APPLIED ISSUES

Animal and vegetation patterns in natural and man-made bog pools: implications for restoration

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SUMMARY

1. Peatlands have suffered great losses following drainage for agriculture, forestry, urbanisation, or peat mining, near inhabited areas. We evaluated the faunal and vegetation patterns after restoration of a peatland formerly mined for peat. We assessed whether bog pools created during restoration are similar to natural bog pools in terms of water chemistry, vegetation structure and composition, as well as amphibian and arthropod occurrence patterns.

2. Both avian species richness and peatland vegetation cover at the site increased following restoration. Within bog pools, however, the vegetation composition differed between natural and man-made pools. The cover of low shrubs, *Sphagnum* moss, submerged, emergent and floating vegetation in man-made pools was lower than in natural pools, whereas pH was higher than in typical bog pools. Dominant plant species also differed between man-made and natural pools.

3. Amphibian tadpoles, juveniles and adults occurred more often in man-made pools than natural bog pools. Although some arthropods, including Coleoptera bog specialists, readily colonised the pools, their abundance was two to 26 times lower than in natural bog pools. Plant introduction in bog pools, at the stocking densities we applied, had no effect on the occurrence of most groups.

4. We conclude that our restoration efforts were partially successful. Peatland-wide vegetation patterns following restoration mimicked those of natural peatlands, but 4 years were not sufficient for man-made pools to fully emulate the characteristics of natural bog pools.

Keywords: arthropods, birds, frogs, peat extraction, ponds, *Sphagnum*

Introduction

Each year, species go extinct because of habitat destruction and fragmentation and our use of natural resources is on the verge of provoking an extinction event which may be comparable with the five massive extinctions of the geological past (Pimm *et al.*, 1995; Mace, Balmford & Ginsberg, 1998). In response to this global trend, conservation biologists have developed numerous strategies to protect threatened populations and species (e.g. Noss, 1987; Scott *et al.*, 1993; Pressey, 1994; Moyle *et al.*, 2003). Among others, setting conservation areas has been a

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general approach adopted by governments and policy makers. Yet, the extent of these conservation areas is often too small for ecological and demographic processes. In other cases, lands may be already too disturbed to offer good conservation opportunities. Thus, restoration may represent an effective alternative to conservation.

Wetlands which have been intensively drained through agriculture, forestry or urban sprawl, have received increasing attention, especially regarding their restoration (e.g. Gibbs, 1993; Rubec, 1996; Zedler, 2000; Dodson & Lillie, 2001; Rozas & Minello, 2001; Sprenger, Smith & Taylor, 2002; Stevens, Diamond & Gabor, 2002; Petranka, Murray & Kennedy, 2003). This is also the case for peatlands, which are acidic freshwater wetlands covering, according to recent estimates, 4 million km^2 (i.e. 3–4%) of the planet's surface (Wheeler & Shaw, 1995; Maltby & Proctor, 1996). Because of the human disturbances mentioned above, as well as the intense mining of the peat deposits for horticultural and energetic purposes, few peatlands remain unaltered in many European countries (Joosten & Clarke, 2002; Chapman *et al.*, 2003). In North America, large expanses of *Sphagnum*-dominated peatlands are still untouched (Daigle, Gautreau-Daigle & Keys, 2001; Joosten & Clarke, 2002). Nonetheless, to supply the world's demand for peat, regions of south-eastern Canada (i.e. Québec and New Brunswick) have been under increasing pressure from peat mining in the last decades.

As currently mined sites become abandoned, there is increasing concern for their restoration potential, because the conditions prevailing at the end of peat mining are generally not favourable to successful recolonisation by flora and fauna (Wheeler & Shaw, 1995; Desrochers, Rochefort & Savard, 1998; Rowlands & Feehan, 2000; Campbell, Rochefort & Lavoie, 2003; Poulin *et al.*, in press). Pools are particularly vulnerable to peatland exploitation or conversion, and will generally not return unless measures are planned specifically for them. Restoration techniques have so far focused on the return of *Sphagnum* mosses and very few efforts have been undertaken to ensure that restored sites are favourable to fauna. In North America, the approach consists mainly in blocking drainage ditches and spreading plant diaspores (i.e. fragments of vascular plants and *Sphagnum* moss) collected in nearby natural peatlands (Rochefort, 2000;

Rochefort *et al.*, 2003). In many parts of Europe, where donor sites are rare, restoration is limited to flooding abandoned peatlands to protect the peat deposits against oxidation and decomposition (Wheeler *et al.*, 1995; Wheeler & Shaw, 1995; Lamers, Smolders & Roelofs, 2002; Smolders *et al.*, 2002, 2003). Although flooded sites may be frequented by aquatic birds, these sites do not present the surface patterns and characteristics found in most natural peatlands. In addition, such flooded areas are far larger than pools of natural peatlands and may prevent associated fauna to recover.

Pools are critical habitats for biodiversity in natural peatlands. They serve as migratory halts for birds (Desrochers, 2001), as foraging sites for amphibians (Mazerolle, 2005) and also as exclusive breeding habitats for certain species of arthropods (Danks & Rosenberg, 1987; Larson & House, 1990). Specific plant communities are also associated with these waterbodies (Barkman, 1992; Guinan *et al.*, 1998; Poulin, Rochefort & Desrochers, 1999). Pools are abundant in northern peatlands and often form large structured networks, but in southern peatlands, they are uncommon. Thus, the creation of pools in abandoned peatlands at these latitudes may significantly contribute to regional biodiversity. Restoration efforts consisting in the creation of bog pools (i.e. expanses of water similar in size and characteristics to those of raised bogs) are at their debut, and most efforts have been directed at the recolonisation of these waterbodies by vegetation (Money, 1995; Money & Wheeler, 1999).

In this paper, we asked how similar bog pools created during restoration are to natural bog pools, regarding their vegetation and faunal assemblages. As part of two independent field studies in south-eastern Canada, we quantified the occurrence of amphibians and arthropods in 70 natural bog pools and the effect of pool-scale variables in explaining the faunal patterns at the pools. Additionally, during a case study innovating on peatland restoration techniques in North America, we created eight bog pools in a restored peatland. We assessed the success of pool creation by monitoring the return of amphibians, arthropods and vegetation to the man-made pools during the following 4 years. Finally, we monitored the colonisation of the entire peatland site by vegetation and birds following restoration.

Methods

Arthropods and amphibians in natural bog pools

Study area. We conducted this work during 1999 and 2000 in three bogs (835–2315 ha) in eastern New Brunswick, with 6–12% of their surface mined for peat. These bogs were mined for peat at the time of the study, but still had large natural bog remnants (>752 ha) adjacent to mined surfaces and contained pools. Each study year, we selected a subset of 10–12 pools in each peatland through randomised stratified sampling across pool size and distance to the mined edge, for a total of 70 pools.

Faunal sampling. Amphibians and arthropods were sampled at each pool using plastic funnel minnow traps (43×23 cm width at largest diameter) with a mesh size of 4.8 mm^2. The number of traps deployed at each pool was proportional to pool size (Mazerolle & Cormier, 2003). Each trap was set for three consecutive nights and checked daily during different periods of the summer (between May and August). Individuals were identified to species and then released immediately. Total trapping effort at the pools varied between 18 and 144 trap nights, where one trap night equates to one trap open for one night.

