 2). Across the transect, water pH in *Sphagnum* bogs was positively correlated with water mineralisation and with local trophic class on the oligotrophic-eutrophic gradient, as indicated by vegetation community (Tables 1, 2). The three southern-most bogs (“Kosulino”, “Belyakovskoe” and “Kuchak”) had much higher water pH and nutrient content (Fig. 2), reflecting latitudinal gradient in productivity. In hummocks, pH was negatively correlated with depth to water table, in pools there were no such relationship (Tables 1, 2).

Among trace elements, Mn, Ni, Zn and Cr in *Sphagnum* moss samples were significantly correlated with latitude and increased North to South (Table 3, Fig. 2). Concentrations of Ti, a conservative lithophile element, are closely correlated with the overall abundance of mineral particles (i. e., dust) arriving into the bog by air (Shotyk et al., 2016). Increased concentrations of potentially toxic trace elements (Cr, Zn, Ni and Sr) in proportion to Ti indicate an enrichment and potentially imply an anthropogenic source of these elements. Among analysed sites, the northern-most site “Tazovsky” had lowest ratios of [Element]/Ti. There was a continuous increase in Cr/Ti ratio from North to South. At higher latitudes concentrations of Zn, Ni, Sr were stable in proportion to those of Ti, but on the southern end of the transect, sites “Kosulino”, “Kuchak” and “Demyanka” were enriched in Sr; sites “Kuchak” and “Demyanka” were also enriched in Zn; site “Abramovo” was enriched in Ni.

### 3.2. Biodiversity gradients: abundance, species richness and community assemblages

The collected *Sphagnum* samples contained 19,822 Oribatida and 618 Mesostigmata individuals. A total of 83 species were found, comprising 65 species of Oribatida and 18 species of Mesostigmata. Site-level species richness ranged from 21 to 39 species. The full species list and species abundance counts are available in the Supplementary Material S2.

Locally, bog micro-topography (depth to water table) was driving abundance patterns, with terrestrial Oribatida and Mesostigmata abundant in drier situations (hummocks) ( $F_{1,162} = 62.25$ ,  $p < 0.001$ ) and limnic Oribatida abundant in wetter situations (pools) ( $F_{1,163} = 393.75$ ,  $p < 0.001$ ). Total species richness of Oribatida and Mesostigmata in *Sphagnum* samples was strongly influenced by water table depth, with dryer areas holding higher biodiversity ( $F_{1,163} = 18.60$ ,  $p < 0.001$ ).



**Fig. 2.** Latitudinal gradients in sampled *Sphagnum* bogs, West Siberian Plain, 2023. All correlations significant at  $\alpha = 0.05$ . Latitudes (North to South) from 68° – southern hypoaarctic tundra to 54° – forest-steppe transition. Units: mineralisation (mg/L); K, P, S, Zn, Cr ( $\mu\text{g/g}$ ); N (%).

**Table 1**  
Pearson correlation coefficients and *p*-values for environmental variables in *Sphagnum* bogs, N = 60 (pools).

	pH	Mineralisation	GW level	Trophic class
Latitude	-0.65, <0.001	-0.64, <0.001	0.06, 0.639	-0.23, 0.083
Mineralisation	0.64, <0.001	1.00		
Water depth	-0.16, 0.232	-0.05, 0.686	1.00	
Trophic class	0.43, 0.001	0.13, 0.315	-0.11, 0.407	1.00

**Table 2**  
Pearson correlation coefficients and *p*-values for environmental variables in *Sphagnum* bogs, N = 120 (hummocks).

	pH	Mineralisation	GW level	Trophic class
Latitude	-0.55, <0.001	-0.49, <0.001	-0.06, 0.554	0.35, <0.001
Mineralisation	0.66, <0.001	1.00		
Water depth	-0.33, 0.001	-0.12, 0.176	1.00	
Trophic class	0.56, <0.001	0.37, <0.001	-0.35, <0.001	1.00

**Table 3**

Mean site-level concentrations ( $\mu\text{g/g}$ ) of nutrients and trace elements in *Sphagnum* moss ( $N = 5$ ) in peatland sites along the West Siberian transect, 2023. Sites are ordered latitudinally North to South, from arctic tundra (s1) to forest-steppe transition (s12). See the Supplementary Material S1 for full names and descriptions of the sites. Trace elements which were below detection levels (n.d.): Al, V, Cu, Co, Ga, Se, Nb, Mo, Pb, Th, U.

