RESEARCH ARTICLE

A New Approach for Tracking Vegetation Change after Restoration: A Case Study with Peatlands

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Abstract

Developing objective tools for tracking progress of restored sites is of general concern. Here, we present an innovative approach based on principal response curves (PRC) and species classification according to their preferential habitats to monitor changes in community composition. Following large-scale restoration of a cut-over peatland, vegetation was surveyed biannually over 8 years. We evaluated whether the establishing plant communities fell within the range of natural variation. We used both general diversity curves and PRC applied on plant species grouped by preferred habitat to compare restored sites and unrestored sites to a reference ecosystem. After 8 years, diversity and richness differed between the sites, with Forest and Ruderal species more prominent in unrestored sites, and *Peatland*, Forest, and Wetland species dominant in restored sites. The PRC revealed that the restored site became rapidly dominated by typical peatland plants, the main drivers

Introduction

For restoration project assessment, the use of natural sites as reference ecosystems is essential when the goal of restoration is to optimize biodiversity rather than maximize it (SER 2004). It provides a target species pool with which the restored species pool can be compared (Belyea 2004). Indices such as richness or Shannon's H are often used as biodiversity indicators, but do not give a complete picture of changes in structural components of the ecosystem. For instance, influences from previous disturbances or surrounding landscape can bring exotic or ruderal species in the restored species pool, which is not desirable to maintain the integrity of the system. Restored systems are following a right trajectory when non-preferential species such as weeds or species not typical of the reference ecosystem decline and when native species of

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of temporal changes being *Sphagnum rubellum*, *Pohlia nutans*, and *Mylia anomala*. Some differences remained between the restored and the undisturbed species pools: the former had more herbaceous species associated with wetlands such as *Calamagrostis canadensis* and *Typha latifolia* and the latter had more forested species like *Kalmia angus-tifolia* throughout the study. PRC revealed to be an efficient tool identifying species driving changes at the community level after restoration. In our case study, examining PRC scores after classifying species according to their preferred habitat allowed to illustrate objectively how restoration promotes target species (associated to peatlands) and how lack of intervention benefits ruderal species.

Key words: cut-over bog, indicator species, multivariate analyses, plant diversity, plant succession, principal response curves, reference ecosystem, restoration ecology, trajectory analysis.

the targeted reference ecosystem increase. We emphasize that species composition should also be part of the evaluation process, and that species may be categorized according to their origin (non-native vs. native), preferred habitat (e.g. peatland specialists, ruderal species, etc.), life history or biological traits (annual vs. perennial), or life form (herbs, shrubs, trees) to better reveal colonization processes and succession patterns.

Monitoring the evolution of plant composition over time in restored sites may benefit from the use of an approach like principal response curves (PRC), a particular case of redundancy analysis (RDA) for which the measured attribute (e.g. species composition) for a given treatment is expressed as deviations from a reference value, at different times (van den Brink & ter Braak 1999; Leps & Smilauer 2003). PRC have been used in different ecosystems to evaluate changes in vegetation assemblages following disturbances (Pakeman 2004; Vandvik et al. 2005; Palik & Kastendick 2010). They have also been used following restoration to evaluate changes in physico-chemistry (Andersen et al. 2010). We propose not only to use them but also to incorporate preferential habitat classification to these integrative statistical analyses in order to investigate the changes in vegetation composition following large-scale restoration of peatlands.

Research in peatland restoration has been carried out since early 1990s. A particular method has been developed

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for cut-over bogs, which allows recreating a moss cover representative of natural bogs within a decade (Quinty & Rochefort 2003). It has also been estimated that 19 years post-restoration will be sufficient to recreate a moss carpet thick enough to offset the water table decrease induced by the summer water deficit (Lucchese et al. 2010), hence to return the system to an effective carbon sink. However, no long-term detailed evaluation of plant composition in restored cutover bogs has been published to date.

The goal of our study is to evaluate vegetation changes following restoration of a cutover bog using objective tools. More precisely, we classified species by their preferential habitats and (1) dissected plant diversity and richness and (2) combined it with PRC to identify drivers (species or group of species) of temporal changes.

