Plant diversity associated with pools in natural and restored peatlands

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SUMMARY

This study describes plant assemblages associated with the edges of peatland pools. We conducted inventories in six natural peatlands in the province of Québec (Canada) in order to measure the contribution of pools to species diversity in climatic regions where peatlands are used for peat extraction. We also carried out vegetation surveys in a peatland that has been restored after peat extraction/harvesting to determine whether pool vegetation establishes along the edges of created pools when dry surface restoration techniques only are used. Pools enhanced plant species richness in natural peatlands. Around created pools, species associated with natural pools were still absent, and non-bog species were present, six years after restoration. On this basis, we emphasise the importance of preserving natural peatlands with pools. In order to restore fully the plant diversity associated with peatlands at harvested sites, it may be necessary to modify pool excavation techniques so that created pools resemble more closely those in natural peatlands. Active introduction of the plant species or communities associated with natural pools may also be needed; candidate species for North America include *Andromeda glaucophylla*, *Cladopodiella fluitans*, *Carex limosa*, *Eriophorum virginicum*, *Rhynchospora alba* and *Sphagnum cuspidatum*.

KEY WORDS: biodiversity, peatland restoration, pond, mire, created pool.

INTRODUCTION

Because of the importance of species diversity for ecosystem functions, the preservation of biodiversity is one of the major long-term goals of ecological restoration (SERi 2004). Creating environmental heterogeneity in restored sites should increase their biodiversity. Although experimental trials or monitoring surveys on habitat heterogeneity in restored habitats are scarce, habitat and environmental heterogeneity has been shown to increase biodiversity in several natural ecosystems (MacArthur & MacArthur 1961, Palmer 1992, Lundholm & Larson 2003, Steiner & Kohler 2003, Statzner & Moss 2004, Dufour *et al.* 2006). Specifically for peatlands, Glaser (1992) found that one of the most important environmental factors for vascular plant richness in the raised bogs of eastern North America was the number of habitats occurring along the wet-to-dry microtopographic gradient of pools, hollows and hummocks; whilst Vitt *et al.* (1995) showed that bryophyte diversity in the peatlands of continental western Canada was generally correlated with habitat diversity. A positive relationship between species diversity and the number of microhabitats has also been shown for birds (Calmé & Desrochers 1999) and macroinvertebrates (Smits *et al.* 2002).

Pool micro-habitats are regarded as hotspots for biodiversity in peatlands. Both generalist and specialist aquatic insects are found here (Danks & Rosenberg 1987, Standen *et al.* 1998), and the intrinsic variety of aquatic invertebrates supports vertebrate diversity *via* trophic links (Murkin & Batt 1987). Despite their acidity, peatland pools are used as foraging sites by amphibians, especially in summer (Mazerolle 2005). They also serve as resting areas for migratory birds (Desrochers 2001) and have been described as the most important feeding areas for greenshank (*Tringa nebularia*) and golden plover (*Pluvialis apricaria*) during the breeding season (Downie *et al.* 1998). It is generally assumed that the topographical and hydrological characteristics of peatland pools influence not only faunal diversity, but also floral diversity. And yet, even though specific plant communities have been described for pool margins (Lindsay *et al.* 1985, Guinan *et al.* 1998, Poulin *et al.* 1999, Poulin *et al.* 2002), the contribution of pools to plant diversity has never been quantified.

Despite the significance of pools for biodiversity, their creation has seldom been included in peatland restoration projects. In Europe, bog restoration usually involves the re-wetting of peat surfaces, and in some cases this has resulted in the development of *Sphagnum* vegetation or the formation of floating rafts with typical hummock-hollow vegetation (Lamers *et al.* 1999). In North America, efforts have been devoted to the re-establishment of suitable hydrological conditions and the accumulation of plant biomass over extensive flat surfaces (Rochefort *et al.* 2003). However, these restoration measures create homogeneous surfaces that do not allow return of the full array of faunal diversity typical of raised bog (van Duinen *et al.* 2003). Verberk *et al.* (2006) recommended that a variety of hydrological conditions should be created in restored sites in order to enhance environmental heterogeneity. The creation of pools would be an efficient means for promoting diverse hydrological conditions in the restoration of dry harvested peatland surfaces. Pools were created on one restored site in Canada, but four years after their establishment, the created pools still differed from natural ones (Mazerolle *et al.* 2006). Amphibian tadpoles were 1–5 times more abundant and arthropods 2–26 times less abundant in created pools than in natural ones, although several bog specialist arthropods had colonised the created pools. The dominant plant species also differed between the two types of pools and the cover of most vegetation strata was lower in created pools.

As the establishment of vegetation around created pools was unsuccessful in preliminary trials, the development of restoration techniques for pool vegetation appears to be important (Mazerolle *et al.* 2006). However, the preliminary trials were very modest, and natural recolonisation of created pools has never been assessed quantitatively. In order to define appropriate goals for pool restoration, a better understanding of the contribution of pools to plant diversity in natural and restored peatlands is required.

We investigated the contribution of pools to natural peatland plant diversity by comparing the vegetation around pools with the vegetation of peatland expanses. To determine whether active plant introduction is needed to restore vegetation around pools in extracted peatlands, we compared plant diversity and vegetation assemblages between natural pools and created pools. For the same purpose, we also estimated how restored pools increase plant diversity within restored peatlands. In the research reported in this paper, three hypotheses are tested, namely:

1. pools increase vegetation diversity in natural peatlands;
2. vegetation diversity around created pools in restored peatlands is similar to vegetation diversity in non-pool habitats; and
3. vegetation diversity around created pools differs from vegetation diversity around natural pools.

METHODS

Vegetation survey in natural peatlands

Site description

We surveyed six natural peatlands in the Low Boreal and Eastern Temperate wetland regions of Canada (Natural Resources Canada 2006) (Figure 1). Annual precipitation ranges from 887 mm to 1170 mm and mean annual temperature from 1.5ºC to 4.7ºC across the sites, and the surveyed peatlands are surrounded by forested or agricultural landscapes with a small fraction of urban land (Table 1). All of them are ombrotrophic and therefore dominated by *Sphagnum* mosses. These peatlands were chosen because they were characterised by pools and because they represent the range of bog vegetation for the main peat harvesting regions of southern Québec.

Sampling

For each peatland, the vegetation cover was evaluated in 60 circular quadrats of area 0.5 m^2. Half of the quadrats were located at pool margins and the other half on two transects at least 25 metres distant from pools. Natural pools in southeast Canadian peatlands are normally between 1 and 100 m^2 in area (PERG unpublished data). The average dimensions of the surveyed pools were 60 m^2 in area and 1 m deep. A sinuous transect was established from aerial photography to follow the margins of adjoining pools and to cover a large number of pools. Pool quadrats were recorded every 20 metres. Each quadrat was placed so that 80% of the sample was adjacent to open water and 20% was in the water to ensure that aquatic vegetation was included. The pool margins were sometimes forested but tree cover never exceeded 50%. We therefore chose to confine the two non-pool transects to open habitats (i.e. with less than 50% tree cover) to make them comparable with the pool quadrats. These two transects were located, again using aerial photographs, to represent the range of open habitats present. Two types of open habitats were distinguished, namely ‘pure herbaceous zones’ and ‘shrub zones with scattered herbs, larches,

