

The impact of peatland afforestation on plant and bird diversity in southeastern Québec¹

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Abstract: Forest expansion (afforestation) is one of the main vegetation changes currently observed in peatlands worldwide in response to natural and anthropogenic disturbances. We examined the relationships between plant and bird richness and frequency and extent of the forest cover in bogs of southeastern Québec to evaluate the impact of forest expansion on typical bog species. A total of 154 plant species and 36 bird species were recorded in the 16 peatlands studied (2-189 ha). Richness and frequency of ombrotrophic plant species were negatively associated with an increase in forest cover. Yet, minerotrophic and minerotrophic-ombrotrophic species did not appear to take advantage of this decline. Afforestation influenced bird species composition by altering the vegetation structure in all strata of the bogs (fewer mosses and shrubs, more trees) and by homogenizing the spatial distribution of plant communities (open patches). Peatlands of southeastern Québec remain islands of boreal vegetation in a matrix of deciduous forests and agricultural fields, but afforestation appears to progressively reduce the diversity of peatland habitats. Afforestation does not imperil plant or bird species across their entire range, but it contributes to impoverishing regional biodiversity.

Keywords: afforestation, biodiversity, Dendroica palmarum, Melospiza lincolnii, ombrotrophic peatland, Sphagnum fuscum.

Résumé : L'augmentation du couvert forestier est l'un des principaux changements écologiques qui s'observent dans les tourbières sujettes à des perturbations naturelles et anthropiques. Nous avons étudié l'impact d'une augmentation du couvert forestier sur les différentes espèces d'oiseaux nicheurs et de plantes de tourbières du sud-est du Québec. Au total, 154 espèces végétales et 36 espèces d'oiseaux ont été recensées dans les 16 tourbières étudiées (2 à 189 ha). L'importance du couvert forestier est associée à une diminution de la richesse et de la fréquence d'apparition des espèces végétales ombrotrophes. Les espèces minérotrophes et minérotrophes-embrotrophes ne semblent pas profiter du déclin des espèces ombrotrophes. L'augmentation du couvert forestier agit sur les espèces d'oiseaux en changeant la structure de la végétation des tourbières (moins de mousses et d'arbustes, davantage d'arbres) et en homogénéisant la répartition spatiale des communautés végétales (aires ouvertes progressivement remplacées par des zones boisées). Les tourbières du sud-est québécois demeurent des îlots de végétation boréale dans une matrice constituée de forêts décidues et de champs agricoles, mais l'augmentation du couvert forestier réduit graduellement la diversité des habitats qu'on y trouve. Cela ne met pas nécessairement en péril les espèces de plantes et d'oiseaux des tourbières, mais cela contribue néanmoins à l'appauvrissement de la diversité régionale.

Mots-clés : biodiversité, boisement, Dendroica palmarum, Melospiza lincolnii, Sphagnum fuscum, tourbière ombrotrophe.

Nomenclature: Stotler & Crandall-Stotler, 1977; Anderson, 1990; Anderson, Crum & Buck, 1990; Esslinger & Egan, 1995; Gauthier & Aubry, 1995; Hinds, 2000.

Introduction

Ombrotrophic (bog) and minerotrophic (fen) peatlands are widespread ecosystems, covering about $3-4 \times 10^6$ km² worldwide (Joosten & Clarke, 2002). Most peatlands are located in the boreal zone, between latitudes 50° and 70° N in Canada, Russia, Fennoscandia, and the northwestern part of Europe (O'Neill, 2000). Peat-accumulating ecosystems are one of the main terrestrial carbon sinks and have accumulated about 455 Gt of carbon over the past 10,000 y (Gorham, 1991). The biodiversity of bogs is low, but they have very distinctive flora and fauna, and many species groups can only be found in these ecosystems (Moore, 2002). This is especially true for southern bogs (Maltby, 1986). They exhibit an array of plant and animal species commonly found at more northern latitudes. Bogs can thus be considered as islands of boreal diversity in a temperate zone (Spitzer, Bezděk & Jaroš, 1999; Calmé, Desrochers & Savard, 2002). Consequently, any natural or anthropogenic disturbance altering the nature and distribution of plant and animal communities in bogs may seriously affect regional biodiversity.

