

# Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light

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## Abstract

**Question:** What are the drivers of bryophyte succession in paludifying boreal *Picea mariana* forests?

**Location:** The Clay-Belt of Québec and Ontario, Canada.

**Methods:** The bryophyte community and habitat variables (forest floor thickness, water table, stand density, canopy openness micro-climate and presence of ericaceous species) were analysed in a chronosequence of 13 stands from 50 to more than 350 years since fire.

**Results:** Across the chronosequence, feathermosses were replaced by shade and desiccation tolerant slower growing hummock *Sphagna* and then by faster growing hollow *Sphagna*. These changes were linked with both increasing light availability and the movement of the water table into the forest floor.

**Conclusions:** As water table rise is dependent on forest floor thickness, which is in turn influenced by the presence of *Sphagna*, this successional sequence represents an example of facilitation. Furthermore, it emphasizes the importance of water table rise in determining stand level, and landscape level variables such as carbon balance.

**Keywords:** Black spruce; Clay Belt; Feathermoss; Habitat variables; *Picea mariana*; Species replacement; *Sphagnum*; Water table.

**Nomenclature:** Anderson (1990) for *Sphagnum*, and Crum & Anderson (1981) for other mosses.

**Abbreviations:** CWD = Coarse woody debris; DCA = Detrended Correspondence Analysis; LCR = Live crown ratio; PAR = Photosynthetically active radiation; pCCA = Partial Canonical Correspondence Analysis; TSF = Time since fire; VPD = Vapour pressure deficit.

## Introduction

Boreal forests are distinguished from many other biomes by the importance of the bryophyte layer in ecosystem functioning. The bryophyte layer constitutes an important component of the biomass, and influences total net primary production (Gower et al. 1997; Bisbee et al. 2001) and soil respiration (O'Connell et al. 2003). An example of the influence of the bryophyte layer is the paludification of boreal forests, a phenomenon by which a forest on mineral soil is transformed into a treed peatland (Crawford et al. 2003) via the accumulation of a thick forest floor and a rising water table (Glebov & Korzukhin 1992). Associated with these changes in the soil there is an establishment and subsequent expansion of *Sphagnum* spp. mosses into the previously bryophyte layer dominated by feathermosses (*Pleurozium schreberi*, *Ptilium crista-castrensis*, *Hylocomium splendens*), occurring ca. 100 years after a fire. The ecosystemic consequences of this change in bryophyte functional groups can be dramatic; as compared to feathermosses, *Sphagnum* has a higher carbon fixation rate (Bisbee et al. 2001; Swanson & Flanagan 2001), a greater buffering effect on soil temperature (Dioumaeva et al. 2002) and a slower decomposition rate (Swanson & Flanagan 2001; Turetsky 2003). Furthermore, wetter *Picea mariana*-*Sphagnum* stands have a longer fire cycle and because of their greater humidity they lose less carbon when they are burned (only 12% vs. 33% of the net primary production according to Harden et al. 2000).

The replacement of species along a successional gradient can be viewed as being driven either by the population life span of individual species, or by interactions among species and habitat conditions (Bazzaz 1990). Bryophyte colonies in forest floors may have almost unlimited life spans due to their continual upward growth as long as conditions remain unchanged, therefore it is unlikely that the shift observed is due to the death of feathermoss colonies. In light of this, the shift in bryophyte functional groups

represents a replacement where the *Sphagna* are capable of overtopping the feathermosses and gain access to an important limiting factor in the boreal forest floor, space (Slack 1990). Replacement by overtopping is a strongly asymmetric (0, -) interaction which, however, may also occur in the reverse direction (*Sphagna* are overtopped by feathermosses in ca. 30% of recorded cases in young forests; Fenton unpubl. data). Such interactions have been referred to as asymmetric competition (Rydin 1997) and as amensalism (Burkholder 1952; Økland 2000). The question that has not been addressed in previous studies is: which environmental change alters the habitat and allows the *Sphagna* to gain an advantage over the feathermosses?

Based on the physiology of the functional groups, two main environmental gradients within ageing forests have been suggested as the causes of change in the bryophyte layer; *Sphagna* growth is favoured by (1) increases in available light (Bisbee et al. 2001), and (2) increases in available moisture (Taylor et al. 1987; Van Cleve & Viereck 1981). However, while these hypotheses have been discussed, their true role in driving successional changes has not been tested. In addition, these environmental gradients have been suggested for successional sequences more than 150 years after fire, and in general have been based uniquely on differences in functional groups (i.e. feathermosses vs. *Sphagnum* spp.) and not on the behaviour of individual species. Therefore the objectives of this study are to document the changes in dominant species composition with increasing time since fire in *Picea mariana* forests, and to determine whether changes in light and/or moisture drive successional changes in paludifying *Picea mariana* forests across an extended time gradient. The role of ericaceous species was also investigated as they may have allelopathic interactions with trees and other species (Inderjit & Malik 1997; Wardle et al. 1998) that may favour *Sphagnum* growth.

## Study area

The Clay Belt of northeastern Ontario and northwestern Québec (Fig. 1) is a major physiographic region created by deposits left by the lakes Barlow and Ojibway after their maximum extension during the Wisconsin glaciation (Vincent & Hardy 1977). In its northern portion, this region is dominated by *Picea mariana*-*Pleurozium schreberi* forests as described by Grondin (1996), and is particularly prone to paludification between fires due to its poorly drained clay-dominated soil, low topographic relief, and moderately humid and cold climate – annual precipitation = 890 mm; annual mean temperature = 0.7 °C (Anon. 2004).

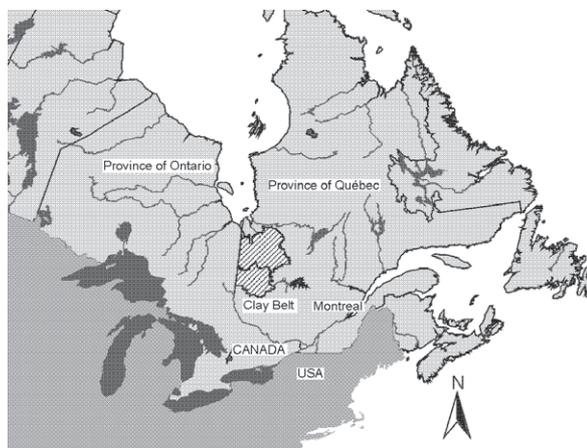
The dominant disturbance types are large fires that kill all above-ground vegetation. Between 1850 and 1920 the fire cycle was ca. 135 years, and it has since increased to ca. 398 years (Bergeron et al. 2004), as a result the average age of the forests is > 100 years. The Clay Belt lies just south of the Hudson Bay-James Bay Lowlands, the second largest peatland complex on the globe.

## Methods

### Sampling

A chronosequence approach was used to address successional changes. The main weakness of this approach is the possibility that initial conditions were not identical for all stands. While this is a valid argument, the chronosequence used here has been extensively validated. This study is part of a larger project, investigating the causes and consequences of paludification on the Clay Belt of Québec and Ontario. A previous study indicated that as these older forests have escaped fire by chance they are as likely to burn as other forests in the landscape, and as such represent a true endpoint to succession and are not topographical escapes (Cyr et al. 2005). The established chronosequence has been validated via stem analysis (Lecomte et al. 2005), and *in situ* analysis of the forest floor (Lecomte et al. in press; Fenton unpubl. data).