Pool characteristics. We measured the following pool characteristics (see descriptive statistics in Table 1): perimeter, water depth within 1-m of pool edge and

Table 1 Descriptive statistics (mean ± SD) of natural bog pools of eastern New Brunswick, Canada ($n = 70$) and man-made pools ($n = 8$) during the restoration of a peatland in eastern Québec

Variable	Natural bog pools	Man-made pools
Perimeter (m)	199.4 ± 161.1	29 ± 0
Mean water depth (cm)	44.0 ± 21.8	44.0 ± 4.1
Distance to mined surface (m)	500 ± 402	–
pH	3.96 ± 0.19	4.52 ± 0.42
Shrub layer cover >50 cm (%)	1.8 ± 5.1	1.0 ± 1.7
Shrub layer cover 30–50 cm (%)	2.2 ± 3.5	0.4 ± 1.0
Shrub layer cover 10–30 cm (%)	14.5 ± 7.2	2.9 ± 4.1
Shrub layer cover <10 cm (%)	8.6 ± 6.5	1.2 ± 1.5
Herb cover (%)	10.3 ± 5.2	4.7 ± 5.3
Sphagnum moss cover (%)	79.6 ± 11.9	9.3 ± 12.2
Emergent vegetation cover (%)	5.4 ± 6.4	0
Floating vegetation cover (%)	8.8 ± 6.9	3.8 ± 10.6
Submerged vegetation cover (%)	14.6 ± 12.6	0

pH, the latter being the most likely to influence arthropod and amphibian occurrence (e.g. Gosner & Black, 1957; Pierce, 1985; van Straalen & Verhoef, 1997; Carbone, Keller & Griffiths, 1998). We surveyed the vegetation on the pool perimeter as well as within the pools (i.e. in water), using two adjacent quadrats set on each side of the water line. Quadrats measured 1×1.5 m, and were deployed proportionally to pool size (two to 36 quadrat pairs per pool). We categorised the percent cover of mosses, herbs, ericaceous shrubs (at four height classes), as well as floating, emergent and submerged vegetation based on the classes used by Mazerolle & Cormier (2003): <1% (individuals rare), 1–5% (individuals abundant but <5% cover), 5–25%, 25.1–50%, 50.1–75% and >75%. To reduce the number of vegetation variables, we summarised the vegetation data with principal components analysis (PCA, Lepš & Šmilauer, 2003). We retained the first four components, which explained a total of 76.6% of the variation of the data. The first axis (VEG1; 29.4%) was an index of tall shrubs and emergent vegetation cover, the second (VEG2; 21.0%) was correlated with low shrubs and moss cover, the third (VEG3; 14.4%) summarised herbs and floating vegetation, whereas the fourth axis (VEG4; 11.8%) was an index of submerged and floating vegetation. The principal component scores were used in subsequent analyses.

Statistical analyses. We quantified the effect of pool perimeter, water depth, distance to mined edge, pH and vegetation structure (i.e. VEG1-VEG4) on the occurrence of both tadpoles and metamorphosed individuals (i.e. adults and juveniles) of green frogs (*Rana clamitans melanota* Rafinesque) and leopard frogs (*Rana pipiens* Schreber) at bog pools. To do so, we used site-occupancy analyses, because we had several trapping periods at each pool within a given sampling year. This type of analysis estimates simultaneously the probabilities of occurrence and detection for a given species or taxa at a given set of sampled sites (for further details, see MacKenzie *et al.,* 2002, 2003; Bailey, Simons & Pollock, 2004; Mazerolle, Desrochers & Rochefort, 2005). It is especially well-suited for ecological scenarios where the probability of detecting individuals is <1. Based on the information-theoretic approach, we considered a set of candidate models (Burnham & Anderson, 2002). In all models, we added the intercept, and the categorical covariables site and year on the probability of

Amphibian data set	Arthropod data set
Site-occupancy models*	Regression models with effort as offset
ψ(site + year + perim) p(effort)	Site + year + perim
ψ(site + year + perim + pH) p(effort)	Site + year + perim + pH
ψ(site + year + perim + distmined) p(effort)	Site + year + perim + distmined
ψ(site + year + perim + watdepth) p(effort)	Site + year + perim + watdepth
ψ(site + year + perim + VEG1 + VEG2) p(effort)	Site + year + perim + VEG1 + VEG2
ψ(site + year + perim + VEG3 + VEG4) p(effort)	Site + year + perim + VEG3 + VEG4
ψ(site + year + pH) p(effort)	Site + year + pH
ψ(site + year + distmined) p(effort)	Site + year + distmined
ψ(site + year + watdepth) p(effort)	Site + year + watdepth
ψ(site + year + VEG1 + VEG2) p(effort)	Site + year + VEG1 + VEG2
ψ(site + year + VEG3 + VEG4) p(effort)	Site + year + VEG3 + VEG4

Table 2 Set of candidate models considered for site-occupancy analyses explaining the probability of occurrence (ψ) and detectability (p) of amphibians, and for regression analyses of the arthropod abundance in 70 natural bog pools of eastern New Brunswick. Notation for site-occupancy models follows Lebreton *et al.* (1992). Intercept included in all models.

Perim, pond perimeter; distmined, distance to mined edge; VEG1, index of tall shrub and emergent vegetation cover; VEG2, index of low shrub and moss cover; VEG3, index of herb and floating vegetation cover; VEG4, index of submerged and floating vegetation cover.
*Models with the same parameters on ψ were also computed for constant probability of detection, i.e. $p(.)$.

occupancy, and the intercept on the probability of detection (Table 2). More complex models were then built by adding combinations of independent variables to the basic models on the probability of occupancy or detection (Table 2). These analyses were conducted with the program PRESENCE 1.0 (MacKenzie *et al.*, 2003).

For arthropods, we could not use site-occupancy analyses because individuals of each arthropod taxa considered were captured at most of the bog pools (96–100%). Thus, we analysed the mean number of arthropods per pools instead, using negative binomial regressions or when appropriate, Poisson regression (McCullagh & Nelder, 1989; White & Bennetts, 1996). We accounted for variations in the sampling effort across pools by including it as an offset variable in all analyses (McCullagh & Nelder, 1989). Here, all models included the intercept, and the categorical covariables site and year (Table 2). For purposes of comparison with the site-occupancy analyses, we considered the same combinations of variables in the regression models. We used the GENMOD procedure of SAS 8.0 for regression analyses (SAS Institute Inc, 1993).

Following the analyses, the models of each data set were ranked according to the second-order Akaike information criterion (AIC$_c$). We then used model-averaging to compute the estimate of each parameter of interest based on the Akaike weight of each model (Burnham & Anderson, 2002).

