Changes in plant communities over three decades on two disturbed bogs in southeastern Québec

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Abstract

Questions: Have the natural plant communities of two mined bogs experienced changes in composition and richness over a three-decade period, and are these changes associated with anthropogenic disturbances?

Location: Bas-Saint-Laurent region, southeastern Québec, Canada.

Methods: We monitored three decades of floristic changes in two disturbed bogs by revisiting 57 plots in 1998, which were previously sampled in 1965 and 1966. Changes in species richness and composition were evaluated using Wilcoxon signed rank tests, principal component analysis and partial redundancy analyses (pRDA). We also used pRDA and an indicator species analysis to determine which species had undergone the greatest changes over time. Variation partitioning was used to evaluate the relative influence of human disturbance in compositional change.

Results: The main changes in the vegetation of the two bogs were 1) a decrease of overall species diversity, 2) an increase in the percent cover of trees and of species tolerant of shade or drought, and 3) a decrease in the cover of heliophilous species. *Picea mariana*, *Sphagnum fuscum* and *Pleurozium schreberi* increased in percent cover while *Chamaedaphne calyculata* and *Sphagnum rubellum* decreased in percent cover. Variation partitioning suggested that human activities had a significant impact on vegetation composition.

Conclusion: The results indicated that substantial changes occurred in the vegetation of the natural fragments of these severely disturbed bogs. Although human activities were partially responsible for the changes, our study suggested that the drying of the peat surface due to drought during the 1960s and 1980s may have contributed to the vegetation changes.

Introduction

Vegetation dynamics are mainly a product of temporal and spatial patterns of disturbance and climate regime (Pickett & White 1985). In addition, the floristic composition and dynamics of numerous ecosystems can be strongly influenced by human disturbances (White & Jentsch 2001). Since plants may take time to react to these disturbances, long term studies are essential to assess the direct or indirect impact of human activities on richness, composition and structure of vegetation assemblages. Although the importance of long term studies is widely recognized, these studies are difficult to perform due to logistical and monetary constraints. Various approaches have been used to overcome these problems including paleoecological analyses (e.g., Foster & Zebryk 1993), aerial photograph analyses (e.g., Peroni et al. 2000; Pellerin & Lavoie 2003a), repeated sampling of permanent plots (e.g., Pyšek et al. 2004; Taverna et al. 2005) and space-for-time substitution (e.g., Rehounkova & Prach 2006).

Long term studies of the vegetation dynamics of ombrotrophic peatlands (bogs) rely almost solely on paleoecological data, although such an approach can not detect changes over relatively short time intervals (<50 years). Recently, some studies have used modern aerial photography to investigate the vegetation dynamics of bogs

(Pellerin & Lavoie 2003a; Linderhom & Leine 2004; Pensa et al. 2004) but this approach generally does not detect subtle changes in species diversity. Therefore, repeated sampling of permanent plots is the most successful approach for quantifying recent compositional changes in peatland vegetation.

Few studies have used permanent plots to monitor changes in bog vegetation for longer than a decade (e.g., Backéus 1972; Frankl & Schmeidl 2000; Gunnarsson et al. 2002). According to these studies, few changes have occurred in the vegetation of bogs subjected to a low level of human disturbance. On the other hand, considerable changes have been observed on sites subjected to intense human activities. For instance, a major increase in the area dominated by *Pinus sylvestris* and *Betula pubescens*, associated with a decrease in the cover of *Sphagnum cuspidatum* and *S. magellanicum*, occurred between 1962 and 1992 in a bog in southern Germany in response to anthropogenic drainage (Frankl & Schmeidl 2000). Tree cover has also increased in drained bogs in Sweden and Switzerland (Freléchoux et al. 2000; Linderholm & Leine 2004). In southern Québec, a shift from bogs dominated by *Sphagnum* mosses to trees occurred between 1948 and 1995, probably resulting from the interaction of drainage, dry climatic periods and fire (Pellerin & Lavoie 2003a; Lavoie & Pellerin 2007).

The objectives of this study were to assess changes over three decades in the vegetation of natural remnants of two bogs that have been severely disturbed by peat mining with regards to: (1) species richness and composition, and, (2) the relationship of species change to anthropogenic disturbance. The vegetation of the two bogs was first described in

1965 and 1966, using several sampling plots. In 1998, we re-surveyed the plots using the same methods and then compared the surveys. We hypothesized that the plant species richness and composition of the two bogs had changed over this period of time and that these changes were related to anthropogenic disturbances.

Materials and Methods

Study sites

The two bogs used in this study were located in an agricultural plain bordering the southern shore of the St. Lawrence River in southeastern Québec, Canada. The original forest cover was mainly composed of *Acer saccharum*, *Betula alleghaniensis* and *Abies balsamea*, and these forests were almost completely cleared for cultivation during the first part of the 19th century. Today, the region is mainly cultivated fields with scattered woodlots, old fields and bogs. Most of the bogs have been disturbed intensively by human activities over the last 200 years through ditching for agricultural drainage, wood gathering, and peat mining (Pellerin & Lavoie 2003a).

