

Fen restoration: defining a reference ecosystem using paleoecological stratigraphy and present-day inventories

Vicky Bérubé, Line Rochefort, and Claude Lavoie

Abstract: Choosing past and present-day indicators could strengthen the reference ecosystem used for ecological restoration projects. Based on the paleoecological analysis of four peat cores and the characterization of 13 contemporary natural sites, the reference ecosystem for minerotrophic peatlands in southeastern Canada is composed of two broad categories of plant assemblages described as tall-sedge and *Sphagnum–Thuja*/brown moss. In paleoecological peat profiles, tall-sedge communities were found at the transition between aquatic and terrestrial, and were associated with high graminoid production, riverine peatlands, and elevated water table in the present-day analyses. *Sphagnum–Thuja* communities resemble the present-day vegetation found in natural basin type peatlands. Except for *Sphagnum warnstorfii* Russ., these communities, with high taxonomical diversity, contain more generalist species from boreal peatland vegetation, such as *Rhododendron groenlandicum* (Oeder) Kron & Judd, *Thuja occidentalis* L., *Linnaea borealis* L., and *Maianthemum trifolium* L. They grow in dryer or shady habitats such as hummocks or forest understory. The importance of brown mosses was revealed by paleoecological analysis. Overall, findings from both approaches are complementary: paleoecological stratigraphy informs us about past ecosystem dynamics, while present-day inventories allow us to define current plant communities and their major environmental characteristics. The range of variability of vegetation and environmental variables found in these studies are essential tools for fen restoration projects.

Key words: rehabilitation, minerotrophic peatland, plant assemblages, plant dynamics, indicator value index (IndVal).

Résumé : Lors d'un projet de restauration écologique, la description de l'écosystème de référence est renforcée par l'utilisation d'indicateurs combinant les études temporelles et spatiales. Se basant sur une étude paléoécologique et la caractérisation de treize sites naturels, la référence pour une tourbière minérotrophe modérément riche située dans le sud-est du Canada se compose de deux types d'assemblages d'espèces végétales : l'assemblage des Grandes-cypéracées et l'assemblage général de *Sphagum–Thuja*/mousse brune. Dans l'étude paléoécologique, la communauté des Grande-cypéracées est observée à la transition entre les écosystèmes de marais et de tourbières. Dans l'étude des sites naturels, cette communauté est associée à une production de biomasse élevée, un niveau d'eau élevé et aux fens de type riparien. L'assemblage *Sphagum–Thuja* est semblable à ceux inventoriés dans les fens de type basin. En faisant l'exception du *Sphagnum warnstorfii* Russ., cet assemblage, très diversifié, inclut surtout des espèces généralistes provenant des tourbières boréales telles le *Rhododendron groenlandicum* (Oeder) Kron & Judd, le *Thuja occidentalis* L., le *Linnaea borealis* L. et le *Maianthemum trifolium* L. L'importance des mousses brunes est révélée dans l'analyse paléoécologique. En somme, les deux approches sont complémentaires : la paléoécologie nous informe sur la dynamique de l'écosystème tandis que les inventaires des sites naturels nous a permis de définir les assemblages et leurs associations aux conditions environnementales. Les étendues de variabilité définies dans ce travail sont un outil à la décision essentiel dans un projet de restauration écologique de fen.

Mots-clés : réhabilitation, tourbière minérotrophe, assemblage de végétaux, dynamique des communautés, index valeur indicatrice (IndVal).

Introduction

Reference ecosystems act as a standard of comparison and evaluation for any restoration project (SERI 2004; Clewell and Aronson 2013; Shackelford et al. 2013). Selecting references among other similar ecosystems located in the same region is a usual starting point for establishing standards (White and Walker 1997; SERI 2004; Hallett et al. 2013). However, the absence or limited

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knowledge of pre-disturbance states, ecosystem dynamics, and cultural services may be responsible for an inappropriate reference selection (Aronson et al. 1995; Birks 1996; Higgs 1997; Jackson and Hobbs 2009; Balaguer et al. 2014). An in-depth knowledge of ecosystem variability with temporal and spatial perspectives is thus recommended for making better choices. Moreover, multiple sources of information improve the quality and accuracy of the data that can be used to build a reliable picture of a reference ecosystem (White and Walker 1997; SERI 2004), and may help to better define realistic restoration objectives (Ehrenfeld 2000; SERI 2004; Hallett et al. 2013; Shackelford et al. 2013).

Data useful for defining a reference ecosystem can be collected using historical records, by studying similar undisturbed ecosystems, or both (Birks 1996; White and Walker 1997; Balaguer et al. 2014). Historical tools include paleoecological studies, past plant or faunal surveys, and aerial and in-situ photographs. One of the advantages of using historical data are that they provide insights into ecosystem dynamics over time (Jackson and Hobbs 2009; Balaguer et al. 2014). They also help to choose the developmental stage at which the ecosystem should be restored. Paleoecological studies are widely used in peatlands to assess past vegetation patterns and succession dynamics (e.g., Glaser and Janssens 1986; Kuhry et al. 1993; Bauer et al. 2003) or climate change (e.g., Halsey et al. 1998; Yu 2006). They proved to be useful to provide a better understanding of the ecosystem functioning over the long term, which can help to evaluate the time frame over which restoration objectives could reasonably be achieved (Lavoie et al. 2001; Blundell and Holden 2015). The response of ecosystems to past disturbance events can also inspire restoration engineers by providing clues on natural recovery processes (Benscoter and Vitt 2008). On the other hand, present-day studies on the existing composition and distribution of species are essential to complete the reference picture. They represent a timescale snapshot but can nevertheless give a precise overview of the spatial distribution of species along a wide range of biotic and abiotic conditions.

In North America, most peatlands that have actively been restored are cutover bogs (ombrotrophic peatlands; Poulin et al. 2013; González et al. 2014). The peat was extracted for horticultural purposes. The most widely used extraction method (vacuum) consists of draining the peatland, removing the living vegetation, and harrowing and vacuuming a thin layer of dried peat. Peat extraction activities cease when peat quality does not correspond to industrial standards (too decomposed, too woody, etc.) and, until recently, at least 50 cm of *Sphagnum* peat was left on-site to ensure that enough material is left for restoration. However, in some cases, the peat industry produces specific growing substrates with the deeper, older peat layers of peatlands. In such cases, ancient minerotrophic peat layers composed of the remains of sedges and brown moss become exposed (Graf et al. 2008). Because the chemical properties of the water and peat then become similar to fen habitats (Wind-Mulder and Vitt 2000), the rehabilitation of the peatland to a minerotrophic developmental stage could be considered if ecological restoration is planned. The challenge under those conditions is to define a reference ecosystem from a series of developmental stages that the ecosystem has experienced in the past, and could experience in the future.