In addition site selection included a detailed analysis of slope and soil texture to determine that the sites established in similar edaphic conditions. Similarly, the presence of charcoal uniquely at the interface between the mineral and organic layers of the soil was verified to establish that the forests issued from a high severity fire



**Fig. 1.** Location of study area within in the province of Québec. The ecoregions where the ClayBelt occurs is indicated; the picture may slightly overestimate the actual area.

(i.e. a fire that affected the ground and not only tree crowns). However, it is conceivable that there were small patches of *Sphagnum* remaining after the previous fire that were not detected by our methods. We believe that their influence on our results would be minimal. A more detailed description of site selection procedures is given by Lecomte et al. (in press).

During the summer of 2003, 13 sites dominated by *Picea mariana*, ranging from 50 to 350 years since fire, were sampled. Sites were chosen based on a stand initiation map of the area (Bergeron et al. 2004) and were selected in the field on the basis of proximity to road, and presence of a mild slope and clay dominated soil. Time since fire (TSF) was established by verification of stand initiation map dates by dating basal cross-sections of a few dominant trees (for more details see Lecomte et al. in press). However, in the oldest stands (> 200 years TSF) C<sup>14</sup> dating of charcoal particles in a few of the sites suggest that the oldest trees were established a considerable period after stand replacing fire. While the C<sup>14</sup> dates suggest that the stands are considerably older than first believed (300-1000 years) they did

not alter the order or the groupings of the sites. For this reason dendrochronology dates were used as they are consistent across the sites.

Within each site, five quadrats of 100 m<sup>2</sup> were established, with four nested quadrats of 25 m<sup>2</sup>. The initial 100-m<sup>2</sup> quadrat was randomly placed at least 50 m from the nearest road, and subsequent quadrats were placed at least 10 m apart along a randomly chosen bearing. Within each 25-m<sup>2</sup> quadrat, all bryophyte species were identified and their percent cover visually estimated. Samples of all non-easily identifiable species were collected for identification in the lab. A representative collection of voucher specimens are stored at the Université du Québec en Abitibi-Témiscamingue. While all of the species data were included in the ordination, only the patterns of the dominant forest floor mosses and *Sphagnum* spp. were analysed in detail.

A series of habitat variables (both abiotic and biotic) affecting substrate availability and microclimate were measured in each 25-m<sup>2</sup> quadrat in order to interpret the bryophyte pattern (Table 1). Steel rods 120 cm long were used to measure the depth of the water table in the

**Table 1.** Abiotic and biotic variables measured within 25-m<sup>2</sup> quadrats in order to interpret patterns in bryophyte species composition. Variables marked with an \* were significant when tested individually in the partial canonical correspondence analysis. Classes of coarse woody debris decomposition were modified from Söderström (1987).

Code	Full variable name	Description
	Forest floor*	Depth from the moss surface to the organic-mineral interface, which is clearly defined on the Clay Belt
	Water table*	The position of the water table in a randomly chosen location within the 25-m <sup>2</sup> quadrat
	Water table index*	The position of the water table relative to the organic matter-mineral soil interface Values < 0 are in the mineral soil, values > 0 are in the organic matter
Coniferous canopy	% coniferous canopy cover	% canopy cover occupied by coniferous trees, measured on a densiometer
Deciduous canopy	% deciduous canopy cover	% canopy cover occupied by deciduous trees, measured on a densiometer
Open canopy	% cover without canopy*	% of canopy that is not covered by coniferous or deciduous trees, and is therefore open to the sky
CWD 1	% cover of coarse woody debris, decay class 1	% of the forest floor covered by coarse woody debris > 5 cm in diameter (CWD) of decay class 1 – freshly fallen
CWD 2	% cover of coarse woody debris, decay class 2	% of the forest floor covered by coarse woody debris > 5 cm in diameter (CWD) of decay class 2 – bark loosening
CWD 3	% cover of coarse woody debris, decay class 3*	% of the forest floor covered by coarse woody debris > 5 cm in diameter (CWD) of decay class 3 bark falling, softening of wood
CWD 4	% cover of coarse woody debris, decay class 4	% of the forest floor covered by coarse woody debris > 5 cm in diameter (CWD) of decay class 4 very soft, shape collapsed
% leaves	% cover of deciduous leaves	% cover of the forest floor covered by deciduous leaves
% pits	% cover peat pits *	Deep water holes formed in the organic matter
% mineral	% cover mineral soil	Mineral soil exposed on the forest floor
BA bS	Basal area <i>Picea mariana</i> (m <sup>2</sup> /ha)	Basal area of all <i>Picea mariana</i> in the quadrat > 8 cm in diameter
BA jP	Basal area <i>Pinus banksiana</i> (m <sup>2</sup> /ha)	Basal area of all <i>Pinus banksiana</i> in the quadrat > 8 cm in diameter
BA bF	Basal area <i>Abies balsamea</i> (m <sup>2</sup> /ha)*	Basal area of all <i>Abies balsamea</i> in the quadrat > 8 cm in diameter
BA tam	Basal area tamarack (m <sup>2</sup> /ha)	Basal area of all <i>Larix laricina</i> in the quadrat > 8 cm in diameter
BA tA	Basal area trembling aspen (m <sup>2</sup> /ha)	Basal area of all <i>Populus tremuloides</i> in the quadrat > 8 cm in diameter
Tot BA	Total basal area (m <sup>2</sup> /ha)	Basal area of all stems > 8 cm in diameter in the quadrat
Mean tree size	Mean tree diameter*	Mean diameter of all trees > 8 cm in the quadrat
LCR bS	% live crown ratio <i>Picea mariana</i> *	Mean % of <i>Picea mariana</i> stems with living foliage, measured as a visual estimate
LCR jP	% live crown ratio <i>Pinus banksiana</i>	Mean % of <i>Pinus banksiana</i> stems with living foliage, measured as a visual estimate
LCR bF	% live crown ratio <i>Abies balsamea</i>	Mean % of <i>Abies balsamea</i> stems with living foliage, measured as a visual estimate
LCR tam	% live crown ratio <i>Larix laricina</i>	Mean % of <i>Larix laricina</i> stems with living foliage, measured as a visual estimate
LCR tA	% live crown ratio <i>Populus tremuloides</i>	Mean % of <i>Populus tremuloides</i> stems with living foliage, measured as a visual estimate
# tip ups	# of tree tip ups	# of tree tip ups per quadrat, which creates variability in the quadrat
# snap offs	# of trees snapped off	# of trees snapped off (rather than tipped up) per quadrat
% ericaceous	% cover of ericaceous species*	% of the forest floor covered by the canopy of ericaceous species, primarily <i>Rhododendron groenlandicum</i> , <i>Kalmia angustifolia</i>

soil. The rods were placed in the soil for several weeks during which orange-brown rust formed at the interface of the oxygenated and non-oxygenated zones of the soil profile (Carnell & Anderson 1986), which approximated the position of the water table. The width of the rusted surface indicates the variation in the water table level during the 40-day period caused by rainfall, drought and seasonal variation. In a previous article (Fenton et al. in press) we demonstrated that the highest point (i.e. closest to the forest floor surface) had the closest relation to the mean actual water table position (which was simultaneously measured in water wells). Therefore in this study the depth to the beginning of the heavily rusted area was used in analyses. In July 2003, 7 of the 13 chronosequence sites were chosen for further study and one steel rod was randomly installed in each 25-m<sup>2</sup> quadrat. The rods were removed 40 days later with locking pliers and the distance from the forest floor surface (i.e. directly above the moss) to the zone of orange-brown rust was immediately identified with colour tape and later measured in the lab.

