FRESHWATER ALGAL ECOLOGY

For richer or poorer: diatoms as indicators of biological condition across a gradient of boreal fen types

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Abstract The goals of this study were to (1) document spatial and temporal variation in diatom species composition across a gradient of northern peatlands and (2) determine how underlying environmental conditions influence diatom species distribution. We sampled three peatlands (a rich, moderate, and poor fen) in interior Alaska during a growing season (May until August). A total of 100 species were observed across all fens, 17 of which were present at > 1% relative abundance, and 15 were selected as indicator species. Based on the differential response of Simpson vs. Shannon diversity metrics, we determined that fen type affected diatom assemblage composition and differences were driven by changes in the most common, but not in the least common species. Diatom species richness declined along a gradient of rich to poor fens. Conductivity, dissolved organic carbon concentration, water temperature, pH, and water depth explained 63% of the total variation in diatom assemblage structure among fens. We identified unique indicator species associated with each fen that either reinforced or expanded current understanding of their environmental thresholds. These results indicate that variation in environmental conditions in boreal fens will be reflected in diatom assemblages, which may be used to monitor biological condition in these ecosystems.

Keywords Alaska · Algae · Biofilm · Fen · Wetland

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Introduction

Peatlands are unique wetland ecosystems that occur across the boreal region (Yu et al., 2010; Xu et al., 2018). Peatlands form when plant productivity has been persistently greater than the rate of plant decay, resulting in the accumulation of peat, or partially decomposed organic material (Vitt, 2006). Peatlands are common in the boreal zone owing in part to conditions that have facilitated the accumulation of peat over time, such as specially adapted plant species and cold, saturated soils that limit decomposition of plant litter (Vitt et al., 2000; Joosten & Clarke, 2002; Bradshaw & Warkentin, 2015). Collectively, northern peatlands tend to operate as a global reservoir for atmospheric carbon (Hugelius et al., 2020; Harris et al., 2022) and they also serve a critical role as hotspots for biodiversity and as habitat for rare and specialized species (Minayeva et al., 2008; Joosten, 2015; Gallé et al., 2019). Many of these attributes are at risk as the boreal zone is experiencing rapid warming, resulting in increased thaw and nutrient release (Olefeldt & Roulet, 2012; Serikova et al., 2019; Qiu et al., 2020), erosion (Li et al., 2017), and changes in

plant communities (Loisel et al., 2012; Lyons et al., 2020; McPartland et al., 2020). The rapidly changing climatic conditions in boreal peatlands have led to a demand for reports on these ecosystems for several groups of organisms that are indicators of biological integrity (UN Environment, 2019).

Using the sensitivity of organisms to environmental variation (i.e., bioindicators) is one of the more common methods for monitoring aquatic ecosystem health (Li et al., 2010; Chen et al., 2020). Regular assessments of freshwater habitats using standardized bioindication methods have been proven to be reliable and reproducible (Kuefner et al., 2020; Zubova et al., 2020; Pérez et al., 2021). Effective bioindicator species typically have a moderate tolerance to environmental variability, as rare species with narrow tolerances are often too sensitive, or too infrequently encountered, to reflect the general biotic response to environmental variance (Holt & Miller, 2011). On the other hand, ubiquitous species with broad tolerances are less sensitive to environmental conditions that otherwise disturb the community as a whole (Holt & Miller, 2011). Owing to the dynamic environmental conditions of peatlands (i.e., frequent water level fluctuation, deep freeze in the winter), it can be difficult or impossible to use bioindicators commonly used in other aquatic environments, such as fish or invertebrates (Kock et al., 2019). In these ecosystems, highly silicified organisms, such as diatoms, may be an alternative owing to their rapid turnover time, sensitivity to environmental conditions, preservation, and extensive taxonomic literature for identification (Stevenson et al., 1999; Battarbee et al., 2010; Küttim et al., 2017).

In northern peatlands, diatoms exist within a biofilm matrix, along with other algae, fungi, and bacteria, and are highly responsive to their environment (Gilbert & Mitchell, 2006; Rober et al., 2014). Previous studies have shown that diatoms comprise between 3 and 36 percent of boreal fen algal communities (Rober et al., 2013, 2014, 2022; Ferguson et al., 2021). Similar to that of lakes and rivers, diversity and richness of peatland diatom assemblages tend to vary according to geology and underlying environmental conditions, as well as according to peatland development and succession (Brugam & Swain, 2000; Fránková et al., 2009; Lento et al., 2022). Compared to other regions, diatom diversity and richness have not been as extensively studied in undisturbed

North American boreal peatlands (Gaiser & Rühland, 2010; Hargan, 2014; Kahlert et al., 2022). Given that linkages between diatom assemblages and environmental variables may differ across localities (Winter & Duthie, 2000), regional reports of diatom species abundance and distribution are crucial for the proper identification and monitoring of peatland ecosystems (Bottin et al., 2014; Oeding & Taffs, 2017).

The aim of this research was to use diatoms to evaluate environmental conditions in a range of undisturbed peatlands (rich, moderate, and poor fens) in interior Alaska where increases in algal biomass and changes in energy flow are predicted to occur with an upsurge in nutrient levels caused principally by changing climatic conditions (Flanagan et al., 2003; Wyatt et al., 2012, 2015, 2021; Rober et al., 2014; Ferguson et al., 2021). Diatoms represent a significant proportion of the algal community in these sites and tend to be most abundant in the early growing season but decline over time, making way for cyanobacteria and filamentous green algae (Ferguson et al., 2021). Despite our knowledge of the algal community as a whole, we know relatively little about diatom species diversity or the factors regulating diatom community composition within the biofilm in peatlands. The objectives of this study were to (1) document spatial and temporal variation in diatom species composition across a gradient of northern peatlands and (2) determine how underlying environmental conditions influence diatom species distribution. We hypothesized that diatom assemblage structure would be heterogeneous across peatland type and driven by underlying environmental conditions that occur in these ecosystems.

Methods

Study site

Samples were collected from three peatlands which represented the dominant peatland types across the boreal landscape (rich, moderate, and poor fens) and were located in a wetland complex located within the Tanana River floodplain just outside the Bonanza Creek Experimental Forest (35 km southeast of Fairbanks) in interior Alaska. Fens are minerotrophic peatlands, receiving nutrients from both groundwater and surface water flow (Rydin & Jeglum, 2013). As

a result, fens are characterized by low pH conditions which influences nutrient availability (i.e., mineral ions become more readily available as pH increases) and thereby plant community composition. As such, rich fens are relatively rich in mineral ions and species diversity whereas poor fens are poor in both mineral ions and species diversity (Rydin & Jeglum, 2013). In this study, rich, moderate, and poor fens were classified prior to the study using water chemistry (e.g., pH) and natural transitions in vegetation community structure (Churchill et al., 2015; McPartland et al., 2019). Fen physical and chemical characteristics have been described in detail elsewhere (Ferguson et al., 2021; Hamilton et al., 2023), but briefly, the rich fen had a water column pH ranging from 5.4 to 8.9 and was comprised of brown moss species (*Amblystegiaceae* and *Brachytheciaceae*) and emergent vascular plants (*Carex atherodes* Spreng*., Equisetum fluviatile* L*.,* and *Potentilla palustris* (L.) Scop.). The moderate fen pH ranged from 5.3 to 8.8 and the plant community was composed of both brown and *Sphagnum* mosses and vascular plants (*C. atherodes, E. fluviatile,* and *P. palustris)*. The poor fen pH ranged from 4.8 to 7.5 and was primarily composed of *Sphagnum* moss species with vascular plants *E. fluviatile, P. palustris,* and *Eriophorum vaginatum* L. All fens were located within ~ 1 km distance from one another and were surrounded by lowland boreal forest composed of spruce and shrub cover. Fen sites remained saturated ($\geq$ 15cm water depth) for the entire growing season.

Environmental variables

Physical and chemical characteristics were measured within each of four evenly spaced plots (1m^2) in each peatland every 10–14 days (4 plots $\times$ 5 sampling dates = 20 samples per fen) beginning after snowmelt in May until August 2017. Water temperature (°C), pH, dissolved oxygen (DO; mg l^{-1}), and conductivity (µScm) were measured with a Hach model 40d multiprobe (Hach Company, Loveland, CO, USA). Water depth (cm) was measured with a meter stick. Photosynthetically active radiation (PAR; µmol m^{-2} s^{-1}) was measured at the peat surface in each plot using a Li-Cor submersible quantum sensor and LI-250 light meter (Li-Cor, Lincoln, NE, USA) attached to a 1-m pole to prevent disturbance of macrophytes. Water samples for dissolved nutrient analysis and dissolved organic carbon (DOC) were collected from 10 cm below the surface and filtered through a 0.45 µm filter (Millipore Corporation, Bedford, MA, USA) into 60 mL acid-washed polyethylene bottles and stored on ice in the field. These samples were kept frozen until analysis for DOC (mg l^{-1}) using a Shimadzu TOC-V carbon analyzer (Shimadzu Scientific Instruments, Columbia, MD, USA). A portion of each filtered sample was analyzed using ion chromatography (Dionex Corporation, Sunnyvale, CA, USA) for nitrate (µg NO$_3^-$ l^{-1}) and phosphate (µg PO$_4^{3-}$ l^{-1}).

Diatom sampling, preparation, and analysis

Attached biofilm was sampled from the same four 1m^2 plots as physical and chemical measurements within each fen on each sampling date. Loosely attached biofilm was collected from the peat surface using a syringe and from the submerged portions of four dead plant stems of the dominant emergent macrophyte using a toothbrush (Rober et al., 2014). The composite sample was preserved in a 2% formalin solution for identification of diatom species composition.

In the laboratory, preserved samples were cleaned by boiling in hydrochloric acid and rinsing the resulting suspension by diluting, settling, and decanting repeatedly until the acid was neutralized (Charles et al., 2002). Rinsed diatom suspensions were placed on three 18 $\times$ 18 mm coverslips per sample and allowed to air dry. They were then scanned to evaluate density (15–30 visible valves per field of view at 400X magnification) before permanent mounting with Naphrax™ mounting medium (Brunel Microscopes Ltd., Chippenham, UK) (Charles et al., 2002).

Diatoms were identified to species level using 1000X oil immersion on a Leica DM750 light microscope (Leica Microsystems, Wetzlar, Germany). Three hundred valves were enumerated for each sample, based on the quantitative method for determining a representative algal sample count (Pappas & Stoermer, 1996). Taxonomic identifications were made using diatoms.org, relevant taxonomic literature, and a voucher flora compiled for Alaskan fens (Hamilton et al., 2023).