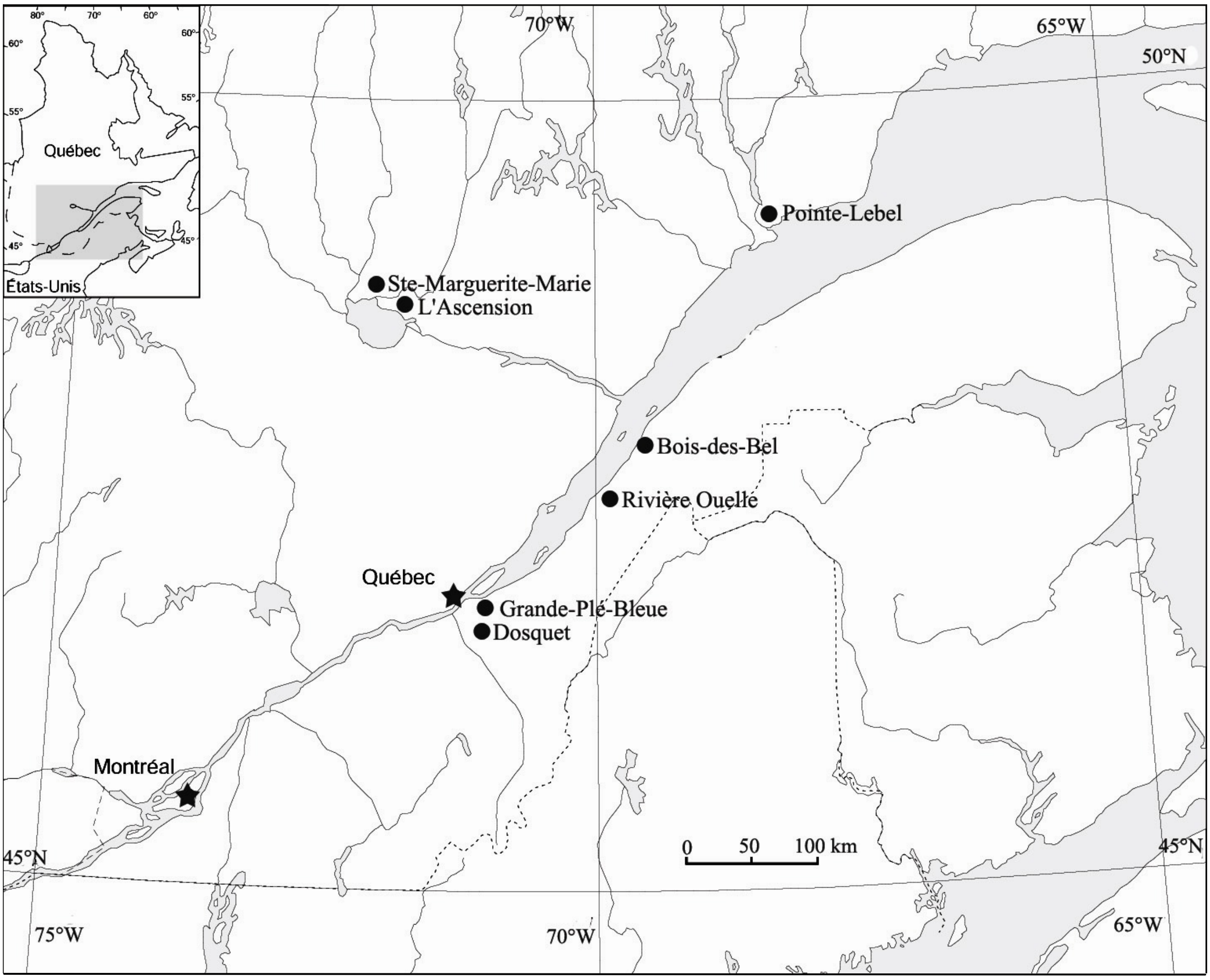

Figure 1. Map of part of the province of Québec, Canada, showing the locations of the Bois-des-Bel restored peatland and the six natural peatlands surveyed during this study.

Table 1. Observed climatic norms for temperature and precipitation, and surrounding landscape types, for the surveyed peatlands.

Sites	Precipitation (mm)	Temperature (ºC)			Landscape (%)		
		Year	Jan	Jul	Forested	Urban	Agricultural
Ste-Marguerite-Marie, L'Ascension	886.9	2.3	-16.4	18.2	54	1	44
Pointe-Lebel	1014.4	1.5	-14.4	14.5	96	3	1
Grande-Plé-Bleue, Rivière Ouelle	1169.6	4.7	-11.9	19.6	27	4	69
Dosquet	1169.6	4.7	-11.9	19.6	60	1	39
Bois-des-Bel	962.9	3.2	-12.6	17.8	30	3	67

Sources: Environment Canada (2006) (precipitation and temperature); Robitaille & Saucier (1998) (landscape types).

and/or spruces'. For the two peatlands (Rivière Ouelle and L'Ascension) with only one open habitat type, the two transects were placed in two different locations but in the same habitat. Quadrats were again placed at 20 metre intervals on each transect. For all quadrats, species cover was evaluated to the nearest 2% for vascular plants, mosses and lichens.

Vegetation survey in the restored peatland

Site description

Bois-des-Bel (BDB) peatland is located in southern Québec (47° 58' N, 69º 26' E; Figure 1, Table 1). The whole peatland covers 189 ha, of which 11.5 ha were harvested for horticultural peat from 1972 to 1980. When peat harvesting activities ceased, a 2 m thick layer of peat remained. A vegetation survey conducted in 1995, 15 years after harvesting ended, revealed that the vegetation was still very sparse due to the harsh environmental conditions typical of abandoned sites (Poulin *et al.* 2005). The cover of the different vegetation strata was less than 5% and *Sphagnum* had not recolonised. Restoration of 8.4 ha of the site was initiated in 1999 in collaboration with the peat industry (PERG undated, Figure 2). The site was levelled to eliminate small-scale microtopography, peat berms were constructed perpendicular to the topographic gradient, plants were collected from a natural bog and spread as fragments on the peatland surface as a restoration measure, a straw mulch was added to protect the plant fragments from desiccation, the drainage ditches were blocked to retain water, and finally a light dressing of phosphorus fertiliser was applied to promote plant establishment. A zone of 3.1 ha was not restored. This zone consisted of three peat fields, one of which serves as a buffer zone between the rewetted and the non-rewetted areas (Figure 2). In an effort to increase site biodiversity and to restore past regional pool diversity, eight pools (6 x 12 m) were dug to a maximum depth of 1.2 m and were shaped with both a shallow and a steep bank to represent the natural variability of pool topography (Figure 3). With a residual peat deposit of two metres, pool bottoms were characteristically peaty, and no mineral soil or deep minerotrophic peat was exposed when digging them. However, Lavoie *et al.* (2001) showed that the transition from fen to bog peat is at 1 m depth in the peat profile. Pool bottoms may thus be close to the fen-bog transition that occurred during development of the peatland. Between 2000 and 2006, mean water pH for pools at Bois-des-Bel was 4.53 (± 0.55; PERG unpublished data). During restoration, a paired design was used in which vegetation was introduced around four pools in 2000 and no introductions were made at the four other pools.

