

TRAJECTORIES OF PLANT RECOVERY IN BLOCK-CUT PEATLANDS 35 YEARS AFTER PEAT EXTRACTION

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Abstract. The initial question of any ecological restoration project should be whether the degraded ecosystem may recover spontaneously in a reasonable time period or active intervention is needed. We examined the successional trajectories of vegetation within peatlands exploited by the traditional block-cut technique in Eastern Canada, with the final purpose of identifying sites which need human intervention to ensure the return of a typical *Sphagnum*-dominated bog community that accumulates C. Ordinations showed that the development of vegetation was different between three block-cut peatland regions. Peatlands of one of the regions were initially colonized by tall, dense ericaceous shrubs. There, communities tended to become increasingly dominated by trees and understories were closing over time, therefore not being on a trajectory toward the recovery of a *Sphagnum*-dominated system that accumulates peat in the future. Intervention is therefore recommended, for example by blocking still active drainage ditches. In the peatlands of the other two regions, *Sphagnum* had a high initial cover and remained dominant ten years later. However, species typically found in hummocks gained relative importance vs. those associated to hollows. More time is needed to decide whether these sites could be left unmanaged as they have remained after their abandonment 35 years ago.

Keywords: *abandoned exploited bogs, cutover peatlands, partial tb-PCA, spontaneous revegetation, mire*

Introduction

Peatlands are severely disturbed by peat extraction for fuel and horticultural purposes, which causes drastic and sometimes irreversible changes in their structure and functioning (Smart et al., 1986; Lavoie and Rochefort, 1996; Rowlands and Feehan, 2000; Girard et al., 2002). Once abandoned, cutover bogs are minimally recolonized by plants because they are left with harsh environmental conditions such as altered hydrology (Price et al., 2003; Price and Whitehead, 2004), surface instability caused by wind, water erosion and frost heaving (Campbell et al., 2002; Groeneveld and Rochefort, 2002), as well as residual peat surfaces with unsuitable physical properties (Price and Whitehead, 2001). However, some plant species are able to colonize abandoned peat fields, especially those where peat was extracted manually using the block-cut method (Girard et al., 2002).

Traditionally, block-cut peat extraction was undertaken by hundreds of workers with shovels, leaving a topography characterized by alternating baulks and trenches (Rochefort, 2001). Unlike modern milling and vacuum techniques, the absence of heavy machinery in block-cut extraction required less intense drainage activities and did not compact soil, in turn resulting in conditions more favorable for plant recolonization (Soro et al., 1999; Price and Whitehead, 2001; van Seters and Price, 2001; Lavoie et al., 2003; Poulin et al., 2005; Konvalinkova and Prach, 2010). As well, plant fragments

were left behind in peat extracted trenches, further promoting natural revegetation. Still, despite effective spontaneous recolonization in block-cut peatlands, species composition and cover differ notably from that found in undisturbed peatlands (Konvalinkova and Prach, 2010), even many decades after abandonment (Soro et al., 1999). Block-cut sites are mostly recolonized by vascular plants, but the cover of the characteristic *Sphagnum* mosses typical of natural ombrotrophic peatlands may vary considerably (Poulin et al., 2005).

The development of *Sphagnum* carpets is essential for restoring the ecological function of carbon accumulation in bogs (Rocheftort, 2000). In the restoration context of Eastern Canada, the short-term goal for cut-over peatlands is to re-establish a plant cover composed of peat bog species dominated by *Sphagnum*, which favours the recovery of the acrotelm and peat accumulation in the long term (Rocheftort et al., 2003). Restoring this ecological service thus represents an “objective-based” strategy in the sense that it does not aim to return to pristine, undisturbed conditions of reference sites but rather focuses on the return of ecosystem functionality, a well-accepted goal by the society at least for irreversibly disturbed sites such as mined peatlands (objective-based restoration, *sensu* Dufour and Piégay, 2009; intervention ecology, *sensu* Hobbs et al., 2011). Knowing more about the fate of such disturbed peatlands is also important for conservation of regional biodiversity. For example, block-cut sites are usually located near current industrial sites. As has been shown to be the case for natural peatland remnants (Poulin et al., 1999; Delage et al., 2000), block-cut sites could potentially play a role in preserving animal and plant populations locally. They could also be a source of plant diaspores during or after restoration work on sites currently abandoned after mechanized peat extraction (see moss transfer layer restoration technique described in Rocheftort et al., 2003).

Development of plant communities in block-cut peatlands, that is, how the trajectories of plant communities evolve after initial establishment, has been even less frequently studied than plant colonization. Assessments using space-for-time substitutions have been applied to block-cut studies occasionally (Konvalinkova and Prach, 2010), but they yield less reliable information than monitoring using permanent plots. Yet, the latter is logistically difficult to implement and therefore infrequent in ecological studies. To our knowledge, there has been no long-term monitoring study of block-cut peatlands left to revegetate spontaneously, particularly on a broad regional scale. As restoration is fundamentally the manipulation of communities towards a desired trajectory, a better knowledge of spontaneous recolonization patterns would provide a reference framework for undertaking restoration action and predict management outcomes (Walker et al., 2007). A fundamental question in the science of ecological restoration is whether we can rely upon spontaneous succession (passive restoration) to restore a disturbed ecosystem or active intervention is needed (Prach and Hobbs, 2008).

In the mid-1990s, a large-scale survey of cutover peatlands, including block-cut sites, was conducted in Eastern Canada (Poulin et al., 2005), one of the primary horticultural peat-producing regions of the world (Warner and Buteau, 2002). At that time, sites had been abandoned for ~25 years and were already at least partly revegetated. We revisited the same block-cut sites ten years later, in 2005-2006 (~35 years after abandonment), to evaluate whether their plant communities were on a trajectory towards the recovery of a *Sphagnum*-dominated system typical of bogs. By answering this question, our ultimate objective was to evaluate whether these sites were self-regenerating or instead active

intervention was needed to ensure the restoration of the key ecological functions of peat accumulation and preservation of regional biodiversity.

Materials and methods

Study sites

The study was carried out in three industrial peatland regions covering a biogeographic gradient from Atlantic to Inland areas in the Eastern Canadian provinces of New Brunswick and Québec (*Fig. 1*). A total of 6800 ha (New Brunswick) and 6000 ha (Québec) of peatland has been mined in these provinces, representing 5% and 0.05% of their total peatland area, respectively (Poulin et al., 2004).

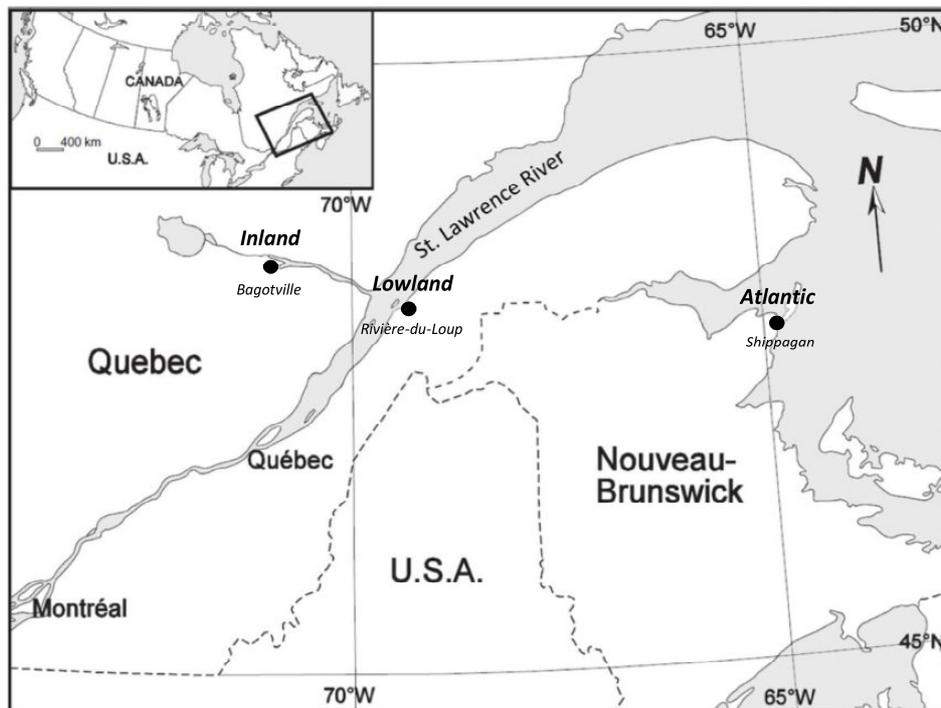


Figure 1. Location of the three abandoned block-cut mined peatland regions in the Eastern Canadian provinces of Québec and New Brunswick. The regions corresponding to major Canadian climatic regions: Atlantic region: Mean annual temperature = 4.5 °C, Total annual precipitation = 1059 mm, Precipitation as snow = 318 mm. Lowland of Great Lakes / St. Lawrence region: Mean annual temperature = 3.2 °C, Total annual precipitation = 963 mm, Precipitation as snow = 270 mm. Inland of Northeastern Forest region: Mean annual temperature = 2.3 °C, Total annual precipitation = 887 mm, Precipitation as snow = 296 mm (Environment Canada, 2012)