The first bog studied, Rivière-Ouelle (47°27′N; 69°57′W), covers an area of 1655 ha (Fig. 1). Peat mining began in 1931, and by 1995 nearly 30% of the site had been mined (Desaulniers 2000). Mining activities are concentrated in the southwestern part of the bog, leaving a large fragment of the bog (1160 ha) unmined. The vegetation of this remnant is mainly dominated by *Sphagnum* mosses and ericaceous shrubs, with several scattered *Picea mariana*
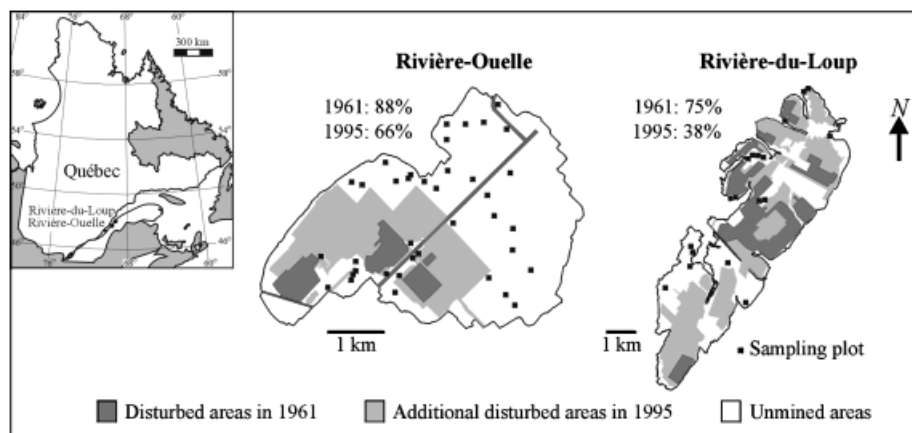

Fig. 1. Location of the Rivière-Ouelle and Rivière-du-Loup bogs (southeastern Québec) and spatial distribution of disturbed areas within each bog in 1961 and 1995. The percentage of unmined area in each bog is indicated for both years.

stands (Gauthier 1967). The second bog, Rivière-du-Loup (47°48′N; 69°30′W), covers an area of 3375 ha (Fig. 1). Peat mining began in the 1940s, and by 1995 approximately 62% of the bog area had been mined (Desaulniers 2000). Mined peat fields were located throughout the site, with several small unmined remnants characterized by dense *P. mariana* stands with some treeless sectors dominated by *Sphagnum* mosses and ericaceous shrubs (Gauthier 1967). Both sites were completely surrounded by agricultural fields, and most of their margins have been converted to agriculture (Desaulniers 2000).

The regional climate is wet and continental. The mean annual temperature is about 3°C. The mean temperatures in January (coldest month) and July (warmest month) are −13 and 18°C, respectively. The mean annual precipitation is 962 mm, 29% of which falls as snow (Environment Canada 2002). Recent analyses of climatological data available for the study area (1913-1995) indicated that the driest period of the record (especially in winter) was from 1955 to 1975. Other dry periods were recorded between 1913 and 1935, and in the 1980s (Girard et al. 2002; Pellerin & Lavoie 2003a).

Vegetation sampling

The two bogs were surveyed initially during the summers of 1965 and 1966 by Gauthier (1967). In these earlier surveys, a total of 101 sampling plots were located towards the center of homogeneous plant communities. The positions of all plots were carefully indicated on aerial photographs (1:15 000) taken in 1961. At each site, the vegetation was sampled within a 5 m×5 m plot using the phytosociological method of Braun-Blanquet (1932). A list of all species present in each plot was drawn up for six vegetation layers: canopy trees (> 250 cm high), lower trees (≤ 250 cm), upper shrubs (> 50 cm), lower shrubs (≤ 50 cm), non-woody vascular herbaceous, and nonvascular species (mosses, liverworts, lichens). The percent cover of each species in each layer was visually estimated according to seven classes, i.e., 0%, <1%, 1-5%, 6-25%, 26-50%, 51-75% and 76-100%.

In the summer of 1998, 57 of the 101 sampling plots (38 at Rivière Ouelle, 19 at Rivière-du-Loup) were relocated and sampled using the same method applied in 1965 and 1966. The vegetation of all the other plots had been eliminated by peat mining or agricultural activities. To ensure accurate comparisons of species composition between sampling years and to avoid edge effects, we located each sampling plot in the center of homogeneous plant commu-

nities. We standardized all species nomenclature to conform to the National PLANTS Database (USDA & NRCS 2006).

Although the 1961 aerial photographs were very useful for relocating the positions of the plots as precisely as possible, this task was difficult in several instances, and location inaccuracy may have introduced errors into the comparison of vegetation surveys. To verify whether differences observed in the vegetation records were due to errors in locating the original plots, we surveyed three additional plots located at 10, 20 and 40 m away from the expected location at four randomly selected sites (two on forest sites and two on treeless sites). These distances were considered reasonable estimates of potential relocation errors. The additional sampling plots were located along a straight line in a random and predetermined direction (North, South, East or West).