Statistical analysis

We found a total of 100 species in 26 genera among all three fen types that were included in the analyses of species diversity (Shannon–Weiner diversity and Simpson's index of diversity $(1-\lambda)$) and evenness (Pielou's evenness) (Boggero et al., 2019; Han et al., 2022). We used boxplots to identify outliers in the measures of richness and diversity and removed them from further analysis; the data points removed were richness values for the poor fen on May 29 and moderate fen on July 19, and Shannon–Weiner diversity, Pielou's evenness, and Simpson's diversity values for the rich fen on May 29. We evaluated differences in measures of diversity and evenness within and among fens and sampling dates using a general linear model (GLM) with fen type and time as fixed factors. When GLM indicated significant differences, Tukey's test for post hoc comparison of means tests was used to discriminate among different factors levels.

We evaluated differences in diatom species composition and environmental conditions within and among peatlands using multivariate GLMs with fen type and time as fixed factors. We included individual diatom species in analyses only when they were present at $> 1\%$ relative abundance to reduce the influence of rare species (Lavoie et al., 2009). Diatom relative abundance was square-root transformed prior to statistical analysis to correct for non-normal distribution and unequal variance. When GLM indicated significant differences, Tukey's test for post hoc comparison of means tests were used to discriminate among different factors levels. Multivariate GLMs were performed using SPSS 28 (SPSS Inc., Chicago, Illinois).

Diatom species present at $> 1\%$ relative abundance were included in indicator species analysis (ISA). This analysis uses a species' relative abundance to estimate the strength of its associations with a defined group (i.e., fen type) and a randomization test to evaluate the probability of association (Dufrêne & Legendre, 1997). An indicator species value (ISV) is then produced (values range from 0 to 1) and is the highest when all individuals of a species occur in a single group of sites (i.e., a rich, moderate, or poor fen) and occurs in all sites of that group (Dufrêne & Legendre, 1997; De Cáceres & Legendre, 2009). For this study, each plot was treated as an individual sample for a total

20 samples (4 plots × 5 sampling dates) per peatland across the study period. Values of ISA were determined using the R package *indicspecies* v1.7.14 (De Cáceres et al., 2023) in RStudio v2023.09.1.494 (RStudio Team, 2023). We calculated weighted average estimates for optima and tolerances of the dominant diatoms following Potapova and Charles (2003) using the R package *optimos.prime* v0.1.2 (Sathicq et al., 2020).

Redundancy analysis (RDA), an extension of multiple regression analysis that is used to model multivariate response data, was used to identify the environmental variables that were significant predictors of diatom species composition (Legendre & Legendre, 2012). Diatom species present at $> 1\%$ relative abundance were included in RDA analysis. Environmental variables were standardized prior to performing RDA using the decostand() function to allow for comparison among variables measured in different units (Legendre & Legendre, 2012). To decide if forward selection of explanatory variables was appropriate, a global test of all variables was run to determine significance (Borcard et al., 2011). To produce a model containing only necessary explanatory variables, the forward.sel() function was applied to the data to devise a parsimonious model with sufficient variables to obtain an R^2_{adj} close to that of the global model (Borcard et al., 2011). The forward.sel() function works by adding variables to the model one-by-one starting with the explanatory variable with the highest R^2 and stops when the adjusted coefficient of multiple determination R^2_{adj} of the global model containing all the potential explanatory variables is reached. The selected explanatory variables were tested for significance using the function anova.cc()**,** similar to an Analysis of Variance (ANOVA) permutation test (Borcard et al., 2011). A parsimonious RDA containing the selected explanatory variables was run and the results were plotted to visualize relationships of diatom assemblages to explanatory variables. Pearson correlations among the first 2 canonical axes and environmental variables were used to interpret the meaning and significance of each axis. Computation of RDA, standardizing and testing significance of variables, and plotting were done in RStudio v2023.09.1.494 (RStudio Team, 2023) using the *vegan* v2.6–4 package, and the *adespatial* v0.3–23 package was used for the selection of variables (Oksanen et al., 2022; Dray, 2023).

Results

Environmental variables

All environmental factors were affected by time (GLM, $F_{36,160} = 8.89$, $P < 0.001$), fen type (GLM, $F_{18,76} = 123.51$, $P < 0.001$), and the combination of fen type and time (GLM, $F_{72,352} = 4.40$, $P < 0.001$; Fig. 1a–i), except for PAR, which was not significantly affected by fen type (GLM, $F_{2,45} = 0.15$, $P = 0.86$; Fig. 1f) and depth, which was not significantly affected by the combined effect of fen type and time (GLM, $F_{8,45} = 1.26$, $P = 0.29$; Fig. 1e). Water temperature (17.25 ± 3.24 °C) increased over the sampling season in all fens, reaching its maximum in late July before declining into August and was on average lowest in the poor fen (15.22 ± 3.53 °C) compared to the rich (18.51 ± 2.29 °C) or moderate fens (18.02 ± 2.88 °C; $P < 0.001$; Fig. 1a). pH ranged from 7.59 to 8.91 among fens at the start of the growing season and decreased over time but was consistently lower in the poor fen (5.77 ± 1.03) compared to the rich (6.46 ± 1.29) or moderate fens (6.42 ± 1.32; $P < 0.001$; Fig. 1b). Dissolved oxygen was most elevated at the beginning of the growing season in all fens and declined over time, but was the highest in the moderate (5.72 ± 1.49 mg l^{-1}) fen compared to the rich (3.92 ± 1.95 mg l^{-1}) and poor fens (3.81 ± 2.42 mg l^{-1}; $P < 0.001$), except for in mid-June, when the poor fen was significantly higher (7.06 ± 1.30 mg l^{-1}) than the rich or moderate fens ($P < 0.001$; Fig. 1c). Conductivity increased over time in both the rich and poor fens, ranging from 31.40 to 48.13 μScm, but decreased over time from 28.48 to 23.81 μScm in the moderate fen (Fig. 1d). Water depth was highest at the beginning of the season in all fens and decreased over time but was consistently higher in the moderate fen (33.98 ± 11.40 cm) compared to the rich (27.51 ± 7.95 cm) or poor fen (26.63 ± 8.86 cm; Fig. 1e). Mean PAR was similar among fen types (254.23 ± 223.16 μmol cm^2 s^{-1}), peaking in mid-June prior to peak macrophyte production and then decreased over the time across all fens ($P < 0.001$; Fig. 1f). Mean DOC was significantly higher in the poor fen (62.38 ± 9.41 mg l^{-1}) than in the rich (32.57 ± 4.32 mg l^{-1}) or moderate fens (29.71 ± 3.14 mg l^{-1}; $P < 0.001$), which were also significantly different from each other ($P < 0.001$; Fig. 1g). Nitrate was the lowest in the rich fen (7.7 ± 2.1 μg NO_3^- l^{-1}) compared to the poor (15.77 ± 9.59 μg NO_3^- l^{-1}) or moderate fens (13.21 ± 7.39; $P < 0.001$), which were not significantly different from each other ($P = 0.10$ Fig. 1h). Phosphate increased over time in the poor fen and was significantly higher (20.9 ± 6.21 μg PO_4^{3-} l^{-1}; $P < 0.001$) than in the rich (8.56 ± 3.40 μg PO_4^{3-} l^{-1}) or moderate (7.54 ± 2.95 μg PO_4^{3-} l^{-1}) fens where phosphate decreased over time (Fig. 1i).

Measures of diversity

Fen type had a significant effect on diatom species richness, Simpson's diversity, and evenness (measured as Pielou's evenness) (Table 1). Time alone had no effect on species richness, diversity, or evenness (Table 1). Therefore, diatom diversity metrics across time were combined to illustrate overall differences among fens (Fig. 2a–d). The interactive effect of fen type and time was significant only for richness (Table 1). A total of 67 species were observed in the rich fen, 66 species in the moderate fen, and 37 species in the poor fen. Mean richness was significantly higher in the moderate fen (17.8 ± 4.28) than in the rich (15.05 ± 3.76) or poor fens (14.60 ± 2.64; $P \leq 0.02$; Fig. 2a). Simpson's diversity was significantly different among fens ($P = 0.03$), but Shannon–Weiner diversity was not different among fens ($P = 0.2$) indicating that there were significant differences in the most common species, but not in the least common species among fens (Fig. 2b–c). Simpson's diversity was significantly higher in the poor fen (0.76 ± 0.08) than in the moderate fen (0.65 ± 0.12; $P = 0.020$; Fig. 2c). Pielou's evenness was significantly lower in the moderate fen (0.59 ± 0.10) than in the poor (0.70 ± 0.09; $P < 0.001$; Fig. 2d) fen, but not significantly different from the rich fen (0.65 ± 0.11; $P = 0.06$; Fig. 2d).

Species composition trends across fen type and over time

We found 17 species were present at > 1% relative abundance and included in analyses of taxonomic composition (Fig. 3). Diatom species present at < 1% relative abundance were grouped as "other" and represented 6–12% of the total relative abundance across all peatland types (Fig. 3). Diatom assemblage composition was significantly affected by fen type