Sampling

Vegetation surveys were conducted around created pools to test whether the re-establishment of pool physical characteristics alone was sufficient for the re-establishment of typical pool vegetation through natural recolonisation. To avoid any sampling bias resulting from plant introduction trials, we chose to survey only the four pools where no interventions were made even though the reintroductions were not effective (Mazerolle *et al.* 2006). The vegetation of these four pools was surveyed using 12 circular quadrats of 0.5 m^2. For comparison, the vegetation was also surveyed along four transects located at least 25 metres from pools on the same four peat fields (Figure 2). Twelve randomly located quadrats were surveyed for each transect. For all quadrats, species cover was evaluated to the nearest 2% for vascular plants, mosses and lichens.

Data analyses

We used species richness as a measure of diversity and compared it between: 1) natural areas with and without pools, 2) restored areas with and without pools, and 3) natural pools and created pools. We used Student's T test to test the significance of these comparisons. Statistical analyses were conducted in SAS software version 8 (SAS Institute 1999–2001).

To assess changes in species diversity among habitats we calculated β-diversity (species turnover between sites) using the method of Harrison *et al.* (1992). We used the following formula:

$$\beta = \{((S/\overline{\alpha})-1)/(N-1)\}\times 100$$

where S = the total number of species recorded, α = mean α-diversity (species richness) for all sites, and N = the number of sites. Values of β range from 0 (no turnover) to 100 (every sample has a unique set of species) (Magurran 2004). Three β-diversity calculations were carried out. The first one included pool quadrats and non-pool quadrats in natural peatlands, the second one included pool quadrats and non-pool quadrats in the restored peatland, and the third one included pool quadrats in natural and restored peatlands. The average species richness for natural pools is based on six peatlands with several surveyed pools for each, while the average species

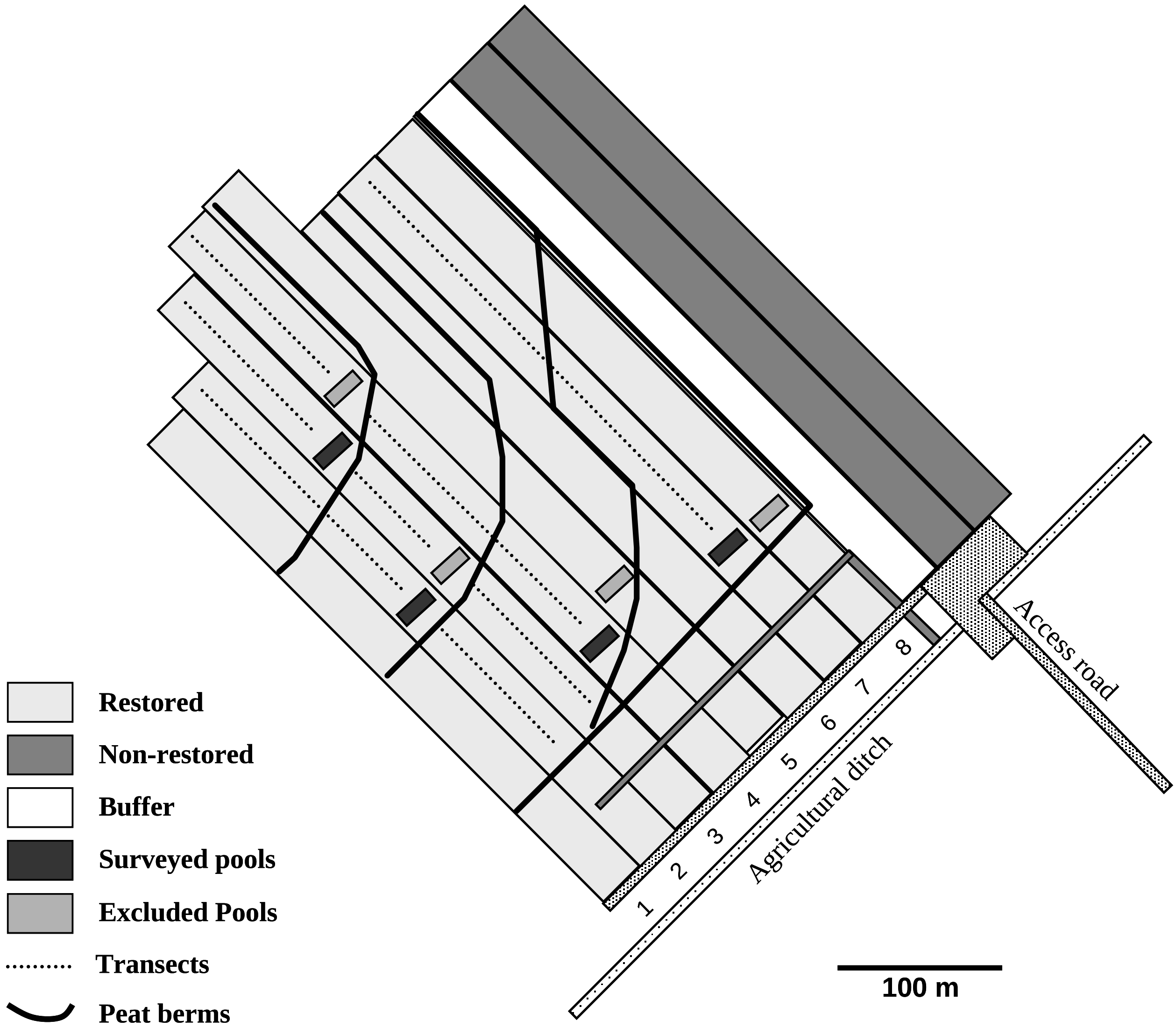

Figure 2. Schematic map of the Bois-des-Bel (BDB) restored peatland, showing the locations of the four surveyed pools and the four vegetation survey transects.

richness for created pools results from a survey conducted around four pools within a single site. We surveyed only one restored site with pools because there is no other restored site with created pools in eastern Canada. This makes the comparison of species richness between natural and created pools conservative because the latter were likely to show lower species richness owing to their location within the same site. For β-diversity measurements, this unbalanced design should not affect the outcome of our study as species did not vary much between the natural peatlands despite the large geographical distances between sites. In fact, few species were restricted geographically. The main differences amongst sites were expressed in terms of species abundance, which was not used for β-diversity calculations.

To assess the influence of pools on plant species composition for both restored and natural peatlands, we conducted two redundancy analyses (RDA) with Hellinger transformed species data, one for natural and one for restored peatlands. This transformation is recommended for RDA, which is a Euclidean-based analysis, as community composition data contain many zero values (Legendre & Gallagher 2001). The presence or absence of pools was used as the only constraining variable and thus only the first axis of the RDA was constrained. Sites were included as covariables in order to partition out variation associated with site location because the

Figure 3. A natural pool (above) and a restored pool (below).

location of the site, with its own climate and local setting, may influence species composition. The analysis thus showed the responses of species to pools alone. We conducted a third RDA analysis with Hellinger transformed species data to assess the variation in species composition around pools associated with the sites *per se*. For this analysis, sites were treated as if they were environmental variables and only pool quadrats from both restored and natural sites were included. All RDA analyses were conducted using Canoco for Windows, version 4.0 (ter Braak & Smilauer 1998) and the significance of the environmental variables was tested with the Monte Carlo re-sampling procedure (999 permutations under the reduced model).