While the randomly placed rods may not have always captured the fine scale spatial variation within the quadrats, these measurements were nevertheless considered to give appropriate indication of relative positions of the water table among quadrats. In order to account for the change in apparent soil surface position (due to increase in forest floor thickness with age), the interface between mineral soil and forest floor was used as a reference point for measurements. This was achieved by subtracting forest floor thickness from depth to the zone of orange/brown rust. Values less than 0 indicate that the water table was in mineral soil, while values greater than zero indicate that the water table was in the forest floor. For more details see Fenton et al. (in press).

In addition to the indirect measures of microclimate explained above, the microclimate of *Sphagnum capillifolium*, *S. magellanicum* and *Pleurozium schreberi* habitats were measured directly in 2004 in two sites (85 and 270 years after fire) between the months of April and September. While equipment limitations restricted the sampling to two sites, these data provide detailed information on the actual microclimate experienced and created by the bryophytes in the two forest types (young and old). Two replicate microclimate stations were installed in each site. Each microclimatic station (Campbell Scientific Dataloggers CR10) was equipped with two photosynthetically active radiation probes (PAR Lite Kipp and Zonen) and two shielded temperature and humidity sensors (CS500 Vaisala 50Y). One PAR and one temperature-humidity probe were installed at moss level in a patch of *Pleurozium schreberi* and *S. capillifolium* and *S. magellanicum* respectively. Therefore, four probe pairs were placed in the young stand and four

probe pairs in the old stand. Temperature (°C), relative humidity and PAR density ( $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ ) were recorded as hourly averages, as well as daily maxima and minima. PAR was also recorded as daily totals ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ). Moss level precipitation, in partially buried rain gauges, was also measured for each species patch, in ml. Relative humidity was converted to vapour pressure deficit (VPD in hPa) by the following formula:

$$VPD = (6.1078) \left\{ \left[ \frac{17.269T}{(273.3 + T)} \right] \right\} (1 - RH) \quad (1)$$

where  $T$  is temperature in Celsius and  $RH$  is relative humidity as a decimal (modified from Tanner 1972).

### Analyses

Species were grouped into two taxonomic and functional guilds (true mosses and *Sphagnum* spp.) in order to facilitate interpretation. Similarly, sites were separated into five age groups:

- 100 TSF (85-95 TSF, 4 sites, quadrats);
- 150 TSF (130-150 TSF, 2 sites, 40 quadrats);
- 200 TSF (180-220 TSF, 3 sites, 60 quadrats);
- 275 TSF (260-300 TSF, 3 sites, 60 quadrats);
- >350 TSF (1 site, 20 80 quadrats).

The cover of a few species was examined in quadrats where the water table was above or below the water table, with the non-parametric Kruskal-Wallis test. Tests with  $p$  values of 0.05 or less are referred to as significant.

In order to summarise overall gradients in species composition, a Detrended Correspondence Analysis (DCA; Hill 1979; Hill & Gauch 1980) was carried out. Only species occurring in a total of 5 or more quadrats, and only quadrats in which  $\geq 5$  or more such species were present, were included in the ordination. CANOCO ver. 4 (ter Braak & Šmilauer 1998) was used for DCA ordination. The ordinated matrix contained 97 species in 253 quadrats (out of 260). Strictly speaking the 20 quadrats from a site are pseudoreplicates, but the variation within sites, and indeed within 100-m<sup>2</sup> quadrats, was very high (Table 2). This justified our treatment of the quadrats as separate samples in exploratory multivariate analyses. Habitat variables were passively fitted to the ordination axes as vectors in the ordination diagram (indirect gradient analysis). As water table depth was measured in only 7 of the 13 sites, the mean value of oxygen depth and oxygen index of the measured sites for each age group was included in the sites where it was not measured directly. A non-metric multidimensional scaling (NMDS) analysis was carried out, using PC-Ord (v.4; McCune & Mefford 1999). As the resultant structure was very similar to that of the DCA, only the DCA is presented.

In order to determine the amount of variation in the species pattern explained by the measured habitat variables, a variation partitioning approach (Borcard et al.

**Table 2.** Mean and standard error of first and second axis scores from the Detrended Correspondence Analysis at different spatial scales. The mean and standard error was calculated for each 100-m<sup>2</sup> plot (from the four component quadrat scores), and then the mean was taken of the plot means and standard errors. A similar analysis was completed for individual sites and age groups.

Scale	Axis 1	Axis 2
100-m <sup>2</sup> plot	1.45 (0.24)	1.85 (0.32)
Site	1.47 (0.35)	1.89 (0.46)
Age group	1.63 (0.43)	1.84 (0.54)

1992; Økland 2003) was undertaken, using (partial) canonical correspondence analysis (CCA; ter Braak 1986). A subset of uncorrelated habitat variables was chosen for each of four categories (see below) through forward selection, using default settings in CANOCO (ter Braak & Šmilauer 1998). Variables were included in the analysis if they explained amounts of residual variation, individually significant at the  $\alpha=0.05$  level. The ten selected variables (Table 1) fell into four categories: canopy (LCR *Picea mariana*, % open canopy, basal area of balsam fir, mean tree size), amount of paludification (organic matter thickness, oxygenated zone thickness, oxygen index), pocket sites (coarse woody debris 3 and % peat pits) and % ericaceous spp. cover. Contributions of categories and their interactions to bryophyte community variation were approximated as a proportion of the sum of Canonical Eigenvalues (the total variation explained), as recommended by Økland (1999).

Spearman correlations between individual species abundance and canopy openness and water table index were calculated (SPSS v.10), and the relationships were graphed for six key species present along the gradient: *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Sphagnum capillifolium*, *S. russowii*, *S. magellanicum* and *S. fuscum*.

Microclimatic variables were analysed by comparing the frequency of values recorded in *Sphagnum* and *P. schreberi* habitats in young and old stands. Because the duration of extreme values are biologically important, in addition to mean values, the duration of high values (upper decile = 90% percentile) were calculated. Values and durations were compared using GLM with age and species as the two factors, and the Julian date as a co-variate (SPSS v. 10). A full factorial model was used, with default settings.

## Results

### Variation in species composition

The dominant pattern in community composition, represented by the first axis of the Detrended Correspondence Analysis [Total inertia ( $TI$ ) = 4.859;  $EV$  = 0.554; gradient length = 3.41 SD units; Fig. 2], was the successional change associated with increasing forest age. Along this gradient, a gradual replacement of a feathermoss dominated community by a *Sphagna* dominated community took place (Fig. 2). Feathermosses (*Pleurozium schreberi*, *Ptilium crista-castrensis*, *Hylocomium splendens*) and *Dicranum polysetum* dominated the youngest sites, resulting in little variation among these plots in the DCA ordination (Fig. 2). While its cover decreased gradually with increasing age, *P. schreberi* remained the most frequent species overall.

There were clear shifts over time in the composition of *Sphagnum* spp. *S. subtile* and *S. girgensohnii* were distinctly associated with young stands (Fig. 2), and larger patches of *Sphagna* contained exclusively *S. capillifolium* and *S. russowii*. With increasing age, *S. capillifolium* and *S. rubellum* or *S. russowii* became more common and abundant (Fig. 2). In the 275 TSF group *S. magellanicum* and *S. fallax* (*sensu lato*) became more abundant. By 350 TSF *Sphagnum fuscum*, and *S. fallax* were the dominant *Sphagna*, while *S. magellanicum* was still frequent, although not abundant (< 5% cover).