Fig. 1 Mean (± 1SD) water temperature (°C) (**a**), pH (**b**), dissolved oxygen (DO; mgL^{-1}) (**c**), conductivity (μS) (**d**), water depth (cm) (**e**), photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}) (**f**), dissolved organic carbon (DOC; mgL^{-1}) (**g**), nitrate (NO$_3^-$ l^{-1}) (h), and phosphate (μg PO$_4^{3-}$ l^{-1}) (i) in each peatland over a sampling season from May to August
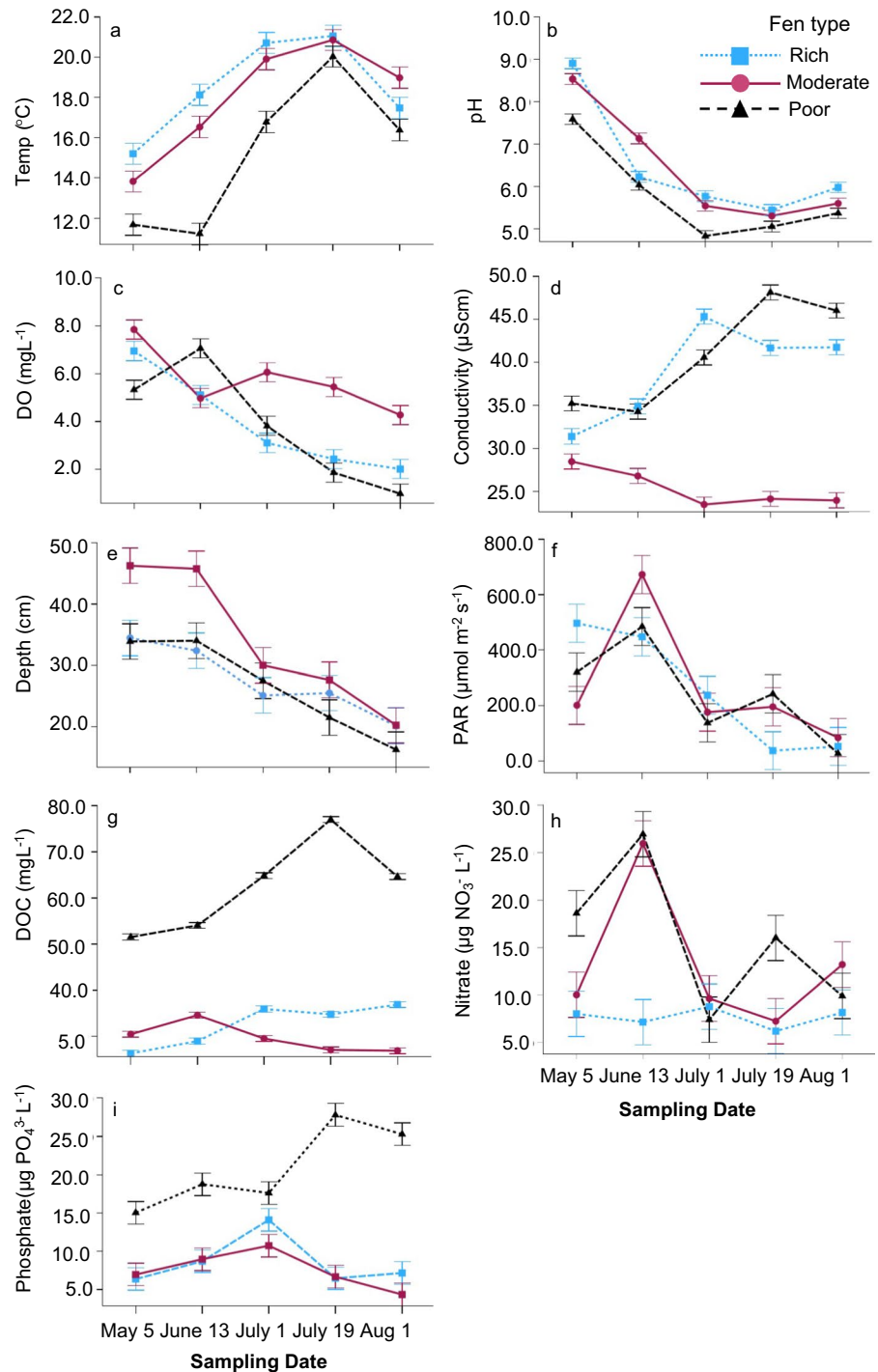
(GLM, $F_{34,60} = 17.108$, $P < 0.001$) and time (GLM, $F_{68,128} = 2.179$, $P < 0.001$), as well as the combined effect of fen type and time (GLM, $F_{136,288} = 1.904$, $P < 0.001$; Fig. 3a-c). Genera observed at the highest

proportion across all fen types were *Eunotia* Ehrenberg (59.2%), *Tabellaria* Ehrenberg ex Kützing (32.9%), and *Gomphonema* Ehrenb. (4.1%). The most specious genera across all fen types were *Eunotia* (34

Table 1 Independent and interactive effects of fen type and time on richness, Shannon–Weiner (S–W) diversity, Simpson's diversity $(1 - \lambda)$, and Pielou's evenness

Effect	df	SS	F	P
Richness				
Fen type	2	120.0	5.12	**0.01**
Time	4	19.7	0.42	0.79
Fen type × time	8	202.0	25.3	**0.05**
Error	45	527.3		
Shannon–Weiner diversity				
Fen type	2	0.40	1.7	0.19
Time	4	0.28	0.59	0.68
Fen type × time	8	1.51	1.59	0.16
Error	45	5.34		
Simpson's diversity $(1 - \lambda)$				
Fen type	2	0.05	3.96	**0.03**
Time	4	0.03	0.62	0.65
Fen type × time	8	0.11	1.06	0.41
Error	45	0.61		
Pielou's evenness				
Fen type	2	0.07	7.29	**< 0.01**
Time	4	0.04	1.01	0.41
Fen type × time	8	0.11	1.37	0.24
Error	45	0.44		

P-value for significant effects are indicated by bold font

species), *Pinnularia* Ehrenb. (14 species), and *Gomphonema* (11 species); however, no *Pinnularia* species nor most *Gomphonema* species (except *G. brebissonii* and *G. lagerheimii*) were included in further analysis due to low relative abundance. In the rich fen, the species in highest proportion were *T. flocculosa* (44.0%), *E. ambivalens* (13.3%), and *E. subcapitata* (8.6%) (Fig. 3a). The taxa observed in highest relative abundance in the moderate fen were *T. flocculosa* (52.8%) and *E. subcapitata* (15.3%) (Fig. 3b). The diatom species in highest relative abundance in the poor fen were *E. mucophila* (39.2%), *E. naegelii* (16.9%), and *E. pseudogroenglandica* (11.1%) (Fig. 3c).

Indicator species and relationship to environmental variables

Ordination analysis revealed clear separation in diatom assemblage structure among fen types and the environmental variables that best explained spatial and temporal variation in community structure

(Fig. 4). Results of forward selection RDA produced a model containing 5 explanatory variables accounting for 63.1% of the total variation in diatom assemblages across all fens: conductivity, DOC, water temperature, depth, and pH ($P \leq 0.05$; Fig. 4). Eigenvalues for the 1st and 2nd axes were 22.8 and 1.8, respectively. The first RDA axis explained 55.4% of variance and was positively correlated with DOC and conductivity and negatively correlated with temperature and pH (Table 2). The first axis differentiated the poor fen with higher DOC concentration and lower pH from the rich and moderate fens with lower conductivity and DOC concentrations (Fig. 4). The second RDA axis explained 4.4% of variance and was positively correlated with conductivity and negatively correlated with depth (Table 2). The second axis differentiated the moderate fen with higher conductivity and shallower depth from the rich fen with higher temperature and lower conductivity (Fig. 4).

The results of ISA, together with results of RDA, reveal reliable bioindicators among the diatoms observed and the environmental variables to which they were most strongly correlated (Table 3; Fig. 4). The results of ISA show that 15 of the 17 species present at > 1% relative abundance were selected as indicator species (i.e., likely to be associated with a particular fen type; Table 3). These species formed distinct clusters within rich, moderate, and poor fen sites. *Gomphonema lagerheimii, G. brebissonii, E. ambivalens,* and *E. cf. glacialispinosa* had significant, high indicator species values (ISVs) for the rich fen and were most strongly influenced by temperature and conductivity ($P < 0.001$; Fig. 4; Table 3), making these species good indicators for boreal rich fens with water temperature in the range of 15–21 °C and conductivity in the range of 31–45 µScm. Our RDA results indicate that variation in diatom species composition in the moderate fen was most strongly influenced by changes in pH and depth (Fig. 4). *Eunotia scandiorussica* and *E. panda* had high, significant ISV for the moderate fen and would make good indicators for inundated moderate boreal fens with pH in the range of 5.3–8.5 ($p \leq 0.002$; Fig. 4; Table 3). Two species (*T. flocculosa* and *E. subcapitata*) were reliable indicators for both rich and moderate boreal fens with pH in the range of 5.3–8.9 ($P < 0.0001$; Fig. 4; Table 3). *Eunotia mucophila, E. pseudogroenglandica, E. paludosa, E. cf. bertrandii, E. krammeri, E. naegelii,* and *E. flexuosa* were most strongly driven
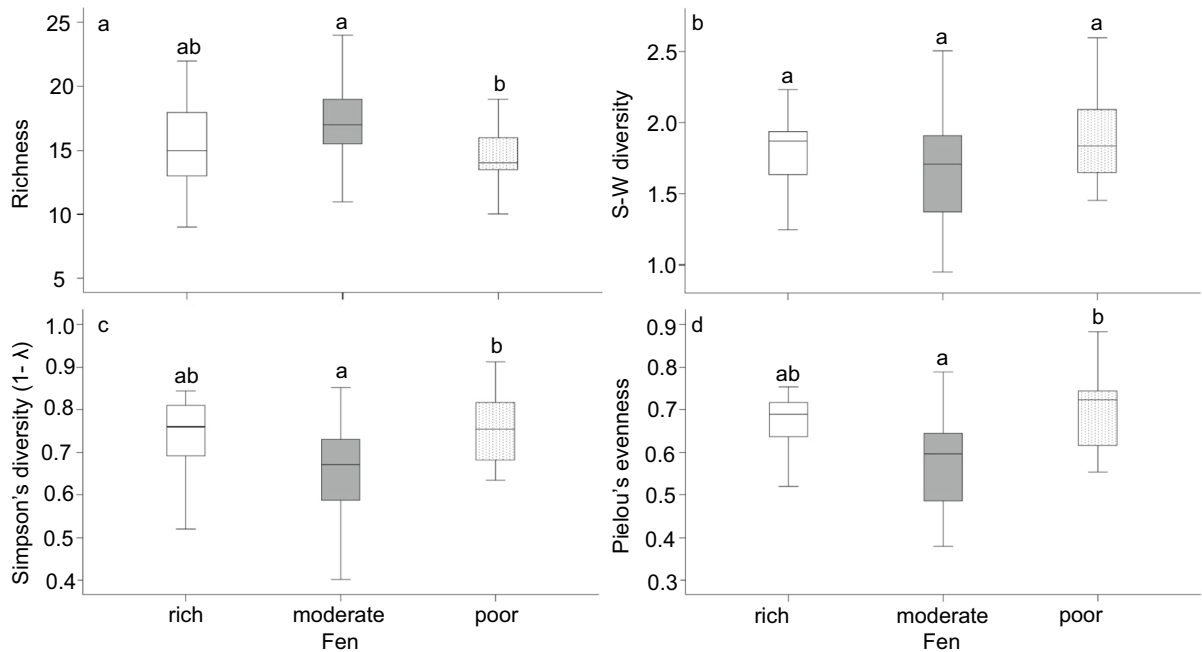
Fig. 2 Diatom species richness (**a**), Pielou's evenness (**b**), Shannon–Weiner diversity index (**c**), and Simpson's index of diversity (1−λ) (**d**) among fen types. Boxplots are mean of 20 replicates (combined over time). Bars with the same letter are not significantly different among treatments (α=0.05)

by variation in DOC (Fig. 4) and had high ISV for the poor fen ($P < 0.001$; Table 3), making them good indicators for boreal poor fens with DOC in the range of 51–77 mg l^{-1}.