The goal of this study was to build a reference ecosystem in the context of fen restoration in southeastern Canada, using paleoecological studies and current regional plant surveys. Specifically, we wanted (i) to describe the historical trajectory of a minerotrophic peatland via its developmental states and its associated plant assemblages; (ii) to assess whether modern plant assemblages are representative of the past; (iii) to evaluate the importance of bryophytes for fen development; (iv) to study natural disturbance regimes and the resilience process, and finally (v) to identify the state to which the disturbed peatland has regressed after the cessation of peat harvesting activities. If the present plant assemblage is representative of a past assemblage, the modern plant surveys should complete the reference by determining the variability in species composition and environmental condition of moderately rich fens. Our overall intent with this study was to demonstrate the usefulness of both approaches to establish precise restoration objectives.

Materials and methods

Study sites

All of the peatlands investigated in this study were located near the south shore of the St. Lawrence River, in the Bas-Saint-Laurent region, Quebec, Canada (Fig. 1). The area was covered by a glacier until 14 000 years BP, and then by the Goldthwait Sea until 10 000 years BP (Locat 1977), leaving clay, sand, and gravel as surficial marine deposits over the St. Lawrence River Lowlands (Fulton 1995). The paleoecological study was conducted in the Bic-Saint-Fabien (BSF) peatland (48°19'22"N, 68°49'52"W). It is part of a peatland complex that developed in a narrow valley (Fig. 2). BSF, which is now included in the Bic National Park, is bordered by steep calcareous hills (340 m a.s.l.) to the north and by agricultural fields to the south. A large pond (about 40 ha) was located in the central part of the peatland but was drained in 1954. The section of the peatland east of the pond was formerly a Sphagnum bog (Scoggan 1942) with a well-defined lagg on its margins. This eastern section had largely been used for peat extraction. The section west of the pond is now a mosaic of peat extraction and few natural (no major disturbance) sites. Peat extraction began in 1946 and ended in the 1990s. The 15 ha area that was targeted for a restoration project has a peat substrate with the following minerotrophic characteristics, as assessed in summer 2011 (L. Rochefort, unpublished data; n = 111): the water pH was





 6.0 ± 0.4 (mean \pm SD) and the electroconductivity was $229 \pm 141 \mu$ S·cm⁻¹. The central section was spontaneously revegetated, mostly with *Typha latifolia*, *Scirpus cyperinus*, *S. atrocinctus*, and *Salix* species, essentially along former drainage ditches. Bare peat covered the last four peat fields of this eastern section.

The northern and eastern sections of BSF bordering the extraction zone still support a moderately rich fen plant community (sensu Chee and Vitt 1989 and Locky and Bayley 2005) dominated by *Thuja occidentalis* (Gauthier and Grandtner 1975). In these sections, the water pH was 6.5 ± 0.8 (mean \pm SD) and the electroconductivity 237 \pm 136 µS·cm⁻¹ (L. Rochefort, unpublished data; n = 41).

Paleoecological analyses

For this study, only the eastern section of the BSF peatland complex has been considered, excluding the former lakebed. Efforts for an ecological restoration project were concentrated in this section (Fig. 2). The condition of the disturbed sector was heterogeneous if we consider the time of abandonment, elevation, and spontaneous vegetation cover. To get a good representation of the site, we divided the area into three more homogeneous subsectors for sampling. One peat core was extracted from each of the three subsectors (R for restored section: R1, R2, and R3). The peat cores were respectively about 700, 950, and 1200 m from the location of the drained pond (Fig. 2). A fourth core (N for natural section) was sampled at a distance of 1300 m, but in the part of the peatland with no peat extraction.

A side-wall peat corer (Jowsey 1966) was used to extract the peat cores from the soil surface to the top of the surficial marine deposit. Each core was cut every 5 cm into subsamples, and each subsample was washed through a series of sieves (2, 1, and 0.5 mm meshes) and then dried. Fossil pieces were sorted and identified to the finest taxonomical level (family, genus, or species when possible). Nomenclature followed the Integrated Taxonomic Information System (2015) for vascular plants and animals, Faubert (2007) for bryophytes, and LoBuglio (1999) for fungi. Pieces were counted under a low power (50x) microscope. When the fossil pieces were too numerous, a subsample of 0.5 g of peat was extracted, the pieces counted, and the total number of pieces was estimated using the total dry weight of the sample. All the results were adjusted to a volume 100 cm³ of peat. Macrofossil zones were defined visually according to changes in the relative abundance of plant remains. Samples at the limits of the zones and at the surface of the peat (for R1, R2, and R3) were dated using accelerator mass spectrometry (AMS) radiocarbon dating. Samples were prepared by the Radiochronology lab at Université Laval, Quebec, Canada, and analyzed by Keck Carbon Cycle AMS Facility (University of California - Irvine, California, USA) Radiocarbon dates were calibrated with CALIB REV 7.0.1 software (Stuiver et al. 2005).

Natural site surveys

A total of 13 fens were found in the vicinity of the BSF peatland (from a 5–30 km distance), with the help of a local bryologist and by looking at satellite maps (Fig. 1).

Fig. 2. Aerial photograph of the Bic-Saint-Fabien (BSF) peatland complex and of the surrounding landscape. The peatland developed in a valley surrounded by a mountain in the north (dark green), part of Bic National Park, and agricultural lands in the south (pale yellow). An ancient lake located in the central part of the peatland, as seen on an aerial photograph taken in 1925, is overlaid in blue. The lake was drained in 1954 and is now covered, in the sections that have not been used for peat extraction, by dense shrubs and wet meadows. The dotted white line delimits the 15 ha area claimed for a restoration project. The peat core locations (R1, R2, R3, N) are also indicated. Source: Orthophoto was used with the permission of the ©Gouvernement du Québec (2001).



Natural peatlands Disturb

Disturbed peatlands

Agricultural lands

Water

Forest

The final selection was based on the presence of indicator plant species of moderately rich fens and water pH above 5.5 (Chee and Vitt 1989). A survey of modern vegetation communities and associated environmental conditions was made during summer 2012. Six of the 13 peatlands were subdivided into two homogeneous units on the basis of their tree cover (with or without) or because they represent different sectors within a peatland complex. The number of quadrats depended on the area of the unit. Between 10 and 12 circular quadrats of 70 cm diameter were positioned equidistant along a linear transect passing throughout the longest axis of the fen (unit), for a total of 200 quadrats. The cover occupied by each species present within the quadrats was visually estimated with the accuracy of ±5% (for more details, see Rochefort et al. 2013). Environmental variables were measured for each peatland unit. The sampling was located in the central part of the peatland unit. Species

richness is defined as the number of species in each quadrat, and diversity was also calculated for each quadrat using the Shannon diversity index (Whittaker 1972). All of the variables are described in Table 1, along with analytical methods used.

