

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

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Abstract: Diatoms collected from 113 surface peat samples from the Boreal Shield and Hudson Plains show taxonomic distributions that are associated with macro-vegetation type, pH, and position relative to the water table, the main environmental variables measured in this study. The overall goal of our research was to determine the ecological distribution and response of diatoms to microhabitat conditions, and to assess the potential for diatoms to be applied as indicators of long-term environmental change in northern peatlands. Our results indicate that diatom assemblage composition was determined by both the broader peatland type (i.e., bog, rich and poor fens) and microhabitats within peatland formations (e.g., hummock, hollow). The diatom assemblages were primarily influenced by pH with the sites divided at a critical pH of 5.5, and secondarily by the depth to the water table. Acidic bog hollow and hummock microhabitats were species-poor and dominated almost exclusively by *Eunotia paludosa* A.Grunow and (or) *Eunotia mucophila* (H.Lange-Bertalot, M.Nörpel-Schempp & E.Alles) H.Lange-Bertalot. These acidophilic and aerophilic diatom species were associated with the narrow pH optima of the dominant *Sphagnum* L. species (e.g., *Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum angustifolium* (C.E.O.Jensen ex Russow) C.E.O.Jensen) found in these bog habitats. Rich and poor fen samples, which were less acidic, supported a more diverse diatom assemblage (>30 species) with greater variability in both diatom and bryophyte pH tolerances. The diatom assemblages recorded in the bogs and fens of our study are similar to those found in peatlands around the world, demonstrating that diatom species are very specialized to exist in these often harsh semi-aquatic environments. Diatoms from peatlands have great potential as biomonitors of environmental change in these important ecosystems.

Key words: diatoms, peatlands, pH and moisture gradient, microhabitat, bryophytes.

Résumé : Les diatomées recueillies de 113 échantillons de surface de tourbe provenant du bouclier boréal et des plaines de la baie d'Hudson présentent des distributions taxonomiques qui sont associées au type de macro-végétation, au pH et à leur position relative par rapport au niveau phréatique, les principales variables environnementales mesurées dans cette étude. Le but global de cette recherche était de déterminer la distribution écologique et la réponse des diatomées aux conditions de micro-habitat, et d'évaluer si les diatomées peuvent constituer des indicateurs de changements environnementaux à long terme dans les tourbières du nord. Les résultats des auteurs indiquent que la composition de l'assemblage des diatomées a été déterminée autant par le type de tourbières le plus large (i.e., bogues, marais riches et pauvres) que par les micro-habitats à l'intérieur des tourbières (butte, niche). Les assemblages de diatomées étaient d'abord influencés par le pH avec des sites divisés à un pH critique de 5,5; puis par la profondeur de la nappe phréatique. Les micro-habitats des bogues à buttes et niches acides étaient pauvres en espèces et étaient presque exclusivement dominés par *Eunotia paludosa* A.Grunow, *Eunotia mucophila* (H.Lange-Bertalot, M.Nörpel-Schempp & E.Alles) H.Lange-Bertalot ou les deux. Ces espèces de diatomées acidophiles et aérophiles étaient associées au pH optimal étroit des espèces de *Sphagnum* L. dominantes (*Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum angustifolium* (C.E.O.Jensen ex Russow) C.E.O.Jensen) trouvées dans ces bogues. Les échantillons de marais riches et pauvres, qui étaient moins acides, supportaient une diversité plus large d'assemblages de diatomées (>30 espèces) avec une plus grande variabilité sur le plan de la tolérance au pH des diatomées et des bryophytes. Les assemblages de diatomées rapportés dans les bogues et les marais étudiés ici sont similaires à ceux trouvés dans les tourbières à travers le monde, ce qui démontre que les espèces de diatomées sont très spécialisées afin de survivre dans ces environnements semi-aquatiques souvent difficiles. Les diatomées des tourbières ont un grand potentiel comme bio-moniteurs des changements environnementaux de ces écosystèmes importants. [Traduit par la Rédaction]

Mots-clés : diatomées, tourbières, gradient de pH et d'humidité, micro-habitat, bryophytes.

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Introduction

With climate change, studies of northern peatlands are now more important than ever owing to the vast quantities of carbon stored within these regions and their future role as net carbon sinks (Roulet 2000; Waddington et al. 2009; Dunn and Freeman 2011). Therefore, attention needs to be directed towards an improved understanding of past peatland successional changes and responses to climate, to more accurately forecast future changes within these sensitive environments. Currently, only a few biological proxies (e.g., macrofossils, testate amoebae, pollen, and humification) are used widely to study historical moisture changes and impacts within northern peatlands, and the full potential archive of peatland biological proxies has not been fully exploited. Diatoms (Bacillariophyceae) are unicellular, siliceous algae that have been used extensively in lake and wetland studies as environmental indicators (Smol and Stoermer 2010). However, diatoms have rarely been used to study past peatland responses to environmental change, despite their presence in peatland systems and their prevalence across a wide range of aquatic habitats, from open water to non-submerged mosses that experience periodic drying (typical of wetland environments) (Gaiser and Rühland 2010; Johansen 2010). Spatial studies exploring modern-day associations between diatoms and differing peatland types are required to interpret long-term peatland changes from diatom stratigraphies.

In the early to mid-20th century, several taxonomic studies examined diatoms found in peatlands, including early work by Hustedt (1927–1966), Krasske (1932, 1936) and Foged (1951), and in early paleoecological studies by Sears and Couch (1932) and Patrick (1954). Later, Kingston (1982) identified characteristic peatland diatom assemblages that were dependent on macro-vegetation type, trophic status, and position relative to the water table, concluding that diatoms are sensitive to microhabitat conditions, and they can be utilized beneficially to analyze environmental gradients in peatlands. Recently, diatom studies have shown that moss-inhabiting diatoms are sensitive to varying moisture conditions and pH (Van de Vijver and Beyens 1997; Poulíčková et al. 2004; Van de Vijver et al. 2008; Chen et al. 2012). Some studies have also emphasized that there may be specific relationships between diatom assemblages and moss species composition, independent of other measured factors (e.g., moisture) (Kingston 1982; Poulíčková et al. 2004; Buczkó 2006; Hájková et al. 2011).

Diatoms have been shown to respond independently to changes in bryophyte assemblages. For example, shifts in diatom assemblages have been found to occur in peat records that are dominated by one moss species (Brown et al. 1994). As well, diatom assemblage shifts have been shown to substantially pre-date shifts in the moss communities, suggesting that diatoms are responding more sensitively to changes in the chemical environment than directly to changes in bryophyte composition (Rühland et al. 2000; Poulíčková et al. 2004). From these few paleoecological studies using diatoms, there appears to be considerable potential for the analysis of the commonly preserved remains of these algae to increase our understanding of the present and historical dynamics of northern environments, particularly when used in tandem with other biotic indicators. In the Boreal Shield and Hudson Plains of Canada, there have been limited modern floristic and faunistic surveys across the varying peatland environments, and those that exist are largely descriptive in nature (e.g., Sjörs 1959; Riley 2011). To our knowledge, there are no current studies on the diatoms living in the peatlands of northern Ontario, which include North America's largest continuous peatland, the Hudson Bay Lowlands.

Modern calibration or training sets explore the distribution of diatom assemblages from surface (i.e., modern) peat samples across a gradient of peat types and provide analogs that can be

used to infer past peat environments from downcore assemblages. Diatom-based calibration models are commonly applied to lake records to infer past environmental changes (Smol and Stoermer 2010), but have rarely been applied to peatland cores. In the few cases where inference models have been applied to diatom peatland records, these models were based on lake calibration sets (Campbell et al. 1997; Kiene et al. 1999; Brugam and Swain 2000), as peatland diatom calibration sets do not yet exist. Exploring modern diatom–bryophyte relationships, together with diatom responses across chemical and physical gradients among peat types, is an important step to gaining a more comprehensive knowledge of peatland developmental history, and possible responses to a changing climate.

The approach for collecting samples for a peatland diatom calibration set differs from the approach for a lake calibration set in a number of ways. Unlike lake sediment samples that represent an integration of all aquatic habitats within a lake (because of sediment focusing toward the center of the depositional basin), numerous samples are typically required to capture the variability in microtopography that exists within a given peatland. In peat calibration sets using testate amoebae, the full range of surface moisture variability is best represented by selecting peatlands that span the gradient from ombrotrophic to minerotrophic, and by sampling the microhabitats within each peatland (e.g., hummocks, hollows, pools) (Booth 2002). This sampling approach should also work best for capturing the full range of diatom microhabitats within peatlands; our methods have been adapted from testate amoebae calibration sets.

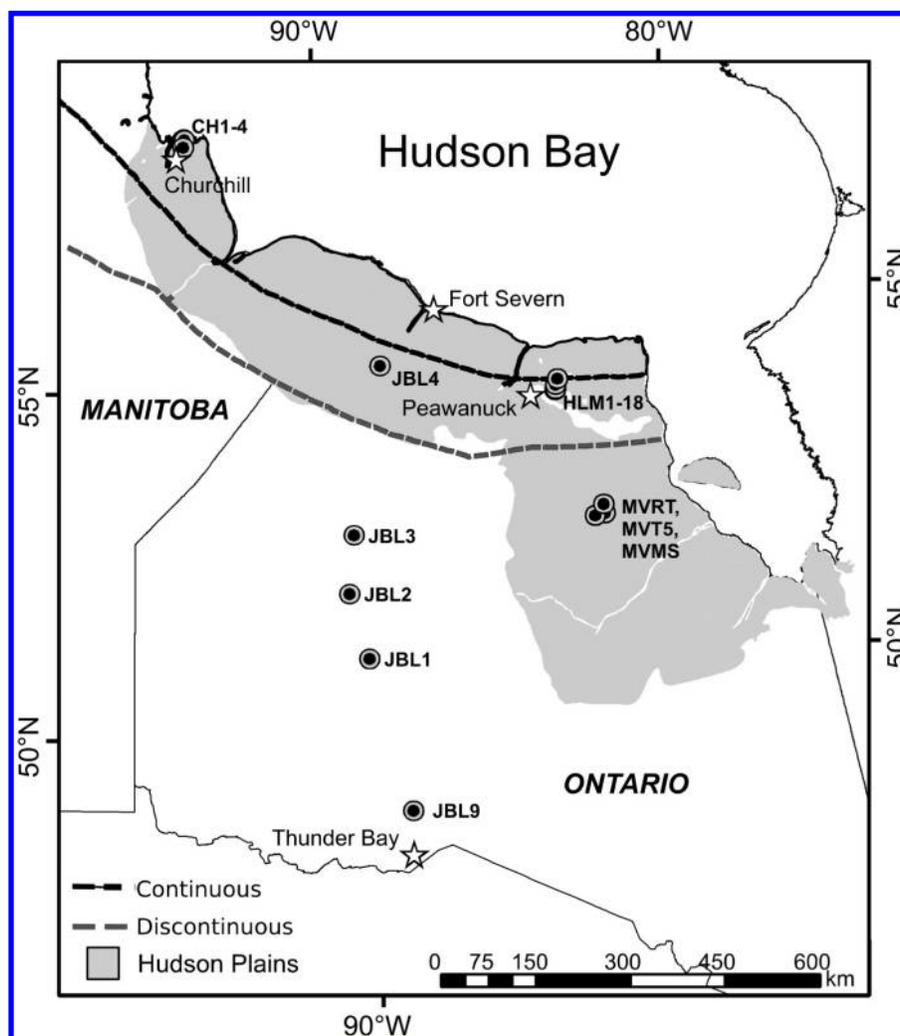
To gain insights into the ecological distribution of diatom taxa across the Boreal Shield of northern Ontario and into the Ontario and Manitoba Hudson Plains (a ~1200 km latitudinal transect), 113 surface peat samples were collected along wide vegetation (e.g., rich fen, poor fen, bog, and associated bryophytes), chemical (e.g., pH range from ~3 to 8), and moisture gradients. Key insights into the relative importance of taxon-specific relationships to either the chemical (pH) or the physical environment (e.g., moisture, and (or) specific vegetation types, *Sphagnum* spp. sensu Kingston 1982) will be central to this study. This study aims to assess the usefulness of diatoms as an environmental proxy for tracking climatic and hydroseral changes in peatlands in the Ontario Boreal Shield and Hudson Plains, Canada. Specifically, the study addresses the following questions: (1) Are there clear associations between diatom assemblages and peatland types? (2) What are the relationships between diatom associations and microhabitat differences observed in the peatlands? (3) Do these associations differ across ecozones (e.g., do fens in subarctic and Boreal Shield regions contain different assemblages)? If so, what are the main environmental variables that may explain these differences? (4) Is there a relationship between diatom species richness and differences in peat microhabitats (e.g., hummocks, hollows)? (5) Is there potential to develop calibration functions based on diatom assemblages to estimate past environmental conditions in peatlands, particularly hydrology?