Site	s1 Taz	s2 Novo	s3 Syv	s4 Gub	s5 Noy	s6 Kog	s7 Nef	s8 Dem	s9 Abr	s10 Kuch	s11 Bel	s12 Kos
P	38.18	94.78	92.92	113.5	53.74	40.14	69.04	80.84	62.02	189.14	136.36	155.94
S	188.32	272.56	293.34	280.12	276.2	240.82	261.26	270.56	337.4	319.38	309.76	372.38
Na	1861.54	2077.3	1824.8	1875.78	2036.02	1866.52	1890.42	2006.44	1844.52	1913.94	1990.98	2082.02
K	486.7	1007.92	1280.12	1040.52	969.5	938.1	1165.42	1404.44	1354.3	2013.84	2433.58	1982.94
Ca	496.64	661.46	556.88	612.58	568.14	276.78	455.1	616.18	620.24	919.98	790.3	881.98
Mg	520.92	576.1	513.92	542.24	595.04	505.34	563.96	544.42	574.32	560.44	637.38	807.1
Cl	n.d	96.36	96.38	160.3	242.44	56.94	80.06	134.1	179.38	167.76	348.34	275
Si	752.74	412.18	208.54	293.8	308.74	365.3	246.46	203.04	364.1	382.32	750.5	1174.38
Ti	32.86	15.32	14.2	14.7	15.78	16.24	15.1	11.1	15.24	14.64	19.38	22.84
Cr	6.04	3.46	3.56	3.66	2.74	3.28	3.42	2.88	5.5	5.44	5.94	9.96
Mn	36.38	53.32	43.26	43.3	25.76	16.42	132.9	43.46	60.76	93.14	100.8	77.62
Fe	504.14	431.1	185.8	379.66	349.74	235.12	343.1	240.08	277.68	341.16	340.14	422.94
Ni	0.26	0.34	0.28	0.2	0.32	0.18	0.34	0.28	0.6	0.34	0.34	0.52
Zn	3.02	4.72	4.86	4.02	6.2	4.2	5.14	6.14	4.7	7.22	6.72	7.64
As	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d	0.08	n.d	n.d
Rb	1.1	3.02	1.98	1.94	1.84	1.78	1.6	1.92	1.76	1.88	0.7	0.6
Sr	0.9	0.98	0.58	0.78	0.76	0.48	0.58	0.82	0.66	1.36	1.36	2.32
Y	n.d	0.2	0.16	0.1	n.d	n.d	0.16	0.1	n.d	n.d	n.d	n.d
Zr	0.82	0.1	n.d	0.14	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d
Ba	n.d	n.d	n.d	n.d	3.36	n.d	n.d	n.d	n.d	n.d	n.d	n.d