Mapping of anthropogenic disturbances

Aerial photographs (scale 1:15 000) taken in 1961 and 1995 (Ressources naturelles Canada 1961; Ministère des Ressources naturelles 1995), were used to map anthropogenic disturbances in the bogs. More precisely, each photograph was digitized, registered in space, corrected to limit geographical distortion (using Geographic Transformer software, Blue Marble Geographics 1998), and integrated into the geographic information system, MapInfo Professional (MapInfo Corporation 2002). The perimeters of disturbed surfaces (mined, cultivated, cut for wood) and drainage ditches located inside or bordering the bogs were then digitized on each of the georeferenced photographs. The smallest distance separating each sampling plot from the nearest disturbed sector and the nearest ditch was then measured. The percentage of disturbed surfaces (mined, cultivated, logging area) within a radius of 20, 50, 100 and 200 m from a sampling plot and the ditch density (m.ha^{-1}) within a radius of 60 m from the plot was also estimated for these aerial photographs. At shorter distances (< 60 m), a drainage ditch has an impact on the water table level of peaty soil significant enough to increase tree growth (Roy et al. 2000).

Data analyses

The midpoint of each cover class was used to evaluate means in statistical analyses. Rare species (percent cover <0.5%) were removed from the analyses (Legendre & Legendre 1998). All analyses

were performed using R software (Casgrain & Legendre 2001).

Relocation errors

Partial redundancy analyses (pRDA) were used to evaluate the potential impact of imprecisely located sampling plots. The pRDA was used as an equivalent of a multivariate ANOVA to look for differences between paired sites at different distances while controlling for temporal variation. For each of the four replicate sampling plots, five vegetation surveys were available: 1965 (survey 1), 1998 (survey 2), and the 1998 replicates sampled at distances of 10 m (survey 3), 20 m (survey 4) and 40 m (survey 5) from the plot used in survey 2. Five species cover matrices were formed by combining corresponding vegetation surveys across plots (e.g., all surveys 1, all surveys 2, all surveys 3). Hellinger's transformations were applied to species cover matrices to account for the presence of double zeros (Legendre & Gallagher 2001). The species cover matrix corresponding to the 1965 surveys was compared successively with the four other species cover matrices by vertically combining them in the pRDAs. Two 4×4 identity matrices were superimposed to pair sites within replicates (constraint matrix). A binary vector corresponding to the year of sampling (0 for 1965-1966 and 1 for 1998) was used as a covariable to remove temporal variation and compare sites with a spatial perspective only. The significance of the adjusted coefficient of determination, or redundancy statistic (Ra^2; Peres-Neto et al. 2006) was tested using permutation analysis of the raw data (Legendre & Legendre 1998). Permutations were tested until the probability differed from the critical level $\alpha = 0.05$ at a type II error of 0.01, or when the number of permutations reached 1000.

Species richness changes

Total species richness and the richness of specific vegetation layers (tree, shrub, non–woody vascular and nonvascular) of 1965-1966 vegetation records were compared to those of 1998 using non-parametric paired Wilcoxon's signed rank tests (normality was rejected for all layers according to Kolmogorov-Smirnov's test). The nonvascular plant layer was divided into categories including liverworts, lichens, *Sphagnum*, and "other" mosses.

Compositional changes

Prior to analyses, species cover matrices of 1965 and 1998 were superimposed vertically and Hellinger's transformations were applied to account for
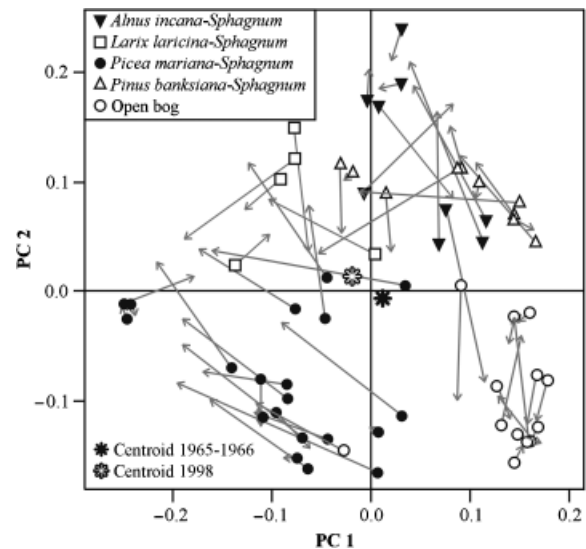

Fig. 2. Direction of vegetation change over time using principal component analysis of vegetation composition of the Rivière-Ouelle and Rivière-du-Loup bogs in 1965-1966 and 1998 (southeastern Québec). The position of the 57 plots sampled in 1965-1966 is represented by symbols (according to vegetation type described by Gauthier (1967)) and arrows indicate the direction of change through time. Centroids of each sampled period are also indicated. Vectors are scaled to unit length to respect relationships between sites.

the presence of double zeros. Changes in species abundances were used to produce an ordination graph using principal component analysis (PCA). In addition, pRDA was used as an equivalent of a multivariate paired *t*-test to statistically verify the effect of time on species composition within sampling plots. To this end, a binary vector corresponding to the year of sampling of each plot was used to constrain the ordination. Additionally, a binary matrix was built by vertically combining two 57×57 identity matrices in order to increase the power of the test by restricting the analysis to paired plots over time. Additional pRDAs were done to verify the effect of time on species composition within sampling plots of each vegetation type described by Gauthier (1967) (Fig. 2). The significance of the Ra^2 of the time vector was tested using permutation analysis as described above.