Optima and tolerance values provide environmental preferences for the 17 dominant diatom species in our study sites (Table 4). Diatom species showed a wide range of optima for DOC concentration, ranging from 30.6 to 61.4 mg l^{-1}. *Eunotia paludosa* and *E. pseudogroenglandica*, indicator species for the poor fen, exhibited tolerance to the highest levels of DOC (76.0 and 77.2 mg l^{-1}, respectively). Conductivity optima ranged from 30.3 to 41.6 µScm among all diatom species (Table 4). *Eunotia flexuosa* had the highest reported tolerance to conductivity (49.5 µScm) and *E. scandiorussica* had the lowest reported tolerance (23.0 µScm). Temperature optima among diatom species ranged from 14.8 to 18.8 °C (Table 4). Tolerance values for temperature were more specific than other environmental variables, with *E. cf. glacialispinosa* exhibiting the narrowest tolerance to temperature (17.6–20.2 °C) and the highest temperature optimum (18.8 °C). Optimal depth ranged from 22.9 to 34.4 cm among all diatom species. *Gomphonema*

brebissonii had the narrowest tolerance to depth (18.9–30.9 cm) and an optimum of 24.2 cm. Optimal pH ranged from 5.41 to 6.96 among all species. *Gomphonema lagerheimii* exhibited the broadest tolerance to pH levels (5.7–8.5) and had a pH optimum of 7.0.

Discussion

Diatom assemblages differed across fen type and were influenced by variation in environmental conditions. A total of 100 species were observed across all fens, 17 of which were present at >1% relative abundance, and 15 were selected as indicator species. Based on the differential response of Simpson vs. Shannon diversity metrics, we determined that differences in assemblage composition among fens were driven by the most common, but not in the least common diatom species. Diatom assemblage composition was related to variation in five explanatory variables accounting for 63.1% of the total variation in diatom assemblages across all fens: conductivity,

Fig. 3 Relative abundance of diatom species present at > 1% relative abundance among the rich (**a**), moderate (**b**), and poor (**c**) fens over a sampling season
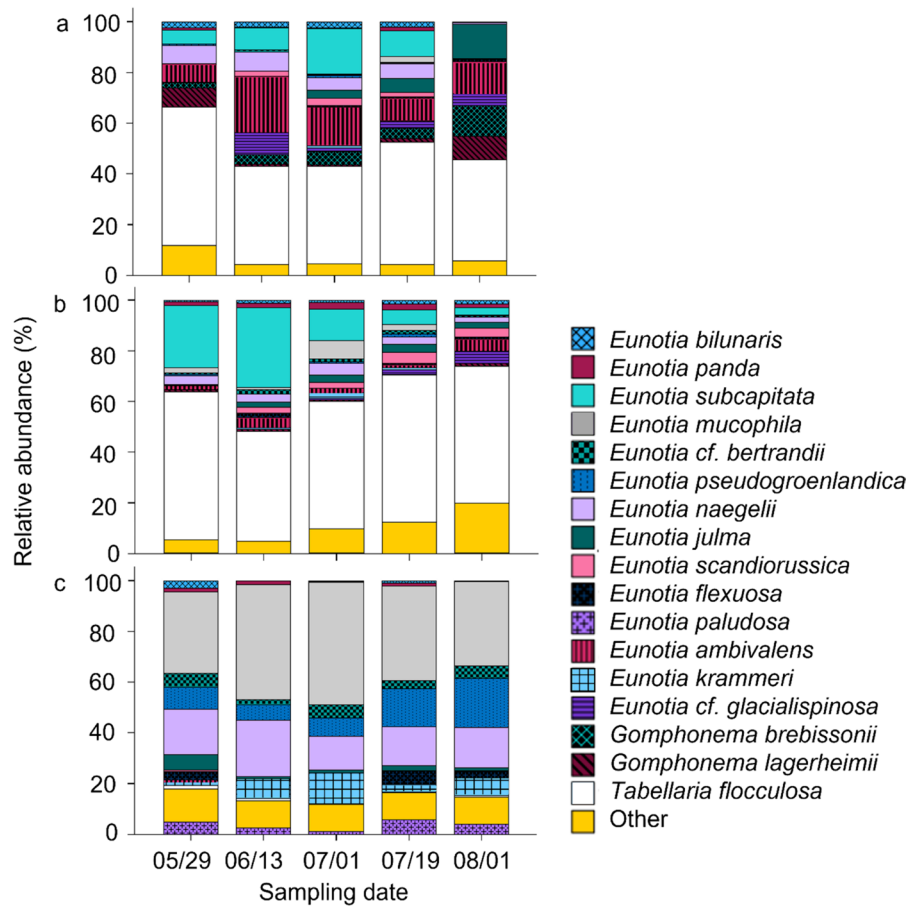

Fig. 4 Redundancy Analysis ordination plot of 17 dominant diatom species with 5 significant environmental predictor variables (conductivity (µScm), DOC (mg l⁻¹), water temperature (°C), depth (cm), and pH). Length of arrows represents the strength of the effect of each variable on the variation in the diatom community matrix. Indicator species clusters for rich, moderate, and poor fens are circled
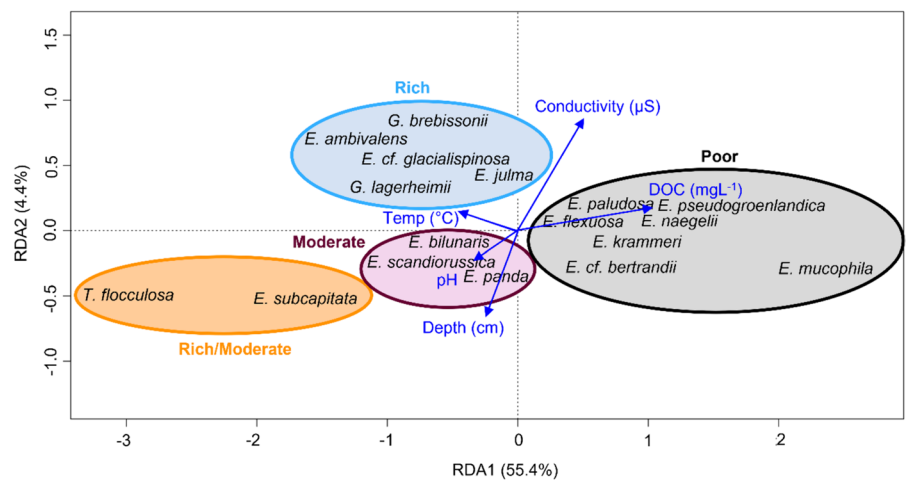
Table 2 Pearson correlations between significant environmental variables and the canonical axes produced by RDA. *$P < 0.05$, **$P < 0.01$

Variable	Axis 1	Axis 2
DOC	0.92**	0.11
Conductivity	0.45**	0.56**
Temp	-0.41**	0.09
Depth	-0.21	-0.41**
pH	-0.3*	-0.14

DOC, temperature, depth, and pH. These findings support our hypothesis that diatom community structure would be different across fen type and driven by underlying environmental conditions.

Diversity of diatom assemblages in rich/moderate/poor fens

Diatom species richness was greater in the rich and moderate fens compared to the poor fen, which aligns with previous studies of peatland diatoms (Pienkowski & Wujek, 1988; Fránková et al., 2009; Hargan et al., 2015; Luna & Bahls, 2017). However, the poor

fen had greater evenness and Simpson's diversity values than the rich and moderate fens, indicating that while there were fewer species, they were distributed more evenly. This may be due to the restrictive environmental conditions which are common to poor fens, such as low pH (Sjörs, 1950; Round, 2004). Environmental conditions that were above or below species tolerance levels could have prevented any species from becoming too abundant in the poor fen, whereas species such as *T. flocculosa* were dominant in the rich and moderate fens. The evenness in the poor fen was driven by the distribution of species within the genus *Eunotia*, which aligns with previous observations made in poor fens in Bosnia (Kapetanović et al., 2011) and the northern Greater Khingan Mountains (Han et al., 2022) and reinforces the idea that *Eunotia* species can better tolerate low pH that typically restricts other diatom taxa.

Tabellaria flocculosa was reported in the greatest abundance among the rich and moderate fens and had the greatest ISV, distinguishing it as a reliable indicator in these fens and warranting a closer look at the environmental measurements that it may infer. *Tabellaria flocculosa* was negatively correlated with conductivity in our study, similar to reports from

Table 3 Diatom species associations with fen type as determined by indicator species analysis (ISA)

Species/author	ISV	P-value	Fen type
Tabellaria flocculosa (Roth) Kützing	0.96	<0.01	Rich/Moderate
Eunotia mucophila (Lange-Bert., Nörpel-Schempp and Alles) Lange-Bert	0.92	<0.01	Poor
Eunotia pseudogroenlandica Lange-Bertalot & Tagliaventi	0.86	<0.01	Poor
Gomphonema brebissonii Kützing	0.84	<0.01	Rich
Eunotia ambivalens Lange-Bertalot & Tagliaventi	0.79	<0.01	Rich
Eunotia paludosa Grunow	0.75	<0.01	Poor
Eunotia cf. bertrandii Lange-Bert	0.71	<0.01	Poor
Eunotia naegelii Migula	0.71	<0.01	Poor
Eunotia krammeri Metzeltin & Lange-Bertalot	0.70	<0.01	Poor
Eunotia subcapitata Kulikovskiy, Lange-Bertalot, Genkal & Witkowski	0.66	<0.01	Rich/Moderate
Gomphonema lagerheimii A. Cleve	0.52	<0.01	Rich
Eunotia flexuosa (Brébisson ex Kützing) Kützing	0.51	<0.01	Poor
Eunotia cf. glacialispinosa Lange-Bertalot & Cantonati	0.48	<0.01	Rich
Eunotia scandiorussica Kulikovskiy, Lange-Bertalot, Genkal & Witkowski	0.49	<0.01	Moderate
Eunotia panda J. Veselá & J.R. Johansen	0.43	<0.01	Moderate
Eunotia bilunaris (Ehrenberg) Schaarschmidt	0.21	0.23	Rich/Moderate
Eunotia julma Lange-Bertalot	0.12	0.65	Rich

Species are sorted from high to low indicator species value (ISV). The ISV ranges from 0 to 1 and high values indicate a stronger association of a species in a particular fen type than lower values

Table 4 Optima and tolerance values for 17 dominant diatom species for explanatory variables: dissolved organic carbon (DOC), conductivity, water temperature, depth, and pH

