# Linkages between spatio-temporal patterns of environmental factors and distribution of plant assemblages across a boreal peatland complex

JEREMY A. GRAHAM, JEREMY A. HARTSOCK, DALE H. VITT, R. KELMAN WIEDER AND JOHN J. GIBSON

**BOREAS**

Here we examine the arrangement of plant species across an oligotrophic bog/poor fen peatland complex in the North American boreal plain and the relationships of these species to their physical and chemical environment. A semi-uniform spatial sampling approach was utilized to describe the species assemblages, pore-water chemistry and physical condition of 100 plots throughout a single peatland complex. Regardless of sharing the same ground cover of *Sphagnum* mosses, the remaining species separated into four distinct assemblages, each with unique indicators. These species groups along with associated chemical and physical factors are organized into four ecosites: bog, margin (edge) and two poor fen ecosites. The plant assemblages of this peatland have a complex relationship with numerous gradients, both physical and chemical, including depth to water table, shade, pH, nutrient and base cation. Rather than being homogenous across the landscape, most environmental variables exhibit distinct spatial patterns and do so in relationship to the plant assemblages, forming spatially distinct ecosites across the complex. Base cation concentrations play a smaller role than previously thought in differentiating these ecosites, and in addition to shade and depth to water table, nitrogen in the form of dissolved organic nitrogen was highly related to the placement of these ecosites. Many significant chemical factors appear related to evaporative water loss within the peatland complex, and these chemical factors are used to differentiate the ecosites. However, the mediation of evaporative water loss is due largely to self-generated responses of the plant assemblages related to shade through plant morphology and peat acrotelm development related to depth to water table. We conclude that plant species and associated environmental gradients act together to form spatially distinct ecosites. The distribution of these ecosites within this large, environmentally complex peatland is largely controlled by differing self-generated responses along the hydrotopographical gradient of differential water loss.

*Jeremy A. Graham (graham19@siu.edu) and Dale H. Vitt, Department of Plant Biology and Center for Ecology, Southern Illinois University Carbondale, 1125 Lincoln Dr., Carbondale IL 62901, USA; Jeremy A. Hartsock and R. Kelman Wieder, Department of Biology, Villanova University, 800 Lancaster Dr., Villanova, PA 19085, USA; John J. Gibson, Department of Geography, University of Victoria, 3800 Finnerty Rd, Victoria, BC V8P5C2, Canada; received 18th March 2015, accepted 14th September 2015.*

Peatlands are distributed across approximately 4.5 million km$^2$ of the earth's surface (Yu *et al.* 2010), with the vast majority at latitudes north of 45° in the northern hemisphere, occupying nearly 3% of global land area. Across North America, peatlands cover $1.37 \times 10^6$ km$^2$, with the majority in Canada's boreal forest (Bridgham *et al.* 2006). Peatlands are most noted for the ability to sequester large stores of carbon, as peat, which is made possible by the combination of peat-forming plant species, those having a positive production to decomposition ratio, and their organization along complex environmental gradients. In boreal regions, peatlands are categorized into two general site types, bogs and fens, based upon specific differences in source of water, vegetation, and chemistry (Sjörs 1950; Zoltai & Vitt 1995; Vitt 2006). Bogs are ombrogenous and receive water and nutrient inputs exclusively from atmospheric sources. Geogenous fens receive water and nutrients from the atmosphere, terrestrial runoff and/ or through either shallow or deep groundwater. Bog and poor fen site types most often have a *Sphagnum*-dominated ground layer and pore-water pH values that generally are below 5.5 (Clymo 1984; Vitt *et al.* 1995).

Characterization of boreal peatland water chemistry (pH, electrical conductivity, base cations/anions, total carbon, ammonium and nitrate) as well as peatland type delineations (bog, poor fen, moderate-rich fen and extreme-rich fen) are historically well studied in the boreal forest region (Sjörs 1950; Vitt & Chee 1990; Zoltai & Vitt 1995). Sjörs (1950), who concluded that peatland types exist along gradients of pH and electrical conductivity (as a surrogate for base cations and their anions), pioneered early studies demonstrating how environmental gradients relate to peatland vegetation. Further research led to the prevailing thought of three primary gradients or 'directions of variation' in peatlands (Sjörs 1950; Horton *et al.* 1979; Malmer 1986). These gradients are (i) microtopographical variation creating the hummock-hollow topography, (ii) peatland expanse to margin, and (iii) degree of minerotrophy. Contemporary methods of peatland delineation integrate these plant and chemical gradients to classify peatlands into their individual types (Vitt & Chee 1990; Zoltai & Vitt 1995; Wieder *et al.* 2006).

The hummock-hollow topography found in peatlands coincides with recognizable differences in species composition at small scales. Conversely, large-scale floristic distinctions at the site level generally divide peatlands into minerotrophic rich fens, dominated

by true mosses, and poor fens and bogs, acidic environments dominated by *Sphagnum*. There are some exceptions to this delineation as some rich fens may have a notable abundance of mesotrophic *Sphagnum* species (Vitt 2006). Malmer (1986) reviewed the connection of scale to peatland gradients, highlighting the complexities in assigning floristic units along these gradients. In continental Canadian bogs and poor fens the dominant sphagna consist primarily of three species, *S. angustifolium*, *S. magellanicum* and *S. fuscum*, which nearly provide the entirety of the ground layer cover. These three mosses are arranged along the hummock-hollow microtopographical gradient suited to their unique differences in morphology, water balance and growth rates (Luken 1985), which reflects competitive differences. Differences at the microtopographical level, that is between hummocks and hollows, are well studied with clear differences in species assemblages (Watt 1947) and function (Belyea & Clymo 2001); however, it is unclear how these small local differences and similarities relate to the larger hydrotopographical gradients found in large peatland complexes. Here we examine how patterns in species compositions along with their associated chemical and physical attributes are organized into ecosites along a hydrotopographical gradient found in a bog/poor fen complex peatland. Whereas peatland site types (bogs, fens, etc.) each have unique attributes, more local, within-site variation, can be defined at the ecosite level. Ecosites are ecological units with similar species assemblages that occur under similar environmental influences (climate, moisture and nutrient regime (Beckingham & Archibald 1996).

Across western Canada interconnected bogs and fens comprising 'peatland complexes' are intrinsically linked owing to their intimate relationships with water table depth, water source and water chemistry, all of which ultimately influence plant assemblage composition (Vitt & Slack 1984; Malmer 1986; Vitt & Chee 1990). These relationships vary between spatial scales, yet there exists no ideal spatial scale to study ecological patterns (Levin 1992). In this study, our objective is to employ a semi-uniform spatial sampling scheme to capture plant species occurrences and abundances, and physical and chemical patterns within a large peatland complex, at a landscape scale beyond that of the hummock-hollow scale. Moreover, this study is a detailed description of a boreal peatland complex capable of providing a comprehensive benchmark for future climate change studies. The following questions were asked to describe how patterns in physical characteristics, water flow, pore-water chemistry and plant assemblages relate to functional attributes across diverse hydrotopographical gradients within a large peatland complex: (i) can species assemblages be sorted into distinct groups within a peatland complex; (ii) do groups of species assemblages have indicator species; (iii) do environmental characteristics exhibit seasonal changes in spatial variation; and (iv) how are species assemblages within the peatland complex linked to environmental gradients found at the site?