Afforestation (increase in tree cover) is one of the main vegetation changes recently observed in peatlands in response to natural and/or anthropogenic disturbances. Raised bogs of western Chile have become increasingly forested near human establishments, probably due to drainage (Pisano, 1983). Large increases in tree cover have been observed in Swedish peatlands over the last 40 y, possibly caused by drainage (Linderholm & Leine, 2004). The proliferation of pine in raised bogs in the Jura Mountains (Switzerland) has also been linked to drainage and peat-cutting activities (Freléchoux *et al.*, 2000). In the last 50 y, many open bogs in the Bas-Saint-Laurent

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region, southeastern Québec (Canada), have undergone major changes in vegetation structure (Figure 1), including large tree cover increases (Pellerin & Lavoie, 2000; Pellerin, 2003b). A dry climatic period during the first part of the 20th century, drainage, and fire events seem to be the main causal factors of these vegetation changes (Pellerin, 2003b; Pellerin & Lavoie, 2003).

Afforestation is expected to be detrimental to peatland biodiversity. Forest expansion has been associated with habitat loss for Sphagnum and other moss species (Frankl & Schmeidl, 2000; Pellerin & Lavoie, 2000), and within temperate regions, several moss species are almost exclusively found in bogs. The influence of forest cover on species distribution in bogs has been studied for plants (Lachance & Lavoie, 2004) and insects (Spitzer, Bezdek & Jaros, 1999). However, to our knowledge, no study has investigated the specific influence of afforestation on bog plant and bird assemblages and its subsequent effect on regional biodiversity. Birds were included in this work because a considerable amount of information on the diversity and ecology of bog avian species has recently been collected in southern Québec (Calmé & Desrochers, 1999; 2000; Calmé, Desrochers & Savard, 2002). The objectives of this study were to examine the relationships between plant and bird richness and frequency and extent of the forest cover in bogs, and to evaluate the impact of forest expansion on typical bog species. We hypothesized that forest expansion is accompanied by significant changes in plant and bird assemblages and that, consequently, these changes are detrimental to regional biodiversity.

Methods

$\ensuremath{S}\xspace{\mathsf{TUDY}}$ area and sampling sites

Ombrotrophic peatlands of the Bas-Saint-Laurent region, in southeastern Québec, Canada (Figure 2), offer a good opportunity to study the influence of forest expansion on species richness and diversity since all have experienced an increase in their forest cover over the past 50 y (Pellerin, 2003b). These peatlands are located in a 4- to 12-km-wide agricultural plain bordering the south shore of the St. Lawrence River. The study area (176 km²) is a narrow strip of agricultural lands located between the cities of Rivière-du-Loup and L'Isle-Verte. Few settlers established in the study area prior to 1800 (Morin, 1993). The original forest cover of the plain was almost completely cleared during the first part of the 19th century, and by 1870 most of the area was used for agriculture (Fortin, 1993a). The peatlands were one of the last ecosystems without agricultural or industrial activities (Fortin,