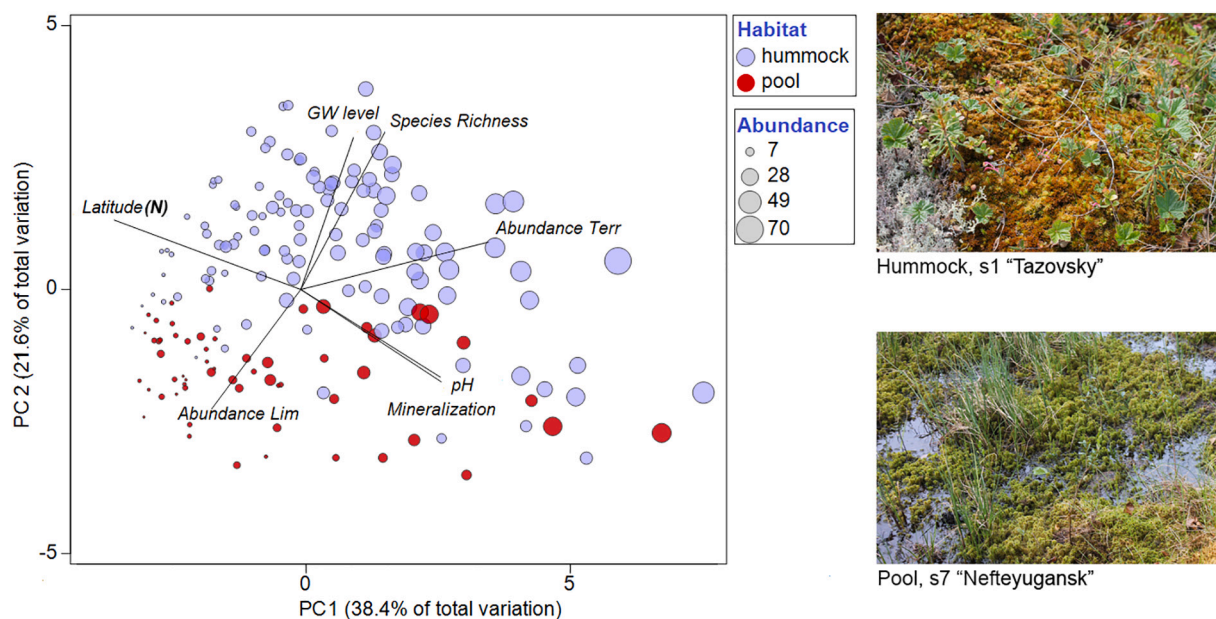
Species richness was not influenced by latitude or any of productivity variables.

Abundance of terrestrial Oribatida and Mesostigmata increased North to South ( $F_{1,163} = 35.48, p < 0.001$ ) and was linked to local trophic class ( $F_{1,163} = 17.43, p < 0.001$ ); it was not influenced by water pH or water mineralisation. Abundance of limnic oribatid mites was also influenced by latitude, but declined North to South ( $F_{1,103} = 5.59, p = 0.020$ ). At the same time, higher abundance of limnic Oribatida was positively linked to higher productivity, indicated by water pH, water mineralisation, and local trophic class (pH:  $F_{1,103} = 7.09, p = 0.009$ ; mineralisation:  $F_{1,103} = 6.31, p = 0.014$ ; trophic class:  $F_{1,103} = 48.70, p < 0.001$ ). This seems counterintuitive, given the latitudinal gradient in productivity on the transect, as demonstrated above. It becomes clearer if we look at the proportion of limnic Oribatida in total Oribatida abundance: along the North-South latitudinal gradient we observed an

increase in total Oribatida abundance ( $F_{1,164} = 29.70, p < 0.001$ ) but a significant decline in proportion of limnic species ( $F_{1,163} = 13.93, p = 0.001$ ), which suggests increasingly dry environments and an overriding impact of that on limnic species.

Fig. 3 presents the PCA ordination of samples in environmental space. The PC1 and PC2 accounted for 38.4 % and 21.6 % of the total variability, respectively. The PC1 appears to largely represent latitude, water pH and water mineralisation, reflecting the influence of the latitudinal gradient in productivity. The PC2 represents the effects of micro-topography (depth to water table). Fig. 3 shows the overall increase in abundance of terrestrial species along the North-South latitudinal gradient, the total species richness linked to drier environments, and the latitudinal increase in terrestrial mites in pools reflecting more xeric conditions overall.