## Site description

In northern Alberta, poor fen/bog complexes are common landscape features, especially on low drainage divides at higher elevations (Vitt *et al.* 1997). We used aerial photography and road reconnaissance to locate a number of peatland complexes in northeastern Alberta. Poor fens and bogs were compared to Vitt *et al.* (1975) and Nicholson & Vitt (1990) for poor fens, and Belland & Vitt (1995) for bogs for comparative chemistry and vegetation. From this set of possible sites, we chose the Mariana Lake complex owing to proximity to roads and representative chemistry and vegetation. The peatland complex is located near Mariana Lake Alberta, Canada, elevation 695 m a.s.l. (latitude 55°89′N, longitude 112°09′W) (Fig. 1). The site includes two peatland site types – a large poor fen (~164 000 m$^2$) connected to two ombrotrophic bogs (~43 290 m$^2$), and the site is bordered by uplands to the north and southeast, continuous poor fen to the west and an access road with culverts along the northeast that separate the study area from a larger peatland complex (Fig. 1). Two fires of recent history have occurred at the study site: the Mariana Lake fire of 1995 (~135 150 ha) and the House River fire of 2002 (~240 000 ha) (Sustainable Resource Development 2010). The southernmost bog at Mariana Lake was partially burned in the latter fire; however, the fire ceased before spreading farther into the peatland complex (Fig. 1). Climate in the Mariana Lake region is typical of the boreal forest Zonobiome VIII (Walter 1979). Mean monthly temperatures range from −16.7 to 16.5 °C and mean annual precipitation is 475 mm (Environment Canada 2010). Annual bulk N deposition at the site is approximately 1 kg N ha$^{-1}$ a$^{-1}$ (Wieder *et al.* 2010).

The bog at Mariana Lake is dominated by *Sphagnum* species, namely *S. fuscum*, *S. angustifolium* and *S. magellanicum*. The dominant vascular plant cover is the tree *Picea mariana*, ericaceous shrub species *Rhododendron groenlandicum*, *Vaccinium vitis-idaea*, *Kalmia polifolia*, and herbs *Rubus chamaemorus* and *Smilacina trifolia*. The large poor fen shares dominant *Sphagnum* species with the bog. Vascular plant cover of the poor fen consists of the graminoids *Eriophorum vaginatum*, *Scheuchzeria palustris*, *Carex aquatilis*, *Carex limosa* and *Carex paupercula*. Poor fen shrub species include *Andromeda polifolia* and *Chamaedaphne calyculata*. The substrate of the surrounding uplands is moist, sandy soil covered largely by the mosses *Pleurozium schreberi*, *Hylocomium splendens*, *Polytrichum commune* and *Dicranum polysetum*. Vascular plants found on the uplands include *Vaccinium myr-*

*Fig. 1.* Orthophoto taken in 2006 of surrounding features with zoomed inset of study area. Large extent scale 1:24 000 and inset 1:6000. Aerial photo obtained from Alberta Environment and Sustainable Resource Development: Air Photo Distribution 2010.

*tilloides, Rhododendron groenlandicum* and *Equisetum pratense. Picea mariana* and *Pinus banksiana* comprise the upland tree cover.

## Methods

### Sampling

Water collection and floristic characterization points (n = 100) were established and geo-referenced in spring 2010 (Fig. 2A). Transects were created across the study site with points placed approximately 30–50 m apart. To capture the ecotone between upland and peatland, points were placed approximately 5 m from the peatland margins, as well as near the margins themselves. Exact plot location was finalized using a number generator to create a random distance and direction from each point on the transect. Each point was marked with surveying flags and GPS coordinates for repeated measurements.

Water samples were collected in acid-washed 60 mL HDPE bottles from each sample plot in early summer

(7th June 2010) and early autumn (9th October 2010). In order for comparison to be made with earlier, regional sampling (e.g. Vitt *et al.* 1975), water was sampled by carefully exposing the water table, waiting for 30 min and sampling from the top 10 cm. Samples for deuterium excess and base cations $Ca^{2+}$, $K^+$, $Mg^{2+}$ and $Na^+$ were collected in June. *d*-excess values can serve as a proxy measurement for evaporative loss from open-water and moss canopies, and can assist in identifying water sources (Whitfield *et al.* 2010). Low *d*-excess values indicate relatively high evaporative losses in areas with open water or emergent sphagna, while high values indicate less evaporative loss – either by water surfaces being protected by the aerobic peat layer or from marginal areas receiving water from shallow groundwater sources. Additionally flow is inferred from elevation data and peatland features, including flarks, shallow linear features that form perpendicular to flow. Water samples were filtered with Whatman 541 filter paper and frozen on the same day as collection. Electrical conductivity was corrected for $H^+$ ions (Miller *et al.* 1988) and pH was measured in the lab at 20 °C.
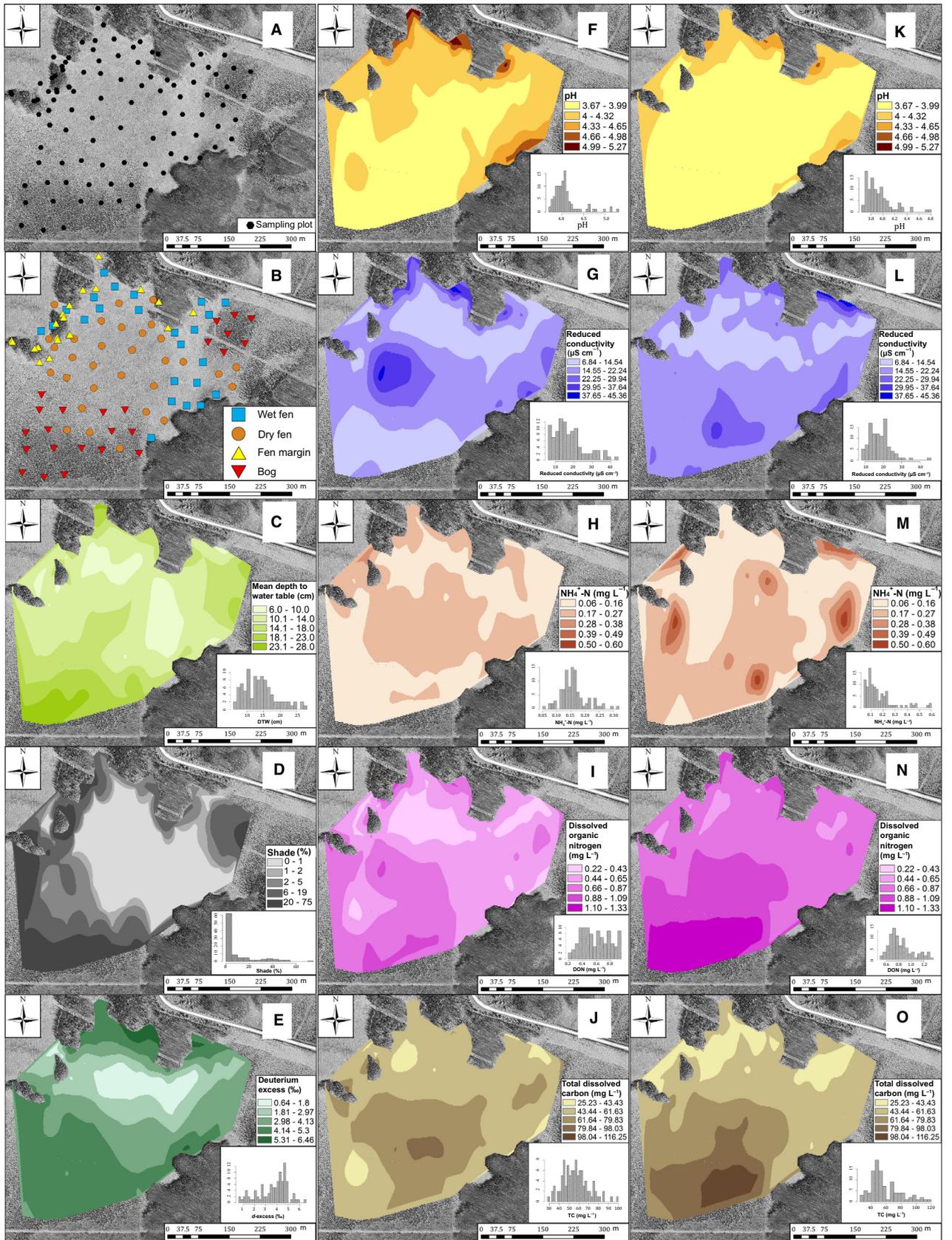
Determination of *d*-excess (*d*-excess: $d(‰) = \delta^2H - \delta^{18}O$) follows Dansgaard (1964) and Whitfield *et al.* (2010). Concentrations of $NH_4^+$-N and $NO_3^-$-N were determined colourimetrically by a Seal III N Analytical AA3 Autoanalyzer using the alkaline phenol and hydrazine reduction methods, respectively. Total dissolved nitrogen (TDN) and total dissolved carbon (TC) were measured using a Shimadzu TN/TC Analyzer. Dissolved organic nitrogen (DON) concentrations were determined by subtracting ($NH_4^+$-N + $NO_3^-$-N) from TDN (Bragazza & Limpens 2004).