Data processing and statistical analyses

The cluster method, specifically *K*-means partitioning, and the indicator value index (IndVal) method (Borcard et al. 2011) were used to define modern plant communities and to identify their associated indicator species. *K*-means are based on species similarity found in each quadrat. To achieve this goal, a truncated species dataset was used for all statistical analyses to avoid biases potentially caused by rare species (Legendre and Gallagher 2001; Borcard et al. 2011); only species with a frequency (occurrence among all the quadrats from all peatlands) and (or) a mean cover (among the quadrats with the species)

Group	Variables	Code	Unit	Range	Notes
Descriptive	Peatland classification*	type	factor	Riverine, basin	Estimated in the field (NWWG 1997)
	Distance to the St. Lawrence	dist_river	km	1 to 21	Estimation based on satellite photographs
	River*				(Google earth V7.1.5.1557)
	Disturbance*	disturb	factor	None, limited	Estimated in the field
Physical	Water level	WT	cm	–35 to 17	Used a ruler within a dug hole
	Peat depth*	depth	cm	42 to 612	Metal rod inserted in the central part of the peatland (unit)
	Bulk density*	BD	g∙mL ^{−1}	0.13 to 0.30	Peat samples dried and weighed in the laboratory
	Organic mater	OM	%	78.6 to 91.9	Dry-ash method (JAOAC 1967)
Water chemistry	pH	рН	_	5.8 to 8.1	Measured in the laboratory (Fisher Scientific Accumet AB150)
	Electroconductivity*	EC	µS·cm ^{−1}	94 to 275	Measured in the laboratory (Orion Model 122) and corrected according to Sjörs (1950)
	Р	Р	mg·L ^{−1}	0 to 1.6	ICP [†]
	Ca*	Ca	mg·L ^{−1}	7.16 to 45.75	ICP
	Mg*	Mg	mg∙L ⁻¹	0.75 to 7.01	ICP
	Fe	Fe	mg·L ^{−1}	0 to 0.26	ICP
	K*	Κ	mg·L ^{−1}	0.21 to 7.90	ICP
	Na*	Na	mg∙L ⁻¹	1.82 to 12.22	ICP
	NH ₄	NH4	mg∙L ⁻¹	0.05 to 5.58	FIA [‡]
	NO ₃ *	NO3	mg∙L ⁻¹	0.01 to 0.14	FIA
	SO ₄ *	SO4	mg∙L ⁻¹	1.13 to 21.64	FIA
Vegetation	Shannon diversity index*	shannon	_	0 to 2.53	$H' = \text{sum}[(p_i) \times \log_2(p_i)]$ calculated with all species per quadrat
	Richness*	rich	_	4 to 22	Number of species per quadrat
	Biomass (graminoid)*	b_gram	g·m ^{−2}	2.92 to 296.50	All living vegetation cut from two
	Biomass (forbs)*	b_forb	g·m ^{−2}	2.92 to 63.71	50 cm × 50 cm quadrats randomly placed
	Biomass (shrubs)*	b_shrub	g·m ^{−2}	0 to 84.50	in a representative homogenous section, dried, and weighed
	General tree cover*	cover	factor	Variable, open	Estimated in the field for each quadrat

Table 1. Description of 23 environmental variables, code names, and units measured in each of the fens (units) surveyed in the Bas-Saint-Laurent region in 2012.

Note: All of the measurements were conducted at the end of July 2012, except for water sampling in Plourde and Aqueduc peatlands, which were conducted in mid-July 2009. Water chemistry samples were analyzed at Laval University. An asterisk (*) indicates the variables kept for the RDA model after forward selection.

[†]ICP, inductively coupled plasma spectroscopy (Optima 4300 DV; Perkin Elmer).

[‡]FIA, flow injection analysis (Quikchem 4000, Lâchât Instrument Division, Milwaukee, Wisconson, USA).

>5% were kept. Hellinger's transformation was conducted to take into account the importance of double zeros and common species (Legendre and Gallagher 2001).

The Calinski-Harabasz criterion (Milligan 1996) was used to determine the adequate number of clusters (plant assemblages). To facilitate the categorization of assemblages, indicator species in each group were identified with the indicator value index (IndVal) developed by Dufrêne and Legendre (1997). This index computes the product of specificity (abundance of a species in all the quadrats of a cluster) and fidelity (presence of a species in a majority of quadrats in a cluster) for every species in each cluster previously delineated with K-means partitioning. IndVal values range from 0 to 1; a value close to 1 for a particular species indicates that the species is present exclusively in this cluster and has a high occurrence. Only species with IndVal values > 0.25, and an associated *P* < 0.001, were used to identify plant communities.

A redundancy analysis (RDA) was performed to understand the influence of environmental variables on plant communities. A forward selection was applied to reduce type I error and select the significant environmental variables. Cumulative r^2 adjusted from this selection must be lower than the r^2 adjusted from the RDA model previously run with all the variables to respect the two stopping criteria (Blanchet et al. 2008). The significant environmental variables issued from the forward selection were used to perform a second RDA and improve model variation. To view the position of the K-means clusters, equiprobability ellipses were created, including 95% of the sites from the same plant community. Finally, the RDA model was submitted to a permutation test with 9999 randomized runs to assess its significance (Legendre and Legendre 2012). All statistical analyses were conducted using R software version 3.0 (R Development Core Team 2016), with the function RDA, Ordistep, and CascadeKM from the vegan package (Oksanen et al. 2011),



Fig. 3. Macrofossil diagrams (selected taxa) of the Bic-Saint-Fabien BSF peatland. (*a*) R1, (*b*) R2, (*c*) R3, and (*d*) N. The broken lines mark the different vegetation zones.

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Fig. 3 (continued).



and IndVal from the labdsv (Roberts 2013) and ellipse package (Murdoch and Chow 2007).

Results

Paleoecological analyses

Four major vegetation zones were identified in N and R3, while only two were observed in R1 and R2. Limnic deposit known as gyttja or coprogenous earth (Groupe de travail sur la classification des sols 2002; Meier-Uhlherr et al. 2015) started to accumulate over a sand and clay marine deposit between 8037 years BP at R1 and 7090 years BP at N (Fig. 3; Table 2; Supplementary data, Fig. S1¹). The closer a peat core was to the pond of BSF peatland, the later peat accumulation was initiated. Rates of peat accumulation for R3 and N varied between 0.31 to 1.12 mm per year, depending on the core sampling location and vegetation assemblage. Peat composed of brown mosses (zones II

and IV) accumulated faster than peat composed only of wood remains (zone III).

At least three major fire events occurred. The peatland burned about 4870 years BP and 2700 years BP at the R3 location. The first fire coincided with the initiation of peat accumulation at this location, and the second with the end of zone II and the beginning of zone III. Around 1930, a fire burned part of the peatland (Scoggan 1942) and left charcoal pieces near the surface of core N. High abundance of *Campylium stellatum* and *Scorpidium cossonii* remains was noticed after this fire. Macrofossils of *Thuja occidentalis* also appeared after the 1930 fire.

The four peat cores followed a similar trajectory concerning the evolution of vegetation assemblages (Fig. 3, and Supplementary data, Fig. S1). Consequently, descriptions of each homogeneous zone identified through time are grouped together to avoid repetition.

¹Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjb-2016-0281.