Methods

Site Description

The study site is located in Eastern Quebec $(47^{\circ}58'N, 69^{\circ}26'W)$ and sits in the Bois-des-Bel natural peatland complex that covers a total of 189 ha (Fig. 1). It corresponds to 11.5 ha that were exploited for horticultural peat between 1972 and 1980, and abandoned thereafter. Spontaneous recolonization was sparse; no *Sphagnum* had colonized the site even 15 years after peat extraction activities stopped and the cover of vascular plants was below 5% (Poulin et al. 2005). The restoration of 8.4 ha has been initiated in 1999 with



Figure 1. Location of the Bois-des-Bel research station and the seven natural peatlands used as the reference ecosystem for evaluating restoration success. The Bois-des-Bel research station includes both the experimental site (with a restored and unrestored section) and a natural site that was part of the reference ecosystem. Numbers in boxes refer to the seven natural peatlands composing the reference ecosystem.

the moss layer transfer technique (Rochefort & Lode 2006), which consists briefly the following: (1) surface preparation; (2) construction of peat berms along topographic gradient; (3) transfer of plant diaspores including Sphagnum collected in a nearby natural peatland-the upper 10 cm of vegetation was cut using a rototiller, collected and spread mechanically onto the residual surfaces at a ratio of 1:10 (1 m² of collected material spread over every 10 m² of the restoration site); (4) spreading of a straw mulch on the introduced plant material for improving microclimatic conditions and protecting plant fragments from desiccation; (5) blocking of the drainage ditches to retain water; and (6) addition of a phosphorus fertilization (150 kg/ha), in June of the following summer. The remaining 3.1 ha that were left unrestored correspond to three peat fields, two of which are used for comparison purposes, and the other one being the buffer area between the restored and the unrestored sites. This set up thus consisted in a quasi-experiment (Manly 1992) as treatment and control were not randomly allocated due to hydrological rewetting constraints. Indeed, peatland restoration implies raising the water table level that impedes working with a complete randomized design within the site. It was judged as the best experimental approach for this large-scale restoration project (Block et al. 2001).

Sampling

A systematic monitoring program was set up to evaluate species composition 1 year before restoration and every 2 years thereafter between 2001 and 2007, using a systematic line-point intercept (LPI) method (Bonham 1989) to detect the presence or absence of plant species. About 60 transects were laid within each peat field, depending on field length, in the restored and unrestored sites. More precisely, every 5 m, a perpendicular line was set across the entire width of the peat field (30 m), and along this line, 10 equidistant points were surveyed, that is, one every 2.7 m. At each sampling point, all plant species intercepted by a vertical rod or by its upward projection were recorded. The same procedure was repeated for the ditches. In this case, however, the perpendicular transects were 10 m apart and only six points (21 cm apart) were surveyed for each 1.5-m wide transect, as ditches are much narrower than peat fields. Every monitoring year, over 5,000 points were surveyed for the peat fields, and over 2,100 points were surveyed for the ditches (for both the restored and unrestored sites combined). The exact number of points varied slightly from year to year due to spatial inaccuracy when moving the lines. For the statistical analyses, the presence-absence data issued from the point survey were converted into frequency data by forming groups of 50 neighboring points for peat fields and 35 points for ditches.

The reference data basis comes from a survey realized in 2007 in seven open and forested peatlands that are found in the region (Fig. 1). Percent cover of all plant species was recorded in 10 equidistant $1-m^2$ plots set along a linear transect crossing each site. In total, seven different peatlands were used to set the range of variability found in the reference ecosystem. Although

LPI may overestimate the cover of some species relatively to direct percent cover data (Kercher et al. 2003), our two datasets should be comparable as LPI data were transformed into more adequate occurrence frequencies.

Statistical Analyses

All statistical analyses were performed with the R version 2.1.10 (R Development Core Team 2009).

Richness and Diversity. We evaluated the changes in richness and diversity (Shannon's H) over time in the restored and unrestored peat fields and ditches in comparison with the reference ecosystem values. Each species was attributed to one of the six following habitat categories: (1) Peatland species (specialist species found preferentially in peatlands, either bogs or fens); (2) Wetland species (specialist species found exclusively in wetlands but not preferentially in peatlands); (3) Facultative wetland species (species that generally prefer, but are not restricted to wetlands); (4) Forest species (species that are found in forested habitat but not preferentially in forested peatlands or wetlands); (5) Ruderal species (species that are found in disturbed environments, such as burned areas, road sides, and eroded sites); and (6) Other species (species that can be found in other habitats such as lakes, cliffs, and alpine habitat). See Appendix S1 for details on sources of information for classifying species. Although some species can be found in more than one category, we used exclusive classification so that each species was attributed to only one category. We calculated Shannon's H diversity index and total species number for each category using the function "diversity" and "specnumber" in the "vegan" library in R (Oksanen et al. 2008).