Plant surveys were carried out in 6.25-m$^2$ plots (2.5×2.5 m) at each of the sampling point locations. Each plot encompassed the entire hydrotopographical gradient present at the sampling point. To rank species abundance, each plot was visually gridded into smaller 0.063-m$^2$ squares. Abundance scores for each species were recorded based on the frequency and dominance of species occurrence within the subplots. Classes were divided using methods modified from Phillips (1959). Class intervals are as follows; 0 – not present, 1 – one or two occurrences, 2 – <10%, 3 – 10–25%, 4 – 26–50%, 5 – 51–80% and 6 – >80%. Shade and depth to water table from the moss surface were measured in June. Shade was measured using a concave spherical densiometer held at chest height. Depth to the water table (here shortened to depth to water (DTW)) was measured at five random locations within each plot. To measure DTW at each location peat was carefully separated to expose the water table, waiting 30 min for water to resettle, with measurement from the top of the living *Sphagnum* to the water table. The mean from the five measurements was calculated to obtain a plot level mean DTW. Shade and DTW were measured in early summer.

### Statistical analyses

To explore relationships of environmental gradients and species composition, ordinations were executed using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities (Bray & Curtis 1957), with the vectors of significant environmental variables ($p < 0.01$) fitted to the ordination. NMDS, vector fitting and complete linkage clustering was performed using the vegan package in R (Oksanen *et al.* 2011), with groups formed at a 0.6 dissimilarity value in the cluster analysis. Vectors for each season were fitted as a different variable and all forms of nitrogen,

including total nitrogen were included in the vector fitting. Analysis of similarity (ANOSIM) was conducted using DECODA (Minchin 1989) to confirm that cluster analysis groups were significantly different in plant species composition. Multi-level indicator species analyses were performed using the indicspecies package in R (De Caceres & Legendre 2009). For seasonal pore-water analysis, 2×4 factorial ANOVAS were performed to determine seasonal differences in pore-water nutrient concentrations between cluster analysis groups. Where data sets failed to meet the assumptions of normality non-parametric tests were performed. Post-hoc comparisons were made using Tukey's HSD test ($p < 0.05$). Maps were generated using ARCMAP 9.3 with nearest neighbour interpolation and classified with equal interval breaks for each variable with the exception of shade, $Ca^{2+}$ and $Na^+$, which were geometrically distributed. These variables were grouped using a geometric interval for shade, and Jenks' natural breaks for $Ca^{2+}$ and $Na^+$. For spring and autumn pore-water maps, equal breaks were determined using the entire range of data from both seasons.

## Results

### Species diversity

The Mariana Lake complex peatland contains 79 species: 21 mosses, four hepatics, 37 vascular plants and 17 lichen species (Table 1). Sixteen of the lichen species belong to the genus *Cladonia*, and due to their high diversity and low abundance all *Cladonia* species were combined for analysis. Of the moss species, nine belong to the genus *Sphagnum* and 13 are true mosses (Table 1). Mean plot (alpha) and beta (species turnover) diversity were 18.0 and 4.5, respectively. The most frequent species is the bryophyte *Sphagnum angustifolium*, occurring in every plot. Other frequent bryophyte species include *Sphagnum magellanicum* and *Pohlia nutans*, present in 92 and 91 of the plots, respectively. Frequent vascular plant species are *Oxycoccos microcarpus* and *Chamaedaphne calyculata*, which occurred in 95 and 94 of the plots, respectively.

### Plant assemblages and ecosites

Complete linkage cluster analysis of the vegetation data at 0.6 dissimilarity distinguished four species assemblages, that were confirmed to be different

*Table 1.* Mean cover class scores of plant abundances of the Mariana Lake peatland complex for the four species assemblages created by complete linkage cluster analysis.

| Species | Wet fen | Dry fen | Fen margin | Bog |
|---|---|---|---|---|
| **Mosses** | | | | |
| *Aulacomnium palustre* | 0.63 | 0.58 | 2.67 | 1.96 |
| *Dicranum polysetum* | 0.00 | 0.00 | 0.48 | 0.00 |
| *Dicranum undulatum* | 0.00 | 0.61 | 0.24 | 2.00 |
| *Hylocomium splendens* | 0.00 | 0.00 | 0.48 | 0.17 |
| *Hypnum lindbergii* | 0.00 | 0.00 | 0.00 | 0.17 |
| *Pleurozium schreberi* | 0.00 | 0.74 | 2.76 | 2.83 |
| *Pohlia nutans* | 3.38 | 2.77 | 2.76 | 2.13 |
| *Polytrichum commune* | 0.00 | 0.00 | 1.76 | 0.00 |
| *Polytrichum strictum* | 1.21 | 0.35 | 1.43 | 0.29 |
| *Ptilium crista-castrensis* | 0.00 | 0.00 | 0.29 | 0.17 |
| *Sphagnum angustifolium* | 5.13 | 4.58 | 4.38 | 5.29 |
| *Sphagnum capillifolium* | 0.00 | 0.00 | 0.10 | 0.00 |
| *Sphagnum fallax* | 0.54 | 1.00 | 0.33 | 0.21 |
| *Sphagnum fuscum* | 1.46 | 4.35 | 2.62 | 3.25 |
| *Sphagnum lindbergii* | 0.08 | 0.39 | 0.00 | 0.00 |
| *Sphagnum magellanicum* | 3.75 | 4.06 | 2.14 | 3.96 |
| *Sphagnum majus* | 0.33 | 0.00 | 0.00 | 0.00 |
| *Sphagnum riparium* | 0.00 | 0.13 | 0.00 | 0.00 |
| *Sphagnum russowii* | 0.29 | 0.13 | 2.57 | 0.00 |
| *Tomentypnum falcifolium* | 0.13 | 0.00 | 0.00 | 0.08 |
| *Warnstorfia fluitans* | 0.08 | 0.13 | 0.29 | 0.08 |
| **Hepatics** | | | | |
| *Calypogeia sphagnicola* | 0.08 | 0.06 | 0.00 | 0.00 |
| *Cladopodiella fluitans* | 0.25 | 1.00 | 0.10 | 0.33 |
| *Mylia anomala* | 0.42 | 1.77 | 0.29 | 1.13 |
| *Ptilidium pulcherrimum* | 0.00 | 0.00 | 0.52 | 0.08 |
| **Lichens** | | | | |
| *Cladonia* species | 0.00 | 0.23 | 0.76 | 1.29 |
| *Peltigera aphthosa* | 0.00 | 0.00 | 0.33 | 0.00 |
| **Vascular plants** | | | | |
| *Alnus rugosa* | 0.00 | 0.00 | 0.10 | 0.00 |
| *Andromeda polifolia* | 4.29 | 4.42 | 0.57 | 3.92 |
| *Betula glandulosa* | 0.54 | 0.00 | 0.29 | 0.00 |
| *Betula papyrifera* | 0.00 | 0.00 | 0.05 | 0.00 |
| *Calamagrostis canadensis* | 0.00 | 0.00 | 1.10 | 0.00 |
| *Carex aquatilis* | 3.83 | 1.42 | 4.52 | 0.38 |
| *Carex canescens* | 0.00 | 0.00 | 0.62 | 0.00 |
| *Carex disperma* | 0.00 | 0.00 | 1.38 | 0.00 |
| *Carex limosa* | 1.38 | 0.39 | 0.14 | 0.00 |
| *Carex livida* | 0.00 | 0.35 | 0.00 | 0.00 |
| *Carex media* | 0.13 | 0.00 | 0.00 | 0.00 |
| *Carex pauciflora* | 0.00 | 0.26 | 0.29 | 0.67 |
| *Carex paupercula* | 0.00 | 0.00 | 0.62 | 0.00 |
| *Carex utriculata* | 1.00 | 0.00 | 0.52 | 0.04 |
| *Chamaedaphne calyculata* | 2.88 | 3.97 | 2.52 | 3.88 |
| *Drosera rotundifolia* | 1.58 | 1.74 | 1.10 | 1.00 |
| *Eleocharis acicularis* | 0.00 | 0.00 | 0.19 | 0.00 |
| *Eleocharis palustris* | 0.00 | 0.00 | 0.14 | 0.00 |
| *Empetrum nigrum* | 0.00 | 0.00 | 0.19 | 0.00 |
| *Equisetum* sp. | 0.00 | 0.00 | 2.10 | 0.00 |
| *Eriophorum angustifolium* | 0.29 | 0.06 | 0.48 | 0.00 |
| *Eriophorum vaginatum* | 2.25 | 4.00 | 1.76 | 2.83 |
| *Kalmia polifolia* | 0.63 | 2.77 | 0.38 | 1.42 |
| *Larix laricina* | 0.33 | 0.23 | 0.24 | 0.00 |
| *Menyanthes trifoliata* | 0.58 | 0.00 | 0.00 | 0.00 |
| *Oxycoccos microcarpus* | 4.21 | 3.87 | 3.05 | 4.08 |
| *Picea mariana* | 1.25 | 2.68 | 2.67 | 3.33 |