Most of the studied peatlands developed in lowlands of sand, silt, and clay marine deposits. Classified as Atlantic boreal peatlands and Maritime Atlantic boreal peatlands, they are primarily rainfed (ombrotrophic bogs; National Wetlands Working Group 1988). The peatlands are concentrated in three main regions, corresponding to major Canadian climatic regions: Atlantic (Atlantic Canada region), Lowland (Great Lakes /

St. Lawrence region) and Inland (Northeastern Forest region). The Atlantic peatland region included two peatlands near the coastal villages of Inkerman Ferry and Shippagan, located ~10 km apart in the province of New Brunswick (*Fig. 1*). The Lowland peatland region was one of the biggest peat production regions in southern Québec and included the six peatlands of Isle Verte, Coteau-du-Tuff, Saint Arsene, Cacouna, Le Parc and Saint Laurent, all located within a ~20 km belt along the south shore of the St. Lawrence River near the town of Rivière-du-Loup (*Fig. 1*, for a more detailed description of this peatland region, the Bas-Saint-Laurent, see Pellerin and Lavoie, 2000; 2003). Peat extraction activities were especially intense in the 1940s and 1950s along the south shore of the St. Lawrence River, particularly in the vicinity of Rivière-du-Loup, resulting in a historically higher concentration of cutover peatlands in the area. The Inland region included the only one extensive traditionally block-cut peatland that was not re-opened for vacuum harvesting and still remained abandoned, located in the proximity of Bagotville (*Fig. 1*). A summary of the characteristics of the nine abandoned bogs in the three peatland regions is provided in *Table 1*. Although the traditional block-cut method severely disturbed the ecosystem, note that the method left in place a peat body of at least 1 m in depth after exploitation, preserving ombrotrophic conditions in all sites and making the spontaneous return of *Sphagnum* a feasible expectation. The pH in residual peat ranged within the typical values for natural bogs (2.9 – 3.2) of the area reported by Andersen et al. (2011) and only EC was slightly higher (40 and 9 $\mu\text{S cm}^{-1}$ in the Lowland and Inland regions respectively, Andersen et al., 2011; no data available for the Atlantic region).

The three peatland regions comprise all of Eastern Canada's abandoned block-cut peatlands. They were totally or partially exploited by the block-cut method before being abandoned to spontaneous revegetation. The first step of the block-cut method involves digging out a network of primary drainage ditches to divide the natural peatland into rectangular sectors and lower the water table level. A first row of peat is then extracted, after removing and setting aside the live surface vegetation. Peat blocks are stacked to dry on racks located on adjacent higher surfaces (baulks) as the surface area under exploitation widens (*Fig. 2a*). The pattern of trenches and baulks resulting from this process remains identifiable decades after abandonment (*Fig. 2b*). A trench is typically ~10-15 m wide, and a baulk ~3-4 m wide. We examined trenches exclusively; we excluded baulks because they are largely devoid of *Sphagnum* (Poulin et al., 2005) and are unlikely to evolve toward plant communities typical of bogs, at least not until such time as the trenches fill up with accumulated organic matter.

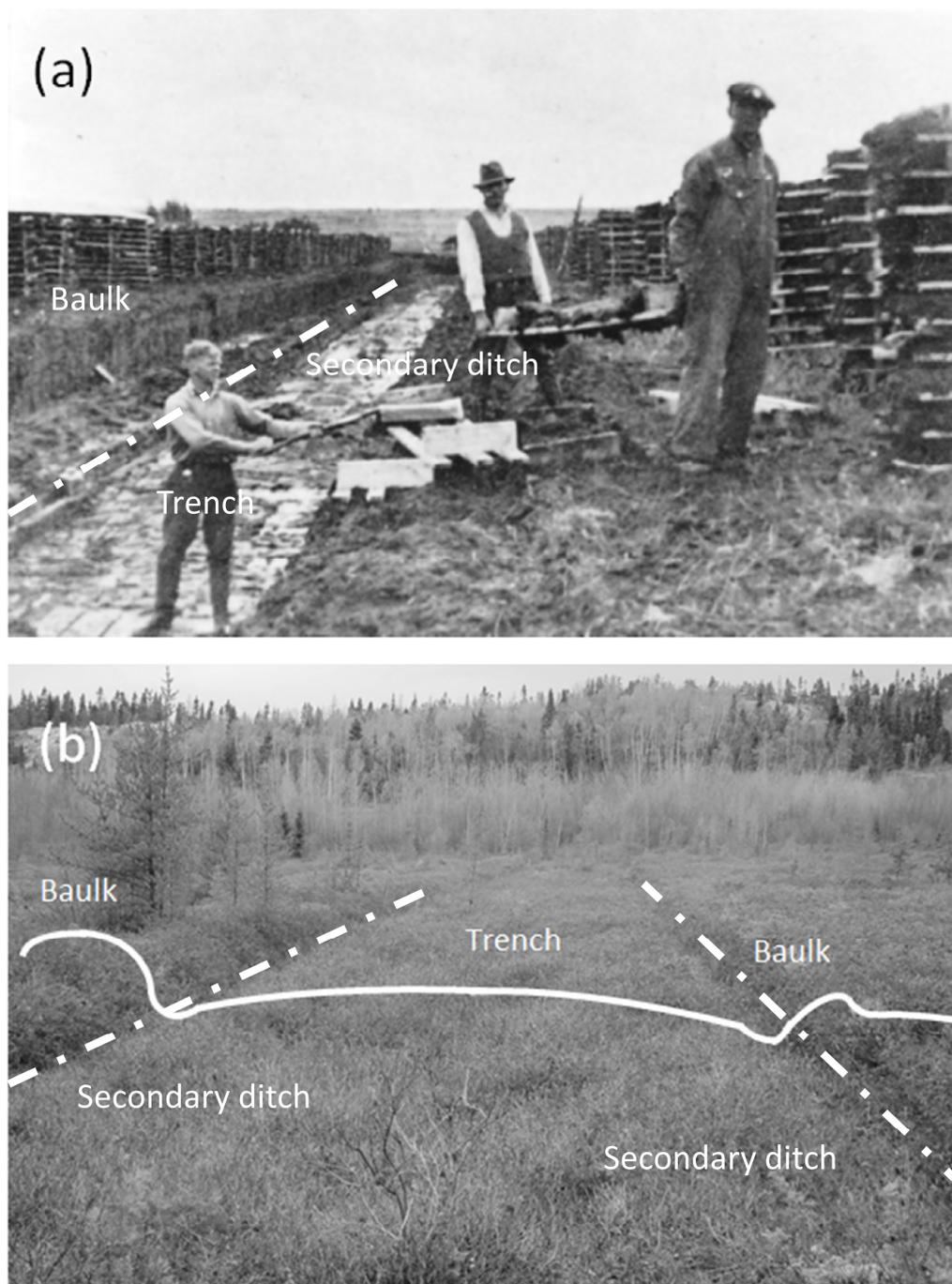


Figure 2. (a) Block-cut exploitation in the Isle Verte peatland (Lowland region) during the 1940s. Workers deposit peat blocks on drying racks (from Risi et al., 1953; courtesy of the Ministère des Ressources Naturelles du Québec); (b) Characteristic topography of alternating baulks and trenches, decades after abandonment and spontaneous recolonization