Temporal Changes in Community Composition. For the subsequent analyses, we reduced the number of plant species by removing all those that were present in less than 10% of the points, leaving a total of 116 species from the 233 original species data. Subsequent analyses are dedicated to identifying the main drivers of community changes over time and rare species would not influence the results. The frequency data were then transformed using the Hellinger's distance using the function "decostand" of the "vegan" package (Legendre & Gallagher 2001; Oksanen et al. 2008). The Hellinger transformation allows giving less weight to abundant species and avoids the problem arising from Euclidean distance, where the distance between two sites sharing no species can be smaller than that between two sites sharing species (Legendre & Gallagher 2001).

To evaluate how communities evolved over time following restoration, we used PRC, a multivariate approach based on constrained ordination techniques, developed by van den Brink and ter Braak (1999). PRC use Monte-Carlo permutations (n = 999) to test the interaction between time and a given treatment, based on the relative changes between this treatment and a control set a priori. In our case, the "control" was the reference ecosystem, and the "treatments" were the restored peat fields (RES-field), restored ditches (RES-ditch), unrestored peat fields (UNR-field), and unrestored ditches (UNR-ditch). The primary result of PRC analysis is one or more sets of curves representing trajectories of community composition for a given treatment over time. In our case, the vegetation was constant in the reference site (data from 2007 used for all years), although this is not an assumption derived from the PRC analysis, simply a constraint of our particular dataset. Along with the curves, the respective scores of each response variable are displayed along a vertical axis, and they indicate how strongly each response variable correlates with the temporal patterns displayed by the treatments.

For the PRC analysis, the response variables were the individual frequencies of each of the 116 species. In addition to the response curves and the species scores, we grouped the species by habitat categories and calculated average group scores, which gave an estimate of the correlation value linking the habitat type with temporal changes in species composition following restoration.

Results

Richness and Diversity

A total of 233 plant species were identified in all the surveys. After 8 years of monitoring, total diversity and richness in all treatments were similar or higher than the reference ecosystem values, with the highest values found in the restored peat fields and the lowest in the reference ecosystem (Fig. 2). The species richness was variable among the habitat preference categories. In the restored sites, Peatland species richness was equal (ditches) or greater (peat fields) than in the reference ecosystem. Forest species were twice more diversified in the unrestored peat fields than in the reference ecosystem but remained similar elsewhere. Ruderal species were found almost exclusively in the unrestored sites, particularly in peat fields. Wetland species contributed to about 15% of the species richness in the restored peat fields and in both the restored and unrestored ditches but were barely present in the reference ecosystem (<1%). The same tendencies were observed for Facultative wetland species.

The temporal evolution of richness and diversity of plant species grouped by habitat preference varied between the sites (Figs. 3 & 4). For *Peatland* species, the values increased rapidly in both the peat fields and ditches of the restored sites, even overreaching the references ones after only 4 years, whereas it remained stable and lower than the reference in the unrestored sites. Two years after restoration, the richness and diversity of *Forest* species started to increase in the peat fields of both the restored and unrestored sites, but not in the ditches, where they remained stable around or below reference ecosystem levels. For *Wetland* species, ditches from both the restored and unrestored sites displayed intermediate values between the richer and more diverse restored peat fields, and the poorer and less diverse unrestored peat fields and reference ecosystem. The species from the *Facultative wetland* category



Figure 2. Average richness (bars) and diversity (Shannon's *H* diversity index: Φ average \pm standard error) 8 years after restoration for the unrestored peat fields (UNR-field), unrestored ditches (UNR-ditch), restored peat fields (RES-field), restored ditches (RES-ditch), and reference ecosystem (REF). Richness has been dissected into groups based on preferred habitat of each species (see Appendix S1). Values were calculated as averages for groups of 50 points (fields) and 35 points (ditches) from the systematic LPI survey (5,000 points were surveyed for the peat fields, and over 2,100 points were surveyed for the ditches for both the restored and unrestored sites combined). Species were grouped according to their preferred habitat: (1) *Peatland* species; (2) *Wetland* species; (3) *Facultative Wetland* species; (4) *Forest* species; (5) *Ruderal* species; and (6) *Other* species. See Appendix S1: Methods for more details on categorization of species. The total number of species recorded is 233.

were relatively stable over time in all sites, with values of richness and diversity only slightly higher in the restored and unrestored sites than in the reference ecosystem. *Ruderal* species were absent from the surveyed reference peatlands. In the restored peat fields, the richness and diversity of those species increased for the first 4 years then started to decrease. In the unrestored peat fields, the values remained more stable throughout the 8 years of monitoring. Very few *Other* species were found in all sites.

