Spontaneous revegetation of mined peatlands in eastern Canada

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Abstract: Many North American peatlands previously mined for horticultural peat have been abandoned recently, allowing natural recolonization to occur. The two dominant methods for peat extraction, hand block-cutting and vacuummining, have created distinctly different abandoned surfaces, leading to different recolonization patterns. Both types of exploitation can be found throughout eastern Canada where we conducted a vast survey of 26 abandoned mined peatlands in the provinces of Québec and New Brunswick. The aim of this study is to describe the revegetation patterns and to assess the impact of local and regional variables as well as the time since abandonment on Sphagnum recolonization. We inventoried the vegetation structure in all trenches (2571) and baulks (2595) of abandoned block-cut areas as well as in all vacuum fields (395) of the mechanically mined areas. We also conducted detailed species relevés in 242 of these peat fields. In comparison to vacuum-mined peatlands, block-cut peatlands regenerated remarkably well. Approximately 80% of all baulks and trenches in block-cut peatlands had 50% or higher cover of ericaceous shrubs compared with only 16% found on vacuum fields. Herb cover in the three types of abandoned fields was similar to that in natural peatlands. However, Sphagnum percent cover was below 2% in baulks and vacuum fields and was 30% on average in the trenches, which is clearly below cover estimates in natural peatlands. Sphagnum cover and richness were both higher in trenches with thin residual peat deposit, and Sphagnum richness increased with latitude. Our surveys revealed that abandoned mined peatlands have a high diversity of peatland vascular plants species and a low diversity of non-peatland species.

Key words: cutover peatlands, regeneration, milled peatlands, block-cut peatlands, vacuum-mined peatlands, colonization patterns.

Résumé : En Amérique du Nord, plusieurs tourbières dont la tourbe a été récoltée à des fins horticoles ont été laissées à l'abandon, ce qui a permis une recolonisation naturelle des surfaces par la végétation. Les deux méthodes d'extraction de la tourbe, soit la coupe manuelle par blocs et la récolte par aspirateur, laissent toutefois des surfaces fort différentes qui ne sont pas recolonisées de la même façon par la végétation. Nous avons mené une vaste étude dans 26 tourbières abandonnées après exploitation, dans les provinces du Québec et du Nouveau-Brunswick, où ces deux types de tourbières sont présents. Nous avons décrit les patrons de recolonisation végétale et déterminé l'influence respective des variables locales et régionales, ainsi que du temps depuis l'arrêt des activités d'extraction de la tourbe sur le succès de colonisation des tranchées par les sphaignes. Nous avons déterminé la structure de la végétation dans toutes les tranchées (2571) et les terre-pleins (2595) des tourbières exploitées par blocs, ainsi que dans les parcelles abandonnées après exploitation par aspirateur (395). Nous avons également fait des relevés détaillés des espèces dans 242 de ces parcelles. Les tourbières dont la tourbe a été récoltée par blocs se régénèrent fort bien comparativement aux tourbières exploitées par aspirateur. Dans les tourbières exploitées par blocs, près de 80 % des terre-pleins et des tranchées sont couverts sur plus de la moitié de leur surface par des éricacées. Un couvert aussi important en éricacées ne s'observe que dans 16 % des parcelles aspirées. Le couvert herbacé des trois types de parcelles abandonnées est semblable à celui des tourbières naturelles. Le couvert des sphaignes est inférieur à 2 % sur les terre-pleins et dans les parcelles exploitées par aspirateur, alors qu'il atteint en moyenne 30 % dans les tranchées. Ces valeurs sont bien en deçà de ce que l'on observe dans les tourbières naturelles. Le couvert et la richesse des sphaignes étaient plus importants dans les tranchées avec un dépôt de tourbe peu épais et la richesse en sphaignes augmentait avec la latitude. Les tourbières abandonnées après exploitation possèdent une grande diversité d'espèces de plantes vasculaires propres aux tourbières et peu d'espèces qui ne se trouvent habituellement pas dans ce milieu.

Mots clés : tourbières abandonnées, regénération, tourbières exploitées par la coupe par blocs, tourbières exploitées par aspirateur, patrons de colonization.

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Introduction

In a world of fragmented and disturbed ecosystems, degraded sites may have significant ecological value and be of great importance for preserving regional biodiversity. For example, forest remnants play a critical role in maintaining animal or plant populations and small forest patches can be beneficial to metapopulation dynamics (Hanski 1998; Hanski and Ovaskainen 2000; Brotons et al. 2003). Peatland remnants could potentially play a similar role (Poulin et al. 1999; Delage et al. 2000), but they are often very small, linear, and located around the periphery of intensely used peatlands. If abandoned mined sites adjacent to peatland remnants could be restored, the residual ecosystems (remnants and restored) would be of greater ecological value. In that respect, peat mining represents a form of exploitation leading to drastic and sometimes irreversible changes in the peatland ecosystems (Smart et al. 1986; Money 1995; Lavoie and Rochefort 1996; Rowlands and Feehan 2000; Girard et al. 2002). Left alone, milled abandoned peat surfaces are barely recolonized by plants because they face harsh environmental filters such as altered hydrology (Price et al. 2003; Price and Whitehead 2004), wind erosion, and frost heaving (Campbell et al. 2002; Groeneveld and Rochefort 2002). Consequently, restoration techniques have been developed to actively revegetate vacuum-milled peatlands, converting them back to peat-accumulating systems (Rochefort 2001; Rochefort et al. 2003). This should, in turn, increase the abandoned peatlands' contribution to regional diversity (Cooper and McCann 1995).

Some vascular and nonvascular plant species are nevertheless able to colonize bare peat fields despite the harsh environmental filters that prevent massive recolonization of abandoned surfaces (Campbell 2002). This is especially true for sites that have been manually mined using the block-cut method (Girard et al. 2002). This method, which was the precursor to mechanized peat mining techniques, consists of extracting peat blocks with shovels, leaving a topography characterized by alternating baulks and trenches (Rochefort 2001). In abandoned trenches, prevailing conditions differ greatly from those of vacuum-mined sites, being more favorable to plant recolonization (Soro et al. 1999; Price and Whitehead 2001; van Seters and Price 2001). With few exceptions, peatlands are no longer excavated by hand. Nonetheless, the study of block-cut peatlands may help understand the factors influencing the natural re-establishment of a vegetation cover, particularly Sphagnum carpets, which are essential for restoring ecological functions of bog ecosystems (Rochefort 2000).

Detailed investigations on the importance of factors influencing the natural revegetation of abandoned peatlands have been undertaken in Europe, especially in Finland (Salonen 1987, 1990, 1992, 1994; Salonen and Setälä 1992; Salonen et al. 1992), Sweden (Soro et al. 1999), Northern Ireland (Cooper et al. 2001), and Switzerland (Buttler et al. 1996; Grosvernier 1996; Matthey 1996). Moist conditions, a nearby plant propagule source, and a less intense exploitation or shorter harvesting period are all factors that promote the recolonization of abandoned surfaces. Other studies involve the manipulation of water table levels prior or during the plant colonization period (Smart et al. 1989; Meade 1992; Tuittila et al. 2000*b*). In North America, Famous et al. (1991) conducted a survey of the natural revegetation of 35 abandoned peatlands (vacuum and block-cut mined) in eastern Canada and United States, but they reported only broad estimates of vegetation cover. Others have studied comprehensively the factors influencing *Sphagnum* establishment in one block-cut mined peatland located in southern Québec (Lavoie and Rochefort 1996; Price and Whitehead 2001, 2004; van Seters and Price 2001; Girard et al. 2002). Only Girard et al. (2002) concurrently looked at the effect of spatio-historical and physicochemical factors on spontaneous revegetation patterns at the same site. Both factors proved to be important in determining recolonization patterns, yet further studies are needed to examine factors acting at different scales.

In 1994, 1995, and 1997, we conducted a large survey of abandoned mined peatlands throughout the provinces of Québec and New Brunswick, where most abandoned peatlands in Canada can be found (Rubec and Thibault 1998; Thibault 2002). This survey included the sites mined by either the vacuum and (or) the block-cut method. Abandoned peat field was evaluated for its vegetation structure and for the plant species that recolonized the site. We first report on the descriptive statistics that illustrate the success of natural revegetation in abandoned peatlands. The survey was used to depict the typical vegetation cover of abandoned baulks, trenches, and vacuum fields. We then used regression models to assess the respective influence of local and regional variables, as well as the time since abandonment, on the success of Sphagnum colonization of block-cut mined peatlands. Although numerous experimental studies on peatland restoration have been conducted since the early stages of this project, few concurrently measured the effects of large and small scale factors, as well as the importance of time, on the revegetation patterns. This study represents, to our knowledge, the most extensive survey on spontaneously revegetated peatlands conducted in North America.