Table 1. Summary of the main characteristics of the nine bogs at three peatland regions of Eastern Canada

	Atlantic			Lowland							Inland
	IF	SH	Total	IV	CT	SA	CA	LP	SL	Total	BA
General characteristics											
Number of trenches	5	10	15	4	4	5	7	11	24	55	10
Size of abandoned peatland (ha)	122	189	-	89	23	20	71	29	220	-	32
UTM coordinates	47°42'N 64°45'W	47°44'N 64°43'W	-	48°02'N 69°18' W	47°58'N 69°22' W	47°56'N 69°26'W	47°54'N 69°27'W	47°52'N 69°30'W	47°49'N 69°29'W	-	48°22'N 70°57'W
Year of abandonment*	1977(0)	1970(0)	1970a(7)	1976(0)	1968(8)	1974(4)	1968(20)	1967(13)	1965(9)	1968b(21)	1970a(0)
Peat properties‡											
Depth of residual peat (cm)	165(67)	163(104)	165a(104)	144(82)	133(78)	101(55)	170(43)	127(160)	182(159)	160a(208)	174a(48)
Von Post	4(3)	3(4)	3b(4)	5(3)	6(2)	5(1)	5(2)	4(0)	5(3)	5a(4)	3b(4)
EC (μScm^{-1})	85(111)	67(133)	71a(135)	60(33)	77(22)	60(41)	81(67)	43(215)	78(103)	76a(216)	36b(49)
pH	3.6(0.9)	3.1(0.7)	3.2b(1.0)	3.9(0.2)	3.8(0.3)	4.0(0.5)	3.5(1.0)	3.9(0.9)	3.7(0.6)	3.7a(1.4)	3.9ab(2.3)
Hydrology†											
Depth of water table (cm)	11(29)	22(29)	17b(29)	7(6)	2(3)	8(5)	26(28)	5(28)	44(102)	25b(109)	47a(18)
Depth of former drainage ditch (cm)	-7(10)	-3(23)	-3b(23)	11(29)	32(21)	30(25)	-9(15)	25(25)	25(36)	25a(54)	-6b(22)
Landscape (ha in 2km radius)§											
Agriculture	26(37)	84(32)	73b(103)	342(47)	912(28)	318(168)	753(106)	736(145)	199(381)	344a(873)	0c(0)
Forest	77(49)	284(208)	233b(331)	520(73)	271(20)	551(125)	229(65)	309(124)	310(161)	309a(407)	363a(32)
Natural	593(74)	706(175)	675a(220)	226(76)	6(0)	86(43)	73(13)	51(1)	100(169)	70c(233)	479b(77)
Abandoned block-cut peatland	122(31)	189(14)	189a(68)	89(0)	23(0)	20(0)	71(0)	29(0)	208(220)	71b(233)	32b(0)
Abandoned vacuum peatland	72(104)	0(0)	0ab(136)	0(0)	0(0)	7(1)	14(0)	7(0)	34(57)	11a(64)	0b(0)
Exploited vacuum peatland	7(4)	167(0)	167a(161)	0(0)	6(0)	155(1)	0(0)	0(0)	334(353)	155a(552)	0b(0)

Numbers are median values for the *n* trenches at each abandoned bog. Range in parentheses. IF – Inkerman Ferry, SH – Shippagan, IV – Isle Verte, CT – Coteau-du-Tuff, SA – Saint Arsene, CA – Cacouna, LP – Le Parc, SL – Saint Laurent, BA – Bagotville. *Information on year of abandonment was gathered from horticultural peat companies. ‡Physicochemical properties were analyzed with three peat samples per trench. The depth of residual peat was measured with an iron bar. Peat EC was measured on samples saturated with distillate water (ratio 1:10) and then corrected according to Sjörs (1952). Peat pH was measured using a portable pH meter on the same 1:10 solution. †The depth of the water table was measured in summer 2005. A negative sign implied that the former drainage ditch (Fig. 2) was completely infilled with peat collapsed from the baulks. §Landscape variables were calculated using ArcGIS 10 on aerial pictures obtained from Google Maps Satellite View, but only the main categories were included in the table to keep them simple. For each variable, letters indicate homogeneous group of peatland regions after Mann-Whitney tests

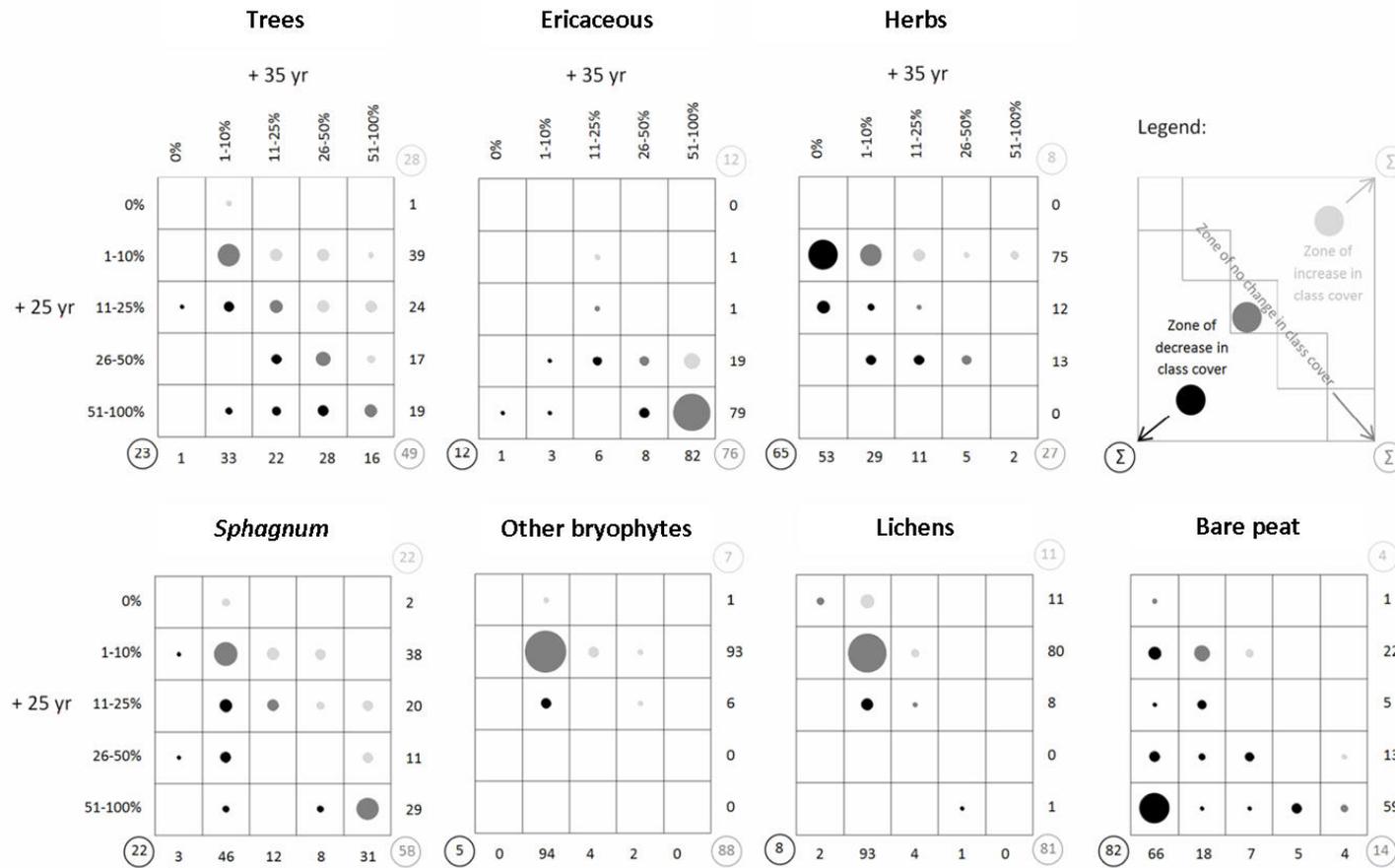


Figure 3. Balloon plots for the cover of six vegetation strata and bare peat in abandoned block-cut peatlands of Eastern Canada. The size of the circles is proportional to the number of trenches ($n = 80$) that were assigned to the cover classes specified in the rows and columns. Column numbers are row sums (frequency of each cover class in 1994-97, ~25 yr after abandonment). Row numbers are column sums (frequency of each cover class in 2005-06: ~35 yr after abandonment). Balloon plots were made using the *gplots* package of R (Warnes, 2011).

