



Hydrology-driven environmental variability determines abiotic characteristics and Oribatida diversity patterns in a *Sphagnum* peatland system

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Abstract

We investigated oribatid mite communities in a *Sphagnum*-dominated boreal peatland system characterised by a mosaic of oligotrophic and meso-eutrophic areas. We aimed to determine the relative importance of environmental factors (pH, *Sphagnum* nutrient content, water table level, diversity of vascular plants and bryophytes in the surrounding plant community) and spatial variation in influencing abundance, diversity and community composition of aquatic and terrestrial oribatid mites. Among environmental variables, water table level (micro-topography), pH, and K in *Sphagnum* tissues were the main predictors of Oribatida community structure. Aquatic species were associated with pools; two terrestrial species—*Hoplophthiracarus illinoisensis* and *Nothrus pratensis*—were associated with oligotrophic hummocks; the rest of terrestrial species were associated with dryer meso-trophic and eutrophic habitats. Low water table depth (hummocks), high local plant diversity, and high P in *Sphagnum* tissues were predictors of high abundance of terrestrial Oribatida. Species richness of terrestrial Oribatida was linked with low water table and high plant diversity. For aquatic Oribatida abundance, water table depth was the single most important predictor variable. Plot trophic class (its status on the peatland poor-rich gradient assigned based on plant indicator species) was also a significant predictor of terrestrial Oribatida abundance, richness, and community structure. Spatial structuring was important for terrestrial Oribatida community composition, weak ($P < 0.10$) for terrestrial Oribatida abundance and richness, and not significant for aquatic Oribatida.

Keywords Microarthropods · Abundance · Species richness · Community structure · Productivity · Habitat diversity

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Introduction

Sphagnum peatlands (raised bogs and transitional mires) occupy extensive areas in the boreal and subarctic regions of Eurasia and North America (Tarnocai and Stolbovoy 2006; Rydin and Jeglum 2013). Precipitation-fed (ombrotrophic) raised bogs generally lack any other hydrological inputs, resulting in acidic and nutrient-poor (oligotrophic) conditions. These environments are characterized by dominance of *Sphagnum* mosses, low pH (<5.0), and scarcity of nutrients (Wheeler and Proctor 2000). Some areas of a peatland may receive supplementary nutrient input from mineral soil, e.g., from ground water seepage (Eurola and Holappa 1985); such areas form patches of nutrient enrichment and provide niches to meso-eutrophic vegetation (Ruuhijärvi and Lindholm 2006). As a result, patches of oligotrophic and meso-eutrophic habitats in a peatland can be complex.

Hydrology and nutrient availability exert a major control on distribution of oligotrophic and meso-eutrophic patches and on patterns of plant and animal diversity in peatlands. Peatland environments are typically described along a poor-rich (acidity–alkalinity) gradient (Ruuhijärvi and Lindholm 2006); it can also be referred to as an oligotrophy–eutrophy gradient (Eurola and Huttunen 2006). This gradient primarily reflects the degree of inflow of mineral soil water, and is best characterised by the pH, with peatland vegetation forming a pH-driven continuum of plant communities (Wheeler and Proctor 2000; Tahvanainen 2004). Perhaps confusingly, ‘oligotrophy–eutrophy’ terminology is also applied to describe the nutrient gradient, which reflects the availability of N, P and K (Ruuhijärvi and Lindholm 2006). The pH gradient and the nutrient availability gradient in peatlands usually coincide, but may be decoupled (Wheeler and Proctor 2000; Bragazza and Gerdol 2002). Different *Sphagnum* and vascular plant species occur at different positions along the pH and nutrient gradients (Limpens et al. 2003; Rydin and Jeglum 2013). Nutrient content in *Sphagnum* tissues has been found to co-vary with local nutrient input within the peatland (Wheeler and Proctor 2000; Limpens et al. 2017; van den Elzen et al. 2018).

Another major gradient in a peatland is the micro-topographic structure of hummocks, hollows, and intermediate lawns. Micro-topography gives peatlands their characteristic patterning and is linked to hydrology, biodiversity and carbon sequestration (Hajkova and Hajek 2007). Different *Sphagnum* species occupy different micro-topographic positions (Gunnarsson 2005; Johnson et al. 2014).

Peatlands contain specialized and highly distinctive assemblages of plants and invertebrates (Tahvanainen 2004; Spitzer and Danks 2006). Oribatid mites are an abundant group of arthropods in boreal peatlands, and their fauna in European peat bogs is well studied (e.g., Tarras-Wahlberg 1961; Markkula 1986; Weigmann 1991; Borcard and von Ballmoos 1997; Stary 2006; Seniczak 2011; Seniczak et al. 2014). At a site level, diversity patterns of Oribatida are influenced by the factors that are recognized as biodiversity drivers for broader groups of peatland organisms, such as ground water level, pH and habitat heterogeneity (Donaldson 1996; Minor et al. 2016).

The drivers of species distribution across environmental gradients continue to be a challenging question in ecology (Sutherland et al. 2013). Environmental conditions, spatial and temporal environmental heterogeneity, biotic interactions, and historical processes are all known to influence the taxonomic and functional structure of communities (Chesson 2000), but the relative contribution of these factors cannot be easily generalised (HilleRisLambers et al. 2012; Cadotte and Tucker 2017). In this study, we measured a set of variables expected to influence patterns of diversity in Oribatida communities in a relatively undisturbed boreal mire system characterised by a mosaic of oligotrophic and meso-eutrophic

areas. We hypothesised that environmental factors such as pH, *Sphagnum* nutrient content, water table level, and plant diversity in the sampling plot will be important contributors to Oribatida diversity patterns, and aimed to quantify relative contribution of these factors to shaping oribatid mite communities.