Species with greatest changes over time

Two different methods were used to identify the species with the greatest changes in cover over time. The first relied on the pRDA of time described earlier. Species with the highest absolute projection on the canonical axis were considered to be the species

with the greatest changes in cover between 1965 and 1998. The second method used the *IndVal* indicator species analysis to examine the relationships of individual species with the sampling period (Dufrêne & Legendre 1997). This method assessed the degree of specificity (uniqueness to a particular group) and fidelity (frequency of occurrence within a particular group) of species in groups defined *a priori*, based on the year of sampling. A high positive difference of *IndVal* between 1998 and 1965 indicated an increase in cover and frequency for a species over this time interval while a negative difference indicated a decrease in species cover.

Human impact

We verified whether any significant impact of time on plant composition was related to human activities using variation partitioning (Borcard et al. 1992). More precisely, we tested whether the variation associated with time remained significant after controlling the joint effect with anthropogenic variables. The species cover matrix described for the previous pRDA analysis was used. The normality of each anthropogenic variable was examined using Kolmogorov-Smirnov tests in the R software. Non-normal variables were transformed to meet assumptions of normality (Table 1). The different fractions of the variation were obtained following the series of RDA and pRDA detailed in Legendre & Legendre (1998) using the binary vector of the sampling year and the matrix formed by all standardized anthropogenic variables. The significance

Table 1. Anthropogenic variables used in variation partitioning to test whether these variables individually or as a whole affected the succession of vegetation between 1965-1966 and 1998 at the Rivière-Ouelle and Rivière-du-Loup bogs (southeastern Québec). ✶ = normality not rejected in Kolmogorov-Smirnov test after transformation ($\alpha = 0.05$). The specific type of transformation used to reduce skewness and maximize normality is also presented.

Variable	Description	Transformation
DDit	Distance from the plot to the closest drainage ditch (m)	BoxCox ($y = 0.079$)✶
DMin	Distance from the plot to a mined or cultivated sector (m)	$y' = \ln(y+1)$
PDis20	Percentage of disturbed area within a 20 m radius from the sampling plot	BoxCox ($y = -7.921$)
PDis50	Percentage of disturbed area within a 50 m radius from the sampling plot	BoxCox ($y = -1.805$)
PDis100	Percentage of disturbed area within a 100 m radius from the sampling plot	BoxCox ($y = -0.381$)
PDis200	Percentage of disturbed area within a 200 m radius from the sampling plot	BoxCox ($y = 0.093$)
DenDit	Drainage ditch density (m/ha) within a 60 m radius from the sampling plot	BoxCox ($y = -1.320$)

of testable fractions was tested using permutation analysis as described above.

To identify which of the anthropogenic variables was most important in the composition of the vegetation, several pRDA's were performed by constraining the species cover matrix with each individual variable in turn, while controlling for time. The severity of the impact on vegetation was evaluated by comparing Ra^2. The significance of each variable was tested by permutation analysis as described above.

Results

Relocation errors

The Ra^2 of the site-pairing matrix (Table 2) was significant for all distances (0, 10, 20 and 40 m). Therefore, the vegetation was more similar over time within the same site (even between those separated by 40 m) than between records from different sites. Even though there was an error of up to 40 m in relocating the original plot from 1965-1966 to 1998, sampling error should have had only a minor impact on the trends in change over time in the vegetation of these sites.

Species richness changes

A total of 125 species were recorded in the 57 plots sampled in 1965 and 1966, while only 92 species were recorded in 1998. The species richness for all sampling times (1965-1966 and 1998) included 139 native species (App. 1). The total richness decreased by a mean of 1.8 (± 4.3) species per plot (5 m × 5 m) between 1965-1966 and 1998 (Table 3), and was apparent especially in stands of *Larix laricina*. In open sites dominated by *Sphagnum* mosses and ericaceous shrubs, the total species richness increased (mean = 0.6 species ± 0.05) between 1965-

Table 2. Adjusted *R*-Square (Ra^2) and associated probabilities of the sampling plot-pairing matrix (n = four sampling plots) used to evaluate the potential impact of a misrelocation of a 1965-1966 sampling plot in 1998 at the Rivière–Ouelle and Rivière-du-Loup bogs (southeastern Québec). ✶ = significant constraint ($\alpha = 0.05$).

Compared matrices	Ra^2 values	Probability
1965-1998 (0 m)	0.246	0.022✶
1965-1998 (10 m)	0.353	< 0.001✶
1965-1998 (20 m)	0.329	0.005✶
1965-1998 (40 m)	0.221	0.014✶

Table 3. Mean species richness changes per plot (57 plots of 5 m×5 m) between 1965-1966 and 1998 in the Rivière-Ouelle and Rivière-du-Loup bogs (southeastern Québec). Associated probabilities of the paired Wilcoxon test, corrected for multiple testing with Holm's procedure, are presented. * = significant difference ($\alpha = 0.05$).