Peatland restoration

Study area. To test the paludification approach to peatland restoration for sites after peat mining (Rochefort, 2000), we studied peatland regeneration and restoration processes at the ecosystem level, at the Bois-des-Bel (BDB) site, located 210 km northeast of Québec City, Canada (Fig. 1). This site of 11.5 ha, which was part of a 189 ha bog, had been mined for peat from 1972 through 1980. It was abandoned when the woody debris in the bottom peat layers became too numerous and decreased the quality of horticultural peat, leaving a deposit of approximately 2 m at the site. Land cover in the vicinity of the site consists of the following: 15% woodlands on well-drained soils, 6% peatlands, 79% agricultural fields (Lachance, Lavoie & Desrochers, 2005). The restoration of 8.4 ha of the site has been initiated in the autumn of 1999 in collaboration with the peat mining industry; the surface was levelled with machinery, drainage ditches were blocked and filled-in with shrubs from the surface of the site and berms were built to promote rewetting of the entire surface of the site. The vegetation was introduced mechanically on the peat
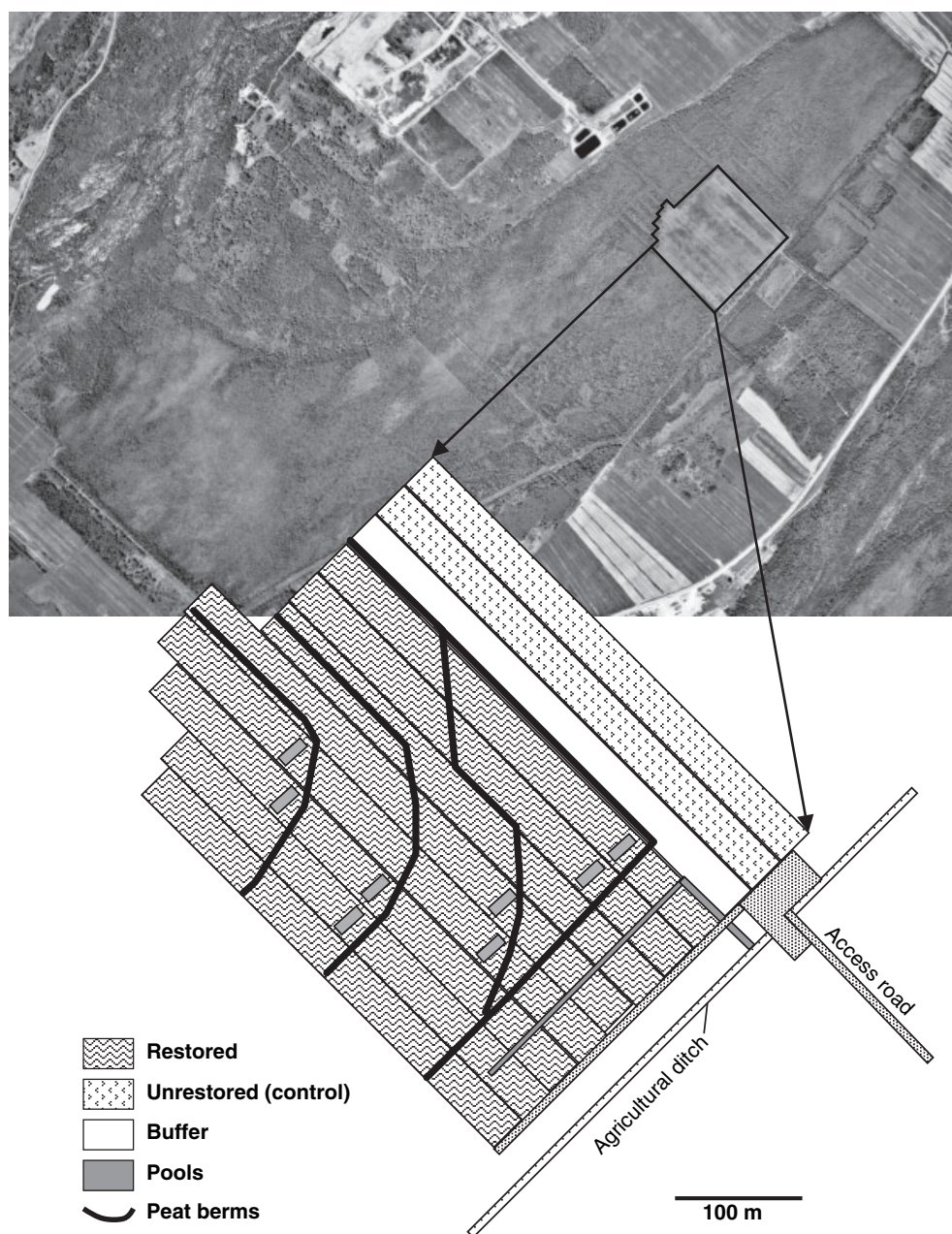
Fig. 1 Schematic representation of Bois-des-Bel (BDB) peatland restoration site in eastern Québec, Canada, illustrating the location of the pools created in 1999, berms and peat fields on which vegetation has been reintroduced.

surface to promote recolonisation. The first 10 cm of vegetation was collected mechanically in a nearby natural peatland. Plant fragments were then sprayed with a manure spreader on the abandoned surface in a ratio of 1 : 10 (1 m^2 collected material spread over every 10 m^2 of the restoration site). We added straw mulch and applied a light phosphorus ferti-lisation to promote plant regeneration.

Because of the long tradition of mining peat for horticulture in the Bas-St-Laurent region, bog pools in the area are rare (Lachance *et al.*, 2005). In an effort to restore past regional pool diversity, eight bog pools (8.5 × 6 m) were created (Fig. 1). We mimicked nat-ural bog pool topography by sloping the bottom of pools to obtain a shallow bank and a steep bank with a maximum pool depth of 1.2 m. Four of the pools

were stocked with aquatic vegetation, whereas we allowed the others to be recolonised through natural processes. We introduced individuals of five plant species in 2000 (taken from natural pools of the region), each were arranged in bunches covering an area of 25×25 cm^2. These consisted of *Sphagnum cuspidatum* G. F. Hoffman (introduced in the water column), *Rhynchospora alba* (L.) Vahl and *Utricularia cornuta* Michx. (introduced on bare peat on pool perimeters), *Carex limosa* L. and *Eriophorum virginicum* L. (planted 50–70 cm from the waterline on pool perimeters).

Colonisation of restored area

Vegetation colonisation. In order to assess site-wide colonisation by vegetation 4 years following restoration, we measured plant cover within 47 quadrats (3×8 m) established permanently at the site. Thirty-two quadrats were set in the restored area of the site, whereas 15 quadrats were established in the non-restored area. Quadrats were distributed so they would include the different plant communities of the site as well as the patterns of bare peat and dead wood ground cover. The percent cover of the following five strata was recorded in late August 2003: (i) mosses, (ii) herbaceous plants, (iii) ericaceous shrubs, (iv) trees and shrubs and (v) litter and bare peat. For comparison, the same strata were sampled in 92 natural peatlands of southern Québec (see Poulin *et al.*, 2002). A total of 214 quadrats (20×20 m) were deployed in these peatlands during the summer of 2000. Quadrats occurring close to open water were omitted to ensure comparison between terrestrial surfaces of BDB and the natural peatlands.

Avian colonisation. From 1993 to 2002, we conducted point count surveys on the BDB site at 3-year intervals to assess avian species richness. During a given year, we conducted surveys at two stations. The first was located in the area of the peatland to be restored, whereas the second was within an undisturbed area of the peatland and served as a reference. Point count surveys consisted in identifying all birds encountered within a 100-m radius at each station during a period of 10 min (Desrochers *et al.*, 1998). We conducted one to three point count surveys at each station each sampling year during the breeding season (28 May to 4 July).

Statistical analyses. We estimated species richness at each station for each sampling year, based on the jacknife estimator (Boulinier *et al.*, 1998; Hines *et al.*, 1999) to account for differences in detection probabilities across species. We then plotted the time series for station 1 and 2, to yield differences in avian community patterns.

Colonisation of man-made pools

Amphibian and arthropod sampling. During the summer months of 2000–2003, we conducted minnow trapping surveys at the pools to assess their subsequent colonisation by amphibians (2000–2003) and aquatic beetles (identified to species in the lab, 2000–2002). Here, we focused on aquatic Coleoptera (i.e. aquatic beetles), because several species of this taxa are peatland specialists (Larson, 1987), and their presence could indicate restoration success for this group. For purposes of comparison with natural bog pools, we also recorded other arthropod taxa present in the man-made pools during the minnow trapping sessions of 2003. Four minnow traps were deployed at each pool for one to three consecutive nights each month from May to August of each year, except in 2003 when we only trapped in June and July. Trap effort at each pool across years varied between 24 and 192 trap nights.

Pool characteristics. From 2000 to 2003, we monitored pH at the pools monthly. In 2003, we also measured vegetation recolonisation in each pool after restoration, by sampling six vegetation quadrats (30×30 cm) equally spaced along each of six transects, crossing the pools from bank to bank. Percent cover of all species was recorded within each quadrat.

