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Is rewetting enough to recover *Sphagnum* and associated peat-accumulating species in traditionally exploited bogs?

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Abstract When restoring ecosystems, the simple removal of stresses causing degradation may seem preferable over other more costly and time consuming approaches. However, some restoration techniques can be implemented at reasonable cost and with increased efficiency in certain cases. We examined the successional trajectories of vegetation within abandoned block-cut peatlands in a major peat-producing region of Eastern Canada to evaluate whether the use of rewetting as a restoration technique can assist in the recovery of a typical bog plant community dominated by *Sphagnum* compared to spontaneous recolonization alone. We surveyed a total of 55 trenches in 6 peatlands twice, ~25 and ~35 years after the cessation of peat extraction. Canonical ordinations evidenced a generalized process of afforestation during the decade studied, partially driven by agricultural drainage in the surrounding landscape. Plant communities were dominated by ericaceous shrubs that hampered the spontaneous recovery of a *Sphagnum*-dominated system typical of bogs in the short and medium-term. Three of the six peatlands surveyed were partially restored by blocking drainage ditches. There, we surveyed plant composition in rewetted (28) and non-rewetted (26) trenches and observed that rewetting mitigated the increase in tree dominance, decreased the dominance by ericaceous shrubs, and favored the spread of non-vascular species with a wet habitat preference (notably *Sphagnum* species from the Cuspidata section). We conclude that the use of low intervention restoration techniques in block-cut bogs, such as the blockage of former drainage ditches, can re-orient undesired vegetation trajectories driven by spontaneous recolonization alone.

Keywords Ecosystem recovery · Mires · Ombrotrophic peatlands · Partial redundancy analysis · Vegetation change · Wetland restoration · Rehabilitation

Introduction

Ecological restoration can assist the recovery of disturbed ecosystems by simply reducing or eliminating the sources of degradation, through grazing exclusion in grasslands (Loydi et al. 2012), levee removal in floodplains (Gergel et al. 2002), or reduction of water pollutants in streams (Clements et al. 2010). Alternatively, restoration sometimes implies more interventionist techniques such as soil amendment, prescribed

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fires, constructions to improve hydrological conditions, and planting or re-introduction of vegetation collected from nearby natural donor sites, usually with a precise goal of attaining a particular structure, composition, or spatial pattern in the targeted community (McIver and Starr 2001). The adequacy of the restoration method chosen and, ultimately, the degree of intervention depend on the starting point of the degraded ecosystem, its trajectory of recovery and its resilience to disturbance. For example, floodplain forests can be successfully restored in only a few years by simply re-naturalizing the river flow regime through dam operations (Rood et al. 2003), provided that undesired species are not already well established at the time of restoration (e.g., *Tamarix* replacing native riparian trees in Western US floodplains, Stromberg et al. 2007).

Restoration of peat bog vegetation in peat-extracted peatlands has been attempted in several countries by different strategies including either hydrological restoration alone or in combination with plant re-introductions (Tuittila et al. 2000a, 2003; Farrell and Doyle 2003; Rochefort et al. 2003; Smolders et al. 2003; Rochefort and Lode 2006; Robroek et al. 2009; Graf et al. 2012; González et al. 2013). Unlike vacuum-extracted sites where propagule limitation is a strong constraint for plant recolonization (Campbell et al. 2003), bogs exploited by the traditional block-cut method are often recolonized, primarily by vascular plants, within a few years following the cessation of peat extraction (Smart et al. 1989; Soro et al. 1999; Lavoie and Rochefort 1996; Girard et al. 2002; Lavoie et al. 2003; Poulin et al. 2005; Konvalinkova and Prach 2010). However, the extent of *Sphagnum* cover varies considerably and may remain too low (<25 %) to achieve two prominent goals of bog restoration, namely, the recovery of self-regulatory mechanisms leading to the re-establishment of an acrotelm, and enhanced carbon accumulation associated with peat forming processes (Rochefort 2000; Rochefort et al. 2003). As some *Sphagnum* nearly always remains after abandonment of peat extraction operations, the restoration of these sites is best approached through low intervention actions such as the blockage of former drainage ditches to re-establish a hydrological regime that promotes *Sphagnum* growth. In some cases, however, no action was taken after abandonment and these sites have become dominated by tall ericaceous shrubs in a few decades (65 % cover, Poulin et al. 2005; González et al. in press), whose tendency to produce substantial amounts of litter may impede the growth of *Sphagnum* and other bog species even after rewetting. Unfortunately, the extent to which the vascular vegetation that had spontaneously established in abandoned peatlands limits the success of simple hydrological restoration actions such as rewetting has not been addressed in the literature.

Eastern Canada is one of the primary horticultural peat-producing regions of the world (Warner and Buteau 2002). In this region, some restoration attempts have been made in formerly block-cut sites to redirect the developing vascular vegetation towards a more *Sphagnum*-dominated ecosystem. Restoration works consisted of the blockage of former drainage ditches to rewet exploited trenches in three bogs that had remained abandoned for $\sim$25 years and were already partly revegetated, primarily by ericaceous shrubs (Poulin et al. 2005). A large-scale survey of cutover peatlands in the region was also conducted with the aim of assessing the spontaneous recovery of *Sphagnum* cover and plant diversity (Poulin et al. 2005). Here, we report on a follow-up study of the same block-cut sites surveyed by Poulin et al. (2005) to evaluate whether their plant communities are on a trajectory towards the recovery of a *Sphagnum*-dominated system typical of bogs. We also evaluate vegetation change following rewetting through the blockage of drainage ditches. The fundamental question addressed by this work is whether we can rely upon spontaneous recolonization alone to restore a *Sphagnum*-dominated plant community in abandoned block-cut sites already revegetated but dominated by vascular plants, and if not, whether the simple blockage of drainage ditches is sufficient to promote *Sphagnum* cover and the return of species assemblages similar to those of a reference bog ecosystem.