Vegetation layer	Mean species richness change per plot	Probability
All layers considered	− 1.754	0.004*
Tree	− 0.053	0.595
Shrub	− 0.614	0.032*
Non woody vascular	− 0.561	0.017*
Nonvascular	− 0.526	0.043*
Liverwort	0.018	1.000
Lichen	− 0.228	0.038*
Sphagnum moss	0.518	0.469
Other mosses	− 0.474	0.007*

1966 and 1998. A significant decrease in species richness also occurred for most vegetation types (Table 3) except for species of trees, liverworts and *Sphagnum* mosses.

Compositional changes

The time-constrained pRDA performed on all sample plots showed that the overall change in species composition over the three–decade period was minor but statistically significant ($Ra^2 = 0.006$; $P < 0.005$). This low level of significance is likely related to the large number of species in the data set (125) and to the small size of the sampling plots (5 m×5 m). The pRDAs constrained by time for stands of *Larix laricina-Sphagnum* and *Picea mariana-Sphagnum* as well as for open bog were also significant ($Ra^2 = 0.015$; $P < 0.03$, $Ra^2 = 0.028$; $P = 0.005$ and $Ra^2 = 0.047$; $P < 0.005$ respectively) while the pRDAs were not significant for stands of *Alnus incana-Sphagnum* and *Pinus-Banksiana-Sphagnum* ($Ra^2 = 0.018$; $P = 0.12$ and $Ra^2 = 0.012$; $P < 0.12$ respectively).

Changes in species composition between 1965-1966 and 1998 at Rivière-du-Loup and Rivière-Ouelle bogs were apparent because the positions changed for the centroids of the plots and for individual plot in the two first axes of the PCA (Fig. 2), which represented 34.5% of the variance (19.5% for axis 1 and 15% for axis 2). The centroid of the plots shifted to the left from 1965-1966 to 1998. This shifting can be interpreted as an overall increase of the cover of tree species, especially *Picea mariana* and of shade or drought-tolerant species such as *Pleurozium schreberi*, *Rhododendron canadense* and *Sphagnum fuscum*. This shift to the left
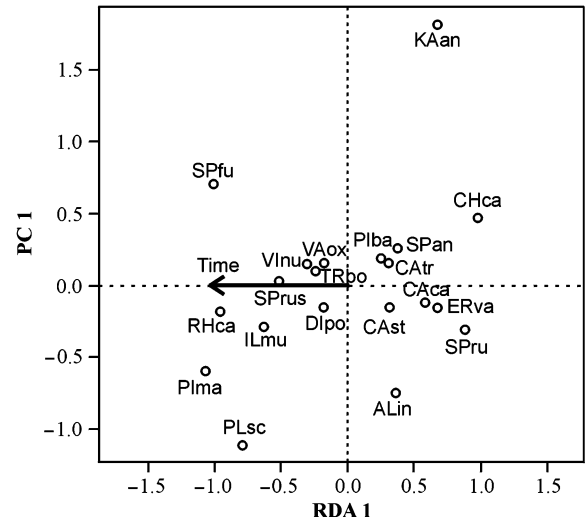

Fig. 3. Species and time vectors of the partial redundancy analysis of species abundances constrained for time realized with the Rivière-Ouelle and Rivière-du-Loup bogs (southeastern Québec) vegetation data set. Only the 10 species with both the highest positive and negative projections on the canonical axis are reported. Species acronyms are based on the first two letters of genus and species name (full names of species are provided in Table 4).

also indicated a decrease of the cover of more shade-intolerant species such as *Sphagnum rubellum* and *Chamaedaphne calyculata* (Fig. 3).

No strong directional change in species composition was detectable by the PCA (Fig. 2). Indeed, the vegetation responses based on individual sampling plots were inconsistent, i.e. the arrows indicating the trends of variation in floristic composition were pointing in several directions. However, most of the 19 plots that were classified as *Picea mariana-Sphagnum* stands by Gauthier (1967) shifted to the left between 1965-1966 and 1998 (Fig. 2). This shifting, including that of the centroid, indicates a densification of the cover of forest species and a decrease of the cover of shade-intolerant species. For instance, the cover of *Pleurozium schreberi* increased between 1965-1966 and 1998 an average by 39% (± 30%) in eight of the *Picea mariana-Sphagnum* stands. On the other hand, the cover of *Chamaedaphne calyculata* decreased an average of 24% (± 20%) in all but one stand where it was present. The cover of *Sphagnum rubellum* also decreased an average by 37% (± 30%) in six of the eight plots where it was recorded.

Most of the plots surveyed in 1998 did not change in vegetation type following Gauthier (1967; Fig. 2). However, one of the *Alnus incana-Sphagnum* plots changed to open bog. This change illustrated

the major decrease of the *Alnus* cover (from 88% in 1965 to 3% in 1998), the complete disappearance of *Carex stricta* (from 88 to 0%) and the important increase of ombrotrophic species such as *Eriophorum vaginatum* ssp. *spissum* (from 0 to 38%) and *Kalmia angustifolia* (from 0 to 40%) in this plot. Lastly, compositional changes in open bogs were minor compared to those in forested stands as based on the length of arrows in the PCA (Fig. 2).