Study sites

The study area encompasses basically all abandoned mined peatlands of three lowland regions of the province of Québec, namely central Québec, Bas-Saint-Laurent, and Lac-Saint-Jean, as well as of the Acadian Peninsula and eastern part of New Brunswick (Fig. 1). Most of the studied peatlands have developed in lowlands of sand, silt, and clay marine deposit. They are classified as Atlantic boreal peatlands and Maritime Atlantic boreal peatlands and are primarily ombrotrophic (bogs; National Wetlands Working Group 1988). They occur in the boreal zone where the spring runoff represents the most important annual hydrological event (National Wetlands Working Group 1988; Price 2001). The mean annual temperature is 3.4 °C and 4.3 °C for the study areas in Québec and New Brunswick, respectively (Environment Canada 1993). Corresponding mean annual precipitations are 937 and 1070 mm. The length of the growing season is 218 and 215 days for these two provinces, respectively.

We surveyed a total of 26 peatlands, which were mined by the block-cut method (Figs. 2a, 2b) and (or) by milling and vacuum machines (Figs. 2c, 2d; Rochefort 2001). In North America, the block-cut method was used until the end of the



Fig. 1. Location of the 26 study peatlands, which corresponds to most of the abandoned mined peatlands of eastern Canada.

1960s (Warner and Buteau 2000). Peat was cut by hand into blocks (ca. 35 cm \times 20 cm \times 15 cm) that were placed on adjacent, raised peat baulks to dry. When abandoned, trenches alternate with baulks, which creates a topography characteristic of all block-cut mined peatlands (Figs. 2b, 2e; Robert et al. 1999; Rochefort 2001; Girard et al. 2002). Living vegetation, including roots and moss fragments, were frequently thrown back in the middle of the excavated trenches where they could potentially initiate the revegetation process.

In the 1960s and 1970s, tractor-drawn vacuum machines replaced shovels and manpower, which required a more complete drainage of extracting sites. To support heavy tractors, V-shaped ditches, with a depth of 1 m in the middle, are regularly spaced every 30 m. The surface vegetation is scraped off and the dry peat deposit is furrowed. The peat is then collected with vacuums, sifted, bagged, and sold mostly to the North American horticultural market. Peat is collected up to a depth of 10 cm per year and mining stops once the basal layer of ombrotrophic peat is less than 50 cm or weakly minerotrophic peat is reached. This method of extracting peat leaves large flat expanses of bare peat devoid of any plant propagules (Fig. 2d).

Materials and methods

We surveyed the vegetation during two consecutive summers (1994 and 1995), as well as in 1997, for some sites located in New Brunswick. We evaluated the vegetation structure of all abandoned fields of the study area. A field consisted of a strip of residual peat that had been mined by the block-cut method (thereafter called trench and baulk fields) or by the vacuum method (thereafter called vacuum fields; Fig. 2e). For each field (i.e., baulk, trench, or vacuum), the percent cover of eight vegetation strata and ground substrate was estimated according to five classes: 0, 0%; 1, 1%-10%; 2, 11%-25%; 3, 26%-50%; 4, 51%-100%. The strata were described as trees, ericaceous shrubs, herbs, Sphagnum, mosses other than Sphagnum, lichens, open water, and bare peat. Because of the substantial number of abandoned fields, we did not proceed with detailed relevés for estimating vegetation structure. Instead, the percent cover of each vegetation strata was estimated visually while walking across every abandoned field. The survey for vegetation structure is thus closer to an inventory than a sample. To compare the regeneration of abandoned peatlands to unmined bog systems, we used vegetation data from Poulin et al. (1999), who surveyed the center and open margins of 24 unmined peatlands in the same regions.

We also conducted detailed species relevés in 242 peat fields (96 baulks, 112 trenches, and 34 vacuum fields). The sampled fields were selected following a stratified random sampling design (Thompson 2002). First, we identified how many types of vegetation structure were present in each peatland. These types were defined according to the two dominating strata. For example, a type E_4B_4 indicates that the two main strata occurring in this peat field were



ericaceous shrubs (E) and bare peat (B), both having a cover >50%. After stratifying each peatland into structure types, we randomly chose a certain number of fields to be sampled. This number was proportional to the surface area occupied by the structure type within the peatland. The vegetation relevés were conducted using a systematic point sampling design (Bonham 1989). Ten equidistant transects were estab-

lished across the field (see Table 3). Along each of these transects, we recorded all plant species, including mosses, liverworts, lichens, and vascular plants, touching a vertical rod placed on ten equidistant positions.

The following physical parameters were measured in the middle of each field sampled for species relevés on the date of the vegetation surveys: thickness of the residual peat de**Fig. 2.** Photographs showing block-cut (*a*, *b*) and vacuum mining (*c*, *d*) in peatlands. When peat was extracted by hand (block-cut), the topography was characterized by alternating trenches and baulks. Baulks are rows of peat that are less deeply mined than trenches and that were used to dry peat blocks. Drainage was more intense for the vacuum method to enable the use of heavy machinery. Trenches, baulks, and vacuum fields were on average 9.9 m (\pm 4.7 m (SD)), 7.2 m (\pm 7.6 m), and 27.5 m (\pm 7.6 m) wide, respectively. The aerial photography of the Cacouna bog studied by Girard et al. (2000) is shown in Fig. 2*e*. Some of the sections are indicated by broken lines. A section encompasses either alternating baulks and trenches (thinner line) or vacuum fields (thicker lines). Here, the vacuum section had been previously exploited by hand before being prepared for vacuum mining, which explains the baulk and trench like patterns. Within each section, fields were abandoned the same year and were subjected to the same treatment (e.g., the amount of peat extracted). Photographs are reproduced with permission from the following: Risi et al. (1953), courtesy of the Ministère des Ressources naturelles et de la faune du Québec (Fig. 2*a*); the Archives provinciales du Nouveau-Brunswick, P93G61, New Brunswick Travel Bureau County Photographs Series (Fig. 2*b*); the Peatland Ecology Research Group from Université Laval (Figs. 2*c* and 2*d*); and the Ministère des Ressources naturelles et de la faune du Québec, aerial photo No. Q83319-55, 1983 (Fig. 2*e*).

posit (using a metal rod), depth of the water table, decomposition state of the surface (10 cm) peat using the von Post scale (Malterer et al. 1992), and surface water pH and conductivity. For the last two parameters, the samples were taken from a hole dug from the surface to the ground water level and stored in polyethylene bottles previously rinsed with distilled water. We stored the samples at a low temperature until they were analyzed in the laboratory. The water pH was measured with an Acumet Model 10 (Fisher Scientific, Pittsburgh, Pennsylvania, USA.). Water conductivity was measured with an Orion conductivity meter, model 122 (Orion Research Incorporated Laboratory Products Group, Boston, Massachusetts, USA.). Conductivity was corrected for the concentration of H⁺ ions (Sjörs 1952). Age of abandonment was estimated by cross-checking information from (1) historical aerial photographs, (2) sampling of the largest trees (1-10) of the peat field to estimate the minimal age of abandonment by dendrochronological analysis, and (3) discussion with industrial site managers (Lavoie and Rochefort 1996; Girard et al. 2002).

Sphagnum recolonization in trenches

We analyzed Sphagnum cover and richness in trenches using Poisson regressions corrected for over dispersion (McCullagh and Nelder 1989). After testing different distributions, we found that Poisson regressions best fit the data that were either categorical data (classes) or integer numbers. We focused mainly on the Sphagnum species because they are considered peatland engineers and are the main focus of North American bog restoration techniques (Rochefort 2000). We restricted our analyses to trenches, where Sphagnum was the most successful. Sphagnum was too sporadic on baulks and on vacuum fields to be statistically analyzed. We used the structure survey for estimating Sphagnum cover and the species relevés for calculating Sphagnum richness. We considered only trenches for which the physical and chemical parameters (n = 112) had been measured. When more than one trench was sampled in the same section (Fig. 2e), we averaged Sphagnum cover and richness for this section to avoid problems related to spatial correlation. This left 105 samples (sections) in the analysis, which corresponded to the 11 block-cut mined peatlands. The cover classes 0 and 1 were merged together because there were too few cases with 0% cover to satisfy the assumptions of the Poisson regression.

