Ecology / Écologie

# Environmental factors explaining the vegetation patterns in a temperate peatland

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## Abstract

Although ombrotrophic temperate peatlands are important ecosystems for maintaining biodiversity in eastern North America, the environmental factors influencing their flora are only partly understood. The relationships between plant species distribution and environmental factors were thus studied within the oldest temperate peatland of Québec. Plant assemblages were identified by cluster analysis while CCA was used to related vegetation gradients to environmental factors. Five assemblages were identified; three typical of open bog and two characterized by more minerotrophic vegetation. Thicker peat deposit was encounter underlying the bog assemblages while higher water table level and percentage of free surface water distinguished the minerotrophic assemblages. Overall, the floristic patterns observed were spatially structured along the margins and the expanse. The most important environmental factors explaining this spatial gradient were the percentage of free surface water and the highest water-table level. *To cite this article: S. Pellerin et al., C. R. Biologies 332 (2009).*
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## Résumé

**Patrons de végétation et gradients environnementaux dans une tourbière tempérée.** Bien que les tourbières ombrotrophes des régions tempérées de l'est de l'Amérique du Nord soient importantes pour le maintien de la biodiversité régionale, les facteurs influençant leurs communautés végétales demeurent peu connus. Les relations entre la végétation et les facteurs environnementaux ont été étudiées dans une tourbière du sud-ouest du Québec. Les assemblages floristiques ont été identifiés à l'aide d'une analyse de groupement tandis qu'une CCA a permis de relier les gradients végétaux aux facteurs environnementaux. Cinq assemblages ont été identifiés ; trois typiques des tourbières ombrotrophes et deux caractérisés par une flore d'appartenance minérotrophique. Les dépôts organiques étaient plus épais sous les assemblages ombrotrophiques alors que les groupements minérotrophiques étaient caractérisés par un pourcentage d'eau libre et une nappe phréatique plus élevés. Globalement, la végétation se répartissait selon un gradient spatial du centre à la bordure. Les principaux facteurs environnementaux sous-jacents ce gradient sont le pourcen-

tage d'eau libre et le niveau le plus élevé de la nappe phréatique. ***Pour citer cet article : S. Pellerin et al., C. R. Biologies 332 (2009).***

## 1. Introduction

A major scientific challenge in plant ecology is to identify and quantify the strength of environmental factors that are responsible for the distribution and abundance of plant species within and among ecosystems. Ecological factors explaining vegetation patterns in peatlands of the northern hemisphere have been investigated in several studies since the 1950s (e.g., [1–7]). According to these studies, the floristic variation in peatlands is mainly controlled by three ecological gradients: acidity–alkalinity, availability of nutrients and water table depth. A margin-expanse gradient is also frequently depicted. However, the ecological factors explaining this gradient are complex and vary from site to site [5,8]. Locally, secondary gradients such as peat thickness or shading may also be important, especially for bryophytes [9–11].

In North America, several studies have attempted to identify the relationships between environmental factors and vegetation patterns on continental western boreal (e.g., [3,12–14]) or maritime peatlands (e.g., [15,16]). In contrast, few studies have been undergone in pristine ombrotrophic temperate peatlands and especially in southern Québec [17] and adjacent New England States [10,18], although those peatlands are very important for maintaining regional biodiversity [19–21]. Such studies are difficult in these regions because most of the peatlands have been disturbed by several anthropogenic activities [19] that altered, or obscured, the controlling influence of environmental factors [20,21]. In this context, the aims of this study were: (1) to describe the plant species assemblages within a temperate peatland of southwestern Québec; and (2) to identify the environmental factors responsible of their distribution patterns. To achieve our objectives, we sampled one of the last nearly untouched peatlands of south-western Québec; the Covey Hill peatland. This peatland is also part of a multidisciplinary research network devote to enhance understanding of hydrological and ecological processes of an important recharge area for the regional aquifer.

## 2. Methods

### 2.1. Study area

Covey Hill, located around 100 km south of Montréal (Québec, Canada) along the Canadian/United States border (New York State), constitutes the northern foothills of the Adirondacks Mountains (Fig. 1). It covers an area of approximately 100 km$^2$ and rises to about 340 m a.s.l. The north and east slopes of the hill are relatively steep (10% slope gradient) while the western slopes gentle down towards the St. Lawrence plain. To the south, the relief is undulating and extends into the next formation of the Adirondacks. The hill is made up of sandstones of the Postdam Group represented by the Covey Hill and Cairnside formations [22]. Thick deposits of reworked till and fluvioglacial sediments are present at the base of the hill [23], while exposed sandstone pavements (known as Flat Rocks) are present locally at its top. On steep slopes, the soils are thin (between 30 and 60 cm thick) or virtually nonexistent whereas pockets of thick soils are present on western slopes [24].

The regional forests belong to the Great Lakes and St. Lawrence region [25] and to the sugar maple-bitternut hickory bioclimatic domain of Québec [26]. On mesic sites, forests are mainly composed of *Acer saccharum*, *Carya cordiformis*, *Tilia americana*, *Fraxinus americana, Fagus grandifolia* and *Betula alleghaniensis*. The hill also shelters some exceptional plant communities not found elsewhere in southern Québec such as Pine Barrens (*Pinus strobus*, *P. resinosa*, *P. banksiana*) and mature hemlock groves (*Tsuga canadensis*).

The regional climate is humid continental with hot summer, cold winter and abundant precipitation. The mean annual temperature is about 6.1 °C. The mean temperatures in January (coldest month) and July (warmest month) are −9.7 and 20.6 °C, respectively. The mean annual precipitation is 929 mm, 17% of which falls as snow [27].