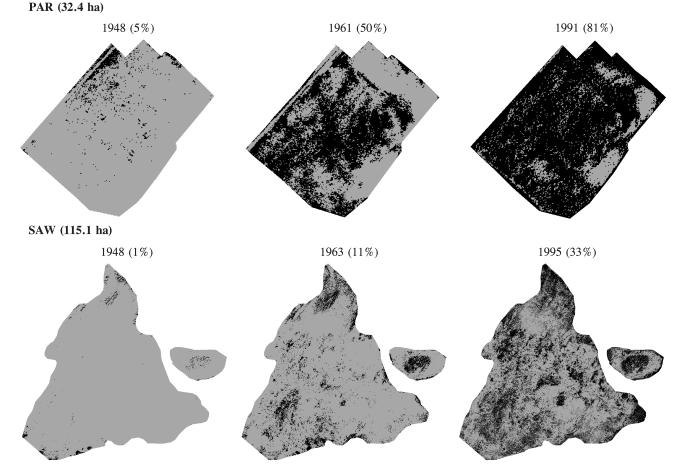


FIGURE 1. Spatio-temporal evolution of the forest cover (black areas) of LeParc (PAR) and Saint-Arsène West (SAW) bogs, Bas-Saint-Laurent region, southeastern Québec, reconstructed from aerial photographs. Percentage of the bog area covered by forest is indicated for each year (modified from Pellerin & Lavoie, 2003).

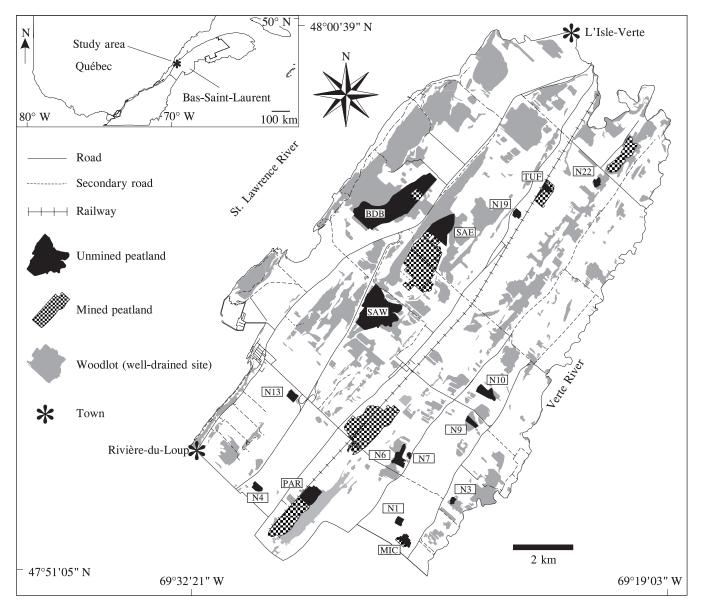


FIGURE 2. Study area, Bas-Saint-Laurent region, southeastern Québec, and spatial distribution of studied bogs, mined peatlands, and woodlots on well-drained sites. Data on woodlots are from Environnement Canada (1999). Peatlands that have been sampled: BDB: Bois-des-Bel; MIC: Michaud; PAR: LeParc; SAE: Saint-Arsène East; SAW: Saint-Arsène West; TUF: Coteau-du-Tuff; N1, N3, N4, N6, N7, N9, N10, N13, N19, and N22: unnamed peatlands.

1993b). Nevertheless, between 1929 and 2000, 62% of the total area covered by bogs was disturbed, by peat mining, logging, or farming activities (Pellerin, 2003a).

Today, the study area is mainly covered by agricultural fields, although woodlots on mesic and xeric sites still occupy about 15% (3,460 ha) of the total area (Figure 2). Woodlot vegetation is dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and balsam fir (*Abies balsamea*) (Robitaille & Saucier, 1998). A total of 18 peatlands are present in the study area. Among those, seven bogs are presently used for the extraction of horticultural peat or are abandoned after decades of mining; mined surfaces occupy an area of 620 ha. Eleven unmined peatlands and five unmined fragments of large bogs are also present, occupying an area of 510 ha. These bogs or bog fragments were never subjected to peat mining, large-scale logging, or farming activities. They range in size from 2 to 189 ha. A mosaic of open and forested patches usually characterizes their vegetation. Dominant tree species include black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*). Ericaceous shrubs, mainly Chamaedaphne calyculata, Kalmia angustifolia, Rhododendron groenlandicum, and Vaccinium angustifolium are widespread in all bogs. In open habitats, Sphagnum mosses, mainly S. capillifolium, S. fuscum, S. magellanicum, and S. rubellum, cover the ground layer, whereas Pleurozium schreberi dominates the ground layer of forested sites.