Among nutrients and trace elements measured in *Sphagnum* moss, Si



**Fig. 3.** PCA ordination for *Sphagnum* bog samples in environmental and biodiversity space (Euclidean similarity), West Siberian Plain, 2023. “Abundance Lim” is the abundance of limnic Oribatida. Bubble size represents combined abundances of terrestrial Oribatida and Mesostigmata (“Abundance Terr”); notice the latitudinal increase in terrestrial mites in pools. Abundance counts were normalized by the dry weight of *Sphagnum* moss in each sample. “GW level”- water table depth.

and C were linked to higher abundance and species richness of terrestrial mites, and to lower abundance of limnic Oribatida; these two elements appear to represent the micro-topography gradient. Abundance of terrestrial mites was not correlated to any other elements. Abundance of limnic Oribatida was linked to higher P and weaker to higher N ( $P: X^2 = 4.79, p = 0.029$ ;  $N: X^2 = 3.88, p = 0.049$ ). Total species richness was positively correlated with K and Zn ( $K: X^2 = 7.89, p = 0.005$ ;  $Zn: X^2 = 10.47, p = 0.001$ ). Overall, the trace elements in *Sphagnum* did not explain a lot of variability in the abundance or species richness data.

Area of the bogs varied from very small (0.07 km<sup>2</sup>, the southern-most site “Kosulino”) to extensive mire systems covering over 100 km<sup>2</sup> (e.g., sites “Demyanka” and “Kogalym”). There was no evidence that larger bogs had larger (or smaller) number of species of either Oribatida or Mesostigmata. There was a significant linear distance decay in community similarity between sites (OLS  $r^2 = 0.56, p < 0.001$ ), suggesting no upper limit beyond which community similarity is relatively independent of distance (Fig. 4).

Among factors tested as potentially influencing site-level community composition of *Sphagnum* bogs (bog area, latitude, site mean for pH, N, P, C:N ratio), the significant factors were latitude (Pseudo-F = 5.86,  $p = 0.001$ ), P (Pseudo-F = 2.92,  $p = 0.016$ ) and C:N ratio (Pseudo-F = 3.59,  $p = 0.020$ ), which together explained 67.2 % variability in community composition. However, it is important to remember that latitude, pH and *Sphagnum* nutrient chemistry were correlated on our transect. Latitude alone explained 37 % variability in community composition.

Assemblages of Oribatida and Mesostigmata appeared to be changing gradually North to South along most of the transect, without clear tendency in total species richness (Fig. 5A). The species assemblages of the three southern-most sites were clearly segregated (Fig. 5A). Mesostigmata assemblages in these three sites were characterized by the absence of any members of Zerconidae or Veigaiidae, which were present and often abundant in most other sites (Fig. 5B) and presence of *Geolaelaps* sp. (absent in other sites). Oribatida assemblages in the three southern-most sites were characterized by presence of some unique species, e.g., *Tyrphonothrus glaber*, *Tyrphonothrus* sp., *Banksinoma akhtyamovi*, larger densities of *Pilgalumna tenuiclava* and *Ramusella furcata*, but also by absence of *Tyrphonothrus foveolatus* and any *Limnozetes*

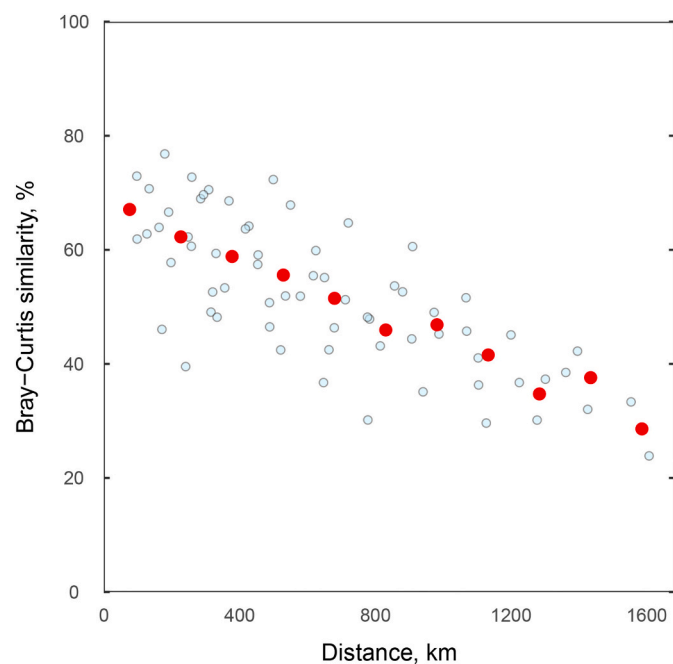


Fig. 4. Distance decay of similarity in site-level species assemblages of Oribatida and Mesostigmata in *Sphagnum* bogs, West Siberian Plain, 2023; red circles are binned averages. OLS regression:  $r^2 = 0.56, p < 0.001$ .

species, which were abundant in all other bogs (Fig. 5C).