The Covey Hill peatland (45°00′29″N; 73°49′36″W) is a 54 ha *Sphagnum*-dominated bog located near the
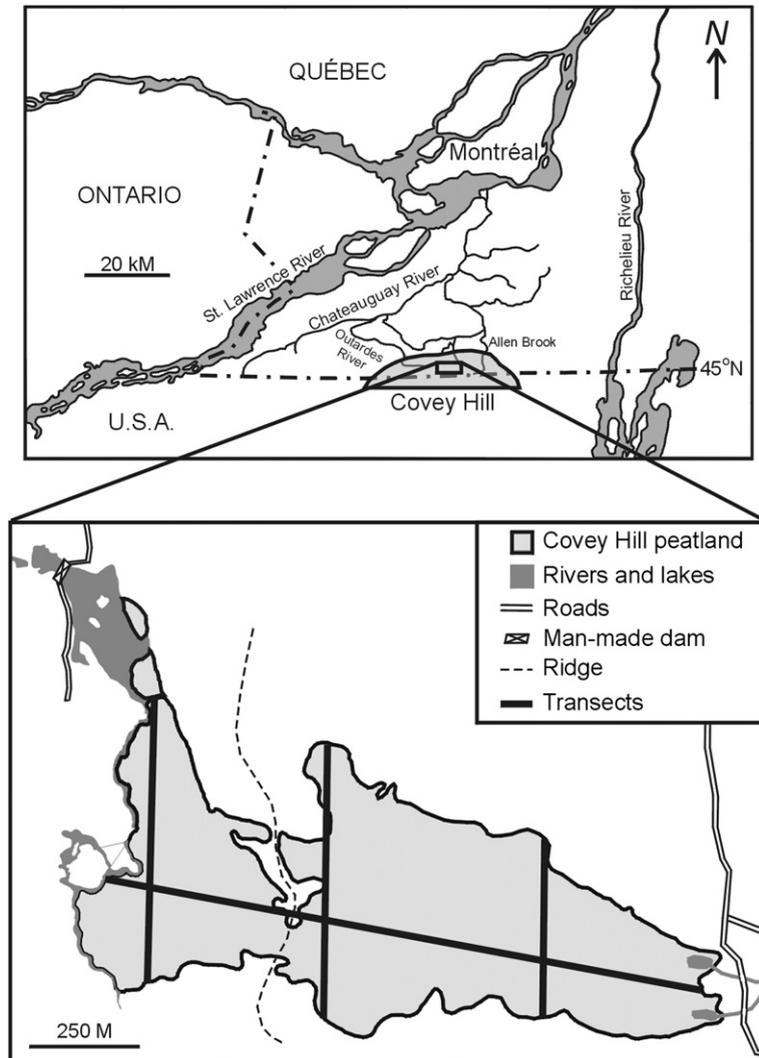
Fig. 1. Location of the study area (south-western Québec, Canada) and spatial distribution of the vegetation transects in the Covey Hill peatland.

summit of the hill, at an elevation of approximately 300 m. The organic deposit lies directly on the fractured sandstone of the Covey Hill formation. Peat thickness reaches a maximum of 360 cm, but thicknesses are highly variable locally due to the step-like morphology of the underlying bedrock [28]. A $^{14}C$ date of 13 925 cal. BP (Beta-245303) was obtained at the bottom of a 350 cm-thick core, making this peatland the oldest known in Québec province (M. Lavoie, unpublished data). The bog is mainly characterized by shrub heath communities with a continuous ground cover of *Sphagnum* mosses and with a well developed hummocks and hollows micro-topography. A ridge divided the bog into two drainage basins (Fig. 1). Outflow from the peatland occurs westward to the Outardes East River and eastward by two outlets that feed Blueberry

Lake and the Allen Brook [29]. A man-made dam was erected at the Outardes East outlet in the 1980s and caused the flooding of the western basin. Small beaver dams are also present at the two eastern outlets creating small pounds (around 10–20 m diameter) of open water. The peatland is fed by direct precipitation and by lateral groundwater input from the surrounding fractured bedrock aquifer [30]. The peatland is located in a headwater basin. The groundwater is therefore not highly mineralized. A shallow well located 200 m from the peatland has a pH of 5 and a corrected electrical conductivity of 28 μS/cm. This pH is higher than those found in the peatland at the same time (<4) while the electrical conductivity is similar [30]. This similarity could be explained by the fact that the groundwater is feeding laterally the upper layers of the peatlands.

In 2006, Nature Conservancy of Canada, which preserved several areas on the hill and one third of the bog, created the Covey Hill Natural Laboratory [29]. This Laboratory aims to generate knowledge that will lead to better protection of the groundwater resources of this important recharge area as well as of exceptional plant and animal communities found on the hill. A multidisciplinary team of ecologists, hydrologists, paleoecologists and conservation managers have now access to permanent sampling stations; several of them being located in the bog.

### 2.2. Vegetation sampling

Vegetation was sampled within 59 plots (5 × 5 m) located 50 m apart along three north–south transects and along an east–west transect (Fig. 1). Only plots located on organic deposits of at least 30 cm-thick were sampled. A point-intercept sampling method was used to estimate the relative cover of each plant species within plots. More precisely, we established six equidistant lines (1 m interval) within each plot and recorded all vascular plants, mosses, liverworts and lichens touching the projection of a vertical rod placed every meter along each lines ($N = 36$ points). Species nomenclature followed the PLANTS Database [31], except for *Rhododendron groenlandicum* (Oeder) Kron & Judd.