VEGETATION SAMPLING

During the summer of 2000, vascular plants, mosses, liverworts, and lichens were sampled in the 16 unmined

peatlands and unmined fragments of large bogs, using the following sampling scheme. The most recent (1995) aerial photograph (1:15,000) covering each bog was digitized, registered in space, and corrected to limit geometrical distortions using Geographic Transformer software (Blue Marble Geographics, 1998). Corrected photographs were imported into a geographic information system (GIS), MapInfo Professional (MapInfo Corporation, 2001). In the GIS, a grid of sampling points located 50 m apart was superimposed on the 12 largest peatlands (6.3-189.2 ha). The four smallest peatlands (2.0-5.8 ha) had a grid with points separated by a distance ranging from 25 to 40 m. in order to have a minimum of 30 sampling points in each bog. The latitude and longitude of each sampling point (n = 2,096) were obtained with the GIS and located in the field using a Global Positioning System receiver.

All plant species present within a 50- \times 50-cm quadrat laid on the ground at each sampling point were identified. The presence of all species covering (at least partly) the vertical projection of the quadrat was also noted. Each plant species was associated with a particular trophic regime (minerotrophic, minerotrophic or ombro-trophic, ombrotrophic; see Appendix I) using the works of Gauthier (1967; 1980), Marie-Victorin (1995), Girard (2000), and Garneau (2001). Species restricted to bog ecosystems in the study area were identified using the work of Blouin and Grandtner (1971), who sampled vegetation communities in all habitat types of the Rivière-du-Loup county.

BIRD SURVEYS

Bird populations were sampled in the 16 unmined peatlands and unmined fragments of large bogs from June 1 to 22, 2001. A grid of sampling stations was superimposed on all sites using the GIS. The stations were located 200 m apart and at least 100 m from the peatland border, except in the three smallest peatlands (2.0-3.3 ha), where a single sampling station was located at the centre of the bog. The latitude and longitude of each sampling station (n = 135) were obtained with the GIS and located in the field using a Global Positioning System receiver. Nesting bird populations were sampled using fixed-radius point counts (Ralph et al., 1993). Point counts were conducted using a 50-m radius and lasted 10 min, during which all birds that were heard were recorded. Point count stations were visited twice during the sampling period, by different observers and at different times between 0400 and 0900, on days without rain and with winds less than 30 km \cdot h⁻¹.

For analyses, we retained only 1) bird species breeding during the sampling period and using peatlands for breeding, according to Gauthier and Aubry (1995), 2) species for which the sampling method was appropriate, thus excluding bird species like purple finch (*Carpodacus purpureus*), whose large territories could induce us to sample the same individual more than once, and 3) species present in more than 5% of the sampling stations. Bogspecialist species were identified according to Calmé, Desrochers, and Savard (2002), who classified bird species sampled in 112 peatlands across the province of Québec (including peatlands of the Bas-Saint-Laurent region) according to their affinity with peatlands. FOREST COVER

Data from Pellerin and Lavoie (2003) were used to estimate the forest cover of the peatlands of the study area. The forest cover of each peatland was calculated using corrected aerial photographs taken in 1995 (the most recent photographs with the highest resolution level) and the EASI/PACE digital image processing software (PCI Remote Sensing Corp., 1997). Although field sampling (plants, birds) was conducted 5 or 6 y later, few changes in the tree cover were expected, since most of the forest cover increase in the Bas-Saint-Laurent peatlands occurred before the 1990s (Pellerin & Lavoie, 2003). A supervised classification approach with a maximum likelihood classifier was used (Campbell, 1996). On aerial photographs, the forested vegetation (trees of all heights, all species considered) could easily be distinguished from open vegetation (i.e., with only small or no trees); hence, these two vegetation types were used to classify the photographs. Each photograph was classified separately to minimize between-image differences in brightness and contrast, and a mask for each bog was created to restrict the analysis to the area of interest. Thus, for each photograph, the area covered by each vegetation type was obtained.