The second DCA axis ( $EV=0.440$ , gradient length = 3.383 SD units) was more difficult to interpret, but mainly reflected differences between quadrats with *S. capillifolium*, *S. rubellum*, *S. fuscum* and *Cladina rangifera* vs. those dominated by *S. russowii*, *S. magellanicum* and *S. fallax*.

### Relationship between community change and habitat variables

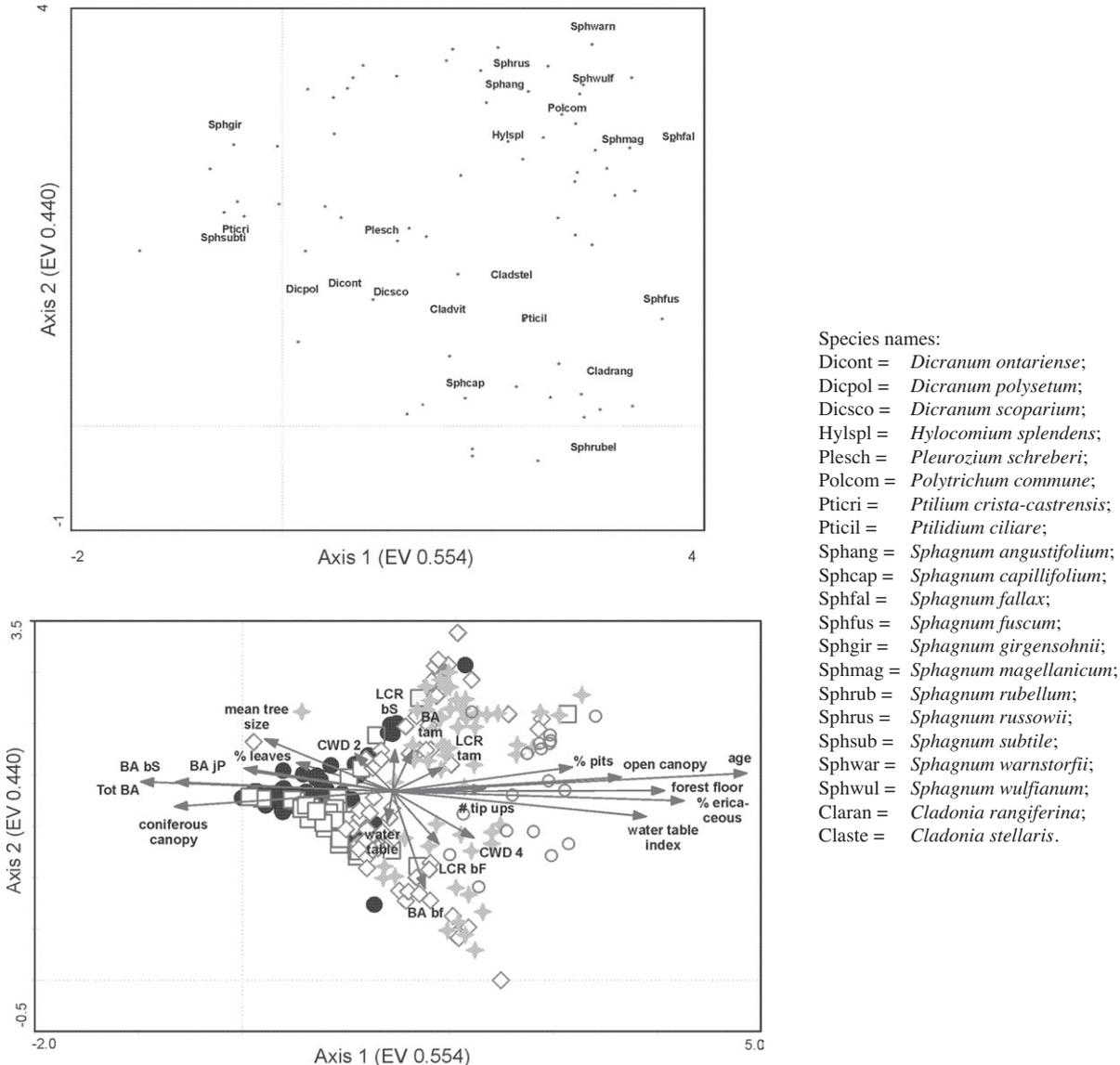
The relationship of habitat variables to the DCA axes (Fig. 2) indicated that the first axis was correlated with increasing forest floor thickness, position of the water table, canopy openness and cover of ericaceous species (primarily *Rhododendron groenlandicum* and *Kalmia angustifolia*; Table 3). DCA axis 2 was correlated with variables related to the habitat, such as live crown ratio of *Picea mariana*, and cover of peat pits.

The relative importance of these habitat variables in shaping the species pattern, as assessed by variation partitioning by CCA, were as follows: The analysis accounted for 22.35% of the variability in the species pattern and of this proportion, canopy cover (LCR *Picea mariana*, % open canopy, basal area of *Abies balsamea*,

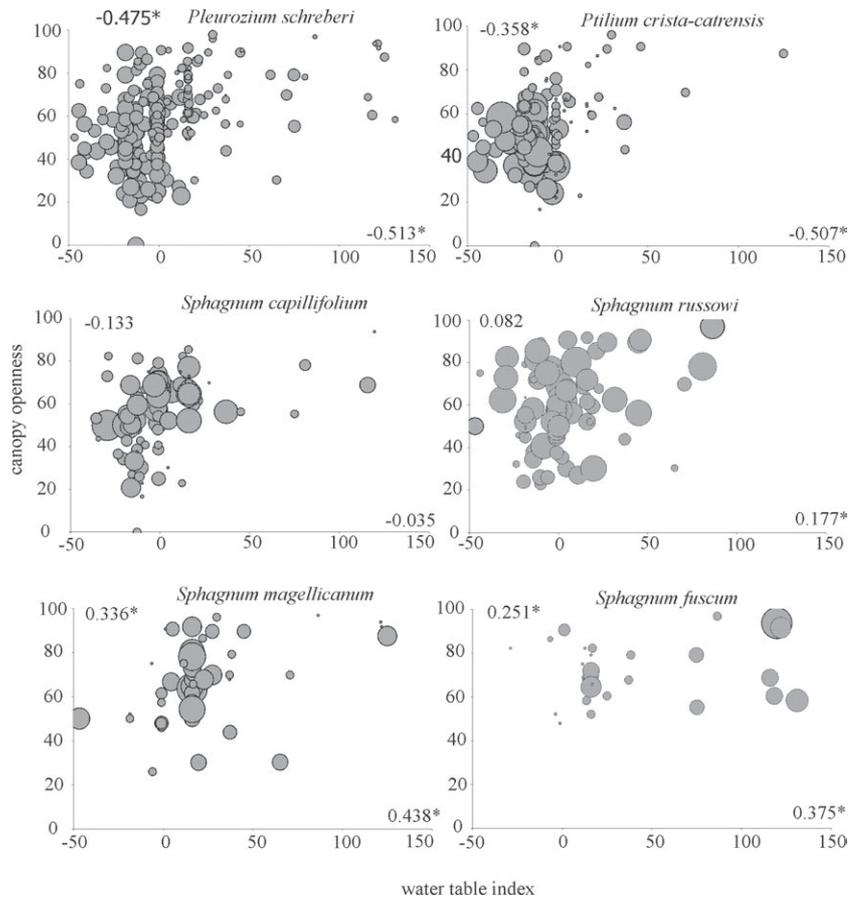
and mean tree size) and paludification (forest floor thickness, water table depth, and water table index) were dominant (19.24 and 14.00% respectively). Cover of ericaceous species, and pocket sites accounted respectively for 8.75 and 10.41% of the explained variation. Interestingly, the interaction (variability explained in addition to the sum of the individual categories) between canopy, paludification and ericaceous species was also important (6.08%).