Table 2. Radiocarbon dates from the four peat cores extracted at the Bic-Saint-Fabien (BSF) peatland.

Core site and		Age	1-sigma range	Calibrated age	1-sigma range	Calibrated	
depth (cm)	Laboratory No.	(¹⁴ C year BP)	(cal. year BP)	(cal. year BP)	(cal. year)	age	Material dated
R1, 2–4	ULA-1627/UCIAMS-76677	3015±15	3175-3221	3198	1272–1226 BC	1249 BC	Moss fragments
R1, 18–20	ULA-1617/UCIAMS-76675	3300±15	3492-3533	3513	1584–1543 BC	1564 BC	Moss fragments
R1, 35–40	ULA-1616/UCIAMS-76674	3360±15	3575-3614	3595	1665–1627 BC	1646 BC	Moss fragments
R1, 155–160	ULA-1626/UCIAMS-76676	7235±20	8001-8052	8027	6103–6052 BC	6078 BC	Wood fragments
R2, 2–4	ULA-1615/UCIAMS-76673	2425±15	2376-2465	2421	516-427 BC	472 BC	Moss fragments
R2, 16–18	ULA-1614/UCIAMS-76672	2660±15	2754-2769	2762	820-805 BC	813 BC	Moss fragments
R2, 165–170	ULA-1582/UCIAMS-76658	7260±20	8019-8055	8037	6106-6070 BC	6088 BC	Wood fragments
R3, 2–4	ULA-1613/UCIAMS-76671	820±15	702–735	719	1215–1248 AD	1232 AD	Moss fragments
R3, 75–80	ULA-1581/UCIAMS-76657	2460±15	2635-2694	2665	754–686 BC	720 BC	Wood fragments
R3, 185–190	ULA-1584/UCIAMS-76660	3955±20	4412-4431	4422	2489-2461 BC	2475 BC	Moss fragments
R3, 235–240	ULA-1564/UCIAMS-75742	4340±20	4854-4886	4870	2937-2905 BC	2921 BC	Moss fragments
R3, 320–325	ULA-1583/UCIAMS-76659	5915±20	6716-6752	6734	4803–4767 BC	4785 BC	Gyttja sediments
N, 105–110	ULA-1567/UCIAMS-75745	1300±15	1256–1281	1269	669–674 AD	672 AD	Moss fragments
N, 195–200	ULA-1566/UCIAMS-75744	3815±15	4158-4205	4182	2256-2209 BC	2233 BC	Moss fragments
N, 275–280	ULA-1565/UCIAMS-75743	4370±15	4927-4960	4944	3011–2978 BC	2995 BC	Moss fragments
N, 335–340	ULA-1563/UCIAMS-75741	4815±20	5488-5505	5497	3556-3539 BC	3548 BC	Wood fragments
N, 445–450	ULA-1562/UCIAMS-75740	6205±20	7067–7112	7090	5163–5118 BC	5141 BC	Wood fragments

Zone I (R1, R2, R3, N)

Gyttja sediments attested to the terrestrialization (infilling) origin of the peatland (Łachacz et al. 2009). The jelly-like sediments included plant species usually found in a shallow water habitat, such as *Najas flexilis*, *Nymphaea* spp., *Potamogeton* spp., *Sparganium* spp., and the bryozoan *Cristatella mucedo*. An assemblage composed of emergent species characterized the end of this zone. Marsh species (*Bidens cernua*, *Dulichium arundinaceum*, and *Sagittaria latifolia*) were sporadically found. The abundance of *Carex* cf. *diandra*, *Carex rostrata*, and *Schoenoplectus* s.l. *acutus* suggested a transition from a shallow lake ecosystem to a fen.

Zone II (R1, R2, R3, N)

Bryophytes were the main components of zone II. High abundance of *Paludella squarrosa*, *Calliergon* spp., and other brown moss fragments from Amblystegiaceae and Calliergonaceae families were recovered. The peat cores closer to the ancient pond (R1 and R2) also included *Sphagnum* stems from Acutifolia section species. At the beginning of zone II, the abundance of remains of matforming species (*Menyanthes trifoliata*, *Comarum palustre*, *Bidens cernua*) decreased. Cyperaceae species such as *Carex diandra*, *C. rostrata*, and *Rhynchospora alba*, along with other unidentified *Carex* species with planoconvex and trigonous shaped seeds, were well-represented for the entire zone.

An abrupt change in plant assemblages was detected in this moss-rich zone of R3, and was characterized by (*i*) a decrease in the number of *Calliergon* sp., *Ptychostomum* s.l. *pseudotriquetrum*, and *Drepanocladus* sp. s.l. remains, followed by (*ii*) the disappearance of *Paludella squarrosa*, and then by (*iii*) the establishment of other brown moss species (Amblystegiaceae spp.) dominated by *Campylium stellatum* and *Pseudocalliergon* trifarium.

Zone III (R3, N)

A major change in the vegetation composition of the peatland occurred about 2665 years BP at R3 and 4182 years BP at N, when bryophytes suddenly disappeared. The highly decomposed peat was mainly composed of small woody debris and no seeds or discernable plant parts were noticed, except for sclerotia of *Cenococcum geophilum*.

Zone IV (R3, N)

A rapid increase in the abundance of bryophytes characterizes the beginning of zone IV. *Sphagnum* spp. were especially abundant at R3, which was also the case for *Paludella squarrosa* at the upper end of the profile. N was dominated by brown mosses (*Campylium stellatum*, *Calliergon giganteum*, and *Straminergon* cf. *stramineum*). The vascular plant assemblages included Rhynchospora alba, Trichophorum alpinum, Eleocharis cf. tenuis, Triglochin maritima and Andromeda polifolia var. latifolia.

Present-day fen surveys

The 13 sampled fens (19 peatland units) had a peat thickness of 345 ± 169 cm (mean \pm SD), water table depth of $10 \pm$ 13 cm below the soil surface, pH of 6.7 ± 0.6 , corrected electroconductivity of 159 ± 53 µS·cm⁻¹, and Ca concentration of 18.1 ± 11.3 mg·L⁻¹. Based on The Canadian Wetland System Classification (NWWG 1997), hydrological regime (terrigenous or littogenous), and topography, there were two main types of fens: basin (n = 8 peatlands or units) and riverine (n = 11). The basin fens were richer in species (17 versus 11), had a deeper water table depth (18 versus 5 cm), a lower pH (6.4 versus 7.0), and a lower electroconductivity (143 versus 171 µS·m⁻¹) than the riverine fens. Levels of elements in the water were also 35% lower (on average) in the basin than in the riverine fens, except for the levels of P and Na, which were higher in the basin fens. Basin fens also occupied a smaller area $(3 ha \pm 3 [SD] versus 5 \pm 4 [SD])$ than the riverine fens.