Methods

Study area

The block-cut sites included in our study were ombrotrophic peatlands of the Bas-Saint-Laurent region located on a 4–10 km wide agricultural plain bordering the south shore of the St. Lawrence River in Quebec, Canada (Fig. 1). This area lies within the Great Lakes/St. Lawrence climatic region, and has a mean annual temperature of 2.7 °C and 999 mm mean total annual

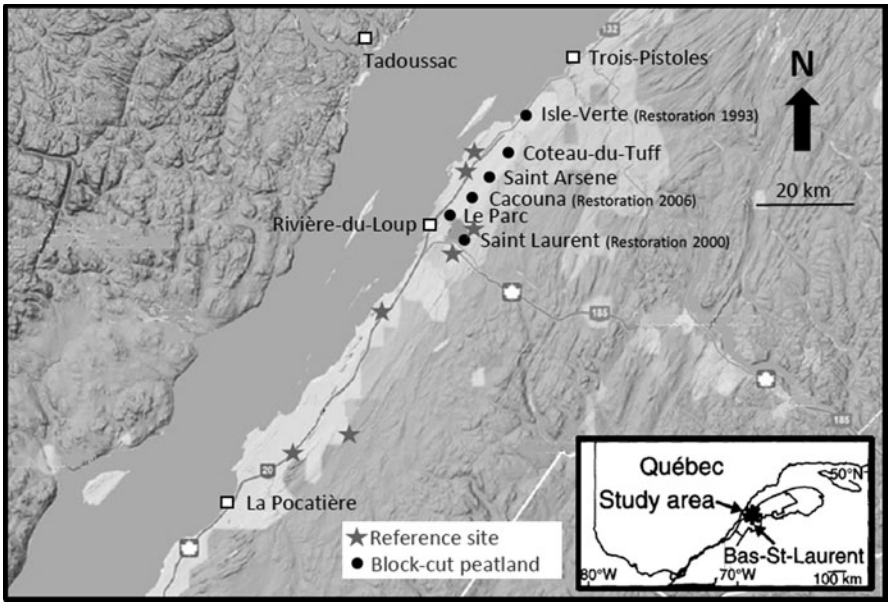


Fig. 1 Location of the six abandoned block-cut peatlands and seven reference sites in the Bas-Saint-Laurent region of Quebec, Canada

precipitation, 28 % of which falls as snow (Rivière Bleue weather station 47 26′N, 69 02′W, Environment Canada 2013). A mosaic of forest and bog originally covered the agricultural plain, although the forest cover was almost completely removed during the eighteenth and nineteenth centuries (Laberge 1993). Most peatlands are currently either being peat-extracted or are in various stages of passive recovery after decades of peat extraction (Desrochers et al. 1998; Lavoie and Saint-Louis 1999); however, some small untouched bog fragments that serve as useful reference sites for evaluation of restoration efforts still remain in the region (Pellerin and Lavoie 2000).

The traditional block-cut method of peat extraction consisted of four main stages: (1) excavation of a network of primary drainage ditches to divide the peatland into rectangular sectors and lower the water table level; (2) removal of surface vegetation in strips to expose the peat surface; (3) extraction of peat blocks in ever widening trenches, stacking the blocks on drying racks located on the higher surface adjacent to trenches (termed "baulks"); and (4) excavation of secondary drainage ditches along the edges of trenches to facilitate drainage (Fig. 2a). The pattern of alternating trenches and baulks resulting from this process remains identifiable decades after abandonment (Rochefort 2001a; Fig. 2b). A trench is typically ~10–15 m wide, and a baulk ~3–4 m wide. Today, secondary ditches are still discernible on both sides of each trench, though they are often filled up with residual peat that collapsed from the baulks (Fig. 2b). In our work, we focused exclusively on the abandoned trenches, as baulks were largely devoid of *Sphagnum* (Poulin et al. 2005) and are unlikely to develop toward plant communities typical of bogs, at least until such time as the trenches fill up with accumulated organic matter.

Study sites spontaneously revegetated

After the survey by Poulin et al. (2005) during the mid-1990s on spontaneous recolonization of block-cut peatlands, we revisited the six sites located in the Bas-Saint-Laurent region 10 years later, in 2005–2006: Cacouna, Isle Verte, Saint Laurent, Coteau-du-Tuff, Le Parc and Saint Arsene (Fig. 1). All are located within a ~20 km belt along the south shore of the St. Lawrence River near the town of Rivière-du-Loup. Most of the studied peat trenches were open to block-cut peat extraction after World War II and were abandoned during the 1960s and 1970s with the arrival of the new vacuum extraction technology. Some sectors within the Cacouna, Isle Verte, and Saint Laurent sites were subjected to low intervention restoration (see below), but no restoration action was implemented in any of the other three sites. The traditional block-cut method left in place a peat body