### 2.3. Environmental variables

We measured the diameter at breast height (dbh) of each tree (dbh $\geqslant$ 1 cm) located in each plot to estimated the tree basal area. Tree basal area was used as an indicator of the importance of tree cover and shading. We also estimated the percentage of free surface water and the groundwater table position below the peat surface every two weeks from excavated wells located in hollows. Only the highest and lowest levels were later used for analyses. Two water samples (25 ml) were collected in May from wells in sterilized polyethylene bottles and store at 4 °C until analyses. The water pH and electrical conductivity were later measured in the laboratory. Conductivity values were adjusted to 20 °C and corrected for the concentration of hydrogen ions [1]. Since corrected conductivity and pH are relatively constant throughout the ice-free season [32], a unique estimation of these variables is sufficient. We did not analyze the water samples for nutrient availability, because it is not consider as a key factor explaining vegetation pattern in poor fens and bogs due to negligible concentrations [6, 33]. Finally, we measured the distance of each sampling plot to the nearest margin (linear transition from peat

deposit to mineral soil) and the peat deposit thickness by manual probing.

### 2.4. Data analyses

Prior to analyses, rare species (sum of percent cover across all plots <10%) were removed from the database (9 species removed). Plant species assemblages were identified using Ward's hierarchical clustering with Euclidean distance which gave the clearest and the more rational results. Then a discriminant analysis was performed to identify which species (hereafter referred to as indicator species) best separate plots between assemblages [34]. The assumptions of normality and homoscedasticity for discriminant analysis were met (Shapiro–Wilk test). Differences in environmental variables and species richness between the species assemblages were tested using one-way ANOVAs. When needed data were rank-average transformed to meet the assumption of normality and homogeneity of variances. Basal area and corrected conductivity variables were not normally distributed even after transformation (too many zeros); we thus did randomization tests for simple one-way ANOVA. Post-hoc multiple comparisons were performed using Tukey HSD. Relationships between vegetation and environmental variables were examined using a canonical correspondence analysis (CCA) [35]. To evaluate the significance of environmental variables within the CCA, a Monte Carlo test was run with 999 unrestricted permutations [36]. Clustering and discriminant analyses were performed using SAS 8.2 (SAS Institute Inc.), ANOVAs and post-hoc comparisons with JMP 7.0.1 (SAS Institute Inc.), randomization tests with ECOSIM 7.0 (Acquired Intelligence Inc.) and CCA and Monte Carlo tests were done with CANOCO 4.5 [Microcomputer Power].

## 3. Results

A total of 56 plant species were recorded in the Covey Hill bog and most of them are typical of ombrotrophic peatland (Table 1). These species comprised seven trees, 16 shrubs, 19 herbs and grasses, two lichens and 12 mosses. They belongs to 25 families; the more common being Ericaceae (nine species), Cyperaceae (nine species) and Sphagnaceae (six species). *Chamaedaphne calyculata* is by far the dominant vascular species covering more than 50% of the sampling plot area in 63% of the plots. *Maianthemum trifolium* is also very common covering more than 50% of the plot area in 24% of the plots. *Sphagnum fallax* is the only

Table 1

Mean percent cover of the species recorded within the five plant species assemblages at the Covey Hill peatland, south-western Québec. Bold indicates indicator species according to discriminant analysis ($p < 0.05$). The habitat preference of each species when growing in peatland is also indicated. Species assemblage number: (1) *Chamaedaphne calyculata–Sphagnum angustifolium* bog, (2) *Chamaedaphne calyculata–Kalmia angustifolia–Sphagnum fallax* bog, (3) *Chamaedaphne calyculata–Sphagnum fallax* bog, (4) *Alnus incana* ssp. *rugosa–Chamaedaphne calyculata–Sphagnum fallax* swamp, (5) *Alnus incana* ssp. *rugosa–Calla palustris–Sphagnum fallax* lagg.