Plant species found in the quadrats (n = 200) surveyed in 2012 were grouped into two vegetation communities (Fig. 4; the complete list of recorded species is available in the Appendix, Table A1), according to the K-means analysis with the highest Calinsky-Harabasz criterion. RDA also divided plant quadrats into two distinct groups (Fig. 5). The first group, named tall-sedge community, was the most widely represented, with 126 quadrats out of 200. Campylium stellatum, Carex lasiocarpa, and C. aquatilis were the indicator species of this group, as revealed by the IndVal analysis (Fig. 4). Other associated species were Myrica gale, Andromeda polifolia var. latifolia, Schoenoplectus acutus var. acutus, and Scorpidium cossonii. These plants were mainly found in sites with a water table close to the surface and open habitats. The high production of graminoid biomass (>120 g·m⁻²), which characterized this group, was positively correlated with electroconductivity, Mg, Ca, and distance to the St. Lawrence River, but negatively with SO₄ concentration, bulk density, and the Shannon diversity index.

The second group, named *Sphagnum–Thuja* community, pooled the other 74 quadrats. *Sphagnum warnstorfii* had the highest species indicator value. Other indicator species were mainly woody species (*Linnaea borealis*, *Rhododendron groenlandicum*, *Thuja occidentalis*, and *Vaccinium oxycoccus*) or forbs (*Maianthemum trifolium* and *Rubus pubescens*). These species usually grew in drier microhabitats like hummocks. *Carex leptalea* and *C. disperma*, also indicator species, were usually associated with mossy and shady forests.

Discussion

We used paleoecological tools and modern (presentday) plant surveys to gain knowledge on plant assemblages occurring in moderately rich fens of St. Lawrence Lowlands. The presence in the gyttja sediments of species thriving in ponds and completing most of their life cycle submerged, such as *Cristatella mucedo* and *Najas flexilis* (Ricciardi and Reiswig 1994; Wingfield et al. 2005) **Fig. 4.** The 40 most frequent species found in fens of the Bas-Saint-Laurent region, classified by life form and grouped into two communities obtained by *K*-means partitioning: (*a*) tall-sedge and (*b*) *Sphagnum-Thuja* communities. Frequency (bar chart) represents, in percentage, the occurrence of each species in all quadrats. Abundance (dots), also in percentage, is the average cover (\pm SD) per quadrat when a species is present. Significant indicator species obtained with the IndVal method are in bold. We retained species with an IndVal > 0.25 and *P* < 0.001 of each community; (***, *P* < 0.001; **, *P* < 0.01; *, *P* < 0.05). The full name of species, coded here by the first three letters for the genus and species, are available in the Appendix Table A1.



b Sphagnum-Thuja community



Fig. 5. Redundancy analysis (RDA) triplot performed with 17 significant environmental variables. RDA explained 33.1% of the total variation ($r^2 = 0.36$, F = 6.348, P < 0.001). Open circles represent centroids of the ellipses and include 95% of the quadrats from the two plant communities obtained by *K*-means partitioning. Only the 16 species with the highest scores (most significant) are shown for clarity. Codes name for species are available in the Appendix Table A1, and for the environmental variables in Table 1.





suggests a limnogenous origin for the Bic-Saint-Fabien peatland. Peatland development followed a successional pathway from a shallow water body to a bryophytedominated habitat. This hydroseral succession is a common form of autogenic development (Kuhry et al. 1993; Charman 2002). In short, paleoecological analyses revealed the existence of three distinct plant assemblages: (*i*) an emergent plant assemblage in the first phase of the peatland history (dominated by *Schoenoplectus acutus* or *S. tabernaemontani* and *Menyanthes trifoliata*); (*ii*) a tallsedge assemblage (dominated by *Carex rostrata* and *Carex diandra*); and (*iii*) a brown moss assemblage with small herbaceous plants, including *Paludella squarrosa*, various species of Amblystegiaceae and Calliergonaceae, *Rhynchospora alba*, and *Trichophorum alpinum*.

Modern plant surveys showed the existence of two distinct plant communities dominated by (*i*) tall sedges or (*ii*) Sphagnum species with Thuja occidentalis. The first community was associated with Carex aquatilis, Carex lasiocarpa, and Campylium stellatum, all species performing better in a high water table and with a high pH (Gignac 1992; Gignac et al. 2004). The analogs to the tallsedge community were found in paleoecological assemblages, especially in zone II. The second community was

Axe II (6.6 %)

strongly associated with *Sphagnum warnstorfii* along with generalist wetland boreal species found in dryer peatland microhabitats (Kenkel 1987; Locky and Bayley 2005).

Relevance of paleoecological analyses

Paleoecological studies are usually used to assess plant succession through the development of the peatland and to identify processes driving this succession. Here, the results were used in a restoration perspective. First, radiocarbon dates of surface peat may provide indications on the amount of time it was necessary to form the peat deposit that was extracted. The 50 years of peat harvesting activities resulted, at R1 and R2, in a loss of about 2500 to 3200 years of peat accumulation. At R3, 10 years of peat harvesting resulted in a loss of about 800 years of peat. At the time peat harvesting stopped, the BSF site at the location of the R1 and R2 cores regressed, from a peat stratigraphy point of view, from a Sphagnum bog to a poor fen. The plant assemblage found at the top part of these cores included species representative of moderately rich to rich fen (e.g., mosses from Amblystegiaceae family, Ptychostomum pseudotriquetrum) but also from poor fen (e.g., Ericaceous species, Comarum palustre). The richness status could be interpreted as the transitional between the two types of fens (rich and poor). The R3 core most probably regressed to a rich fen. According to successional patterns observed in the paleoecological analyses, target plant assemblage for reference purposes should be inspired from moderately rich fen in the eastern part (R3 location). The same assemblage could be introduced in the central part (R1 and R2) as long as the water chemistry and hydrology fall into the range seen in natural fens. As the paleoecological status was not clear-cut, if the environmental conditions at BSF are closer to poor fen characteristics, we advised targeting this specific assemblage.

High occurrence of bryophytes in zones II and IV generated a higher peat accumulation rate, averaging respectively 1.1 and 0.6 mm per year compared with 0.05 mm for zone III where bryophytes were absent. Even though brown mosses decompose at a faster pace than *Sphagnum* species (Vitt 1990), they decompose at a slower rate than vascular plants (Bartsch and Moore 1985), and thus generate significant peat accumulation. If the most important objective of a peatland restoration plan is to restore the carbon sequestration function, then particular attention should be given to the return of the bryophytes.