Species with greatest changes over time

Based on their projection on the canonical axis representing time, the cover of 84 species declined while that of 55 species increased between 1965-1966 and 1998. Similarly, differences in indicator values showed that 88 species declined, 11 remained stable and 40 species increased in cover and frequency (number of sampling plots where a species was identified) between 1965-1966 and 1998. The ten species with the greatest degree of both positive and negative changes generally stood out from the distribution of values in the two analyses and consequently were kept for interpretation (Fig. 3; Table 4). *Ledum groenlandicum* was a notable exception, having contradictory responses in the two analyses; the pRDA indicated a slight increase over time while the *IndVal* suggested a significant decrease of the cover and frequency of this species. A mean decline of 0.4% per sampling plot was observed for this species, although marked differences were found between individual plots (from -37.5 to $+49.5\%$), which could explain the discrepancy between the analyses.

Human impact

Anthropogenic variables and time explained a significant, albeit small, part of the vegetation composition of the two bogs studied (Fig. 4). Variables associated with anthropogenic disturbances, regardless of the year of sampling, had a greater impact on the composition of vegetation than change over time. However, removing the joint effect of time and anthropogenic variables attributed equally (i.e., the impact of increased human activities over time on vegetation) left the impact of time still significant, corresponding to 0.9% of the total variance of the matrix. This means that some of the changes in species composition between 1965-1966 and 1998 could not be ascribed to the increase of human disturbances in the bogs studied as measured by our variables. The Ra^2 of this time-structured anthropogenic impact was very low and negative,

Table 4. List of the species that experienced the highest increase and decrease (cover and frequency) between 1965-1966 and 1998 in the Rivière-Ouelle and Rivière-du-Loup bogs (southeastern Québec) based on A) their projection on the time axis in the partial redundancy analyses and B) their difference of indicator values over time in the *IndVal* indicator species analysis. Only the ten species with the highest decrease or increase in cover and frequency are presented.

| Rank	(A) Projection on time axis		(B) Difference of indicator values	
	Species	Projection	Species	Difference
Increase in cover and frequency				
1	*Picea mariana*	-1.074	*Sphagnum fuscum*	22
2	*Sphagnum fuscum*	-1.010	*Sphagnum russowii*	18
3	*Rhododendron canadense*	-0.959	*Rhododendron canadense*	16
4	*Pleurozium schreberi*	-0.791	*Ilex mucronata*	15
5	*Ilex mucronata*	-0.637	*Pleurozium schreberi*	11
6	*Sphagnum rusowii*	-0.517	*Trientalis borealis*	10
7	*Viburnum nudum* var. *cassinoides*	-0.309	*Dicranum undulatum*	9
8	*Trientalis borealis*	-0.245	*Vaccinium oxycoccos*	9
9	*Dicranum polysetum*	-0.187	*Dicranum polysetum*	9
10	*Vaccinium oxycoccos*	-0.179	*Picea mariana*	1
Decrease in cover and frequency				
1	*Chamaedaphne calyculata*	0.972	*Eriophorum vaginatum* ssp. *spissum*	-27
2	*Sphagnum rubellum*	0.880	*Chamaedaphne calyculata*	-24
3	*Kalmia angustifolia*	0.672	*Carex trisperma*	-17
4	*Eriophorum vaginatum* ssp. *spissum*	0.668	*Sphagnum angustifolium*	-15
5	*Calamagrostis canadensis*	0.580	*Calamagrostis canadensis*	-15
6	*Sphagnum angustifolium*	0.377	*Sphagnum rubellum*	-14
7	*Alnus incana* ssp. *rugosa*	0.359	*Kalmia angustifolia*	-12
8	*Carex stricta*	0.314	*Alnus incana* ssp. *rugosa*	-10
9	*Carex trisperma*	0.300	*Ledum groenlandicum*	-9
10	*Pinus banksiana*	0.243	*Polytrichum commune*	-9
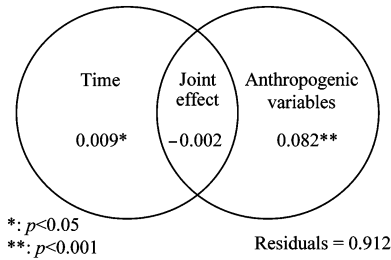
Fig. 4. Venn diagram showing the partition of the total variation (Ra^2) in vegetation composition of the Rivière-Ouelle and Rivière-du-Loup bogs (southeastern Québec). The joint fraction and residuals could not be tested for significance because these were obtained by subtraction.

Table 5. Importance of the single effects of anthropogenic variables on the vegetation of the Rivière-Ouelle and Rivière-du-Loup bogs (southeastern Québec) according to partial redundancy analyses where time is a covariable. ∗ = constraint is significant ($\alpha = 0.05$).

Anthropogenic variables	Ra^2	Probability
Distance from the plot to the closest drainage ditch (m)	0.03571	< 0.001*
Distance from the plot to a mined or cultivated sector (m)	0.03504	< 0.001*
Drainage ditch density (m/ha) within a 60 m radius from the sampling plot	0.03411	< 0.001*
Percentage of disturbed area within a 200 m radius from the sampling plot	0.02192	< 0.001*
Percentage of disturbed area within a 100 m radius from the sampling plot	0.01672	0.003*
Percentage of disturbed area within a 50 m radius from the sampling plot	0.00616	0.061
Percentage of disturbed area within a 20 m radius from the sampling plot	− 0.00025	0.453

showing that time and human activities had different individual effects on the vegetation of the two bogs.