**Table 3.** Correlation coefficients (Spearman's  $\rho$ ) between DCA axes 1 and 2 and environmental variables. Variables in italics indicate that they are significant.

Environmental variable	DCA axis 1	DCA axis 2
Forest floor thickness	<i>0.697 (&lt;0.001)</i>	<i>0.181 (0.004)</i>
Water table	0.051 (0.418)	<i>-0.140 (0.026)</i>
Water table index	<i>0.650 (&lt;0.001)</i>	<i>0.138 (0.029)</i>
Canopy openness	<i>0.544 (&lt;0.001)</i>	0.112 (0.072)
Cover of ericaceous species	<i>0.680 (&lt;0.001)</i>	0.087 (0.165)
LCR <i>Picea mariana</i>	0.017 (0.782)	<i>0.125 (0.047)</i>
Cover of peat pits	<i>0.535 (&lt;0.001)</i>	<i>0.209 (0.001)</i>



**Fig. 2.** Detrended Correspondence Analysis of the total matrix of 253 quadrats; axes 1 and 2. **A.** Species plot. Only dominant species are indicated, position of other species are indicated by \*. **B.** Quadrat plot with age classes indicated as follows: ● = < 100 TSF; □ = 150TSF; ◇ = 200 TSF; \* = 275 TSF; ○ = > 350 TSF. Vectors for environmental variables were passively fit into the diagram. The arrows indicate strength of relationship with axes and direction of maximum change in the variable in question. Abbreviations are as follows: BA bF = Basal area *Abies balsamea*; BA bS = Basal area *Picea mariana*; BA jP = Basal area *Pinus banksiana*; Total BA = Total basal area; LCR bF = Live crown ratio *Abies balsamea*; LCR bS = Live crown ratio *Picea mariana*, CWD 2 = Coarse woody debris 2; CWD 4 = Coarse woody debris 4. See Table 1 for a complete description of variables.



**Fig. 3.** Abundance of six species in response to canopy openness and water table index. Circles indicate abundance and the Spearman correlation between species abundance and canopy openness and water table index are indicated in the corners of the respective axes. Significant relationships are indicated with \*. The dotted line indicates where the water table moves from the mineral soil to the organic forest floor.

*Species-habitat relationships*

In light of the strong relationships indicated by the pCCA between community composition and ericaceous species, water table position and light, these factors were examined in greater detail. The cover of ericaceous species was strongly correlated with forest floor thickness ( $R^2 = 0.528$ ;  $p < 0.001$ ) and position of the water table ( $R^2 = 0.362$ ;  $p < 0.001$ ). Similarly the cover of *S. rubellum* ( $R^2 = 0.19$ ;  $p = 0.03$ ) and *S. russowii* ( $R^2 = 0.19$ ;  $p = 0.02$ ) were positively, and *P. schreberi* was negatively partially correlated with ericaceous cover ( $R^2 = -0.291$ ;  $p < 0.001$ ), even when forest floor thickness, water table position and canopy cover were accounted for. Interestingly, the abundances of *Sphagna* found in more illuminated habitats (*S. magellanicum*, *S. fallax*) were uncorrelated with ericaceous species cover when forest floor thickness, water table position and canopy opening had been accounted for (not shown). The relationship between canopy cover, water table index and species abundance was investigated for key species along the successional gradient (Table 4; Fig. 3). The abundance of *P. schreberi* and *P. crista-castrensis* was generally negatively related to canopy openness and water table index (Fig. 3) and these species were

more common in quadrats where the water table was in the mineral soil (Table 4). However, *P. schreberi* was found in a variety of habitats as is indicated by the wide spread of points in Fig. 3. *S. capillifolium* did not have a significant correlation with canopy ( $R^2 = -0.133$ ) or water table index ( $R^2 = -0.035$ ), and was found both in quadrats under closed and open canopies. *S. russowii*

**Table 4.** Cover of selected species in sites where the water table is present in the mineral soil, compared to sites where it is present in the forest floor. Values are means and standard error, and letters indicate significant differences; a < b.

Species	Water table mineral	Water table forest floor
Feathermosses:		
<i>Pleurozium schreberi</i>	46.20 ± 1.50 b	24.70 ± 1.99 a
<i>Ptilium crista-castrensis</i>	11.37 ± 1.21 b	2.35 ± 0.54 a
<i>Hylocomium splendens</i>	1.48 ± 0.31 a	2.71 ± 0.54 b
<i>Ptilidium ciliare</i>	4.46 ± 0.52 a	5.02 ± 0.62 b
<i>Sphagna</i>		
<i>Sphagnum capillifolium</i>	6.45 ± 1.02	6.35 ± 1.41
<i>Sphagnum russowii</i>	10.10 ± 1.59 a	13.06 ± 2.44 b
<i>Sphagnum rubellum</i>	2.82 ± 0.84 a	6.56 ± 1.83 b
<i>Sphagnum magellanicum</i>	1.00 ± 0.40 a	8.33 ± 1.61 b
<i>Sphagnum fallax</i>	2.30 ± 0.78 a	12.06 ± 2.31 b
<i>Sphagnum fuscum</i>	0.0017 ± 0.00058 a	4.40 ± 1.20 b

showed an intermediate pattern, present in quadrats with the water table in the mineral soil, but predominantly where the canopy was relatively open, and also present in quadrats where the water table was in the forest floor. *S. magellanicum* and *S. fuscum* were significantly less frequent in quadrats where the water table was not in the forest floor, and were restricted to quadrats with high levels of open canopy cover.

The difference between habitats indicated above was confirmed with direct microclimate measurements made in one young and one old stand. The microclimate (mean total daily PAR, temperature, and vapour pressure deficit or VPD; Table 5) measured in the habitats of *P. schreberi* and *S. capillifolium* in the young stand and in the habitats of *P. schreberi* and *S. magellanicum* in the old stand were significantly different for total daily PAR while only subtle differences in the frequencies of temperature and VPD were observed (data not shown). Interestingly, precipitation was greater in *Sphagnum* spp. patches in both young and old stands.

While mean conditions give a general picture of the microclimate in these habitats, extreme conditions, and their duration may be more relevant for the performance of the species (Table 5). Duration of high PAR followed a similar pattern as the mean while a different pattern was observed for temperature, with longer duration of extreme temperatures in the *Sphagnum* patches in the young stand, while actual temperatures were greater in the older stand. Interestingly, while incident light and temperature were consistently higher in the older stand, duration of high VPD values was greater in the younger stand, and higher in *Pleurozium schreberi* compared to the *Sphagnum* spp. in the older stand.