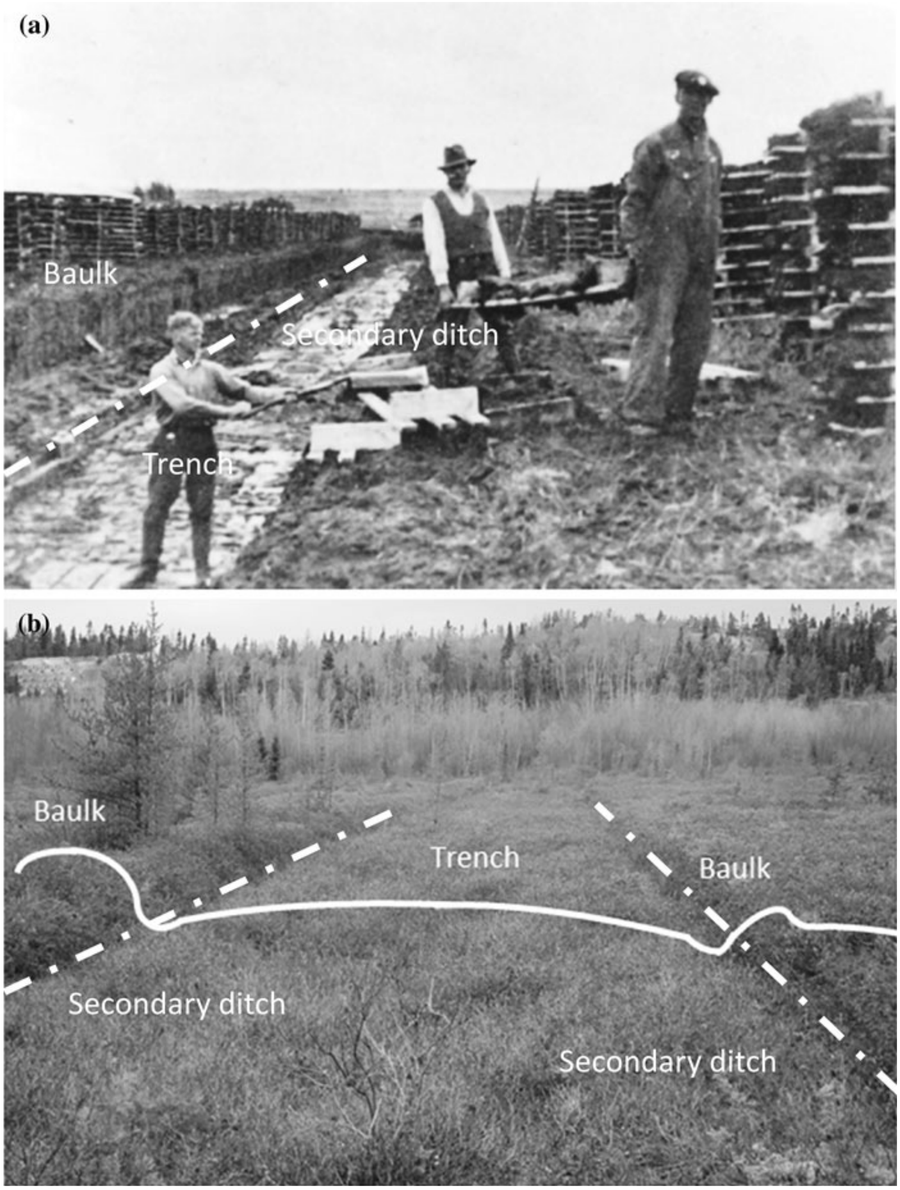


Fig. 2 **a** Block-cut exploitation in the Isle Verte peatland (Lowland region) during the 1940s. Workers deposit peat blocks on drying racks (from Risi et al. 1953; courtesy of the Ministère des Ressources Naturelles du Québec). **b** Characteristic topography of alternating baulks and trenches, decades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

of at least 1 m in depth after exploitation, preserving ombrotrophic conditions in all sites and making bog restoration a feasible target. A summary of the peat chemistry, hydrological and landscape characteristics of the six peatlands is provided in Table 1. In all cases, the pH of residual peat was within the range of typical values reported for natural bogs in the Bas-Saint-Laurent region (2.9–3.2), and EC was only slightly higher (40 $\mu S\ cm^{-1}$) (Andersen et al. 2011).

The exhaustive survey conducted in the 1990s (1994, 1995, and 1997) by Poulin et al. (2005) described the vegetation structure of all trenches in all block-cut peatlands left to spontaneous revegetation in Eastern Canada, including our six study peatlands. This inventory

Table 1 Summary of the main characteristics of the six abandoned block-cut bogs in the Bas-Saint-Laurent region

	Partially restored			Non-restored		
	IV	SL	CA	CT	SA	LP
General characteristics						
Beginning of peat extraction works	1935	1939	1942	1948	1959	1962
Year of abandonment[a]	1976 (0)	1965(9)	1968 (20)	1968 (8)	1974 (4)	1967 (13)
Number of surveyed trenches ~25 and ~35 year after abandonment	4	24	7	4	5	11
Size of abandoned peatland (ha)	89	220	71	23	20	29
UTM coordinates	48°02′N 69°18′W	47°49′N 69°29′W	47°54′N 69°27′W	47°58′N 69°22′W	47°56′N 69°26′W	47°52′N 69°30′W
Year of restoration	1993	2000	2006	–	–	–
Number of surveyed rewetted trenches ~40 year after abandonment	4	18	6	–	–	–
Number of surveyed non-rewetted trenches ~40 year after abandonment	7	6	13	–	–	–
Peat properties[b]						
Depth of residual peat (cm)	144 (82)	182 (159)	170 (43)	133 (78)	101 (55)	127 (160)
Peat decomposition (Von Post scale)	5 (3)	5 (3)	5 (2)	6 (2)	5 (1)	4 (0)
EC (μS cm^{-1})	60 (33)	78 (103)	81 (67)	77 (22)	60 (41)	43 (215)
pH	3.9 (0.2)	3.7 (0.6)	3.5 (1.0)	3.8 (0.3)	4.0 (0.5)	3.9 (0.9)
Hydrology[c]						
Depth of water table (cm)	7 (6)	44 (102)	26 (28)	2 (3)	8 (5)	5 (28)
Depth of former drainage ditch (cm)	11 (29)	25 (36)	−9 (15)	32 (21)	30 (25)	25 (25)
Landscape (ha in 2 km radius)[d]						
Agriculture	342 (47)	199 (381)	753 (106)	912 (28)	318 (168)	736 (145)
Forest	520 (73)	310 (161)	229 (65)	271 (20)	551 (125)	309 (124)
Natural	226 (76)	100 (169)	73(13)	6(0)	86 (43)	51 (1)
Abandoned block-cut peatland	89 (0)	208 (220)	71 (0)	23 (0)	20 (0)	29 (0)
Abandoned vacuumed peatland	0 (0)	34 (57)	14 (0)	0 (0)	7 (1)	7 (0)
Exploited vacuum peatland	0 (0)	334 (353)	0 (0)	6 (0)	155 (1)	0 (0)

Numbers are median values for the n trenches at each abandoned bog. Range in parentheses

IV Isle Verte, *CT* Coteau-du-Tuff, *SA* Saint Arsene, *CA* Cacouna, *LP* Le Parc, *SL* Saint Laurent

[a] Information on year of abandonment was gathered from horticultural peat companies

[b] 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 distilled 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

[c] The depth of the water table was measured during vegetation inventories conducted in the summer of 2005. A negative sign implies that the former drainage ditch (Fig. 2) was completely infilled with peat collapsed from the baulks

[d] 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 and in analyses to reduce problems associated with non-normality

was used to stratify each peatland according to the main vegetation structure types and to select representative trenches for species inventories. In the Bas Saint-Laurent region, a total of 1,721 trenches was surveyed for vegetation structure, of which 77 were selected for conducting species inventories. Some sectors were reopened for vacuum extraction after the 1990s survey, but we were able to revisit 55 of these initial trenches during our 2005–2006 survey (see number of surveyed trenches in Table 1).