Natural disturbance events are of interest for restoration ecologists. By looking at the evolution of an ecosystem after disturbance, one may detect which species help system recovery and the potential trajectories that a restored ecosystem can potentially take (Robert et al. 1999). Fires are a common natural disturbance in peatlands (Turetsky and St. Louis 2006; Lavoie and Pellerin 2007) and past fire events (charcoal layers) are easily detectable in paleoecological analyses. For instance, Polytrichum strictum grew in abundance after fire in ombrotrophic peatlands (as indicated by paleoecological studies: Kuhry et al. 1993, Lavoie et al. 2001, Benscoter 2006), which suggests that it helps to reestablish the plant cover. The same species was also found to be an excellent nurse plant for Sphagnum reestablishment during the restoration of harvested peatlands (Rochefort et al. 2003; Groeneveld et al. 2007; González et al. 2014). Fire events were not frequent at BSF, probably because the water level in the peatland was probably very close to the surface most of the time (as inferred by the species assemblages), or because the tree cover was too sparse to generate detectable amounts of charcoal. However, at N, Campylium stellatum appeared just after the last fire (1930). This species often colonizes bare peat surface soon after a disturbance (Tyler 1984; Arnesen 1999; Mälson et al. 2010) and can grow on mineral ground (Gauthier 2014; Borkenhagen and Cooper 2016). Campylium stellatum was observed, during vegetation surveys in 2012, growing abundantly in disturbed locations such as all-terrain vehicles trails where the surface vegetation cover disappeared. Even if there was no evidence of its role in the facilitation of plant reestablishment, C. stellatum could be a candidate to test in this respect.

Usefulness of modern plant surveys

We surveyed a wide range of minerotrophic peatland types in the BSF region, but only two distinct plant communities were identified, i.e., tall-sedge and Sphagnum-Thuja communities. These communities are similar in species composition to those found in open, moderatelyrich to extremely-rich fens of western boreal Canada (Chee and Vitt 1989; Locky and Bayley 2005), and in the forested cedar swamp of northern Ontario (Kenkel 1987; Jeglum 1991). Although similarities have been found, reference system determination should essentially be based on local surveys, because species habitat requirements may change from region to region (Clewell and Aronson 2013). Moreover, modern plant surveys may also highlight discrepancies between past vegetation assemblages (which are always only a partial record of real communities, because not all plants produce well-preserved macrofossils) and modern vegetation. For instance, Thuja occidentalis was very abundant in the peatlands in 2012 but was not found in the macrofossil analyses.

Knowledge of the environmental variables in undisturbed natural sites can be used as a guideline for evaluating the success of a restoration project (Ruiz-Jaen and Aide 2005; Shackelford et al. 2013). In Table 1 and summary Fig. 6, we showed the range of variability for several environmental variables for fens of the BSF area. The characteristics of the restored site should perhaps fall within this range. The nutrients and mineral water concentrations fall within the range seen in the literature for fen (compilation from Andersen et al. 2011), especially moderately rich fen (Chee and Vitt 1989). Among interesting observations that should be considered **Fig. 6.** Schematic representations of the plant assemblages and their associated habitats within a moderately rich fen ecosystem as described by the paleoecological stratigraphies and present-day studies. The range of variability of the main water chemical elements and biomass are also summarized for two main fen types.



during the restoration, there was the higher nitrate concentrations that favored shrub growth. Although it is recognized that high nitrate concentrations can negatively impact plant diversity in fens (Drexler and Bedford 2002; Bobbink et al. 2010), that was not the case in our study. However, in the long term, shrub expansion might be detrimental to plant diversity, by diminishing moss abundance for example (Pedrotti et al. 2014). As moss cover is a difficult characteristic to re-establish in disturbed fens, nitrogen concentration should be considered carefully before implementing a restoration project. A second observation concerns the possible link between the high sulfate concentrations in water, such as seen in riverine fens, and poor species richness. There are numerous factors that affect species richness, and we do not suggest that sulfate is the explanation. However, there is a paucity of research on the direct impact of sulfate on vegetation communities in peatlands, as most studies on the influence of the sulfur cycle looked at microorganisms (Andersen et al. 2013) and the impact on the C cycle (Vile and Novák 2006). Since sulfate concentrations increased with time after the restoration

(Andersen et al. 2010), the interaction between sulfate and vegetation should be examined closer.

In summary, our present-day study succeeded in establishing relationships between plant assemblages and a set of environmental conditions (Fig. 6). These relationships are the foundation of a reference system for restoration. Therefore, to expect success, the reference system for restoration should match up with the environmental conditions in the disturbed site to be restored. In the BSF case study, for example, if a high water table is predicted, tall-sedge assemblage will be more successful than a *Sphagnum warnstorfii* dominated assemblage. Thus, it is only after evaluation of the disturbed site conditions that we can determine the best plant assemblage to introduce (Clewell and Aronson 2013).

Application of the results: BSF case-study

As seen previously in both paleoecological and presentday studies, a total of four fen plant communities were described as possible references for the BSF restoration project. We should then target one or several of these communities for this project. At BSF, the topography of

the disturbed area is one of the main constraints influencing the choice of an appropriate reference. The central section of BSF, where R1 and R2 were cored, is in a lower position compared with the eastern section (R3, N). The monitoring of the water table depth and water chemical analyses indicated that the blockage of the drainage ditches in 2009 consistently maintained a high water table in the central section (Malloy and Price 2014), which was facilitated by the fact that mineral-rich water is continuously flowing toward this section (L. Rochefort, unpublished data). Spontaneous revegetation, mostly with Typha latifolia, Scirpus cyperinus, S. atrocinctus, and Salix species, already occurred along former drainage ditches in the central section. Reintroducing small herbaceous plants and bryophytes could be risky because they will likely be out-competed. Paleoecological analyses would suggest the restoration of a poor fen assemblage in the central section (R1 and R2 cores), but modern data would instead point toward the restoration of a tallsedge community. Species from this community are probably competitive enough to cope with the other species already established.

Peat harvesting did not last long in the eastern section of BSF where R3 was cored. However, negative impacts are important: peat compaction and subsidence on the first metre of the peat profile, low water table depth, frost heaving, no spontaneous vegetation, etc. These impacts are commonly seen in post-harvested cutover peatlands (Price 1996; Poulin et al. 2005). At R3, a *Sphagnum*–brown moss community with more hummock species and with a better survival in driest conditions would consequently be an objective that can realistically be achieved with the moss layer transfer technique currently used in North American bogs (Rochefort et al. 2003).

Complementarity of both methods

The selection of species to introduce during the restoration process is the key to reach broader functional and ecosystem stability objectives (Clewell and Aronson 2013; Shackelford et al. 2013). We focused on the gaining information on minerotrophic peatland plant communities, as this is becoming a more prominent goal as well as a tool for peatland restoration planning. Present-day studies produce more applied outcomes but only illustrated a snapshot in the sequence of changing species. Paleoecological tools informed us about the succession of communities and link them to autogenic or allogenic processes. In our study, long persistence in some communities indicated stability. Emergent species were replaced by mat species, then bryophytes and small herbaceous plants. The present-day vegetation at BSF still supports this last community. The disadvantages of paleoecological analyses center on the time required to process cores, and the need to train people. Therefore, paleoecological analyses are less applicable or accessible for smaller restoration projects. But, once it is done in a region, one can assume similar dynamics for similar hydrogeomorphological settings of peatlands (e.g., Swinehart and Parker 2000; Arlen-Pouliot 2009). In this sense, field vegetation surveys have the benefits of being faster and have more direct applied outcomes than paleoecological studies, mostly to describe environmental variables associated with vegetation. Paleoecology extrapolates peatland development from one precise point, and the interpretation of cores is based on actual knowledge of the peatland ecology. Still, understanding ecosystem dynamics is an important component of restoration, (SERI 2004; Shackelford et al. 2013), and this understanding is best achieved with paleoecology. For example, in our study, the structure of a plant community was shown to be stable in time where tall-sedge community did initiate peat accumulation and brown moss was an essential component. From our present-day study, we were able to compare distance between reference and disturbed sites and make clearer restoration objectives.