| Plant species assemblages | | | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|---|---|
| Average species number | | | 11 | 11 | 10 | 15 | 18 |
| Number of stations | | | 3 | 21 | 6 | 15 | 14 |
| Plant species | Family | Habitat[a] | | | | | |
| **Acer rubrum** | Sapindaceae | Poor fen | – | 0.4 | – | 2.6 | 19.7 |
| **Alnus incana** ssp. **rugosa** | Betulaceae | Poor fen | 0.9 | 3.8 | 6.4 | 19.6 | 23.3 |
| **Andromeda polifolia** var. **glaucophylla** | Ericaceae | Bog | 24.1 | – | – | 1.6 | – |
| Aulacomnium palustre | Aulacomniaceae | Bog | – | 0.9 | 0.9 | 2.4 | 2.1 |
| Betula alleghaniensis | Betulaceae | Rich fen | – | – | – | – | 0.6 |
| **Betula populifolia** | Betulaceae | Poor fen | 1.9 | 0.8 | 0.5 | 6.6 | 1.7 |
| **Calla palustris** | Araceae | Moderate fen | – | 0.3 | 9.3 | 4.4 | 37.2 |
| Carex aquatilis | Cyperaceae | Poor fen | – | – | 0.5 | 6.4 | 12.6 |
| **Carex brunnescens** | Cyperaceae | Poor fen | – | – | – | – | 23.5 |
| Carex canescens | Cyperaceae | Poor fen | – | – | – | 0.8 | 0.2 |
| Carex crinita | Cyperaceae | Rich fen | – | – | – | – | 0.2 |
| **Carex magellanica** ssp. **irrigua** | Cyperaceae | Poor fen | – | – | – | 0.8 | 8.9 |
| Carex oligosperma | Cyperaceae | Poor fen | – | 0.3 | – | 10.3 | – |
| Carex trisperma | Cyperaceae | Bog | – | 0.1 | 2.3 | 2.6 | 11.3 |
| **Chamaedaphne calyculata** | Ericaceae | Bog | 53.7 | 76.0 | 91.2 | 66.5 | 4.9 |
| Cladina rangiferina | Cladoniaceae | Bog | – | – | – | 0.8 | – |
| Cladina stellaris | Cladoniaceae | Bog | – | – | – | 0.2 | – |
| Cornus canadensis | Cornaceae | Rich fen | – | – | – | – | 0.4 |
| Dicanum undulatum | Dicranaceae | Bog | – | – | – | 0.2 | – |
| Drosera rotundifolia | Droseraceae | Bog | – | 1.5 | – | – | 0.4 |
| **Eriophorum vaginatum** ssp. **spissum** | Cyperaceae | Bog | 10.2 | 23.2 | – | 0.6 | 1.1 |
| Gaultheria procumbens | Ericaceae | Bog | – | 1.0 | – | – | – |
| Hypericum ellipticum | Clusiaceae | Moderate fen | – | – | – | – | 0.6 |
| **Ilex mucronata** | Aquifoliaceae | Poor fen | – | 0.4 | – | 4.2 | 6.0 |
| **Ilex verticillata** | Aquifoliaceae | Moderate fen | – | 0.3 | – | 0.2 | 10.7 |
| **Iris versicolor** | Iridaceae | Rich fen | – | 0.1 | – | 0.8 | 18.2 |
| **Kalmia angustifolia** | Ericaceae | Bog | 10.2 | 27.2 | 5.1 | 11.1 | 9.0 |
| **Kalmia polifolia** | Ericaceae | Bog | – | 9.9 | 1.4 | 7.1 | – |
| **Larix laricina** | Pinaceae | Bog | – | – | 0.5 | 4.8 | – |
| Leersia oryzoides | Gramineae | Poor fen | – | – | – | – | 0.9 |
| Maianthemum trifolium | Liliaceae | Poor fen | 21.3 | 35.7 | 21.8 | 20.2 | 30.8 |
| **Osmunda cinnamomea** | Osmundaceae | Rich fen | – | 0.1 | 0 | 1.0 | 5.1 |
| Photinia melanocarpa | Rosaceae | Poor fen | – | 0.4 | – | 4.9 | 4.3 |
| Picea mariana | Pinaceae | Bog | 0.9 | – | – | – | – |
| Pinus resinosa | Pinaceae | Poor fen | – | – | – | 1.9 | 0.9 |
| Pinus strobus | Pinaceae | Bog | 1.9 | 0.4 | – | 1.2 | – |
| Pleurozium schreberi | Hylocomiaceae | Bog | – | – | – | 0.6 | – |
| Pohlia nutans | Bryaceae | Bog | – | 2.5 | – | 1.6 | – |
| Polytrichum commune | Polytrichaceae | Bog | – | 4.3 | 1.4 | 0.2 | 1.5 |
| **Polytrichum strictum** | Polytrichaceae | Bog | 14.8 | 35.2 | 3.7 | 3.2 | 5.1 |
| Rhododendron groenlandicum | Ericaceae | Bog | – | 12.9 | 0.9 | 11.7 | – |
| **Rubus hispidus** | Rosaceae | Rich fen | – | – | – | – | 4.7 |
| **Salix pyrifolia** | Salicaceae | Rich fen | – | – | – | 0.6 | 1.9 |
| Sarracenia purpurea | Sarraceniaceae | Bog | 0.9 | 0.9 | – | – | – |
| Scirpus cyperinus | Cyperaceae | Rich fen | – | – | – | – | 1.5 |
| **Sphagnum angustifolium** | Sphagnaceae | Bog | 78.7 | 0.6 | 1.8 | 14.8 | 12.2 |
| **Sphagnum capillifolium** | Sphagnaceae | Bog | 11.1 | 4.1 | – | – | 0.2 |
| **Sphagnum compactum** | Sphagnaceae | Poor fen | – | – | 1.9 | 0.4 | – |
| **Sphagnum fallax** | Sphagnaceae | Poor fen | 14.8 | 79.6 | 88.4 | 61.1 | 62.2 |

Table 1 (*continued*)

| Plant species assemblages | | | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|---|---|
| Average species number | | | 11 | 11 | 10 | 15 | 18 |
| Number of stations | | | 3 | 21 | 6 | 15 | 14 |
| Plant species | Family | Habitat[a] | | | | | |
| *Sphagnum magellanicum* | Sphagnaceae | Bog | – | 7.9 | 9.7 | 12.3 | 3.2 |
| **Sphagnum rubellum** | Sphagnaceae | Bog | – | 23.1 | 0.5 | 0.2 | – |
| **Spiraea alba var. latifolia** | Rosaceae | Poor fen | – | – | – | 0.8 | 4.1 |
| *Trientalis borealis* | Primulaceae | Rich fen | | | | | |
| **Vaccinium angustifolium** | Ericaceae | Bog | 2.8 | 2.8 | 2.8 | 35.7 | 9.0 |
| **Vaccinium myrtilloides** | Ericaceae | Bog | – | – | – | – | 0.9 |
| *Vaccinium oxycoccos* | Ericaceae | Bog | – | 2.7 | – | 0.2 | – |