Statistical analyses. For each sampling year, we used single season site-occupancy analyses *sensu* MacKenzie *et al.* (2002) to evaluate the probability of occurrence (corrected for detection) of amphibians at the man-made bog pools. We analysed tadpoles and metamorphosed individuals separately. For each group, we pooled all species together, as single-species data were too sparse. In our analysis, we considered four trapping periods (May, June, July and August). For each year, we compared a set of six models consisting of the following with either detectability constant or varying with trap effort: (i)

probability of occurrence constant, (ii) probability of occurrence depending on pH and (iii) probability of occurrence depending on plant introduction.

We evaluated the change in beetle species richness across years with respect to plant introduction, as single species were either too rare or too abundant for site-occupancy analyses. We used the program SPECRICH2 (Hines *et al.*, 1999) which employs the jacknife estimator technique of Burnham & Overton (1979) to compute species richness over several visits and to account for different probabilities of detection among species. We then used Poisson regression with trapping effort as an offset to assess changes in the species richness of aquatic beetles at each pool each year. We considered three models: (i) intercept only, (ii) intercept with pH and (iii) intercept with plant introduction.

We assessed the effect of pH and plant introduction on the occurrence of arthropod taxa in the pools 4 years after their creation. We considered three models with detectability constant because all pools were surveyed with the same effort in 2003: (i) probability of occurrence varying with plant introduction in the pools, (ii) probability of occurrence varying with pH and (iii) the probability of occurrence constant.

Results

Patterns at natural bog pools

Amphibian occurrence. Captures consisted mostly of green frogs and leopard frogs, as either metamorphosed individuals (juveniles and adults) or tadpoles (Table 3). Wood frogs (*Rana sylvatica* LeConte) also occurred at the pools, but in too few numbers for analyses. Based on minnow trapping data, the probability of amphibian occurrence varied across groups. Indeed, 20% of the pools in the study were occupied by green frog tadpoles, whereas the probability of occurrence was 0.48 for green frog adults and juveniles (Table 4). The algorithms for the analyses of leopard frog tadpoles did not converge, so we do not report these. Leopard frog adults and juveniles, however, had a probability of 0.7 of occurring at a pool (Table 4). Although models including vegetation structure variables sometimes ranked highly, we only detected a strong relationship in green frog tadpoles, which was influenced by the vegetation structure (VEG3 model-averaged estimate ± unconditional SE: 7.232 ± 2.612). That is, tadpole occurrence decreased with cover of

Table 3 Amphibian and arthropod abundance in 70 natural and eight man-made bog pools created in 1999 during a peatland restoration effort

Taxon	Mean individuals 100 trap nights^{-1} ± SD	
	Natural bog pools (1999–2000)	Man-made bog pools*
Amphibian tadpoles		
Green frog	2.1 ± 10.8	22.9 ± 64.8
Leopard frog	1.7 ± 7.4	0
Wood frog	0.01 ± 0.1	126.7 ± 195.8
American toad	0	13.3 ± 43.4
Amphibian juveniles/adults		
Green frog	1.6 ± 3.0	4.8 ± 5.2
Leopard frog	2.4 ± 3.0	–
Wood frog	1.0 ± 0.1	1.0 ± 1.9
American toad	0	0
Arthropods		
Coleoptera	62.3 ± 35.4	21.4 ± 18.0
Zygoptera	28.3 ± 21.4	0
Anisoptera	67.5 ± 40.6	2.6 ± 5.9
Hemiptera	44.0 ± 30.3	23.4 ± 34.0
Other arthropods	26.4 ± 27.1	0

*Mean for 2003, except for wood frog and toad tadpoles with means for 2000–2003.

herbs and floating vegetation (i.e. herbs and floating vegetation were negatively related to VEG3). Based on our minnow trapping data, we did not detect any effects of pool size, pool depth and distance to mined edge or pH on amphibian occurrence. Detection probability ± SE (obtained from 10 000 bootstraps) was 0.42 ± 0.003, 0.36 ± 0.01 and 0.48 ± 0.01, for green frog adults/juveniles, green frog tadpoles and leopard frog adults/juveniles, respectively.

Arthropod abundance. Several arthropod taxa were captured in bog pools (Table 3). These consisted of Coleoptera (Dytiscidae, Gyrinidae, Hydrophilidae), Zygoptera, Anisoptera (Aeshnidae, Libelulidae), Hemiptera (Belostomatidae, Corixidae, Gerridae, Nepidae, Notonectidae) as well as other arthropods (Diptera, Ephemeroptera, Hymenoptera, Orthoptera, Trichoptera, and Arachnida). Coleoptera abundance was only influenced by tall shrubs and emergent vegetation cover (VEG1) (Table 5). Zygoptera larvae captures increased with distance to the mined edge, pool pH and water depth, and were also influenced by vegetation structure at the pools (VEG1, VEG3, VEG4, Table 4). Anisoptera larvae abundance, on the other hand, was independent of all the variables

Table 4 Three highest-ranked site-occupancy models (i.e. based on Akaike weight) for amphibians in natural bog pools of eastern New Brunswick, Canada. Note that amphibian occurrence (ψ) was not influenced by any of the independent variables, with the exception of VEG3 for green frog tadpoles (see text for details). See Table 2 for variable names; $p(.)$ indicates that detectability was constant across periods.

Group	Highest-ranked model	Number of parameters	Akaike weight	P of occurrence*
Green frog tadpoles	ψ(site + year + perim + VEG3 + VEG4) $p(.)$	8	0.37	0.20 ± 0.05
	ψ(site + year + perim) $p(.)$	6	0.12	
	ψ(site + year + perim + pH) $p(.)$	7	0.11	
Green frog adults and juveniles	ψ(site + year + distmined) $p(.)$	7	0.30	0.48 ± 0.12
	ψ(site + year + VEG3 + VEG4) $p(.)$	8	0.13	
	ψ(site + year + distmined) p(effort)	8	0.10	
Leopard frog adults and juveniles	ψ(site + year + distmined) $p(.)$	7	0.23	0.70 ± 0.07
	ψ(site + year + distmined) p(effort)	8	0.14	
	ψ(site + year + VEG1 + VEG2) $p(.)$	8	0.10	

*Model-averaged estimates ± unconditional SE.

Table 5 Model-averaged regression estimates ± unconditional SE of variables explaining the abundance of arthropods in natural bog pools of eastern New Brunswick. Characters in bold indicate that 0 is excluded from the 90% confidence interval. All parameters were obtained with negative binomial regressions, except for damselflies estimated more efficiently with Poisson regression

	Perimeter	Water depth	pH	VEG1	VEG2	VEG3	VEG4	Distance to mined edge
Coleoptera	−0.040 (0.070)	−0.003 (0.071)	0.314 (0.437)	**−0.152 (0.051)**	0.033 (0.056)	−0.036 (0.064)	0.096 (0.072)	0.063 (0.071)
Zygoptera	0.103 (0.075)	**0.211 (0.069)**	**0.984 (0.408)**	**−0.159 (0.062)**	0.011 (0.064)	**0.152 (0.077)**	**0.254 (0.084)**	**0.151 (0.076)**
Anisoptera	0.0003 (0.056)	−0.038 (0.062)	−0.313 (0.376)	−0.025 (0.046)	0.003 (0.050)	0.074 (0.058)	0.061 (0.069)	0.053 (0.060)
Hemiptera	**0.110 (0.067)**	−0.117 (0.089)	0.365 (0.458)	0.043 (0.051)	**−0.118 (0.043)**	0.007 (0.074)	−0.001 (0.080)	**−0.142 (0.079)**
Other arthropods	−0.120 (0.115)	0.135 (0.112)	0.942 (0.713)	**0.138 (0.076)**	−0.084 (0.071)	0.132 (0.108)	**0.234 (0.127)**	−0.052 (0.110)

VEG1, tall shrubs, emergent vegetation; VEG2, low shrubs, moss; VEG3, herbs, floating vegetation; VEG4, submerged and floating vegetation.

considered (Table 5). Hemiptera abundance increased with pool perimeter, decreased with distance to mined edge, but was also influenced by the cover of low shrubs and mosses (VEG2). Finally, the captures of other arthropods (e.g. Diptera, Ephemeroptera, Trichoptera and Arachnida) depended only on the cover of tall shrubs, emergent vegetation, submerged and floating vegetation (VEG1 and VEG4).