## 4. Discussion

### 4.1. Latitudinal productivity gradient

Nutrient content in *Sphagnum* tissues has been found to co-vary with nutrient input within the peatland, with increased N concentration reflecting increased N inputs (Aerts et al., 1992; van der Heijden et al., 2000; Limpens et al., 2017; van den Elzen et al., 2018). Our results show a consistent increase in nutrient content of *Sphagnum* tissues and water pH along the North to South latitudinal gradient. The three southern-most sites were highest in N and P and were classified as mesotrophic based on pH and vegetation. The northern-most site “Tazovsky” had lowest N and highest C:N ratio, indicating potential N limitation influenced by the cold climate.

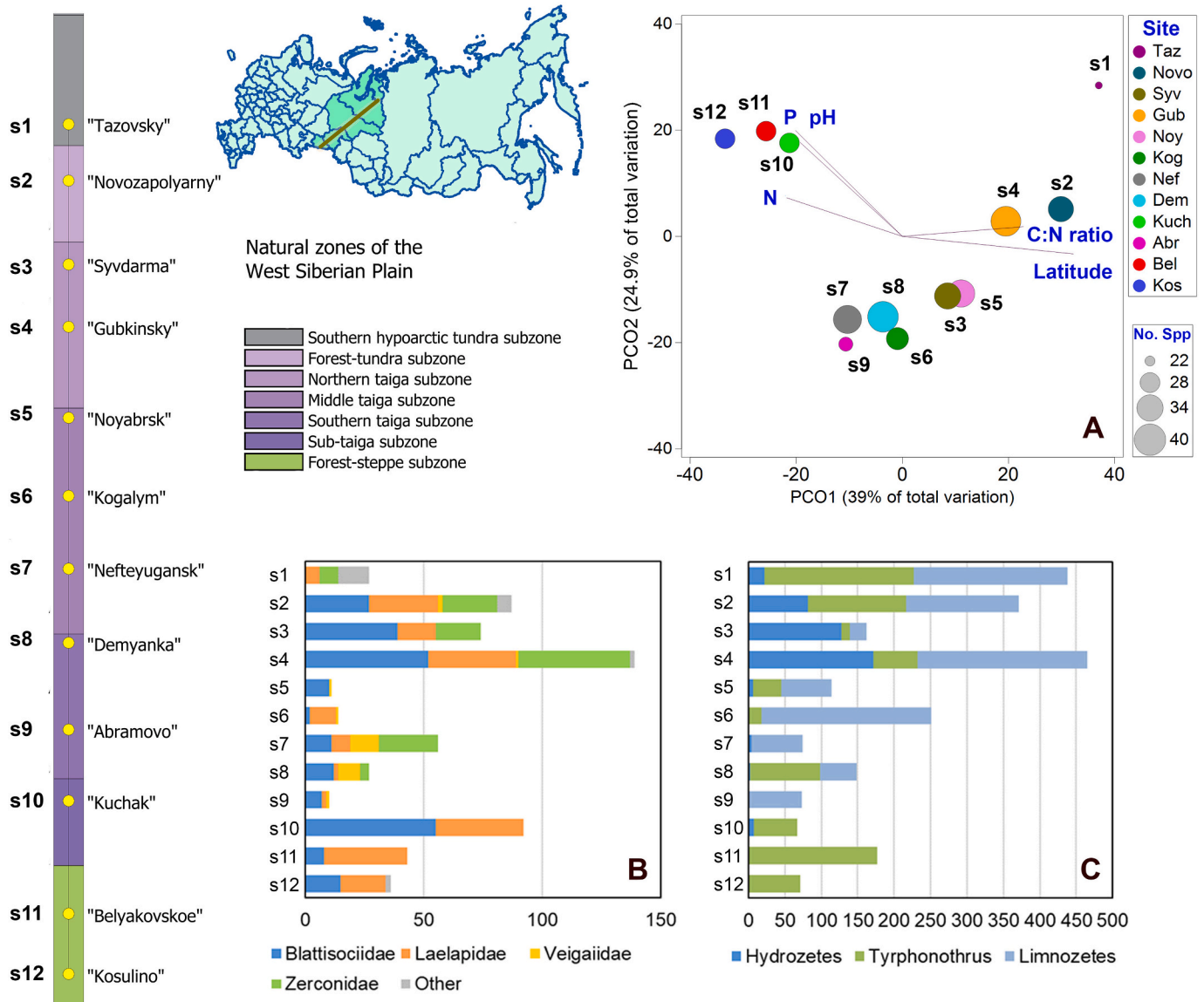
In the Northern hemisphere, higher latitudes are associated with decreased soil pH, decomposition, and mineralisation rates (Gholz et al., 2000; Pärtel, 2002; Stark et al., 2014). Research in NW Europe and Western Siberia indicates lower total N concentrations, lower N mineralisation rates and higher C:N ratios in high-latitude subarctic peatlands compared to cool-temperate or warm-temperate ones, indicating strong N limitation at high latitudes (Dorrepaal et al., 2005; Meyer et al., 2006). The findings that N might be the main limiting factor at high latitudes are consistent across studies reporting on N in boreal and tundra ecosystems (Van Cleve and Alexander, 1981; Clein and Schimel, 1995; Reich and Oleksyn, 2004; Kaiser et al., 2005; Lovelock et al., 2007; Stark et al., 2014).