Methods

Study site

The sampled mire system ('Boloto Shichenskoe', 59°56'30.4"N, 41°16'57.1"E) is located in Vologda oblast in the north-western Russia (Fig. 1a). The climate in the region is humid continental (Köppen climate classification: Dfb), with long moderately cold winter (mean temperature of January $-12\text{ }^{\circ}\text{C}$) and short warm summer (mean temperature of July $16\text{--}17\text{ }^{\circ}\text{C}$). Annual precipitation is 500–650 mm as rain and snow; snow cover lasts 165–170 days of the year. The mire is a large (15,900 ha) wetland system of predominantly lacustrine origin, formed in the large glacial lake basin (Philippov 2015). The central part of the mire is occupied by a shallow oligotrophic lake Shichenskoe (1060 ha). The mire occupies a transitional-accumulative position on the local landscapes, with distribution of ombrotrophic and minerotrophic areas in the mire system reflecting the flows of gravitational and ground water (Fig. 1b). Significant area of the mire is occupied by the ombrotrophic peat bog, dominated by *Pinus*-shrubs-*Sphagnum* and *Eriophorum*-shrubs-*Sphagnum* associations. The bog ridges and hummocks are dominated by *Sphagnum fuscum*, less frequently by *Sphagnum angustifolium* and *S. medium*; hollows are occupied by *S. cuspidatum*, *S. balticum*, less frequently by *S. majus* and *S. fallax*; nine other species of *Sphagnum* occur sporadically (Philippov and Boychuk 2015). Within the ombrotrophic bog there are several ground water seeps, usually associated with forested mineral islands, the seeps are visible in Fig. 1b. Present in or near the seeps are meso- and eutrophic *Sphagnum* mosses. The south-eastern part of the mire system, where three rivers flow, is

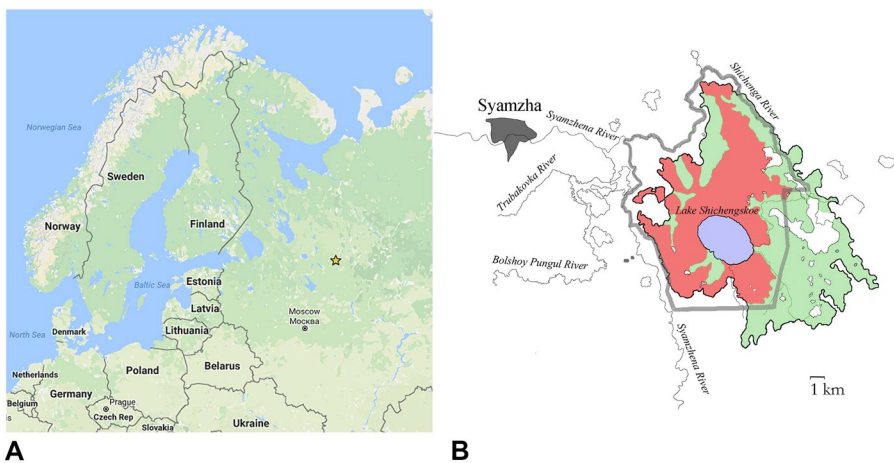


Fig. 1 Sampling area: **a** map of Europe by GoogleMaps; **b** Shichenskoe mire; red (b/w: dark grey) — ombrotrophic peat bog, green (b/w: light grey) —minerotrophic areas; grey line is the boundary of the Shichenskoye regional landscape reserve. (Color figure online)

meso- and eutrophic. The eutrophic edges of the mire are forested with *Betula pubescens*, *Salix pentandra*, and *Alnus glutinosa* (Philippov 2015).

Sampling

Sampling was conducted in July 2016 and limited to *Sphagnum*-dominated communities in ombrotrophic (western) part of the mire. Samples were collected from 48 plots (1 m^{-2}), each plot dominated by one of the 16 *Sphagnum* species present in the mire, with three replicated plots per *Sphagnum* species. The stratification by *Sphagnum* species was used to achieve balanced sampling. The minimum distance between some conspecific *Sphagnum* plots was 5–7 m, but usually over 30 m. *Sphagnum* mosses were identified using Ignatov and Ignatova (2003), and classified into phylogenetic sections and preferred habitat types (Table 1); nomenclature follows Ignatov et al. (2006). In each sampling plot GPS coordinates, *Sphagnum* moss identity, and plant diversity (as simple species richness of vascular plants, bryophytes and liverworts) were recorded.

Other variables recorded at a plot level were water table level, water pH, and *Sphagnum* nutrient content (C, N, P, K). Water table depth was measured in each sampling plot using temporary wells. The upper layers of peat were removed and the water level allowed to stabilize; the depth from the water table to the top of *Sphagnum* capitula was measured with a ruler. Water pH samples (one compound sample per plot, squeezed from the relevant *Sphagnum* moss species) were collected in 15 ml plastic vials into the portable chiller, stored in the dark at 4 °C and analysed the next day in the lab using Sartorius PB-11 benchtop pH meter. Nutrient content (C, N, P, K) of *Sphagnum* moss from all plots was analysed in duplicate samples. The moss samples were air-dried at room temperature and homogenised. Total organically bound carbon (TOC) and nitrogen (TN_b) were measured using ‘Vario TOC cube’ analyser (Elementar Analysensysteme). Phosphorous (as P_2O_5) was quantified colorimetrically in a spectrophotometer using molybdenum-blue method from samples prepared by wet digestion (H_2SO_4 plus 30% H_2O_2 with Se as a catalyst). Potassium (as K_2O) was measured using atomic absorption spectrophotometer AA-6300 (Shimadzu) from samples prepared by wet digestion (same method as for P). All nutrient content results were converted to dry-matter basis (determined by drying subsamples at 105 °C to a constant weight).