## Discussion

### *The role of the environment in changes in community composition*

Even though the species composition varies considerably within each age group, our results reveal a consistent gradient of change in the bryophyte community from feathermosses to hummock *Sphagna* (*S. capillifolium*, *S. rubellum*) and then to hollow *Sphagna* (*S. magellanicum*, *S. fallax*) along the first DCA ordination axis. This compositional gradient may be brought about by changes in available light due to the opening of the forest canopy and/or by changes in available moisture due to the rising water table; both of these variables are correlated with the first DCA axis (Fig. 2) and both are shown directly to explain variation in species' presence and abundance (Fig. 3, Tables 2, 4). Results of this study are thus consistent with both of the main hypotheses concerning the driving forces in the successional community changes in paludifying forests. The abundance of ericaceous species (*Rhododendron groenlandicum* and *Kalmia angustifolia*) is also strongly correlated with the main compositional gradient and may thus be an additional driving force for successional changes in the bryophyte community.

### *Available light*

Light availability triples between young dense stands and old open stands (Table 5). A possible explanation for the observed successional replacement is that changes in light availability results in altered growth rates of

**Table 5.** Means and standard error for microclimatic variables in young (85 years) and old (270 years) stands, for *Sphagnum* spp. and *Pleurozium schreberi* patches. Significant differences ( $p < 0.05$ ) between species are indicated with capital letters, while differences between age classes are indicated with lower case letters ( $a < b$ ). GLM model for rows in italics are significant, as is the interaction term between age and species, for more details on the model, see the Methods section. The N for high values indicates the number of times values exceeded the cut-off point. Values are means  $\pm$  SE.

Variable	Young		Old	
	<i>S. capillifolium</i>	<i>P. schreberi</i>	<i>S. magellanicum</i>	<i>P. schreberi</i>
Daily total PAR	2540.0 $\pm$ 98.9	2876.7 $\pm$ 119.3	8319.7 $\pm$ 334.5	12157.3 $\pm$ 602.1
Temperature	12.9 $\pm$ 0.079	12.92 $\pm$ 0.079	12.96 $\pm$ 0.13	13.38 $\pm$ 0.14
VPD	2.78 $\pm$ 0.044	2.73 $\pm$ 0.043	2.82 $\pm$ 0.068	3.56 $\pm$ 0.086
Precipitation	3335 $\pm$ 245Ba	2985 $\pm$ 297Aa	3932 $\pm$ 113Ba	3083 $\pm$ 308Aa
High PAR (N)	37 $\pm$ 3.5	48.5 $\pm$ 31.5	84	84
Duration (hours)	2.12 $\pm$ 0.13Aa	2.09 $\pm$ 0.11Aa	6.35 $\pm$ 0.23Ab	6.37 $\pm$ 0.21Ab
Mean value ( $\mu\text{molm}^{-2}\text{s}^{-1}$ )	230.50 $\pm$ 6.23	274.70 $\pm$ 11.18	284.11 $\pm$ 9.15	462.80 $\pm$ 23.25
High temperature (N)	63 $\pm$ 7.0	52.5 $\pm$ 4.5	34 $\pm$ 12.0	38.5 $\pm$ 14.0
Duration (hours)	10.01 $\pm$ 1.57	7.68 $\pm$ 0.39	7.69 $\pm$ 0.39	7.68 $\pm$ 0.41
Mean value ( $^{\circ}\text{C}$ )	21.663 $\pm$ 0.13Aa	21.61 $\pm$ 0.15Aa	22.83 $\pm$ 0.23Ab	23.22 $\pm$ 0.25Ab
High VPD (N)	36 $\pm$ 2.0	34.5 $\pm$ 4.5	32.0 $\pm$ 16.5	40.0 $\pm$ 18.0
Duration (hours)	6.40 $\pm$ 0.35Ab	6.61 $\pm$ 0.35Ab	4.52 $\pm$ 0.32Aa <sup>§</sup>	5.33 $\pm$ 0.27Aa <sup>§</sup>
Mean value (KPa)	11.18 $\pm$ 0.26	11.16 $\pm$ 0.26	11.02 $\pm$ 0.30	12.28 $\pm$ 0.33

<sup>§</sup> The  $p$  value for the difference between these two values when tested with a  $t$ -test is 0.0

both groups, allowing the *Sphagna* to overtop the feathermosses and therefore claim their space. In dark young forests, feathermosses with maximum photosynthetic capacity at low light levels dominate (Williams & Flanagan 1998). The *Sphagna* present in these forests are capable of tolerating shade – *S. capillifolium*, *S. subtile*, *S. russowii*; Fig. 3 (Hayward & Clymo 1983; Gignac 1992) and, consequently, are found in habitats not significantly more illuminated than those of the feathermosses. With increasing light availability due to canopy break-up, the established *Sphagna* are likely to take advantage of the newly available light resource, as their maximum photosynthetic rate is higher than that of the feathermosses and is reached at a higher illumination level (Silvola 1991; Williams & Flanagan 1998). This may facilitate an increase in growth rate, allowing them to physically overtop the feathermosses and occupy their space. Once abundant light levels have been reached species that are not tolerant of shade, such as *S. magellanicum*, *S. fallax* and *S. fuscum* (Fig. 3; Gignac 1992) became dominant. The continued presence and even importance of *P. schreberi* in the older stands is interesting, and may be due to its tolerance of high light levels and temperatures (and associated desiccation, see below), as the light levels are significantly higher in the *P. schreberi* habitat than in the *S. magellanicum* habitat in the old forest.

#### Available moisture

Along with changes in light availability, moisture increases strongly along the age gradient. In young stands the water table is in the mineral soil and the soil environment is dry with a high vapour pressure deficit (VPD; Table 5). The species composition includes species tolerant of or resistant to desiccation. Feathermosses are capable of tolerating desiccation and of reactivating their photosynthetic apparatus in a relatively short period (Silvola 1991; Williams & Flanagan 1998; Bisbee et al. 2001). In contrast *Sphagna* are less tolerant of desiccation (Silvola 1991; Gerdol et al. 1996), but more capable of resisting desiccation, by means of their colonial structure, particularly in hummock species, such as *S. capillifolium* and *S. subtile*, with tight interlacing branches and densely packed individuals (Hayward & Clymo 1983; Schipperges & Rydin 1998). While the habitats of *P. schreberi* and *S. capillifolium* are not significantly different in the young stands, more precipitation is collected in *S. capillifolium* patches than in *P. schreberi* carpets. This may indicate that the *Sphagna* establish in microhabitats that are slightly more humid than the surrounding matrix.

With increasing time since fire the forest floor thickness increases and eventually the pore size of the basal

layers of the forest floor decreases during decomposition. This is likely to bring about a gradual upward movement of the water table into the forest floor via capillary action (Fenton et al. in press), whereby the immediate environment of the forest-floor bryophytes becomes more humid. Position above water table has been shown to be one of the main structuring features in peatlands (Hayward & Clymo 1983; Rydin 1987; Gignac et al. 1991) and in swamp forests (Jeglum 1991; Økland et al. 2001).