Species	DOC			Conductivity			Temperature			Depth			pH		
	Opt	High	Low	Opt	High	Low	Opt	High	Low	Opt	High	Low	Opt	High	Low
Tabellaria flocculosa	30.6	35.0	26.8	30.5	39.0	23.8	18.0	21.1	15.3	29.5	41.1	21.2	6.37	7.74	5.24
Eunotia cf. glacilalispinosa	30.9	35.1	27.2	33.4	43.0	25.9	18.8	20.2	17.6	27.0	34.4	21.3	5.88	6.43	5.38
Gomphonema lagerheimii	31.0	36.1	26.7	34.8	42.5	28.6	17.1	19.3	15.2	26.3	37.5	18.5	6.96	8.49	5.71
Eunotia scandiorussica	31.6	38.1	26.1	29.6	38.1	23.0	18.8	22.0	16.0	27.7	37.3	20.7	5.84	6.62	5.15
Eunotia subcapitata	32.0	35.5	28.8	30.7	38.5	24.5	17.2	21.0	14.2	34.4	46.2	25.5	6.65	7.98	5.55
Eunotia ambivalens	32.1	36.8	27.9	36.2	44.1	29.7	18.4	21.0	16.4	27.6	36.3	21.0	6.24	7.20	5.41
Gomphonema brebissonii	34.4	38.7	30.5	40.6	45.9	36.0	18.3	20.2	16.7	24.2	30.9	18.9	6.10	6.91	5.39
Eunotia bilunaris	35.5	47.9	26.4	33.3	41.9	26.4	17.0	21.2	13.7	30.1	40.2	22.5	6.43	7.74	5.33
Eunotia panda	35.7	50.0	25.5	30.3	38.1	24.0	16.9	21.2	13.5	28.5	39.7	20.5	6.10	7.38	5.05
Eunotia julma	38.7	50.8	29.5	36.2	45.8	28.6	17.4	21.2	14.3	25.2	33.4	19.1	5.98	6.80	5.25
Eunotia naegelii	48.3	68.7	34.0	37.1	45.3	30.3	15.5	19.6	12.2	26.5	37.8	18.6	5.99	7.17	5.00
Eunotia cf. berrrandii	51.7	72.2	37.0	37.0	46.3	29.5	15.7	19.7	12.5	25.5	35.7	18.2	5.88	7.02	4.92
Eunotia flexuosa	52.9	75.4	37.1	38.7	49.5	30.3	16.5	20.6	13.3	24.4	34.5	17.2	5.85	6.91	4.94
Eunotia krammeri	55.3	74.7	41.0	38.0	46.6	31.0	15.7	19.2	12.8	25.3	34.5	18.6	5.41	6.13	4.78
Eunotia mucophila	58.6	73.8	46.5	39.1	46.5	32.8	15.2	19.2	12.1	26.7	36.7	19.5	5.63	6.59	4.82
Eunotia pseudogroenglandica	61.0	77.2	48.3	41.6	49.0	35.3	15.8	19.7	12.6	22.6	30.9	16.6	5.60	6.54	4.79
Eunotia paludosa	61.4	76.0	49.5	40.7	48.2	34.4	14.8	18.8	11.7	22.9	31.8	16.4	5.80	6.90	4.88

Diatom species are in order of increasing DOC optima. Optima (Opt.) and tolerances (High and Low) are back transformed from weighted average and weighted standard deviation values of log-transformed measurements

lakes with low conductivity across Russia (Maslennikova, 2020) and north-eastern Siberia (Pestryakova et al., 2018). Previously reported pH tolerance for *T. flocculosa* ranged from 4.6 to 7.04 across studies of streams (Pan et al., 1996; Dixit et al., 2002; Kovács et al., 2006), lakes (Bigler & Hall, 2002; Cheng et al., 2022; Duda et al., 2023), and bogs (Kim et al., 2007). pH tolerance values recorded for *T. flocculosa* in our study ranged from 5.2 to 7.7, suggesting that the tolerance for this species may be broader than initially thought. This finding indicates that levels of tolerance for diatom species may vary by habitat (Winter & Duthie, 2000), demonstrating that additional support is needed for updated regional reports of diatom taxa for accurate biomonitoring.

Indicator species related to environmental variables

Our observations of rich fen indicator species suggest expanded tolerance limits and habitat preferences than have been previously reported. For example, water temperature, rather than pH, was the common regulatory factor among the rich fen indicator species in this study. For example, *Gomphonema lagerheimii* (often reported as *G. hebridense*) was previously shown to be an indicator species for coastal poor fens in the Hudson Plains in Canada and tends to be sensitive to changes in pH (Hargan et al., 2015). However, *G. lagerheimii* was identified as a rich fen indicator in our study and was correlated with changes in water temperature rather than pH. These findings align more closely with observations made by Van Dam et al. (1994) and Wojtal (2003), suggesting that factors that affect abundance of this species may be unique to different habitats. Another rich fen indicator in our study, *Gomphonema brebissonii*, was correlated with changes in both water temperature and conductivity. *G. brebissonii* was most abundant at the end of the sampling season when water temperature was 17.5 °C and conductivity was 41.8 μScm. These findings expand previous observations in which this species was found in cold waters (6.2–9.0 °C) of moderate conductivity (360–480 μScm; Wojtal 2003). Finally, we observed *Eunotia ambivalens* to be positively correlated with water temperatures in the range of 16.4–21.0 °C, which is consistent with the reports of temperature preferences for this species observed in Romanian peat bogs (10–21 °C; Szigyártó et al., 2017). Although previous research indicates that *E.*

ambivalens is acidophilous (i.e., organisms that thrive in a relatively acidic environment), this species did not vary principally in relation to pH in our study. These findings suggest that pH may not be the primary factor regulating the growth and abundance of *E. ambivalens* in this rich fen as has been previously reported in bogs (Szigyártó et al., 2017).

We identified two moderate fen indicator species and the environmental variables to which they are correlated. *Eunotia scandiorussica* was identified as a moderate fen indicator and has previously been reported as an indicator species for streams and ponds of the high Arctic (Pla-Rabés et al., 2016) and was observed in *Sphagnum* bogs of the Russian Arctic (Kulikovskiy et al., 2010) and in the buccal cavity of a Siberian mammoth (Genkal et al., 2020). Although these previous studies do not report tolerance values related to water chemistry, we can infer some information, such as a preference for low pH and conductivity which are common features of *Sphagnum*-dominated bogs (Clymo, 1984; Bleuten et al., 2006). While our findings align with a preference for low conductivity, *E. scandiorussica* was positively correlated with pH, suggesting that pH was a stronger driving factor for *E. scandiorussica* in this moderate fen. *Eunotia panda* was the other moderate fen indicator and was negatively correlated with conductivity and positively correlated with water depth. These findings align with observations of *E. panda* in acidic (4.5–6.0), low conductivity (9.0–73.5 μScm) peat bogs, streams, and ponds in Acadia National Park, Maine (Veselá & Johansen, 2014).

Owing to overlap in hydrological and chemical characteristics between the rich and moderate fen, some species were found to be indicators of both fen types. In addition to *T. flocculosa,* described above, we observed *E. subcapitata* as an indicator for both the rich and moderate fens. We found *E. subcapitata* in highest relative abundance in the first half of the sampling season and it was positively correlated with variation in pH (5.6–8.0) and water depth (25.5–46.2 cm). The environmental tolerance and optima of *E. subcapitata* are not well known as they have been rarely observed (Kulikovskiy et al., 2010). Therefore, the results of our study shed some light on the preference of this rare species.

We identified seven indicator species in the poor fen across a range of pH tolerance limits that reinforce current understanding of acidophilous diatom

species. *Eunotia mucophila* was consistently the most abundant species found in the poor fen, representing 55–69% of the diatom community. Similar to our findings, *E. mucophila* was found to be negatively correlated with conductivity and positively correlated with DOC in shallow lakes of the Hudson Bay lowlands (Jacques et al., 2016) and associated with low pH (5–6) in peatlands in the northern Greater Khingan mountains (Han et al., 2022). *Eunotia paludosa* and *E. flexuosa* have been reported in bogs and acidic rich fens of the Hudson Bay lowlands (Hargan et al., 2015) and acidic peatlands and bogs in the northern Greater Khingan Mountains (Liu et al., 2011; Han et al., 2022), which corroborates our findings of these species being negatively correlated with pH. Another indicator species, *E. krammeri,* has been reported in *Sphagnum* samples from circumneutral rivers and lakes in Chukotka Peninsula, NE Siberia (Kulikovskiy et al., 2010). We observed *E. krammeri* in greatest abundance at the lowest pH (4.8) and clustered with other poor fen indicator species, suggesting this is an acidophilous species. Similarly, we observed *E. naegelii* to be negatively correlated with pH, which aligns with previous observations of this species in acidic mountain peatlands (pH 4.65–6.81; Kim et al., 2007), rivers (pH 4.3; Glushchenko & Kulikovskiy, 2017), and bogs (pH 4.5–6.5; Liu et al., 2011). Although previously reported in neutral to slightly alkaline (pH 6.07–8.0) lakes and ponds (Luo et al., 2019; Cantonati et al., 2021), we found that *E. pseudogroenlandica* was negatively correlated with pH, which aligns with observations of this species in acidic ponds with pH in the range of 5.55–6.20 (Stanković et al., 2022).

Interestingly, water column DOC concentration was a predictor of poor fen diatom species composition. This finding was surprising given that DOC is rarely identified as an explanatory variable for diatom assemblage composition in previous studies where poor fen indicator species were reported (Cheng et al., 2022; Stanković et al., 2022). Boreal peatlands contain high concentrations of terrestrially derived organic matter that can reduce light penetration and thereby algal photosynthesis (Ask et al., 2009; Rober et al., 2015; Gu & Wyatt, 2016). There has been much work investigating the role of DOC in general biofilm ecology in northern peatlands (Gu & Wyatt, 2016; Myers et al., 2021; Rober et al., 2023), but none of which has looked specifically at the effects of DOC on diatom species composition. We do know that DOC concentrations in the poor fen (51–77 mg l^{-1}) were

consistent with the levels previously shown to reduce light availability for algal production (Gu & Wyatt, 2016) and allow heterotrophic members of the biofilm to outcompete autotrophs (Myers et al., 2021). This is an area where additional study is needed to better understand the association between DOC and diatom communities in northern peatlands, especially given that DOC levels are expected to increase in this region with processes associated with ongoing climate change (Freeman et al., 2001; Wyatt et al., 2012; Fenner et al., 2021).