Temporal Changes in Community Composition

As PRC are measuring a temporal change, one has to remember that the curves for each treatment need to be interpreted in relation to the zero line (which represents the composition of the reference peatlands; Figs. 5a & 6a). To enhance the interpretation of those changes, the individual plant species more

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strongly correlated with the temporal trajectory, either positively or negatively, are displayed (as species scores) on the one-dimensional diagram (Figs. 5b & 6b).

Figure 5a and 5b shows the most prominent changes in species composition over time: Sphagnum rubellum, Pohlia nutans, Mylia anomala, Sphagnum magellanicum, and Vaccinium oxycoccos were initially unfrequent (negative PRC score at time 0) but were favored by restoration and became even more frequent in the restored peat fields and ditches than in the reference ecosystem after 2 and 6 years, respectively (Fig. 5a; PRC axis 1 = 23%; F = 36.95, p = 0.005). However, the unrestored peat fields and ditches (with constant negative PRC scores) had higher frequencies of Vaccinium angustifolium, and, to a lesser extent, Ledum groenlandicum, Typha latifolia, Larix laricina, Equisetum arvense, Calamagrostis canadensis, and Betula papyrifera than the reference peatland throughout the 8 years of monitoring. When grouping species according to their preferred habitat and calculating an average correlation with the temporal changes (average species score), it becomes obvious that restoration modifies species composition by promoting Peatland specialist species (highest positive correlation with the temporal trajectory), while not restoring after peat mining (unrestored sites) benefits ruderal species (Fig. 5c).

The second set of curves (axis 2) reveals that some other species were more frequent in the restored sites than in the reference ecosystem from the start of the monitoring after restoration, namely, *C. canadensis*, *Pohlia nutans*, *Eriophorum vaginatum* var. *spissum*, *Polytrichum strictum*, *T. latifolia*, *M. anomala*, *Drosera rotundifolia*, and *V. oxycoccos* (Fig. 6; PRC axis 2 = 14%; F = 23.75, p = 0.005). On the contrary, *Kalmia angustifolia*, *Sphagnum fuscum*, *Cladina rangiferina*, and *S. magellanicum* were less frequent in all sites than in the reference ecosystem for the 8 years of the study, hence were not promoted by restoration. Overall, the differences that remained in the species composition between the restored sites and the reference ecosystem were mostly due to the higher frequencies of *Wetland* species in the former (Fig. 6c).

Discussion

Richness data or Shannon's diversity indices are general indicators often used to evaluate the progress of plant communities following restoration. Some studies have split indices into habitat preference groups to examine plant succession after restoration or spontaneous recolonization but habitat categories remain often very broad (e.g. native vs. alien species), which prevents detailed examination of successional patterns. Our case study on bog restoration reasserts the importance of dissecting species diversity into distinct groups based on habitat preferences to achieve a better description of the evolution of the restored site.

In effect, we demonstrated here that although the unrestored sites had a similar richness and diversity (H) to the restored and reference ecosystem after 8 years, the richness



Figure 3. Evolution of the average richness (and standard error) over the 8 years of monitoring, measured separately for each habitat category. The grey line is the average value (and standard error) of the reference ecosystem (see Fig. 2 and Appendix S1 for more details). Note that scale varies among subgraphs. PreR corresponds to the year before restoration. *Ruderal* and *Other* species were absent from the reference ecosystem, as shown by the zero line for both graphs.

and diversity of particular groups based on habitat preferences was different across sites. Indeed, restoration mainly favored Peatland species but also allowed Wetland (obligate and facultative) species to establish. Restoration also helped suppressing undesirable species such as ruderal plants, which are adapted to disturbed areas and are usually eliminated throughout competition when environmental conditions specific to an ecosystem improve. In restored bogs, the moss Polytrichum strictum becomes rapidly dominant from reintroduction of the diaspores (L. Rochefort 2012, Laval University, Québec, Canada, unpublished study), which may hinder the spreading or persistence of Ruderal species like Equisetum arvense, which was by far the most frequent Ruderal species in the unrestored sites. Site preparation followed by wetter conditions brought upon by restoration (Shantz & Price 2006) significantly reduced richness and diversity of *Forest* species compared with the unrestored peat fields where trees have been growing since the abandonment of peat extraction activities in 1980.