Despite the relative coarseness of the measures of water table position (one observation per 25-m<sup>2</sup> plot), we are able to document that a number of hollow *Sphagna* (*S. magellanicum*, *S. rubellum*, *S. angustifolium* and *S. fallax*), that are less efficient at resisting desiccation because they form looser colonies (Schipperges & Rydin 1998), are most likely able to colonize and expand after, or immediately before the movement of the water table into the forest floor. Once established these species may be able to overtop feathermosses and hummock *Sphagnum* species due to their higher growth rates (Moore 1989; Rochefort et al. 1990; Vitt 1990). Furthermore, feathermosses such as *P. schreberi* (Mulligan & Gignac 2002) and *Hylocomium splendens* (Busby et al. 1978) have been found to be intolerant of very high water tables. A deviant pattern is shown by *P. ciliare* as it is equally abundant in quadrats with low and high water tables. The ultimate dominance of *S. fuscum* and *S. fallax* in very old stands may be due to their relatively broad tolerance of water table position compared to *S. magellanicum* and the other hollow species present (Gignac 1992), as the height above water table increased dramatically over time, as organic material continued to accumulate in the forest floor.

#### Ericaceous species

Two different hypotheses may account for the strong correlation between ericaceous species and the successional changes in the community. Firstly, a negative effect of ericaceous species, including *Kalmia angustifolia* and *Ledum groenlandicum*, on the growth of vascular plants and decomposition of *P. schreberi* litter is well-documented (Inderjit & Malik 1997; Wardle et al. 1998). Therefore, it is possible that the strong positive correlations of ericaceous cover with forest floor thickness and the water table is related to its effects on decomposition. However, 11.4% of the explained variation in bryophyte species composition is explained by ericaceous cover alone. This may be due to the ladder effect, described by Malmer et al. (2003), i.e. that *Sphagna* use vascular plants as ladders and consequently they increase their annual growth. According to this hypothesis, and considering the poor ability of feathermosses

to use ladders, the presence of ericaceous species will favour the growth of *Sphagna* over that of *P. schreberi*. This is also supported by significant partial correlation coefficients between ericaceous cover and abundances of *S. rubellum* and *S. russowii* and the negative partial correlation coefficient with *P. schreberi*.

#### *The role of non-equilibrium factors in changes in community composition*

This study supports the theory that equilibrium factors such as habitat changes are important drivers of successional change in this system. However, a large percentage of the variation in the community is not explained by the habitat factors examined. This may be due to stochastic factors affecting species establishment within the community. An example may be remnant patches of *Sphagna* that have survived from the previous stand and which may influence the composition of the community in the regenerating forest. Furthermore, establishment factors may play an important role. The mechanism of establishment of *Sphagna* patches in the feathermoss carpet is still unknown, although it is believed that *Sphagnum* spores cannot germinate in the carpet (Sundberg & Rydin 2002) because they require a specific substrate. Noble et al. (1984) observed that *S. girgensohnii* establishes in tip-ups, while Lawrence (1958) suggested that *Sphagna* establish in holes in the carpet formed by animal urine. In our sites, *Sphagna* seem to establish in sites with a microclimate almost identical to that of the surrounding feathermosses (Table 5), although the establishment substrate was not identified. The true role of establishment dynamics (e.g. availability of spores or asexual propagules and establishment sites) in driving the community pattern is yet unknown.

#### *Succession and competition theory*

The sequential replacement of bryophyte species in coniferous boreal forests after fire has been described as a typical successional sequence; unlike the cyclical succession or initial floristics that frequently dominates the tree and shrub layers (Heinselman 1981; Foster 1985). In this study, the type of succession appears to fit the model of facilitation as described by Connell & Slatyer (1977), where later species are dependent on habitat changes produced by the initial colonizers. The hollow *Sphagna* would be unable to establish in the older stands if the forest floor had not developed to the thickness required for the water table to rise and the accumulation of material in the forest floor is accelerated by the presence of *Sphagna* (Fenton et al. 2005). Therefore, the presence of the hollow *Sphagna* is dependent on the

precedent group of hummock *Sphagna*. Examples of facilitative secondary succession (as described by Connell & Slatyer 1977) are rare, and their existence in bryophyte communities has been questioned (Rydin 1997).

It is unclear whether species displacement is due to an altered realized niche – because of interactions with newly established species – or to limits of the fundamental niche. It has been suggested that habitats of hummock species are restricted by competition in poor fens and bogs (Mulligan & Gignac 2001). The true role of competition in species displacement along this gradient can only be tested experimentally with reciprocal transplants (Rydin 1997; Bisbee et al. 2001).

Our results demonstrate that *Sphagnum* spp. are not only structured spatially along environmental gradients (i.e. water table), but that they are also temporally structured within an evolving forest habitat. The dynamism of this system emphasizes the importance of water table movement in determining the outcome of succession, and in a landscape dominated by forests that are prone to paludification ultimately ecosystemic and landscape dynamics such as carbon balances and fire cycles.

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#### **References**

- Anon. (Environment Canada) 2004. [http://www.climate.weatheroffice.ec.gc.ca/climate\\_normals/results\\_e.html](http://www.climate.weatheroffice.ec.gc.ca/climate_normals/results_e.html)
- Anderson, L.E. 1990. A checklist of *Sphagnum* in North-America north of Mexico. *Bryologist* 93: 500-501.
- Bazzaz, F.A. 1990. Plant-plant interactions in successional environments. In: Grace, J. & Tilman, D. (eds.) *Perspectives on plant competition*, pp. 239-263. Academic Press, San Diego, CA, US.
- Bergeron, Y., Gauthier, S., Flannigan, M. & Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forests in northwestern Quebec. *Ecology* 85: 1916-1932.
- Bisbee, K., Gower, S., Norman, J. & Nordheim, E. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. *Oecologia* 120: 261-270.
- Boudreault, C., Bergeron, Y., Gauthier, S. & Drapeau, P.