RESULTS

The analysis of species diversity allowed us to evaluate the role of pools in increasing the number of species present in both natural and restored peatlands. Pools significantly increased species richness in both natural and restored peatlands ($P < 0.01$; Table 2, Appendix 2). Natural peatlands had an average of 35 species and this figure dropped to 24 when data from pool quadrats were omitted. The same pattern was found in the restored peatland, where there was an average of 34 species per peat field when all quadrats were considered and this number dropped to 27 when pool quadrats were excluded. Created pools were as diverse as natural pools since both showed a species richness of 24 species. However, the high β-diversity between natural and restored pools (β_p = 54; Table 2) indicates a high species turnover between these two habitats, and thus that their species assemblages differed greatly. The β-diversity within natural peatlands including pools and non-pool areas was lower (β_p = 32.6; Table 2) than between natural and restored pools, which indicates that species assemblages in pool and non-pool areas in natural peatlands had more species in common than did the species assemblages of natural and restored pools. Habitats within the restored peatland were the most similar, as indicated by the lowest β-diversity (23.8; Table 2). This implies that although pools increased the species diversity of the restored site, the species assemblages of pool and non-pool samples within the restored site had many species in common.

The ordinations indicate that the presence of pools explained 16.3% of the variation in species distribution in natural peatlands ($P < 0.01$; Figure 4). Some species, such as the bryophytes *Cladopodiella fluitans* and *Sphagnum cuspidatum* and the cyperaceous species *Carex limosa* and *Rhynchospora alba*, were associated with pools. Others, for example the ericaceous species *Kalmia angustifolia* and *Rhododendron groenlandicum* and the moss *Sphagnum fuscum*, were found mostly in open habitats distant from pools. Factors affecting the distributions of *Sphagnum rubellum* and *Sphagnum magellanicum* appear not to have been measured in this study since these two species are placed vertically, more or less parallel with the second axis of the ordination, which represented 11.6% of the variation in plant distribution.

The presence of pools in the restored peatland was as important as their presence in natural peatlands in explaining the variation in species distribution, as it accounted for 16.4% of the plant species distribution ($P < 0.01$; Figure 5). Only *Typha latifolia,* a species that does not grow in natural bogs, was associated with pools. The peatland species *Chamaedaphne calyculata*, *Eriophorum vaginatum*, *Polytrichum strictum* and *Rhododendron groenlandicum* were more abundant in non-pool areas. Other species like *Drosera*

Table 2. Values of species richness (± SD) for all quadrats sampled in the six natural peatlands and one restored site as well as for non-pool quadrats and pool quadrats in the same sites. Values of β-diversity, which indicates species turnover amongst habitats, are shown for different pairs of habitats ($\boldsymbol{\beta_n}$: pool and non-pool habitats in natural peatlands; $\boldsymbol{\beta_r}$: pool and non-pool habitats in the restored peatland; $\boldsymbol{\beta_p}$: pools in natural and restored peatlands).

	*N**	Quadrats/*N***	All quadrats	Non-pool quadrats	Pool quadrats	
Natural	6	60	34.8 (± 3.4)	24.0 (± 2.8)	24.0 (± 3.0)	**$\boldsymbol{\beta_n}$ = 32.6**
Restored	4	24	34.0 (± 1.8)	27.3 (± 2.2)	24.0 (± 5.6)	**$\boldsymbol{\beta_r}$ = 23.8**
					$\boldsymbol{\beta_p}$ = 54.0	

* For natural sites *N* = 6 peatlands; for the restored site *N* = 4 peat fields within the same peatland.
** 60 quadrats were recorded in each natural site (30 around pools and 30 distant from pools) and 24 quadrats were surveyed on each restored peat field (12 around pools and 12 distant from pools).

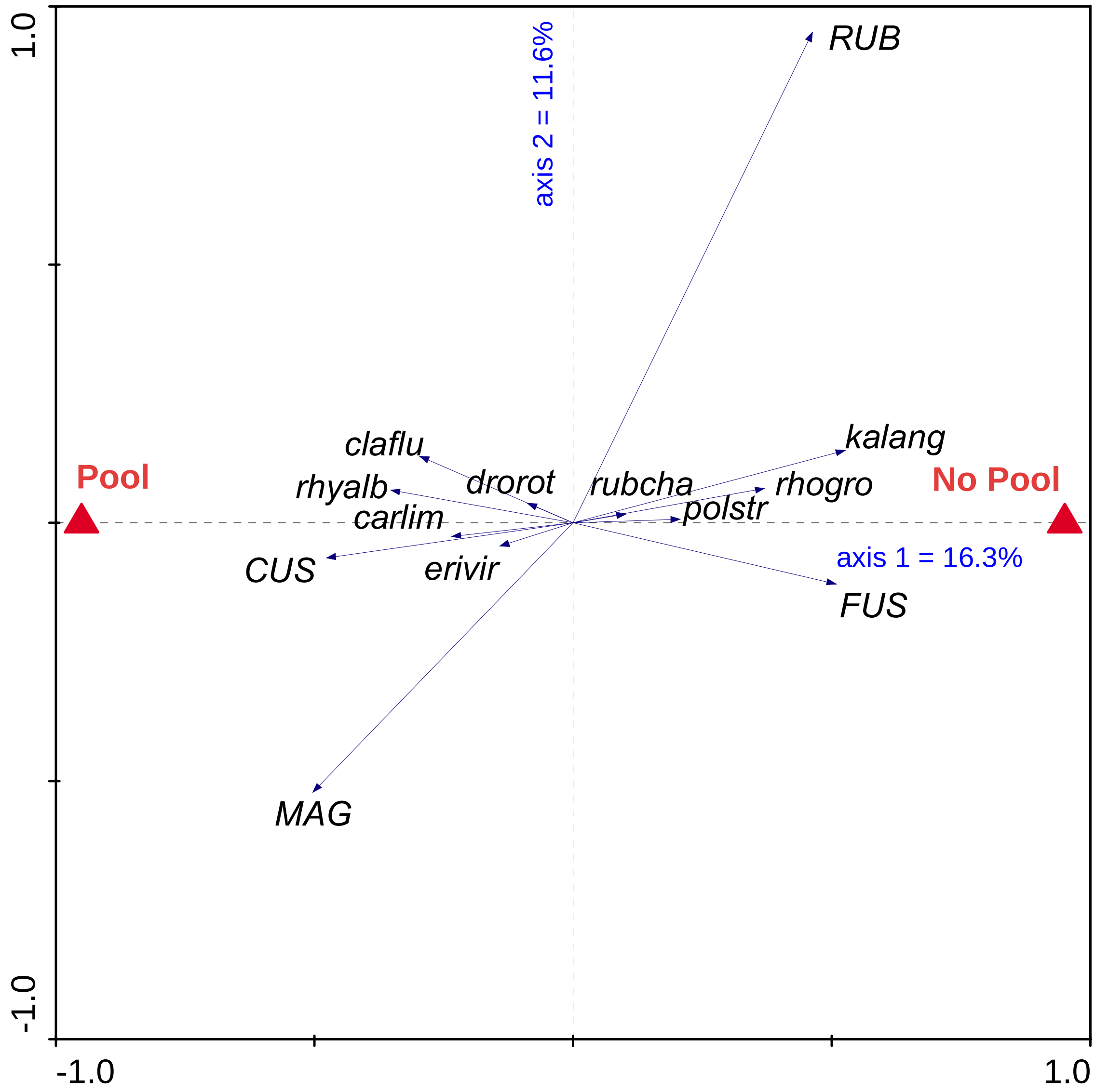

Figure 4. RDA of species distribution in relation to the presence of pools in natural peatlands. Only species with a species fit higher than 10% are shown. See Appendix 1 for species codes.