(continued)

*Table 1.* (continued).

| Species | Wet fen | Dry fen | Fen margin | Bog |
|---|---|---|---|---|
| *Pinus banksiana* | 0.00 | 0.00 | 0.48 | 0.00 |
| *Rhododendron groenlandicum* | 0.33 | 1.26 | 4.29 | 3.54 |
| *Rubus chamaemorus* | 0.33 | 1.94 | 1.76 | 3.96 |
| *Salix pedicellaris* | 0.00 | 0.00 | 1.67 | 0.00 |
| *Sarracenia purpurea* | 0.08 | 0.06 | 0.00 | 0.00 |
| *Scheuchzeria palustris* | 2.38 | 1.65 | 0.00 | 0.13 |
| *Scirpus caespitosus* | 0.00 | 0.00 | 0.14 | 0.00 |
| *Smilacina trifolia* | 1.63 | 2.48 | 3.86 | 4.17 |
| *Vaccinium myrtilloides* | 0.00 | 0.00 | 1.10 | 0.00 |
| *Vaccinium vitis-idaea* | 0.13 | 0.26 | 3.90 | 3.21 |

Wet fen (WF) n = 24, dry fen (DF) n = 31, fen margin (M) n = 21, bog (B) n = 24.

(ANOSIM $R^2 = 0.67$, $p < 0.0001$). Pairwise comparisons indicated that all four assemblages were significantly different from one another ($p < 0.05$). Three of these assemblages are found in the peatland interior; the fourth exists exclusively within 10 m from the peatland margin. Of the three interior assemblages one is graminoid-dominated, one shrub-dominated and one tree-dominated. Two of these occur in the poor fen area and one in the bog area. We identify these four spatially distinct plant assemblages along with their associated environmental attributes as ecosites using hydrotopographical features as follows: 'Fen margin' (FM) (n = 21), 'bog' (n = 24), 'dry fen' (DF) (n = 31) and 'wet fen' (WF) (n = 24). The DF ecosite occupies the large central area of the peatland. The WF ecosite is localized adjacent to the north upland margin (Fig. 2B). Cover class scores are provided in Table 1. Several species were identified as ecosite indicators at varying hierarchical levels (Table 2). *Andromeda polifolia* was designated an indicator of the three peatland interior ecosites. *Rubus chamaemorus* was the only other indicator species of three groups, being absent only from the WF. Amongst the remaining hierarchical combinations, the FM had the greatest number of indicators and the DF the least (Table 2). The only indicator species unique to the DF was the regionally rare, yet locally abundant *Sphagnum lindbergii* (Vitt & Andrus 1977).

## Environmental factors

Throughout the site, DTW ranged from 6.4 to 27.8 cm. There was no significant departure from normal precipitation amounts in the months preceding DTW measurements (Environment Canada 2010); therefore values found here are believed to be representative of normal conditions at the site. Shade values varied from 0 to 73.5%, with only eight plots having shade values exceeding 40%. The majority of plots (n = 62) exhibited shade values below 5%. All shade

*Table 2.* Multiple level indicator species analysis with groups in left column and indicator values in right column.

| Species | Group | Indicator value |
|---|---|---|
| *Andromeda polifolia* | WF, DF, BG | 0.97 |
| *Rubus chamaemorus* | DF, BG, FM | 0.82 |
| *Scheuchzeria palustris* | WF, DF | 0.66 |
| *Carex aquatilis* | WF, FM | 0.9 |
| *Polytrichum strictum* | WF, FM | 0.61 |
| *Carex utriculata* | WF, FM | 0.44 |
| *Betula glandulosa* | WF, FM | 0.4 |
| *Kalmia polifolia* | DF, BG | 0.76 |
| *Mylia anomala* | DF, BG | 0.71 |
| *Vaccinium vitus-idaea* | BG, FM | 0.94 |
| *Rhododendron groenlandicum* | BG, FM | 0.88 |
| *Pleurozium schreberi* | BG, FM | 0.85 |
| *Aulacomnium palustre* | BG, FM | 0.85 |
| *Cladonia* spp. | BG, FM | 0.65 |
| *Carex limosa* | WF | 0.58 |
| *Menyanthes trifoliata* | WF | 0.41 |
| *Sphagnum lindbergii* | DF | 0.37 |
| *Dicranum undulatum* | BG | 0.73 |
| *Salix pedicellaris* | FM | 0.87 |
| *Sphagnum russowii* | FM | 0.83 |
| *Equisetum* sp. | FM | 0.82 |
| *Polytrichum commune* | FM | 0.72 |
| *Calamagrostis canadensis* | FM | 0.62 |

All reported species were significant at $p < 0.01$. WF = Wet fen; DF = dry fen; BG = bog; FM = fen margin.

was from *Picea mariana*, and was limited to bogs or areas near the FM. Shade occurring from the uplands declines precipitously moving towards the fen, whereas shading in the bog declines gradually towards the centre of the fen (Fig. 2D).