To characterise the status of each sampled peatland plot on the poor-rich continuum, each plot was assigned to a qualitative ‘trophic class’ based on plant community features (Rydin et al. 1999; Euroala and Huttunen 2006). We used oligotrophy-eutrophy terminology and included intermediate categories to separate five trophic classes: oligotrophic, oligomesotrophic, mesotrophic, meso-eutrophic, eutrophic. Note that ‘trophic class’ here does not directly reflect nutrient status, but instead is based on plant indicator species of the poor-rich (acidity–alkalinity) gradient; we then compared resulting trophic classes with pH and *Sphagnum* nutrient content measurements.

Sphagnum moss for mite extraction was collected as 10×10 cm samples to the depth of living moss plants (including capitula and the length of stems). Mites from moss samples were extracted in modified Berlese funnels until samples were fully dry. Adult Oribatida were counted, identified to a species level, and classified into two functional groups—‘aquatic’ (species living on submerged vegetation in freshwater habitats, following Weigmann and Deichsel 2006; Seniczak 2011), and ‘terrestrial’ (all other species). Nomenclature system is mostly following Subías (2018).

Table 1 *Sphagnum* mosses sampled in the Shichengskoe mire, July 2016, their habitat and related environmental variables (mean ± SD, n = 3)

Section	<i>Sphagnum</i> species	Habitat	Water table (cm)	pH	TN _b (% dry weight)	ω (P ₂ O ₅) (% dry weight)	ω (K ₂ O) (% dry weight)	TOC (% dry weight)	Plant diversity	Trophic class
Cuspidata	<i>S. angustifolium</i> ^a	Lawns	- 15.0 ± 3.61	3.93 ± 0.09	2.357 ± 0.807	0.1651 ± 0.1083	0.4794 ± 0.0904	47.28 ± 2.131	6.67 ± 1.53	O
	<i>S. balticum</i> ^a	Hollows	- 9.67 ± 3.21	4.02 ± 0.31	2.544 ± 0.657	0.1756 ± 0.1696	0.4303 ± 0.0693	47.19 ± 0.725	7.33 ± 0.58	O
	<i>S. cuspidatum</i>	Hollows	- 7.33 ± 4.04	4.00 ± 0.40	2.340 ± 0.326	0.1469 ± 0.1489	0.8036 ± 0.2308	48.72 ± 3.510	6.67 ± 2.08	O
	<i>S. fallax</i> ^a	Lawns	- 12.0 ± 2.65	5.03 ± 0.34	2.094 ± 0.773	0.1167 ± 0.0392	0.7926 ± 0.0175	46.57 ± 2.891	10.67 ± 0.58	M
	<i>S. flexuosum</i>	Hollows	- 12.67 ± 3.79	4.60 ± 0.22	2.322 ± 0.511	0.1487 ± 0.0906	0.7533 ± 0.0483	48.39 ± 5.404	11.33 ± 2.08	OM
	<i>S. lindbergii</i>	Hollows	- 6.0 ± 1.00	4.87 ± 0.20	2.762 ± 0.222	0.0594 ± 0.0029	0.6566 ± 0.0608	48.07 ± 4.958	8.67 ± 2.08	O
Sphagnum	<i>S. majus</i> ^a	Hollows	- 9.33 ± 1.15	4.77 ± 0.29	2.160 ± 0.106	0.0904 ± 0.0055	0.7286 ± 0.0073	49.33 ± 2.351	10.67 ± 1.53	OM
	<i>S. centrale</i>	Hummocks	- 29.0 ± 7.94	4.55 ± 0.44	2.771 ± 0.389	0.1366 ± 0.0407	1.3499 ± 0.2436	52.85 ± 1.776	6.0 ± 0	M
Acutifolia	<i>S. medium</i>	Hummocks	- 30.67 ± 9.81	3.79 ± 0.09	2.505 ± 0.690	0.2005 ± 0.2036	0.6225 ± 0.0673	47.98 ± 2.910	11.33 ± 2.89	O
	<i>S. fuscum</i>	Hummocks	- 36.67 ± 2.89	3.78 ± 0.16	2.584 ± 0.420	0.1353 ± 0.1468	0.5368 ± 0.0876	49.15 ± 2.538	8.0 ± 1.00	O
	<i>S. rubellum</i>	Hummocks	- 25.0 ± 2.00	4.03 ± 0.08	2.595 ± 0.691	0.0678 ± 0.0106	0.5048 ± 0.0107	48.99 ± 2.536	9.0 ± 1.00	O
	<i>S. russowii</i>	Hummocks	- 37.67 ± 2.52	4.10 ± 0.26	2.848 ± 0.755	0.1031 ± 0.0093	0.6552 ± 0.1620	51.51 ± 0.468	8.0 ± 1.00	M
	<i>S. warnstorffii</i>	Lawns	- 13.33 ± 1.53	5.75 ± 0.21	3.504 ± 0.164	0.2006 ± 0.0363	0.7603 ± 0.0678	51.22 ± 2.616	15.0 ± 3.00	E
Squarrosa	<i>S. squarrosom</i>	Various	- 20.0 ± 8.66	4.80 ± 0.32	4.018 ± 1.142	0.1895 ± 0.0994	1.1245 ± 0.3184	47.55 ± 3.951	5.67 ± 1.53	E
Subsecunda	<i>S. subsecundum</i>	Hollows	- 7.0 ± 1.00	5.08 ± 0.13	3.145 ± 0.658	0.0855 ± 0.0112	0.8132 ± 0.0635	52.36 ± 3.948	10.67 ± 2.08	ME
Polyclada	<i>S. wulfianum</i>	Hummocks	- 33.33 ± 2.89	3.68 ± 0.19	2.581 ± 0.706	0.1568 ± 0.0336	0.5528 ± 0.0587	47.48 ± 1.516	9.33 ± 1.15	M