We considered 18 models, for which we had a biological rationale, to explain *Sphagnum* cover and richness, and we ranked the models based on the second-order Akaike Infor-

mation Criterion corrected for over dispersion (QAICc; Pan 2001). The models were built with different combinations of groups of variables that consisted of regional localities (latitude and longitude), hydrology (depth of the water table), physical aspects of the peat deposit (thickness and decomposition state of the residual peat), local spatial parameters (width of sampled fields), chemistry of surface water (pH and conductivity), and time (since abandonment of peat mining activities; Table 4). Each group of variables was included or not included in a specific model according to its biological role and its complementarity with the other groups already in the model. The models with $QAIC_c < 2$ and high Akaike weights (interpreted as a probability) are considered to be the models that best approximate the information contained in the data, relative to the other candidate models and given a trade-off between bias and variance (Burnham and Anderson 1998). We then used modelaveraging techniques to obtain estimates for each variable and their standard errors (Burnham and Anderson 2002). The Poisson regressions were fitted using the GENMOD procedure of SAS 8.01 (SAS Institute Inc. 1993).

Results

Statistics on abandoned peatlands

In the studied peatlands, peat harvesting ceased 1 to 59 years ago (mean \pm SD: 23 \pm 8 years), leaving a total abandoned area of 1654 ha (Table 1). The current exploited area adjacent to the now abandoned peatlands represented 7764 ha. The mean area of each exploited peatland was 907 \pm 1032 ha (mean \pm SD). For the vegetation structure, we surveyed a total of 5166 block-cut fields (2571 trenches and 2595 baulks) and 395 vacuum fields. At the time that the block-cut method was abandoned to the profit of the more efficient way of harvesting peat with vacuum machines, the average width of trenches was 9.9 \pm 4.7 m (mean \pm SD). For vacuum fields the average width was 27.5 \pm 7.6 m (mean \pm SD).

Vegetation structure

The regeneration of typical peatland plants was remarkably successful in the block-cut peatlands as compared with that of the vacuum-mined peatlands. Indeed, ericaceous shrubs were highly successful in colonizing abandoned block-cut areas: 91% and 79% of all baulks and trenches, respectively, showed a 50% or higher cover of ericaceous shrubs (Table 2). Block-cut areas had an even greater cover of ericaceous shrubs than unmined peatlands, which had a

	Québec	New Brunswick	Total ^a
Number of study peatlands	13	13 ^b	26 ^b
Total exploited area (ha) ^c	5172	2592	7764
Total abandoned area $(ha)^d$	798	857	1654
Total block-cut area (ha)	671	478	1149
Total vacuum area (ha)	127	378	505
Mean area of each surveyed peatland $(ha)^e$	936 (±1188)	877 (±897)	907 (±1032)
Time since abandonment (years) ^f	24 (±8)	19 (±8)	23 (±8)
For block-cut area	26 (±6)	24 (±3)	25 (±5)
For vacuum area	11 (±7)	11 (±7)	11 (±7)

Table 1. Main characteristics of the study sites.

^aData for Québec and New Brunswick combined together.

^bOne of these 26 peatlands was sampled for vegetation structure only (and not for species diversity and environmental variables).

[°]This corresponds to the current exploited section of each surveyed peatland, summed for Québec, New Brunswick, and the two regions together.

^{*d*}This corresponds to the abandoned area, after exploitation, of each surveyed peatland, summed for Québec, New Brunswick, and the two regions together.

^eThe total area (including exploited, abandoned, and natural sections) of all surveyed peatlands was averaged for Québec, New Brunswick, and the two regions together.

^fMeans were calculated on the basis of sections (e.g., 133 sections in the 13 peatlands in Québec and 66 sections in the 13 peatlands in New Brunswick). A section is a series of fields (baulks, trenches, or vacuum fields) having received homogeneous treatment (e.g., the amount of peat harvested and the number of years of exploitation). Sections are usually separated by large drainage ditches (see Fig. 2).

mean ericaceous shrub cover of 48% (Fig. 3). In comparison, ericaceous shrubs usually covered between 1% and 25% of the vacuum-mined surfaces, and only 16% of the fields had more than 50% cover.

Despite the recolonization success of typical ericaceous shrubs in abandoned peatlands, *Sphagnum* re-establishment was far less successful. Only 21% of the vacuum fields were colonized by *Sphagnum* and most of them showed a *Sphagnum* cover of less than 10% (Table 2). Moreover, only two vacuum fields out of 395 (<1%) had more than 25% *Sphagnum* cover. *Sphagnum* establishment was more successful in the trenches resulting from block-cutting. Practically all trenches (98%) were colonized by *Sphagnum*, and 23% of them had a *Sphagnum* cover of more than 50%. Yet, *Sphagnum* cover averaged 66% in unmined peatlands of the same regions, whereas it averaged only 29% within abandoned trenches (Fig. 3).

Although lichens and non-*Sphagnum* mosses were present in most sites, especially on baulks and in trenches, they rarely covered more than 10% of the abandoned fields. Their distribution was also limited in unmined peatlands, though slightly more abundant (Fig. 3). For most of the abandoned peat fields more than 50% of their surface was characterized by bare peat, whereas bare peat was absent in unmined peatlands (Table 2, Fig. 3). Herb cover was similar in mined and unmined sites while trees were more common on blockcut surfaces than in unmined peatlands and vacuum fields (Fig. 3).

In summary, a typical trench had a 29% cover of *Sphagnum* and a 65% cover of ericaceous shrubs; trees and herbs were less dominant with 21% and 12% cover, respectively (Fig. 3). Still, 50% of the ground layer of a typical trench consisted of bare peat. A typical baulk was characterized by 65% cover of bare peat for the ground layer, with 1% cover of *Sphagnum* and 71% cover of ericaceous shrubs. A typical vacuum field was also characterized by large surfaces of bare peat (67%) with only 1.7% cover of *Sphagnum*. They

appeared more denuded than baulks because of the highly reduced cover of ericaceous shrubs (20%). Herbs were also not very abundant on vacuum fields (16%).

Species richness

In general, vacuum fields showed a lower species richness than block-cut areas (Table 2, Appendix A). In that respect, Sphagnum mosses were the most affected by the modernization of peat mining activities. Indeed, only two Sphagnum species colonized more than one vacuum field compared with five and 17 species for baulks and trenches of block-cut areas, respectively (Appendix A). The main Sphagnum species found in all types of abandoned fields were S. rubellum, S. magellanicum, S. fallax, S. fuscum, S. russowii, and S. angustifolium. Sphagnum rubellum was by far the most successful species at colonizing abandoned surfaces. Few additional Sphagnum species occurred in unmined peatlands of the same region (Poulin et al. 1999; Lavoie et al. 2001). Likewise, ericaceous shrub species richness was slightly higher in block-cut sites than in vacuum surfaces (Table 2). However, the most common ericaceous shrub species were the same for the three types of abandoned sites (baulk, trench, and vacuum), that is, Kalmia angustifolia, Ledum groenlandicum, *Chameadaphne calyculata*, Vaccinium angustifolium, and Rhododendron canadense. In unmined peatlands of the same region, these species are also the most common shrubs. Yet, Andromeda polifolia and Vaccinium oxycoccos, are more abundant on unmined peatlands than on the abandoned sites (Poulin et al. 1999). Lichen species richness was high in baulks and trenches, whereas only one species, Cladina rangiferina, was commonly found on vacuum sites, despite the dry prevailing conditions. Lichens do not cover a large extent in unmined peatlands of the same regions but can be frequent, especially in Atlantic bogs (Dignard and Grondin 1996; Poulin et al. 1999). Herbs were most diverse in trenches. The main species were the same as those found in unmined peatlands (Poulin et al. 1999).