Across the peatland complex, *d*-excess values plotted spatially reveal areas of differing evaporation/inflow, especially in marginal areas that receive water from shallow groundwater (thus having lower evaporation/inflow due to higher inflow) (Fig. 2E). The southern bog and transitioning DF plots form a zone of high DTW (and thus little evaporative loss), with water losses occurring mainly through evapotranspiration from vascular plants and evaporation from moss canopies. A zone of evaporatively enriched water having low *d*-excess exists on an east–west axis. This water is inferred to have relatively high evaporative losses, and from the southwest of the study site to the northeast, there is a gentle transition in *d*-excess values, highlighting a gradient of increased evaporative loss. Topographical maps and aerial photographs indicate that water exits through the northeastern corner of the peatland through two culverts. Small flarks orientated north–south are found from the northernmost upland island across to the protruding upland on the north edge of the study area. Flarks orientated east–west are found in the location of the WF plots located towards the eastern side of the study area. They also exist in a northwest–southeast orientation in the WF area between the northeast bog and upland in the northeastern area of the study site.

Concentrations of $Mg^{2+}$ and $Na^+$ across the peatland were generally low with only a few high values, while $K^+$ and $Ca^{2+}$ were more widely distributed (Fig. 3A, C). For pore-water base cation content, mean $Mg^{2+}$, $Na^+$, $K^+$ and $Ca^{2+}$ concentrations were 0.42, 1.03, 0.43 and 1.36 mg $L^{-1}$, respectively. Pore-water ranges for $Mg^{2+}$, $Na^+$, $K^+$ and $Ca^{2+}$ concentrations were 0.29–2.50, 0.59–5.64, 0.04–1.36 and 0.38–3.46 mg $L^{-1}$, respectively (Table 3). All base cations demonstrated spatial patterning within the study area. The high values of $Mg^{2+}$ were located in the bog ecosite at the far southern portion (Fig. 3B). Other than two high values of $Mg^{2+}$ all other values were <1 mg $L^{-1}$ and similar across the complex. All pore-water $Na^+$ concentration spikes were located along the fen margins with little variation within the peatland complex (Fig. 3D). Higher values of $K^+$ were mostly found along the FM with some higher values in the southern bog, but not the northeastern bog. Many of the higher concentrations of $Ca^{2+}$ were found in the southern bog and near uplands, declining in concentration towards the convergence of the WF and DF ecosites.

Most other water-chemistry parameters exhibited some degree of temporal variation and also demonstrated spatial patterning in the peatland complex (Fig. 2F–N). Across the entire peatland and both seasons, pH ranged from 3.7 to 5.3. pH declined from summer to autumn, with nearly the entire study area exhibiting pH <4.0 in the autumn. The range of reduced conductivity was similar in both seasons, ranging from 8.3 to 45.4 μS cm$^{-1}$ in the summer and 6.8 to 42.3 μS cm$^{-1}$ in the autumn, with shifts in spatial patterns, with the southern bog increasing and the DF showing some reduction in conductivity. DON was the dominant N form in pore water followed by $NH_4^+$-N and lastly $NO_3^-$-N. DON concentrations were lower in summer than autumn, ranging from 0.21 to 0.94 and 0.52 to 1.33 mg $L^{-1}$, respectively. The range of $NH_4^+$-N values increased slightly from 0.05 to 0.32 mg $L^{-1}$ in the summer to 0.05 to 0.59 mg $L^{-1}$ in the autumn. Summer concentrations of $NO_3^-$-N ranged from 0.0 to 0.28 mg $L^{-1}$ while autumn levels dropped to nearly undetectable concentrations. Early summer $NH_4^+$-N values were fairly uniform across the peatland complex, yet in the autumn there appeared to be localized hotspots of elevated $NH_4^+$-N. DON had mostly low values to the north and east regions of the study area. This pattern generally remained similar while concentrations increased from summer to autumn. At the pH levels found at this study site, total dissolved carbon is in the form of dissolved organic carbon (DOC). Ranges for DOC were similar for both seasons, from 29.3 to 98.0 and 25.2 to 116.3 mg $L^{-1}$ for summer and autumn, respectively. A spatial clustering of high DOC concentrations was located in the central and southern areas of the study site.
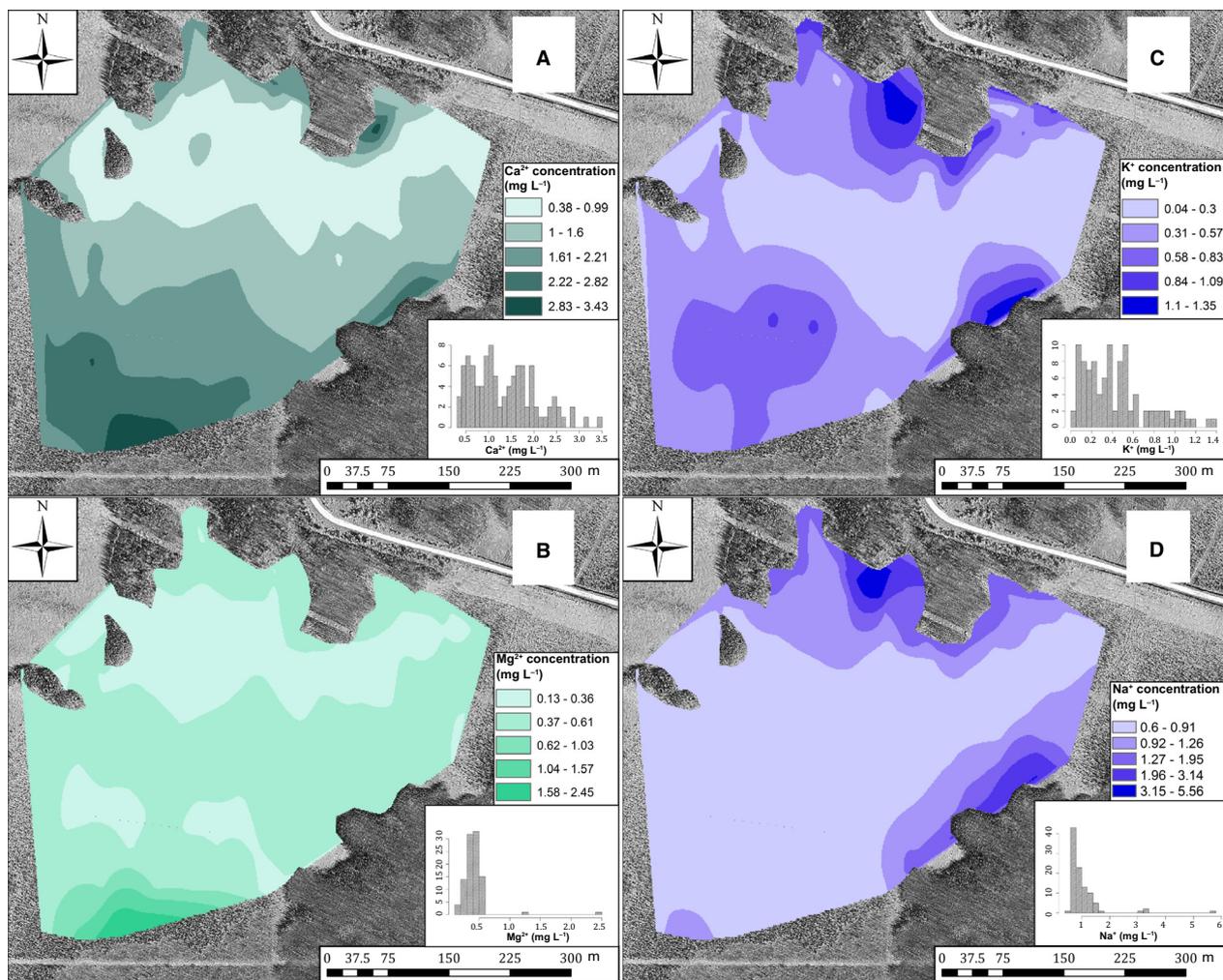
*Fig. 3.* Spatial representation of base cation concentrations (mg L$^{-1}$) in pore water at the Mariana Lake peatland complex: (A) calcium, (B) magnesium, (C) potassium and (D) sodium. Distribution of each variable shown on each map in embedded histogram with frequencies on the y-axis across the data range on the x-axis. For all maps lower values are characterized by lighter colours and higher values by darker colours. Spring water-chemistry maps are found in the left column, and autumn in the right column.