Nutrients measured in *Sphagnum* tissues: TN_b total bound nitrogen, TOC total organic carbon. *Plant diversity* quantified as the number of species of vascular plants and bryophytes in a 1 × 1 m sampling plot. *Trophic class* refers to the status of sampling plots on the poor-rich gradient based on plant community features: O oligotrophic, OM oligo-mesotrophic, M mesotrophic, ME meso-eutrophic, E eutrophic

^aIndicates peat-forming species

Statistical analysis

A multicollinearity analysis (SAS v.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 in this analysis. Although different *Sphagnum* species were sampled as a stratification measure, we did not focus on the effect of *Sphagnum* species identity on Oribatida due to (1) low replication for *Sphagnum* species, and (2) strong confounding effect of environmental variables for *Sphagnum* species (see Table 1; Fig. 2a).

The environmental variables best explaining the abundance of aquatic and terrestrial Oribatida and species richness of terrestrial Oribatida were identified using random forests regression (randomForest package in R) (Genuer et al. 2010); richness for aquatic Oribatida was not analysed due to the overall low number of aquatic species. Random forests (RF) is

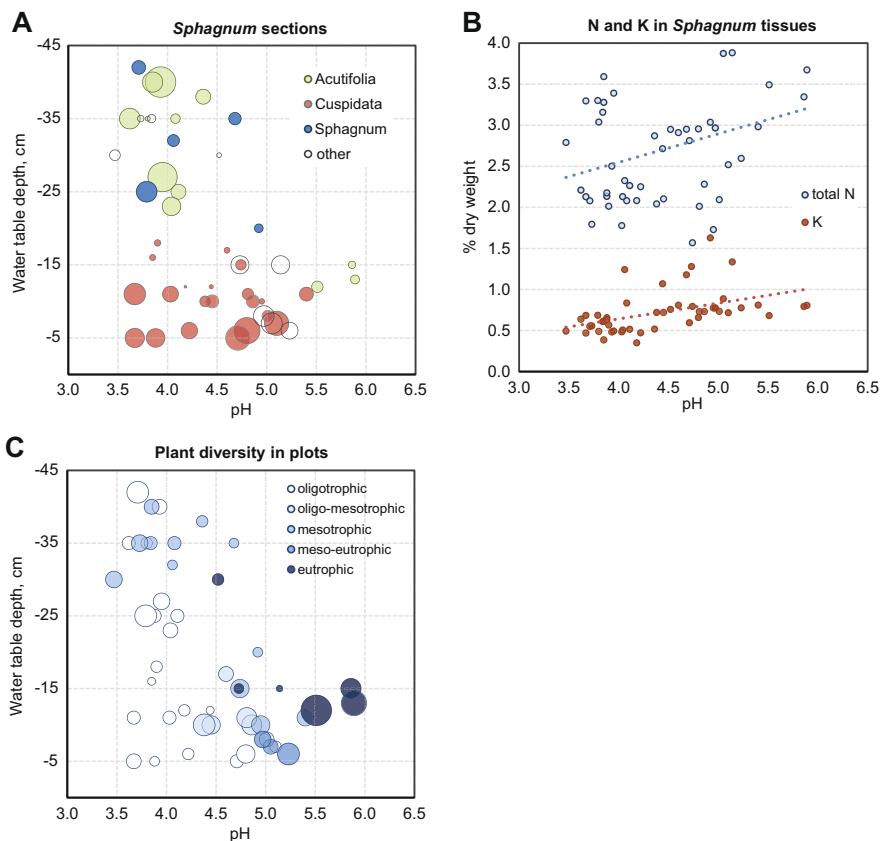


Fig. 2 Ecological gradients in the mire: **a** distribution of the three major *Sphagnum* phylogenetic clades (sections) along the pH-water table gradients, symbol size represents N:P ratio in *Sphagnum* tissues. **b** N and K in *Sphagnum* tissues along the pH gradient, OLS reg (N) $r^2 = 0.09$, $P < 0.005$, (K) $r^2 = 0.21$, $P < 0.001$. Note: there was no significant relationship between P in *Sphagnum* tissues and the pH gradient. **c** Plant diversity (symbol size) in sampling plots of different trophic classes along the pH-water table gradients, OLS reg (pH) $r^2 = 0.17$, $P = 0.003$, (water table) $r^2 = 0.02$, $P = 0.33$. Plot trophic class ('oligotrophic-eutrophic') is based on plant indicator species and reflects plot status on the peatland poor-rich gradient. (color figure online)

a classification and regression tree method that makes no distributional assumptions, has the ability to incorporate non-linear relationships between dependent and independent variables, can combine both quantitative (e.g., environmental) and qualitative (e.g., plot trophic class) variables, and is suitable for ecological data which are correlated. The RF creates multiple regression trees (the default is 500 trees, we adjusted this number for each model) fitting each tree to a randomly selected sample of the data; all trees are then averaged. The output provides the total % variance explained, and the importance score for each explanatory variable. The importance scores can be used to select the variables most important for interpretation of observed patterns. The significance of RF forests models was tested using permutation procedure (rfUtilities package; Murphy et al. 2010). Random forests can be also used for developing predictive models, but in our case the sample number is too low to train this algorithm to develop meaningful prediction, and the method was used for variable selection. Since consistency of results across statistical methods gives indication of robustness, we used the generalized linear regression (gamma distribution with log-link, SAS v.9.4, proc hpgenselect) to check for variable significance for top five most important variables identified by random forests.