	Perce	nt cover clas	ses ^a			
	0%	1-10%	11–25%	26-50%	51-100%	Mean (± SD) species richness
Trees						
Total	2	49	24	16	9	2.9 (±1.7)
Trench	1	46	25	17	11	3.2 (±1.5)
Baulk	1	50	25	16	8	3.0 (±1.8)
Vacuum	17	63	10	05	5	1.9 (±1.8)
Ericaceous	s shrubs					
Total	1	4	4	11	80	6.9 (±2.5)
Trench	0	1	4	16	79	7.9 (±2.0)
Baulk	0	1	1	7	91	6.6 (±1.7)
Vacuum	22	35	21	6	16	4.3 (±3.6)
Herbs						
Total	1	71	16	11	1	1.7 (±1.7)
Trench	0	70	16	12	2	2.3 (±1.8)
Baulk	0	76	14	9	1	$0.9(\pm 1.2)$
Vacuum	3	53	25	13	6	2.3 (±1.6)
Sphagnum						
Total	47	25	10	7	11	$2.4(\pm 2.6)$
Trench	2	39	20	16	23	4.6(+2.2)
Baulk	86	12	2	0	0	0.5(+0.9)
Vacuum	79	15	5	1	0	$0.4 (\pm 1.1)$
Mosses						
Total	5	89	5	1	0	2.8 (±1.6)
Trench	3	90	6	1	0	$3.2(\pm 1.5)$
Baulk	4	93	3	0	0	$2.7 (\pm 1.6)$
Vacuum	27	59	7	4	3	1.5 (±1.7)
Lichens						
Total	7	76	14	3	0	2.7 (±2.5)
Trench	6	82	10	2	0	$2.2(\pm 2.0)$
Baulk	1	75	20	4	0	3.9 (±2.6)
Vacuum	63	35	2	0	0	0.5 (±1.2)
Water						
Total	88	12	0	0	0	_
Trench	76	22	1	1	0	_
Baulk	98	2	0	0	0	_
Vacuum	94	6	0	0	0	_
Bare peat						
Total	1	9	6	16	68	
Trench	2	17	9	15	57	_
Baulk	0	1	5	18	77	_
Vacuum	0	3	4	9	84	_

Table 2. Vegetation cover in abandoned peatlands after hand block-cutting (trenches and baulks) or vacuum mining in eastern Canada.

Note: Each number represents the proportion of the fields surveyed (%) that was colonized by each of the eight vegetation strata or ground substrate, according to five cover categories. These descriptive statistics are shown for all fields of the 26 surveyed peatlands as well as separately for trenches (n = 2571), baulks (n = 2595), and vacuum fields (n = 395). The species richness for all vegetation strata is given in the last column. The average area of an abandoned trench or baulk is 0.22 ha and of an abandoned vacuum field is 1.28 ha.

^{*a*}All strata and ground substrate do not sum to 100% cover because we took into consideration the vertical structure of the vegetation when estimating percent cover (e.g., it is possible to find 75% cover of ericaceous shrubs and 50% cover of *Sphagnum* within the same trench because the shrubs overlay mosses).



Fig. 3. Mean vegetation cover in 26 abandoned mined peatlands and 24 nearby natural peatlands in eastern Canada. Means (\pm SD) are shown separately for eight vegetation strata and ground substrates in three types of abandoned fields (trench, baulk, vacuum) and in natural peatlands. Surveys in natural peatlands were conducted in 1997 and include peatland expanse and peatland open margins (see Poulin et al. 1999 for more details).

Regarding non-bog species, *Agrostis scabra*, *Calamagrostis canadensis*, and *Typha* spp. were slightly more common on vacuum surfaces than in block-cut areas. Yet, our survey revealed that abandoned peatlands were not massively invaded by non-bog species (Appendix A).

Physical parameters

The three types of fields (baulk, trench, and vacuum) showed on average the same degree of peat acidity (pH) and peat decomposition (von Post scale; Table 3). In contrast, the electrical conductivity of surface water was higher in vacuum sites than in block-cut areas while baulks and trenches were similar in that respect. Vacuum mining left thinner residual peat deposits than did hand block-cutting, for which residual peat deposits were slightly thicker in baulks than in trenches (Table 3). Following this topography, the water table was lower for baulks than for trenches whereas vacuum sites had an intermediate water level.

Sphagnum recolonization in trenches

We tested the effect of regional and local variables, as well as time since abandonment, on the recolonization success of Sphagnum in trenches. Among the 18 models considered, the ones best explaining Sphagnum cover (those with a delta $QAIC_c \leq 2$ are considered equivalent) included the thickness and decomposition state of the residual peat deposit as well as the width of the fields sampled (Table 4a). For Sphagnum richness, the best models included latitude and longitude as well as the thickness and decomposition state of the residual peat deposit (Table 4b). Yet, according to the model averaging approach, only two of the nine variables considered were found to be important (Table 5). Sphagnum cover and richness were both influenced by the thickness of the residual peat deposit, whereas latitude influenced only Sphagnum richness. More precisely, Sphagnum covered larger areas in trenches with a thin residual peat deposit. Sphagnum richness was also higher in trenches with thinner residual peat deposits and at higher latitudes. There was considerable correlation between the observed values and predicted values based on model averaging $(R^2 = 0.40)$ for Sphagnum cover; $R^2 = 0.34$ for Sphagnum richness), which indicates that the global model fitted the data well.

Discussion

To our knowledge, this study is the first to survey abandoned peatlands on such an extensive scale. The picture presented here is in accordance with previous findings in Europe and North America: our survey also showed that peatlands can regenerate spontaneously under certain conditions. Abandoned vacuum surfaces remained essentially void of vegetation while block-cut areas were generally well

	Abbreviation used in			
Variable	other tables (units)	Trenches	Baulks	Vacuum
No. of peatlands sampled	_	11	11	18
No. of fields sampled	_	105	96	34
Depth of the water table	Wtable (cm)	56 (±28)	96 (±13)	82 (±26)
Thickness of the residual peat deposits	Peat_depth (m)	3.0 (±1.1)	3.7 (±1.1)	1.7 (±1.3)
Decomposition state of the residual peat ^a	VonPost (von Post scale)	3.5 (±0.9)	3.6 (±1.0)	3.5 (±0.9)
Width of sampled fields	Width (m)	9.9 (±4.7)	7.2 (±7.6)	27.5 (±7.6)
pH of the surface water	pH	3.9 (±0.4)	3.9 (±0.3)	3.7 (±0.5)
Conductivity of the surface water ^b	Conduct (µS)	7.4 (±14.1)	9.3 (±21.8)	50.3 (±96.4)

Table 3. Physical conditions of fields (means \pm SD) in abandoned peatlands after hand block-cutting (trenches and baulks) and vacuum mining in eastern Canada.

^{*a*}Measured 10 cm from the surface according to the Von Post scale (Malterer et al. 1992). ^{*b*}Measure of the total amount of ions in the water.

recolonized. Yet, our results refine statistics found in the cited literature. For instance, we estimated that 15% of the total area of all block-cut mined peatlands has been colonized by Sphagnum in eastern Canada, a slightly better value than the 10% value calculated for Cacouna bog, which is commonly used as a reference (Girard et al. 2002). Regarding vacuum-mined peatlands, 20% of the fields we surveyed showed between 1% and 25% of Sphagnum cover. Yet, the average cover of Sphagnum was 2%. This is consistent with Lavoie and Bérubé (2000) who did not find any Sphagnum colonization on a vacuum-mined peatland in Québec eight years after exploitation activities stopped. The high variability of vegetation cover among abandoned peatlands, in addition to the lack of data reported in the literature, emphasizes the importance of conducting large-scale surveys to evaluate the capacity of peatlands to recover from disturbances.

It has been suggested that other mosses could be beneficial for Sphagnum colonization through the stabilization of the substrate and consequent reduction of the detrimental effects of frost heaving, the depletion of peat crust formation, and the increase in soil moisture content (Groeneveld 2002; Groeneveld and Rochefort 2002). Although mosses and liverworts did not invade the abandoned peatlands studied, Polytrichum strictum, Mylia anomala, and Pleurozium schreberi were frequent in our species relevés. While these mosses (and liverworts) may be potential companion species in abandoned peatlands (Robert et al. 1999), we found only a weak positive correlation between Polytrichum strictum and Sphagnum occurrences in our study (Pearson correlation, $R^2 = 0.15$). Additional surveys should be conducted to clarify their role in natural recolonization processes. In addition to mosses, Eriophorum vaginatum has been studied to understand its role in facilitating Sphagnum establishment (Grosvernier et al. 1995; Boudreau and Rochefort 1999; Tuittila et al. 2000a; Lavoie et al. 2003a). Our study reaffirms the high capacity of E. vaginatum to colonize mined peatlands. Yet, the weak correlation between E. vaginatum and Sphagnum occurrences in our survey (Pearson correlation, $R^2 = 0.2$) neither confirms nor refutes the role of E. vaginatum as a companion species.