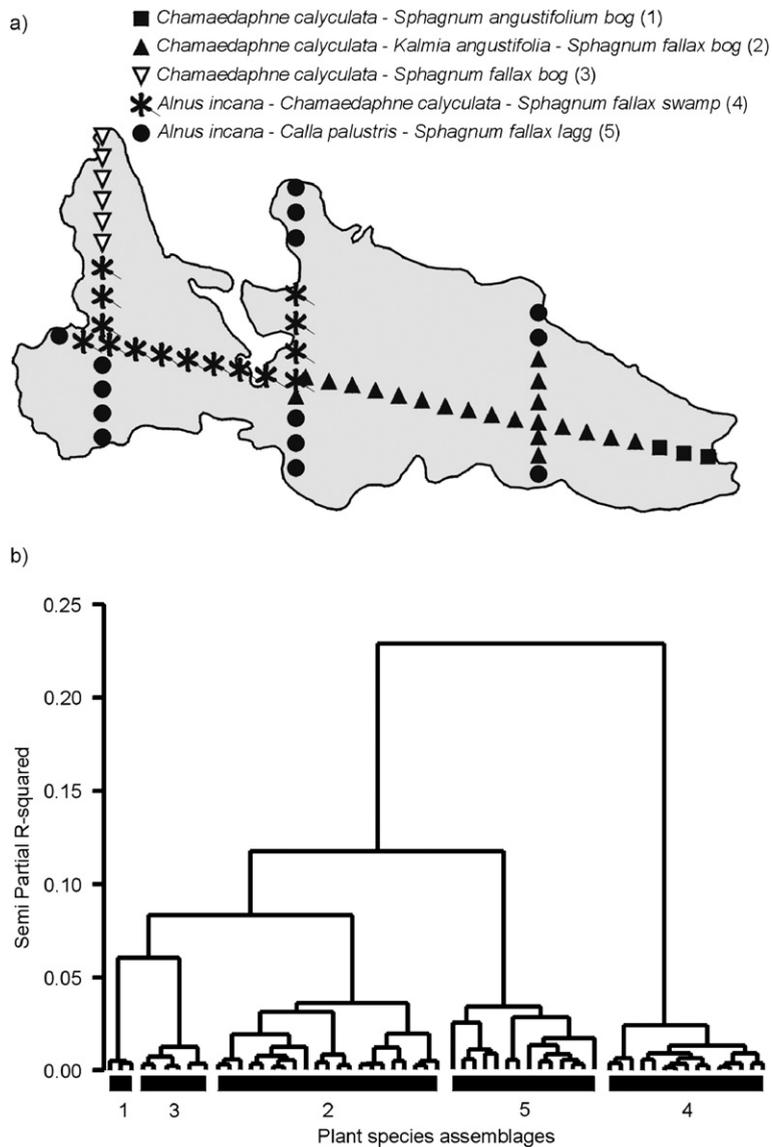[a] The habitat preference follows Marie-Victorin [55] and Garneau [58].



Fig. 2. Spatial distribution (a) and Ward's dendrogram (b) of the plant species assemblages in the Covey Hill peatland.

dominant bryophyte species. It covers more than 50% of the plot area in 78% of the plots.

### 3.1. Plant species assemblages

Five geographically distinct plant species assemblages (or clusters) were identified within the Covey Hill bog (Table 1; Fig. 2). The three first assemblages are typical of open bog habitats characterized by hummock and hollow surface microtopography, by a dense ground cover of *Sphagnum* mosses and by the abundance of ericaceous shrubs. The first assemblage (*Chamaedaphne calyculata–Sphagnum angustifolium* bog) occupies the extreme east edge of the bog. Fifteen species were identified in this assemblage and the dominant (mean cover >20%), in order of decreasing average cover, are *Sphagnum angustifolium*, *Chamaedaphne calyculata*, *Andromeda polifolia* var. *glaucophylla* and *Maianthemum trifolium*. The best indicators species are *A. polifolia*, *S. angustifolium* and *S. capillifolium*. The second assemblage (*Chamaedaphne calyculata–Kalmia angustifolia–Sphagnum fallax* bog) is located in the center of the eastern basin. Of the 32 species identified in this assemblage, *S. fallax*, *C. calyculata*, *M. trifolium, Polytrichum strictum*, *Kalmia angustifolia* and *Eriophorum vaginatum* ssp. *spissum* are dominant, while the principal indicator species are *E. vaginatum*, *K. angustifolia*, *P. strictum* and *S. rubellum*. The third assemblage (*Chamaedaphne calyculata–Sphagnum fallax* bog) is situated on a large floating mat in the north section of the western basin. This assemblage shares many species with the previous assemblage, but it is characterized by a higher mean cover of *C. calyculata*, a much lower mean cover of *K. angustifolia* and of *P. strictum* and by the absence of *E. vaginatum*. Among the 20 species recorded, only *C. calyculata*, *S. fallax* and *M. trifolium* are dominant. In addition to those species, indicator species included *S. compactum*. The fourth and fifth assemblages are characterized by more minerotrophic conditions than the three previous ones. They are also characterized by the presence of tall shrubs (>1 m) and by the abundance of cyperaceous and more aquatic species, such as *Calla palustris* and *Iris versicolor*. The fourth assemblage (*Alnus incana* ssp. *rugosa–Chamaedaphne calyculata–Sphagnum fallax* swamp) is located in the center of the western basin. A total of 41 species were identified within this assemblage. The dominant are *C. calyculata*, *S. fallax*, *Vaccinium angustifolium*, *M. trifolium* and *A. incana* while principal indicators species included *Betula populifolia*, *Larix laricina* and *V. angustifolium*. Finally, the fifth assemblage (*Alnus incana* ssp. *rugosa–Calla palustris–*

*Sphagnum fallax* lagg) is composed of 14 plots located at the margins of the bog. This lagg ranged between 10 to 150 m wide. Among the 38 species recorded, *S. fallax*, *M. trifolium*, *A. incana* ssp. *rugosa* and *Acer rubrum* are dominant, while *A. rubrum*, *A. incana* ssp. *rugosa*, *C. palustris* and *I. versicolor* are the principal indicator species. Large standing dead trees were also observed within this assemblage. Overall, the two minerotrophic assemblages were more diverse in term of mean number of species per plot than the three ombrotrophic assemblages ($F = 18.56$, $p < 0.001$).