Since the contribution of abiotic and biotic factors can be complex, we used path analysis to quantify relative contribution of environmental variables which form a network of causal relationships (Hatcher 1996). We constructed a hypothetical model of causal relationships underlying the observed diversity patterns in oribatid mites (see examples in Fig. 4) and used path analysis to calculate coefficients associated with each path in the diagram (proc CALIS in SAS v.9.4). Abundance of terrestrial and aquatic Oribatida, and species richness of terrestrial Oribatida were modelled; count variables were \sqrt{x} transformed for this analysis.

Principal coordinate analysis (Bray–Curtis distance on square root transformed species abundance counts) was used to construct ordination plot of samples and environmental variables in species space. Because Oribatida communities are affected not only by environmental gradients, but also by autocorrelation, we checked for spatial structuring in Oribatida communities using the Principal Coordinates of Neighbouring Matrices (PCNM) method (Borcard et al. 2004). The PCNM was applied to the matrix of pairwise Euclidean distances between sampling plots calculated from GPS coordinates, resulting in two orthogonal vectors (PCNM1, PCNM2) which were used to represent independent spatial variables. The distance-based linear modelling (DistLM) in PRIMER 7 (Clarke et al. 2014) with step-wise variable selection using AICc criterion was used to test which variables best explain Oribatida community composition. Taxa with low abundance (less than 5 individuals from all samples) were excluded from community analysis. Significance level $\alpha=0.05$ was used for all statistical tests.

Results

Environmental gradients in the mire

Sphagnum mosses and their related environmental and biological variables are reported in Table 1. Figure 2 outlines the main ecological gradients in the mire. There was a considerable correlation between taxonomic sections within the genus *Sphagnum* and their position along the pH-wetness gradients (Fig. 2a): species from Cuspidata section occupied the wetter positions (hollows and lawns), while Acutifolia and *Sphagnum* sections occurred

Table 2 Spearman's rank correlations (ρ , P -value; $n=48$) for plot trophic class vs. local environmental and productivity data

	Water table	pH	Plant diversity	Nutrients in <i>Sphagnum</i> tissues			
				N	P	K	C:N
ρ	-0.070	0.571	0.188	0.370	0.390	0.645	-0.307
P	0.64	<0.001	0.20	0.010	0.006	<0.001	0.034

Table 3 Variables best explaining Oribatida assemblages (all species) in *Sphagnum* plots (marginal tests, distance-based linear model)

Parameter	Pseudo- F	P	% Variance explained	
			This variable	Cumulative
Water table level	23.66	0.001	33.97	33.97
pH	4.46	0.003	8.84	42.81
K	3.87	0.007	7.77	50.58
PCNM1	3.75	0.017	7.54	58.12
N	2.52	0.042	5.19	63.31
PCNM2	2.55	0.053	5.25	68.56
P	1.37	0.21	2.89	71.45
Plant diversity	0.91	0.41	1.95	73.40

Plot trophic class is not included here as it is correlated with pH, N, P and K

PCNM1, *PCNM2* variables representing spatial variability

at the dry end of the gradient (hummocks), which is a known trend (Anderson et al. 1995; Johnson et al. 2014). The exception was *S. warnstorffii* (Acutifolia section), which was only found in eutrophic lawns. A multicollinearity analysis (SAS v.9.4, proc reg) checking simple correlations and variance inflation factors for plot-level variables showed that pH was significantly correlated with water table level (in drier habitats pH was more acidic, $r=0.51$, $P<0.001$), with N (0.30, $P=0.037$) and K (0.4, $P=0.001$) in *Sphagnum* tissues (Fig. 2b), and with plot-level plant diversity (0.35, $P=0.015$) (Fig. 2c). The variance inflation factor 3.05 for pH was only moderate; other variables were not significantly collinear.

Plot trophic class index, based on plant indicator species, was significantly correlated with local environmental variables representing both the acidity–alkalinity (pH) gradient and the nutrient availability (N–P–K) gradient in the mire, but was not related to the water table (micro-topography) gradient (Table 2).

Oribatida community composition, abundance and species richness

We collected 8048 adult Oribatida individuals, representing 52 species (Table S1). Water table level, pH, and K in *Sphagnum* tissues were three best environmental predictors of Oribatida assemblages, explaining 50.6% of the variance in community structure (combined aquatic and terrestrial species) (Table 3; Fig. 3). Aquatic species were associated with pools; two terrestrial species—*Hoplophthiracarus illinoisensis* and *Nothrus pratensis*—were associated with dry oligotrophic hummocks; the rest of terrestrial species were associated with drier mesotrophic and eutrophic habitats (Fig. 3). Plot trophic class