In our survey the high diversity of *Sphagnum* is noteworthy in comparison to other studies. We found 17 species in abandoned peatlands of eastern Canada, whereas only two species were found in an abandoned milled peatland in Finland (*S. russowii* and *S. riparium*; Tuittila et al. 2000*b*) and only one (S. papillosum) in a vacuum-mined bog in southern Ontario (Jonsson-Ninniss and Middleton 1991). It was especially surprising to observe that hollow species such as S. cuspidatum and S. riparium colonized trenches. The margins of trenches are often much wetter than the higher central area and these two species may have been favored by the microtopography of trenches (Price and Whitehead 2001; Girard et al. 2002). The two main species used for active restoration, S. rubellum and S. fuscum (Quinty and Rochefort 2003), were among the four most common species found on abandoned mined peatlands. Yet, Sphagnum fuscum colonized trench surfaces less frequently and extensively than did S. rubellum despite the fact that S. fuscum has been shown experimentally to be the most resistant species to dry conditions of bare peat surfaces (Chirino et al. 2005).

The thickness of the peat deposit was the most important factor explaining Sphagnum cover in trenches, whereas both peat depth and latitude influenced Sphagnum richness. Still, it was surprising to find that Sphagnum cover decreased with increasing peat thickness. This result is not as counterintuitive as it might seem. Indeed, deep peat deposits at our study sites tended to be dryer than thin peat deposits (correlation between peat depth and water table: $R^2 = 0.22$), although other factors not directly measured here must be involved since this correlation was weak. Peat thickness has been shown to strongly influence vegetation recolonization in abandoned peatlands (Girard et al. 2002). When examining carefully the results from Girard et al. (2002), we find that the occurrence of four of the five most common Sphagnum species was correlated with thin peat deposits. Areas where peat has been harvested to deeper levels may accumulate more water, which is favorable to Sphagnum. Regarding the influence of latitude on Sphagnum richness, our survey partly covered the Atlantic oceanic to continental gradient, which can explain differences in species distribution and therefore, the higher species richness at higher latitude. In regard to the peat deposits, the decrease of Sphagnum richness with peat deposit thickness is probably related to the trophic status of the peat, where minerotrophic conditions are usually associated with higher species richness.

Detailed hydrological studies of the Cacouna bog in southern Québec revealed that hydrology is a critical factor in determining *Sphagnum* recolonization success in abandoned trenches (Price and Whitehead 2001; van Seters and

Table 4. Ranking of Poisson regression models (based on QAICc) explaining Sphagnum recolonization in trenches
of abandoned peatlands after hand block-cutting in eastern Canad	la.

Model					OAIC
No.	Model ^a	K^b	QAIC _c ^c	$QAIC_{c}^{d}$	weight ^e
(a) Res	oonse variable: Sphagnum cover				
3	Lat Long Wtable Peat_dep VonPost Width	8	107.236	0.000	0.346
6	Lat Long Peat_dep VonPost Width	7	107.679	0.443	0.278
11	Peat_dep VonPost Width	5	109.299	2.063	0.124
17	Wtable Peat_dep VonPost Width	6	110.447	3.211	0.070
14	Peat_dep VonPost Width pH Conduct	7	110.661	3.425	0.062
2	Lat Long Wtable Peat_dep VonPost Width pH Conduct	10	111.760	4.524	0.036
16	Wtable Peat_dep VonPost Width pH Conduct	8	112.291	5.055	0.028
1	Lat Long Wtable Peat_dep VonPost Width pH Conduct Age_aban	11	112.739	5.503	0.022
15	Wtable Peat_dep VonPost Width pH Conduct Age_aban	9	112.780	5.544	0.022
18	Wtable pH Conduct	3	115.497	8.261	0.006
13	Age_aban	5	117.379	10.143	0.002
10	Wtable	3	118.109	10.873	0.002
12	pH Conduct	5	118.989	11.753	0.001
5	Lat Long Wtable	4	119.196	11.960	0.001
7	Lat Long pH Conduct	5	120.150	12.914	0.001
4	Lat Long Wtable pH Conduct	6	120.442	13.206	0.000
8	Lat Long Age_aban	7	120.709	13.473	0.000
9	Lat Long	4	121.531	14.295	0.000
(b) Res	ponse variable: Sphagnum richness				
6	Lat Long Peat_dep VonPost	6	-630.013	0.000	0.675
3	Lat Long Wtable Peat_dep VonPost	7	-628.106	1.907	0.260
2	Lat Long Wtable Peat_dep VonPost pH Conduct	9	-625.023	4.990	0.056
1	Lat Long Wtable Peat_dep VonPost pH Conduct Age_aban	11	-621.145	8.868	0.008
11	Peat_dep VonPost	4	-615.361	14.652	0.000
17	Wtable Peat_dep VonPost	5	-613.156	16.857	0.000
14	Peat_dep VonPost pH Conduct	6	-611.654	18.359	0.000
16	Wtable Peat_dep VonPost pH Conduct	7	-609.371	20.642	0.000
15	Wtable Peat_dep VonPost pH Conduct Age_aban	9	-605.857	24.155	0.000
5	Lat Long Wtable	5	-603.276	26.737	0.000
9	Lat Long	4	-600.526	29.487	0.000
4	Lat Long Wtable pH Conduct	7	-599.444	30.569	0.000
7	Lat Long pH Conduct	6	-598.057	31.956	0.000
10	Wtable	3	-597.011	33.002	0.000
12	pH Conduct	4	-596.533	33.479	0.000
8	Lat Long Age_aban	6	-596.529	33.484	0.000
18	Wtable pH Conduct	5	-595.916	34.097	0.000
13	Age_aban	4	-591.811	38.202	0.000

Note: 105 trenches were used for the analyses, which correspond to the 105 sections sampled in the 11 peatlands mined by hand with the block-cut method (see Fig. 2, Table 3). Models with a delta $QAIC_c \le 2$ are considered equivalent.

^aLat, latitude; Long, longitude; Wtable, depth of the water table (cm); Peat_dep, thickness of the residual peat deposit (m); VonPost, decomposition state of the residual peat (von Post scale; Malterer et al. 1992); Width, width of sampled fields (m); pH, pH

of the surface water; Conduct, conductivity of the surface water (μ S, measure of the total amount of ions in the water); Age_aban, time since the abandonment of peat-mining activities.

^bNumber of estimable parameters (including intercept and the correction factor *c*).

^cAkaike's information criterion (AIC) adjusted for over dispersion and for small sample size (Burnham and Anderson 1998).

^dDifference between the $QAIC_c$ value for this model and that of the model with the lowest $QAIC_c$ value.

^eEstimates of the likelihood of the model, given the data, normalized to sum to one.

Price 2001; Girard et al. 2002). In this bog, *Sphagnum* was most commonly found in zones where the water table was less than 40 cm below the ground surface, the soil moisture was greater than 50%, and the soil–water pressure was greater than 100 mbar (1 mbar = 100 Pa). In our study, we did not take detailed, repeated measures of hydrology during the summers. This probably explains why our analyses did

not reveal the importance of hydrology for the recolonization of mined peatlands, although water table was a variable included in the main models explaining *Sphagnum* cover and richness.