We used the same sampling protocol for the species inventories as in the earlier survey (known as the line-point intercept method; 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 along each transect. Strictly speaking, this method yields a measure of the frequency of occurrence of a species within each trench, which we will refer to as "species cover". Because of taxonomic difficulties in the field, *Amelanchier, Cladonia*, *Carex,* and *Salix* were identified to the genus level only. The total number of cases of our vegetation (species cover) dataset for the assessment of spontaneous recolonization alone was, therefore, 110 (i.e., 2 surveys $\times$ 55 trenches).

Restoration sites

Some sectors of the peatlands at Isle Verte, Saint Laurent and Cacouna were subject to restoration by the peat industry, which involved blocking the former primary drainage ditches to decrease runoff and increase water levels in the residual peat body. In 1993, two sectors comprising 25 trenches ($\sim$3 ha) at the Isle Verte peatland were rewetted after infilling of drainage ditches with decomposed peat and construction of a plywood weir to retain water. In 2000, a total of $\sim$150 trenches ($\sim$20 ha-sector) at the Saint Laurent peatland were rewetted by blocking the primary drainage ditch network with 20 peat dams. As a result of these actions, water table levels rose $\sim$15 cm in both peatlands (S.W. Henstra, field observations). In October 2006, a total of 29 dams was installed in the primary drainage ditch network at the Cacouna peatland, raising the water table level an average of 32 cm in $\sim$80 trenches (10 ha) (Ketcheson and Price 2011).

A vegetation survey was carried out during the 2010 growing season ($\sim$40 yr. after abandonment) to assess the effects after 4, 10 and 17 years of rewetting, respectively for Cacouna, Saint Laurent and Isle Verte. A total of 28 rewetted trenches was surveyed following the same methodology used for the surveys of the sites subject to spontaneous recolonization alone: 6 rewetted trenches in Cacouna, 18 in Saint-Laurent, and 4 in Isle Verte. The number of trenches was chosen as a function of the size of the restored sector at each peatland and the heterogeneity of vegetation in the trenches observed in the field during preliminary visits. Additionally, 26 trenches were surveyed in non-rewetted sectors of these same peatlands, as a control in the evaluation of rewetting success (Table 1). The trenches that had been used previously for evaluation of spontaneous recolonization alone at Cacouna (7) and Isle Verte (4) were re-sampled. At Saint-Laurent, the largest of the peatlands included in this study, composed of North, South and West sectors, we did not re-sample any of the 24 trenches surveyed in 1994 and 2005 because they were located in a different sector from the one where the rewetting experiment was implemented (West); instead, 6 new trenches were surveyed in the West sector for use as a control.

Reference sites

Seven unmanaged bog fragments in the vicinity of the studied peatlands were used as reference sites to contextualize the outcomes of the rewetting (Fig. 1). These sites were not pristine, as they had been affected by human activities in the region (e.g. fragmentation and drainage for agriculture); however, we considered that their plant communities could serve as appropriate targets for evaluating restoration success.

Plant species cover in the reference sites was estimated visually in 2007 using ten equidistant 0.5 m^2 circular plots systematically placed in a rectangular grid at each site (Rochefort et al. 2013). Although this method underestimates the cover of certain species compared to the line-point intercept method used in the trenches (Rochefort et al. 2013), we considered these data as an acceptable reference in our study.

Data processing and statistical analyses

We used redundancy analysis (RDA) to assess the development of plant composition in the trenches of the six abandoned peatlands that had been left exclusively to spontaneous recolonization and which were surveyed $\sim$25 and $\sim$35 years after abandonment. Vegetation data were Hellinger transformed to account for the presence of double zeros (Legendre and Gallagher 2001), while the peat properties, hydrological and landscape descriptors of Table 1 were used as explanatory variables. The year of abandonment was included in the model as a covariable because we were interested in the temporal development of the plant communities and their controlling factors, rather than in their differences due to age. Highly correlated variables ($r > 0.7$) were removed and those remaining were subjected to a forward selection in order to avoid multi-collinearity in the models. Log and polynomial transformations of the explanatory variables were considered but abandoned, because no enhanced linearity of the relationship or normality of error was noted. Significance of the RDA was assessed using a permutation test with 9,999 randomized runs (Legendre and Legendre 2012). As the RDA explained only a low percentage of the variability in species composition, the first two unconstrained axes of the model (PC axes, also referred to as residuals of the RDA model), which correspond with the patterns in species composition unexplained by the environmental variables, also were explored. The site scores of the trenches on the main axes of the RDA and their residuals were 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.

The success of restoration was evaluated by comparing species with >1 % cover within seven vegetation strata (trees, ericaceous shrubs, shrubs, herbs, *Sphagnum* mosses, bryophytes other than *Sphagnum* and lichens) in the rewetted and non-rewetted trenches of each of the three partially restored peatlands surveyed in 2010. The criteria for judging success was based on the increase in cover of typical bog species, especially species of *Sphagnum* associated with wet microhabitats (i.e., depressions and hollows). To that end, the non-parametric Mann–Whitney test was used. The natural variability of species cover at the seven nearby unmanaged bog fragments was used as a reference and plotted in graphs showing the effect of rewetting to contextualize the experiment; however, the differences between restored and reference sites were not tested statistically because of the different techniques used for species cover estimation in the restored (line-point intercept) and reference sites (visual estimation in plots). For the same reason, the reference sites were not included in the RDA analyses described above for the sites subjected to spontaneous recolonization alone and, additionally, because exploratory analyses showed that their inclusion would obscure the successional patterns summarized by the ordinations.

The RDAs 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. The forward selection procedure was available in the packfor package (Dray et al. 2009), though the function forward.sel. SPSS v 13.0 was used to run the univariate non-parametric tests.

Results

Development of vegetation in bogs subjected to spontaneous recolonization alone

A total of 89 plant species were identified during the two surveys in the 55 trenches of the six peatlands. Once the effect of trench age was removed, sites were separated by a combination of peat properties, hydrology and landscape predictors along a vegetation gradient that followed a closed to open canopy (RDA1, 9 %, Fig. 3a, b), with the ericaceous shrubs *Kalmia angustifolia* and *Ledum groenlandicum* and the bryophyte *Polytrichum strictum* having the most positive scores (open canopy, absence of overstory layer); and with some tree species, namely *Picea mariana* and *Betula papyrifera* contributing to the closed-canopy side of the gradient. Trees were more frequently found when the landscape was composed of agricultural fields and at trenches having higher peat-EC and deeper secondary ditches. In contrast, open canopies were correlated with more decomposed peat (higher Von Post) and the amount and proximity of natural areas (peatland and open water) in the surroundings. The tendency of these peatlands over the decade considered was to develop a more closed canopy layer (arrows, Fig. 3a).