### 3.2. Environmental factors

The Covey Hill bog is mainly characterized by an open structure with few trees as indicated by the extreme low value of tree basal area in all plant assemblages (Fig. 3a). The organic deposit thickness varied from 30 to 226 cm across the sampling stations. The peat deposit was thickest in the two *Chamaedaphne–Sphagnum fallax* assemblages and the thinnest in the lagg (Fig. 3b). Water pH was low in all sampling stations, ranging between 3.8 and 4.7, but it was significantly lower in the *Chamaedaphne–Kalmia angustifolia–Sphagnum fallax* bog (Fig. 3c). Water corrected conductivity was also very low in all plant assemblages, ranging between 0 and 19 μS/cm (Fig. 3d). Although the average lowest groundwater table levels were not statistically different between assemblages (Fig. 3e), the mean highest levels were closer to the peat surface in the *Chamaedaphne–Sphagnum fallax*, swamp and lagg assemblages (Fig. 3f). Similarly, the percentage of free surface water was higher in the *Chamaedaphne–Sphagnum fallax* and the lagg assemblages than in the other two bog assemblages (Fig. 3g). Finally, the sampling stations within the *Chamaedaphne calyculata–Kalmia angustifolia–Sphagnum fallax* bog were located farther to the peat margins than those within the *Chamaedaphne–Sphagnum fallax*, swamp and lagg assemblages (Fig. 3h).

### 3.3. Vegetation–environment relationships

The eight environmental variables used in the CCA explain 30% of the variance in the floristic composition of the Covey Hill peatland. The permutation test based on the sum of all canonical eigenvalues is highly significant (*p* value = 0.001) indicating a strong relationship between species and the variables measured. The eigenvalues of the two first axes (0.364 and 0.141) are markedly higher than those of the two following axes (0.084 and 0.0067), indicating that they contributed
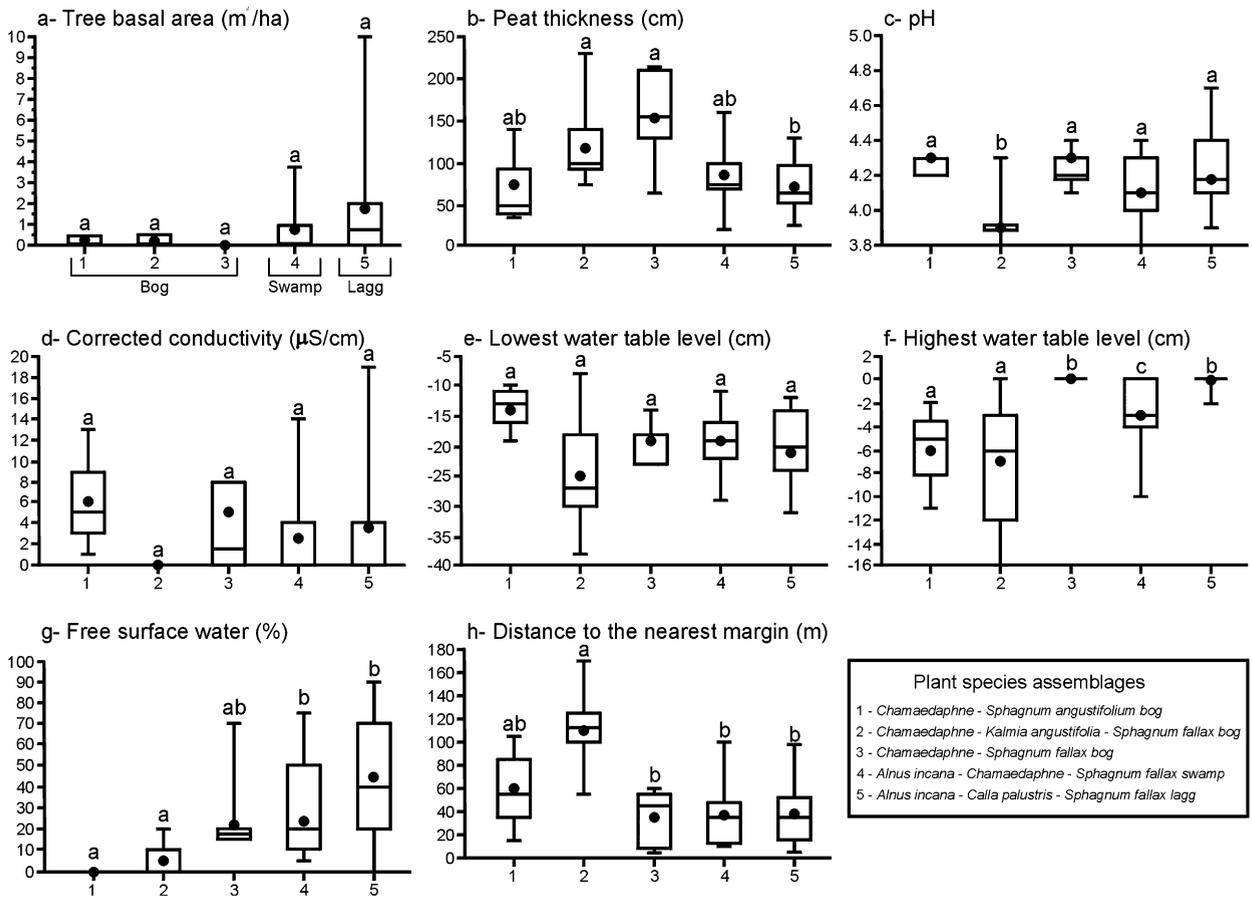
Fig. 3. Distribution of environmental variables in the five plant species assemblages identified in the Covey Hill peatland. The upper, lower and middle lines of the box correspond, respectively, to the 75th, 25th and 50th percentile (median). The lower and upper whiskers extend from the maximum and minimum values. The means are represented by the black dot. Significant differences (one-way ANOVA or randomization test, $p < 0.05$) between assemblages were found for all variables, except the tree basal area, the corrected conductivity and the lowest water table level. Means with different letters differ significantly.