rotundifolia, *Lophozia incisa*, *Mylia anomala*, *Sphagnum fuscum*, *Sphagnum magellanicum*, *Sphagnum rubellum*, *Vaccinium angustifolium* and *Vaccinium oxycoccos* were less influenced by pools and thus had a broader spatial distribution within the restored peatland. Because *T. latifolia* was remarkably abundant in created pools (69% occurrence; Appendix 1, Figure 3), we removed this species from the data set and ran the same RDA again to see whether *T. latifolia* was the main factor explaining the differences in species assemblages between pool and non-pool quadrats at the restored site. Without *T. latifolia*, the presence of created pools still explained 12.4% of the variation within the vegetation of the restored site. Since no particular species seemed to be associated with pools, species abundances and frequencies rather than the species themselves were affected by the presence of pools in the restored site. Pools thus exert a quantitative rather than a qualitative influence on species occurrence at the restored site.

The third RDA was conducted to compare sites on the basis of the vegetation found around pools (Figure 6). The plant composition of pools varied significantly between sites ($P < 0.01$). Despite the great regional variation of pool plant diversity between sites, the Bois-des-Bel (BDB) restored site was well separated from natural peatlands in the ordination. Even the centroid for Rivière Ouelle (RO), a geographically close site to BDB (Figure 1),

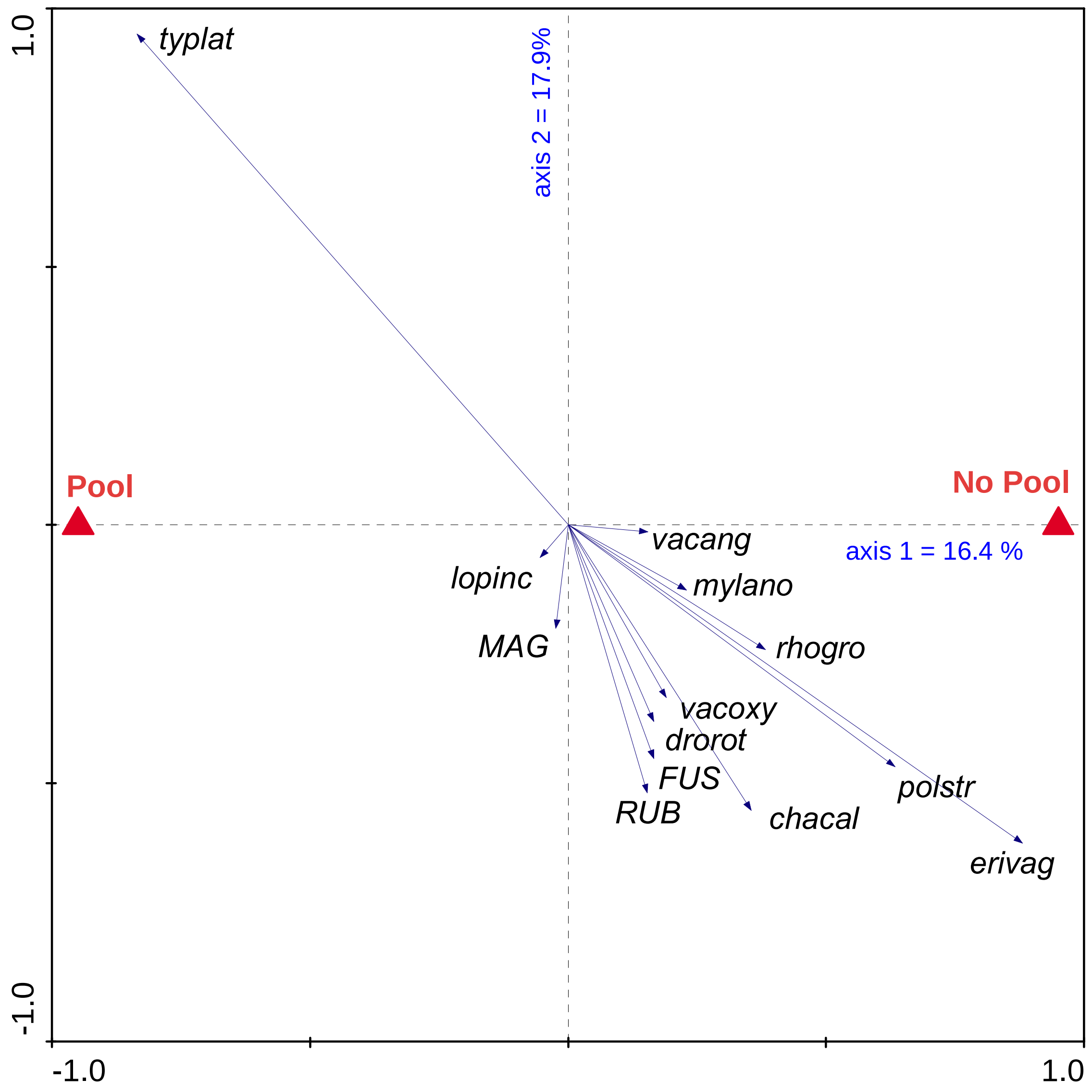

Figure 5. RDA of the species distribution in relation to pools in a restored peatland (Bois-des-Bel). Only species with a species fit greater than 10% are shown. See Appendix 1 for species codes.

was distant from BDB's centroid on the ordination biplot. The species assemblages of created pools thus differed from species assemblages found around natural pools, although the latter were variable in their own right.

DISCUSSION

The presence of pools was an important factor in explaining the variation of species distribution in natural peatlands. Some species grew around pools and nowhere else, for example *Drosera anglica*, *Drosera intermedia*, *Nuphar lutea* ssp. *variegata*, *Rhynchospora alba*, *Sphagnum cuspidatum*, *Utricularia cornuta*, *Vaccinium macrocarpon*, and *Warnstorfia fluitans* (Appendix 1). Pools thus increased the species richness of natural sites, and this was reflected by the high β-diversity between areas with and without pools. Some other species were not found exclusively around pools but their occurrence was much higher around pools than in other areas of open peatland; these included *Andromeda glaucophylla*, *Carex limosa*, *Cladopodiella fluitans*, *Drosera rotundifolia*, *Eriophorum virginicum*, *Sphagnum fallax, and S. papillosum* (Appendix 1). Therefore, pools provide suitable conditions for plants that are not widespread elsewhere in peatlands. These results are in agreement with other studies on species diversity