Materials and methods

Site description

Surface peat samples were collected across a broad latitudinal gradient from northern Ontario near Thunder Bay in the Ontario Boreal Shield, and crossing the Hudson Bay Lowlands from James Bay in Ontario into northern Manitoba near Churchill (48°50' to 58°43'N and 83°55' to 93°50'W; Fig. 1). The study area spans two main ecozones within Canada known as the Boreal Shield and Hudson Plains (Ecological Stratification Working Group 1996; Fig. 1). The study sites cross a number of environmental gradients both within and across these ecozones including climate, permafrost, vegetation, and bedrock (Holmquist et al. 2014), and are discussed below.

Fig. 1. Locations of peatland sampling sites across Ontario and Manitoba, with the Hudson Plains and the southern limit of the continuous and discontinuous permafrost boundaries delineated.



The study region transitions from a continental to a marine climate, as well as from a temperate to a subarctic climate from the Boreal Shield to the Hudson Plains. The climate of the Hudson Plains is characterized by a humid, microthermal Arctic climate with relatively short, mild summers and long, cold winters (Martini 2006). Across the Hudson Plains, from south (southern James Bay region) to north (Churchill region), mean annual temperatures are $-1\text{ }^{\circ}\text{C}$ and $-5\text{ }^{\circ}\text{C}$, respectively, with mean daily winter minima reaching $-27\text{ }^{\circ}\text{C}$ in the south and $-30\text{ }^{\circ}\text{C}$ in the north (Martini 2006; McKenney et al. 2010; Holmquist et al. 2014). The climate of the Hudson Plains is influenced by both Arctic air masses that move south, and sea and fluvial currents that move counterclockwise in Hudson Bay resulting in a cooling effect along the western coasts of Hudson Bay and James Bay (Martini 2006). In Polar Bear Provincial Park, located on the western shores of Hudson Bay in Ontario, mean annual precipitation (1970–2000) is 519 mm and is predicted to increase to 542 mm over the next three decades (McKenney et al. 2010). West of the Hudson Plains, in the northern limits of the Boreal Shield Ecozone within Ontario, temperatures are similar to those of the southern James Bay region with a mean annual temperature (1970–2000) of $-1.7\text{ }^{\circ}\text{C}$, annual average temperature maxima of $23\text{ }^{\circ}\text{C}$ and minima of $-29\text{ }^{\circ}\text{C}$; mean annual precipitation however, is higher at 630 mm (McKenney et al. 2010). Compared with the rest of our study area, Thunder Bay (Ontario), where the most southern peatlands were

sampled, has warmer and longer summers, a higher mean annual temperature ($0.7\text{ }^{\circ}\text{C}$) and a greater mean annual precipitation (739 mm) (McKenney et al. 2010).

Boreal Shield Ecozone

The sampled peatlands within this region have been designated “JBL1”, “JBL2”, “JBL3”, and “JBL9” (Holmquist et al. 2014) and are situated on Precambrian Shield, composed primarily of granitic bedrock. Surficial deposits include extensive areas of bare rock with thin veneers of Laurentide till to variably thick deposits of till, glaciomarine and transgressive marine sediments, and glaciolacustrine sediments from glacial lakes Agassiz and Ojibway (Fulton 1995). Across this ecozone (part of the Canadian Shield physiographic region), permafrost is absent in the south and is sporadic at its northern limit. North-central Ontario (JBL1, JBL2, JBL3) is characterized by low ridges of clay and sand, and extensive peatlands in low-lying areas. Within this region of Ontario, forest cover is sparse ($\sim 21.4\%$) and more than 30% of the area is covered by wetlands (Crins et al. 2009). The depth of peat accumulation within these peatlands ranges between ~ 285 and 421 cm with estimated basal peat ages between ~ 6242 and 7835 (JBL3) cal. year. BP (Holmquist et al. 2014). The most southern peatland sampled in the Boreal Shield (JBL9), located just north of Lake Superior, has climatic differences between immediately adjacent areas of similar latitude, exhibiting a stronger boreal climate with lower mean

Table 1. Peatland sampling locations across Ontario and Manitoba, and corresponding latitude, longitude, elevation, and number of samples collected at each peatland.

Region	Province	Year	Peatland site code	Latitude (°N)	Longitude (°W)	Elevation (m a.s.l.)	No. of samples
Attawapiskat watershed	ON	2010	MVRT-01	52.8519	83.9242	87	1
	ON	2010	MVRT-02	52.8507	83.9252	124	3
	ON	2010	MVRT-03	52.8467	83.9272	83	1
	ON	2010	MVRT-04	52.8455	83.9272	78	2
	ON	2010	MVRT-05	52.8438	83.9285	78	3
	ON	2010	MVRT-06	52.8435	83.9285	81	2
	ON	2010	MVRT-07	52.8417	83.9263	82	1
	ON	2010	MVRT-08	52.8398	83.9303	53	1
	ON	2010	MVT5-01	52.7201	83.9426	87	2
	ON	2010	MVT5-02	52.7205	83.9431	84	2
	ON	2010	MVT5-03	52.7205	83.9418	89	2
	ON	2010	MVT5-04	52.7211	83.9390	87	2
	ON	2010	MVMS-01	52.7126	84.1752	104	4
	ON	2010	MVMS-02	52.7119	84.1743	103	3
	ON	2010	MVMS-03	52.7130	84.1753	102	2
Hawley Lake area	ON	2010	MVM-01	52.8502	83.9292	83	1
	ON	2011	HLM1-3	54.5992	84.6403	135	3
	ON	2011	HLM4-9	54.6100	84.6088	103	6
	ON	2011	HLM10-15	54.6771	84.5995	105	6
Churchill	MB	2008	CH1	58.7261	93.8416	18	4
	MB	2008	CH2	58.7343	93.8051	16	6
	MB	2008	CH3	58.7293	93.7937	17	20
	MB	2008	CH4	58.6181	93.8322	24	3
Boreal Shield	ON	2008	JBL1	51.0648	89.7926	371	6
	ON	2008	JBL2	52.0185	90.1313	362	8
	ON	2008	JBL3	52.8604	89.9293	270	5
Severn River watershed	ON	2008	JBL4	55.2692	88.9306	108	6
Boreal Shield	ON	2008	JBL9	48.8400	89.1200	488	6

annual temperatures (−1.7 to 2.1 °C) (Crins et al. 2009). This region of the Ontario Boreal Shield is distinct from more northern Boreal Shield sites (JBL1, JBL2, JBL3) due to temperature and precipitation gradients and associated changes in estimated net primary productivity (Crins et al. 2009). Further details on the JBL sites and their environmental setting are available from Holmquist et al. (2014).

Hudson Plains Ecozone

Peatlands were sampled in four regions of the Hudson Plains Ecozone (also known as the Hudson Bay Lowlands physiogeographic region, HBL): the Attawapiskat River watershed (MVRT, MVT5, MVMS), the Hawley Lake area (HLM1–18), the Severn River watershed (JBL4), and Churchill, Manitoba (CH1–4) (Table 1). The Hudson Plains contains steep transitions across sporadic, discontinuous and a narrow band of continuous permafrost close to the Hudson Bay coast and into Manitoba. The area just inland of Hudson Bay (MVRT, MVT5, MVMS, HLM peatlands) is characterized by discontinuous permafrost linked to peat plateaus in the north, and patterned bogs and fens (without permafrost) in the south (Tam et al. 2014). Basal dates from both a 256 cm long fen core and a 303 cm long bog core collected from the Attawapiskat watershed estimate that peatland accumulation began ~6700 years ago (Bunbury et al. 2012; O'Reilly et al. 2014). The lowlands located west of James Bay (JBL4 peatlands) are characteristic of open patterned bogs and ribbed and netted fens, underlain by sporadic permafrost. Wooded peat plateaus and palsa fields occur northward, with evident collapse features and initiation phases (Riley 2011). The peat in the JBL4 core was ~175 cm deep and had an estimated basal age of ~5570 cal. year BP (Holmquist et al. 2014). At the most northern site in the Manitoba region of the Hudson Plains (CH1–4 peatlands), broad areas of polygonal peat plateaus, immature fens, and shore fen and inter-ridge fen cover the landscape (Riley 2011). Initial stages of peat accumulation and palsa

development are typical of immature fens, with deeper peatlands maturing to peat plateaus (Riley 2011). The northern extent of the Hudson Plains contains continuous permafrost and the northward shift towards greater fen than bog peat reflects the cooler climate, which decelerates peat growth (Riley 2011). Although the basal ages for CH1–4 peatlands sampled in this study are not known, as they have not been ¹⁴C dated, a study by Dredge and Mott (2003) estimated the peatlands in this region to be slightly younger than northern Ontario peatlands with basal ages estimated between 3120 and 6280 years BP. Along the Hudson Bay coast, fens also rim the coastal freshwater marshes and cover the area slightly inland, which drains many of the major rivers of the Hudson Plains (Martini 2006). Bedrock of the Hudson Plains consists predominantly of sedimentary carbonate rock (dolostone and limestone), with some sandstone, shale, and siltstone, and is of Middle to Lower Silurian age (Ontario Geological Survey 1991). Much of the HBL was flooded by the post-glacial Tyrrell Sea marine incursion (Peltier and Andrews 1983; Dredge and Cowan 1989), which laid down silty clays of lacustrine or marine origin, and these deposits underlie peat sections of 2–3 m thickness (Fulton 1995).

Sample collection

From 2008 to 2011, 113 peat samples were collected from eight locations across the two large ecozones (Table 1, Fig. 1). In 2008, an extensive peatland survey (Holmquist et al. 2014) yielded a total of 64 surface peat samples from Ontario's Boreal Shield (samples within areas labeled JBL1, JBL2, JBL3, and JBL9 in Fig. 1), Ontario's northwestern Hudson Plains (JBL4 in Fig. 1), and the most northerly point of the Hudson Plains located near Churchill, Manitoba (CH1–4 in Fig. 1). These samples were collected using a steel knife, sealed in plastic sample bags, and stored in a cooler until transferred to a laboratory refrigerator. Water-table depth was measured with a meterstick several minutes after removing the

surface sample to allow recharge. For JBL2 and JBL7, pH was measured in the field using a handheld Fisher Scientific accumet pH and conductivity meter, calibrated at pH 4.0 and 7.0. For samples near Churchill, pH was measured in the field using an Ecotest pH2. The dominant vegetation collected with the sample was identified to the genus or species level. Sampling was organized so as to collect material from the range of water depths and peatland types encountered at each site.

In 2010, a total of 31 surface peat samples were collected from the Hudson Plains Ecozone in the area surrounding the Victor Diamond Mine, within the Attawapiskat River watershed (samples labeled MVRT, MVT5, MVMS; Table 1, Fig. 1). The sampling approach was designed to maximize our ability to capture the variability in the community across multiple scales in a given peatland. For example, when visiting these peatlands, sample points were organized along transects. At each point along the transect, samples were collected to capture variability across wetland mesoform types; however, at some sample points, only one mesoform type was present so only one sample was taken. At other sample points, multiple mesoform types were present in immediate proximity, so multiple samples were taken (e.g., MVRT-02 hummock, hollow, and pool habitats were present, and so individual samples were taken from each). Sample points where only one sample was taken were relatively uniform in terms of mesoform type on the scale of 1–3 m.

In 2011, 17 surface peat samples were collected from the Hawley Lake area within the Sutton River watershed (samples labeled HLM1–18; Table 1, Fig. 1). For both of these field sampling seasons (2010, 2011), a 10 cm × 10 cm × 10 cm of surface peat (i.e., peat sampling depth was 10 cm) was removed using a steel knife, placed in plastic Ziploc bags, and stored in coolers until they were transported to the laboratory cold room where they were kept at <10 °C until the samples were processed. If the water table was lower than 10 cm (the depth of the peat collection), the hole was deepened to allow measurement of the depth to the water table (DWT) and pH (using Hanna handheld pH meters that were calibrated with buffers at a pH of 4.0 and 7.0). Negative values were assigned to water-table depths that were above the vegetation surface (i.e., standing water was present and the collected sample was submerged). The dominant vegetation type at each microsite was determined by placing a 1 m² quadrat centered around the sample location and ranking the dominance of the vegetation (to the genus level) within this quadrat on a scale from 1 to 5.