Time since abandonment did not influence *Sphagnum* cover and richness in our study. Similarly, Girard et al. (2002) found that *Sphagnum* were either not influenced by

	Regional varia	bles ^a	Local variables	q^{i}					Time
Response variables	Latitude	Longitude	Wtable	Peat_dep	VonPost	Width	рН	Conduct	$A bandon^c$
Sphagnum cover	0.6753	0.0669	-0.0052	-0.3268	-0.0306	0.0400	0.1831	0.0054	-0.0345
)	(± 0.4880)	(±0.0749)	(± 0.0033)	(± 0.0857)	(± 0.0966)	(±0.0257)	(±0.2935)	(± 0.0063)	(± 0.023)
Sphagnum richness	0.5751	0.0504	-0.0012	-0.2406	0.0345	0.0074	-0.0346	-0.0034	0.0097
1	(±0.2478)	(± 0.0365)	(± 0.0017)	(± 0.0446)	(±0.0470)	(± 0.0107)	(± 0.1415)	(± 0.0034)	(± 0.003)

Tocality of each peatland sampled (see Fig. 1). *Wtable, depth of the water table (cm); Peat_dep, thickness of the residual peat deposit (m); VonPost, decomposition state of the residual peat (Von Post scale; Malterer et al. 1992); Width, width th

each field sampled (m); pH, pH of the surface water; Conduct, conductivity of the surface water (µS, measure of the total amount of ions in the water). abandonment of peat-mining activities years since 'Number of

of

time since abandonment or favored by short periods of abandonment, which can be surprising a priori. As Sphagnum can directly colonize bare peat surfaces (Robert et al. 1999), it seems that prevailing conditions when mining activities are abandoned are more important than time for the development of extensive Sphagnum carpets. Thus, prevailing conditions at the site as well as climate during the period of abandonment may play a critical role (Girard et al. 2002). In other words, mined sites with appropriate hydrological conditions are rapidly (<10 years) recolonized by Sphagnum species, while others will probably remain devoid of mosses for several decades, if not centuries (Lavoie and Rochefort 1996, Girard et al. 2002). For instance, long-term monitoring of vegetation cover in vacuum-mined bogs indicates that very few Sphagnum colonies become established in sites with a water table level more than 40 cm below the soil surface, and that established colonies were still declining 18 years after abandonment (Lavoie et al. 2005).

In terms of biodiversity, abandoned peatlands were colonized by species typically found in unmined peatlands. Very few non-bog species were recorded in our survey. Regarding herbs, only Agrostis scabra, Calamagrostis canadensis, and Typha spp. colonized either trenches or vacuum fields and their cover was very restricted. Girard et al. (2002) also found that non-bog species generally do not invade mined peatlands except for Pteridium aquilinum, which had 21% cover in one section of the studied bog. There are several cases in Europe where peatlands have been invaded by weeds after mining (Fojt and Harding 1995). Moreover, peatlands used by sheep are largely modified by Molinia caerulea, which eventually dominates the vegetation after intense grazing (Grant et al. 1985; Hobbs and Gimingham 1987; Bragg and Tallis 2001; Hulme et al. 2002). However, abandoned peatlands in general appear to be highly resistant to invasive species and weeds when compared with other ecosystems such as marshes (Lavoie et al. 2003b). Even birches (Betula spp.) were not abundant, although they occurred in half of the fields. Birches can reach high (Lavoie and Rochefort 1996) or even extreme (80 000 stems/ha; C. Lavoie, unpublished data) densities, but this phenomenon seems to be restricted to only a few sites in southeastern Canada.

Conclusion

Mined peatlands can spontaneously regenerate under certain conditions. Yet, almost no Sphagnum species were able to recolonize vacuum-mined peat fields (1.7%) or the baulks of block-cut mined peatlands (1%). Within trenches, Sphagnum carpets still only cover 29% of the ground surface. Sphagnum colonization of abandoned sites does not appear to be a question of time but rather of the immediate climatic, historic, and environmental conditions following the cessation of peat-extracting activities. This reasserts the need for restoration measures in both block-cut and vacuum-mined peatlands to revert them to functional peat-accumulating ecosystems. Active restoration is essential to re-establish the fundamental carbon sequestration function associated with unmined peatlands.

On the other hand, the diversity of plants in abandoned mined peatlands was high, particularly in trenches of blockcut sites. In this regard, block-cut mined peatlands should be considered sites contributing to regional biodiversity in human-modified landscapes. This may have great implications for regions with high disturbance. For instance, in an agricultural plain of 176 km² in southern Québec, 62% of the initial peatland area has been disturbed by human activities (Pellerin 2003). Half of these sites were exploited for horticultural peat and were abandoned during the past 30 years. In this context, abandoned peatlands could play a significant role in the preservation of peatland plant diversity, which should increase regional biodiversity.

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Appendix A

Appendix appears on the following pages.

Brunswick, Can	ada.														
Total $(n = 242)$				Baulk $(n =$	96)			Trench $(n =$	112)			Vacuum (n	= 34)		
Species		ε			Ľ	5			Ľ	Ę			Ē	Ę	
code FI	equency	%	Mean	Species	Frequency	%	Mean	Species	Frequency	%	Mean	Species	Frequency	%	Mean
Mosses and live	erworts	Ċ	2 20			ĊĹ	11	1-0	20	20	0 1 5	Ĺ	5	чc	101
Mvl and 13		77	90.5 00.5	POL_SU Pla_sch	0/	5 5	4.11 2 36	Pol_str Mv1_ano	00	C8 08	61.8 88.3	Dic_cer Pol_etr	10	رد ۲	1.21
Ple sch 11	2 9	5 4 8 4	1.65	Mvl ano	32	66	1.08	Ple sch	15	46	1.36	Mvl ano	2 ∞	24	1.24
Dic und 5	4	22	0.42	Dic und	28	29	0.64	Dic pol	24	21	0.31	Ple sch	5	15	0.62
Dic_pol 5	2	21	0.39	Dic_pol	26	27	0.58	Dic_und	24	21	0.34	Poh_nut	3	6	1.74
Poh_nut 4	1:	17	0.51	Poh_nut	17	18	0.31	Poh_nut	21	19	0.3	Dic_pol	2	9	0.12
Pti_cil 2	2	6	0.14	Pti_cil	13	14	0.26	Cla_flu	19	17	0.94	Dic_und	2	9	0.06
Cla_flu 2	0	8	0.45	Ste_ser	5	5	0.05	War_flu	10	6	0.15	Aul_pal	1	С	0.03
Dic_cer 1	5	9	0.18	Tet_pel	5	5	0.07	Pti_cil	9	8	0.08	Dic_sco	1	З	0.06
Tet_pel 1	3	5	0.07	Dic_sco	3	ŝ	0.03	Tet_pel	8	Г	0.09	War_flu	1	З	0.03
War_flu 1	2	5	0.08	Dic_cer	1	-	0.01	War_exa	4	4	0.05				
Dic_sco	L	Э	0.03	War_exa	1	1	0.01	Dic_sco	Э	ю	0.03				
Ste_ser	9	0	0.03	War_flu	1	1	0.01	Aul_pal	2	0	0.02				
War_exa	5	0	0.03	Cla_flu	1	1	0.03	Dic_cer	2	0	0.02				
Aul_pal	3	1	0.01					Ste_ser	1	-	0.02				
Lichens															
Cla_ran 12	6	53	2.22	Cla_ran	62	65	2.74	Cla_ran	64	57	2.34	Cla_ran	3	6	0.35
Cla_mit 5	6	24	0.57	Cla_def	38	40	1.2	Cla_mit	25	22	0.43	Cla_cen	1	Э	0.06
Cla_def 5	8	24	0.6	Cla_crt	37	39	1.72	Cla_def	20	18	0.28	Cla_coc	1	ю	0.03
Cla_crt 5	4	22	0.83	Cla_mit	33	34	0.92	Cla_crt	16	14	0.28	Cla_crt	1	З	0.12
Cla_chl 4	0:	17	0.36	Cla_cri	31	32	0.79	Cla_chl	15	13	0.24	Cla_fim	1	З	0.03
Cla_cri 3	6	16	0.37	Cla_chl	25	26	0.63	Cla_coc	6	8	0.25	Cla_mit	1	З	0.09
Cla_ste 2	5	10	0.14	Cla_mac	20	21	0.68	Cla_cri	8	L	0.13	Cla_phy	1	б	0.03
Cla_mac 2	5	10	0.29	Cla_ste	20	21	0.27	Cla_cen	9	S	0.05	Cla_sp.	1	б	0.03
Cla_cen 2	3	10	0.16	Cla_cen	16	17	0.32	Cla_sp.	9	S	0.07	Cla_ste	1	б	0.03
Cla_fim 2	1	6	0.18	Cla_fim	15	16	0.35	Cla_fim	5	4	0.08				
Cla_coc 2	1	6	0.25	Cla_sp.	13	14	0.18	Cla_mac	5	4	0.04				
Cla_sp. 2	0	×	0.11	Cla_coc	11	11	0.33	Cla_cor	4	4	0.14				
Cla_gra 1	0	4	0.06	Cla_gra	9	9	0.11	Cla_fur	4	4	0.04				
Cla_cor	6	4	0.12	Cla_bot	5	5	0.06	Cla_gra	4	4	0.04				
Cla_phy	8	б	0.04	Cla_cor	5	5	0.15	Cla_ste	4	4	0.06				
Cla_bot	9	0	0.03	Cla_con	4	4	0.04	Cla_dig	3	б	0.03				
Cla_fur	5	0	0.02	Cla_par	4	4	0.04	Cla_phy	3	б	0.04				
Cla_par	4	0	0.02	Cla_phy	4	4	0.04	Cla_bot	1	1	0.01				
Cla_dig	4	0	0.02	Cla_dig	1	1	0.01								
Cla_con	4	0	0.02	Cla_fur	1		0.01								