## Multivariate linkages

In ordination space, the three peatland interior ecosites have little overlap, yet form a continuous gradient (Fig. 4). Plots belonging to the FM were separate from the peatland interior groups. Bog plots demonstrated the least variable placement in ordination space, while those in the DF, WF and FM ecosites were more variable in ordination space. The first (x) NMDS axis distinguishes the FM from the WF ecosite, as well as separating the bog from the DF ecosite. The second (y) axis divides the WF and FM from the DF and bog.

Fourteen vectors have highly significant fit to the ordination ($p < 0.01$). Vector bearing is indicative of the direction of maximum correlation of increasing values in ordination space and the length of the vector represents the strength of correlation. Spring and autumn pH had the strongest fit to the ordination –

highest in FM plots and lowest in DF plots. DOC (TC) orientation changed little between seasons, but approximately doubled in strength in the autumn in the direction of the bog, indicating strong DOC increases in the bog plots in autumn. The two physical parameters, shade and DTW, both fit in a similar fashion, increasing towards the bog and FM. Total nitrogen and DON were probably autocorrelated because DON is the dominant component of total nitrogen (75% – spring, 83% – autumn) in the peatland complex. Total nitrogen demonstrated a shift in orientation from FM in the spring towards the bog plots in the autumn. Inorganic N forms failed to produce significant vectors. Of the base cation vectors, only Ca$^{2+}$ and Na$^+$ were highly significant, and orientated in perpendicular directions. Elevated Ca$^{2+}$ concentrations were strongly associated with the FM and to a lesser extent the bog along the first NMDS axis, whereas high Na$^+$

*Table 3.* Mean values of environmental variables and seasonal pore-water chemistry across the Mariana Lake complex peatland ecosites.

| Parameter | Wet fen Spring | Wet fen Autumn | Dry fen Spring | Dry fen Autumn | Bog Spring | Bog Autumn | Fen margin Spring | Fen margin Autumn |
|---|---|---|---|---|---|---|---|---|
| Depth to water (cm) | 10.9$^c$ (3.3) | | 12.9$^{b,c}$ (3.6) | | 18.5$^a$ (4.9) | | 14.7$^{a,b}$ (4.1) | |
| Shade (%) | 0.03$^b$ (0.15) | | 0.9$^b$ (2.1) | | 17.1$^a$ (15.3) | | 27.2$^a$ (19.1) | |
| Ca$^{+2}$ (mg L$^{-1}$) | 1.06$^b$ (0.65) | | 1.17$^b$ (0.56) | | 1.82$^a$ (0.72) | | 1.44$^{a,b}$ (0.67) | |
| K$^+$ (mg L$^{-1}$) | 0.53 (0.40) | | 0.37 (0.29) | | 0.40 (0.24) | | 0.46 (0.29) | |
| Mg$^{+2}$ (mg L$^{-1}$) | 0.38 (0.12) | | 0.38 (0.11) | | 0.51 (0.46) | | 0.41 (0.10) | |
| Na$^+$ (mg L$^{-1}$) | 1.42$^a$ (1.09) | | 0.88$^b$ (0.25) | | 0.79$^b$ (0.10) | | 1.09$^{a,b}$ (0.59) | |
| $d$-excess (‰) | 3.73$^{a,b}$ (1.39) | | 3.06$^b$ (1.29) | | 3.97$^a$ (0.71) | | 4.12$^a$ (1.38) | |
| $\delta^2$H | −137.45 (1.57) | | −137.06 (1.92) | | −137.14 (2.36) | | −136.86 (1.71) | |
| $\delta^{18}$O | −17.65 (0.31) | | −17.51 (0.36) | | −17.64 (0.29) | | −17.62 (0.30) | |
| Species richness | 13.83$^c$ (2.53) | | 16.77$^b$ (3.04) | | 18.08$^b$ (2.36) | | 21.43$^a$ (2.38) | |
| pH | 4.15$^{b,1}$ (0.16) | 4.00$^{b,2}$ (0.16) | 4.00$^{b,1}$ (0.16) | 4.00$^{b,2}$ (0.16) | 3.94$^{c,1}$ (0.14) | 3.82$^{c,2}$ (0.09) | 4.33$^{a,1}$ (0.43) | 4.14$^{a,2}$ (0.28) |
| Reduced conductivity (µS cm$^{-1}$) | 18.3$^{a,b}$ (6.9) | 15.4$^b$ (7.6) | 16.7$^b$ (8.5) | 17.9$^{a,b}$ (5.6) | 19.1$^{a,b}$ (4.5) | 14.3$^b$ (4.4) | 17.9$^a$ (9.9) | 23.1$^a$ (5.6) |
| NH$_4^+$-N (mg L$^{-1}$) | 0.17$^{a,b}$ (0.03) | 0.14$^{b,c}$ (0.11) | 0.17$^a$ (0.05) | 0.20$^a$ (0.14) | 0.13$^{a,b,c}$ (0.04) | 0.20$^b$ (0.13) | 0.18$^a$ (0.05) | 0.12$^c$ (0.08) |
| NO$_3^-$-N (mg L$^{-1}$) | 0.02$^a$ (0.04) | 0.00$^b$ (0.00) | 0.05$^{d,e}$ (0.08) | 0.00$^b$ (0.00) | 0.02$^a$ (0.02) | 0.00$^b$ (0.00) | 0.06$^a$ (0.06) | 0.01$^b$ (0.02) |
| DON (mg L$^{-1}$) | 0.46$^c$ (0.13) | 0.70$^{b,c,d}$ (0.09) | 0.56$^{d,e}$ (0.19) | 0.83$^b$ (0.15) | 0.68$^{c,d}$ (0.20) | 1.00$^a$ (0.23) | 0.71$^{b,c,d}$ (0.17) | 0.82$^{b,c}$ (0.14) |
| TC (mg L$^{-1}$) | 51.34$^{b,c}$ (9.8) | 41.83$^c$ (8.9) | 58.97$^b$ (12.2) | 59.51$^b$ (19.2) | 58.04$^b$ (14.5) | 75.22$^a$ (20.6) | 57.82$^b$ (16.1) | 53.50$^{b,c}$ (13.5) |
| TC/DON | 115.6$^a$ (16.6) | 59.9$^d$ (7.4) | 110.1$^a$ (21.0) | 70.2$^{c,d}$ (10.8) | | | | |

SDs in parentheses. Superscript letters/numbers indicate post hoc differences (Tukey's HSD). Letters denote differences in community and numbers indicate seasonal differences.
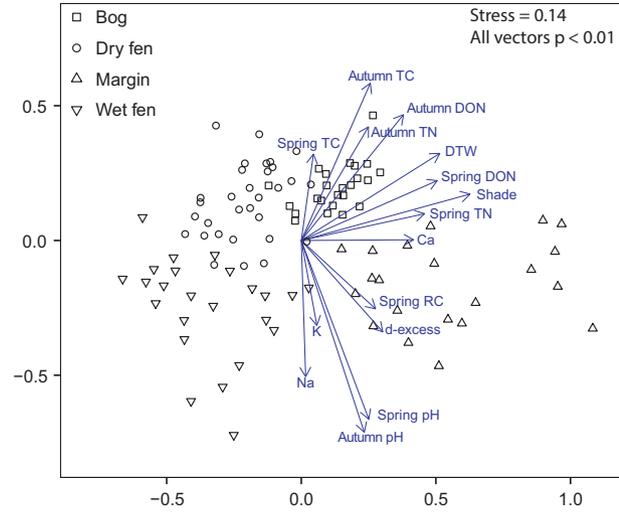


*Fig. 4.* NMDS ordination based on Bray–Curtis dissimilarity of the 100 plots in the peatland complex. Symbols represent the four species assemblages and vectors represent significant environmental vectors ($p < 0.01$). Vector bearing is orientated in direction of increasing values and length is proportional to the strength of fit to the ordination. TN = total nitrogen; TC = total carbon; DTW = mean depth to water table; RC = reduced conductivity; DON = dissolved organic nitrogen. $R^2$ of ordinations in decreasing strength are: autumn pH = 0.56, spring pH = 0.50, shade = 0.42, autumn TC = 0.41, DTW = 0.37, autumn DON = 0.36, spring DON = 0.30, Na = 0.26, autumn TN = 0.24, spring TN = 0.22, $d$-excess = 0.21, Ca = 0.17, spring RC = 0.14, spring TC = 0.10.

concentrations fit between the FM and WF along the second NMDS axis.