2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. *Can. J. For.* 32: 1080-1093.
- Burkholder, P.R. 1952. Cooperation and conflict among primitive organisms. *Am. Sci.* 40: 601-631.
- Busby, J.R., Bliss, L.C. & Hamilton, C.D. 1978. Microclimatic control of growth rates and habitats of the boreal forest mosses *Tomenthypnum nitens* and *Hylocomium splendens*. *Ecol. Monogr.* 48: 95-110.
- Carnell, R. & Anderson, A. 1986. A technique for extensive field measurements of soil anaerobism by rusting of steel rods. *Forestry* 59: 129-140.
- Connell, J.H. & Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.
- Crawford, R.M., Jeffree, C.E. & Rees, W.G. 2003. Paludification and forest retreat in northern oceanic environments. *Ann. Bot.* 91: 213-226.
- Crum, H. & Anderson, L.E. 1981. *The mosses of eastern North America*. Columbia University Press, New York, NY, US.
- Cyr, D., Bergeron, Y., Gauthier, S. & Larouche, A. 2005. Are old-growth forests of the Clay Belt part of a fire-regulated mosaic? *Can. J. For. Res.* 35: 65-73.
- Dioumaeva, I., Trumbore, S., Schuur, E., Goulden, M., Litvak, M. & Hirsch, A. 2002. Decomposition of peat from upland boreal forest: temperature dependence and sources of respired carbon. *J. Geophys. Res.* 108(D3): Art. 8222.
- Fenton, N., Lecomte, N., Légaré, S. & Bergeron, Y. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. *For. Ecol. Manage.* 213: 151-159.
- Fenton, N., Légaré, S., Bergeron, Y. & Paré, D. Soil oxygen within boreal forests across an age gradient. *Can. J. Soil. Sci.* In press.
- Foster, D. 1985. Vegetation development following fire in *Picea mariana* (Black spruce) – *Pleurozium* forests of south-eastern Labrador, Canada. *J. Ecol.* 73: 517-534.
- Gerdol, R., Bonora, A., Gualandri, R. & Pancaldi, S. 1996. CO<sub>2</sub> exchange, photosynthetic pigment composition and cell ultrastructure of *Sphagnum* mosses during dehydration and subsequent rehydration. *Can. J. Bot.* 74: 726-734.
- Gignac, D. 1992. Niche structure, resource partitioning and species interactions of mire bryophytes relative to climatic and ecological gradients in western Canada. *Bryologist* 95: 406-418.
- Glebov, F. & Korzukhin, M. 1992. Transitions between boreal forest and wetland. In: Shugart, H., Leemans, R. & Bonan, G. (eds.) *A systems analysis of the global boreal forest*, pp. 241-266 Cambridge University Press, Cambridge, UK.
- Gower, S., Vogel, J., Norman, J., Kucharik, C., Steele, S. & Stow, T. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *J. Geophys. Res.* 102: 29029-29041.
- Grondin, P. 1996. Écologie forestière. In: Bérard, J.A. & Côté, M. (eds.) *Manuel de foresterie*, pp. 133-279. Le Presse de l'Université Laval, Québec, CA.
- Harden, J., Trumbore, S., Stocks, B., Hirsch, A., Gower, S., O'Neill, K. & Kasischke, E. 2000. The role of fire in the boreal carbon budget. *Global Change Biol.* 6 (Suppl. 1): 174-184.
- Hayward, P. & Clymo, R. 1983. The growth of sphagnum: experiments on, and simulation of, some effects of light flux and water table depth. *J. Ecol.* 71: 845-863.
- Heinselman, M. 1981. Fire and succession in the conifer forests of North America. In: West, D.C., Shugart, H.H. & Botkin, D.B. (eds.) *Forest succession: concepts and applications*, pp. 374-405. Springer-Verlag, New York, NY, US.
- Hill, M.O. 1979. *DECORANA – A FORTRAN program for detrended correspondence analysis: and reciprocal averaging*. Cornell University, Ithaca, NY, US.
- Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.
- Inderjit & Mallik, A.U. 1997. Effects of *Ledum groenlandicum* amendments on soil characteristics and black spruce seedling growth. *Plant Ecol.* 133: 29-36.
- Jeglum, J. 1991. Definition of trophic classes in wooded peatlands by means of vegetation types and plant indicators. *Ann. Bot. Fenn.* 28: 175-192.
- Lawrence, D. 1958. Glaciers and vegetation in south-eastern Alaska. *Am. Sci.* Summer: 89-122.
- Lecomte, N., Simard, M., Bergeron, Y., Larouche, A., Asnong, H., & Richard, P.J.H. 2005. Effects of fire severity and initial tree composition on understory vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data. *J. Veg. Sci.* 16: 665-674.
- Lecomte, N., Simard, M. & Bergeron, Y. In press. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of north western Quebec, Canada. *Ecoscience*
- Malmer, N., Albinsson, C., Svensson, B. & Wallén, B. 2003. Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. *Oikos* 100: 469-482.
- McCune, B. & Mefford, M.J. 1999. *PC-Ord. Multivariate Analysis of Ecological Data for Windows, ver. 4*. MJM Software Design, Gleneden Beach, OR, US.
- Moore, T. 1989. Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. *Can. J. Bot.* 67: 1203-1207.
- Mulligan, R. & Gignac, D. 2001. Bryophyte community structure in a boreal poor fen: reciprocal transplants. *Can. J. Bot.* 79: 404-411.
- Noble, M., Lawrence, D. & Streveler, G. 1984. *Sphagnum* invasion beneath an evergreen forest canopy in southeastern Alaska. *Bryologist* 87: 119-127.
- O'Connell, K., Gower, S. & Norman, J. 2003. Net ecosystem production of two contrasting boreal black spruce forest communities. *Ecosystems* 6: 248-260.
- Økland, R. 1999. On the variation explained by ordination and constrained ordination axes. *J. Veg. Sci.* 10: 131-136.
- Økland, R.H. 2000. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. 5. Consequences of the vertical position of individual shoot segments. *Oikos* 88: 449-469.
- Økland, R. 2003. Partitioning the variation in a plot-by-species

- data matrix that is related to  $n$  sets of explanatory variables. *J. Veg. Sci.* 14: 693-700.
- Økland, R., Økland, T. & Rydgren, K. 2001. Vegetation-environment relationships of boreal spruce swamp forests in Østmarka Nature Reserve, SE Norway. *Sommerfeltia* 29: 1-190.
- Reiners, W., Worley, I. & Lawrence, D. 1971. Plant diversity in a chronosequence. *Ecology* 52: 55-69.
- Rocheffort, L., Vitt, D. & Bayley, S. 1990. Growth, production and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology* 71: 1986-2000.
- Rydin, H. 1997. Competition among bryophytes. *Adv. Bryol.* 6: 135-168.
- Schipperges, B. & Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. *New Phytol.* 140: 677-684.
- Silvola, J. 1991. Moisture dependence of CO<sub>2</sub> exchange and its recovery after drying in certain boreal forest peat mosses. *Lindbergia* 17: 5-10.
- Slack, N. 1990. Bryophytes and ecological niche theory. *Bot. J. Linn. Soc.* 104: 187-213.
- Söderström, L. 1987. Dispersal as a limiting factor for distribution among epixylic bryophytes. *Symp. Biol. Hung.* 35: 475-483.
- Sundberg, S. & Rydin, H. 2002. Habitat requirements for establishment of *Sphagnum* from spores. *J. Ecol.* 90: 268-278.
- Swanson, R. & Flanagan, L. 2001. Environmental regulation of carbon dioxide exchange at the forest floor in a boreal black spruce ecosystem. *Agric. For. Meteorol.* 108: 165-181.
- Tanner, C. 1972. Application of psychometry to micrometeorology. In: Brown, R. & Van Haveren, B. (eds.) *Psychometry in water relations research*, pp. 239-247. Utah Agricultural Experiment Station. Utah State University, Salt Lake City, UT, US.
- Taylor, S., Carleton, T. & Adams, P. 1987. Understorey vegetation change in a *Picea mariana* chronosequence. *Vegetatio* 73: 63-72.
- ter Braak, C. & Šmilauer, P. 1998. *CANOCO for Windows Version 4.2*. Centre for Biometry Wageningen, CPRO-DLO, Wageningen, NL.
- Turetsky, M. 2003. The role of bryophytes in carbon and nitrogen cycling. *Bryologist* 106: 395-409.
- Van Cleve, K. & Viereck, L. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. In: West, D., Shugart, H. & Botkin, D. (eds.) *Forest succession: Concepts and applications*, pp. 185-211. Springer-Verlag, New York, NY, US.
- Vincent, J. & Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. *Geogr. Phys. Quart.* 31: 357-372.
- Vitt, D. 1990. Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients. *Bot. J. Linn. Soc.* 104: 35-59.
- Wardle, D., Nilsson, M.C., Gallet, C. & Zackrisson, O. 1998. An ecosystem-level perspective of allelopathy. *Biol. Rev.* 73: 305-319.
- Williams, T. & Flanagan, L. 1998. Measuring and modelling environmental influences on photosynthetic gas exchange in *Sphagnum* and *Pleurozium*. *Plant Cell Environ.* 21: 555-564.

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