Many studies have also used reference ecosystems for evaluating restoration but we are aware of only one other study using PRC to follow restoration success through time, namely, on chemical aspects of bog restoration (Andersen et al. 2010). Most studies addressing vegetation changes in restored sites remain mainly descriptive. When more data are available, results are often presented in large tables (Konisky et al. 2006). Such tables are useful for short-term assessment but could not be extended for multiyear datasets without getting too complicated. In cases where a long-term monitoring has been carried out, it is also common to present multivariate response of communities over time with graphs that become packed with symbols and lines and where the main information is difficult to extract (Tuittila et al. 2000; Tangen et al. 2003; Palik & Kastendick 2010; Haapalehto et al. 2011). We believe that the present study clearly shows the applicability of PRC to restoration evaluation because it allows the following: (1) reporting temporal changes of the restored site on a comparative basis with the reference ecosystem; (2) performing multitreatment comparisons; (3) directly identifying the main species driving the changes; and (4) giving enough flexibility to focus either on individual species or any other group of ecological significance.

Indeed, by using PRC in this case study, we were able to demonstrate that restoration promoted a small number of species, particularly those strictly associated with peatlands and to prove that the site is on the right trajectory compared with the unrestored site. Establishing a *Sphagnum* carpet is one of the main targets of bog restoration. Indeed, *Sphagna* are keystone plants for the return of bog functions such as peat accumulation and water regulation (van Breemen 1995).



Figure 4. Evolution of the average Shannon's H diversity index (and standard error) over the 8 years of monitoring, measured separately for each habitat category (see Figs. 2 & 3 and Appendix S1 for more details).

Sphagnum rubellum appeared to be even more frequent in the restored fields than in the reference ecosystem, although similar quantities of S. fuscum and S. rubellum fragments were introduced, as indicated by their ground cover in the donor site $(39 \pm 27\%$ for S. rubellum and $26 \pm 32\%$ for S. fuscum). Interestingly, other sites restored with the same techniques in Québec are also dominated by S. rubellum (average covers between 28 and 49%), S. fuscum having significant lower cover in those sites (average covers between 21 and 25%; Pouliot et al. 2011b). Sphagnum rubellum is known to have fairly broad ecological amplitudes (Gignac 1992), which might give it a competitive advantage in early stages of the restoration where the water table is still fluctuating (Shantz & Price 2006). We believe that S. fuscum, which has a greater ability to transport water by capillarity (Rydin 1993), may become more frequent in time, as hummocks will grow larger and higher, a process evaluated to take 10-20 years for reaching the same size as in natural bogs (Pouliot et al. 2011a). The same may hold true for hollow species that should expand as wetter microhabitats develop.

One important concern in this particular site that was highlighted by the PRC is that *Wetland* species atypical of bogs established particularly well in both the restored peat fields and ditches (Fig. 6). For example, *Typha latifolia* densely recolonized the site in its early stage after restoration (rhizomes were present pre-restoration) and proliferated along ditches and adjacent peat field surfaces as well as along pools. *Typha latifolia* occurs usually immediately or soon after disturbance in moist or wet habitats. Its growth has been shown to be optimal in soils of pH between 5 and 6.5 (Brix et al. 2002), which may explain its capacity to invade cut-over sites once rewetted. Indeed, the water pH in Bois-des-Bel ranges from 4.5 to 6, with higher pH in mid-summers (Andersen et al. 2010). However, Sphagnum has the capacity to acidify its environment (Clymo 1964); therefore, the pH should decrease toward values more typical of bog waters over time (below 4.2; Vitt & Chee 1990). Typha latifolia has already started to decrease in both restored ditches and peat fields (Appendix S2), possibly in more acidic areas as it loses its capacity to uptake nitrates at pH 3.5 (Dyhr-Jensen & Brix 1996). The Facultative wetland species Calamagrostis canadensis also differentiated the restored sites from the references ecosystem where it was not frequently found. This species needs nutrientrich conditions to proliferate (Lieffers et al. 1993). In addition, it does not tolerate competition for light and thus might not survive at the restored site as Ericaceae, shrubs, and trees develop (Powelson & Lieffers 1992; Appendix S2). Overall, although some species not associated with peatlands have developed widely at the restored sites, it did not preclude the establishment of Peatland species which reassert the efficiency of the moss layer transfer technique for restoring peatlands.