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Appendix A

Appendix Table A1 appears on the following pages.

suitability for the rare European macrophyte *Najas flexilis* (Willd.) Rostk. & Schmidt. Aquat. Conserv. **15**(3): 227–241. doi: 10.1002/aqc.673.

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Table A1. List of species identified during present-day inventories in 19 moderately rich to rich minerotrophy
peatlands (and units) located around Rimouski, Quebec, Canada.

1 · · · · · · · · · · · · · · · · · · ·	,		
Form	Code	Species names	Authority names
Bryophyte	aul_pal	Aulacomnium palustre	(Hedw.) Schwaegr.
Bryophyte	pty_pse	Ptychostomum s.l. pseudotriquetrum	(Hedw.) J.R. Spence & H.P. Ramsay
Bryophyte	bryo_sp	Bryophyte sp.	
Bryophyte	cal_cus	Calliergonella cuspidata	(Hedw.) Loeske
Bryophyte	cal_gig	Calliergon giganteum	(Schimp.) Kindb.
Bryophyte	cal_lin	Calliergonella lindbergii	(Mitt.) Hedenäs
Bryophyte	calli_sp	Calliergon s.l. sp.	(Sull.) Kindb.
Bryophyte	cam_ste	Campylium stellatum	(Hedw.) Lange & C.E.O. Jensen
Bryophyte	cli_den	Climacium dendroides	(Hedw.) Web. & Mohr
Bryophyte	dic_pol	Dicranum polysetum	Sw. ex anon.
Bryophyte	dre_adu	Drepanocladus aduncus	(Hedw.) Warnst.
Bryophyte	dre_unc	Sanionia uncinata	(Hedw.) Loeske
Bryophyte	drep_sp	Depanocladus s.1. sp.	(C. Müll.) G. Roth
Bryophyte	fis_sp	Fissidens sp.	Hedw.
Bryophyte	ham_ver	Hamatocaulis vernicosus	(Mitt.) Hedenäs
Bryophyte	hel_bla	Helodium blandowii	(Web. & Mohr) Warnst.
Bryophyte	hep_sp	Hepatic sp.	
Bryophyte	hyl_spl	Hylocomium splendens	(Hedw.) Schimp.
Bryophyte	hypn_sp	Hypnaceae sp.	
Bryophyte	mni_pun	Rhizomnium punctatum	(Hedw.) T.J. Kop.
Bryophyte	mni_sp	Mnium sp.	Hedw.
Bryophyte	pal_squ	Paludella squarrosa	(Hedw.) Brid.
Bryophyte	ple_sch	Pleurozium schreberi	(Brid.) Mitt.
Bryophyte	pol_str	Polytrichum strictum	Brid.
Bryophyte	pti_cri	Ptilium crista-castrensis	(Hedw.) De Not.
Bryophyte	rhy_tri	Rhytidiadelphus triquetrus	(Hedw.) Warnst.
Bryophyte	sco_cos	Scorpidium cossonii	(Schimp.) Hedenäs
Bryophyte	sco_sco	Scopidium scorpioides	(Hedw.) Limpr.
Bryophyte	sph_ang	Sphagnum angustifolium	(C. Jens. ex Russ.) C. Jens.
Bryophyte	sph_cen	Sphagnum centrale	C. Jens
Bryophyte	sph_fim	Sphagnum fimbriatum	Wils.
Bryophyte	sph_fus	Sphagnum fuscum	(Schimp.) Klinggr.
Bryophyte	sph_mag	Sphagnum magellanicum	Brid.
Bryophyte	sph_pal	Sphagnum palustre	L.
Bryophyte	sph_squ	Sphagnum squarrosum	Crome.
Bryophyte	sph_sub	Sphagnum subsecundum	Nees.
Bryophyte	sph_ter	Sphagnum teres	(Schimp.) Angstr.
Bryophyte	sph_war	Sphagnum warnstorfii	Russ.
Bryophyte	thu_del	Thuidium delicatulum	(Hedw.) Schimp.
Bryophyte	tom_nit	Tomenthypnum nitens	(Hedw.) Loeske.
Bryophyte	tor_tor	Tortella tortuosa	(Hedw.) Limpr.
Graminoid	cal_can	Calamagrostis canadensis	(Michx.) Nutt.
Graminoid	car_aqu	Carex aquatilis	Wahl.
Graminoid	car_aur	Carex aurea	Nutt.
Graminoid	car_dia	Carex c.f. diandra	Schrank
Graminoid	car_dis	Carex disperma	Dewey