Despite the statistical significance of the full RDA model (adjusted $r^2 = 0.14$, $F = 4.6767$, $P < 0.001$), overall explanatory power was low making an examination of the unexplained proportion of variability pertinent. The two first axes of the residual variability also reflected light availability (Fig. 3c, d). A closed-open canopy gradient was still identifiable along PC1 of the RDA residuals. In fact, it included a slightly higher variability in the plant community than RDA1 (13 vs. 9 %). Tree species dominated the left side of the axis, associated with mosses that typically appear under dense canopies and tolerate shading (e.g., *Pleurozium schreberi*). As in RDA1, ericaceous species appeared on the right side and the six peatlands seemed to develop more closed canopies (arrows, Fig. 3c). An open-closed understory gradient remained unexplained by the environmental variables but also integrated a higher proportion of variability

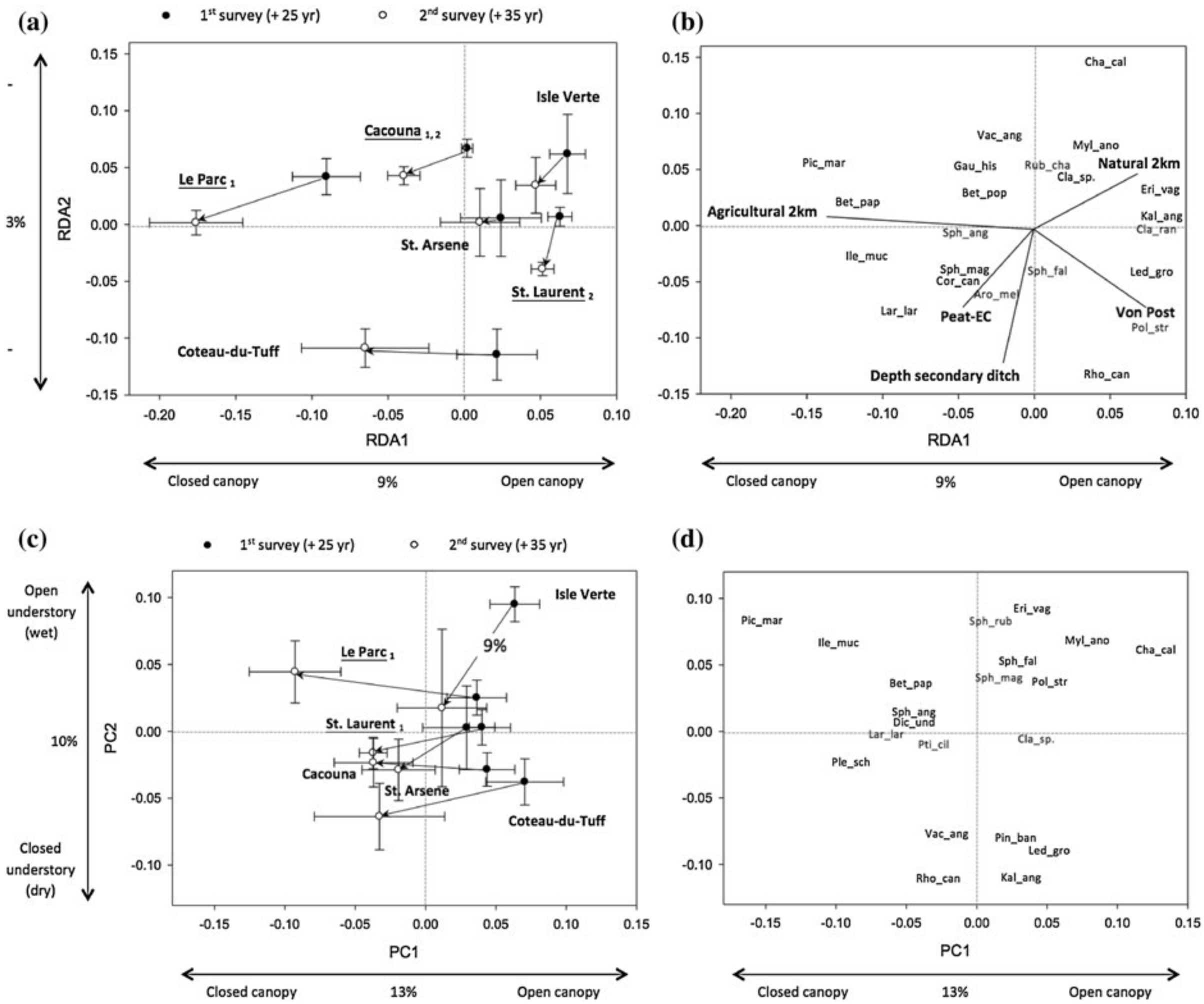


Fig. 3 **a** RDA site scores (Scaling = 1) for the six abandoned block-cut peatlands of the Bas-Saint-Laurent region **b** RDA species and environmental parameters scores (Scaling = 1), **c** Sites scores of the first and second axes of the residuals of the RDA model, **d** Species scores of the residuals of the RDA model. Plant species cover matrices were built from 110 trench-time surveys (55 trenches x two surveys, Table 1). To improve visual clarity of the diagrams, only the centroids (site scores means) of each peatland during each of the two surveys (*filled circles* = 1994–1997, *open circles* = 2005–2006), and the standard errors of the mean were drawn. Arrows were drawn to link the two sampled periods. *Underlined peatland names* indicate that the sites scores were significantly different between the two sampled periods according to Wilcoxon tests ($P < 0.05$). *Subscript number* nearby the peatland name indicates the axis whose site scores significantly differed. Species scores were scaled by multiplying by 1/7 and are represented by codes detailed in Table 2. For simplicity, only the 20 species with the highest scores are represented on each figure. The year of abandonment, whose effect on the vegetation was partialled out before implementing the RDA, explained only 6 % of the vegetation variability among trenches

than RDA1 (PC2, 10 %, Fig. 3c, d). Three ericaceous species forming tall, dense shrub thickets (*Rhododendron canadense*, *K. angustifolia* and *L. groenlandicum*) had the most negative scores (closed understory). The herb *Eriophorum vaginatum* and some bryophytes (*Mylia anomala* and some *Sphagnum* spp.), in association with shorter ericaceous shrub species such as *Chamaedaphne calyculata*, had the most positive scores (open understory). This gradient of variability could also be interpreted as a wet to dry gradient, since species dominating the open understories had an overall higher preference for wet soils (e.g., *Sphagnum* spp., *C. calyculata*) than those prevailing in the closed understory. The six peatlands remained stable along the axis from the first to the second survey (arrows, Wilcoxon tests, Fig. 3c).