Measures of distances to disturbance, in particular to the closest drainage ditch, better predicted the impact of human disturbances on vegetation than the percentage of disturbed areas around a site (Table 5). Variables with the largest impact were, in decreasing order, the distance to the closest drainage ditch (*DDit*), the distance to a mined or agricultural sector (*DMin*), the ditch density (*DenDit*), the percentage of disturbed area within a 200-m radius (*PDis200*), and the percentage of disturbed area within a 100-m radius (*PDis100*). However, the impact of these disturbance variables remained low, with an Ra^2 varying between 0.04 and 0.02. For most plots, the value for the distance to a mined or agricultural sector was equivalent to the distance to the closest drainage ditch, explaining the similar

impact of these variables on vegetation. Drainage ditches are usually constructed for mining or agricultural purposes. Human disturbance still had an impact on vegetation at 200 m from a sampling plot, as the Ra^2 increased between a radius of 100 and 200 m (Table 5) and remained significant ($Ra^2 = 0.010$, $P = 0.01$), even when removing the effect of disturbances present at a shorter distance. The impacts of disturbances within radii of 20 and 50 m were not significant (Table 5). The small number of plots affected by disturbances within such short distances (three plots in radius of 20 m and 15 plots in radium of 50 m) could partially explain the lack of significance.

Discussion

Vegetation dynamics

Recent shifts in the vegetation composition of disturbed bogs associated with a decrease in the diversity of true ombrotrophic species have been demonstrated in both Europe (Frankl & Schmeidl 2000; Freléchoux et al. 2000; Linderhom & Leine 2004) and North America (Pellerin & Lavoie 2003a). We also observed rapid changes within the natural plant communities of the two bogs in our study in southeastern Québec. The main changes observed were a decrease in the overall species diversity, and a general increase in the cover of tree and shade-tolerant species (e.g., *Picea mariana*, *Pleurozium schreberi*) associated with a decrease in the cover of more heliophilous species (e.g., *Chamaedaphne calyculata*). These changes were likely the result of tree–cover densification and tree stand aging. The increase of shading associated with a growing tree layer is known to lead to the replacement of lower vegetation layers typical of bogs by forest floor species such as *Pleurozium schreberi* (Laine & Vanha-Majamaa 1992; Laine et al. 1995; Frankl & Schmeidl 2000; Gunnarsson et al. 2002; Lachance et al. 2005), and to the reduction of the regional biodiversity (Laine et al. 1995; Lachance et al. 2005). Observed changes in this study were less evident in open *Sphagnum*-dominated sites than in forested sites. Resistance to change, or the stability, of *Sphagnum*-dominated ecosystems has been demonstrated in other studies (e.g., Backéus 1972; Klinger 1996). This resistance is likely related to the fact that *Sphagnum*-dominated ecosystems are nutrient-poor, and with a slow nutrient turnover rate and low production, even though small changes in vegetation might indicate enduring

changes in the environment (Gunnarsson et al. 2000).

Over the 32-year period, many more species decreased (decreasers) than increased (increasers) in cover and frequency. More than 80 species were decreasers in both analyses while between 40 and 50 species were increasers. The two methods used to identify increasers and decreasers produced nearly identical results, which ensured their reliability. All of the top ten increasers and decreasers were perennial species and almost all were clonal. These characteristics should favour their persistence and resistance to environmental changes (Gunnarsson et al. 2002). Thus, the observed changes in this study likely reflected long term directional changes in the vegetation communities rather than inter-annual fluctuations (Nordbakken 2001; Gunnarsson & Flodin 2007).

The composition of the top ten increasers and decreasers reflected the overall changes in the vegetation of the two bogs, i.e. an increase or densification of the forest cover. Almost all increasers (e.g., *Picea mariana*, *Rhododendron canadense*, *Sphagnum russowii*, *Pleurozium schreberi*, *Trientalis borealis*, *Dicranum polysetum*) were forest species, which were able to tolerate shade and drought (Damman & Dowhan 1981; Gignac 1992; Laine & Vanha-Majamaa 1992; Lachance & Lavoie 2004). The increaser *Sphagnum fuscum* does not tolerate shade, its cover increased almost exclusively in open habitats (between 3 and 63%). Since *S. fuscum* is one of the most drought-tolerant *Sphagnum* species in North America (Vitt & Slack 1984; Gignac et al. 1991); its cover increase therefore likely indicated that the *Sphagnum*-dominated sites of the bogs studied were drying out. In contrast, most decreasers (e.g., *Chamaedaphne calyculata*, *Kalmia angustifolia*, *Eriophorum vaginatum* ssp. *spissum* and *Calamagrostis canadensis*) are shade-intolerant species associated with open and more humid habitats (Lieffers & Stadt 1994; Malik 1994; Lachance & Lavoie 2004). The decrease or disappearance of *Chamaedaphne calyculata* in bogs due to an increase of shading following their colonisation by trees and tall shrubs, such as *Rhododendron canadense* has also been demonstrated in other disturbed peatlands of North America (Mitchell & Niering 1993; Pellerin & Lavoie 2003b; Lachance & Lavoie 2004).