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Table A1 ($c \epsilon$	ontinued).														
Total $(n = 24)$	12)			Baulk $(n = 0)$	96)			Trench $(n =$	112)			Vacuum (n	= 34)		
Species code	Frequency	%	Mean	Species	Frequency	%	Mean	Species	Frequency	%	Mean	Species	Frequency	%	Mean
Sphagnum					4				4				4		
Sph_rub	141	58	6.58	Sph_rub	29	30	0.69	Sph_rub	108	96	13.41	Sph_rub	5	15	0.76
Sph_mag	69	29	2.19	Sph_mag	4	4	0.06	Sph_fal	67	60	3.04	Sph_fal	2	9	0.35
Sph_fal	69	29	1.46	Sph_fus	3	С	0.05	Sph_mag	64	57	4.67	Sph_sp	1	С	0.12
Sph_fus	67	28	1.85	Sph_ang	3	С	0.07	Sph_fus	63	56	3.93	Sph_pap	1	С	0.03
Sph_rus	50	21	0.7	Sph_sp	2	2	0.29	Sph_rus	49	44	1.51	Sph_mag	1	С	0.03
Sph_ang	30	12	0.33	Sph_rus	1	1	0.01	Sph_ang	27	24	0.64	Sph_fus	1	С	0.03
Sph_cus	20	8	0.15	Sph_pap	1	1	0.01	Sph_cus	19	17	0.29	Sph_fim	1	3	0.06
Sph_sp	19	8	0.34	Sph_gir	1	1	0.01	Sph_fim	18	16	0.25	Sph_cus	1	б	0.12
Sph_fim	19	8	0.12					Sph_sp	16	14	0.44				
Sph_rip	10	4	0.1					Sph_rip	10	6	0.21				
Sph_pap	6	4	0.07					Sph_pul	8	L	0.43				
Sph_pul	8	б	0.2					Sph_pap	7	9	0.13				
Sph_gir	L	б	0.03					Sph_gir	9	5	0.06				
Sph_fla	5	7	0.14					Sph_fla	5	4	0.29				
Sph_lin	4	0	0.02					Sph_lin	4	4	0.04				
Sph_squ	3	1	0.02					Sph_squ	3	3	0.04				
Herbs and fo	erns														
Rub_cha	105	43	1.71	Rub_cha	44	46	2.22	Eri_vag	58	52	4.14	Eri_vag	21	62	8.97
Eri_vag	101	42	3.77	Eri_vag	22	23	1.49	Rub_cha	49	44	1.3	Eri_ang	12	35	2.85
Dro_rot	59	24	0.56	Cor_can	21	22	0.92	Dro_rot	46	41	0.91	Rub cha	12	35	1.61
Car_sp.	48	20	1.09	Car_sp.	6	6	0.24	Car_sp.	34	30	1.82	Jun_bre	6	26	5.12
Eri_ang	41	17	1.68	Dro_rot	6	6	0.13	Eri_ang	23	21	2.64	Car_sp.	5	15	1.06
Cor_can	40	17	0.6	Eri_ang	9	9	0.14	Cor_can	16	14	0.48	Dro_rot	4	12	0.65
Eri_vir	17	7	0.33	Pte_aqu	5	5	0.26	Eri_vir	14	13	0.63	Agr_sca	3	6	0.09
Rhy_alb	16	7	0.55	Mel_lin	б	Э	0.04	Rhy_alb	14	13	1.18	Cor_can	ю	6	0.12
Pte_aqu	15	9	0.24	Tri_bor	С	Э	0.03	Pte_aqu	8	Г	0.25	Eri_vir	ю	6	0.26
Mel_lin	6	4	0.04	Mai_can	2	2	0.02	Mel_lin	9	5	0.06	Cal_can	2	9	0.26
Jun_bre	9	4	0.72	Cop_gro	1	1	0.04	Car_can	4	4	0.25	Car_can	2	9	0.24
Car_can	9	7	0.15	Dro_int	1	1	0.01	Osm_cin	4	4	0.04	Pte_aqu	2	9	0.12
Typ_sp.	5	7	0.03	Labiaea	1	1	0.01	Car_dis	ю	Э	0.15	Mai_tri	2	9	0.09
Spi_alb	5	7	0.16	$Rhy_{-}alb$	1	1	0.01	Cyp_aca	ю	Э	0.03	Spi_alb	2	9	0.71
Mai_tri	S	7	0.06					Dro_int	3	Э	0.11	Typ_sp.	2	9	0.06
Osm_cin	5	0	0.04					Labiaea	3	б	0.03	Cop_gro	1	б	0.03
Mai_can	5	0	0.02					Mai_tri	3	б	0.1	Mai_can	1	б	0.03
Tri_bor	4	7	0.02					Spi_alb	3	Э	0.13	Osm_cin	1	ю	0.18
Labiaea	4	7	0.02					Typ_sp.	3	ю	0.05	Rhy_alb	1	Э	0.03
Dro_int	4	7	0.05					Cop_gro	7	0	0.05				
Cop_gro	4	0	0.05					Mai_can	2	0	0.03				
Agr_sca	4	7	0.02					Agr_sca	1	-	0.02				