DATA ANALYSIS

Since peatlands are of variable sizes (2.0-189.2 ha) and sampling points and stations were established from regular grids, large peatlands would appear to have more species simply because much more effort was spent on sampling (Connor & McCoy, 1979). To correct plant species richness for sampling effort, a Monte Carlo procedure was applied (Sokal & Rohlf, 1981). One hundred samples of 30 randomly selected points were extracted from peatlands containing more than 30 sampling points. Relative richness was established for each of these peatlands by calculating the mean species richness from the extracted samples. A similar procedure was applied to correct bird species richness. However, since small peatlands had only one sampling station, relative richness for larger peatlands was simply the mean species richness of all sampling stations.

Species richness alone can be a misleading measure of biodiversity, since resistance to disturbances, primary productivity, and adequate functioning of an ecosystem depend not only on the number of species, but also on other factors, including species abundance or frequency (Magurran, 1988; Cardinale, Nelson & Palmer, 2000; McCann, 2000; Purvis & Hector, 2000; Tilman, 2000; Loreau et al., 2001). To account for plant species frequency as well as the frequency of trophic groups (minerotrophic, minerotrophic-ombrotrophic, or ombrotrophic), an additional index was required. We took the number of sampling points where a species was found and divided it by the total number of sampling points in the peatland to correct for sampling effort and obtain the species' frequency. The same procedure was applied for trophic groups, albeit with the frequency calculated for all species belonging to a particular group. Thus, the relative frequency of a species (F_{rs}) and the relative frequency of a trophic group (F_{rt}) can be defined by two equations:

$$F_{rs} = \frac{N}{N_P}$$
[1]

where N is the number of sampling points at which a given species was recorded in a particular peatland and N_P is the total number of sampling points in the same peatland, and:

$$F_{rt} = \sum_{i=1}^{S_t} \frac{N_{it}}{N_P}$$
[2]

where N_{it} is the number of sampling points at which the species *i* of the trophic group *t* was recorded in a particular peatland, S_t is the number of species of the same trophic group recorded in the same peatland, and N_P is the total number of sampling points used in this peatland. Thus, F_{rs} and F_{rt} are simple measures of relative frequency, calculated for each species and each trophic group.

Linear regressions were used to assess relationships between plant and bird species richness (after correction for sampling effort) F_{rs} and F_{rt} , with forest cover. For birds, studying relationships between single bird species occurrences and forest cover leads to inconclusive results, since many bird species are uncommon. An alternative for studying such relationships is the use of logistic regression, where the dependent variable is categorical. Logistic regression was used to study the relationship between total species frequency (dependent variable, categorical) and forest cover (independent variable) while considering each species as a category (Tabachnick, 1996). Statistical analyses were conducted using SPSS software (SPSS, 2001), except for the logistic regression, which was computed using the CATMOD procedure in the SAS software (SAS Institute, 1999).

Results

A total of 154 plant species were recorded in the peatlands (Appendix I). Of the 76 minerotrophic species, *Carex trisperma, Coptis trifolia,* and *Cornus canadensis* were the most abundant. *Dicranum polysetum, Nemopanthus mucronatus,* and *Pleurozium schreberi* were the most abundant of the 26 species that can be considered either minerotrophic or ombrotrophic. Finally, among the 38 ombrotrophic species, *Kalmia angustifolia, Picea mariana,* and *Vaccinium angustifolium* were the most abundant. Remaining plant species could not be classified in any group because of the lack of autecological information.

A total of 36 bird species were detected, but only 15 species were included in the analyses. Of these, eight are known as bog specialists at the regional level. The most frequent species were Nashville warbler (*Vermivora ruficapilla*), common yellowthroat (*Geothlypis trichas*), and magnolia warbler (*Dendroica magnolia*).