Diatom sample preparation

At the Paleocological Environmental Assessment and Research Laboratory (PEARL), Queen's University, approximately 0.3 g of peat was digested in 10 mL of concentrated nitric acid (HNO₃) using a microwave digestion technique that is well-suited for digesting highly organic material such as peat samples (Parr et al. 2004). Digested samples were transferred from the Teflon tubes to glass scintillation vials. The resulting slurries were allowed to settle for 24 h, the supernatant was removed, and the sample was rinsed by adding deionized water. This procedure was repeated until the diatom samples approached circum-neutral pH. Slurries were concentrated by aspirating most of the water from the glass vials prior to making diatom strews. Concentrated strews were dried on cover slips and mounted onto microscope slides using the mounting medium Naphrax. Diatoms were identified to the lowest taxonomic level possible (often variety) using an assortment of taxonomic references, including Krammer and Lange-Bertalot (1986–1991); Camburn and Charles (2000); Kulikovskiy et al. (2010); Hamilton and Siver (2010); and Antoniadou et al. (2008). A minimum of 400 diatom valves were counted for each sample, unless diatoms were scarce and species richness was

low (<10 species), in which case a minimum of 200 valves were counted. Samples that yielded counts fewer than 200 diatom valves were not included in the data analyses. Photomicrographs of the most common diatom taxa, including diatom species identified as indicator taxa for each cluster, were constructed to increase taxonomic clarity and comparisons among researchers.

Data analysis

All statistical analyses were completed using CANOCO version 4.5 (ter Braak and Šmilauer 2002) and R version 2.11.1 (R Development Core Team 2010). The following R packages were used: (1) vegan (Oksanen et al. 2010) for transformations, canonical correspondence analysis (CCA) and associated permutation tests, (2) ade4 (Chessel et al. 2004; Dray et al. 2007) and mvpart (De'ath 2002) for a multivariate regression tree, and (3) labdsv to identify indicator species (Dufrene and Legendre 1997; Roberts 2010).

To eliminate rare taxa, a cutoff criterion of at least 1% relative abundance in at least one site was applied to the diatom data. To explore the distribution of diatoms among peatland habitats and to help visualize the differences and similarities amongst sites, we examined several methods of multivariate analyses, including a multivariate regression tree approach (MRT), indicator species analysis, and CCA.

Prior to clustering and indicator species analysis, diatom count data were converted to percent relative abundances and were Hellinger transformed to minimize the effects of the large number of zeroes that are common to species relative abundance data (Legendre and Gallagher 2001) and to give low weight to rare species. A MRT approach (De'ath 2002) was applied to allow for the inclusion of the two measured variables (DWT and pH). Strong environmental interactions between the diatom assemblages and each of the two variables were therefore modeled. The MRT technique employs Euclidean distance to summarize between-site differences in assemblage composition (De'ath 2002). The method identifies splits along measured environmental gradients that explain the greatest amount of variation in the species assemblages, and minimizes the sum of squared Euclidean distance (SSD) within the resultant groups. The indicator value method (Ind-Val; Dufrene and Legendre 1997) was then used to identify indicator diatom taxa within each of these groups of sites. Ind-Val is a method used to identify indicator species and species assemblages that characterize groups of samples (Dufrene and Legendre 1997). The indicator value of a species in a particular group of sites is the product of both specificity, which estimates to what extent a species is found only in one specific group, and fidelity, which measures what proportion of the sites of that specific group the species of interest is found in. The indicator value of a species is then the largest value found for that species among all groups identified in the study (Legendre and Birks 2012). A *p* value with a cut-off criterion of *p* ≤ 0.05 was used to select significant indicator diatom taxa and the Ind-Val values are reported for each species.

CCA using the program CANOCO, version 4.5 (ter Braak and Šmilauer 2002) was used to examine DWT, pH, and vegetation type in relation to the diatom data (including those diatoms not identified as significant indicator taxa in the Ind-Val analysis). Vegetation data were treated as nominal variables and transformed into an absence–presence matrix for each site and plotted passively (i.e., were treated as supplementary data) in the ordination analysis. Diatom percent relative abundance data were square-root transformed prior to applying this unimodal ordination method. For the JBL and Churchill samples, only one vegetation species was sampled (see Supplementary Table S1¹), whereas for all other samples from the Hudson Plains, dominant species within the 1 m² quadrat (ranked between 3 and 4) were given a “1” in the matrix. Species scores, site constraints (linear combinations

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjb-2014-0138>.

of the constraining variables), and supplementary vegetation data from the CCA analyses were plotted in the ordination with the sites and species identified based on the MRT groups.

Results

The study sites span broad gradients in pH (3.3 to 8.5) and DWT (−37 cm (water table above the vegetation surface) to 59 cm) (Supplementary Table S1¹). Across all peatland samples (including those excluded from diatom analyses), the mean pH value and DWT were 5.1 and 13 cm, respectively (Supplementary Table S1¹).

A total of 208 diatom taxa were identified from 32 genera. Photomicrographs of 20 common *Eunotia* taxa, and diatom species from 18 other genera are depicted in Figs. 2 and 3, respectively. Authorities for the common diatom species in this study are presented in Table 2. Diatoms were present in all but 20 surface peat samples where they were very rare or occurred in low abundances, although there was little evidence of dissolution in the few valves encountered (Supplementary Table S1¹). After eliminating these 20 samples, 93 surface peat samples were amenable for further data analyses. Approximately half (~10) of the surface peat samples that were removed from further data analysis were composed primarily of club lichen, specifically *Cladonia* P. Browne spp., and the other half removed were composed of the ribbed bog moss *Aulacomnium* Schwägr. Of the 93 peat samples with diatoms present, acidophilous and epiphytic taxa, mainly from the genera *Eunotia* (25 taxa) and *Pinnularia* (11 species) were best represented across peat samples, although not present in every sample. Cosmopolitan aerophilic diatom taxa (e.g., *Luticola mutica*, *Hantzschia amphioxys*, and *Pinnularia borealis*) were present across many peat samples, but were never the dominant species.

Based on cross validation within one SE, the best predictive model relating diatom assemblages to peatland habitats identified by the MRT analysis (De'ath 2002) was a model with five clusters (four splits) (Fig. 4a). This model therefore captures five distinct peatland habitats that were associated with distinct diatom assemblages. The MRT shows that pH is a more important variable than DWT at explaining diatom distributions across these peatland habitats, with a pH value of 5.5 identified as the critical threshold value splitting the classes of peatlands. This initial split in the MRT thus separates the diatom assemblages that occurred in highly acidic and bog-like sites from those found in the more pH-neutral fen-like sites (Fig. 4b). Clusters 1 to 5 follow a gradient of pH, with Clusters 1 and 2 containing the most acidic sites and Clusters 3 to 5 containing slightly alkaline to circum-neutral sites respectively. Following this first split, all preceding splits are defined based on DWT. There is an overlap in the DWT of Clusters 3 to 5 with Clusters 1 and 2, indicating that DWT was less distinct between peatland habitats (Fig. 4c). However, Cluster 1 contained the driest microhabitats, and Cluster 5 the wettest microhabitats. The mean pH value of Clusters 1 through 5 was 4.0, 4.2, 7.0, 6.8, and 6.1, and DWT was 34.2, 4.5, 22, 5.1, and −5.6 cm, respectively (Supplementary Table S1¹). Sites are not evenly distributed throughout the clusters, with approximately twice as many bog-like samples ($n = 61$) in Clusters 1 and 2 than fen-like samples ($n = 32$) in Clusters 3 to 5.

CCA axis 1 separated sites and species along the pH gradient and explained 65% of the diatom variation (Figs. 5a–5c). Cluster 4 sites are most strongly linked to a circum-neutral pH (and moderate surface wetness), composed largely of *Aulacomnium* and *Drepanocladus* (Müll. Hal.) G. Roth vegetation, and represented by more circum-neutral epiphytic diatom taxa (Figs. 5a–5c). CCA axis 2 separated sites and species along the DWT gradient, and explains 21% of the variation in diatom assemblage composition. This gradient distinguishes the driest, acidic sites of Cluster 1 from Cluster 2 and the wetter sites of Cluster 5 from Cluster 4 sites (Fig. 5a). *Cladina* spp. and *Sphagnum fuscum* (Schimp.) Klinggr. were the dominant vegetation types sampled for the Cluster 1 sites and *Sphagnum*

angustifolium (C.E.O. Jensen ex Russow) C.E.O. Jensen and *Sphagnum magellanicum* Brid. were the main vegetation types sampled in Cluster 2 sites. Although Cluster 3 sites and species scores have the greatest variability in pH and DWT, the largest overlap with sites in this group occurs with the hollow sites of Cluster 2 and the hummock sites of Cluster 1. It is difficult to identify Cluster 3 sites as belonging to one particular peatland type, and it is possible they represent an intermediate microhabitat between bog hollows and hummocks. The shrub *Chamaedaphne calyculata* (L.) Moench plots between the bog hollow and hummock sites in ordination space. Cluster 5 sites are distinct from other clusters and form a tight grouping in the bottom left quadrant of the CCA (Fig. 5a) and are associated with slightly acidic pH and higher DWT, and are mainly composed of sedges (Cyperaceae).

The number of significant indicator species ($p \leq 0.05$) increases substantially from Cluster 1 to Cluster 5 (Table 2). Bog-hummock sites of Cluster 1 ($n = 24$) were dominated almost exclusively by *Eunotia paludosa* (Fig. 2), and thus this diatom was the sole indicator species for Cluster 1. However, aerophilic taxa (e.g., *P. borealis*, *L. mutica*, *H. amphioxys*; Fig. 3) plot in the upper right quadrant of the CCA, closely tied to DWT or the low moisture levels associated with sites grouped in Cluster 1 (Fig. 5c). The bog-hollow Cluster 2 sites ($n = 37$) were represented by two significant indicator taxa: acidophilous and aerophilic *Eunotia mucophila* (van Dam et al. 1994) followed by marginally significant indicator *E. paludosa* var. *trinacria* ($p = 0.05$, Table 2, Fig. 2). The more acid-neutral sites in Clusters 3 to 5 had a greater diversity and abundance of diatoms that commonly co-occur across all sites within a cluster (Table 2). Cluster 3 ($n = 4$) contains five significant indicator species that had a wide spread in the CCA ordination space including: benthic fragilarioid taxa, *Auloseira subarctica*, *Eunotia exigua*, and *Gomphonema* cf. *bohemicum*, (Table 2; Figs. 2 and 3). Significant indicator species in Cluster 4 fen sites ($n = 19$) are largely epiphytic species that prefer acid-neutral conditions from the genera *Cymboplectura*, *Encyonema*, *Encyonopsis*, *Gomphonema*, and *Nitzschia* (van Dam et al. 1994; Fig. 3). However, many indicator taxa in this cluster have a wide range of tolerance for pH. Cluster 5 wet fen sites ($n = 9$) were mainly characterized by acidophilic *Eunotia* and *Tabellaria* indicator taxa (Table 2, Fig. 5c). Diatom species that plotted together in the CCA ordination space tended to be the same species the MRT identified as belonging to a specific cluster of the tree (Fig. 5c). The ordination visually demonstrates which diatom species, both indicator and non-indicator species, are more closely associated with a particular habitat and vegetation type.

Discussion

Diatoms are sensitive to the differing environmental conditions found in broad peatland types (bog, rich and poor fens) and microhabitats (hummocks, hollows) at both the Boreal Shield and Hudson Plains ecozone sites. This consistent environmental sensitivity at both the Boreal Shield and Hudson Plains ecozones demonstrates that diatoms have potential to be powerful paleo-ecological proxies of local peatland type and hydrological conditions. The five distinct peatland habitat types identified by MRT distinguish the diatom assemblages found in true bog sites from more fen-like sites, which is primarily based on pH differences between habitats. Subsequent habitat types are distinguished based on DWT. Both the MRT and CCA analyses identify pH as a more important variable than moisture in explaining the variation among diatom assemblages and distinguishing the peatland sites. The extreme environment of the dry, acidic bog sites contain depauperate diatom assemblages that are dominated by one or two species of *Eunotia*, whereas the wetter, less acidic fen sites support a relatively rich variety of diatom taxa.

The reported importance of pH versus moisture in structuring bryophyte and microorganism assemblages in peatlands varies across the literature. A critical pH value of 5.5 has been described

Fig. 2. Common *Eunotia* taxa encountered in northern Ontario peatlands. Image 1a–1f. *Eunotia paludosa*; 2a–2b. *Eunotia paludosa* morphotype 2; 3a–3b. *Eunotia paludosa* var. *trinacria*; 4a–4b. *Eunotia bilunaris*; 5a–5b. *Eunotia mucophila*; 6a–6b. *Eunotia fennica*; 7. *Eunotia implicata*; 8. *Eunotia argus*; 9a–9b. *Eunotia nymanniana*; 10. *Eunotia incisa*; 11. *Eunotia praerupta*; 12. *Eunotia serra*; 13. *Eunotia hexaglyphis*; 14a–14b. *Eunotia exigua*; 15. *Eunotia glacialis*; 16. *Eunotia flexuosa*; 17. *Eunotia pectinalis*; 18. *Eunotia lapponica*; 19. *Eunotia fallax*; 20a–20b. *Eunotia septentrionalis*.