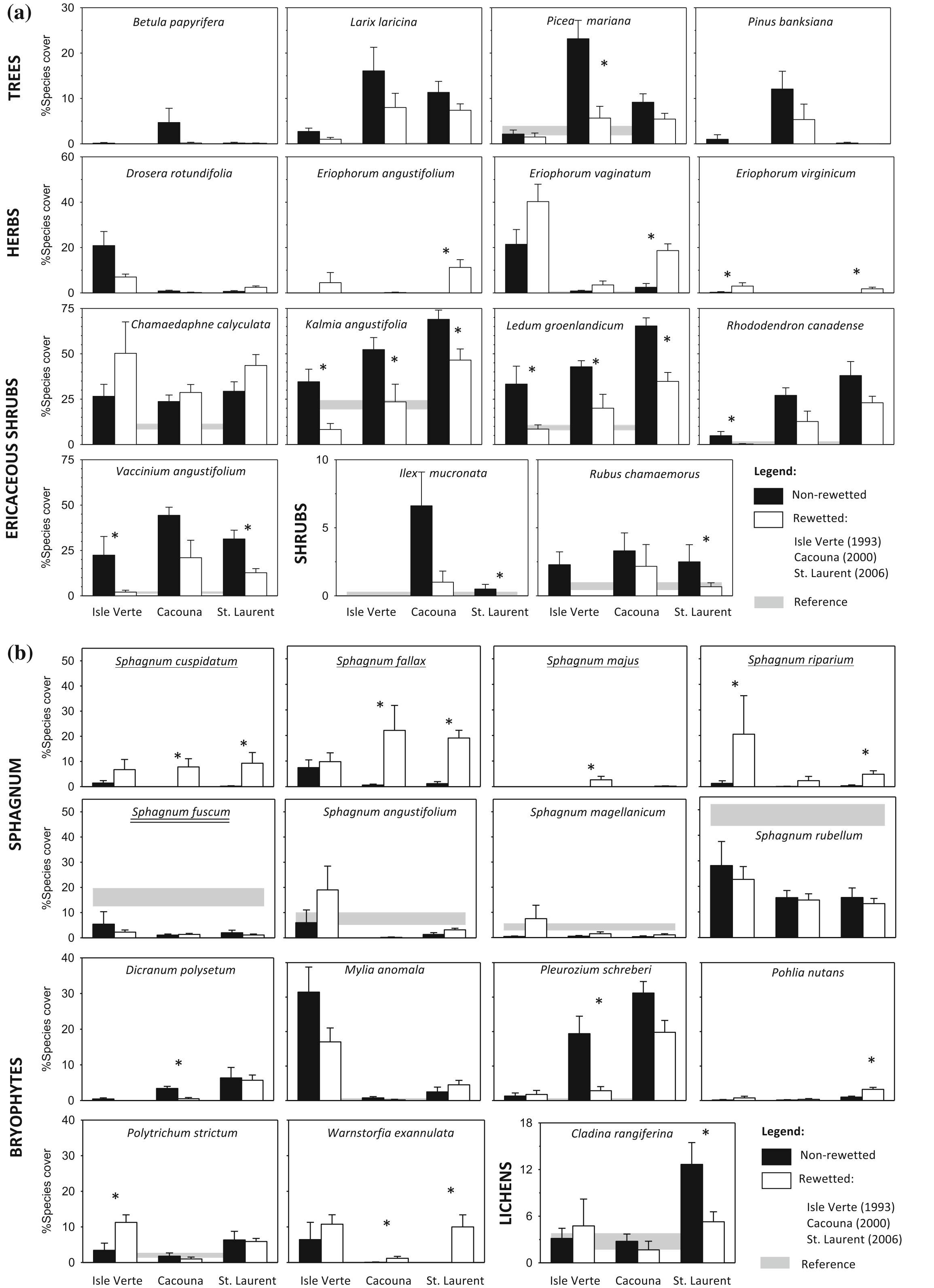
Table 2 Species codes for species presented in Fig. 3

Bryophytes	
Dic_und	*Dicranum undulatum*
Myl_ano	*Mylia anomala*
Pol_str	*Polytrichum strictum*
Ple_sch	*Pleurozium schreberi*
Pti_cil	*Ptilidium ciliare*
Ericaceous shrubs	
Cha_cal	*Chamaedaphne calyculata*
Gau_his	*Gaultheria hispidula*
Kal_ang	*Kalmia angustifolia*
Led_gro	*Ledum groenlandicum*
Rho_can	*Rhododendron canadense*
Vac_ang	*Vaccinium angustifolium*
Herbs	
Cor_can	*Cornus canadensis*
Eri_vag	*Eriophorum vaginatum*
Lichens	
Cla_sp.	*Cladonia species*
Cla_ran	*Cladina rangiferina*
Sphagna	
Sph_ang	*Sphagnum angustifolium*
Sph_fal	*Sphagnum fallax*
Sph_mag	*Sphagnum magellanicum*
Sph_rub	*Sphagnum rubellum s.l.*
Shrubs	
Aro_mel	*Aronia melanocarpa*
Ile_muc	*Ilex mucronata*
Rub_cha	*Rubus chamaemorus*
Trees	
Bet_pap	*Betula papyrifera*
Bet_pop	*Betula populifolia*
Lar_lar	*Larix laricina*
Pic_mar	*Picea mariana*
Pin_ban	*Pinus banksiana*