Warmer temperatures, either due to climate or raised in experimental settings, accelerate nitrogen cycling in peatlands and promote higher nitrogen mineralisation rates (Peterjohn et al., 1994; Hobbie, 1996; Rustad et al., 2001; Weedon et al., 2012). Furthermore, increased nitrogen availability at lower latitudes can be exacerbated by anthropogenic nitrogen deposition (Aerts et al., 1992). Atmospheric N deposition rates were not measured in our study, but the decades-long research on N deposition in industrialized regions suggests a broad-scale covariance between anthropogenic N inputs and latitude (Bobbink et al., 2010; Peñuelas et al., 2012). For example, strong gradients in wet and dry total N deposition rates exist from the central Europe towards northern Europe, and from central China towards Siberia (Bobbink et al., 2010).

Many plants found in oligotrophic *Sphagnum* peatlands are adapted to low pH and low N availability. Acting together, warmer temperatures and increased N deposition can transform *Sphagnum*-dominated oligotrophic peatlands into mesotrophic systems dominated by vascular plants (Limpens et al., 2003; Gunnarsson et al., 2004; Bragazza et al., 2006; Bubier et al., 2007; Juutinen et al., 2010). This transformation leads to shifts in ecosystem functioning and services, for example affecting C sequestration dynamics, which is a critical environmental concern.

### 4.2. Trace elements

*Sphagnum* samples collected from twelve peat bogs on the West Siberian transect provide insights on atmospheric deposition of trace elements. The variation in Ti concentrations observed along our transect reflects the distribution and quantity of airborne dust deposition from the atmosphere (Shotyk et al., 2016; Kempter et al., 2017). *Sphagnum* mosses are reliable bioindicators for monitoring atmospheric deposition of trace metals and other contaminants, as concentrations in moss tissue closely reflect deposition rates (Berg and Steinnes, 1997; Gerdol et al., 2000; Steinnes et al., 2011; Shotyk et al., 2016; Kempter et al., 2017). Our results indicate an increase in deposition levels of potentially toxic Zn, Ni and Sr in proportion to the abundance of lithophile Ti in some sites on the southern end of the transect. Additionally, there was a continuous increase in Cr/Ti from North to South. However, in absolute