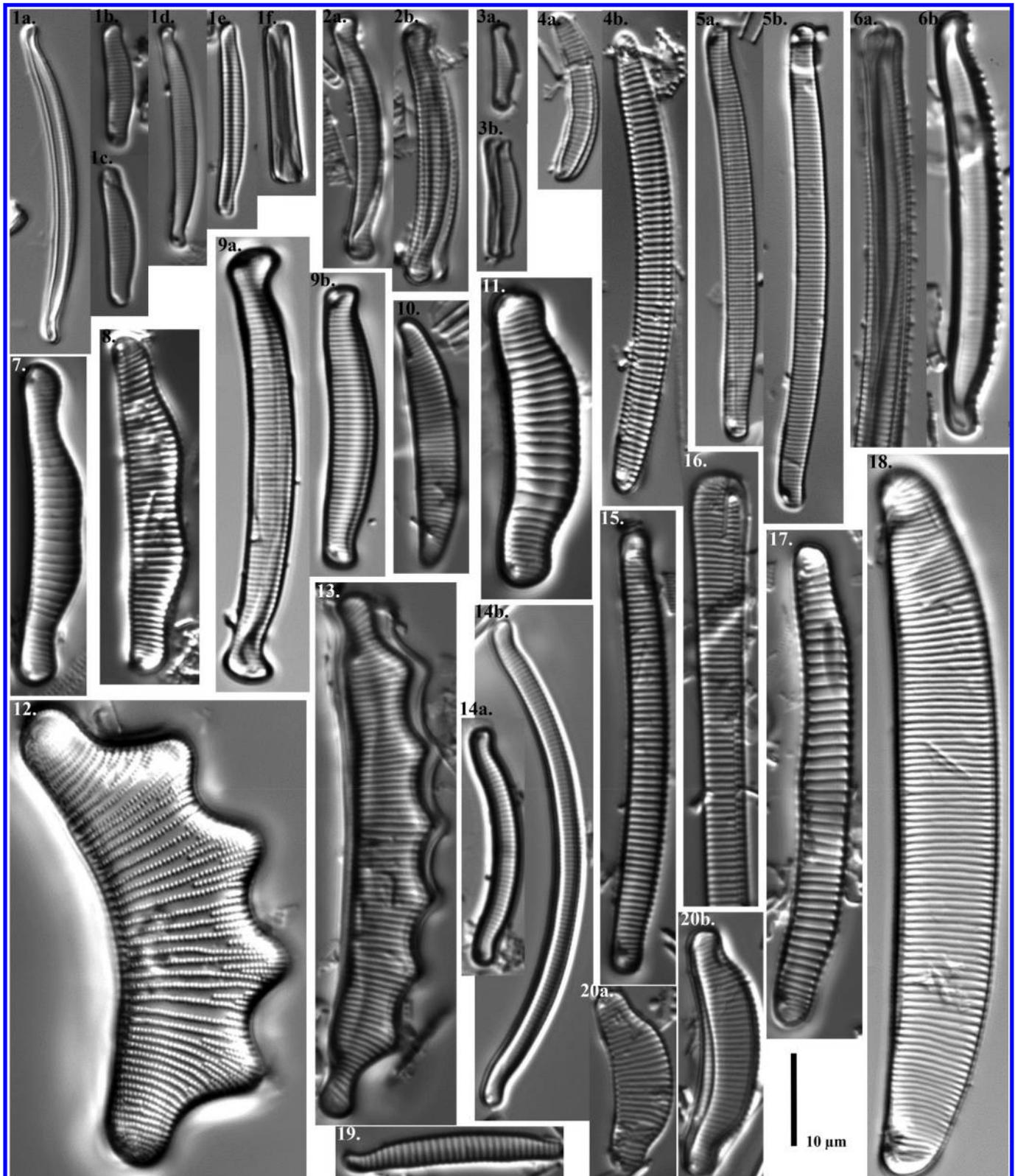


Fig. 3. Common diatom taxa found in northern Ontario peatlands. Image 1. *Rhopalodia gibba*; 2. *Epithemia adnata*; 3. *Brachysira brebissonii*; 4. *Caloneis undulata*; 5. *Caloneis tenuis*; 6. *Nitzschia alpina*; 7. *Nitzschia frustulum*; 8a–8c. *Nitzschia perminuta*; 9. *Hantzschia amphioxys*; 10. *Luticola mutica*; 11. *Encyonopsis descripta*; 12. *Chamaepinnularia mediocris*; 13. *Denticula kuetzingii*; 14. *Fragilaria ulna*; 15. *Encyonema silesiacum*; 16. *Encyonema paucistriatum*; 17. *Kobayasiella subtilissima*; 18. *Adlafia bryophila*; 19. *Gomphonema acuminatum*; 20. *Encyonema gracile*; 21. *Encyonopsis microcephala*; 22. *Achnanthisidium minutissimum*; 23. *Chamaepinnularia soehrensii*; 24. *Encyonema latens*; 25. *Aulacoseira subarctica*; 26. *Encyonema norvegicum*; 27. *Pinnularia borealis*; 28a–28b. *Gomphonema parvulum*; 29. *Gomphonema intricatum*; 30. *Gomphonema hebridense*; 31. *Gomphonema lagerheimii*; 32a–32b. *Gomphonema angustatum* var. *undulatum*; 33. *Gomphonema angustatum*; 34a–34b. *Gomphonema gracile*; 35. *Gomphonema* cf. *bohemicum*.

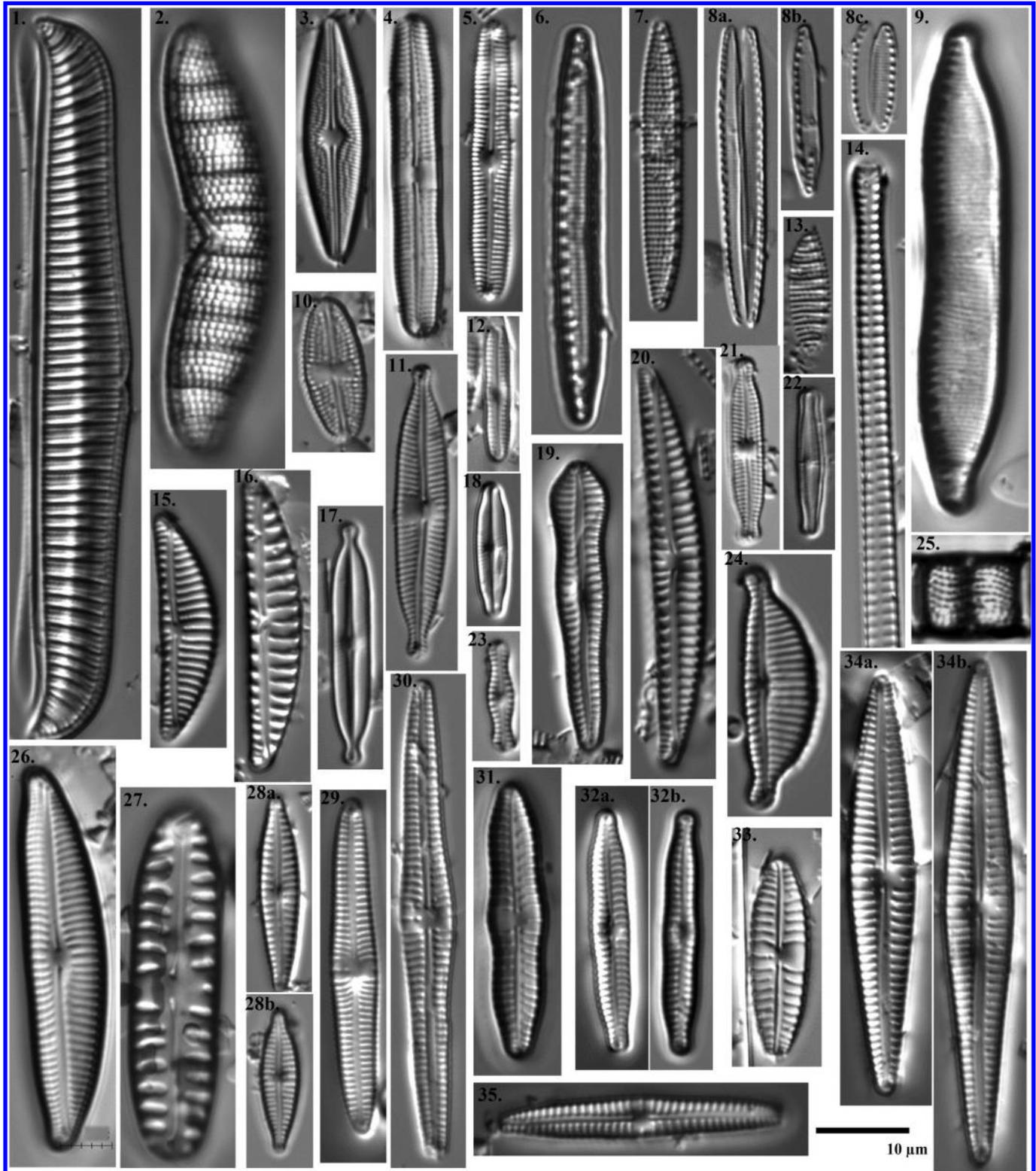


Table 2. Common diatom species (present in at least 1% relative abundance in one site) found in peatland habitats across the Ontario Boreal Shield and the Hudson Plains.