Vegetation surveys

The exhaustive survey conducted in the 1990s (1994, 1995 and 1997) described the vegetation structure of all trenches in all three peatland regions. This inventory was used to stratify each peatland according to main vegetation structure types and to select representative trenches for species relevés. A total of 2571 trenches were surveyed for vegetation structure, of which 112 were selected for conducting species relevés. Some sectors were reopened for vacuum extraction after the 1990s survey, but we could still revisit 80 of these initial trenches in our 2005-2006 survey (Number of trenches, *Table 1*).

The same protocol was used for the two surveys. When walking across each trench, the percent cover of six vegetation strata and ground substrate was visually estimated according to the following five percent 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* bryophytes, bryophytes other than *Sphagnum*, lichens and bare peat. Two or more categories could overlap vertically and therefore obtain a value of 4 within the same trench.

For species relevés, the Line-Point Intercept method was used (Bonham, 1989). Ten equidistant transects were established across each trench, such that all plant species including mosses, liverworts, lichens and vascular plants touching a vertical rod were recorded on ten equidistant positions. Species counts over the 100 pinpoints corresponded to the frequency of occurrence of a species within each trench, which we will refer to as “species cover” (as distinct from “species frequency”, i.e., the proportion of trenches where the species appeared), even though the Line-Point Intercept method tends to overestimate the cover of some species, such as small ericaceous shrubs (Rocheffort et al., in press). Because of taxonomic difficulties in the field, *Amelanchier*, *Cladonia*, *Carex*, *Drepanocladus*, *Lycopodium*, *Salix* and *Typha* were identified to the genus level only.

The total number of cases of our vegetation (species cover) dataset was therefore 160 (i.e., two surveys x 80 trenches). Additionally, in the second survey, the thickness of the new organic matter accumulated since abandonment (OM) was measured at the central point of transects 2, 5 and 9 of each trench with a ruler.

Data processing and statistical analyses

We used partial transformed-based principal component analysis (partial tb-PCA; Legendre and Legendre, 2012) to assess the similarity of plant composition between peatlands as well as their successional trajectories. Before looking at plant composition and trajectories, the effect of time since abandonment was partialled out by running a RDA, for which the year of abandonment was used as the only explanatory variable; a Hellinger’s transformation was applied to species cover in order to account for the occurrence of double zeros (Legendre and Gallagher, 2001). Rare species (occurring in less than 5% of the trenches) were removed from the vegetation matrix before transformation. The significance of the RDA was assessed using a permutation test with 9999 randomized runs (Legendre and Legendre, 2012). A PCA was then carried out on the residuals of the RDA (completing the last step of the partial tb-PCA). The PCA revealed the major community gradients and reflected their temporal evolution (from 25 yr to 35 yr). The scores of the trenches on the main axes of the PCA (sites scores, scaling = 1) were then compared between the two surveys using non-parametric

Wilcoxon matched-pairs tests to assess the degree of community change along the ecological gradients given by the ordination. Finally, the capacity of peatlands to accumulate OM along the identified ecological gradients was evaluated. The three OM thickness measurements at each trench were averaged to adjust the best multiple linear function “ $OM = f(\text{PCA sites scores with scaling } 1)$ ”. Only the site scores of the second survey were used, as OM was measured during the second survey only. These steps were carried out for the three peatland regions separately, as preliminary analyses showed a strong regional component in plant composition that drove ordinations when the three regions were analyzed together. Ordinations were carried out using R (version 2.14.0) software (R Development Core Team, 2011), more precisely the *vegan* (Oksanen et al., 2011) and *ade4* (Dray and Dufour, 2007) packages. SPSS v 13.0 was used to run the univariate non-parametric tests.

Results

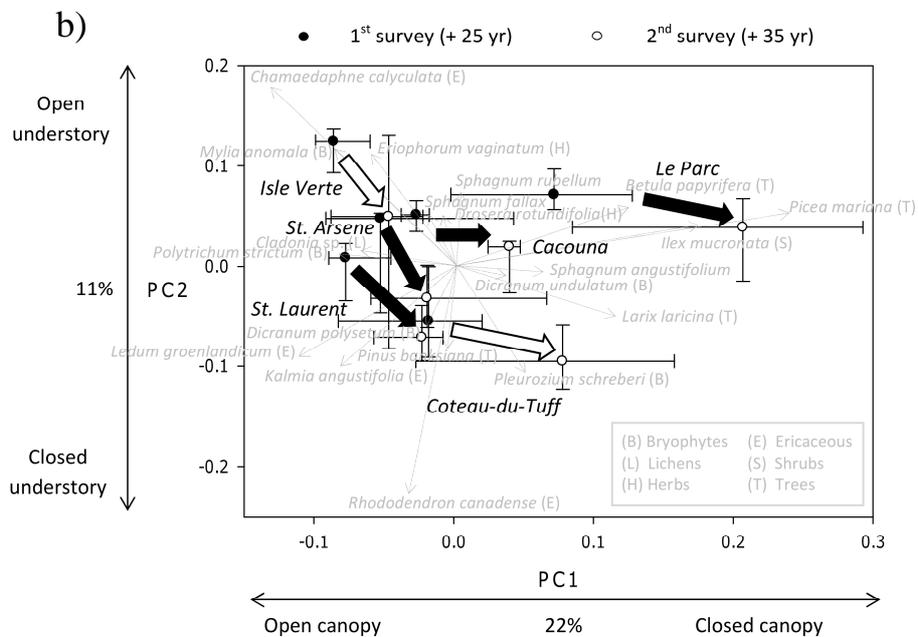
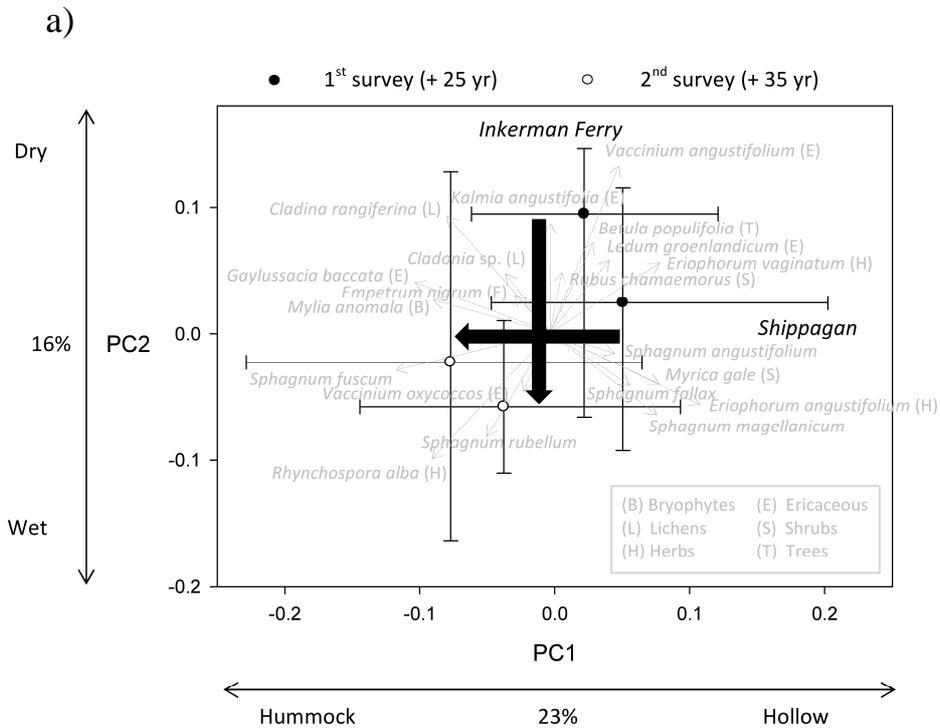
Overview of vegetation strata evolution