Colonisation of restored area. Four years following restoration, vegetation cover had greatly increased on the site (Fig. 2). For instance, moss cover was almost 50% on the restored area, 25 times greater than in the non-restored area. Similarly, herb cover in the restored area was 19%, approximately twice that of the non-restored area. Furthermore, vegetation patterns in the restored area were closer to those of natural peatlands of the area than the non-restored area (Fig. 2).
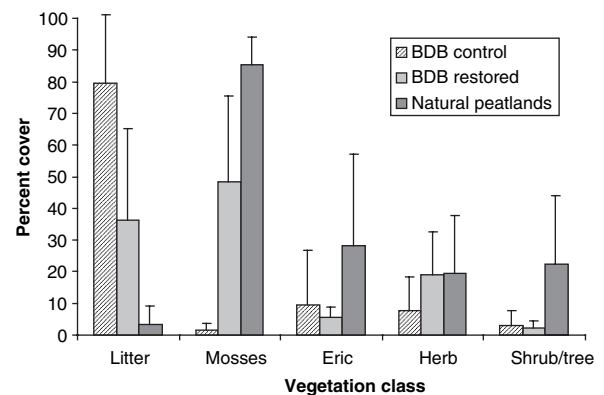

Fig. 2 Vegetation patterns in the control and restored areas of BDB compared with those of natural peatlands in the same geographic area.

Fewer bird species occurred in the area of BDB to be restored than in the undisturbed area, but we noted a net species increase in both areas in the years
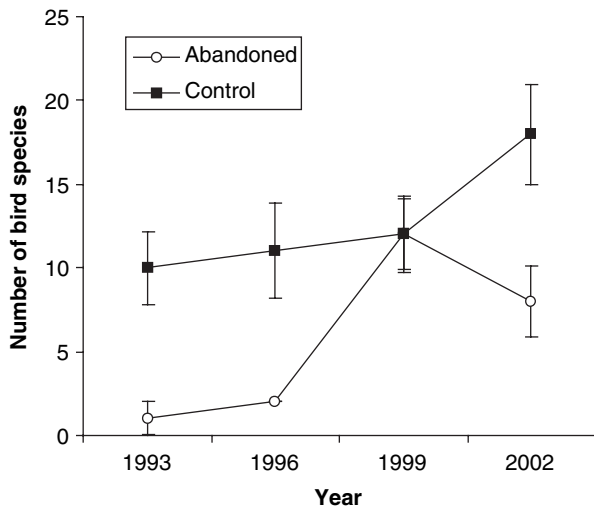
Fig. 3 Bird species richness accounting for species' detectability (*sensu* Hines *et al.*, 1999) based on point count surveys conducted between May and July in the area of the site abandoned after peat mining but restored in the autumn of 1999 and an undisturbed control area at the BDB site.

following the restoration of BDB in the autumn 1999 (Fig. 3). A number of peatland specialists, based on species' affinity for peatlands (Calmé, Desrochers & Savard, 2002), occurred at BDB. Lincoln's sparrow (*Melospiza lincolnii* Audubon), hermit thrush (*Catharus guttatus* Pallas), Nashville warbler (*Vermivora ruficapilla* Wilson) and common yellowthroat (*Geothlypis trichas* Linnaeus) were detected at the station within the area to be restored both before and after restoration. They were also detected in the undisturbed area of the peatland. In contrast, the palm warbler (*Dendroica palmarum* Gmelin), the magnolia warbler (*Dendroica magnolia* Wilson), the golden-crowned kinglet (*Regulus satrapa* Lichenstein), the ruby-crowned kinglet (*R. calendula* Linnaeus) and the white-winged crossbill (*Loxia leucoptera* Gmelin) were reported only in the undisturbed area.

Colonisation patterns of pools created during restoration

Pool characteristics. Pools quickly filled with water after their creation and maintained their shape (B. Drolet, unpublished bathymetric data). They retained water for the whole duration of the study, as is typical of natural bog pools. The mean pH of the pool water fluctuated slightly across and within years, without any general trend, with most measures lying between pH 4 and 5. Nonetheless, pH was consistently lower
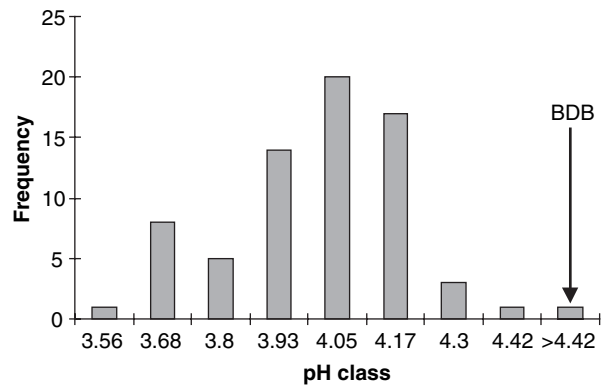

Fig. 4 Mean pH at the man-made pools at the Bois-des-Bel site (BDB) 4 years after restoration compared with the distribution of pH in 70 natural bog pools of eastern New Brunswick.

in natural pools than in the eight man-made pools 4 years after restoration, as the mean pH of the restoration site lay in the higher 1% of the tail of the distribution of the pH of natural bog pools (Fig. 4).

Vegetation structure at the pools 4 years following restoration differed significantly from the first year of restoration for all vegetation classes, but plant introduction had no influence on vegetation recolonisation (Fig. 5). Similarly, a DCA analysis (results not shown) revealed that there was no segregation between pools that were stocked with vegetation and those that were not. Although high shrub cover (>30 cm) at the man-made pools was similar to that of natural pools, the cover of low shrubs (<30 cm), submerged vegetation, emergent vegetation, floating vegetation and *Sphagnum* moss was consistently lower than in natural pools (Fig. 6). Dominant species also differed between man-made and natural pools (Table 6). *Typha latifolia*, seldom found in bogs, rapidly colonised pools and became dominant along with *Sphagnum* species and other mosses such as *Polytrichum strictum*. The other species colonising the man-made pools probably originated from the restored surfaces where a high diversity of plants was recorded only 4 years after restoration (J. Zhou, L. Rochefort, M. Poulin & U. Laval, unpublished data).