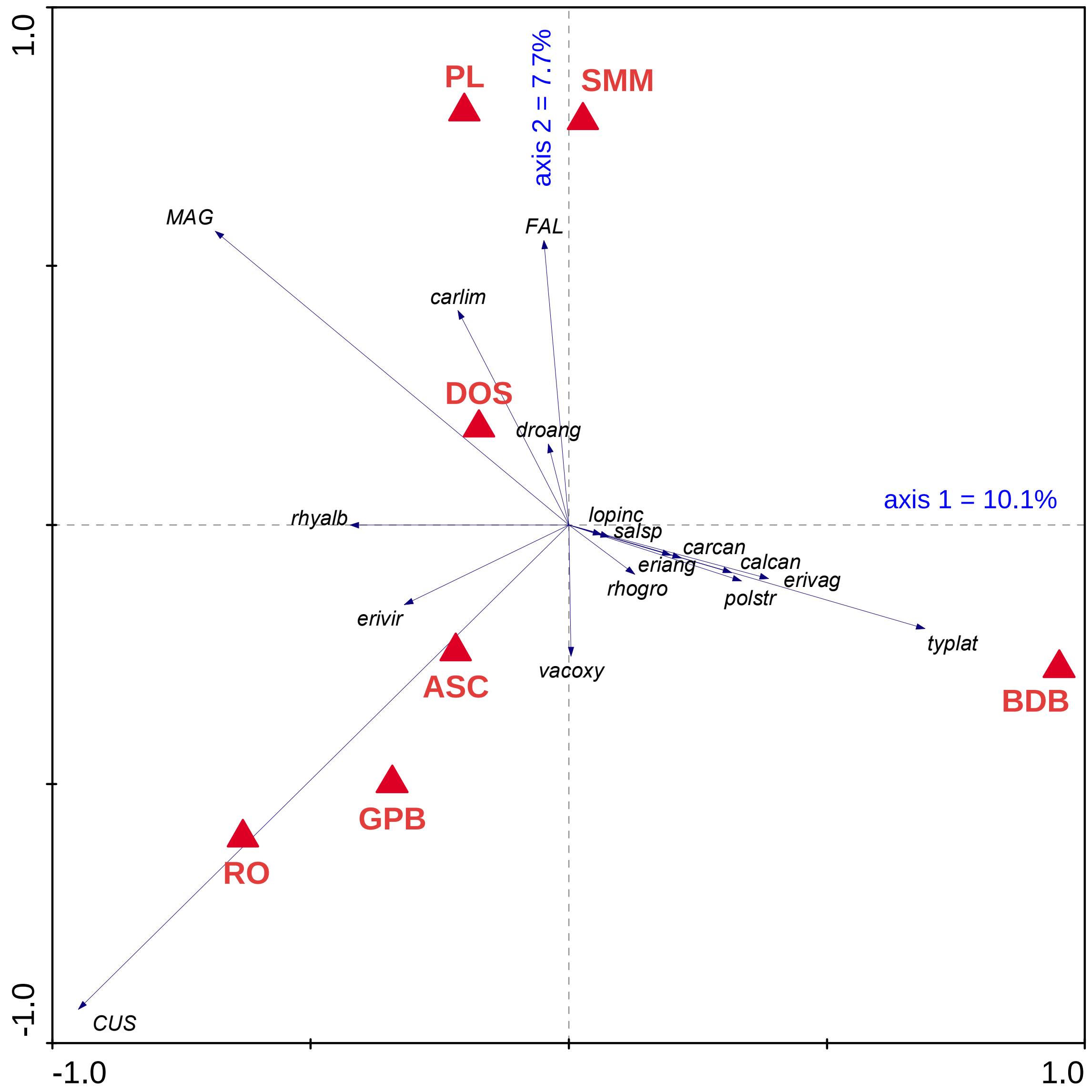

Figure 6. RDA of the pool vegetation of natural peatlands (Pointe-Lebel = PL, Ste-Marguerite-Marie = SMM, Dosquet = DOS, L'Ascension = ASC, Grande-Plé-Bleue = GPB, Rivière Ouelle= RO) and the restored peatland (Bois-des-Bel = BDB). Only species with a species fit higher than 10% are shown. See Table 1 for site characteristics and Appendix 1 for species codes.

of ponds in different ecosystems. Palmer *et al.* (1992) have suggested that ponds contribute significantly to wetland plant diversity in Great Britain, whilst William *et al.* (2004) have shown that ponds and other small water bodies can contribute significantly to regional plant diversity in agricultural landscapes. For peatlands, Lindsay *et al.* (1985) found that particular species are associated with different types of pools in Britain. Our results also corroborate previous Canadian peatland studies. In their study on the reliability of satellite imagery for defining peatland vegetation diversity, Poulin *et al.* (2002) showed that *C. fluitans, D. rotundifolia, Nuphar lutea* ssp. *variegata, R. alba, S. cuspidatum* and *U. cornuta* were associated with pools on natural peatlands in Southern Québec. Mazerolle *et al.* (2006) published a list of dominant species for natural pools in eastern New Brunswick that includes several species associated with pools in the present study. These two studies were rather descriptive, however, and were not designed specifically to quantify the contribution of pools to peatland plant diversity by directly comparing areas with and without pools. From our study, it becomes obvious that pools play a major role in increasing plant diversity in peatlands.

For the restored peatland, both the relatively low β-diversity and the ordination indicated that areas with and without pools shared a great many species. This is not surprising because the same restoration technique was applied uniformly over the site (PERG unpublished data). However, as in natural peatlands, the presence of pools was still an important contributory factor to variation in species distribution. Some species were associated with created pools so that the species richness of the site was higher when quadrats placed around pools were considered. Yet an increase in species diversity associated with the presence of pools does not necessarily mean that restoration has been successful. For that, the restored ecosystem must show species assemblages and community structure similar to those of the reference ecosystem (SERi 2004). At the Bois-des-Bel restored site, the vegetation around created pools included both peatland and non-peatland species that established following the restoration of flat, dry areas. The species that grew only or mostly around created pools were not peatland plants (*Carex canescens, Juncus brevicaudatus, Lophozia incisa, Lycopus uniflorus, Salix sp*., and *Typha latifolia*; Appendix 1). Although most of these species were too rare or their distributions too variable to stand out in the ordination, pools were clearly characterised by high abundance of *Typha latifolia*. This very competitive species is not associated with bogs but forms monotypic stands in areas of shallow open water (Grace & Wetzel 1981) leading to low vegetation diversity (McNaughton 1968, Drexler & Bedford 2002). It follows that *T. latifolia* might compete with peatland species to colonise created pools at Bois-des-Bel. Its presence could in turn have an impact on the hydrological characteristics of created pools as the quality and quantity of the vegetation cover usually influences the physical and chemical characteristics of ponds (Angélibert *et al.* 2004). Conversely, the pool characteristics at Bois-des-Bel could themselves be an ecological filter limiting plant establishment. Peat areas near the steep banks of the pools may have been elevated slightly when peat was scooped out to form the pools, even though it was spread as uniformly as possible. This effect may explain the differences in species frequency between pool and non-pool samples from the restored site, a suggestion that is supported by the fact that bog species associated with drier microsites, like *Sphagnum fuscum*, were more common around pools than elsewhere. Also, the pH of water in created pools was higher than that of natural pools (Mazerolle *et al.* 2006). The mean water pH for pools at BDB (4.53 ± 0.55 for the years 2000 to 2006; PERG unpublished data), corresponds to the highest 1% of the pH of natural bog pools (Mazerolle *et al.* 2006). This could also have hampered the establishment of bog plants and promoted the occurrence of non-peatland species.

Non-peatland species may disappear with time as they are not adapted to peatland conditions. In particular, as *T. latifolia* is not adapted to acidic environments which are nutrient poor (Brix *et al.* 2002), it should decrease in abundance with time as *Sphagnum* mats develop. Indeed, *Sphagnum* is known to be a key ecosystem engineer that acidifies the ecosystem due to its high ion exchange capacity (Clymo 1964). Since 1999, the occurrence of *Sphagnum* at the site has increased steadily to 55% in 2005 and some *Sphagnum* cushions are now up to 20 cm thick (PERG unpublished data).