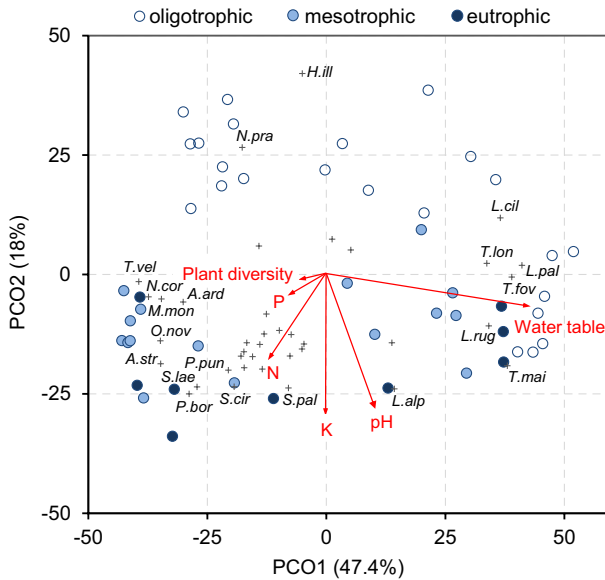


Fig. 3 Ordination tri-plot (principal coordinate analysis, Bray–Curtis distance) for Oribatida assemblages, showing sampling plots (circles) in species space. Plot trophic class (‘oligotrophic–eutrophic’) is based on plant indicator species and reflects plot status on the peatland poor-rich (acidity–alkalinity) gradient. Mesotrophic and oligo-mesotrophic plots grouped as ‘mesotrophic’, eutrophic and meso-eutrophic plots grouped as ‘eutrophic’. Environmental variables are overlaid as vectors. Only species with >50% correlation with axes are labelled: *A. ard*—*Acrotritia ardua*, *A. str*—*Atropacarus striculus*, *H. ill*—*Hoplophthiracarus illinoisensis*, *L. alp*—*Liochthonius alpestris*, *L. cil*—*Limnozetes ciliatus*, *L. pal*—*Limnozetes palmerae*, *L. rug*—*Limnozetes rugosus*, *M. mon*—*Malacoonthrus monodactylus*, *N. cor*—*Nanhermannia coronata*, *N. pra*—*Nothrus pratensis*, *O. nov*—*Oppiella nova*, *P. bor*—*Phthiracarus boresetosus*, *P. pun*—*Parachipteria punctata*, *S. cir*—*Schelorbates circumcarinatus*, *S. lae*—*Schelorbates laevigatus*, *S. pal*—*Suctobelbella palustris*, *T. fov*—*Trimalaconothrus foveolatus*, *T. lon*—*Trhypochthoniellus longisetus*, *T. mai*—*Tyrphonthrus maior*, *T. vel*—*Tectocepheus velatus*. (Color figure online)

by itself explained 14.7% of the variance in community structure (pseudo- $F = 7.93$, $P = 0.002$). Spatial structuring in Oribatida communities was significant but explained only a small proportion of the total variability in community structure (Table 3). However, for terrestrial Oribatida spatial variables accounted for 16.6% of community variability, and three terrestrial species (*H. illinoisensis*, *Adoristes ovatus*, *Parachipteria punctata*) showed strong correlation (>0.55) with spatial variables. There was no significant spatial structuring in communities of aquatic Oribatida.

Among environmental variables, water table depth, local plant diversity, and P in *Sphagnum* tissues best explained the abundance of terrestrial Oribatida (Figs. 4a, 5a). Low water table depth and increased diversity of plants were also linked to increased richness of terrestrial Oribatida (Figs. 4b, 5b). Plot trophic class was a significant predictor of terrestrial Oribatida abundance and richness (Fig. 4a, b). For aquatic Oribatida abundance, high water table was the single most important predictor (Figs. 4c, 5c). Spatial variables were weakly significant for terrestrial Oribatida abundance and richness ($P < 0.10$), and not significant for aquatic Oribatida.

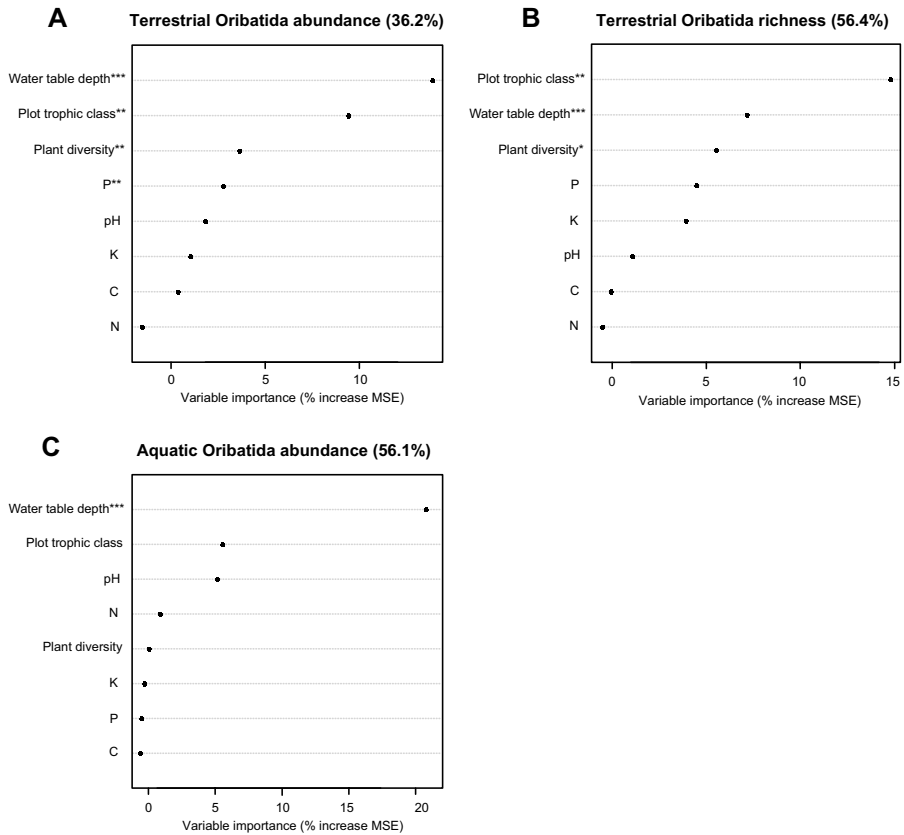


Fig. 4 Environmental variables best explaining Oribatida abundance and species richness in *Sphagnum* samples: **a** terrestrial Oribatida abundance; **b** terrestrial Oribatida richness; **c** aquatic Oribatida abundance. The percentage in parentheses is the total % variance explained. Plotted are variable importance scores (% increase MSE) from random forests regressions; the variables with higher % increase MSE are more important in explaining observed patterns; all random forests models significant, $P < 0.05$ with 999 permutations. Variable significance checked using generalized linear regression: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Plant diversity refers to the number of species of vascular plants and bryophytes in 1×1 m sampling plots. Plot trophic class, based on plant indicator species, reflects plot status on the peatland poor-rich gradient. Nutrients (N, C, P and K) were measured in *Sphagnum* tissues. Richness of aquatic Oribatida was not analysed due to the overall low number of aquatic species

Discussion

Oribatida diversity patterns in the Shichenskoe mire corresponded with environmental gradients such as ground water level, pH, plant diversity, nutrients, and were less influenced by spatial structuring, which was significant only for some terrestrial species.