Amphibian occurrence. Three species of amphibians were captured, as either tadpoles or metamorphosed individuals, in the minnow traps set in the pools of the restoration site: wood frogs, American toads (*Bufo americanus* Holbrook) and green frogs. Wood frogs and green frogs successfully bred in the pools, as
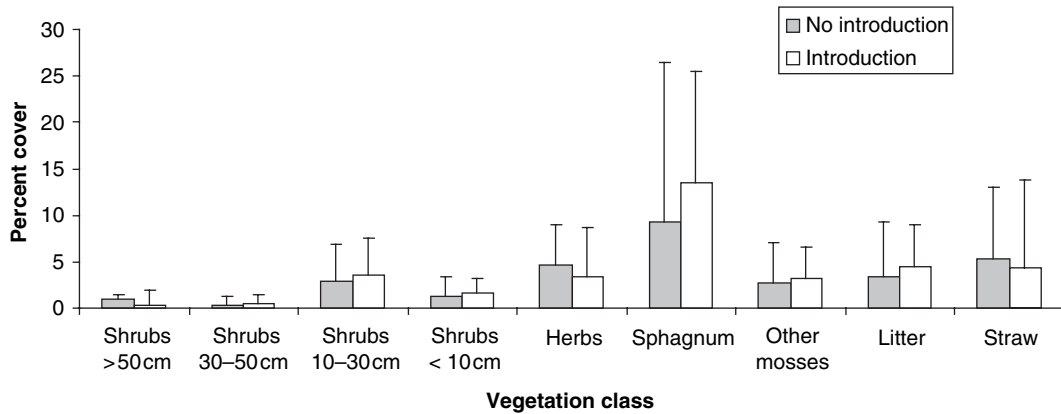
Fig. 5 Mean vegetation structure (±SD) at the pools 4 years after restoration differed significantly from that at the pools at the time of pool creation in 1999 (paired *t*-test with 7 d.f.). Note that no vegetation cover was present at the start of restoration. All variables were log-transformed except shrubs 10–30 cm, which already met normality requirements. Shrub layer >50 cm: $t = 2.95$, $P = 0.0214$; shrub layer 30–50 cm: $t = 2.95$, $P = 0.0214$; shrub layer 10–30 cm: $t = 5.49$, $P < 0.001$; shrub layer <10 cm: $t = 9.79$, $P < 0.0001$; herbs: $t = 17.25$, $P < 0.0001$; *Sphagnum* moss: $t = 11.78$, $P = 0.0214$; other mosses: $t = 11.78$, $P < 0.0001$; litter: $t = 8.97$, $P < 0.0001$; straw: $t = 4.61$, $P = 0.0025$. Vegetation cover 4 years after pool creation was independent of plant introduction ($P > 0.05$) and test statistics are not shown for brevity.

tadpoles and young-of-the-year were captured in subsequent years. Adult and juvenile amphibians were only captured in 2003 (green frogs and wood frogs), although based on tadpole captures, they frequented the site at the onset of the study (Table 3). Captures of green frog tadpoles and wood frogs were one to five orders of magnitude greater in man-made pools than in natural bog pools. Similarly, captures of green frog adults and juveniles were three times greater than in natural pools, whereas those of wood frogs were similar in both pool types.

After accounting for detectability, 60–88% of the pools was occupied each year by tadpoles. Because the maximum-likelihood estimations for adults and juveniles at the pools did not converge, we do not report on them here. Tadpole occurrence in 2000 was lower in the pools that had been stocked with plants (model-averaged estimate ± unconditional SE: −33.132 ± 5.435), but neither plant introduction nor pH had an influence on tadpole occurrence for any other year. Detectability of tadpoles with minnow traps in the man-made pools varied greatly across years, ranging from 0.43 to 0.75.

Aquatic beetle species richness. Nine out of the 12 species of aquatic beetles captured in minnow traps at the man-made pools were peatland-associated species (Larson, 1987; Smetana, 1988; Larson, Alarie & Roughley, 2000). These consisted of *Acilius semisulcatus* Aubé, *Colymbetes paykulli* Erichson, *C. sculptilis* Harris, *Dytiscus cordieri*

Aubé, *D. dauricus* Gebler, *D. harrisii* Kirby, *D. verticalis* Say, *Gyrinus sayi* Aubé and *Hydrobius fuscipes* (L.), whereas the species not associated with peatlands consisted of *D. fasciventris* Say, *Graphoderus perplexus* Sharp and *Gyrinus affinis* Aubé. The estimated species richness of aquatic beetles varied between one and nine species per pool in any given year, with considerable fluctuations within years. Neither pH nor plant introduction influenced species richness at the pools, regardless of the years after restoration. Indeed, for all 3 years, the intercept-only model was consistently the highest-ranked, being between 2.6 and 6.4 times better than the second-ranked model (i.e. based on the ratio of Akaike weights).

Arthropod occurrence. Four years after creation, the pools were occupied by Coleoptera, Anisoptera as well as Hemiptera (Belostomatidae, Nepidae) (Table 3). Captures of these species in man-made pools were 2–26 times fewer than in natural bog pools. The probability of occurrence of Hemiptera was 0.67 ± 0.19 (model-averaged estimate ± unconditional SE), whereas that of Coleoptera was 0.88 ± 0.13. Anisoptera were captured too infrequently to undergo site-occupancy analyses. This contrasts with the occurrence of these three taxa in the natural bog pools, which was between 96 and 100%. Regardless of the taxa, there was very little evidence for an effect of plant introduction on the probability of occurrence at the pools. Indeed, for Hemiptera and Coleoptera, the
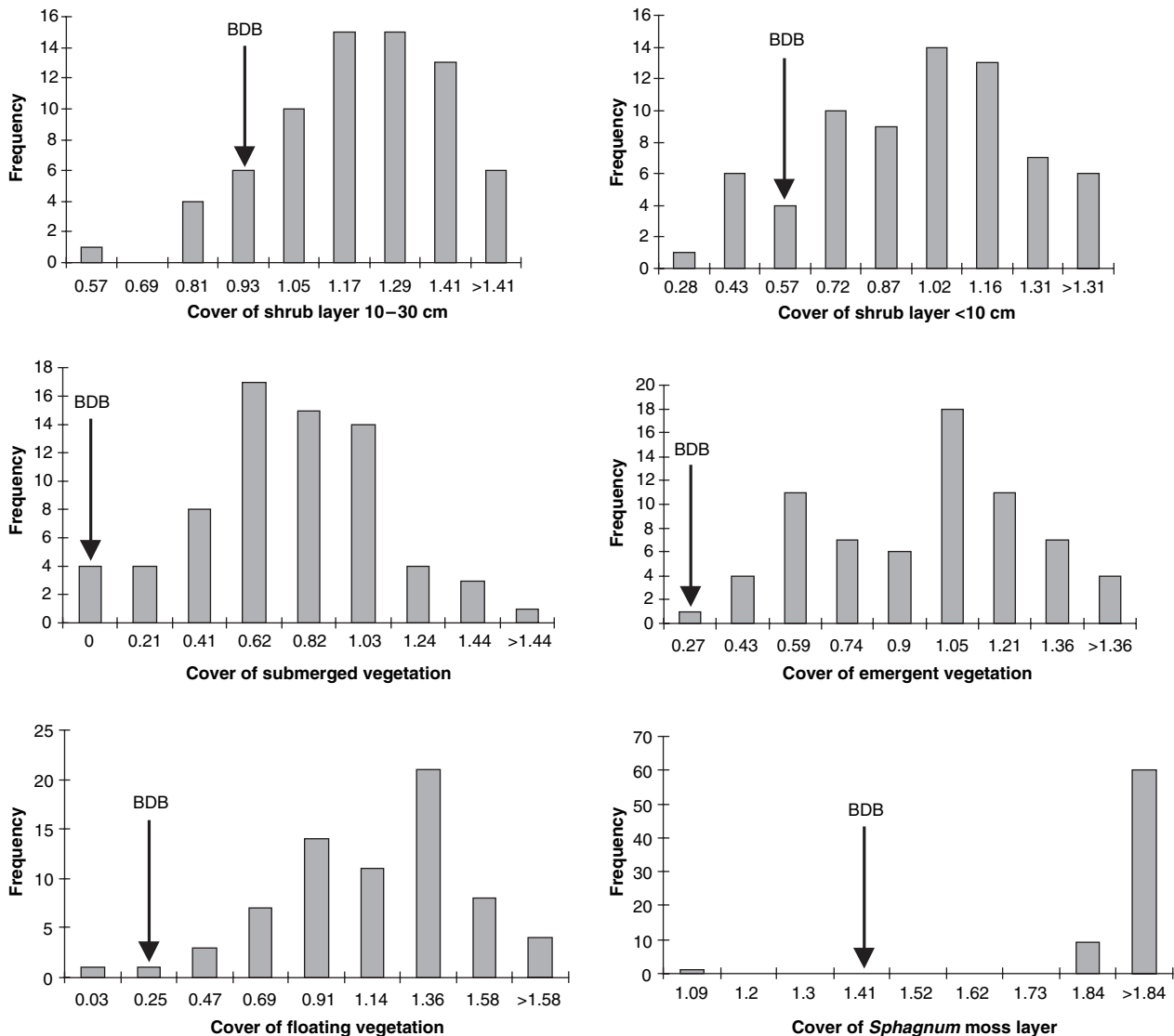
Fig. 6 Mean vegetation cover at the eight man-made pools at the Bois-des-Bel site (BDB) 4 years after restoration compared with the distribution of cover in 70 natural bog pools of eastern New Brunswick. All variables were log-transformed. For the sake of brevity, we only show the vegetation strata for which cover in man-made pools lay in the 15% of the tails of the distribution of natural pools.

intercept-only models were 13.3 and 49 times better than the ones with plant introduction (i.e. based on the ratio of Akaike weights), respectively.