CCA Abbrev.	Diatom species	Indicator value	<i>p</i>	Mean % Clus.1	Mean % Clus.2	Mean % Clus.3	Mean % Clus.4	Mean % Clus.5
1	<i>Eunotia paludosa</i> A.Grunow	0.48	0.001	95.5	66.7	34.5	0.6	0.0
2a	<i>Eunotia mucophila</i> (H.Lange-Bertalot, M.Nörpel-Schempp & E.Alles) H.Lange-Bertalot	0.60	0.001	1.9	19.4	3.3	0.0	0.0
2b	<i>Eunotia paludosa</i> var. <i>trinacria</i> (Krasske) M.Nörpel & E.Alles	0.26	0.05	0.0	3.8	0.0	0.0	0.0
3a	<i>Aulacoseira subarctica</i> (O.Müller) E.Y.Haworth	0.20	0.035	0.5	0.3	4.7	0.2	0.0
3b	<i>Staurorsira construens</i> Ehrenberg	0.25	0.043	1.3	1.0	4.5	2.3	0.0
3c	<i>Eunotia exigua</i> (L.A.Brébisson) G.L.Rabenhorst	0.52	0.005	1.9	4.9	22.7	0.2	3.3
3d	<i>Staurorsirella pinnata</i> (Ehrenberg) Williams & Round	0.35	0.016	0.7	1.7	8.9	0.8	0.7
3e	<i>Gomphonema bohemicum</i> H.Reichelt & F.Fricke	0.23	0.041	0.0	0.0	3.7	0.4	0.0
4a	<i>Achnanthydium minutissimum</i> (Kützing) D.B.Czarnecki	0.72	0.001	0.0	0.7	8.4	23.9	0.0
4b	<i>Rossethidium peterseii</i> (Hustedt) Round & Bukhtiyarova	0.37	0.015	0.0	0.0	0.0	3.4	0.0
4c	<i>Cymbopleura angustata</i> (W.Smith) K.Krammer	0.32	0.015	0.0	0.0	0.0	3.4	0.0
4d	<i>Encyonema aueri</i> (Krasske) Krammer	0.21	0.009	0.0	0.0	0.0	3.7	0.0
4e	<i>Cymbella cistula</i> (Hemprich & Ehrenberg) Kirchner	0.19	0.04	0.0	0.0	1.5	2.3	0.0
4f	<i>Cymbopleura incerta</i> (Grunow) K.Krammer	0.57	0.001	0.0	0.2	0.0	7.9	0.0
4g	<i>Encyonema latens</i> (Krasske) D.G.Mann	0.32	0.019	0.0	0.0	0.0	2.1	0.0
4h	<i>Encyonopsis microcephala</i> (Grunow) Krammer	0.55	0.002	0.0	0.2	10.7	18.7	0.0
4i	<i>Encyonema paucistriatum</i> (Cleve-Euler) D.G.Mann	0.21	0.014	0.0	0.0	0.0	3.0	0.0
4j	<i>Encyonema silesiacum</i> (Bleisch) D.G.Mann	0.73	0.001	0.0	0.7	0.0	16.3	1.9
4k	<i>Cymbopleura subaequalis</i> (Grunow) K.Krammer	0.42	0.004	0.0	0.0	0.0	3.7	0.0
4l	<i>Denticula kuetzingii</i> Grunow	0.59	0.001	0.3	0.2	9.9	17.2	0.0
4m	<i>Diatoma tenuis</i> C.A.Agardh	0.31	0.026	0.0	0.0	3.4	4.9	0.0
4n	<i>Epithemia adnata</i> (Kützing) Brébisson	0.30	0.026	0.2	0.2	0.0	5.3	0.0
4o	<i>Fragilaria capucina</i> J.B.H.J.Desmazières	0.45	0.005	0.0	0.4	6.7	9.7	1.4
4p	<i>Fragilaria tenera</i> (W.Smith) H.Lange-Bertalot	0.82	0.001	0.2	0.5	1.5	14.0	0.0
4q	<i>Gomphonema acuminatum</i> C.G.Ehrenberg	0.29	0.025	0.0	0.2	0.0	5.6	1.3
4r	<i>Gomphonema angustatum</i> (F.T.Kützing) G.L.Rabenhorst	0.41	0.004	0.0	0.2	0.0	4.3	0.0
4s	<i>Gomphonema angustatum</i> var. <i>undulatum</i>	0.29	0.015	0.0	0.8	0.0	7.6	0.0
4t	<i>Gomphonema gracile</i> C.G.Ehrenberg	0.59	0.001	0.0	0.6	0.0	10.1	0.0
4u	<i>Gomphonema lagerheimii</i> A.Cleve	0.32	0.019	0.0	0.0	0.0	2.9	0.0
4v	<i>Adlafia bryophila</i> (J.B.Petersen) G.Moser, H.Lange-Bertalot & D.Metzeltin	0.37	0.013	0.0	0.0	0.0	3.9	0.0
4w	<i>Navicula cryptocephala</i> Kützing	0.72	0.001	0.0	0.2	4.3	14.6	0.0
4x	<i>Navicula cryptotenella</i> Lange-Bertalot	0.24	0.026	0.0	0.2	0.0	2.2	0.0
4y	<i>Sellaphora pupula</i> (Kützing) Mereschkovskiy	0.29	0.024	0.0	0.4	1.5	3.0	0.0
4z	<i>Navicula radiosa</i> Kützing	0.63	0.001	0.0	0.0	0.0	5.7	0.0
4i	<i>Navicula tuscula</i> (Ehrenberg) Grunow	0.42	0.004	0.0	0.0	0.0	2.5	0.0
4ii	<i>Nitzschia frustulum</i> (Kützing) Grunow	0.46	0.002	0.0	0.3	0.0	6.0	0.0
4iii	<i>Nitzschia intermedia</i> Hantzsch ex Cleve & Grunow	0.47	0.002	0.0	0.0	0.0	4.5	0.0
4iv	<i>Nitzschia linearis</i> W.Smith	0.37	0.007	0.0	0.2	2.1	5.5	0.0
4v	<i>Nitzschia perminuta</i> (Grunow) M.Peragallo	0.65	0.001	0.0	2.0	8.6	54.7	14.9
4vi	<i>Rhopalodia gibba</i> (Ehrenberg) O.Müller	0.25	0.026	0.0	0.1	0.0	3.0	0.0
4vii	<i>Stauroneis phoenicenteron</i> (C.L.Nitzsch) C.G.Ehrenberg	0.28	0.04	0.3	0.2	2.1	4.7	3.5
5a	<i>Brachysira brebissonii</i> R.Ross	0.51	0.003	0.0	1.5	0.0	0.0	16.2
5b	<i>Brachysira hofmanniae</i> H.Lange-Bertalot	0.22	0.05	0.0	0.0	0.0	0.0	1.8
5c	<i>Caloneis tenuis</i> (Gregory) Krammer	0.40	0.004	0.0	0.0	0.0	2.7	6.5
5d	<i>Encyonema gracile</i> Rabenhorst	0.76	0.002	0.0	0.2	0.0	2.9	18.6
5e	<i>Eunotia arcus</i> C.G.Ehrenberg	0.31	0.005	0.0	0.0	0.0	0.4	5.1
5f	<i>Eunotia argus</i> C.G.Ehrenberg	0.76	0.001	0.0	0.0	0.0	0.3	12.5
5g	<i>Eunotia bilunaris</i> (C.G.Ehrenberg) J.Schaarschmidt	0.58	0.003	1.1	2.0	2.4	2.4	14.8
5h	<i>Eunotia faba</i> (C.G.Ehrenberg) A.Grunow	0.54	0.001	0.0	0.1	0.0	0.0	4.4
5i	<i>Eunotia fallax</i> A.Cleve	0.33	0.022	0.0	1.3	0.0	0.0	3.9
5j	<i>Eunotia flexuosa</i> (Brébisson ex Kützing) Kützing	0.70	0.002	0.0	0.7	0.0	0.3	9.3
5k	<i>Eunotia glacialis</i> F.Meister	0.85	0.001	0.0	0.2	0.0	2.6	16.0
5l	<i>Eunotia hexaglyphis</i> C.G.Ehrenberg	0.67	0.001	0.0	0.0	0.0	0.0	5.9
5m	<i>Eunotia incisa</i> W.Smith ex W.Gregory	0.67	0.002	0.0	0.0	0.0	0.0	13.9
5n	<i>Eunotia maior</i> (Smith) Rabenhorst	0.33	0.007	0.0	0.0	0.0	0.0	3.3
5o	<i>Eunotia naegelli</i> Migula	0.43	0.006	0.0	0.1	0.0	0.0	3.8
5p	<i>Eunotia nymanniana</i> Grunow	0.42	0.007	0.3	3.7	0.0	2.5	11.4
5q	<i>Eunotia paludosa</i> morphotype 2 sensu lato Hamilton and Siver 2010	0.54	0.004	0.4	3.4	3.7	2.6	15.2
5r	<i>Eunotia pectinalis</i> (Kützing) Rabenhorst	0.32	0.01	0.0	0.0	1.5	0.2	4.3
5s	<i>Eunotia praeurupta</i> C.G.Ehrenberg	0.84	0.001	0.0	0.0	0.0	3.8	19.5
5t	<i>Eunotia septentrionalis</i> E.V.Østrup	0.85	0.001	0.0	0.8	0.0	0.0	16.5
5u	<i>Eunotia serra</i> C.G.Ehrenberg	0.56	0.001	0.0	0.0	0.0	0.0	5.7
5v	<i>Fragilaria ulna</i> (C.L.Nitzsch) H.Lange-Bertalot	0.64	0.001	0.3	0.6	2.4	2.2	13.6

Table 2 (concluded).

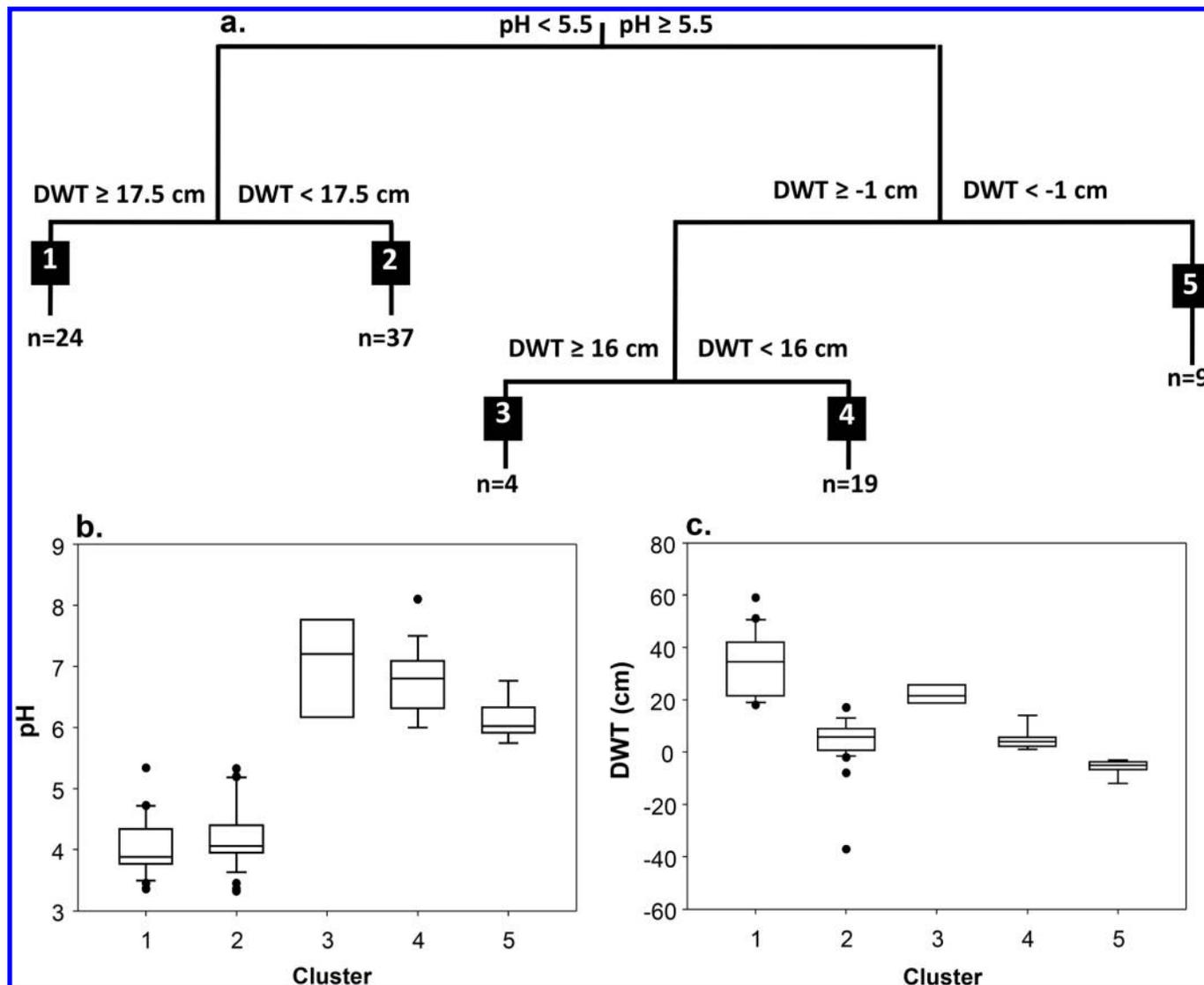
CCA		Indicator	Mean %	Mean %	Mean %	Mean %	Mean %	
Abbrev.	Diatom species	value	<i>p</i>	Clus.1	Clus.2	Clus.3	Clus.4	Clus.5
5w	<i>Frustulia rhomboides</i> (Ehrenberg) De Toni	0.57	0.003	0.3	1.6	1.7	0.3	23.5
5x	<i>Gomphonema intricatum</i> Kützing	0.72	0.001	0.0	0.1	0.0	0.6	9.3
5y	<i>Gomphonema parvulum</i> (Kützing) Kützing	0.64	0.001	0.0	0.0	1.5	2.1	9.0
5z	<i>Diadesmis gallica</i> (W.Smith) Lagerstedt	0.33	0.014	1.2	0.1	2.1	0.6	6.2
5i	<i>Chamaepinnularia mediocris</i> Krasske	0.53	0.002	0.0	1.1	2.4	0.0	13.5
5ii	<i>Chamaepinnularia soehrensensis</i> Krasske	0.55	0.001	0.3	1.1	0.0	0.0	6.5
5iii	<i>Pinnularia divergens</i> W.Smith	0.29	0.012	0.0	0.1	0.0	0.3	2.9
5iv	<i>Pinnularia microstauron</i> (C.G.Ehrenberg) P.T.Cleve	0.27	0.05	0.9	0.8	2.4	0.9	4.5
5v	<i>Pinnularia streptoraphe</i> P.T.Cleve	0.72	0.001	0.0	0.4	0.0	0.3	7.5
5vi	<i>Tabellaria fenestrata</i> (H.C.Lyngbye) F.T.Kützing	0.67	0.001	0.0	0.0	0.0	0.0	7.2
5vii	<i>Tabellaria flocculosa</i> (A.W.Roth) F.T.Kützing	0.70	0.001	0.7	0.4	3.3	2.1	24.8
5viii	<i>Tabellaria flocculosa</i> var. <i>linearis</i> J.D.Koppen	0.67	0.001	0.0	0.0	0.0	0.0	15.4
6	<i>Aulacoseira</i> spp. Thwaites			1.5	0.9	3.3	1.1	0.7
7	<i>Aulacoseira ambigua</i> (Grunow) Simonsen			0.0	0.3	0.0	0.0	0.0
8	<i>Brachysira zellensis</i> (Grunow) Round & D.G.Mann			0.2	0.2	4.4	3.4	12.0
9	<i>Caloneis bacillum</i> (Grunow) Cleve			0.0	0.2	0.0	0.0	0.0
10	<i>Caloneis molaris</i> (Grunow) Krammer			0.0	0.0	0.0	3.4	0.0
11	<i>Caloneis undulata</i> (Gregory) Krammer			0.0	0.0	0.0	1.6	2.5
12	<i>Encyonopsis descripta</i> (Hustedt) Krammer			4.4	0.0	4.0	4.7	0.0
13	<i>Cymbopleura lapponica</i> (Grunow) K.Krammer			0.0	0.0	4.3	4.1	0.0
14	<i>Encyonema minutum</i> (Hilse) D.G.Mann			0.0	0.1	5.2	6.4	3.9
15	<i>Cymbella naviculacea</i> Grunow			0.0	0.0	0.0	0.4	3.4
16	<i>Cymbopleura naviculiformis</i> (Auerswald ex Heiberg) K.Krammer			0.0	0.0	0.0	0.4	0.0
17	<i>Encyonema norvegicum</i> (Grunow in A.Schmidt et al.) Bukhtiyarova			0.0	0.2	1.5	4.7	1.4
18	<i>Cymbella subarctica</i> Cleve-Euler			0.0	0.0	0.0	0.6	0.0
19	<i>Eunotia arculus</i> Lange-Bertalot & M.Nörpel			0.0	0.0	0.0	0.0	1.4
20	<i>Eunotia femica</i> (Hustedt) H.Lange-Bertalot			0.0	7.9	2.9	0.0	0.4
21	<i>Gomphonema subtile</i> Ehrenberg			0.0	0.0	0.0	0.4	0.0
22	<i>Eunotia implicata</i> M.Nörpel, E.Alles & H.Lange-Bertalot			0.0	0.0	0.0	0.0	3.6
23	<i>Eunotia lapponica</i> A.Grunow			0.3	2.9	0.0	0.0	0.0
24	<i>Pseudostaurosira brevistriata</i> (Grunow) Williams & Round			0.4	0.2	0.0	0.0	0.0
25	<i>Gomphonema amoenum</i> H.Lange-Bertalot			0.0	0.0	0.0	0.8	0.0
26	<i>Gomphonema angustum</i> C.A.Agardh			0.2	0.0	0.0	1.1	0.0
27	<i>Gomphonema clavatum</i> C.G.Ehrenberg			0.0	0.0	0.0	0.3	0.0
28	<i>Gomphonema hebridense</i> W.Gregory			0.0	0.0	0.0	0.6	0.0
29	<i>Gomphonema longiceps</i> C.G.Ehrenberg			0.0	0.0	0.0	0.4	0.0
30	<i>Hantzschia amphioxys</i> (Ehrenberg) Grunow			3.9	4.9	5.6	7.5	0.0
31	<i>Navicula eidrigiana</i> J.R.Carter			0.0	0.0	0.0	0.9	0.0
32	<i>Navicula festiva</i> Krasske			0.0	1.5	0.0	0.0	0.0
33	<i>Kobayasiella jaegii</i> (Meister) H.Lange-Bertalot			0.0	0.0	0.0	1.5	1.7
34	<i>Navicula lanceolata</i> (Agardh) Edrenberg			0.0	0.0	0.0	0.7	0.0
35	<i>Luticola mutica</i> (Kützing) D.G.Mann			3.9	4.8	2.6	5.4	1.8
36	<i>Navicula peregrina</i> (Ehrenberg) Kützing			0.0	0.0	3.7	2.6	0.0
37	<i>Navicula rhynchocephala</i> Kützing			0.0	0.2	0.0	0.8	0.0
38	<i>Navicula striolata</i> (Grunow) Lange-Bertalot			0.0	0.0	0.0	1.3	0.0
39	<i>Kobayasiella subtilissima</i> (Cleve) H.Lange-Bertalot			1.9	36.2	48.3	1.3	22.6
40	<i>Navicula viridula</i> (Kützing) Ehrenberg			0.0	0.0	3.0	3.6	0.0
41	<i>Navicula vulpina</i> Kützing			0.0	0.0	0.0	0.6	0.0
42	<i>Neidium</i> spp. Pfitzer			0.0	0.0	0.0	0.8	0.4
43	<i>Nitzschia alpina</i> Hustedt			0.3	0.0	3.0	1.4	0.0
44	<i>Pinnularia biceps</i> W.Gregory			1.0	0.1	0.0	0.0	0.0
45	<i>Pinnularia borealis</i> C.G.Ehrenberg			1.3	2.8	3.9	4.3	0.0
46	<i>Pinnularia gibba</i> Ehrenberg			0.0	0.6	0.0	0.0	1.1
47	<i>Pinnularia interrupta</i> W.Smith			1.8	0.5	1.5	0.0	0.5
48	<i>Pinnularia maior</i> (Kützing) Cleve			0.0	3.7	0.0	0.4	0.6
49	<i>Pinnularia</i> cf. <i>microstauron</i> (small size)			2.1	0.6	0.0	0.0	0.0
50	<i>Pinnularia rupestris</i> Hantzsch			0.0	2.3	0.0	0.3	0.0
51	<i>Pinnularis supcapitata</i> W.Gregory			0.5	0.4	0.0	0.0	0.0