Form	Code	Species names	Authority names
Graminoid	car_ech	Carex echinata	Murray
Graminoid	car_exi	Carex exilis	Dewey.
Graminoid	car_fla	Carex flava	L.
Graminoid	car_gyn	Carex gynocrates	Wormsk. ex Drejer
Graminoid	car_int	Carex interior	L.H. Bailey
Graminoid	car_lac	Carex lacustris	Willd.
Graminoid	car_las	Carex lasiocarpa	Ehrh.
Graminoid	car_lep	Carex leptalea	Wahl.
Graminoid	car_lim	Carex limosa	L.
Graminoid	car_mag	Carex magellanica	Lam.
Graminoid	car_pra	Carex prairea	Dewey ex Alph. Wood
Graminoid	car_pse	Carex pseudocyperus	L.
Graminoid	car_sp	Carex sp.	L.
Graminoid	car_vag	Carex vaginata	Tausch
Graminoid	eri_viri	Eriophorum viridicarinatum	(Engelm.) Fernald.
Graminoid	gly_can	Glyceria canadensis	(Michx.) Trin.
Graminoid	mul_glo	Muhlenbergia glomerata	(Willd.) Trin.
Graminoid	poa_sp	Poaceae sp.	
Graminoid	rhy_alb	Rhynchospora alba	(L.) Vahl.
Graminoid	rhy_fus	Rhynchospora fusca	(L.) W.T. Aiton
Graminoid	sci_acu	Schoenoplectus acutus var. acutus	(Muhl. ex Bigelow) Á. Löve & D. Löve
Graminoid	tri_alp	Trichophorum alpinum	L.
Graminoid	tri_ces	Trichophorum cespitosum	L.
Forb	gal_rot	Galearis rotundifolia	(Banks ex Pursh) R.M. Bateman
Forb	ara_nud	Aralia nudicaulis	L.
Forb	are_bul	Arethusa bulbosa	L.
Forb	ast_novb	Symphyotrichum novi-belgii var. novi-belgii	(L.) G.L. Nesom
Forb	ast_pun	Symphyotrichum puniceum	(L.) Á. Löve & D. Löve
Forb	ast_sp	Aster s.l. sp.	
Forb	doe_umb	Doellingeria umbellata	(Mill.) Nees
Forb	ath_fil	Athyrium filix-femina	(L.) Roth
Forb	cal_pal	Calla palustris	L.
Forb	cic_bul	Cicuta bulbifera	L.
Forb	cli_bor	Clintonia borealis	(Aiton) Raf.
Forb	con_chi	Conioselinum chinense	(L.) Britton, Sterns & Poggenb.
Forb	cop_tri	Coptis trifolia	L.
Forb	cyp_par	Cypripedium parviflorum	Salisb.
Forb	cyp_reg	Cypripedium reginae	Walter
Forb	dro_int	Drosera intermedia	Hayne.
Forb	dro_rot	Drosera rotundifolia	L.
Forb	epi_pal	Epilobium palustre	L.
Forb	equ_pal	Equisetum palustre	L.
Forb	eup_mac	Eutrochium maculatum	(L.) E.E. Lamont
Forb	fra_vir	Fragaria virginiana	Duchesne.
Forb	gal_lab	Galium labradoriricum	(Wiegand) Wiegand
Forb	gal_sp	Galium sp.	L.
Forb	gal_tri	Galium triflorum	Michx.
Forb	geu_riv	Geum rivale	L.
Forb	tri_vir	Triadenum virginicum	(L.) Raf.
Forb	iri_ver	Iris versicolor	L.
Forb	neo_con	Neottia convallariodes	(Sw.) Rich.
Forb	lob_kal	Lobelia kalmii	L.
Forb	lyc_uni	Lycopus uniflorus	Michx.
Forb	mai_can	Maianthemum canadense	Desf.
Forb	mal_uni	Malaxia unifolia	Michx.
Forb	men_tri	Menyanthes trifoliata	L.
Forb	mit_nud	Mitella nuda	L.
Forb	nup_var	Nuphar variegata	Engelm.

Table A1 (continued).

Form	Code	Species names	Authority names
Forb	orch sp	Orchidaceae	
Forb	osm_cin	Osmundastrum cinnamomea	(L.) C. Presl
Forb	osm_reg	Osmunda regalis	L.
Forb	par_gla	Parnassia glauca	Raf.
Forb	phr_aut	Phragmites australis subsp. americanus	(Cav.) Trin. ex Steud.
Forb	gym_cla	Gymnadeniopsis clavellata	(Michx.) Rydb.
Forb	pla_dil	Platanthera dilatata	(Pursh) Lindl. ex L.C. Beck
Forb	pog_oph	Pogonia ophioglossoides	(L.) Ker-Gawl.
Forb	per_amp	Persicaria amphibia	(L.) DelTree
Forb	com_pal	Comarum palustre	L.
Forb	pota_sp	Potamogeton sp.	L.
Forb	pyr_asa	Pyrola asarifolia	Michx.
Forb	pyr_ell	Pyrola elliptica	Nutt.
Forb	ran_acr	Ranunculus acris	A. Gray
Forb	rub_pub	Rubus pubescens	Raf.
Forb	sag_lat	Sagittaria latifolia	Willd.
Forb	san_can	Sanguisorba canadensis	L.
Forb	sar_pur	Sarracenia purpurea	L.
Forb	scu_gal	Scutellaria galericulata	L.
Forb	sel_sel	Selaginella selaginoides	(L.) Link.
Forb	mai_tri	Maianthemum trifolium	L.
Forb	sol_uli	Solidago uliginosa	Nutt.
Forb	tha_pub	Thalictrum pubescens	Pursh
Forb	the_pal	Thelypteris palustris	Schott
Forb	thy_lat	Typha latifolia	L.
Forb	tof_glu	Tofieldia glutinosa	(Michx.) Pers.
Forb	tri_bor	Trientalis borealis	Raf.
Forb	tri_mar	Triglochin maritima	L.
Forb	utr_int	Utricularia intermedia	Hayne.
Forb	val_uli	Valeriana sitchensis subsp. uliginosa	(Torr. & A. Gray) F.G. Mey.
Forb	vic_cra	Vicia cracca	L.
Forb	vio_sp	Viola sp.	L.
Shrub	and_pol	Andromeda polifolia var. latifolia	Aiton
Shrub	cha_cal	Chamaedaphne calyculata	(L.) Moench.
Shrub	cor_can	Cornus canadensis	L.
Shrub	cor_ser	Cornus sericea	
Shrub	gau_his	Gaultheria hispidula	(L.) Muhl. ex Bigelow
Shrub	gay_bac	Gaylussacia baccata	(Wang.) K. Koch.
Shrub	kal_ang	Kaimia angustifona	L.
Shrub	kal_pol	Kalmia polifolia	Wang.
Shrub	rno_gro	Knoaoaenaron groenianaicum	(Oeder) Kron & Judd
Shrub	lin_dor	Linnaea boreaiis	L. $(\mathbf{M}; \mathbf{h}; $
Shrub	ION_VII	Lonicera villosa	(MICIIX.) K. & S.
Shrub	myr_gai	Myrica gale	L.
Shirub	doi fra	Desighang frutisons	(L.) IIel.
Shrub	dal_iru	Dasiphora francosa Dhammus almifolia	(L.) Kydd. L'llón
Shrub	rib lac	Niuminus umijonu Pihas la custra	L HEL.
Shrub	roc bla	Rides ucusite	(reis.) roll. Marshall
Shrub	ros_Dia	Kosu pulustris Saliy habianna	Nidi Sildii Sang
Shrub	sal_UEU	Salix discolor	Jarg. Mühl
Shrub	sal_uis	Salix sp	I
Shrub	sai_sp spi lat	Suur sp. Sniraea latifalia	(Ait) Borkh
Shrub	spi_iat	Vaccinium angustifolium	Ait
Shrub	vac_ang	Vaccinium angustyonum Vaccinium oxycoccos	I I
Shrub	vib cas	Vihurnum cassinoides	L.
Tree	abi bal	Ahies halsamea	L. (I.) Mill
Tree	ace nen	Acer nensylvanicum	L.
	acc_Pen	ree renstrancent	L ,

Table A1	(concluded).
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Form	Code	Species names	Authority names
Tree	ace_rub	Acer rubrum	L.
Tree	aln_rug	Alnus incana	(L.) Moench.
Tree	bet_pap	Betula papyrifera	Marsh.
Tree	fra_nig	Fraxinus nigra	Marsh.
Tree	lar_lar	Larix laricina	(DuRoi) Koch.
Tree	pic_mar	Picea mariana	(Mill.) BSP.
Tree	sor_dec	Sorbus decora	(Sarg.) C.K. Schneid.
Tree	thu_occ	Thuja occidentalis	L.

Note: Nomenclature follows the Integrated Taxonomic Information System (2015) for vascular plants, and Faubert (2007) for bryophytes.

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