Effects of rewetting abandoned block-cut sites on established vegetation

Rewetting of abandoned block-cut trenches had a substantial impact on the cover of most vascular plant species (Fig. 4a). With the sole exception of *Picea mariana* at Cacouna, tree cover did not differ significantly between rewetted and non-rewetted sites in 2010; however, restoration seemed to have reversed the tendency towards more closed canopies observed within the sites subjected to spontaneous recolonization alone over the study decade. In fact, cover values of the most abundant tree species (*B. papyrifera*, *Larix laricina*, *Picea mariana* and *Pinus banksiana*) returned to levels similar to or below those recorded during the first vegetation survey in 1994, and approached those observed in the reference sites. The cover of two of the most abundant ericaceous shrubs (*Kalmia angustifolia* and *L. groenlandicum*) was significantly lower in the three rewetted peatlands compared to that recorded in non-rewetted trenches. *Rhododendron canadense* and *Vaccinium angustifolium* also had a significantly lower cover in the Isle Verte rewetted trenches than in the non-rewetted ones, and for the latter species, in Cacouna as well. Overall, cover of ericaceous species after rewetting was closer to that found in reference sites, with the remarkable exception of *C. calyculata*, a species that copes well with wet conditions and which was apparently favored by rewetting. The shrub species *Rubus chamaemorus* and *Ilex mucronata* also decreased to natural levels in Saint Laurent. The latter species had been increasing with greater canopy closure in sites subjected to spontaneous recolonization alone (Fig. 3d). In Saint Laurent, three species of the genus *Eriophorum* experienced a net increase, despite being rare in the reference sites (herbs, Fig. 4a).

Rewetting also had a significant effect on the cover of non-vascular species (Fig. 4b). Despite being almost absent in the reference sites, wetter habitat *Sphagnum* species from the Cuspidata section experienced a high overall increase in cover after rewetting. For example, cover of *S. fallax* was 36 and 17 times greater in rewetted than in non-rewetted trenches at Cacouna and Saint Laurent, repectively. Similarly, *S. riparium* appeared ~15 times more abundant in rewetted than in non-rewetted trenches at Isle Verte (Fig. 4b). Another species typical of depressions and pools species, *S. cuspidatum*, had 54 times greater cover in rewetted than in non-rewetted trenches of the Saint Laurent peatland. *S. majus*, frequent in depressions, appeared in the rewetted trenches of Cacouna in 2010, while it was not found in the non-rewetted trenches in any of the three surveys. In contrast, no significant increases were observed for *Sphagnum* species not associated with hollows and depressions. Indeed, the cover values of the typical hummock species, *S. fuscum,* the widespread *S. magellanicum*, as well as *S.*


(a)
TREES
HERBS
ERICACEOUS SHRUBS
SHRUBS
%Species cover
Betula papyrifera
Larix laricina
Picea mariana
Pinus banksiana
Drosera rotundifolia
Eriophorum angustifolium
Eriophorum vaginatum
Eriophorum virginicum
Chamaedaphne calyculata
Kalmia angustifolia
Ledum groenlandicum
Rhododendron canadense
Vaccinium angustifolium
Ilex mucronata
Rubus chamaemorus
Isle Verte
Cacouna
St. Laurent
Legend:
Non-rewetted
Rewetted:
Isle Verte (1993)
Cacouna (2000)
St. Laurent (2006)
Reference
(b)
SPHAGNUM
BRYOPHYTES
LICHENS
Sphagnum cuspidatum
Sphagnum fallax
Sphagnum majus
Sphagnum riparium
Sphagnum fuscum
Sphagnum angustifolium
Sphagnum magellanicum
Sphagnum rubellum
Dicranum polysetum
Mylia anomala
Pleurozium schreberi
Pohlia nutans
Polytrichum strictum
Warnstorfia exannulata
Cladina rangiferina

◀**Fig. 4** Cover of **a** vascular and **b** non-vascular species (i.e., mean number of counts in trenches, including those where the species was not present) in the rewetted and non-rewetted peatlands of the Bas-Saint-Laurent region in 2010. Only species with cover >1 % are shown. The numbers of non-rewetted trenches for Isle Verte (restoration in 1993), Saint Laurent (restoration in 2000) and Cacouna (restoration in 2006) were 7, 6 and 13. Rewetted trenches surveyed in 2010 were 4, 18 and 6 for the three peatlands, respectively. Asterisks indicate significant differences between rewetted and non-rewetted trenches after Mann–Whitney tests ($P < 0.05$) for the given peatland. Note that *Sphagnum* names singly underlined are wetter liking species from the Cuspidata section and the *S. fuscum* underlined twice is a species preferring drier habitats from the Acutifolia section, the other three species being topographically widespread along the hummock-hollow gradient. Note that the scale of the Y-axis is different for each vegetation type. The grey line represents mean cover in the seven nearby reference sites and its thickness ±1 SE of the mean

rubellum, largely dominant in block-cut sites, remained well under the values observed in nearby reference sites. However, other bryophytes such as *Pohlia nutans, Polytrichum strictum* and *Warnstorfia exannulata*, which were infrequent in reference sites, increased in cover after rewetting in some peatlands. In fact, only a few non-vascular species had a notably reduced cover in rewetted versus non-rewetted sites (e.g., the mosses *Dicranum polysetum* and *Pleurozium schreberi* at Cacouna, and the lichen *Cladina rangiferina* at Saint Laurent).

Discussion

Spontaneous recolonization alone is insufficient for the recovery of Sphagnum-dominated vegetation in abandoned block-cut sites

The vegetation communities in these six peatlands showed remarkable development for the time frame (10 yr.) considered in this study, which is very brief on the time scale of peatland succession. Some clear trends common to all these peatlands were identified. Peatlands were initially colonized by tall, dense ericaceous shrubs. Communities maintained predominantly ericaceous vegetation over time and hence were not on a trajectory toward the recovery of a *Sphagnum*-dominated system. In fact, only one species of *Sphagnum* (*S. rubellum*) had a mean cover >10 %, and rarely exceeded 20 %, while ericaceous species covered more than 50 % of the surface in 80 % of the trenches. Our analyses also revealed an increasing dominance of the tree stratum, a result in accordance with that found by Pellerin and Lavoie (2000, 2003), who reported the afforestation of undisturbed bogs and bog remnants surrounding industrial peatlands used for the production of horticultural peat in the Bas-Saint-Laurent region. They suggested that this afforestation phenomenon may have been driven by multiple factors, including drainage related to agriculture and peat extraction, fire events (especially promoting *Pinus banksiana*), and a dry climatic period in the region during the first part of the 20th century. In our study, the greater presence of trees at the sites surrounded by agriculture could thus be due to drainage activities associated with the production of land crops. Although slight, the correlation of closed canopies to the depth of former drainage ditches reinforced this finding.