Note: The numbers in the first column refer to diatom taxa that were identified by the indicator value method (Ind-Val) (i.e. diatom indicator species) for each cluster (Clus.) of the Multivariate Regression Tree up until 5viii. Species numbers below the horizontal line (6–51) refer to diatom taxa not identified as an indicator species by Ind-Val, but that were included in the canonical correspondence analysis (CCA) ordination plot (Fig. 5c). Ind-Val indicator value, associated *p* value, and mean percent relative abundance of each species in each cluster are also included in the table.

previously for explaining the separation of brown mosses (higher pH) and *Sphagnum* spp. (lower pH) abundances (Gignac and Vitt 1990), as well as for the separation of acidophilous taxa within diatom (Battarbee et al. 2010) and chrysophyte (Smol 1995) lake

calibration sets. Generally, many *Sphagnum* species have optima within a small pH range, but have broader tolerances to water-table depth (Booth 2002), whereas brown mosses have a relatively wide range in pH and water-table depth. In contrast to testate

Fig. 4. (a) Multivariate regression tree (MRT) for the diatom assemblages from the 93 surface peat data set with the measured environmental variables pH and depth to water table (DWT). For each cluster, the number of samples (n) are identified below. (b) and (c) Boxplots of pH and DWT organized by MRT cluster.



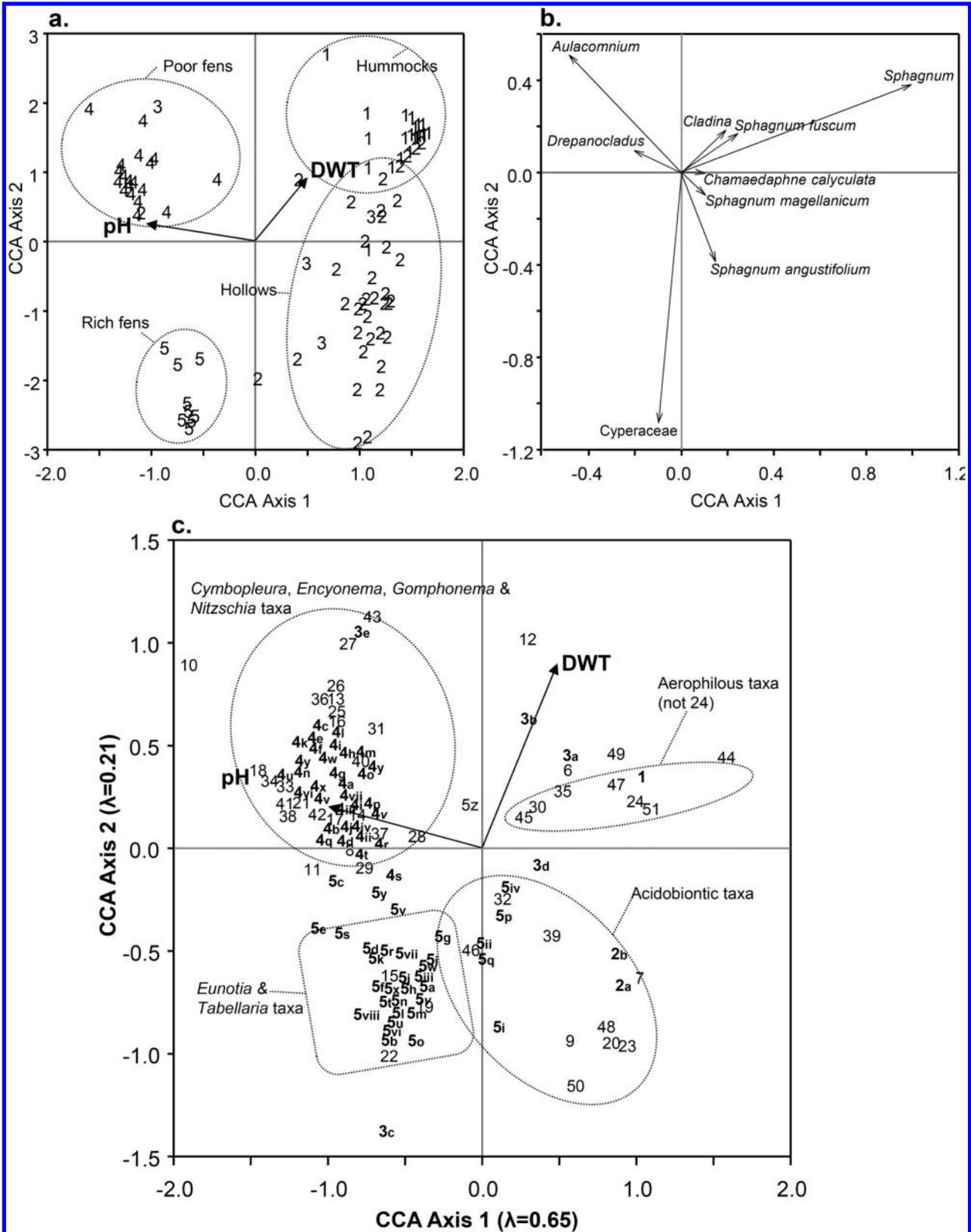
amoebae, a common microorganism found in peat environments that has been shown to be sensitive to moisture (e.g., Booth 2002; Charman et al. 2007), diatoms respond sensitively to both physical (e.g., vegetation type, moisture) and chemical (e.g., pH and nutrients) environmental factors. It is thus not surprising that there have been variable findings regarding diatom distributions across peat environments, with reports of moisture being the primary gradient influencing diatom assemblages in some studies (Chen et al. 2012) and water chemistry, especially pH, being important in other studies (Pouličková et al. 2004; Fránková et al. 2009). In our study, although somewhat limited in terms of measured variables, diatoms appear to respond primarily to pH and secondarily to moisture, regardless of the dominant bryophyte type. It is important to note that DWT measurements are more likely to vary through the year and between years depending on changes in hydrology (e.g., precipitation, runoff, etc.), and thus pH is probably a more consistent and reliable measurement to base inferences. Nevertheless, it is likely that both are important as some microhabitats (e.g., bog sites) contain diatom species that are able to withstand both a dry and a very acidic environment, indicating that they are both aerophilic and acidophilous.

Habitats with depauperate diatom flora

The dry bog hummock environments across our study region contained depauperate diatom flora that were typically dominated by one or two *Eunotia* species (*E. paludosa* and (or) *E. mucophila*). These diatom species are likely tolerant of both the extreme dry and acidic conditions of this peat habitat. The lack of species-rich assemblages, and in some cases the complete absence of diatoms from certain peat deposits, have been noted in other studies and is likely due to a variety of reasons including harsh (i.e., dry) environments unsuitable for diatom survival, low availability of silica that limits growth, and (or) taphonomic processes that may lead to the dissolution of siliceous diatom valves. In environments with these conditions, diatoms may be a difficult proxy to examine within peat deposits, and their absence during certain portions of peat cores do pose problems for paleoecological reconstructions. However, this study demonstrates that diatoms are highly sensitive to the main chemical gradients across peat habitats and, when present, could be a valuable supplementary biological proxy for inferring environmental changes in peatlands.

Of the 20 samples in which diatoms were absent or occurred in very low abundances (Supplementary Table S1¹) in this study,

Fig. 5. Canonical correspondence analysis (CCA) ordination plots for: (a) sites scores with numbers representing multivariate regression tree clusters; (b) supplementary vegetation data for the dominant vegetation sampled at each site; and (c) diatom species scores with significant species for each cluster **bolded**. Species scores are represented with numbers, letters, and Roman numerals and the corresponding names can be found in Table 2. DWT, Depth to water table.