The high β-diversity between natural and created pools indicates that their vegetation communities are quite different from one another. After six years of restoration, only four species that grow exclusively or mostly in natural pools were found in created pools, namely *Sphagnum cuspidatum, S. fallax, S. papillosum* and *Drosera rotundifolia* (Appendix 1). *Sphagnum* species were found in very few samples (between 2% and 8% occurrence) whereas *D. rotundifolia* was present everywhere in the restored peatland, with a higher percentage occurrence in non-pool quadrats than in pool quadrats. Other species associated with natural pools were absent from created pools, irrespective of whether they were common or rare in natural pools. These results were predictable as there is no seed bank in mined peatlands to facilitate rapid plant colonisation (Salonen 1987, Huopalainen *et al.* 1998, Huopalainen *et al.* 2000). Moreover, there are no pools at the donor site where the plant fragments that were spread at Bois-des-Bel were collected. Nonetheless, spores and seeds from natural peatlands could colonise created pools, as peatland mosses and shrubs have high dispersion potential (Campbell *et al.* 2003, Sundberg *et al.* 2006). However, the time since restoration is probably too short for plant propagules to have colonised created pools and, moreover, the closest and second closest bog pools are located 40 and 70 km respectively from the study site. In fact, BDB is located within a region where peatlands have been either lost or greatly disturbed through peat mining, forestry and agricultural activities (Pellerin 2003). Thus, limitation of natural sources of plant propagules for species associated with peatland pools may greatly impede the natural colonisation of created pools.

CONCLUSION

Our study emphasised the importance of pools for preserving peatland plant diversity. As restoration techniques for pools have not yet been developed, the most reliable way to preserve plant species associated with pools would be to protect peatlands with pools from industrial activities. Our study has shown that, when pools are created in mined peatlands, natural pool vegetation does not return within six years. This may be due to unfavourable physical and chemical attributes of the created pools, which may or may not diminish with time; but propagule availability is another potential issue. One approach to reducing the problem would be through altering the method used for creating pools so that they physically resemble more closely pools in natural peatlands. However, active plant introduction may also be needed to promote the establishment of species associated with pools. *Andromeda glaucophylla*, *Cladopodiella fluitans*, *Carex limosa*, *Eriophorum virginicum*, *Rhynchospora alba* and *Sphagnum cuspidatum* would be good target species since they are associated with and common in natural peatland pools and they do not seem to colonise created pools spontaneously. These species could be introduced as mixtures in order to re-create pool edge habitat, which would be consistent with the coarse filter approach of Noss (1987). Additional species that would be of high interest as fine filters owing to their rarity and their strict association with pools are *Drosera intermedia*, *D. anglica*, *Nuphar variegatum*, *Sphagnum papillosum*, *Utricularia cornuta* and *Vaccinium macrocarpon*.

We restricted our survey to bogs because this is the type of peatland that is mined for horticultural peat in Québec and for which restoration techniques are now available. However, a number of abandoned peatlands and sectors of peatland complexes contain minerotrophic peat, and restoration approaches are currently being developed for these. As pools or flarks also occur in fens, the restoration of abandoned peatlands with minerotrophic peat may also benefit from interest regarding pool restoration.

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Appendix 1. List of species and their percentage occurrence in quadrats around pools and distant from pools in six natural and one restored peatlands. Species are ordered according to their occurrence around natural pools in order to aid interpretation. Species in bold type are those mentioned in the text and shown in the Figures.

Code	**Species**	**Natural pool**	**Natural non-pool**	**Restored pool**	**Restored non-pool**
	number of quadrats	180	180	48	48
chacal	***Chamaedaphne calyculata* (L.) Moench**	**71**	**86**	**58**	**92**
rhyalb	***Rhynchospora alba* (L.) Vahl.**	**69**	**0**	**0**	**0**
MAG	***Sphagnum magellanicum* Brid.**	**69**	**46**	**56**	**71**
vacoxy	***Vaccinium oxycoccos* L.**	**54**	**72**	**50**	**83**
CUS	***Sphagnum cuspidatum* Ehrh. ex Hoffm.**	**51**	**0**	**2**	**0**
RUB	***Sphagnum rubellum* Wils.**	**50**	**82**	**85**	**100**
carlim	***Carex limosa* L.**	**46**	**1**	**0**	**0**
erivir	***Eriophorum virginicum* L.**	**46**	**11**	**0**	**0**
drorot	***Drosera rotundifolia* L.**	**36**	**9**	**46**	**85**
andgla	***Andromeda polifolia* L. var. *glaucophylla* (Link) DC.**	**30**	**12**	**0**	**0**
claflu	***Cladopodiella fluitans* (Nees) H. Buch**	**30**	**1**	**0**	**0**
FAL	***Sphagnum fallax* (Klinggr.) Klinggr.**	**25**	**9**	**8**	**0**
sarpur	*Sarracenia purpurea* L.	19	10	10	19
kalang	***Kalmia angustifolia* L.**	**16**	**82**	**10**	**42**
kalpol	*Kalmia polifolia* Wangenh.	16	51	0	8
PAP	***Sphagnum papillosum* Lindb.**	**14**	**1**	**2**	**0**
droint	***Drosera intermedia* Hayne**	**13**	**0**	**0**	**0**
droang	***Drosera anglica* Huds.**	**12**	**0**	**0**	**0**
FUS	***Sphagnum fuscum* (Schimp.) Klinggr.**	**11**	**59**	**71**	**42**
nuplut	***Nuphar lutea* (L.) Sm. ssp. *variegata* (Dur.) E.O. Beal**	**11**	**0**	**0**	**0**
warflu	***Warnstorfia fluitans* (Hedw.) Loeske**	**9**	**0**	**0**	**2**
rhogro	***Rhododendron groenlandicum* (Oeder) K.A. Kron & Judd**	**7**	**77**	**29**	**90**
caroli	*Carex oligosperma* Michx.	6	16	0	0
utrcor	***Utricularia cornuta* Michx.**	**5**	**0**	**0**	**0**
vacmac	***Vaccinium macrocarpon* Ait.**	**5**	**0**	**0**	**0**
MAJ	*Sphagnum majus* (Russ.) C. Jens.	4	1	0	0
vacang	***Vaccinium angustifolium* Ait.**	**4**	**21**	**4**	**33**
betmic	*Betula michauxii* Spach	4	8	0	0
ANG	*Sphagnum angustifolium* (C. Jens. ex Russ.) C. Jens. in Tolf	3	20	10	33
polstr	***Polytrichum strictum* Brid.**	**3**	**48**	**48**	**100**
mylano	***Mylia anomala* (Hook.) Gray**	**3**	**14**	**25**	**44**
plable	*Platanthera blephariglottis* (Willd.) Lindl.	3	1	0	0
eriang	*Eriophorum angustifolium* Honckeny	3	0	23	15
FIM	*Sphagnum fimbriatum* Wils. in Wils. & Hook. f. in Hook. f.	3	0	0	0
erivag	***Eriophorum vaginatum* L.**	**2**	**22**	**35**	**90**
picmar	*Picea mariana* (P. Mill.) B.S.P.	2	20	0	10
dicund	*Dicranum undulatum* Brid.	2	6	0	0
cartri	*Carex trisperma* Dewey	1	4	4	27
rubcha	*Rubus chamaemorus* L.	1	27	0	4
larlar	*Larix laricina* (Du Roi) K. Koch	1	8	0	0