Across the ecosite groups, mean DTW decreased from bog>FM>DF>WF. Only in a few instances (n = 5) did either the WF or DF have any measureable shade. $d$-excess values were highest in the FM and lowest in the DF and bog ecosites. Both Ca$^{2+}$ and Na$^+$ had differences between groups, while Mg$^{2+}$ and K$^+$ did not differ. Ca$^{2+}$ concentrations were highest in the bog and FM and lowest in the DF and WF. Na$^+$ concentrations were highest in WF and FM ecosites and lowest in the DF and bog (Table 3).

Many pore-water parameters differed between the ecosites and season (Table 3). Seasonal pore-water variables changed differently between the ecosite groups, resulting in interactions for all parameters, with the exception of pH and NO$_3^-$-N. The FM had the highest pH; the lowest pH values were in the DF and bog. A near uniform drop of pH occurred in all ecosites from the summer to the autumn. No ecosites had a significant seasonal change in reduced conductivity. Differences in reduced conductivity only existed in the autumn, with the FM having higher conductivity compared to the WF and bog. NH$_4^+$-N values increased from summer to autumn in the bog, decreased in the FM and remained similar in the WF and DF. Levels of NO$_3^-$-N were extremely low in both seasons, but dropped to near-undetectable levels in the autumn.

All ecosites with the exception of the FM experienced a significant increase in DON concentration, most notably the bog. Summer DOC concentrations were similar for all groups. Autumn DOC concentrations in the FM and DF did not change seasonally, dropped slightly in the WF and increased significantly in the bog.

## Discussion

### Description of plant assemblages and ecosites

The common peat mosses, *Sphagnum angustifolium*, *S. magellanicum* and *S. fuscum*, form a near-continuous undulating cover across the study site (Table 1). Amongst these dominating *Sphagnum* species, multivariate techniques segregate four floristically distinct species assemblages (Figs 2B, 3), each having unique indicator species (Table 2). Due to plot areas that encompass both hummocks and hollows, these findings suggest the existence of independent species associations within the Mariana Lake peatland complex that extend beyond the traditional generalized view of upland, poor fen and bog, as well as hummock and hollow topography.

Species assemblages in the fen margin were the most variable, indicated by the large spread in ordination space (Fig. 4). The fen margin assemblage often contains a mixture of sphagna, true mosses and vascular species not found in the peatland interior (i.e. *Sphagnum russowii*, *Polytrichum commune*, *Salix pedicellaris* and *Calamagrostis canadensis*), as well as sharing species with the other assemblages (i.e. *Rubus chamaemorus*, *Vaccinium vitis-idaea*, *Rhododendron groenlandicum* and *Aulacomnium palustre*). The fen margin has a shallower organic layer than that of the interior fen and bog and is influenced by shallow groundwater, both factors contributing to differing edaphic and hydrological conditions.

The wet fen–dry fen–bog gradient formed by the three peatland interior species assemblages signifies a gradual species transition from a wet mesotrophic environment to a drier ombrotrophic environment. Species assemblages in the wet fen are characterized by lawns and carpets of *S. angustifolium*, and occasionally *Sphagnum fallax*, with *Carex aquatilis* as the dominant vascular species. *Carex limosa* and *Scheuchzeria palustris* are also constant throughout the wet fen. The carpets and lawns of *S. angustifolium* in the wet fen are nearly always at full water saturation. Compared to the other assemblages, the wet fen is lacking in ericaceous shrubs such as *Rhododendron groenlandicum*, and herbaceous species such as *Smilacina trifolia* and *Rubus chamaemorus*. The wet fen also contains low hummocks with *S. magellancum* on the sides, which are occasionally topped by *S. fuscum* and *Polytrichum strictum*.

The dry fen assemblage becomes apparent farther into the fen expanse (Fig. 2B), and represents the largest number of sample units in the study (n = 31). The main floristic distinction of the dry fen from the wet fen is the lack of cover from the robust sedges *Carex aquatilis* and *C. utriculata*; these species being replaced with an abundance of the tussock-forming *Eriophorum vaginatum*. Extensive lawns of *S. fuscum* and an abundance of dwarf shrubs are dominant features across the dry fen. Wet lawns of *Sphagnum lindbergii* and *S. angustifolium*, and a few occurrences of *Sphagnum riparium* occasionally interrupt the drier *S. fuscum* lawns. Smaller graminoids such as *Scheuchzeria palustris*, *Carex limosa* and *Carex livida* are often found on these lawns, along with a mixture of liverworts including *Mylia anomala* and *Cladopodiella fluitans*, and occasionally the bryophyte *Warnstorfia fluitans*. The increase in depth to water table near the southern edge of the dry fen is met with a gradual increase in size and density of *Picea mariana* as the dry fen slowly transitions to bog vegetation. The dry fen is set apart from the bog by a lack of *L. groenlandicum* and *V. vitis-idaea*, and a lesser abundance of true mosses. The presence of *R. chamaemorus*, a species representative of ombrotrophic conditions, as a shared indicator of the dry fen and bog represents a shift towards ombrotrophy in the dry fen (Vitt 2006). A few large remnant tree snags (standing but dead trees) are present in the dry fen, suggesting that at one point this area supported large individuals of *P. mariana*.

At the dry end of the interior peatland gradient are two bogs. The most prominent feature of these areas is the presence of mature *Picea mariana*. Tree rings indicate that the bogs have not burned recently and that the mature *P. mariana* date to 110 years (J. A. Graham, unpublished data). In addition to *P. mariana*, the bogs differ from the other ecosites by the appearance of true mosses, abundant cover of ericaceous shrubs, and the herbaceous species *S. trifolia* and *R. chamaemorus*. Shrubs in the bog are much larger than in the dry fen. The burn line seen at the southern edge of the aerial photo separates an area burned by a recent fire (Fig. 1), and high cover of *P. strictum* in the burned area indicates that the fire occurred 10–15 years ago (Benscoter & Vitt 2008). This recent fire (i.e. The House River fire) may have resulted in a local water-table rise, leaving the study site slightly wetter than in the recent past. The mean depth to water table in the bog (18.5 cm) is markedly shallower than bogs from other studies (~20–70 cm; Vitt & Slack 1984; Thormann & Bayley 1997; Turetsky *et al.* 2008; Wieder *et al.* 2009). Wetter conditions in this bog may have potentially slowed the proliferation of mature dry bog species such as *Pleurozium schreberi* and *Dicranum undulatum*, while still favouring *Sphagnum* dominance, in particular *S. angustifolium*. Nevertheless, the mature bog still contains characteristic bog species, including

several members of the lichen genus *Cladonia*, all of which prefer drier habitats. The northeastern bog lying near the road is slightly wetter compared to the southern bog (Fig. 2C). Parameters similar between the two bogs are depth to water table, shade, pH and sodium. Depth to water table, shade and pH are amongst the most significant variables associated with species occurrences in the two bogs, suggesting that the differences in other attributes are less likely to alter species composition. The northeastern bog lacks the abundance of *Cladonia* species and has present *Carex pauciflora*, a small sedge not present in the southern bog. Regardless of these differences, the tight clustering of the bog sample units in the ordination demonstrates the relatively consistent species composition found in the species assemblages of the bog ecosite.