Although the trajectories of the plant communities were informative, the percentages of variability explained by the environmental variables were low. In such an extensive study, environmental parameters, especially those related to peatland hydrology, were difficult to assess precisely and consequently have limited explanatory power. In addition, we think that the range of environmental variation within peat properties was too narrow to accurately explain changes in vegetation composition over only 10 years. With only 14 % of variability explained by the RDA, it is therefore not surprising that the first two axes of the residuals of the RDA explained a higher amount of variability than the first two axes of the RDA. Factors controlling the development of vegetation communities must be considered with caution, as our study mainly aimed to identify general revegetation patterns in order to contextualize restoration efforts, rather than to disentangle the drivers of spontaneous recolonization. Studies at finer spatial scales are more appropriate for the latter objective (e.g., microtopographic scale, Tuittila et al. 2000b; Pouliot et al. 2012; paleoecological analyses, Robert et al. 1999; Pellerin and Lavoie 2000, 2003).

Regardless of the drivers of vegetation recovery, it seems unlikely that peatlands in the Bas-Saint-Laurent region will progress naturally toward *Sphagnum*-dominated systems in the coming decades. The dominant tree and ericaceous species may inhibit future *Sphagnum* establishment. For example, *Picea mariana*, one of the species that experienced a higher increase in frequency and cover and played a key role in the ordinations (Fig. 3), is known to increase dryness by enhancing evapotranspiration (van Seters and Price 2001). The same impact has also 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). In short, the examination of spontaneous recolonization patterns revealed that successional trajectories were not oriented toward *Sphagnum*-dominated functional bogs and that intervention by rewetting is highly recommendable in the abandoned block-cut sites.

Rewetting changed spontaneous recolonization trajectory

Our results showed that rewetting of abandoned trenches could modify the undesired trajectory observed in abandoned block-cut peatlands. First, the spread of trees seemed to be controlled and even reversed locally, as in Cacouna peatland where *Picea mariana* cover experienced a dramatic four-fold decline to the levels observed in nearby reference sites. The mitigation of the trajectory toward more closed canopies, observed after rewetting, also was consistent with the decline of shade-tolerant species such as the moss *Pleurozium schreberi* and the shrub *Ilex mucronata* (both highly associated with trees in our ordinations). Declines were much more pronounced for ericaceous species forming taller and denser thickets (*Rhododendron canadense*, *Kalmia angustifolia* and *Ledum groenlandicum*), which were largely dominant in abandoned trenches before rewetting. A similar report of shrub decline following rewetting and an increase in water table level in abandoned cut-away peatlands was described by Tuittila et al. (2000a). In our case, water table increases of 15–32 cm were attained after rewetting, with presumably negative consequences for shrub growth.

Second, *Sphagnum* itself, which had remained marginal (cover <10 %) in the trenches left to spontaneous recolonization alone, started to show encouraging signs of development. The success of rewetting was especially evident with the great increase of *Sphagnum* species such as *S. fallax*, *S. riparium* and, to a lesser extent, *S. cuspidatum* and *S. majus*, all of which are typical of wet habitats (Rochefort 2001b). Even though the presence of the wet *Sphagnum* species from the Cuspidata section was marginal in reference sites, their recovery in rewetted sites may indicate successful hydrological restoration and, therefore, that rewetted sites are on track toward a desired successional trajectory. This, and the other discrepancies between rewetted and unmanaged sites suggest that strict comparisons of plant composition between treatment and reference sites must be made with caution. Pristine, undisturbed bogs do not occur in the study area and criteria to confirm success can not be based entirely on mimicking plant composition of those target ecosystems; rather, the return of ecosystem functionality should be the primary goal (objective-based restoration, sensu Dufour and Piégay 2009; intervention ecology, sensu Hobbs et al. 2011). Restoration will produce 'novel' plant communities that contain at least some species not found in the reference communities but that may be accepted as a valuable restoration outcome (Toth and van der Valk 2012). For example, the continued development of the wet *Sphagnum* species from the Cuspidata section might contribute to the return of the peat accumulation function and compensate for the lack of recovery of the hummock and widespread *Sphagnum* mosses. Recovery of hummock species may take longer, given that a minimum period of 10–30 yr. is necessary for a typical hummock-hollow-microtopography to develop in restored cutover bogs (Pouliot et al. 2011). This time lag may explain why *S. angustifolium, S. magellanicum*, *S. fuscum* and *S. rubellum* have not yet shown strong signs of recovery. Unfortunately, as the restoration projects were not replicated within time periods for each restored peatland, we were unable to assess the general effect of time elapsed since rewetting on the recovery and development of the plant communities. One might have expected, for example, that differences in species cover between rewetted and non-rewetted sites would have been higher at Isle Verte (17 years) than at Saint Laurent (10 years) and Cacouna (4 years), but that was not always the case; nevertheless, this fact does not exclude the possibility that there were site-specific responses to rewetting (e.g., increase in *Eriophorum* spp. at St. Laurent, increase in some non-*Sphagnum* bryophytes at certain sites).

Finally, it is worth mentioning that the positive response of other vascular and non-vascular species with wet preferences, such as the ericaceous shrub *C. calyculata,* the herb *Eriophorum* spp. and the mosses *Pohlia nutans*, *P. strictum* and *Warnstorfia* *exannulata*, and the decline of species more tolerant of dry conditions, such as the lichen *Cladina rangiferina*, collectively support the effectiveness of rewetting as a restoration strategy.

Active plant reintroductions and more complex hydrological restoration techniques, such as constructing shallow retention basins, berms, terracing or polders, and even irrigation, might be considered to enhance the trends initiated by rewetting and to restore a more diverse bog vegetation (Robroek et al. 2009; Graf et al. 2012; González et al. 2013). We conclude, however, from our study, that an improvement of hydrological conditions by a relatively simple operation such as the blockage of former primary drainage ditches can effectively counteract undesired trajectories and promote the recovery of typical bog vegetation. With minimal economic cost and relatively fast response after implementation, such restoration measures could notably improve the ecological value of highly altered ecosystems such as block-cut cutover bogs that are initially recolonized by vascular plants. Our results suggest that this approach should certainly be prioritized over spontaneous recolonization alone.

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