Discussion

Colonisation of restored area

Vegetation patterns at the scale of the site showed marked differences between the restored and non-restored areas. Furthermore, the restored area of BDB was more similar to natural peatlands than to the non-restored area, which indicates that successful vegetation recolonisation was occurring, even only 4 years after restoration. In order for the recolonisation of peatland vegetation to occur, the site must be sufficiently rewetted. Wet conditions can be achieved in 3–7 years following restoration (Wheeler & Shaw, 1995; Price, Heathwaite & Baird, 2003). At BDB, the restoration practices, particularly those consisting in blocking drainage ditches and applying mulch to the surface, reduced the water lost from the peat and contributed to the establishment and growth of the vegetation. To our knowledge, no other restoration

	Natural	Man-made
Cover of species common to both pool types		
Sphagnum mosses	89.5 ± 20.2	21.6 ± 18.6
Mosses and liverworts	81.3 ± 12.4	4.4 ± 1.5
Chamaedaphne calyculata (L.) Moench.	11.2 ± 8.4	3.6 ± 1.7
Carex sp.	8.5 ± 9.0	0.5 ± 0.6
Nuphar variegatum Engelm.	6.6 ± 7.6	0.1 ± 0.3
Vaccinium oxycoccos L.	6.4 ± 4.9	0.5 ± 0.4
Drosera rotondifolia L.	3.2 ± 3.5	0.4 ± 0.3
Kalmia angustifolia L.	2.2 ± 2.6	0.1 ± 0.2
Litter	2.1 ± 9.5	2.2 ± 1.8
Kalmia polifolia Wangenh.	1.5 ± 1.7	0.1 ± 0.1
Eriophorum vaginatum L.	1.4 ± 2.2	2.8 ± 2.3
Eriophorum angustifolium Honckeny.	1.2 ± 2.6	2.5 ± 4.6
Algae	0.5 ± 1.9	0.9 ± 1.9
Ledum groenlandicum Oeder.	0.3 ± 0.6	0.6 ± 0.5
Cover of species only in natural bog pools		
Myrica gale L.	4.4 ± 7.8	
Andromeda polifolia L.	3.5 ± 3.7	
Gaylussacia baccata (Wangenh.) K. Koch	3.1 ± 4.6	
Empetrum nigrum L.	2.1 ± 3.2	
Picea mariana (Miller.) B.S.P.	2.1 ± 6.0	
Vaccinium macrocarpon Ait.	1.8 ± 3.5	
Gaylussacia dumosa (Andr.) Torr. & Gray	1.7 ± 2.4	
Rubus chamaemorus L.	1.0 ± 1.4	
Sarracenia purpurea L.	0.7 ± 1.2	
Xyris montana Ries	0.7 ± 1.5	
Lichen	0.6 ± 1.7	
Aronia melanocarpa (Michx.) Ell.	0.6 ± 1.7	
Utricularia cornuta Michx.	0.4 ± 1.0	
Eriphorum vaginatum L.	0.2 ± 0.5	
Larix laricina (DuRoi) Koch.	0.1 ± 0.6	
Calopogon tuberosus (L.) B.S.P. var. *tuberosus*	0.1 ± 0.2	
Cover of species only in man-made pools		
Typha latifolia L.		5.8 ± 5.1
Calamagrostis canadensis (Michx.) Beauv.		1.4 ± 2.0
Equisetum arvense L.		0.9 ± 1.2
Lycopus uniflorus Michx.		0.5 ± 0.9
Scirpus atrovirens Willd.		0.4 ± 1.0
Maianthemum trifolium (L.) Sloboda.		0.3 ± 0.8
Euthamia graminifolia (L.) Nutt.		0.3 ± 0.3
Salix myricoides Muhl.		0.2 ± 0.4
Solidago rugosa Miller.		0.2 ± 0.3
Betula papyrifera Marsh.		0.1 ± 0.2
Agrostis scabra Willd.		0.1 ± 0.3
Lysimachia terrestris (L.) B.S.P.		0.1 ± 0.3
Populus tremuloides Michx.		0.1 ± 0.1
Epilobium angustifolium L.		0.1 ± 0.1

Table 6 Mean percent cover ± SD of dominant species of natural bog pools of eastern New Brunswick, Canada ($n = 70$) and of man-made pools ($n = 8$) 4 years after the restoration of a mined peatland in eastern Québec

program has systematically assessed the restoration success of peatland vegetation at a large scale (>5 ha) and compared it to an undisturbed ecosystem. Subsequent vegetation surveys conducted in BDB in 2004 and 2005 revealed that the site is converging further towards natural peatland ecosystems.

Avian species richness increased at the site after restoration but several peatland specialists were never observed in the restored site. In a study in the same region, Desrochers *et al.* (1998) observed that bird species richness in natural peatlands was greater than in peatlands abandoned after having been mined for peat with the vacuum method. Because this method of peat extraction was used at BDB, our results suggest that habitat quality improved for birds at the site, but whether it was reverting to the characteristics of a

natural peatland remains to be determined by a more thorough analysis of species composition. Furthermore, the occurrence of certain peatland specialists increases with forest cover (Lachance *et al.*, 2005) and could explain their absence from the recently restored site.

Amphibians in natural versus man-made pools

Based on our analyses, amphibian tadpoles were more likely to occur in man-made pools than natural pools. This is not surprising as the man-made pools had not yet undergone full transformation into bog pools during our study, and specifically, the pH of the water was generally higher in the man-made pools than in bog pools. Acidity is an important parameter regulating amphibian distribution (e.g. Pierce, 1985; Wyman, 1988; Dunson, Wyman & Corbett, 1992) and likely explains the higher occurrence of amphibian tadpoles in the man-made pools. Indeed, typically fewer amphibians occur and breed in bog pools than in upland pools (Mazerolle, 2005).

In our study, amphibian species composition varied between natural bog pools and man-made pools. American toads first colonised the man-made pools, whereas they were absent from natural bog pools. In addition, no leopard frogs occurred at the restored site after 4 years, whereas they were frequent in natural bog pools. Restoration studies have documented that although amphibians quickly colonise man-made wetlands, composition differs with that of reference wetlands (Lehtinen & Galatowitsch, 2001; Pechmann *et al.*, 2001; Petranka, Kennedy & Murray, 2003; Hazell *et al.*, 2004). Yet, Stevens *et al.* (2002) observed that wetlands 2–7 years following restoration yielded higher anuran species richness and abundance than wetlands that had not been restored. Because of the low pH, bog pools are devoid of fish, and this feature of bog pools distinguishes them from permanent upland wetlands of the study area. This characteristic should be kept in mind when generalising from peatlands to other habitat types.