## Environmental factors – physical

The physical factors in this study, depth to water table and shade, have clear spatial patterning, differ between species assemblages and are strongly linked to ecosite patterns. The spatial patterning of depth to water table is closely related to the patterning of the species assemblages, most notably those within the bog, wet fen and dry fen. It has been previously noted that both shade and depth to water table are closely related to the local arrangement of *Sphagnum* species (Vitt & Slack 1984; Gignac 1992), as well as members of the Cyperaceae (Gignac *et al.* 2004). The positioning of these *Sphagnum* species, each with unique morphologies and population characteristics, interacts with the distribution of the vascular plant morphologies, particularly the rooting strategies. In hummocks, vascular plants, mostly dwarf shrubs of the Ericaceae, provide supportive frameworks for *Sphagnum* species that retain water by forming dense canopies, allowing *Sphagnum* growth at higher distances from the water table. Conversely, in lawns and carpets, where sedges generally have deep penetrating aerenchymatous roots, which provide little structure, flat wet depressions filled with loose canopies of *Sphagnum* are found (Malmer *et al.* 1994). At the Mariana Lake peatland complex, depth to water table is a major factor delimiting species occurrence along the wet fen–bog gradient.

Shade was also a key environmental variable. This is due to the strong association of shade with the fen margin and bog ecosites, with the two habitats differing both chemically and floristically. Shade and depth to water table are highly correlated, which can be attributed to the presence of *Picea mariana* that only occurs on aerobic substrates (Islam *et al.* 2003); thus, shade and depth to water table have a synergistic relationship relating to both floristic and chemical surroundings.

Based on the Global Network for Isotopes in Precipitation database (https://www.iaea.org/water), Edmon-

ton precipitation sampled in the 1960s had a *d*-excess value averaging close to 5.5‰ whereas Fort Smith had a value of 4.6‰. We can expect similar values for non-evaporated waters in the Mariana lakes area. In comparison, *d*-excess values in the wetland ranged from 0.64 to 6.46‰. Higher values apparently reflect a long-term mixture of precipitation and groundwater sources, whereas low *d*-excess is associated with summer rainfall and evaporative isotopic enrichment, which occurs in proportion to evaporation/inflow. The systematic *d*-excess patterns observed across the wetland suggest that these variations arise more from mixing conditions and evaporation than due to short-term variations in precipitation input. Spatially, we can infer that evaporation/inflow is reduced in the southern bog, along much of the western edge of the study area, and along the perimeter of the northern upland where higher *d*-excess is found. The west to east 'bulls-eye' of low *d*-excess values corresponds well with low values of most ions and may be attributed to lower residence time, ponding/evaporation and ions being moved farther along the drainage path. High *d*-excess values are linked to high depth to water-table values and shade, both factors that limit evaporative loss.

## Environmental factors – pore-water chemistry

The seasonal averages of pH were consistent with previous measurements of poor fens and bogs of western Canada (Vitt & Chee 1990; Malmer *et al.* 1992; Vitt 2006). In contrast to Vitt *et al.* (1995), who found very little seasonal change in pH, all of the ecosites in the Mariana Lake complex demonstrated an overall decline in pH over the course of the growing season (Table 3). Vector orientation was consistent for both seasons, and pH had the strongest fit to the ordination, suggesting that while the variation of pH in the peatland complex is small, the subtle gradients of pH are strongly linked to ecosite patterns.

With the exception of a few outliers, all four base cation concentrations fell within Albertan bog and poor fen ranges (Malmer *et al.* 1992). Of interest are calcium concentrations in the bog ecosites that are significantly higher than the remaining interior poor fen ecosites. Spatially this is most evident in the large southern bog (Fig. 3A). This is unlike patterns shown in other Albertan peatlands, where higher calcium values are associated with more minerotrophic habitats (Malmer *et al.* 1992; Vitt *et al.* 1995). Similar to that of Vitt & Chee (1990), calcium has the highest mean concentration across the peatland complex, whereas sodium has the single highest concentration along the fen margin. Although the entire site is within the calcium tolerance range for *Carex aquatilis*, albeit the lower end (Gignac *et al.* 2004), *C. aquatilis* is confined to the wet fen and fen margin, where sodium and potassium concentrations are higher, suggesting that

these cations exert some influence in governing the distribution of this regionally abundant sedge. The higher concentrations of sodium and to a lesser extent potassium are probably the result of their spatial proximity to uplands with mineral soil, while higher concentrations of calcium in the southern bog may be the result of stagnation (Fig. 3). The influence of mineral soil uplands on the peatland interior weakens rapidly, within 5–20 m, with increasing distance from the upland.

Pore-water inorganic nitrogen levels within the complex are characteristic of nutrient concentrations previously measured in western Canadian bogs and poor fens (Vitt *et al.* 1995; Bayley *et al.* 2005) (Table 3). Due to low pH levels, nitrification and denitrification are both unimportant in poor fens and bogs; thus, nitrate is generally lacking in pore water. Nitrate concentrations can spike in spring owing to snow-melt (Driscoll *et al.* 2001; Basiliko *et al.* 2005), providing additional nitrate inputs. At the Mariana Lakes site, nitrate was only detectable in early summer, and absent in autumn, suggesting that new inputs of nitrate are rapidly taken up and removed from the pore-water column. With the exception of a few autumn hotspots, ammonium concentrations were stable and uniform.

The greatest proportion of total dissolved nitrogen at this site is DON. Bragazza & Limpens (2004) found similar proportions across European bogs and concluded that DON concentrations are partly due to growth response and leaching from *Sphagnum*. At our peatland DON concentrations increased in all ecosites except the fen margin over the growing season (Table 3). The greatest seasonal DON concentration increase occurred in the bogs, markedly so in the southern bog (Figs 2I, N, 4B). Spatially, patterns of DOC seasonal increase were similar to that of DON. Ongoing decomposition and high residence time of water in the southern section of the study area are strongly associated with high levels of DOC and DON.

## Conclusions

In summary, our study site at Mariana Lake is hydro-topographically typical of oligotrophic poor fen/bog peatland complexes of the western Canadian boreal plain. Here, for the first time, we describe the ecological intricacies of such a complex. Species assemblages are organized into four significantly unique ecosites within this peatland complex and are also differentiated based on a complex set of variables, including a combination of shade, depth to water table, pH, evaporative losses and nutrient variables. Base cations play only a small role in differentiating these ecosites. The four ecosites have clear spatial patterns across the peatland landscape, and are spatially related to a number of environmental factors. Of most importance are two factors: (i) increases in pH and sodium along marginal areas due to influences from mineral substrates, and (ii) more importantly, differences in evaporative loss of water within the complex, with areas of vascular plant canopies or marginal areas associated with a number of key water-chemistry parameters. These include conductivity, DON, calcium and potassium, all higher in areas with low evaporative loss compared to those with higher evaporative loss and flow. Thus, in this peatland complex, areas within the bog and marginal ecosites have higher amounts of these chemical factors when compared to the two poor fen ecosites. We conclude that differences in evaporative loss are a major factor in explaining pore-water patterns; however, the control of evaporative loss is largely due to a complex set of autogenic processes of plant assemblage development linked to interactions with shade and depth to water table, and/or shallow groundwater influences.

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