Causes of changes

Recent forest expansion, biodiversity losses or species composition changes in bogs are increasingly associated with direct (e.g., drainage) or indirect (e.g., air pollution) anthropogenic disturbances (Frankl & Schmeidl 2000; Lachance & Lavoie 2004; Linderhom & Leine 2004; Pensa et al. 2004; Lachance et al. 2005). In our study, according to variation partitioning, the variables that were used to quantify human activities (mainly the distance to the closest drainage ditch or to a disturbed sector and the ditch density) had a greater impact on vegetation composition than change over time (Fig. 4). We expected a larger anthropogenic control on the vegetation of the natural bog remnants because the two bogs were highly disturbed. Nevertheless, most of the sampling plots were located far away from a disturbance (31 sampling sites were located at > 500 m from a disturbance in 1998 while only 14 were located at < 100 m), and thus were probably not too influenced by human activities. For instance, effects of drainage on bog water table, and indirectly on vegetation communities, are rarely perceptible > 100 m away from a ditch (Hillman 1992; Poulin et al. 1999; Roy et al. 2000). However, considering that spatial and compositional heterogeneities were not controlled for in this analysis, and that those heterogeneities were likely responsible for a large portion of the variation among sampling plots, 8% of the total variation explained by human activities was rather important. It is also likely that our variables did not capture all the driving force behind the changes observed, since the effect of time on plant composition was also significant and because a large fraction of the variance remained unexplained (Fig. 4). These changes may thus have been faint indicators of an external factor such as atmospheric pollution or climate change.

In Europe, recent changes in the vegetation of apparently undisturbed peatlands have been attributed to an additional supply of nitrogen and sulphur due to atmospheric pollution (Gunnarsson et al. 2000, 2002; Ohlson et al. 2001). In the Bas-Saint-Laurent region, the atmospheric input of nitrogen and sulphur is lower than critical loads for soil acidification (Ouimet et al. 2001). Therefore, in this study it was unlikely that the observed changes were also associated with airborne pollutants. Therefore, the part of the observed change not explained by our anthropogenic variables likely was associated to some extent to climate drying.

Vegetation in bogs is particularly sensitive to climate as they receive almost all their water and nutrient supply from atmospheric precipitation. Several paleoecological studies have reported vegetation modifications (e.g., tree colonization and/or expansion) in bogs in response to climate change (e.g., Barber 1981; Ellis & Tallis 2000; Lavoie &

Richard 2000). For example, *Pinus sylvestris* colonisation in peatlands of Europe during the Holocene was usually ascribed to warmer and/or dryer climatic periods (e.g., Gear & Huntley 1991; Pilcher et al. 1995). In Québec, recent forest expansion associated with significant *Sphagnum* decrease has been attributed, in part, to climate drying in the early 20th century (Pellerin & Lavoie 2003a). Weltzing et al. (2000, 2003) also found that an increase in temperature along with a decrease in water–table induced an increase of around 50% in shrubs cover and a similar decrease in graminoid and moss cover. Also, Thormann & Bayley (1997) found an increase in shrub cover under drier conditions. In our study area, long drier-than-average climatic periods were recorded in the 1960s and the 1980s (climatic records are available in Girard et al. 2002; Pellerin & Lavoie 2003a). Although we did not have hydrological measurements, it seemed likely that the surface peat layers of the bogs studied were wetter in 1965-1966 than in 1998 due to these long-term water input deficits. In addition, the creation of large mined fields in the two bogs during the studied period might have created dry conditions by modifying the microclimate of the unmined fragments, which were then more exposed to wind (Campbell et al. 2002). For instance, Mitchell et al. (2001) found that the drying of the peat surface of a bog in Switzerland was likely caused by an increased exposure to desiccating winds due to deforestation.

Conclusion

Significant changes occurred in the vegetation communities of natural fragments of two highly disturbed bogs in southeastern Quebec over a 32-year period. The general trend was toward a densification of woody forest cover, a decrease in the cover of shade-intolerant species and an increase in the cover of drought or shade-tolerant species. Although some of the vegetation changes can be associated with anthropogenic activities, an increase in the peat surface dryness due to climate change may also have enhanced the phenomenon. In regions where several peatlands are available for various land uses (mining, conservation), it would be more appropriate to concentrate mining activities within particular sites to preserve other bogs. Conserving several fragments of natural habitats within disturbed sites, even large fragments, as a replacement for the total preservation of particular peatlands, does not appear as a suitable conserva-

tion option. Pristine bogs are indeed more likely to preserve their ecological integrity over a long time frame (Poulin et al 1999; Pellerin & Lavoie 2000; Lachance & Lavoie 2004), especially in the context of climate change.

Supporting information

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

App. 1. Change in species cover between 1965-1966 and 1998 within each sampling plot at the Riviere-du-Loup and Riviere-Ouelle bogs (southeastern Québec).

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