Diatom heterogeneity within and among peatlands

The heterogeneity in diatom species composition among fens observed in this study was consistent with a voucher flora of diatoms in an Alaskan rich, moderate, and poor fen (Hamilton et al., 2023), across a gradient of rich and poor boreal spring fens of Europe (Fránková et al., 2009), and with rich and poor fens of sub-boreal Canada (Hargan, 2014). Likewise, diatom assemblages displaying heterogeneity across different peatland types (i.e., rich fens, moderate fens, poor fens, and bogs) have been reported in modern (Pienkowski & Wujek, 1988; Fránková et al., 2009; Hargan et al., 2015) and paleoecological (Rühland et al., 2018) studies of peatlands. Within fen type, we found similar dominance of *Tabellaria* and *Eunotia* as those that have been previously reported in rich and poor fens (Fukumoto et al., 2014; Hargan et al., 2015; Rühland et al., 2018). These genera have been described as generalists in their preference to pH (Hargan et al., 2015), which aligns with our findings and may help explain their broad distribution. However, we observed lower species richness than previous studies and while patterns observed in this study were consistent with the literature at the genus level, our findings frequently differed at the species level (Fukumoto et al., 2014; Hargan et al., 2015; Rühland et al., 2018). These differences may indicate that broad environmental tolerances drive similarities at the genus level, but species may differ across regions owing to localized environmental conditions (Antoniades et al., 2004; Rober et al., 2014; Soininen & Teittinen, 2019).

Conclusion

Overall, our data provide insight into patterns of natural variation in diatom species abundance and

composition across a gradient of northern peatland types and provide insight into the underlying environmental conditions that influence diatom species distribution in our study area. Further, we identified several diatom species that may be useful as bioindicators for these fens. Our findings expand current understanding of environmental tolerance for several diatom species of high indicator value. These data also help to explain previously observed successional trends in diatom relative abundance in these fens (Ferguson et al., 2021) and improve our ability to use environmental metrics (e.g., DOC, temperature) to predict shifts in the dominant algal functional groups that have consequences for ecosystem function (Wyatt et al., 2015; Rober et al., 2022). Taken together, these results contribute to a growing awareness of peatlands as hotspots for biodiversity and as habitat for rare and specialized species (Minayeva et al., 2008). Given that the ability to predict ecosystem resilience requires characterization of spatial and temporal variability in species abundance and composition, the results of this study may facilitate monitoring of diatom communities in response to environmental variation in undisturbed northern fens.

Data availability The data are available from the authors upon reasonable request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

References

Antoniades, D., M. S. Douglas & J. P. Smol, 2004. Diatom species–environment relationships and inference models from Isachsen, Ellef Ringnes Island, Canadian High Arctic. Hydrobiologia 529: 1–18. https://doi.org/10.1007/s10750-004-4942-8.

Ask, J., J. Karlsson, L. Persson, P. Ask, P. Byström & M. Jansson, 2009. Terrestrial organic matter and light penetration: Effects on bacterial and primary production in lakes. Limnology and Oceanography 54: 2034–2040. https://doi.org/10.4319/lo.2009.54.6.2034.

Battarbee, R. W., C. F. Donald, C. Bigler, B. F. Cumming & I. Renberg, 2010. Diatoms as indicators of surface-water acidity. In Smol, J. P. & E. F. Stoermer (eds), The Diatoms: Applications for the Environmental and Earth Sciences Cambridge University Press, Cambridge: 98–121.

Bigler, C. & R. I. Hall, 2002. Diatoms as indicators of climatic and limnological change in Swedish Lapland: a 100-lake calibration set and its validation for paleoecological reconstructions. Journal of Paleolimnology 27: 97–115. https://doi.org/10.1023/A:1013562325326.

Bleuten, W., W. Borren, P. H. Glaser, T. Tsuchihara, E. D. Lapshina, M. Mäkilä, D. Siegel, H. Joosten & M. J. Wassen, 2006. Hydrological processes, nutrient flows and patterns of fens and bogs. In Verhoeven, J. T. A., B. Beltman, R. Bobbink & D. F. Whigham (eds), Wetlands and Natural Resource Management Springer, Berlin: 183–204.

Boggero, A., S. Zaupa, S. Musazzi, M. Rogora, E. Dumnicka & A. Lami, 2019. Environmental factors as drivers for macroinvertebrate and diatom diversity in Alpine lakes: New insights from the Stelvio National Park (Italy): Biodiversity of mountain Alpine lakes. Journal of Limnology 78: 147–162. https://doi.org/10.4081/jlimnol.2019.1863.

Borcard, D., F. Gillet & P. Legendre, 2011. Canonical Ordination In Numerical Ecology with R, Springer, New York:, 203–297.

Bottin, M., J. Soininen, M. Ferrol & J. Tison-Rosebery, 2014. Do spatial patterns of benthic diatom assemblages vary across regions and years? Freshwater Science 33: 402–416. https://doi.org/10.1086/675726.

Bradshaw, C. J. A. & I. G. Warkentin, 2015. Global estimates of boreal forest carbon stocks and flux. Global and Planetary Change 128: 24–30. https://doi.org/10.1016/j.gloplacha.2015.02.004.

Brugam, R. B. & P. Swain, 2000. Diatom indicators of peatland development at Pogonia Bog Pond, Minnesota, USA. The Holocene 10: 453–464. https://doi.org/10.1191/095968300668251084.

Cantonati, M., R. Zorza, M. Bertoli, P. Pastorino, G. Salvi, G. Platania, M. Prearo & E. Pizzul, 2021. Recent and subfossil diatom assemblages as indicators of environmental change (including fish introduction) in a high-mountain lake. Ecological Indicators 125: 107603. https://doi.org/10.1016/j.ecolind.2021.107603.

Charles, D. F., C. Knowles, & R. S. Davis, 2002. Protocols for the analysis of algal samples collected as part of the US Geological Survey National Water-Quality Assessment Program: 1–124. Retrieved from http://diatom.ansp.org/nawqa/pdfs/ ProtocolPublication.pdf.

Chen, X., S. McGowan, Z. J. Bu, X. D. Yang, Y. M. Cao, X. Bai, L. H. Zeng, J. Liang & Q. L. Qiao, 2020. Diatom-based water-table reconstruction in Sphagnum peatlands of northeastern China. Water Research 174: 115648. https://doi.org/10.1016/j.watres.2020.115648.

Cheng, Y., N. Michelutti, A. M. Paterson, C. Meyer-Jacob & J. P. Smol, 2022. Developing diatom-based inference models to assess lake ecosystem change along a gradient of metal smelting impacts: Sudbury lakes revisited. Journal

of Phycology 58: 530–542. https://doi.org/10.1111/jpy.13257.

Churchill, A. C., M. R. Turetsky, A. D. McGuire & T. N. Hollingsworth, 2015. Response of plant community structure and primary productivity to experimental drought and flooding in an Alaskan fen. Canadian Journal of Forest Research 45: 185–193. https://doi.org/10.1139/cjfr-2014-0100.

Clymo, R. S., 1984. Sphagnum-dominated peat bog: a naturally acid ecosystem. Philosophical Transactions of the Royal Society of London B, Biological Sciences 305: 487–499. https://doi.org/10.1098/rstb.1984.0072.

De Cáceres, M., F. Jansen, & N. Dell, 2023. indicspecies: Relationship Between Species and Groups of Sites. R package version. https://CRAN.R-project.org/package=indicspecies.

De Cáceres, M. & P. Legendre, 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90: 3566–3574. https://doi.org/10.1890/08-1823.1.

Dixit, S. S., A. S. Dixit & J. P. Smol, 2002. Diatom and chrysophyte transfer functions and inferences of post-industrial acidification and recent recovery trends in Killarney lakes (Ontario, Canada). Journal of Paleolimnology 27: 79–96. https://doi.org/10.1023/A:1013571821476.

Dray, S., 2023. adespatial: Multivariate Multiscale Spatial Analysis. R package version. https://CRAN.R-project.org/package=adespatial.

Duda, M. P., B. Sivarajah, K. M. Rühland, A. M. Paterson, J. L. Barrow, Y. Cheng, E. J. Favot, K. R. Hadley, R. I. Hall, K. E. Hargan, C. Nelligan, E. D. Reavie, R. E. Valleau, P. Werner, C. Wilkins & J. P. Smol, 2023. Environmental optima for common diatoms from Ontario lakes along gradients of lakewater pH, total phosphorus concentration, and depth. Journal of Paleolimnology 70: 131–158. https://doi.org/10.1007/s10933-023-00288-7.

Dufrêne, M. & P. Legendre, 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.

Fenner, N., J. Meadham, T. Jones, F. Hayes & C. Freeman, 2021. Effects of climate change on peatland reservoirs: a DOC perspective. Global Biogeochemical Cycles 35: e2021GB006992. https://doi.org/10.1029/2021GB006992.

Ferguson, H. M., E. J. Slagle, A. A. McCann, J. T. Walls, K. H. Wyatt & A. R. Rober, 2021. Greening of the boreal peatland food web: Periphyton supports secondary production in northern peatlands. Limnology and Oceanography 66: 1743–1758. https://doi.org/10.1002/lno.11719.

Flanagan, K. M., E. McCauley, F. Wrona & T. Prowse, 2003. Climate change: the potential for latitudinal effects on algal biomass in aquatic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 60: 635–639. https://doi.org/10.1139/f03-062.

Fránková, M., J. Bojková, A. Poulíčková & M. Hájek, 2009. The structure and species richness of the diatom assemblages of the Western Carpathian spring fens along the gradient of mineral richness. Fottea 9: 355–368. https://doi.org/10.5507/fot.2009.035.

Freeman, C., C. D. Evans, D. T. Monteith, B. Reynolds & N. Fenner, 2001. Export of organic carbon from peat soils. Nature 412: 785–785. https://doi.org/10.1038/35090628.

Fukumoto, Y., K. Kashima & U. Ganzorig, 2014. The Holocene environmental changes in boreal fen peatland of northern Mongolia reconstructed from diatom assemblages. Quaternary International 348: 66–81. https://doi.org/10.1016/j.quaint.2014.05.029.

Gaiser, E. & K. Rühland, 2010. Diatoms as indicators of environmental change in wetlands and peatlands. In Smol, J. P. & E. F. Stoermer (eds), The Diatoms: Applications for the Environmental and Earth Sciences Cambridge University Press, Cambridge: 473–496.

Gallé, R., F. Samu, A. R. Zsigmond, N. Gallé-Szpisjak & I. Urák, 2019. Even the smallest habitat patch matters: On the fauna of peat bogs. Journal of Insect Conservation 23: 699–705. https://doi.org/10.1007/s10841-019-00164-8.

Genkal, S. I., V. A. Gabyshev & A. V. Protopopov, 2020. Findings of diatom algae in the trunk and buccal cavity content of a mammoth from sediments of the late pleistocene of Yakutia. Paleontological Journal 54: 552–559. https://doi.org/10.1134/S0031030120050056.