The block-cut peatlands were largely revegetated by the time of the first survey, ~25 years after exploitation finished. The majority of trenches (79%) had a cover of ericaceous shrubs higher than 50%, and a great proportion of trenches (60%) had been colonized by *Sphagnum*, with a cover higher than 10% (Fig. 3). Ten years later, 76% of the trenches had not experienced any change in ericaceous class cover, which was still by far the dominant plant stratum (Fig. 3). *Sphagnum* was still very common in 2005-06, although variability was very high among trenches, both in terms of cover (with two peaks at 1-10 and > 50%) and development. That is, *Sphagnum* cover remained stable in only 58% of the trenches and increased and decreased in the same proportion of trenches (22%) (Fig. 3). A similar pattern was observed for trees, for which a high variety of situations was observed as well. There was no predominant class cover either in 1994-97 or 2005-06. The main tendency for tree cover, however, was to remain stable (49%), while increases (28%) were slightly more frequent than decreases (23%) (Fig. 3). As observed for ericaceous shrubs, cover of bryophytes other than *Sphagnum* and lichens had changed little ten years after the first survey (88% and 81% of the trenches remained stable, respectively) (Fig. 3). Their cover remained < 10% in practically all trenches. Finally, herbs and especially bare peat showed a remarkable and generalized decrease in 65 and 82% of the trenches (Fig. 3).

Development of peatland plant communities

A total of 119 plant species (Appendix 1) were identified during the two surveys in the 80 trenches of the three peatland regions. For the Atlantic region, the first gradient seemed to represent the vertical zonation of *Sphagnum* species along hummock-hollow microtopography (PC1, 23%; Fig. 4a). The hummock species *S. fuscum* associated with the liverwort *Mylia anomala*, and the shrub *Gaylussacia baccata* appeared on the negative side of the gradient. Hollow/lawn associations *Eriophorum angustifolium*, *Sphagnum magellanicum*, *S. fallax*, *S. angustifolium* dominated the positive side of the gradient. Trenches were alternatively ordinated into a wet to dry gradient (PC2, 16%; Fig. 5a). *Sphagnum* spp. and herbs with humid preferences (*Rhynchospora alba* and *Eriophorum angustifolium*) had the most negative scores (wet); while ericaceous species, trees and lichens more typical of relatively drier environments appeared on the

positive end of the gradient (dry). The trajectories of the two Atlantic peatlands diverged over time: Inkerman Ferry became more dominated by plants with wet preference and Shippagan by hummock species (Fig. 4a).



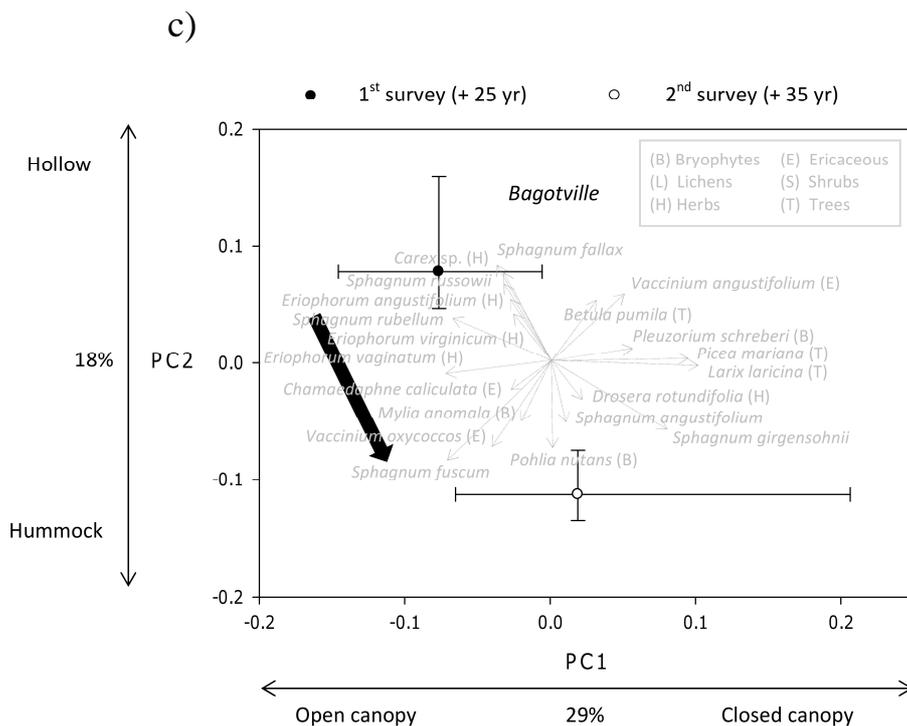


Figure 4. PC1 vs. PC2 biplots of respective partial *tb*-PCA ordinations (scaling = 1) for the plant community at (a) Atlantic, (b) Lowland and (c) Inland abandoned block-cut mined peatlands of Eastern Canada. Plant species cover matrices were built from 30, 110 and 20 cases (two surveys \times 15, 55 and 10 trenches, Table 1). To improve visual clarity of the PCA diagram, only the centroids (site scores medians) of each peatland at each one of the two surveys (filled circles = 1994-1997, open circles = 2005-2006), and the first and third percentile representing the errors, were drawn. Species scores were scaled by multiplying by 1/5 and are represented by dashed grey arrows. Removal of infrequent species resulted in a total of 62 (Atlantic), 55 (Lowland), and 55 (Inland) species for inclusion in the ordination analyses, but only the 20 species with the highest scores are represented at each figure for simplicity. Black arrows indicate that site scores between the two surveys at a given peatland were significantly different (Wilcoxon tests not shown, $P < 0.05$). Note that if the test was only significant for one of the axes, the arrow was drawn perpendicular to the one with no significance. White arrows were drawn to facilitate identification of the peatlands when the temporal change along the ordination was not significant on either of the two axes. The year of abandonment, whose effect on the vegetation was cancelled out before running the PCA, explained only 9 and 6% of the vegetation variability among trenches of the Atlantic and Lowland regions, respectively (RDA, permutation test, 9999 runs, $F = 2.8017$, $P = 0.004$; and RDA, permutation test, 9999 runs, $F = 7.0382$, $P < 0.001$). The RDA was not necessary in the Inland peatland region as it only included one peatland where all trenches were abandoned the same year

The two main gradients detected in the Lowland region reflected light availability (Fig. 4b). An open-closed canopy gradient explained the highest proportion of variability in the plant community (PC1, 22%), with ericaceous shrubs *Chamaedaphne calyculata* and *Ledum groenlandicum* having the most negative scores (open canopy); and with tree species contributing to the closed-canopy side of the gradient. Alternatively, sites were separated along a closed to open understory gradient (PC2,

11%). Three ericaceous species forming thick, taller populations (*Rhododendron canadense*, *Kalmia angustifolia* and *Ledum groenlandicum*) had the most negative scores (closed understory), associated with the tree *Pinus banksiana* and the moss *Pleurozium schreberi* that typically appears under dense canopies and tolerates shading. Short ericaceous species such as *Chamaedaphne calyculata*, the herb *Eriophorum vaginatum* and some bryophytes (*Mylia anomala* and some *Sphagnum* spp.) had the most positive scores (open understory). The general tendency of the six peatlands in the Lowland region was to become more closed both in the canopy and understory layers (Fig. 4b).