Among measured environmental variables, abiotic factors (water table level and pH) were important in explaining Oribatida assemblages in mire environments. With respect to Oribatida assemblages, sampled habitats fell into three groups—(1) dry and oligotrophic hummocks, characterised by the presence of *Sphagnum medium*, *S. fuscum* and *S. rubrum*; characteristic Oribatida species were tyrophilic *N. pratensis* and *H. illinoisensis*; (2)

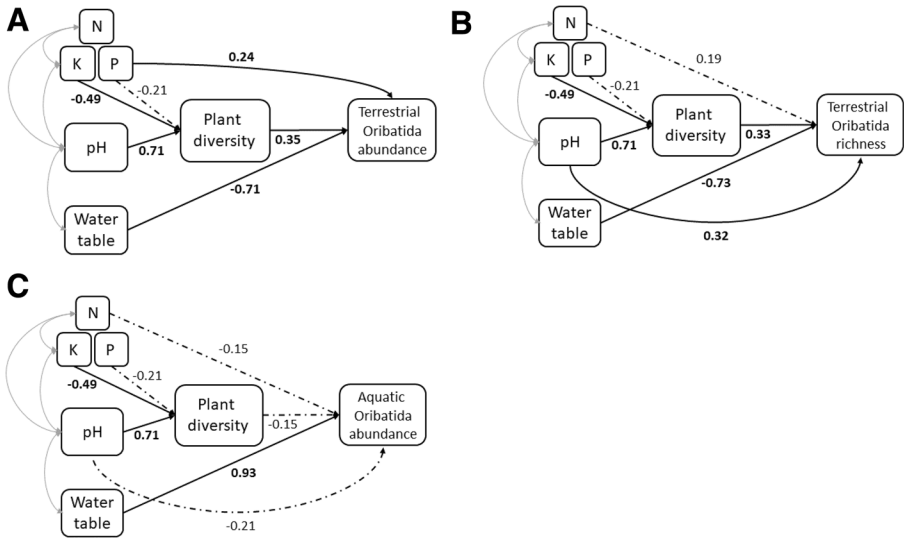


Fig. 5 Standardized path coefficients for environmental factors affecting Oribatida diversity in *Sphagnum* samples: **a** terrestrial Oribatida abundance; **b** terrestrial Oribatida richness; **c** aquatic Oribatida abundance. Plant diversity refers to the number of species of vascular plants and bryophytes in 1 × 1 m sampling plots. Richness of aquatic Oribatida was not analysed due to the low number of aquatic species. Single-headed arrows represent paths; grey double-headed arrows represent correlations. Solid paths are significant, $P < 0.05$, dashed paths have $P < 0.10$; other paths not shown

mesotrophic and eutrophic, with a gradient from dry hummocks (characterised by *S. wulfianum* and *S. russowii*) to wetter lawns (*S. squarrosum*, *S. warnstorffii*), and characterised by presence of tyrophilic and eurybiontic Oribatida species; (3) pool communities, characterised by *S. majus*, *S. subsecundum*, *S. lindbergii*, *S. flexuosum*, *S. balticum*, *S. cuspidatum*, *S. fallax*; characteristic Oribatida were aquatic species *Trimalaconothrus foveolatus*, *Trhypochthoniellus longisetus*, *Hydrozetes lacustris*, *Limnozetes* spp., *Malaconothrus* spp. which typically inhabit submerged vegetation in European *Sphagnum* bogs (Weigmann 2006; Seniczak 2011; Seniczak et al. 2014).

The depth of the water table is one of the most ecologically significant hydrologic properties in peatlands (Lafleur et al. 2005). In our study at the wet end of the water table gradient Oribatida communities converge to a small set of aquatic species, presenting an example of environmental filtering. Environmental filtering (Keddy 1992; Lavorel and Garnier 2002) refers to species-sorting whereby an abiotic filter (here, the high water table) limits communities to species with specific tolerances (here, the ability to survive underwater). In drier environments (higher micro-topographic position), more species are able to pass through the filter, and the resulting outcome is a less predictable community, which reflects an interplay of all local biotic and abiotic factors (Comte et al. 2016). As a result, ‘dry’ Oribatida assemblages vary, but all ‘wet’ assemblages are strongly homogeneous, irrespectively of other local factors such as nutrient status (see Fig. 3). The concept of environmental filtering has been criticized (e.g., Kraft et al. 2014; Cadotte and Tucker 2017), who argued that it is not possible to conclude whether a species is excluded from a community due to an environmental filter, dispersal limitation, or local competition. However, we suggest that a strong abiotic gradient can have a deciding influence in species-sorting.