Amphibian movements are generally under 1 km (Dodd, 1996; Semlitsch & Bodie, 2003). Thus, the proximity of wetlands, and consequently, of colonising populations, are an important component of wetland restoration. In our study, the closest wetlands consisted of agricultural drainage ditches, artificial filtration pools and a freshwater marsh, 100 m, 300 m and 4 km from the restoration site, respectively. Amphibians occurring at the man-made pools of BDB may have originated from one or more of these sites.

Arthropods in natural versus man-made pools

Arthropod abundance was considerably lower in man-made pools than in natural pools. Nonetheless, Hemiptera and Coleoptera readily colonised the man-made pools. A number of pool characteristics, such as vegetation structure and pH, were important in determining arthropod abundance in natural bog pools. Although the occurrence of arthropods within coarse habitat types (e.g. fen, bog, marsh) is relatively well established (Danks & Rosenberg, 1987), detailed accounts on the effect of vegetation structure at bog pools remain scarce but are presently the focus of investigations in Europe (van Duinen, *personal communication*). For instance, in a peatland abandoned after the peat had been cut by hand, Cooper *et al.* (2005) reported that vegetation structure in ditches and peat pits strongly influenced the species composition of aquatic beetles. In the man-made bog pools of BDB, however, neither aquatic beetle species richness nor the occurrence of different arthropod taxa were influenced by plant introduction. This suggests vegetation in the man-made pools was not sufficiently developed to influence arthropod assemblages.

Based on our aquatic beetle data set, several peatland specialists colonised the man-made bog pools. This is not surprising for aquatic beetles, as most species fly during their adult life to colonise new habitats, find overwintering sites and leave pools that are changing or drying up (Larson *et al.*, 2000). Nevertheless, it is interesting to find highly specialised bog species only 2 years after the creation of pools at BDB. For instance, three individuals of *C. paykulli*, a species almost entirely restricted to the cold water of *Sphagnum* bogs (Larson *et al.*, 2000), were present at BDB in 2001. Considering that the nearest natural bog pools are located 40 km from the BDB peatland, this suggests that aquatic beetles have dispersal abilities to colonise newly created bog pools within this distance range.

Our results concur with those of numerous restoration studies on arthropods in terrestrial systems. In such systems, arthropods rapidly colonise restored sites, but species composition differs with that of

reference sites (Nelson & Andersen, 1999; Webb, Oliver & Pik, 2000; Mortimer *et al.*, 2002; Andersen, Hoffmann & Somes, 2003; Longcore, 2003; Nakamura, Proctor & Catterall, 2003; Nichols & Nichols, 2003; but see Grimbacher & Hughes, 2002). Data are scarce for restored wetlands. Some suggest that an invertebrate species richness and composition similar to reference sites can be achieved as quickly as 4 years following restoration (Stanczak & Keiper, 2004), whereas in other cases 17 years might still be insufficient (D'Amico *et al.*, 2004). In one of the rare peatland restoration efforts focusing on arthropods, van Duinen *et al.* (2003) documented that the species richness of bog-associated species was greater at sites restored between 1 and 29 years than at unrestored sites that had been abandoned before 1950. This may have resulted from a combination of variations in age, humidity, water chemistry and size of unrestored sites relative to restored sites (van Duinen *et al.*, 2003). In contrast with the whole site-rewetting approach used in Europe (e.g. Smolders *et al.*, 2002, 2003), we created different habitat types (i.e. pools versus drier adjacent areas with *Sphagnum* and other bog vegetation), and results suggest our approach facilitates colonisation by arthropods. Additional investigations are required to assess if this is the case for other taxa.

Peat mining proximity versus amphibians and arthropods

Although amphibian capture rates in open bog habitat are lower than in mined bog remnants (Mazerolle, 2003), we did not observe any effect of peat mining proximity on the occurrence of amphibians in pools of natural bog remnants. Similarly, during a landscape-scale study Mazerolle *et al.* (2005), using a combination of frog call and visual surveys, observed that distance to mined edge was not a good predictor of frog occurrence at bog pools, but depended mostly on the amount of pools and forest cover 100–1000 m from the pools. In contrast, mining proximity influenced some arthropod species in our study. Zygoptera larvae were most abundant at pools far from the mined edges, whereas Hemiptera were most abundant close to mined edges. Certain Zygoptera species are peatland specialists (Hilton, 1987; Larson & House, 1990). Thus, disturbances associated with peat mining such as peat dust fallout into pools may disrupt larval development and could explain the

negative influence of mining proximity, but this remains speculative and warrants further work. Hemiptera, on the other hand, are not bog-obligate species and occur in different wetland types (Scudder, 1987), which may explain the greater abundance of these taxa in pools near mined edges.

Management implications

Accounting for species' detectability. Our results highlight the importance of measuring detectability of the organisms under study, as most analyses assume it to be one. For instance, the probability of detection of amphibians in minnow traps in our study varied between 0.36 and 0.75. Mazerolle *et al.* (2005) have shown that assuming that species are detected perfectly when in fact detectability <1, increases the chance of reaching the wrong conclusions. Techniques to estimate species' detectability (e.g. MacKenzie *et al.*, 2002, 2003; Kéry, 2004) can be used with data based on repeated inventories (i.e. at least two visits/site) of fauna as well as vegetation and should be implemented whenever possible.

Stocking with vegetation. Of all the variables we considered for natural pools, vegetation cover both in the pool (floating vegetation) and on the perimeter (herb cover) decreased the occurrence of green frog tadpoles and did not influence adult or juvenile amphibians, whereas its effects varied across the arthropod taxa. Vegetation structure was more limited in the man-made pools, and there was generally little effect of plant introduction on vegetation as well as faunal recolonisation. Although bog plant species will return, this process will be slower than for fauna, as plants have lower dispersal rates than animals. Our results also indicate that to actually promote plant recolonisation in created bog pools, one should deploy greater effort than in our study by increasing the initial stocking density.

Long-term monitoring. Long-term monitoring is primordial in wetland restoration and a number of investigators make a strong case for it. Mitsch & Wilson (1996) maintain that wetland restoration projects should be evaluated after 15–20 years. In some cases, certain wetland characteristics sought (e.g. a given species assemblage or water quality) might not be attained even after 50 years (Zampella &

Laidig, 2003). For peatlands, Rochefort *et al.* (2003) suggested a functional ecosystem accumulating peat might be achieved 30 years after restoration. However, longer periods might even be needed for bog pool restoration. More importantly, periodical assessment is required to evaluate the dynamics of wetland restoration through time. Periodical assessments can help to identify problems early-on in the project, consequently reducing costs in time and resources, but also increasing the chances of restoration success.

Conclusion

Comparing the patterns and processes in restored wetlands with those in reference wetlands is crucial (Brinson & Rheinhardt, 1996), and some criteria of success must be established *a priori* to evaluate a given restoration effort. Gorham & Rochefort (2003) suggest that successful restoration of peatlands can be achieved when: (i) animal and plant species associated with peatlands of the same geographic area recolonise the site, (ii) the trophic structure of the organisms is similar to that before disturbance and (iii) productivity, decomposition and biogeochemical cycles typical of the original ecosystem before disturbance are balanced in order for peat to accumulate. Based on the first criterion, our restoration efforts have proved useful to some extent. Monitoring site-wide avian and vegetation patterns revealed that restoration increased bird species richness and promoted vegetation recolonisation by peatland specialists, although bird species richness in the restored area was lower than in the undisturbed area. At the scale of bog pools, however, our efforts were not as successful. Although some of the amphibian and arthropod species occurred in both natural and man-made pools, water quality and vegetation structure (particularly in the low shrub and moss layers), still differed between pool types. Nonetheless, this will undoubtedly change as the man-made pools progressively adopt bog pool characteristics but indicate that more than 4 years are required for bog pool restoration.

Acknowledgments

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