The Inland region included only one peatland whose trenches were mainly ordinated along an open to closed canopy gradient as well (PC1, 29%; Fig. 4c). Here, *Sphagnum rubellum*, *S. fuscum* and the tussock-forming sedge *Eriophorum vaginatum* dominated the negative side of the gradient; the trees *Picea mariana* and *Larix laricina*; and *Sphagnum girgensohnii* and *Pleurozium schreberi*, bryophytes typical of forested peatlands, dominated the positive end of the gradient. Secondly, a hummock-hollow gradient seemed to emerge, as in the Atlantic peatlands. Species typically associated with hummocks, such as *S. fuscum*, *Vaccinium oxycoccos*, *Pohlia nutans* and *Mylia anomala* dominated the negative end of the figure. Conversely, the hollow/lawn *Sphagnum fallax* and *S. russowii* species had the highest positive scores, in conjunction with the wetland herbs *Carex* spp. and *Eriophorum angustifolium*. The trajectory of the peatland was to become slightly more forested and to be more dominated by hummock-species (Fig. 4c).

New organic matter accumulation

The organic matter layer was 13 cm thick on average, but could vary notably among trenches (range 0-35 cm) and peatland regions, with Inland peatland thickness doubling that found in Lowland peatlands (Mean, Table 2). Organic matter tended to accumulate more in open systems (Best function, Table 2). However, the hummock-hollow and dry-wet gradients did not contribute to explain organic matter accumulation in any of the peatland regions.

Table 2. New organic matter accumulated in the three abandoned peatland regions in 2005-2006 as a function of their position along the ecological gradients given by the partial tb-PCA ordinations

	Mean ± SE (cm)	PC axis	Succession gradient	Best function	Adj R ²	F	P
Atlantic	16 ± 2	PC1	Hummock-hollow	Organic matter = 16 (mean)	-	-	-
		PC2	Wet-dry				
Lowland	10 ± 1	PC1	Open-closed canopy	Organic matter = 25*PC2 + 11	0.04	3.04	0.087
		PC2	Closed- open understory				
Inland	21 ± 2	PC1	Open -closed canopy	Organic matter = -27*PC1 + 23	0.43	7.87	0.023
		PC2	Hummock-hollow				

Note: In bold, the direction of the gradient with higher organic matter accumulation. When adjusting the functions, limits for P values were set up at 0.1 because a higher error type I was considered acceptable for such an exploratory analysis.

Discussion

Development of plant communities in abandoned block-cut peatlands

The vegetation communities in the three peatland regions showed remarkable changes for the time period (10 yr.) considered in this study, despite being very short in the time scale of peatland succession. Overall, among the three peatland regions studied, the Atlantic seemed to be most clearly on a trajectory toward recovery, with a higher abundance of moss species relative to ericaceous shrubs and trees. The greater abundance of hummock species in the second survey could indicate the initiation of a hummock-hollow gradient, as it takes only 10–30 yr for a microtopography typical of bogs to develop in restored cutover bogs (Pouliot et al., 2011). However, some caution is warranted since the increased dominance of hummock species could also simply reflect a decrease in hollow species, associated with drier conditions. In fact, this second hypothesis appears more plausible, because the most representative hollow species (e.g., *S. fallax*, *S. magellanicum* and *S. angustifolium*) were decreasing slightly in terms of frequency and/or cover (Appendix 1). The region's other peatland (Inkerman Ferry), however, showed a tendency toward increased wetness. We know that this was the peatland more frequently inundated among the nine included in this study (field observations).

Peatlands of the Lowland region were initially colonized by tall, dense ericaceous shrubs. There, communities maintained an ericaceous dominance over time and hence were not on a trajectory toward the recovery of a *Sphagnum*-dominated system. The analyses also revealed an increasing dominance of the tree strata, a result in accordance with that by Pellerin and Lavoie (2000; 2003), who reported the afforestation of undisturbed bogs and bog remnants within surfaces mined for the production of horticultural peat within our Lowland region. They suggested that this afforestation phenomenon may have been driven mainly by drainage related to agriculture and peat extraction, fire events (especially promoting *Pinus banksiana*) and a dry climatic period during the first part of the 20th century in the Bas-Saint-Laurent region. Recently, González et al. (In press) have also suggested that agricultural activities may be favoring afforestation in abandoned block-cut peatlands of the same region. It thus seems very unlikely that Lowland region peatlands evolve naturally toward *Sphagnum*-dominated systems. Moreover, the dominant tree and ericaceous species may even inhibit future *Sphagnum* establishment. For example, *Picea mariana*, one of the species that experienced a higher increase in frequency and cover (Fig. 5b, Appendix 1), is known to increase dryness by enhancing evapotranspiration (van Seters and Price, 2001). The same process has been described for *Betula* trees (Fay and Lavoie, 2009). Likewise, living biomass and litter produced by the increasingly dominant vascular species may limit light availability for *Sphagnum* (Berendse et al., 2001).

The detailed examination of the Inland peatland showed that it was also subjected to an afforestation process (PC1, Fig. 4c). However, the greater presence of trees in this case did not prevent *Sphagnum* establishment. As in the Shippagan peatland, a hummock-hollow successional trend was identified as well. In this case, the hypothesis that hollow species are disappearing seems more plausible than the hypothesis that a hummock-hollow microtopography could be recovered. Frequency and cover of the most representative hollow species, *S. fallax*, decreased dramatically from the first to the second survey (Appendix 1), while other hollow/lawn species remained stable (e.g.,

S. magellanicum, Appendix 1) or increased only slightly (e.g., *S. angustifolium*, Appendix 1).

Understanding succession to reach Sphagnum-dominated systems

It is widely agreed that hydrological conditions (i.e., water table depths and fluctuations, and peat water content) as well as the quality and depth of the peat remaining after exploitation play a critical role in the establishment and succession of plant communities in peatlands, including block-cut sites (Rochefort and Lode, 2006). To verify this, canonical analyses for all peatland regions altogether and separately were carried out with the species cover as matrix Y and the peat, hydrology and landscape descriptors of *Table 1* as matrix X, but models could only explain a marginal proportion of the variability and therefore are not shown. Lack of replication for the Inland region and the only two peatlands surveyed in the Atlantic region limited the explanatory power of our predictors, especially the landscape variables, which did not differ much between trenches of the same peatland. On the other hand, environmental parameters such as those related to hydrology are hard to be characterized precisely in such an extensive study and our data were probably too restricted in time and space to allow a comprehensive understanding of factors controlling secondary succession. In addition, we think that the range of environmental variation within peat properties was too narrow to explain such similar trajectories. Nevertheless, our study only aimed at identifying general revegetation patterns to optimize the choice of restoration sites and not at disentangling the drivers of spontaneous recolonization. Studies at finer spatial scales are more appropriate in that case (e.g., microtopography scale, Tuittila et al., 2000; Pouliot et al., 2012; paleoecological analyses, Robert et al., 1999; Pellerin and Lavoie, 2000; 2003). With this limitation in mind, however, one point related to possible drivers of recolonization deserved to be mentioned. Given that the development of vegetation was different between the three block-cut peatland regions but similar within the same region, we suggest that supra-regional factors (e.g., climate, landscape) were probably among the main drivers of post-abandonment succession. For example, drier conditions in Lowland peatlands compared to the other two regions could have been exacerbated by intensified drainage of agricultural lands surrounding the trenches and by deeper secondary ditches within peatlands (*Table 1*, González et al. in press).

Regardless of cause, the different trajectories reported here suggest criteria for the identification of sites that require active intervention to ensure the recovery of the ability to accumulate peat, a key ecological function of bogs, and to detect trends essential to biodiversity conservation. For example, the trajectory of the Lowland peatlands will contribute little to the conservation of biodiversity and peat-accumulation functions in the region, given undesired evolution toward closed understories and canopies, and the lowest OM accumulation (*Table 2*). Consequently, intervention is highly recommended. In fact, some restoration measures, such as the blockage of former drainage ditches, have been carried out in three of the Lowland peatlands (Isle Verte in 1993, Saint Laurent in 2000 and Cacouna in 2006), with promising results for successful restoration: reduced runoff and a raised water-table, which improve the hydrological conditions for *Sphagnum* recolonization, have been reported by Ketcheson and Price (2011) for Cacouna peatland. González et al. (in press) and Henstra (2012) described positive responses of rewetting on plant composition in the three restored peatlands, namely a decrease in the dominance by trees and ericaceous shrubs, in parallel with an increase in the occurrence of hollow *Sphagnum* species. The Inland and,

especially the Atlantic region peatlands are, however, on a better trajectory of recovery and intervention does not seem critical. There, future studies are needed to document long-term evolution of the transition from hollow to hummock species we observed, as well as the impact on peat accumulation.