Our results demonstrate that abundance and species richness of terrestrial Oribatida in the Shichengskoe mire can be linked to local plant diversity. More diverse plant communities create greater small-scale heterogeneity, which can provide a richer habitat structure and a more diverse range of food resources to soil fauna (Perez-Harguindeguy et al. 2000; Hättenschwiler et al. 2005; Nielsen et al. 2010). Vegetation composition and type have been shown to have strong influence on Oribatida communities (Nielsen et al. 2010, 2012; Minor et al. 2016). Greater litter diversity has been associated with greater species richness (but not abundance) of oribatid mites (Hansen and Coleman 1998; Kaneko and Salamanca 1999). However, some studies showed no correlation between plant or litter diversity and species richness or community composition of oribatid mites (Kaneko et al. 2005; Winkler et al. 2018).

Our results also identify P as an important element in predicting terrestrial Oribatida abundance in the mire. Strong links (both positive and negative) between P and abundance of bog Oribatida species have been observed elsewhere (Seniczak 2011). Both N and P are important nutrients affecting growth of *Sphagnum* and vascular plants in peatlands (Limpens et al. 2004; Hill et al. 2014; Toberman et al. 2015). In ombrotrophic peat bogs the input of P is limited to dry atmospheric deposition and biological sources (Rydin and Jeglum 2013; Tipping et al. 2014). As a result, P is an important limiting element in N cycling in bogs, controlling net primary production (Limpens et al. 2004), organic N mineralization (White and Reddy 2000) and microbial N-fixation (Toberman et al. 2015; van den Elzen et al. 2017). Local P enrichment, for example, can increase N uptake and lead to higher N concentrations in *Sphagnum* tissue, which in turn promotes faster *Sphagnum* litter decomposition and stimulates local nutrient cycling (Gerdol et al. 2007).

The P input within the Shichengskoe mire is linked to the land relief and the local hydrology. Within the oligotrophic ombrotrophic bog there are several ground water seeps associated with forested mineral islands. Such seeps of ground water provide sources of nutrient enrichment in an otherwise oligotrophic environment (Ruuhijärvi and Lindholm 2006). Ground water seeps of the Shichengskoe mire create localised patches of nutrient enrichment within the oligotrophic bog, with higher pH, eutrophic and mesotrophic *Sphagnum* species, and characteristic plant species (e.g., *Equisetum* spp.) more common for fens. When combined with higher micro-topographic position, these seeps provide niches for more abundant and diverse Oribatida communities.

The relationship between local pH, nutrient availability, and Oribatida diversity patterns can reflect indirect effects on the local food web structure. Recent stable isotope data (Lehmitz and Maraun 2016) show that the majority of Oribatida typical for *Sphagnum* peatlands are primary and secondary decomposers with heterogeneous $\delta^{15}\text{N}$ values, suggesting that they use a variety of resources, including plant fragments and associated bacteria, fungi, micro-algae and protozoa. Some species (aquatic *Limnozetes ciliatus* and *H. lacustris*, terrestrial *Acrotritia ardua* and *Pergalumna nervosa*) had wide trophic niches, indicating feeding on more than one trophic level. Abundant in our samples *Tyrphonothrus maior* had $\delta^{13}\text{C}$ signal close to that of *Sphagnum*, which suggested that it feeds directly on *Sphagnum*. Species such as *Limnozetes rugosus* and *H. lacustris* were enriched in $\delta^{15}\text{N}$, suggesting they are predators or scavengers. At all trophic levels the $\delta^{15}\text{N}$ values of oribatid mites were significantly correlated with the $\delta^{15}\text{N}$ values of the *Sphagnum* in respective samples, indicating that the local food web is based on *Sphagnum* moss, with bacteria, fungi and microfauna that oribatid mites consume also deriving their nutrients from *Sphagnum*.

Bacteria, microalgae and protozoa make up the majority of microbial biomass in *Sphagnum* peatlands (Gilbert et al. 1998; Jassey et al. 2013) and are sensitive to pH, water table

depth, and nutrient availability (Andersen et al. 2013). Nutrient enrichment can lead to an overall increase in microbial biomass (Gilbert et al. 1998), algal biomass (Guasch et al. 1995), and change the taxonomic composition and functioning of peatland microbial community (Andersen et al. 2013; Mieczan et al. 2015), which then affects Oribatida through bottom–up interactions.

The effects of acidity, nutrient availability and habitat heterogeneity are difficult to separate in a peatland. *Sphagnum* mosses are adapted for high uptake and retention of N, and in nutrient-poor ombrotrophic bog they are able to outcompete other plants (Hájek 2009; Turetsky et al. 2012). Additional input of nutrients (e.g., from ground water seeps), especially in the rhizosphere, depresses *Sphagnum* growth and favours vascular plants, therefore increasing habitat heterogeneity (Berendse et al. 2001; Bragazza et al. 2006; Limpens et al. 2011). Our data show that within the Shichengskoe mire system the pH gradient and the nutrient availability gradient were linked, which is common but not universal in peatlands (Wheeler and Proctor 2000; Bragazza and Gerdol 2002). This is highlighted by the result that the trophic class of sampled plots (based on plant community features) was correlated to both pH and nutrient measurements, and was one of the best predictors of abundance and species richness of terrestrial Oribatida. Other indirect factors may have a role in shaping local communities—for example, litter type (i.e., plant species) was the main factor affecting activity of aerobic decomposers in a boreal peatland, more important than local nutrients and water table regime (Straková et al. 2011).

To conclude, if we were to suggest best predictors of Oribatida community structure, abundance and diversity in the Shichengskoe mire, it would be two variables—water table depth (micro-topography) and plot trophic class (combined pH and nutrient availability gradients). With their defined environmental gradients and well-known assemblages of plants and animals, peatlands are unique model systems for investigating questions related to the community assembly rules and niche-based species coexistence. Information on functional traits of individual Oribatida species (e.g., Lehmitz and Maraun 2016) offers a further opportunity for understanding the species coexistence processes and hyperdiversity among Oribatida.

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