Gilbert, D. & E. A. D. Mitchell, 2006. Microbial diversity in Sphagnum peatlands. In Martini, I. P. & A. M. Cortizas (eds), Developments in Earth Surface Processes Elsevier, Amsterdam: 287–318.

Glushchenko, A. M. & M. S. Kulikovskiy, 2017. Taxonomy and distribution of the genus Eunotia Ehrenberg in aquatic ecosystems of Vietnam. Inland Water Biology 10: 130–139. https://doi.org/10.1134/S1995082917020055.

Gu, L. Y. & K. H. Wyatt, 2016. Light availability regulates the response of algae and heterotrophic bacteria to elevated nutrient levels and warming in a northern boreal peatland. Freshwater Biology 61: 1442–1453. https://doi.org/10.1111/fwb.12783.

Hamilton, V. A., S. S. Lee, A. R. Rober, P. C. Furey, K. M. Manoylov & K. H. Wyatt, 2023. A voucher flora of diatoms from fens in the Tanana River Floodplain. Alaska. Water 15: 2803. https://doi.org/10.3390/w15152803.

Han, D., Y. Sun, J. Cong, C. Gao & G. Wang, 2022. Ecological distribution of modern diatom in peatlands in the northern Greater Khingan Mountains and its environmental implications. Environmental Science and Pollution Research 30: 36607–36618. https://doi.org/10.1007/s11356-022-24910-9.

Hargan, K. E., 2014. Diatoms as indicators of environmental and climatic change in peatlands and lakes located across the boreal shield and Hudson Bay lowlands of Canada. PhD Thesis, Queen's University. Retrieved from https://www.proquest.com/dissertations-theses/diatoms-as-indicators-environmental-climatic/docview/1819494008/se-2.

Hargan, K. E., K. M. Rühland, A. M. Paterson, S. A. Finkelstein, J. R. Holmquist, G. M. MacDonald, W. Keller & J. P. Smol, 2015. The influence of water-table depth and pH on the spatial distribution of diatom species in peatlands of the Boreal Shield and Hudson Plains, Canada. Botany 93: 57–74. https://doi.org/10.1139/cjb-2014-0138.

Harris, L. I., K. Richardson, K. A. Bona, S. J. Davidson, S. A. Finkelstein, M. Garneau, J. McLaughlin, F. Nwaishi, D. Olefeldt, M. Packalen, N. T. Roulet, F. M. Southee,

M. Strack, K. L. Webster, S. L. Wilkinson & J. C. Ray, 2022. The essential carbon service provided by northern peatlands. Frontiers in Ecology and the Environment 20: 222–230. https://doi.org/10.1002/fee.2437.

Holt, E. A. & S. W. Miller, 2011. Bioindicators: Using organisms to measure environmental impacts. Nature Education Knowledge 2: 8–13.

Hugelius, G., J. Loisel, S. Chadburn, R. B. Jackson, M. Jones, G. MacDonald, M. Marushchak, D. Olefeldt, M. Packalen, M. B. Siewert, C. Treat, M. Turetsky, C. Voigt & Z. Yu, 2020. Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. Proceedings of the National Academy of Sciences 117: 20438–20446. https://doi.org/10.1073/pnas.1916387117.

Jacques, O., F. Bouchard, L. A. MacDonald, R. I. Hall, B. B. Wolfe & R. Pienitz, 2016. Distribution and diversity of diatom assemblages in surficial sediments of shallow lakes in Wapusk National Park (Manitoba, Canada) region of the Hudson Bay Lowlands. Ecology and Evolution 6: 4526–4540. https://doi.org/10.1002/ece3.2179.

Joosten, H., 2015. Peatlands, Climate Change Mitigation and Biodiversity Conservation. Nordic Council of Ministers. Retrieved from http://urn.kb.se/resolve?urn=urn:nbn:se:norden:org:diva-3879.

Joosten, H., & D. Clarke, 2002. Wise Use of Mires and Peatlands: Background and Principles Including a Framework for Decision-Making. International Peat Society and International Mire Conservation Group 304.

Kahlert, M., K. M. Rühland, I. Lavoie, F. Keck, E. Saulnier-Talbot, D. Bogan, R. B. Brua, S. Campeau, K. S. Christoffersen, J. M. Culp, S. M. Karjalainen, J. Lento, S. C. Schneider, R. Shaftel & J. P. Smol, 2022. Biodiversity patterns of Arctic diatom assemblages in lakes and streams: Current reference conditions and historical context for biomonitoring. Freshwater Biology 67: 116–140. https://doi.org/10.1111/fwb.13490.

Kapetanović, T., R. Jahn, S. Redžić & M. Carić, 2011. Diatoms in a poor fen of Bijambare protected landscape, Bosnia & Herzegovina. Nova Hedwigia 93: 125–151. https://doi.org/10.1127/0029-5035/2011/0093-0125.

Kim, Y., J. Suk Choi, H. Sin Kim & Soon, 2007. Epiphytic diatom communities from two mountain bogs in South Korea. Nova Hedwigia 84: 363–379. https://doi.org/10.1127/0029-5035/2007/0084-0363.

Kock, A., J. C. Taylor & W. Malherbe, 2019. Diatom community structure and relationship with water quality in Lake Sibaya, KwaZulu-Natal, South Africa. South African Journal of Botany 123: 161–169. https://doi.org/10.1016/j.sajb.2019.03.013.

Kovács, C., M. Kahlert & J. Padisák, 2006. Benthic diatom communities along pH and TP gradients in Hungarian and Swedish streams. Journal of Applied Phycology 18: 105–117. https://doi.org/10.1007/s10811-006-9080-4.

Kuefner, W., S. Ossyssek, J. Geist & U. Raeder, 2020. The silicification value: a novel diatom-based indicator to assess climate change in freshwater habitats. Diatom Research 35: 1–16. https://doi.org/10.1080/0269249X.2020.1722246.

Kulikovskiy, M., H. Lange-Bertalot, S. Genkal & A. Witkowski, 2010. Eunotia (Bacillariophyta) in the Holarctic:

New species from the Russian Arctic. Polish Botanical Journal 55: 93–107.

Küttim, L., M. Küttim, L. Puusepp & S. Sugita, 2017. The effects of ecotope, microtopography and environmental variables on diatom assemblages in hemiboreal bogs in Northern Europe. Hydrobiologia 792: 137–149. https://doi.org/10.1007/s10750-016-3050-x.

Lavoie, I., P. J. Dillon & S. Campeau, 2009. The effect of excluding diatom taxa and reducing taxonomic resolution on multivariate analyses and stream bioassessment. Ecological Indicators 9: 213–225. https://doi.org/10.1016/j.ecolind.2008.04.003.

Legendre, L. & P. Legendre, 2012. Numerical Ecology, Elsevier, Amsterdam:

Lento, J., S. M. Laske, I. Lavoie, D. Bogan, R. B. Brua, S. Campeau, K. Chin, J. M. Culp, B. Levenstein, M. Power, É. Saulnier-Talbot, R. Shaftel, H. Swanson, M. Whitman & C. E. Zimmerman, 2022. Diversity of diatoms, benthic macroinvertebrates, and fish varies in response to different environmental correlates in Arctic rivers across North America. Freshwater Biology 67: 95–115. https://doi.org/10.1111/fwb.13600.

Li, L., B. Zheng & L. Liu, 2010. Biomonitoring and bioindicators used for river ecosystems: definitions, approaches and trends. Procedia Environmental Sciences 2: 1510–1524. https://doi.org/10.1016/j.proenv.2010.10.164.

Li, P., J. Holden, B. Irvine & X. Mu, 2017. Erosion of northern hemisphere blanket peatlands under 21st-century climate change. Geophysical Research Letters 44: 3615–3623. https://doi.org/10.1002/2017GL072590.

Liu, Y., Q. Wang & C. Fu, 2011. Taxonomy and distribution of diatoms in the genus Eunotia from the Da'erbin Lake and surrounding bogs in the Great Xing'an Mountains, China. Nova Hedwigia 92: 205–232. https://doi.org/10.1127/0029-5035/2011/0092-0205.

Loisel, J., A. V. Gallego-Sala & Z. Yu, 2012. Global-scale pattern of peatland Sphagnum growth driven by photosynthetically active radiation and growing season length. Biogeosciences 9: 2737–2746. https://doi.org/10.5194/bg-9-2737-2012.

Luna, T. & L. Bahls, 2017. An extremely rich fen on the plains of the Blackfeet Indian Reservation, Montana. Natural Areas Journal 37: 457–473. https://doi.org/10.3375/043.037.0403.

Luo, F., Q. You, P. Yu, W. Pang & Q. Wang, 2019. Eunotia (Bacillariophyta) biodiversity from high altitude, freshwater habitats in the Mugecuo Scenic Area, Sichuan Province. China. Phytotaxa 394: 133. https://doi.org/10.11646/phytotaxa.394.2.2.

Lyons, C. L., B. A. Branfireun, J. McLaughlin & Z. Lindo, 2020. Simulated climate warming increases plant community heterogeneity in two types of boreal peatlands in north–central Canada. Journal of Vegetation Science 31: 908–919. https://doi.org/10.1111/jvs.12912.

Maslennikova, A. V., 2020. Development and application of an electrical conductivity transfer function, using diatoms from lakes in the Urals, Russia. Journal of Paleolimnology 63: 129–146. https://doi.org/10.1007/s10933-019-00106-z.

McPartland, M. Y., E. S. Kane, M. J. Falkowski, R. Kolka, M. R. Turetsky, B. Palik & R. A. Montgomery, 2019.

The response of boreal peatland community composition and NDVI to hydrologic change, warming, and elevated carbon dioxide. Global Change Biology 25: 93–107. https://doi.org/10.1111/gcb.14465.

McPartland, M. Y., R. A. Montgomery, P. J. Hanson, J. R. Phillips, R. Kolka & B. Palik, 2020. Vascular plant species response to warming and elevated carbon dioxide in a boreal peatland. Environmental Research Letters 15: 124066. https://doi.org/10.1088/1748-9326/abc4fb.

Minayeva, T., O. Bragg, O. Cherednichenko, J. Couwenberg, G. A. (Gert-J. Duinen, W. Giesen, A. P. Grootjans, P. Grundling, V. Nikolaev, & S. van der Schaaf, 2008. Peatlands and biodiversity In Parish F., A. Sirin, D. Charman, H. Joosten, T. Minayeva, M. Silvius, & L. Stringer (eds) Assessment on Peatlands, Biodiversity and Climate Change. Global Environment Centre, Kuala Lumpur & Wetlands International: 60–98. Retrieved from https://search-ebscohost-com.proxy.bsu.edu/login.aspx?direct=true&db=sch&AN=30046996&site=ehost-live&scope=site.