**Fig. 5.** Biodiversity patterns of Acari (Oribatida, Mesostigmata) in *Sphagnum* bogs along the sampled transect, West Siberian Plain, 2023. Sites are numbered North to South from s1 – southern hypoarctic tundra to s12 – forest-steppe transition. (A) Principal Coordinates Analysis based on Bray-Curtis similarity showing sites in species space; bubble size (No. spp.) represents the combined (Oribatida + Mesostigmata) total species richness in each site; vectors represent major gradients. (B) Abundance of Mesostigmata families. (C) Abundance of limnic Oribatida genera.

terms and when compared to recent data from mosses collected in Canada (Shotyk et al., 2016), Germany (Kempter et al., 2017) and remote regions of Norway (Steinnes et al., 2011), the mean concentrations of Zn, Sr, Ni, and As in the *Sphagnum* moss from the West Siberian transect were very low. In fact, the average Ni concentrations in our *Sphagnum* samples are comparable to the mid-Holocene reference values (Ni  $0.46 \pm 0.09 \mu\text{g/g}$ ) from an ombrotrophic peat bog at Etang de la Gruère, Jura Mountains, Switzerland (Krachler et al., 2003).

On the other hand, relatively higher concentrations of Cr, ranging between 2.74 and 9.96  $\mu\text{g/g}$  in our samples compared to 0.42–17.38  $\mu\text{g/g}$  in *Sphagnum* from industrialized Southern Germany (Kempter et al., 2017), and a consistent increase in Cr/Ti ratios from North to South suggest an anthropogenic source. Natural Cr content in the Earth's crust falls between 0.35 and 0.83  $\mu\text{g/g}$  (Yaroshevsky, 2006). Chromium primarily enters the air from industrial sources (iron and steel production, coal combustion), and from other more minor sources such as dyes and road dust (Pacyna and Pacyna, 2001; Ullah et al., 2023), and it is probably linked to the oil and gas production in the West Siberian

petroleum province (Brekhtunsov et al., 2011). The World Health Organization sets the permissible limit of Cr in the soil at 100  $\mu\text{g/g}$ , although lower (and higher) limits are set by many countries (Ding et al., 2014) – this renders the Cr concentrations in our samples still very low.

### 4.3. Biodiversity patterns

Latitude and productivity gradient were correlated on the West Siberian transect. Terrestrial abundance appears to be influenced both by productivity gradient and by water depth. As we expected, latitude (and linked productivity gradient) significantly influenced the total abundance of terrestrial mites (terrestrial Oribatida and all Mesostigmata), which increased North to South. Higher abundance of limnic oribatid mites was linked with higher productivity (N, P, water pH, water mineralisation), but declined North to South in absolute numbers and as proportion of total Oribatida abundance – which suggests increasingly drier environments. Latitude accounted for 37 % variability in community composition. Assemblages of Oribatida and Mesostigmata

changed gradually North to South, with assemblages of the three southern-most mesotrophic sites (“Kosulino”, “Belyakovskoe” and “Kuchak”) distinctly segregated.

Minor et al. (2016) observed a North-to-South increase in Oribatida abundance in *Sphagnum* bogs, probably reflecting the productivity gradient. While latitudinal gradients in species richness have been confirmed for a range of organisms, some evidence suggests that this phenomenon may not fully apply to soil organisms such as ECM fungi (Tedersoo and Nara, 2010) or soil oribatid mites (Maraun et al., 2007).

We found no effect of latitude on species richness along a 1600 km transect. Instead, the main driver for species richness appeared to be the local depth to water table, with dryer areas colonised by a wider range of species. The decrease in abundance of limnic (aquatic) Oribatida from North to South in our study, as well as absence/near absence of *Limnozetes* and *Hydrozetes* in the three southern-most sites, also suggest an overriding influence of increasingly xeric conditions. Similarly, Barreto et al. (2021) found that warming-induced drying of a peatland increased species richness of terrestrial Oribatida due to enhanced colonization and at the expense of moisture-loving limnic species, which declined. Recent modelling suggests that the southern edge of boreal peatlands would experience the greatest decline in the suitable *Sphagnum* habitat with the rising temperatures, with warmer growing season and drier conditions giving competitive advantage to vascular plants (Dieleman et al., 2015; Ma et al., 2022).