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Table A1. (continued).														
Total $(n = 2$	42)			Baulk $(n = 9)$	(96			Trench $(n =$	112)			Vacuum (n	= 34)		
Species code	Frequency	%	Mean	Species	Frequency	%	Mean	Species	Frequency	%	Mean	Species	Frequency	%	Mean
Cyp_aca	3		0.01					Cal_can	1	1	0.02				
Car_dis	\mathfrak{S}	1	0.07					Tri_bor	1	1	0.01				
Cal_can	3	-	0.05												
Shrubs and	subshrubs														
Kal_ang	228	94	38.63	Kal_ang	96	100	44.53	Kal_ang	112	100	42.64	Kal_ang	20	59	8.73
Led_gro	226	93	33.47	Led_gro	96	100	32.35	Led_gro	112	100	42.42	Led_gro	18	53	7.12
Cha_cal	222	92	21.6	Vac_ang	95	66	40.71	Cha_cal	111	66	25.5	Cha_cal	20	59	6.58
Vac_ang	220	91	29.47	Cha_cal	91	95	22.36	Vac_ang	109	76	26.93	Vac_ang	16	47	6.12
Rho_can	177	73	9.95	Rho_can	70	73	10.22	Rho_can	96	86	12.32	Vac_mac	11	32	2.09
Kal_pol	96	40	1.82	Pyr_arb	32	33	1.26	Kal_pol	63	56	3.21	Rho_can	11	32	1.4
Pyr_arb	67	28	1.06	Kal_pol	28	29	0.77	Gau_his	35	31	0.93	Emp_nig	8	24	1.71
Vac_mac	52	21	1.3	Nem_muc	18	19	1.77	Vac_mac	34	30	2.06	Pyr_arb	9	18	1.68
Nem_muc	43	18	1.5	Bet_pum	11	11	1.06	Pyr_arb	29	26	0.7	Kal_pol	5	15	0.21
Gau_his	42	17	0.49	Vib_nud	9	6	0.36	Nem_muc	22	20	1.55	Myr_gal	5	15	0.74
Emp_nig	32	13	1.79	Emp_nig	7	L	1.9	Emp_nig	17	15	1.72	Vac_myr	5	15	0.88
Vac_myr	26	11	1	Vac_mac	7	L	0.15	Vac_myr	17	15	1.56	Nem_muc	3	6	0.56
Vac_oxy	25	10	0.96	Vac_oxy	9	9	0.09	Vac_oxy	17	15	1.93	Sal_sp.	3	6	0.15
Myr_gal	23	10	0.69	Gau_his	5	5	0.14	Myr_gal	14	13	1.15	Gau_his	2	9	0.09
Bet_pum	22	6	0.81	Gay_bac	4	4	0.5	Bet_pum	11	10	0.85	Vac_oxy	2	9	0.21
Vib_nud	19	8	0.2	$Myr_{-}gal$	4	4	0.15	Vib_nud	10	6	0.11	Gay_bac	1	Э	0.03
Gay_bac	13	2	0.54	Sal_pyr	4	4	0.07	And_pol	8	L	0.21	Rub_set	1	ŝ	0.47
Sal_pyr	10	4	0.08	Vac_myr	4	4	0.4	Gay_bac	8	Г	0.73	Sal_pyr	1	С	0.03
And_pol	6	4	0.11	Gay_dum	3	С	0.07	Sal_pyr	5	4	0.1				
Sal_sp.	7	Э	0.07	And_pol	1	1	0.04	Sal_sp.	4	4	0.11				
Gay_dum	9	0	0.04	Rub_set	1	1	0.01	Gay_dum	3	ю	0.03				
Vac_mac	ŝ	1	0.03					Vac_mac	ŝ	б	0.06				
Rub_set	3	1	0.07					Rub_set	1	1	0.01				
Trees															
Lar_lar	165	68	5.93	Lar_lar	64	67	6.45	Lar_lar	06	80	7.05	Bet_pop	16	47	4.36
Pic_mar	152	63	6.48	Pic_mar	63	99	6.4	Pic_mar	80	71	8.34	Bet_pap	14	41	1.74
Bet_pap	137	57	3.17	Bet_pap	55	57	3.53	Bet_pap	68	61	3.29	Lar_lar	11	32	0.77
Pin_ban	73	30	2.33	Pin_ban	39	41	3.95	Bet_pop	34	30	1.32	Pic_mar	9	26	0.56
Bet_pop	69	29	1.57	Bet_pop	19	20	0.88	Pin_ban	33	29	1.64	Pru_pen	4	12	0.21
Pru_pen	28	12	0.2	Pru_pen	16	17	0.3	Abi_bal	14	13	0.27	Bet_cae	3	6	0.15
Abi_bal	27	11	0.23	Abi_bal	12	13	0.26	Ame_sp.	8	L	0.1	Pic_gla	2	9	0.09
Ame_sp.	16	Г	0.1	Ame_sp.	7	7	0.13	Pru_pen	8	L	0.11	Pop_tre	2	9	0.12
Sor_ame	11	S	0.06	Pop_tre	9	9	0.18	Sor_ame	7	9	0.08	Abi_bal	1	Э	0.03
Pop_tre	11	S	0.12	Pic_gla	5	5	0.09	Pic_gla	4	4	0.09	Ame_sp.	1	б	0.06
Pic_gla	11	S	0.09	Sor_ame	4	4	0.05	Pop_tre	3	З	0.06	Pin_ban	1	Э	0.03
Bet_cae	9	0	0.07	Bet_cae	1	1	0.04	Bet_cae	2	0	0.06				

*

Total $(n = 1)$	242)			Baulk $(n = 0)$	96)			Trench $(n =$: 112)			Vacuum (n	= 34)		
Species code	Frequency	%	Mean	Species	Frequency	%	Mean	Species	Frequency	%	Mean	Species	Frequency	%	Mean
Other															
Bpeat	139	57	13.65	Bpeat	62	65	9.27	Bpeat	46	41	4.4	Bpeat	31	91	56.5
Water	18	٢	0.31	Lyc_ann	9	9	0.31	Water	16	14	0.58	Lyc_sp.	1	ю	0.03
Note: Spe	cies codes are the	e first th	ree letters	of the genus nai	me and the first t	free lette	ers of the a	specific epithet.	Frequency, numb	er of fiel	ds colonize	ed by each spec	sies; %, proportio	n of all	ields

 Table A1. (concluded)

bei species; cacn coronized by Table A2. The complete list of species.

Mosses and liverworts

Aulacomnium palustre (Hedw.) Schwaegr. Cladopodiella fluitans (Nees) Jörgensen Dicranella cerviculata (Hedw.) Schimp. Dicranum polysetum Swartz Dicranum scoparium Hedw. Dicranum undulatum Brid. Mylia anomala (Hook.) S. Gray Pleurozium schreberi (Brid.) Mitt. Pohlia nutans (Hedw.) Lindb. Polytrichum strictum Brid. Ptilidium ciliare (L.) Hampe Steerecleus serrulatus (Hedw.) Robins. Tetraphis pellucida Hedw. Warnstorfia exannulata (W. P. Schimp.) Loeske Warnstorfia fluitans (Hedw.) Loeske

Lichens

Cladina mitis (Sandst.) Hustich Cladina rangiferina (L.) Nyl. Cladina stellaris (Opiz) Brodo Cladonia botrytes (K. Hagen) Willd. Cladonia cenotea (Ach.) Schaerer Cladonia chlorophaea (Flörke ex Sommerf.) Sprengel Cladonia coccifera (L.) Willd. Cladonia conista A. Evans Cladonia cornuta (L.) Hoffm. Cladonia crispata (Ach.) Flotow Cladonia cristatella Tuck. Cladonia deformis (L.) Hoffm. Cladonia digitata (L.) Hoffm. Cladonia fimbriata (L.) Fr. Cladonia furcata (Hudson) Schrader Cladonia gracilis (L.) Willd. Cladonia macilenta Hoffm. Cladonia parasitica (Hoffm.) Hoffm. Cladonia phyllophora Hoffm.

Sphagnum

Sphagnum angustifolium (C. Jens.) C. Jens Sphagnum cuspidatum G. F. Hoffman Sphagnum fallax Klinggräff Sphagnum fimbriatum Wilson & JDHooker Sphagnum flavicomans (Card.) Warnst. Sphagnum fuscum (W. P. Schimp.) Klinggräsff Sphagnum girgensoniii Russow Sphagnum lindbergii W. P. Schimp. Sphagnum magellanicum Brid. Sphagnum papillosum Lindb. Sphagnum pulchrum (Lindb.) Warnst. Sphagnum riparium Ångstr. Sphagnum rubellum^a Sphagnum russowii Warnst. Sphagnum squarrosum Crome.

Herbs and ferns

Agrostis scabra Willd. Calamagrostis canadensis (Michx.) P.Beauv. Carex sp. Carex canescens L.

Table A2 (continued).

Carex disperma Deway Coptis groenlandica (Oeder) Fernald Cornus canadensis L. Cypripedium acaule Aiton Drosera intermedia Hayne Drosera rotundifolia L. Eriophorum angustifolium Honckeny Eriophorum vaginatum L. subsp. spissum (Fernald) Hultén. Eriophorum virginicum L. Juncus brevicaudatus (Engelm.) Fernald Maianthemum canadense Desf. Maianthemum trifolium (L.) Sloboda Melampyrum lineare Desr. Osmunda cinnamomea L. Pteridium aquilinum (L.) Kuhn Rubus chamaemorus L. Rhynchospora alba (L.) Vahl Trientalis borealis Raf.

Shrubs and subshrubs

Amelanchier sp. Andromeda polifolia L. Betula pumila L. Chamaedaphne calyculata (L.) Moench Empetrum nigrum L. Gaultheria hispidula (L.) Muhl. Gaylussacia dumosa (Andr.) A. Gray Gaylussacia baccata (Wang.) K.Koch Kalmia angustifolia L. Kalmia polifolia Wangenh. Ledum groenlandicum Oeder

Table A2 (concluded).

Myrica gale L.

Nemopanthus mucronatus (L.) Trel. Pyrus arbutifolia (L.) L. f. Rhododendron canadense (L.) Torr. Rubus setosus Bigelow Salix sp. Salix pyrifolia Andersson Spirea alba Du Roi Vaccinium angustifolium Aiton Vaccinium macrocarpon Aiton Vaccinium myrtilloides Michx. Vaccinium oxycoccos L. Viburnum nudum L. var. cassinoides (L.) Torr. & A. Gray Trees

Abies balsamea (L.) Miller Betula × caerulea-grandis Blanch. Betula papyrifera Marshall Betula populifolia Marshall Larix laricina (Du Roi) Koch Picea mariana (Mill.) Britton, Stems & Poggenb. Pinus banksiana Lamb. Populus tremuloides Michx. Prunus pensylvanica L.f. Sorbus americana Marshall Picea glauca (Moench) Voss

"Same species as S. capillifolium sensu lato in previous publications from the Peatland Ecology Research Group, Université Laval, Quebec, Canada.