predominantly to explain species composition. The percentages of variance explained by the first two CCA axes (calculated using eigenvalues and total inertia) are 14% and 5.4% respectively. The variables with the highest correlation with the first axis are the distance to the nearest margin ($r = -0.74$), the highest water table level ($r = 0.75$), pH ($r = 0.73$) and the percentage of free surface water ($r = 0.66$). This axis thus principally depicts a spatial gradient (from the margins to the center) but also moisture and acidity gradients. The lowest water table level ($r = 0.61$) is the only variable associated with the second axis.

According to the ordination, the five plant species assemblages are mainly located along the distance to peatland edge and the wetness gradient (Fig. 4a). The wettest plant species assemblage (lagg) was found at the edge of the bog on the right side of the ordination while the more typical open bog assemblage

(*Chamaedaphne–Kalmia angustifolia–Sphagnum fallax* bog) was found in the driest innermost part of the bog and on the left side of the ordination. The *Chamaedaphne–Sphagnum fallax* bog seems to be a transitional assemblage between the lagg and the *Chamaedaphne–Kalmia angustifolia–Sphagnum fallax* bog while plots of this assemblage are located in the central portion of the ordination. This cluster indeed shares many species with the later (Table 1), but its environmental conditions are more similar to those of the lagg (Fig. 3). Although surface water chemistry (pH, conductivity) and tree cover variables do not vary much between assemblages (Fig. 3), they tend to follow the gradient usually described in the literature [2,32], i.e. a decrease along the swamp-to-bog gradient (Fig. 4a).

The species–environment CCA biplot (Fig. 4b) shows the relationship among species and environmental conditions that gave rise to the differences in plant species
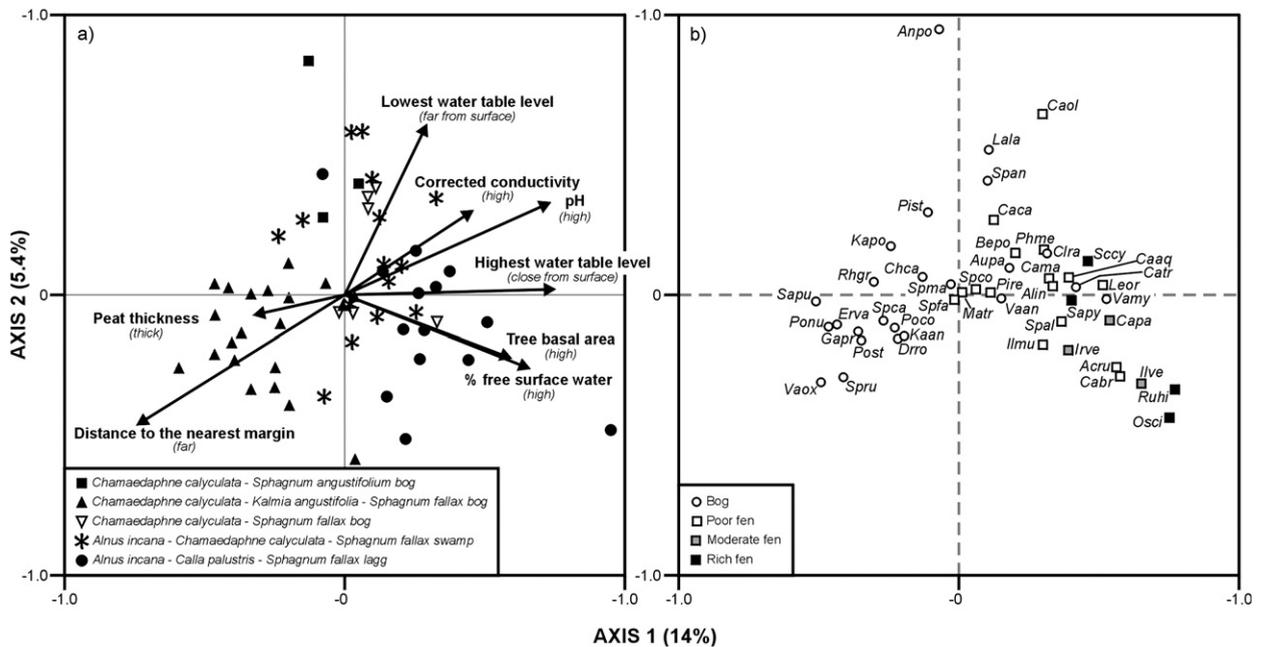
Fig. 4. Biplot of the canonical correspondence analysis examining the strength of association between environmental variables and a) the plant species assemblages, and b) the species in the Covey Hill peatland. Environmental vectors have been taken off the species–environment biplot for clarity. Species acronyms are based on the first two letters of genus and species name (full names of species are provided in Table 1).

assemblages. True ombrotrophic species such as *Vaccinium oxycoccos*, *Sphagnum rubellum*, *Sarracenia purpurea* and *Drosera rotundifolia* tend to be located toward the central section of the bog (left side of the ordination) while minerotrophic species such as *Ilex verticillata*, *Iris versicolor*, *Calla palustris*, *Alnus incana* ssp. *rugosa* and *Carex aquatilis* occurred more frequently at the margin (right side of the ordination). Trees (*Betula populifolia*, *Larix laricina, Pinus resinosa, Pinus strobus*), tall shrubs (*I. verticillata*, *Ilex mucronata*, *A. incana* ssp. *rugosa*, *Salix pyrifolia*) as well as aquatic species such as *I. versicolor* and *C. palustris* are also more associated with the wet margins.