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Appendix 1. List of species identified in the three peatland regions during the two surveys (1st survey = 25 yr after abandonment, 2nd survey = 35 yr after abandonment) and classified by vegetation strata. Freq. is the “species frequency” (i.e., the proportion of trenches where the species appeared). Cover is the “species cover” (i.e., mean percentage of counts within the trenches where the species was present)

Species name	Atlantic				Lowland				Inland			
	1 st survey		2 nd survey		1 st survey		2 nd survey		1 st survey		2 nd survey	
	Freq.	Cover										
<i>Sphagnum</i>												
<i>Section Acutifolia</i>												
<i>Sphagnum fimbriatum</i> Wils. in Wils. & Hook. f. in Hook. f.	7	2	7	1	18	2	5	3	40	1	0	-
<i>Sphagnum flavicomans</i> (Cardot) Warnst.	13	4	47	4	0	-	0	-	0	-	0	-
<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	80	8	100	11	40	2	35	4	100	21	100	30
<i>Sphagnum girgensohnii</i> Russ.	0	-	0	-	4	1	18	6	20	2	60	14
<i>Sphagnum rubellum</i> Wils. (<i>Sphagnum capillifolium sensu lato</i>)	100	22	100	29	93	11	96	15	100	49	100	41
<i>Sphagnum russowii</i> Warnst.	13	2	0	-	35	3	5	1	90	7	0	-
<i>Section Cuspidata</i>												
<i>Sphagnum angustifolium</i> (C. Jens. ex Russ.) C. Jens. in Tolf	80	3	33	4	15	2	45	6	30	5	90	4
<i>Sphagnum cuspidatum</i> Ehrh. ex Hoffm.	7	3	13	2	18	2	7	1	10	1	10	1
<i>Sphagnum fallax</i> (Klinggr.) Klinggr.	47	7	20	2	51	5	22	3	80	7	0	-
<i>Sphagnum lindbergii</i> Schimp. in Lindb.	0	-	0	-	2	1	4	1	10	2	0	-
<i>Sphagnum majus</i> (Russ.) C. Jens.	0	-	13	2	2	1	2	1	0	-	0	-
<i>Sphagnum pulchrum</i> (Lindb. ex Braithw.) Warnst.	0	-	0	-	11	8	0	-	10	1	0	-
<i>Sphagnum riparium</i> Ångstr.	0	-	0	-	9	3	2	1	30	2	0	-
<i>Section Sphagnum</i>												
<i>Sphagnum magellanicum</i> Brid.	100	13	100	12	42	3	53	4	100	14	100	15
<i>Sphagnum papillosum</i> Lindb.	0	-	20	8	5	1	2	2	10	2	0	-
<i>Section Squarrosa</i>												
<i>Sphagnum squarrosum</i> Crome	0	-	0	-	0	-	2	1	0	-	0	-
<i>Bryophytes other than Sphagnum</i>												

Species name	Atlantic				Lowland				Inland			
	1 st survey		2 nd survey		1 st survey		2 nd survey		1 st survey		2 nd survey	
	Freq.	Cover										
<i>Aulacomnium palustre</i> (Hedw.) Schwaegr.	0	-	0	-	2	1	2	1	0	-	0	-
<i>Calliergon stramineum</i> (Brid.) Kindb.	0	-	7	1	0	-	0	-	0	-	0	-
<i>Dicranella cerviculata</i> (Hedw.) Schimp.	7	1	0	-	0	-	0	-	10	1	0	-
<i>Dicranum montanum</i> Hedw.	0	-	0	-	2	1	0	-	0	-	0	-
<i>Dicranum polysetum</i> Sw.	20	1	7	2	20	1	33	4	30	1	30	2
<i>Dicranum spadicum</i> J.E. Zetterst.	0	-	7	1	0	-	0	-	0	-	0	-
<i>Dicranum undulatum</i> Ehrh. ex Web. & Mohr non Brid.	7	1	27	1	18	2	53	3	0	-	50	2
<i>Drepanocladus species</i>	0	-	0	-	0	-	0	-	10	1	0	-
<i>Gymnocolea inflata</i> (Huds.) Dumort.	0	-	13	5	0	-	0	-	0	-	0	-
<i>Mylia anomala</i> (Hook.) S. Gray	87	9	87	9	82	6	44	6	40	4	80	4
<i>Plagiothecium laetum</i> Schimp. in B.S.G.	0	-	0	-	0	-	2	1	0	-	10	2
<i>Pleurozium schreberi</i> (Brid.) Mitt.	0	-	20	1	53	3	87	8	90	4	80	10
<i>Pohlia nutans</i> (Hedw.) Lindb.	7	1	0	-	15	2	22	3	30	2	90	6
<i>Polytrichum commune</i> Hedw.	0	-	0	-	0	-	2	1	0	-	0	-
<i>Polytrichum juniperinum</i> Hedw.	0	-	0	-	0	-	2	1	0	-	0	-
<i>Polytrichum strictum</i> Brid.	67	3	60	4	85	7	69	6	100	25	100	26
<i>Ptilidium ciliare</i> (Hedw.) Lindb.	0	-	13	12	7	1	45	3	0	-	30	2
<i>Ptilium crista-castrensis</i> (Hedw.) De Not.	0	-	0	-	0	-	2	2	0	-	0	-
<i>Ptilidium pulcherrimum</i> (G. Web.) Hampe	0	-	0	-	0	-	5	1	0	-	0	-
<i>Sanionia uncinata</i> var. <i>uncinata</i> (Hedw.) Loeske	0	-	0	-	0	-	0	-	10	1	0	-
<i>Steerecleus serrulatus</i> (Hedw.) H. Rob.	0	-	0	-	2	2	0	-	0	-	0	-
<i>Tetraphis pellucida</i> Hedw.	0	-	0	-	7	1	2	1	10	1	0	-
<i>Warnstorfia exannulata</i> (Schimp. in B.S.G.) Loeske var. <i>exannulata</i>	7	3	7	1	2	1	2	3	0	-	30	1
<i>Warnstorfia fluitans</i> (Hedw.) Loeske	7	1	0	-	7	1	5	3	20	2	10	1
Lichens												
<i>Cladina mitis</i> (Sandst.) Hustich	40	4	47	2	25	1	55	6	10	1	0	-
<i>Cladina rangiferina</i> (L.) Nyl.	73	7	87	8	56	4	49	6	30	1	40	2
<i>Cladonia species</i>	93	13	80	9	69	3	53	6	40	1	30	1
Herbs												