The approach presented here is greatly influenced by the choice of the reference ecosystem. In this case study, it comprised data from seven natural peatlands of the Bas-St.-Laurent region of Québec, where peatland afforestation is a well-documented phenomenon arising from a combination of factors, including fire and drier-than average climate (Pellerin & Lavoie 2003). It is unlikely that restored sites can



Figure 5. PRC for the first axis of the RDA testing the effect of treatment \times time on the species composition and representing the dominant temporal trajectory in species composition. (a) Response curves of each treatment with the 0 line representing the reference ecosystem; (b) species scores representing correlation (positive score = positive correlation, 0 = no correlation, negative score = negative correlation) with the temporal trends displayed in (a); and (c) average species score grouped by preferred habitat representing average correlation of all species belonging to a group with the temporal trends (Fac. Wet is for Facultative wetland). Treatments were as follows: restored peat fields (RES-field), restored ditches (RES-ditch), unrestored peat fields (UNR-field), and unrestored ditches (UNR-ditch). PreR corresponds to the year before restoration. For species names, refer to Appendix S1.



Figure 6. PRC for the second axis testing the effect of treatment \times time on the species composition and representing a secondary temporal trajectory in species composition. See Figure 5 for details on curves and species scores. For species names, refer to Appendix S1. Note the difference of scale with Figure 5a.

reach a forested state similar to that of the reference ecosystem within less than 10 years following restoration, explaining why species associated with a forest habitat, such as *Vaccinium angustifolium* and *Kalmia angustifolia*, were still more frequent in the reference ecosystem.

Overall, we believe that dissecting diversity into groups based on habitat preferences and using approaches such as PRC are simple yet very efficient ways of enhancing our understanding of how biodiversity or plant community composition evolves over time following restoration. There are increasing numbers of restoration projects in a wide variety of ecosystems, and we advocate that an essential part of ecological restoration is the adequate and informative monitoring of changes in community composition against references.

Implications for Practice

- PRC are efficient tools to integrate to the monitoring in order to identify successful or problematic species in a given restored site but has specific requirements: at least two points in time, a matrix of response variables (e.g. species) including data for a reference system (or control), and a number of replicates (or lines) greater than the number of response variables. The analysis itself can be performed using the free software R.
- The systematic vegetation survey should start prior to restoration to capture the initial conditions and reflect the "no intervention" scenario, and should include at least one reference ecosystem (target for restoration). Further to the identification of the species, managers should classify the species according to ecologically relevant groups such as habitat preference.
- Restoration should take place as quickly as possible after disturbance to limit the possibility for ruderal species to establish and compete with target species (in this case, *Peatland* species). Following initial restoration, further management of undesirable species (e.g. *Wetland* species like *Typha latifolia*) could speed up the vegetation succession and prevent invasion, but costs might not be justified if time is not an issue.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of the 233 species found with the LPI method for the restored and unrestored sites and in quadrats sampled in seven natural peatlands composing the reference ecosystem. Each species was attributed to one of the six habitat preference categories. For Peatland species, both bryophytes and vascular plants were identified according to Payette and Rochefort (2001). For Wetland and Facultative wetland species, vascular plants were identified according to the Ministère du Développement durable, de l'Environnement et des Parcs du Québec (2008). For the rest of the vascular plants, we referred to Boivin (1992; for Cyperaceae) and to Marie-Victorin (1995). For nonvascular plants other than those found preferentially in peatlands, we referred to Sims and Baldwin (1996) for Sphagnum, to Ireland et al. (1987) and J. Faubert (2010, Société québécoise de bryologie, Québec, Canada, personal communication) for mosses, to Jean Faubert for liverworts, and to Brodo et al. (2001) for lichens. The species classification into the six habitat preference categories was based on habitat species preferences in regions South of the 48° parallel. Although some species can be found in more than one category, we used exclusive classification so that each species was attributed to only one category. We chose not to associate Picea mariana to Facultative wetland category and classified it as a Forest species. Some species were too generalists to be attributed to a particular category and were classified as Other species.

Appendix S2. Frequencies of occurrence of species identified as indicator species by the principal response curve (see Figs. 5 & 6) from the year prior to restoration (0) and the years after (2, 4, 6, and 8). Values for the restored and unrestored sites are from the LPI method (presence–absence) and those for the reference ecosystem are from percent cover in 1-m^2 quadrats (see Methods). The grey line is the average value (and standard error) of the reference ecosystem.

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