## 4. Discussion

The water chemistry and the position of the water table are very important environmental factors controlling the vegetation distribution within homogeneous peatlands (e.g., [2,7,37–41]). The results of our study suggest that water chemistry had probably only a minor influence on the vegetation distribution within the Covey Hill bog, since corrected conductivity and pH did not vary much between the five plant species assemblages. The range of variation in both pH and corrected conductivity within the Covey Hill bog is however very small compared with those found in others studies [1,13,16,

21,37,41]. Furthermore, although not analyzed in the scope of this study, concentrations of major ions ($Ca^{+2}$, $K^+$, $Mg^{+2}$, $Na^{+2}$, $Cl^-$, $SO_4^{-2}$) are available through a hydrological study made in the same bog [42]. Those concentrations were obtained from water sampled extracted from six surface piezometers located throughout the site (i.e. two in the *Chamaedaphne–Kalmia* bog, one in the *Chameadaphne–Sphagnum fallax* bog, two in the swamp and one in the lagg). Concentrations of major ions were similar in all piezometers [42]. On the other hand, our results suggest that the highest water table level is an important gradient explaining the floristic variation within the studied bog. The highest water table level has also been identified as an important factor controlling the vegetation distribution and composition in wetlands of the Netherlands [43].

The floristic patterns observed within the Covey Hill bog are spatially structured; the distance to the nearest margin being highly correlated with the first axis of the CCA. The central portion of the bog was mainly characterized by true ombrotrophic species (mainly *Sphagnum* and ericaceous shrubs species) while minerotrophic, aquatic and tall shrub species were more often found near its margins. Similar shifts in plant species composition between peatland margin and peatland expanse have been frequently depicted worldwide (e.g., [1,2, 4,16,38,44]). According to Wheeler and Proctor [8],

the underlying ecological factors explaining the floristic variation along this margin-expanse gradient are site dependant. However, the water table level and its fluctuation as well as the nutrient availability are the factors more often cited. For instance, the position of the water table below the surface is usually deeper and more fluctuating at the margins than at the center [7,44,45]. Consequently, the aeration of the peat substrate is greater at the margins [2,5,46]. Furthermore, the margins are often richer than the center since they receive mineral rich water from the uplands (and from the center in raised bog) and due to the proximity of the mineral soil [10,44, 47]. Those environmental conditions are known to favor the establishment and growth of trees and tall shrubs in peatlands [48,49].

Water table level and peat surface wetness are likely the principal ecological factors underlying the expanse-margin gradient within the vegetation of the Covey Hill bog since the percentage of free surface water and the highest water table level were also highly correlated with the primarily axis of the ordination. However, contrary to what we could expect, the margins are characterized by much wetter hydrological conditions than its expanse as indicated by higher water table levels, larger proportions of free surface water and higher relative cover of swamp shrubs (e.g., *Alnus incana* ssp. *rugosa*; *Ilex verticillata*, *I. mucronata*) and aquatic species (e.g., *Calla palustris*). The wet conditions and the associated plant assemblages found at the margins of the Covey Hill bog have likely been induced, or at least favored, by the man-made and beaver dams that are blocking the natural flow in the three outlets of the site. Shallow flooding in ombrotrophic peatlands following damming is indeed known to favor the spread of minerotrophic, marshes or aquatic vegetation [50–53]. It also usually induces tree mortality and creates floating mats in open or low-density treed bogs [51–53]. Dead standing trees were found in the lagg while floating mats were observed in the *Chamaedaphne–Sphagnum fallax* assemblage located in the northwest portion of the bog; i.e. near the large reservoir upstream of the man-made dam. *Chamaedaphne calyculata* is a pioneer ericaceous shrub typical of floating mats [54,55]. This species can easily invade open water due to its ability to produce extensive adventitious root system that grows laterally above the water surface [54]. Its establishment can then promote the colonization of pioneer *Sphagnum* species, mainly *S. fallax*, and eventually the establishment of other mosses and woody plant species [52,54, 56]. Therefore, it is plausible that the floating mats observed in the western basin will continue to expand through the open water of the reservoir. Furthermore,

the *Chamaedaphne–Sphagnum fallax* assemblage will likely continue to evolve into a more complex and diverse community as the one found in the undisturbed central portion the bog; i.e. the *Chamaedaphne–Kalmia angustifolia–Sphagnum fallax* assemblage. A quick re-establishment of typical open bog vegetation upon floating mats and rapid increase of floristic diversity was also observed in a boreal peatland complex of northwestern Ontario (Canada) following experimental flooding [52].

In conclusion, our study has demonstrated that even a seemingly homogeneous bog, like the Covey Hill peatland, can support heterogeneous plant species assemblages. This heterogeneity is spatially structured and mainly controlled by water table level and peat surface wetness. Moreover, our results suggest that the damming of seepage outlets has favored the establishment of swampy vegetation at the margins of the site. If the water table continues to rise, it can induce more conversion of bog areas to swamp areas. It may also facilitate paludification of surrounding mineral soils [57]. Several pockets of thin *Sphagnum* mats ($<$30 cm) were observed at the edge of the Covey Hill bog likely indicating lateral growth of the peatland. On the other hand, if the water table stays stable, swampy plant communities may continue to evolve to more typical ombrotrophic communities [52]. Long term monitoring plots have been established within the studied bog to investigate its future vegetation dynamics.

## Acknowledgements

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