Code	Species	Natural pool	Natural non-pool	Restored pool	Restored non-pool
	number of quadrats	180	180	48	48
maitri	*Maianthemum trifolium* (L.) Sloboda	1	6	0	0
sciatr	*Scirpus atrocinctus* Fern.	1	0	8	15
junpel	*Juncus pelocarpus* E. Mey.	1	0	0	0
xyrmon	*Xyris montana* Ries	1	0	0	0
claran	*Cladina rangiferina* (L.) Nyl.	0	16	2	8
plesch	*Pleurozium schreberi* (Brid.) Mitt.	0	9	0	0
calmit	*Cladina mitis* (Sandst.) Hustich	0	8	0	8
claste	*Cladina stellaris* (Opiz) Brodo	0	7	0	10
empnig	*Empetrum nigrum* L.	0	6	0	0
rhocan	*Rhododendron canadense* (L.) Torr.	0	4	2	8
clachl	*Cladonia chlorophaea* (Florke ex Sommerf.) Sprengel	0	3	0	0
clacri	*Cladonia crispata* (Ach.) Flotow	0	3	0	0
elequi	*Eleocharis quinqueflora* (F.X. Hartman) Schwarz	0	3	0	0
gauhis	*Gaultheria hispidula* (L.) Muhl. ex Bigelow	0	3	0	0
nemmuc	*Nemopanthus mucronatus* (L.) Loes.	0	3	0	0
aromel	*Aronia melanocarpa* (Michx.) Ell.	0	2	2	0
dicpol	*Dicranum polysetum* Sw.	0	1	0	0
pticil	*Ptilidium ciliare* (L.) Hampe	0	1	0	0
clasqu	*Cladonia squamosa* Hoffm.	0	1	0	0
RIP	*Sphagnum riparium* Ångstr.	0	1	0	0
vibcas	*Viburnum cassinoides* L.	0	1	0	0
typlat	***Typha latifolia* L.**	**0**	**0**	**69**	**2**
calcan	*Calamagrostis canadensis* (Michx.) Beauv.	0	0	38	27
carcan	***Carex canescens* L.**	**0**	**0**	**23**	**6**
lopinc	***Lophozia incisa* (Schrad.) Dumort.**	**0**	**0**	**19**	**4**
salsp	***Salix sp.***	**0**	**0**	**19**	**4**
junbre	***Juncus brevicaudatus* (Engelm.) Fern.**	**0**	**0**	**10**	**0**
equiarv	*Equisetum arvense* L.	0	0	6	4
lycuni	***Lycopus uniflorus* Michx.**	**0**	**0**	**6**	**0**
solgra	*Solidago graminifolia* (L.) Salisb.	0	0	4	6
aulpal	*Aulacomnium palustre* (Hedw.) Schwaegr.	0	0	4	0
onosen	*Onoclea sensibilis* L.	0	0	4	0
rumcri	*Rumex crispus* L.	0	0	4	0
betpap	*Betula papyrifera* Marsh.	0	0	2	10
arahis	*Aralia hispida* Vent.	0	0	2	4
astpun	*Aster puniceus L.*	0	0	2	2
betcor	*Betula cordifolia* Regel	0	0	2	2
diccer	*Dicranella cerviculata* (Hedw.) Schimp.	0	0	2	2
solrug	*Solidago rugosa* P. Mill.	0	0	2	2
SQU	*Sphagnum squarrosum* Crome	0	0	2	0
warexa	*Warnstorfia exannulata* (Schimp. in B.S.G.) Loeske	0	0	2	0
poptre	*Populus tremuloides* Michx.	0	0	0	21
spilat	*Spiraea latifolia* (Ait.) Borkh.	0	0	0	4
rubida	*Rubus idaeus* L.	0	0	0	2

Appendix 2. Statistical comparisons of species richness (diversity) between: 1) natural peatland areas with and without pools, 2) areas in the restored Bois-des-Bel (BDB) peatland with and without pools, and 3) natural pools and created (at BDB) pools. N: number of observations; CL: confidence limits; SD: standard deviation; SE: standard error; DF: degrees of freedom. The analyses were conducted using SAS 8 software (SAS Institute 1999–2001).

1. NATURAL PEATLANDS			2. BDB (RESTORED PEATLAND)			3. POOL QUADRATS		
quadrats	obs	no. species	quadrats	obs	no. species	site	obs	no. species
all	1	39	all			BDB		
	2	34		1	35		1	26
	3	39		2	33		2	29
	4	33		3	36		3	25
	5	31		4	32		4	16
	6	33						
non-pool	7	27	non-pool			natural peatlands	5	29
	8	24		5	28		6	26
	9	26		6	24		7	23
	10	25		7	28		8	22
	11	23		8	29		9	21
	12	19					10	23

1. Comparison of species numbers in natural peatlands

variable	quadrats	N	range	mean	CL of mean	SD	CL of SD	SE
species	non-pool	6	19–27	24	21.032 to 26.968	2.8284	1.7655 to 6.937	1.1547
species	all	6	31–39	34.833	31.295 to 38.371	3.3714	2.1045 to 8.2689	1.3764
species	Diff (1-2)			-10.83	-14.84 to -6.83	3.1118	2.1743 to 5.461	1.7966

	method	variances	DF	t	Pr > |t|
T-TESTS	Pooled	equal	10	-6.03	0.0001
	Satterthwaite	unequal	9.71	-6.03	0.0001
EQUALITY OF VARIANCES	method	DF (numerator)	DF (denominator)	F value	Pr > F
	Folded F	5	5	1.42	0.7093

2. Comparison of species numbers at BDB

variable	quadrats	N	range	mean	CL of mean	SD	CL of SD	SE
species	non-pool	4	24–29	27.25	23.722 to 30.778	2.2174	1.2561 to 8.2675	1.1087
species	all	4	32–36	34	31.095 to 36.905	1.8257	1.0343 to 6.8074	0.9129
species	Diff (1-2)			-6.75	-10.26 to -3.236	2.031	1.3088 to 4.4724	1.4361

	method	variances	DF	t	Pr > |t|
T-TESTS	Pooled	equal	6	-4.70	0.0033
	Satterthwaite	unequal	5.79	-4.70	0.0037
EQUALITY OF VARIANCES	method	DF (numerator)	DF (denominator)	F value	Pr > F
	Folded F	3	3	1.48	0.7571

3. Comparison of species numbers between created pools at BDB and natural pools

variable	site	N	range	mean	CL of mean	SD	CL of SD	SE
species	BDB	4	16–29	24	15.093 to 32.907	5.5976	3.171 to 20.871	2.7988
species	natural	6	21–29	24	20.887 to 27.113	2.9665	1.8517 to 7.2756	1.2111
species	Diff (1-2)			0	-6.182 to 6.1823	4.1533	2.8054 to 7.9568	2.681

	method	variances	DF	t	Pr > |t|
T-TESTS	Pooled	equal	8	0.00	1.000
	Satterthwaite	unequal	4.14	0.00	1.000
EQUALITY OF VARIANCES	method	DF (numerator)	DF (denominator)	F value	Pr > F
	Folded F	3	5	3.56	0.2053