Evidence supporting latitudinal gradients in community assemblages of terrestrial arthropods is accumulating (Andrew and Hughes, 2004; Bowden and Buddle, 2010; Aslani et al., 2022). Previous studies on Oribatida in a variety of habitats demonstrated a strong spatial effect on community composition (Borcard and Legendre, 2002; Lindo and Winchester, 2008; Caruso et al., 2012, 2019). Caruso et al. (2019) found a large-scale North to South gradient in assemblages and species diversity of soil Oribatida across Great Britain. However, the direct effect of latitude on Oribatida diversity was not statistically significant, implying that “latitudinal” changes were driven by other variables, such as precipitation and organic matter. Similarly, at the regional scale of the Netherlands, Zaitsev et al. (2013) found significant changes in oribatid mite communities East to West along the gradient in the quantity and quality of organic matter. On a much smaller scale, Chen (2014) found that macro-climatic factors had no effect on structuring Oribatida communities. Overall, latitudinal effects appear stronger when several gradients (e.g., precipitation and organic matter) are coupled (e.g., Caruso et al., 2019).

Our study along the West Siberian transect showed a linear distance decay in mite community similarity with increased geographical distance. Other scientists also found distance decay in peatland Oribatida community similarity at a larger scale (Mumladze et al., 2013), although at smaller scales it may not be as evident (Minor et al., 2016). Chen et al. (2014) found a decline in microarthropod community similarity with geographic distance, with species composition based on presence-absence better predicted by spatial distance than environmental similarity. In contrast, environmental variables explained more variance in the community composition in terms of relative abundance of taxa.

## 5. Conclusions

In summary, we confirmed the presence of large scale latitudinal gradients in productivity and biodiversity in peatlands on the West Siberian Plain. A consistent increase in N, P, K content of *Sphagnum* tissues, water pH and water mineralisation indicated a North to South increase in productivity, which can be linked to increased abundance of terrestrial mites (terrestrial Oribatida and all Mesostigmata). Abundance of limnic Oribatida declined North to South, reflecting increasingly xeric conditions. The latitudinal gradient in species richness was not evident; the main driver for species richness was the local microtopography, with dryer areas colonised by more species. There was an increase in deposition levels of potentially toxic trace elements Cr, Zn, Ni and Sr on the

southern end of the transect, although in absolute terms concentrations of these elements in *Sphagnum* tissues were low.

The transect studies allow us to elucidate constraints on productivity and biodiversity dynamics, understand how organisms may adapt to changing conditions and provide a checkpoint in the timeline of global change (Steffen et al., 1999; Meyer et al., 2006). Although at closer approximation the conditions in each peatland reflect a set of local factors such as climate, geology, topography, hydrology and history, the general patterns observed over large spatial extent provide broad insights, even considering a single sampling campaign. As intrazonal ecosystems with limited adaptability, peatlands are sensitive to local environmental conditions – changes in climate, land management or atmospheric deposition of nutrients and pollutants can lead to noticeable shifts in ecological processes and species assemblages (Parish et al., 2008), potentially more quickly and in a more predictable way than in broader zonal systems. Considering expected changes in climate, especially in arctic and subarctic zones (Maxwell, 1992; Niskanen et al., 2019; IPCC, 2019), peatlands can be particularly useful as early warning systems on a landscape scale, providing information about the state of the environment and the effects of human activities.

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## CRediT authorship contribution statement

**M.A. Minor:** Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Conceptualization. **S.D. Sheykin:** Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **V.A. Stolbov:** Writing – review & editing, Project administration, Methodology, Investigation, Conceptualization. **S.G. Ermilov:** Writing – review & editing, Investigation. **O. Joharchi:** Writing – review & editing, Investigation. **A.S. Afonin:** Investigation. **O. S. Shvartseva:** Investigation. **A.V. Tolstikov:** Resources, Project administration, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Sample-level georeferenced datasets are available from the corresponding author upon request. All specimens (ethanol with drop of glycerol) are deposited in the Tyumen State University Museum of Zoology, Tyumen, Russia.

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