Species name	Atlantic				Lowland				Inland			
	1 st survey		2 nd survey		1 st survey		2 nd survey		1 st survey		2 nd survey	
	Freq.	Cover										
<i>Agrostis hyemalis</i> (Walter) Britton, Sterns & Poggenb	7	2	0	-	0	-	0	-	0	-	0	-
<i>Doellingeria umbellata</i> (Mill.) Nees	0	-	0	-	0	-	0	-	0	-	10	1
<i>Calamagrostis canadensis</i> (Michx.) P. Beauv.	0	-	0	-	0	-	0	-	10	2	0	-
<i>Carex species</i>	33	6	0	-	24	4	4	1	80	12	40	1
<i>Geocaulon lividum</i> (Richardson) Fernald	0	-	0	-	0	-	0	-	0	-	10	2
<i>Coptis trifolia</i> (L.) Salisb.	0	-	0	-	2	5	4	1	10	1	0	-
<i>Cornus canadensis</i> L.	0	-	0	-	20	4	13	4	10	1	0	-
<i>Cypripedium acaule</i> Ait.	0	-	13	2	5	1	4	1	0	-	0	-
<i>Drosera intermedia</i> Hayne	20	4	20	1	0	-	0	-	0	-	0	-
<i>Drosera rotundifolia</i> L.	80	3	87	5	31	2	11	15	10	1	90	2
<i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs	0	-	0	-	2	2	0	-	0	-	0	-
<i>Eleocharis parvula</i> (Roem. & Schult.) Link ex Bluff, Nees & Schauer	7	1	0	-	0	-	0	-	0	-	0	-
<i>Eriophorum angustifolium</i> Honck.	53	17	33	14	5	14	5	3	70	7	50	4
<i>Eriophorum vaginatum</i> L.	87	6	60	7	40	8	35	5	80	8	70	6
<i>Eriophorum virginicum</i> L.	13	1	40	3	4	11	0	-	80	5	50	5
<i>Lycopodium annotinum</i> L.	7	1	0	-	2	1	2	2	30	1	0	-
<i>Lycopodium species other than Lyc_ann</i>	0	-	7	1	0	-	0	-	30	1	10	1
<i>Maianthemum canadense</i> Desf.	0	-	0	-	4	2	0	-	0	-	0	-
<i>Maianthemum trifolium</i> (L.) Sloboda.	13	5	13	6	0	-	0	-	0	-	0	-
<i>Melampyrum lineare</i> Desr.	0	-	7	1	9	1	2	4	0	-	0	-
<i>Osmunda cinnamomea</i> L.	7	1	0	-	4	1	0	-	0	-	0	-
<i>Pteridium aquilinum</i> (L.) Kuhn	0	-	0	-	5	6	2	2	20	2	0	-
<i>Puccinellia laurentiana</i> Fernald & Weath.	7	9	0	-	0	-	0	-	0	-	0	-
<i>Rhynchospora alba</i> (L.) Vahl	87	10	67	18	0	-	0	-	0	-	0	-
<i>Sarracenia purpurea</i> L.	0	-	40	1	4	6	4	4	0	-	0	-
<i>Scirpus microcarpus</i> J. Presl & C. Presl	0	-	0	-	0	-	2	3	0	-	0	-
<i>Smilacina trifolia</i> (L.) Desf.	13	5	0	-	0	-	0	-	0	-	0	-
<i>Solidago rugosa</i> Mill.	0	-	0	-	0	-	0	-	20	1	0	-
<i>Solidago uliginosa</i> Nutt.	0	-	0	-	2	1	0	-	0	-	0	-
<i>Spartina alterniflora</i> Loisel.	7	1	0	-	0	-	0	-	0	-	0	-

Species name	Atlantic				Lowland				Inland			
	1 st survey		2 nd survey		1 st survey		2 nd survey		1 st survey		2 nd survey	
	Freq.	Cover										
<i>Spartina pectinata</i> Bosc ex Link	7	1	0	-	0	-	0	-	0	-	0	-
<i>Thelypteris noveboracensis</i> (L.) Nieuwl.	0	-	0	-	2	1	0	-	0	-	0	-
<i>Trientalis borealis</i> Raf.	0	-	0	-	2	1	2	1	0	-	0	-
<i>Trichophorum cespitosum</i> (L.) Hartm.	7	2	27	1	0	-	0	-	0	-	0	-
<i>Typha</i> species	13	3	0	-	0	-	0	-	10	1	0	-
<i>Utricularia cornuta</i> Michx.	0	-	7	4	0	-	0	-	0	-	0	-
Ericaceous shrubs												
<i>Andromeda polifolia</i> L. var. <i>glaucophylla</i> (Link) DC.	0	-	53	5	2	1	0	-	40	3	70	2
<i>Chamaedaphne calyculata</i> (L.) Moench	100	27	100	21	100	23	95	17	100	34	100	41
<i>Empetrum nigrum</i> L.	93	11	93	7	0	-	0	-	0	-	0	-
<i>Gaultheria hispidula</i> (L.) Muhl. ex Bigelow	0	-	0	-	40	3	33	3	20	2	10	2
<i>Gaultheria procumbens</i> L.	0	-	0	-	0	-	4	5	0	-	0	-
<i>Gaylussacia baccata</i> (Wangenh.) K. Koch	47	10	93	24	0	-	0	-	0	-	0	-
<i>Gaylussacia dumosa</i> (Andrews) Torr. & A. Gray	20	1	0	-	0	-	0	-	0	-	0	-
<i>Kalmia angustifolia</i> L.	100	19	100	16	100	50	100	48	100	16	100	17
<i>Kalmia polifolia</i> Wangenh.	100	7	100	8	38	3	49	3	100	12	100	14
<i>Ledum groenlandicum</i> Oeder	100	11	100	8	100	47	98	42	100	52	100	54
<i>Rhododendron canadense</i> (L.) Torr.	87	6	80	4	96	17	96	26	0	-	0	-
<i>Vaccinium angustifolium</i> Ait. s.l.	93	22	87	7	100	35	100	30	80	10	80	9
<i>Vaccinium macrocarpon</i> Ait.	20	2	53	4	0	-	4	2	0	-	10	1
<i>Vaccinium oxycoccos</i> L.	100	13	93	16	25	3	22	3	100	12	100	25
Shrubs												
<i>Amelanchier</i> species	0	-	0	-	13	1	2	1	0	-	0	-
<i>Aronia melanocarpa</i> (Michx.) Ell.	20	5	27	3	31	3	31	4	0	-	0	-
<i>Ilex mucronata</i> (L.) Powell, Savolainen & Andrews	73	10	93	7	0	-	0	-	10	3	0	-
<i>Myrica gale</i> L.	7	1	0	-	27	9	35	13	0	-	0	-
<i>Rubus chamaemorus</i> L.	40	3	47	3	36	3	36	3	30	1	20	4
<i>Salix pyrifolia</i> Anderss.	20	3	0	-	2	1	0	-	10	2	10	2
<i>Salix</i> species other than <i>Sal_pyr</i>	0	-	0	-	2	1	0	-	20	4	10	3
<i>Spiraea alba</i> var. <i>latifolia</i> (Ait.) Dippel	13	2	0	-	2	11	4	5	0	-	10	14

Species name	Atlantic				Lowland				Inland			
	1 st survey		2 nd survey		1 st survey		2 nd survey		1 st survey		2 nd survey	
	Freq.	Cover										
<i>Viburnum nudum</i> L. var. <i>cassinoides</i> (L.) Torr. & A. Gray	0	-	0	-	11	1	11	6	0	-	0	-
Trees												
<i>Abies balsamea</i> (L.) P. Mill.	13	2	13	2	15	3	18	3	0	-	10	1
<i>Acer rubrum</i> L.	0	-	0	-	0	-	5	3	0	-	0	-
<i>Betula papyrifera</i> Marsh. var. <i>cordifolia</i> (Regel) Fernald	0	-	0	-	0	-	4	1	0	-	0	-
<i>Betula hybride</i>	0	-	0	-	2	1	2	6	10	6	0	-
<i>Betula papyrifera</i> Marsh.	7	1	20	2	71	5	58	7	80	2	60	2
<i>Betula populifolia</i> Marsh.	93	5	73	5	20	4	15	3	0	-	0	-
<i>Betula pumila</i> L.	0	-	7	1	0	-	0	-	100	8	90	8
<i>Larix laricina</i> (Du Roi) K. Koch	60	2	47	4	84	9	89	11	100	15	100	29
<i>Picea glauca</i> (Moench) Voss	0	-	0	-	4	2	7	4	0	-	0	-
<i>Picea mariana</i> (P. Mill.) B.S.P.	33	2	33	1	84	13	87	19	60	3	70	10
<i>Picea rubens</i> Sarg.	0	-	13	3	0	-	0	-	0	-	0	-
<i>Pinus banksiana</i> Lamb.	20	5	13	1	42	6	55	9	0	-	20	2
<i>Populus tremuloides</i> Michx.	0	-	0	-	5	2	2	5	0	-	0	-
<i>Prunus pensylvanica</i> L. f.	0	-	0	-	11	2	9	2	0	-	10	2
<i>Prunus virginiana</i> L.	0	-	0	-	0	-	4	1	0	-	0	-
<i>Sorbus americana</i> Marsh.	0	-	0	-	5	1	9	2	0	-	0	-
<i>Thuja occidentalis</i> L.	0	-	0	-	0	-	2	2	0	-	0	-