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10 were composed primarily of club lichen, specifically *Cladonia* spp. In the Hudson Plains, *Cladonia* is often indicative of the extensive permafrost peatlands called peat plateaus and palsas where the hummocks typically freeze (Riley 2011). The freezing of hummocks draws down water, minimizing surface water availability and resulting in very dry and possibly silica-depleted environments. The remaining 10 peat samples with insufficient diatoms were collected from fens in the northern-most part of the study region near Churchill (Manitoba) and one sample from a rich fen near Hawley Lake (Ontario). Interestingly, these sites would not be considered environmentally harsh (pH and moisture) for the growth of diatoms as they were circum-neutral to slightly alkaline. Unlike the *Cladonia*-dominated bog samples, they did not experience extreme dry conditions as the water tables were higher. Given that the physical and chemical environments from these particular samples should be suitable for diatoms to occur, it is not clear why diatoms are sparse or absent within these samples. It is possible that diatom valves did not preserve at these sites because dissolution and solubility of silicate minerals (including diatom valves) is greatly enhanced under environments that are anoxic and highly organic with a circum-neutral pH (Bennett et al. 1991), conditions that may occur seasonally within these fen peat habitats. However, there was no evidence of etched valves, which may occur with silica dissolution.

Bog-hummock microhabitats

The driest (mean DWT = 34 cm) and most acidic (mean pH value = 4.0) peatland habitats that contained diatoms (i.e., Cluster 1, $n = 24$) were dominated by *Sphagnum*, particularly *S. fuscum*. This species is commonly found in dense hummocks in boreal regions (Bauer et al. 2007). All of our bog hummock microhabitat samples contained depauperate diatom floras that were dominated by one particular species: *Eumotia paludosa*. Diatom communities associated with the specific bryophyte *S. fuscum* have not been studied previously, but *E. paludosa* has been documented to be associated with other *Sphagnum* species such as *S. fibriatum* in Hungary (Buczko 2006) and *S. papillosum* in the Czech Republic (Pouličková et al. 2004). Although this association between *Sphagnum* and *E. paludosa* has been reported in the literature, it is still unclear whether this diatom species is truly “bryophytic/sphagnophilous”, or has a preference for the acidic and dry habitats that are closely linked to *Sphagnum* hummocks (Kingston 1982; De Vries 1984; Van de Vijver and Beyens 1997; Pouličková et al. 2004; Novakova and Pouličková 2004; Buczko 2006). De Vries (1984) noted that, although *E. paludosa* was dominant in the ombrotrophic habitat of emerged (i.e., dry) peat moss (mean pH value was 3.1), it was also present (but not dominant) in *Sphagnum* zones occurring above the water table of fen lakes, irrespective of the floral composition of their aquatic habitats. This suggests that the species may be more closely linked to the dry and acidic habitat provided by *Sphagnum* mosses.

Aside from *E. paludosa* and *E. paludosa* var. *trinacria*, we were also able to distinguish a third form of *E. paludosa* in our samples (Fig. 2) that Hamilton and Siver (2010) named *E. paludosa* morphotype 2, based on its larger size and more prominent striae. This taxon was identified as a significant indicator taxon for Cyperaceae-dominated rich fens (i.e., Cluster 5). Aside from reports of multiple forms of *E. paludosa*, large variations in cell size have also been attributed to differences in microhabitat moisture. For example, dry habitats can limit sexual reproduction and associated cell size restoration and (or) small-sized diatoms can acclimate to moisture-limited habitats owing to their high resources absorption efficiencies (Chen et al. 2012). In our study, *E. paludosa* morphotype 2 was present in the drier microhabitats within rich fen sites, similar to that observed in the fen sites studied by De Vries (1984).

It is likely that the dominance of *E. paludosa* in dry, acidic, bog habitats stems from the fact that *Sphagnum* species are able to

retain moisture through capillarity, and that *E. paludosa* secretes a copious external sheath (Beyens 1985; Chen et al. 2012). *Sphagnum fuscum* and other *Sphagnum* species provide the greatest competitive microhabitat for this diatom species and allow it to resist periods of desiccation.

Although *E. paludosa* is often the dominant taxon in dry, acidic bog environments, it may also occur in a variety of peat habitats that are not necessarily dominated by *Sphagnum* species. In these less extreme peat habitats, other acidophilous and aerophilous diatoms will be able to compete and may therefore be better indicator taxa. For example, in this study *E. paludosa* co-occurs with widespread euterrestrial (present in environments/soils that periodically dry out) species, albeit in low relative abundances: *Hantzschia amphioxys*, *Luticola mutica*, and *Pinnularia borealis* (Johansen 2010; Gaiser and Rühland 2010; Fig. 5c). Aside from these aerophilous taxa, *E. paludosa* was also found to co-occur with *Pinnularia rupestris* and *Achnanthes lanceolata* in Czech Republic peatlands (Pouličková et al. 2004), and with *E. exigua* in sub-Antarctic mosses (Van de Vijver and Beyens 1997). All three of these taxa are found mainly in water bodies, but also occur regularly on wet and moist places, suggesting they are tolerant of some drying or emergent environments (van Dam et al. 1994). Although we consider the samples with close to 100% abundance of *E. paludosa* to be the driest microhabitats in this study, other diatom peatland studies with even drier microhabitats have reported dominance by euterrestrial diatom species (Van de Vijver and Beyens 1997). This is also true for coastal marshlands, where Gaiser et al. (1998, 2001) found that *L. mutica*, *P. borealis*, and *H. amphioxys* are diatoms that can withstand the shortest hydroperiod or time without flooding. In our peat samples, it is possible that the hummock sites were too acidic for these particular euterrestrial diatom species to dominate. For example, although *H. amphioxys* is considered to have a circum-neutral pH optimum (van Dam et al. 1994) and a broad pH tolerance, it is rarer in acidic soils and reaches high densities in dry, neutral to slightly alkaline soils (Johansen 2010). Additionally, the low abundance or absence of common euterrestrial species has also been attributed to lack of sufficient mineral material (Lund 1945; Van de Vijver and Beyens 1998, 1999).

Bog-hollow microhabitats

Wet, acidic bog sites in our study (i.e., Cluster 2 identified by the MRT analysis) differ from the dry, acidic bog sites described above (i.e., Cluster 1) in that they have a water table closer to the vegetation surface (mean DWT = 4.5 cm). The less extreme periodic drying in these sites will likely provide a more amenable environment for diatoms to grow than bog-hummock microhabitats. Despite the relatively large number of peat samples ($n = 37$) containing a greater variety of vegetation types (e.g., *Carex* spp., *S. angustifolium*, *S. magellanicum*), these samples share only two diatom indicator species, dominant across the 36 samples: *E. mucophila* and *E. paludosa* var. *trinacria* (Table 2). This suggests that, although these wetter microhabitats were not as harsh as the raised bog-hummock microhabitats (Cluster 1), they are nevertheless challenging environments for diatom survival.

It is plausible that *E. mucophila* and *E. paludosa* var. *trinacria* occur in these microhabitats because the pH level and mineral content is optimal for their survival, and their association to these bryophyte species occurs because of overlap in their ranges of pH and moisture tolerance. Alternatively, bog-hollow microhabitats may not be optimal conditions for these diatom species, but they are still capable of outcompeting other diatom taxa in dry and acidic environments. It is possible that *E. mucophila* and *E. paludosa* are opportunists for these particularly harsh peat environments and thus occur at abundances close to 100%, but can also survive in other less acidic and dry environments where they are found at lower abundances in this study. *Sphagnum angustifolium*, often associated with *S. magellanicum*, is found in poor fen lawns, the hol-

lows of bogs, and open bog pools with discontinuous permafrost, but rarely grows in carpets and on bog hummocks sampled in Cluster 1 (Bauer et al. 2007; Riley 2011). Given the higher water table, and that the dominant bryophytes sampled in this study tend to grow in more moist environments, the diatom species identified in Cluster 2 are indicative of the hollow microhabitats found within bogs, but likely do not have a particular affinity to a given bryophyte type as these diatoms were found in association with all vegetation types within these acidic (pH < 5.5) bog samples.

Cluster 2 samples are distinguished from Cluster 1 samples by the appearance and high abundances of the rarely cited but morphologically distinct *E. mucophila*. Our study suggests that *E. mucophila* maintains a close association to particular *Sphagnum* species found growing in bog hollows due to overlap in pH and moisture preferences. For example, this species was found in our habitats with pH values of about 4.2, and *S. angustifolium* and *S. magellanicum* have reported narrow pH optima, often between 3.6 and 4.0 (Booth 2002). When identified, *E. mucophila* has been found in a fen dominated by *S. angustifolium* (Buczkó 2006), and in association with *Sphagnum* species but independent of the moisture regime (Pouličková et al. 2004). In general, bog diatoms in our study are responding to chemical cues in their environment, and secondarily to changes in moisture regime, both of which can influence the moss communities. Similar to what we suggest for the two diatom taxa, *E. paludosa* and *E. mucophila*, Hájková et al. (2011) found for the entire diatom assemblage that the highest proportion of diatom variation was explained by water chemistry rather than bryophyte characteristics.

In our northern Ontario peatland sites, other diatom species that also show possible associations to peat hollow microhabitats include *Eunotia lapponica*, *E. fennica*, and *Caloneis bacillum*. These species were often found to co-occur with *E. mucophila* and may be other potential indicator species for hollow microhabitats. Similar to this study, *E. lapponica* has previously been found to co-occur with *E. mucophila* and was associated with bogs containing *S. angustifolium*, as well as *Carex* by Buczkó (2006) and Chen et al. (2012). *Eunotia fennica* is also commonly found in *Sphagnum* ponds, and thus may also be associated with the bryophytes growing in bog hollows or share a similar pH optima to hollow *Sphagnum* spp. (Hamilton and Siver 2010). Although this species was not common across all samples, it was found in three highly acidic samples (pH ~4) with varying DWT at relative abundances exceeding 30%, suggesting that it has a narrow optimum and tolerance for pH. *Caloneis bacillum* was also often found with the hollow-indicator diatom taxa in the species ordination plot (Fig. 5c). This species has been reported to be able to sustain large osmotic changes from increasing dryness but cannot support long periods of desiccation (Van de Vijver et al. 2003), and thus may be more common in hollow habitats that are transitioning to drier hummock microhabitats. Collectively, our results suggest that *E. mucophila* is the best diatom indicator of bog-hollow microhabitats, but its occurrence with some of the other aforementioned diatom species (e.g., *E. lapponica*, *E. fennica*, *C. bacillum*) may provide further details on the specific hollow microhabitat.

Hollow-hummock transition microhabitats

Samples that were dominated by the bryophyte *S. magellanicum* (i.e., Cluster 3, $n = 4$) may capture microhabitats occurring between bog hummock and hollow environments. The occurrence of *S. magellanicum* in this transitional habitat is consistent with its broad ecological range, occurring in relatively acidic habitats, on the tops and sides of hummocks in older bogs, as well as in pioneering sites in wetter, more mineral-rich habitats that are more strongly connected to the water table (Gignac and Vitt 1990). Given that *S. magellanicum* is considered a generalist species found in a wide variety of peat habitats, it is not surprising that the diatom indicator species associated with this group of peat sites

likewise vary substantially in their autecology. The five indicator diatom species for hollow-hummock transition microhabitats (widely scattered in the CCA ordination plot) include: acidobiontic *Eunotia exigua* and *Gomphonema cf. bohemicum*, benthic; often alkaliphilous fragilarioid taxa; and *Aulacoseira subarctica* (Fig. 5c). In our study, *E. exigua* was associated with acidic but wetter sites associated with rich fen habitats (Cluster 5; Fig. 5c). Although, *E. exigua* has been reported extensively in floristic surveys of wetlands (e.g., de Vries 1984; Buczkó 2006), it has also been found to thrive in a variety of acidic, low-mineral habitats such as in acid mine drainage with high mineral content and particularly high metal loads (van Dam et al. 1981; DeNicola 2000; Liu et al. 2011). Therefore, it is doubtful that this diatom species has an affiliation with *S. magellanicum*, but rather the acidic and wet microhabitats of these peat sites were ideal for its growth. In contrast to *E. exigua*, indicator taxon *Gomphonema cf. bohemicum*, classified as acidobiontic by van Dam et al. (1994), occurs with other epiphytic diatom taxa associated with more circum-neutral to slightly acidic pH (i.e., Cluster 4). *Gomphonema bohemicum* has previously been reported in the literature to be acidobiontic but in the spatial distribution of this taxon across peatland habitats in our study suggest that it may also be limited by moisture. The present study adds to the known autecology of this species, as it clearly has a preference for sites that are less acidic and have a water table higher than bog sites and co-occurs with *S. magellanicum*.