Myers, J. M., K. A. Kuehn & K. H. Wyatt, 2021. Carbon subsidies shift a northern peatland biofilm community towards heterotrophy in low but not high nutrient conditions. Freshwater Biology 66: 589–598. https://doi.org/10.1111/fwb.13663.

Oeding, S. & K. H. Taffs, 2017. Developing a regional diatom index for assessment and monitoring of freshwater streams in sub-tropical Australia. Ecological Indicators 80: 135–146. https://doi.org/10.1016/j.ecolind.2017.05.009.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, P. Solymos, M. H. H. Stevens, E. Szoecs, & H. Wagner, 2022. vegan: Community Ecology Package. R package version. https://CRAN.R-project.org/package=vegan.

Olefeldt, D. & N. T. Roulet, 2012. Effects of permafrost and hydrology on the composition and transport of dissolved organic carbon in a subarctic peatland complex. Journal of Geophysical Research: Biogeosciences 117: G01005. https://doi.org/10.1029/2011JG001819.

Pan, Y., R. J. Stevenson, B. H. Hill, A. T. Herlihy & G. B. Collins, 1996. Using diatoms as indicators of ecological conditions in lotic systems: a regional assessment. Journal of the North American Benthological Society 15: 481–495. https://doi.org/10.2307/1467800.

Pappas, J. L. & E. F. Stoermer, 1996. Quantitative method for determining a representative algal sample count. Journal of Phycology 32: 693–696. https://doi.org/10.1111/j.0022-3646.1996.00693.x.

Pérez, L., A. Correa-Metrio, S. Cohuo, L. M. González, P. Echeverría-Galindo, M. Brenner, J. Curtis, S. Kutterolf, M. Stockhecke, F. Schenk, T. Bauersachs & A. Schwalb, 2021. Ecological turnover in neotropical freshwater and terrestrial communities during episodes of abrupt climate change. Quaternary Research 101: 26–36. https://doi.org/10.1017/qua.2020.124.

Pestryakova, L. A., U. Herzschuh, R. Gorodnichev & S. Wetterich, 2018. The sensitivity of diatom taxa from Yakutian lakes (north-eastern Siberia) to electrical conductivity and other environmental variables. Polar Research 37: 1485625. https://doi.org/10.1080/17518369.2018.1485625.

Pienkowski, T. P. & D. E. Wujek, 1988. The diatom flora of the Red Lake Peatland, Minnesota. Journal of the Minnesota Academy of Science 53: 7–13.

Pla-Rabés, S., P. B. Hamilton, E. Ballesteros, M. Gavrilo, A. M. Friedlander & E. Sala, 2016. The structure and diversity of freshwater diatom assemblages from Franz Josef Land Archipelago: a northern outpost for freshwater diatoms. PeerJ 4: e1705. https://doi.org/10.7717/peerj.1705.

Potapova, M. & D. F. Charles, 2003. Distribution of benthic diatoms in U.S. rivers in relation to conductivity and ionic composition. Freshwater Biology 48: 1311–1328. https://doi.org/10.1046/j.1365-2427.2003.01080.x.

Qiu, C., D. Zhu, P. Ciais, B. Guenet & S. Peng, 2020. The role of northern peatlands in the global carbon cycle for the 21st century. Global Ecology and Biogeography 29: 956–973. https://doi.org/10.1111/geb.13081.

Rober, A. R., K. H. Wyatt, M. R. Turetsky & R. J. Stevenson, 2013. Algal community response to experimental and interannual variation in hydrology in an Alaskan boreal fen. Freshwater Science 32: 1–11. https://doi.org/10.1899/11-131.1.

Rober, A. R., K. H. Wyatt, R. J. Stevenson & M. R. Turetsky, 2014. Spatial and temporal variability of algal community dynamics and productivity in floodplain wetlands along the Tanana River, Alaska. Freshwater Science 33: 765–777. https://doi.org/10.1086/676939.

Rober, A. R., R. J. Stevenson & K. H. Wyatt, 2015. The role of light availability and herbivory on algal responses to nutrient enrichment in a riparian wetland, Alaska. Journal of Phycology 51: 528–535. https://doi.org/10.1111/jpy.12298.

Rober, A. R., K. S. McCann, M. R. Turetsky & K. H. Wyatt, 2022. Cascading effects of predators on algal size structure. Journal of Phycology. 58: 308–317. https://doi.org/10.1111/jpy.13235.

Rober, A. R., A. J. Lankford, E. S. Kane, M. R. Turetsky & K. H. Wyatt, 2023. Structuring life after death: plant leachates promote CO_2 uptake by regulating microbial biofilm interactions in a northern peatland ecosystem. Ecosystems 26: 1108–1124. https://doi.org/10.1007/s10021-023-00820-w.

Round, F. E., 2004. pH scaling and diatom distribution. Diatom 20: 9–12. https://doi.org/10.11464/diatom1985.20.0_9.

RStudio Team, 2023. RStudio: Integrated Development for R. PBC, Boston, MA, http://www.rstudio.com/.

Rühland, K. M., K. Rentz, A.M. Paterson, J. T. Teller, & J. P. Smol. 2018. The post-glacial history of northern Lake of the Woods: A multi-proxy perspective on climate variability and lake ontogeny. Journal of Great Lakes Research 44: 367–376. https://doi.org/10.1016/j.jglr.2018.04.002

Rydin, H. & J. K. Jeglum, 2013. The Biology of Peatlands, Oxford University Press:

Sathicq, M, B., M. M. N. Gelis, J. Cochero, 2020. optimos. prime: Optimos prime helps calculate autoecological data for biological species. R package version. https://CRAN.R-project.org/package=optimos.prime.

Serikova, S., O. S. Pokrovsky, H. Laudon, I. V. Krickov, A. G. Lim, R. M. Manasypov & J. Karlsson, 2019. High carbon emissions from thermokarst lakes of Western Siberia.

Nature Communications 10: 1552. https://doi.org/10.1038/s41467-019-09592-1.

Sjörs, H., 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2: 241. https://doi.org/10.2307/3564795.

Soininen, J. & A. Teittinen, 2019. Fifteen important questions in the spatial ecology of diatoms. Freshwater Biology 64: 2071–2083. https://doi.org/10.1111/fwb.13384.

Stanković, I., M. G. Udovič, M. Šušnjara, A. Alegro & Z. Levkov, 2022. Diversity and ecology of benthic diatoms in a mire with narrow pH gradient. Fottea 22: 39–55. https://doi.org/10.5507/fot.2021.015.

Stevenson, R. J., Y. Pan & H. Van Dam, 1999. Assessing environmental conditions in rivers and streams with diatoms. In Smol, J. P. & E. F. Stoermer (eds), The Diatoms: Applications for the Environmental and Earth Sciences Cambridge University Press, Cambridge: 11–40.

Szigyártó, I.-L., K. Buczkó, I. Rákossy, Z. May, I. Urák & A.-R. Zsigmond, 2017. Contrasting diatom diversity in lentic and lotic habitats of Romanian peat bogs and the relation to environmental variables. Fundamental and Applied Limnology 189: 137–151. https://doi.org/10.1127/fal/2016/0943.

UN Environment (ed), 2019. Global Environment Outlook–GEO-6: Summary for Policymakers. Cambridge University Press, Cambridge. https://doi.org/10.1017/9781108639217.

Van Dam, H., A. Mertens & J. Sinkeldam, 1994. A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. Netherlands Journal of Aquatic Ecology 28: 117–133. https://doi.org/10.1007/BF02334251.

Veselá, J., & J. R. Johansen, 2014. Three new Eunotia (Bacillariophyta) species from Acadia National Park, Maine, USA. Phytotaxa 175: 181–200. https://doi.org/10.11646/phytotaxa.175.4.1.

Vitt, D. H., 2006. Functional characteristics and indicators of boreal peatlands. In Wieder, R. K. & D. H. Vitt (eds), Boreal Peatland Ecosystems Springer, Berlin: 9–24.

Vitt, D. H., L. A. Halsey, I. E. Bauer & C. Campbell, 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. Canadian Journal of Earth Sciences 37: 683–693. https://doi.org/10.1139/e99-097.

Winter, J. G. & H. C. Duthie, 2000. Stream epilithic, epipelic and epiphytic diatoms: habitat fidelity and use in biomonitoring. Aquatic Ecology. https://doi.org/10.1023/A:1011461727835.

Wojtal, A., 2003. Diatoms of the genus Gomphonema Ehr. (Bacillariophyceae) from a karstic stream in the Krakowsko-Częstochowska Upland. Acta Societatis Botanicorum Poloniae 72: 213–220. https://doi.org/10.5586/asbp.2003.028.

Wyatt, K. H., M. R. Turetsky, A. R. Rober, D. Giroldo, E. S. Kane & R. J. Stevenson, 2012. Contributions of algae to GPP and DOC production in an Alaskan fen: effects of historical water table manipulations on ecosystem responses to a natural flood. Oecologia 169: 821–832. https://doi.org/10.1007/s00442-011-2233-4.

Wyatt, K. H., J. S. Bange, A. S. Fitzgibbon, M. J. Bernot & A. R. Rober, 2015. Nutrients and temperature interact to regulate algae and heterotrophic bacteria in an Alaskan poor fen peatland. Canadian Journal of Fisheries and Aquatic Sciences 72: 447–453. https://doi.org/10.1139/cjfas-2014-0425.

Wyatt, K. H., K. S. McCann, A. R. Rober & M. R. Turetsky, 2021. Letter: Trophic interactions regulate peatland carbon cycling. Ecology Letters 24: 781–790. https://doi.org/10.1111/ele.13697.

Xu, J., P. J. Morris, J. Liu & J. Holden, 2018. PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. Catena 160: 134–140. https://doi.org/10.1016/j.catena.2017.09.010.

Yu, Z., J. Loisel, D. P. Brosseau, D. W. Beilman, & S. J. Hunt, 2010. Global peatland dynamics since the Last Glacial Maximum. Geophysical Research Letters 37: 2010GL043584. https://doi.org/10.1029/2010GL043584.

Zubova, E. M., N. A. Kashulin, V. A. Dauvalter, D. B. Denisov, S. A. Valkova, O. I. Vandysh, Z. I. Slukovskii, P. M. Terentyev & A. A. Cherepanov, 2020. Long-term environmental monitoring in an Arctic lake polluted by metals under climate change. Environments 7: 34. https://doi.org/10.3390/environments7050034.