Benthic indicator species, such as *Staurosira construens* and *Staurosirella pinnata*, are more commonly found in standing water, which suggests fluctuations in water-table depth within the hollow-hummock transition sites. *Staurosira construens* and, to a lesser degree *Staurosirella pinnata*, are positively influenced by shallow water tables. Small benthic fragilarioid taxa are known to be opportunistic, pioneering diatoms that tend to outcompete other diatoms when conditions are unfavourable (e.g., low light availability, short growing seasons, low nutrients; Lotter and Bigler 2000; Smol and Douglas 2007; Finkelstein and Gajewski 2008), and also found in very high abundances in not only alkaline conditions but also circum-neutral and slightly acidic lakes and ponds across temperate to Arctic regions (Smol et al. 2005; Karst-Riddoch et al. 2009). It is also not uncommon for these taxa to be present in depleted nutrient and mineral environments (e.g., ombrotrophic conditions), provided that there is sufficient moisture to survive (Rühland et al. 2009). Low-lying regions of the Hudson Plains are common and local connections to groundwater across small distances can be sporadic (Wolfe et al. 2011), yielding areas that have periodic contact with groundwater allowing the formation and disappearance of surface pools. This is consistent with the findings of Weihoefer and Pan (2007), who found that *Staurosira construens* and *Staurosirella pinnata* were the dominant diatom species in wetlands with relatively high water tables.

Aulacoseira subarctica is present, albeit in low abundances (maximum of 5% mean abundance in one sample) with a low indicator F value (Table 2), within hummock-hollow transition microhabitats. The occurrence of this tychoplanktonic diatom in our peat sample is somewhat surprising as it has been reported to occur in the open-water environment of well-mixed, relatively deep lakes with low light conditions (Kilham et al. 1996; Gibson et al. 2003) as well as in lakes with high concentrations of dissolved organic carbon (DOC) (Rühland and Smol 2002). The occurrence of *Aulacoseira* species in this peat environment is likely due to its ability to survive in low light environments, similar to the benthic fragilarioid taxa mentioned above. *Aulacoseira* species were also found in peat cores collected from the HBL, and attributed to a wetter, more fen-like environment prior to bog-hollow establishment (Hargan et al. 2015). In addition, higher DOC may result from the humification of older peat, and (or) groundwater contact with the surface vegetation, both of which would further limit light penetration.

Kobayasiella subtilissima, although not a significant indicator species for these habitats ($p = 0.053$), was dominant (mean abundance 48%) in Cluster 3 samples. This species was likely not an indicator taxon for these microhabitats due to its incidence across many other peat types. This species occurs most often with the bog-hollow species suggesting its preference for more acidic environments than typically found in fen habitats, but wetter conditions than bog hummock sites (Table 2, Fig. 5c). Similar to our observations of *K. subtilissima* in this study, this diatom is considered to be an acidobiontic species typically inhabiting bogs and nutrient-poor lakes and often co-occurs with small species of *Eunotia* (van Dam et al. 1981; Walker and Paterson 1986; Dixit et al. 1993). Unlike the epiphytic *Eunotia* taxa, *K. subtilissima* is an unattached benthic species and thus is likely more closely associated to the pH and DWT (as well as nutrients, although not measured) that the bog-hollow microhabitats yield as opposed to a bryophytic association (Fig. 5c).

Given that *S. magellanicum* can grow in a variety of peat habitats, the low pH tolerances of *E. exigua*, *K. subtilissima*, and *G. cf. bohemicum*, and low-light adaptations of small, benthic fragilarioid taxa and *A. subarctica*, it is most likely that these acidic microhabitats were either humified, thereby reducing the clarity of surface water (and also potentially further increasing acidity), and (or) receiving some nutrient and mineral inputs from groundwater sources or overland flow. The strong association of a few of the diatom species to either low or high water tables also suggests that water tables are unstable and these habitats may be prone to periodic drying.

Aulacomnium poor-fen habitats

Circum-neutral, poor-fen peat samples dominated by the moss *Aulacomnium* or by *Carex* contained distinct diatom assemblages (i.e., Cluster 4 MRT analysis; $n = 19$) and a rich variety of significant indicator species. All but one of these samples (HLM16) were collected in the Hudson Plains Ecozone near coastal Churchill within continuous permafrost. *Aulacomnium palustre* is known to be a common moss species of western Canadian peatlands that tends to occur frequently in drier fen microsites (Bauer et al. 2007), but has also been reported to grow on a variety of microhabitats with a wide-range of canopy and moisture conditions (Gignac 1992; Bauer et al. 2007). *Aulacomnium palustre* and species of the brown moss *Drepanocladus* are known as “strong fen indicators” in the Hudson Plains (Riley 2011). These have been observed to occur in peatlands close to the Hudson Bay coast that typically have a pH above 6.0 and a range in DWT, varying between 0.5 and 20 cm (Riley 2011). In this study, *Aulacomnium*-dominated sites had a mean pH value of 6.8 and although relatively dry, were wetter than the bog-hummock sites with a mean of DWT of 5.1 cm (i.e., water table slightly below the living vegetation surface), representing habitats more indicative of poor fens (Zoltai and Vitt 1995; Riley 2011).

A total of 33 significant diatom indicator taxa represent this group of poor-fen samples (Cluster 4), which includes distinct diatom assemblages consisting of a variety of mostly epiphytic taxa from the genera *Encyonema*, *Gomphonema*, and *Nitzschia* (Table 2). Given that many of the significant species within this cluster are either pH-indifferent, (e.g., *Achnantheidium minutissimum*; van Dam et al. 1981), or alkaliphilous (e.g., *Navicula* taxa particularly *N. cryptocephala*, *N. vulpina*, and *N. radiosa*; van Dam et al. 1981; Rühland et al. 2000; Weillhoefer and Pan 2007), diatom assemblage composition appears to be most strongly associated with the greater connection to the water table in these fen peat sites and related chemical characteristics such as relatively high levels of conductivity, minerals, and nutrients. The high number of diatom indicator taxa (e.g., *Achnantheidium minutissimum*, *Denticula kuetzingii*, *Epithemia adnata*, *Diatoma tenuis*, *Nitzschia perminuta*, and *Fragilaria capucina*) that are common in environments that are not as chem-

ically restrictive as in bog environments such as ponds and lakes, is consistent with the stronger connection to groundwater.

All of the coastal fens from the Churchill region shared similar diatom assemblages but were distinct from the rest of our study samples, suggesting that coastal peatlands of this region are both relatively homogenous and yet dissimilar to the other peatlands in the study region. Many of the poor fen, epiphytic indicator diatom taxa found at Churchill have been commonly reported from other wetland types (particularly fens) across the globe. For example, *Encyonopsis microcephala* was co-dominant with *Achnantheidium minutissimum* in Dutch moorland pools (van Dam et al. 1981), *Gomphonema* and *Nitzschia* taxa were found to typically co-occur in peat records from Siberia and Alaska during fen periods dominated by sedge peat (Rühland et al. 2000; Myers-Smith et al. 2007), and *A. minutissimum* and *Fragilaria capucina* co-occurred during a section in an Ontario peatland core when *Drepanocladus* and *Carex* macrofossils were present (i.e., fen stages) (Campbell et al. 1997). Additionally, *Fragilaria tenera* was identified as a significant indicator species occurring in Arctic moss substrates (Michelutti et al. 2003), and although it is often considered planktonic, its presence in our subarctic brown moss environments appears to be common across the Arctic.

In general, there are more fens along the Hudson Bay coast than bogs, as the shore of Hudson Bay represents the most recent state of peat and substrate in the study region, whereas regions farther inland from the coast have experienced a lengthened period of emergence from the Tyrrell Sea and hence a longer period for peat to accumulate and ombrotrophication to occur (Martini 2006; Crins et al. 2009; Holmquist et al. 2014). It is of interest to note that coastal fens occur throughout the Hudson Plains along the coast of Hudson Bay (Riley 2011), but in this study this fen type was only sampled near Churchill. If homogeneity of coastal fens is indeed the case in the Hudson Plains, then we might expect to find similar diatom assemblages throughout both the Ontario and Manitoba coastal fen sites.

Wet fen habitats

Wet fen habitats (Cluster 5; $n = 9$) had the greatest connection to the water table with the living vegetation at the surface typically submerged (mean DWT = -5.6 cm). These samples had the highest diatom diversity of all of our samples and yielded the largest number of significant indicator taxa, despite having a mean pH value lower than the hummock-hollow transition microhabitats and poor fen habitats (i.e., Clusters 3 and 4). This is interesting considering that pH is driving most of the clusters and secondarily DWT, but here it seems that the stronger connection to the water table prevails for species richness. However, pH data are probably more reliable than the water table depth data, as the DWT varies considerably through the year. Given the DWT and vegetation, these sites are likely rich fens; however, the pH is more acidic than typical rich fen habitats, which tend to have a pH > 7. The high diatom diversity observed in these peat samples is consistent with the flora reported in other rich fen environments (Kingston 1982; Pouličková et al. 2004). The dominant vegetation type sampled was Cyperaceae, but fen samples also included *Drepanocladus*, *Equisetum*, and *Carex*, taxa typical of a rich fen environment (Riley 2011). A total of 34 significant diatom taxa from 10 genera represent this habitat including 17 *Eunotia* taxa, 3 *Pinnularia* taxa, 3 *Tabellaria* taxa, 2 *Brachysira* taxa, and *Frustulia rhomboides* (Table 2). The high number of indicator taxa identified in this group was likely due to more peatland habitats, including favourable conditions for diatom growth, including a higher water table, less acidic pH than bogs, and higher nutrients and minerals, for both vegetation and diatom growth resulting in a more diverse and complex variety of peat vegetation types and thus a greater assortment of diatom microhabitats.

In these wet, poor to rich fen environments, diatom species appear to be generalists in their preference for pH, as they tend to

occur over a relatively wide range of pH from alkaliphilous to acidophilous environments. Several of the taxa dominant in these fens have previously been reported to be closely associated with fen peatland habitats, including *Tabellaria flocculosa*, *Eunotia hexaglyphis*, *E. incisa*, and *Pinnularia brevicostata*, which are often indicative of wetter and more acidic conditions (Fukumoto et al. 2012). Many diatom calibration sets and studies on peatland carbon corroborate the presence of many of these indicator diatom taxa in slightly acidic and humic sedge environments. For example, *Frustulia rhomboides*, *Brachysira brebissonii*, and *Chamaepinnularia soehrensii* were associated with humic waters and frequently found in mosses growing on rocks in modern peat samples and peat core records (Kokfelt et al. 2009). Many *Eunotia* taxa (*E. praerupta*, *E. incisa*, *E. tenella*, *E. hexaglyphis*, *E. arcus*, and *E. subarcuatoidea*), *Stauroneis phoenicenteron*, and *Pinnularia* taxa were present in both modern sedge peat samples and during the sedge-dominant period depicted in a peat cores (Myers-Smith et al. 2007; Kokfelt et al. 2009). Pienitz and Smol (1993) found that coloured lakes located in peaty areas contained benthic acidophilic diatoms, such as *Brachysira* spp., *Encyonopsis microcephala*, *E. exigua*, *E. praerupta*, *Frustulia rhomboides*, *Chamaepinnularia mediocris*, *C. soehrensii*, *K. subtilissima*, *Neidium ampliatum*, and *Stauroneis phoenicenteron*. Although dissolved organic carbon (DOC) was not measured, groundwater flow is significant in the redistribution of carbon and determining spatial patterns of carbon concentration (Waddington and Roulet 1997), indicating that higher DOC concentrations at these rich fen sites, as indicated by the diatom assemblages, are highly probable. As well, decomposition rates are much higher in sedges than in *Sphagnum* mosses (Moore and Basiliko 2006), which could contribute to higher DOC or humic waters in these rich fens. Although we suggest that pH is the main driver clustering our sites, and secondarily DWT, the diatom assemblages highlight the strong importance of groundwater connection in fens, which has a strong influence on species richness.

Conclusions

We demonstrate striking microhabitat specificity of diatom assemblages across the Boreal Shield and subarctic peatlands of Ontario and Manitoba. The uniformity in diatom preferences for these microhabitats across the large expanse of our study region (~800 km) suggests that the temperature and precipitation differences associated with the Boreal Shield or Hudson Plains ecozones have minor influences on diatom distributions in these surface peat samples. Distinct diatom assemblages captured the transition between *Sphagnum*-dominated bog microhabitats and *Aulacomnium* and brown-moss dominated fens. Diatom species diversity and richness decreased from rich-fen to bog environments and from hummocks to hollows. MRT analysis was particularly well-suited to identifying associations between diatom assemblages and peat type at each site. Water-table depth and pH were found to clearly define microhabitat type and the diatoms associated with these. This study demonstrates that diatoms are highly sensitive to peat microhabitat environments and can and should be more widely used for paleoecological studies to track peatland hydroseral changes.

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