Linear regressions showed no significant relationship between forest cover and relative richness (Figure 3) except for ombrotrophic plant species, whose richness significantly dropped as forest cover increased. Relative frequency for ombrotrophic species was significantly and negatively correlated with forest cover (Figure 4). This result is noteworthy since forest cover increase was mainly associated with black spruce (Pellerin & Lavoie, 2003), classified in this study as an ombrotrophic species. It

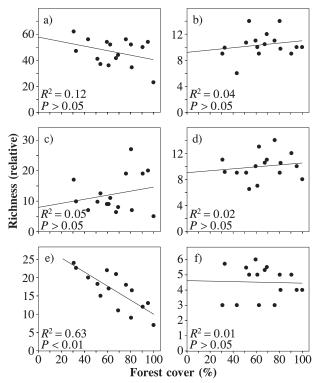


FIGURE 3. Effect of forest cover (percentage of the area of the peatland covered by trees in 1995) on relative richness of a) all plant species, b) all bird species, c) minerotrophic plant species, d) minerotrophic-ombrotrophic plant species, e) ombrotrophic plant species, and f) bog-specialist bird species sampled in bogs of the Bas-Saint-Laurent region, southeastern Québec.

strengthens the evidence of a loss of diversity for all other ombrotrophic species. The relative frequency of the minerotrophic and minerotrophic-ombrotrophic groups did not exhibit any significant relationship, but both trends were similar, *i.e.*, an increase in frequency with forest cover.

The relative frequency (F_{rs}) of 14 of the 38 ombrotrophic plant species was significantly correlated with forest cover (Table I). As expected, only *Picea mariana* was favoured by forest cover increase. Among the 13 species significantly impeded by forest expansion, five were restricted to ombrotrophic sites within the study area: *Kalmia polifolia*, *Mylia anomala*, *Rubus chamaemorus*, *Sphagnum fuscum*, and *Vaccinium oxycoccos*.

The occurrence of four of the 15 bird species analyzed was significantly correlated with forest cover (Table II). Among regional bog specialists, common yellowthroat and Lincoln's sparrow (*Melospiza lincolnii*) showed a significant decrease in occurrence in response to an increase in forest cover. In contrast, winter wren (*Troglodytes troglodytes*) and yellow-rumped warbler (*Dendroica coronata*) showed a significant increase in occurrence.

Discussion

AFFORESTATION AND PLANT DIVERSITY

Only the richness and frequency of ombrotrophic species were negatively associated with forest cover. Minerotrophic and minerotrophic-ombrotrophic species

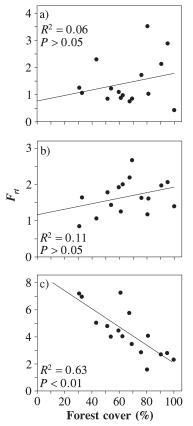


FIGURE 4. Effect of forest cover (percentage of the area of the peatland covered by trees in 1995) on the relative frequency (F_{rt}) for a) minerotrophic plant species, b) minerotrophic-ombrotrophic plant species, and c) ombrotrophic plant species sampled in bogs of the Bas-Saint-Laurent region, southeastern Québec.

did not appear to take advantage of this decline. The afforestation process that occurred during the last century influenced both shade and water table, two environmental parameters particularly important in determining the distribution of peatland plant species (Sjörs, 1950; Vitt et al., 1990; Gignac, 1994; Lachance & Lavoie, 2004). Forest cover increase affects lower vegetation strata through alteration of light quality (increased shade), which influences the photosynthetic activities of plants. This may result in a decline of open-bog Sphagnum species (Gauthier, 1980), an increase in coverage of shade-tolerant mosses such as Dicranum polysetum and Pleurozium schreberi (Laine & Vanha-Majamaa, 1992), and a decrease in regional diversity as bog vegetation becomes similar to that of surrounding landscape dominated by coniferous forests (Laine, Vassander & Sallantaus, 1995).

Among plant species affected by an increase in the forest cover, Sphagnum fuscum is one of the most important species because it is the dominant Sphagnum species in raised bogs of eastern Canada (Gauthier, 2001). Although this species can withstand a wide range of environmental conditions (Mulligan & Gignac, 2001), it does not tolerate shade (Gauthier, 2001). Sphagnum fuscum typically forms hummocks (Gauthier, 2001), which provide adequate habitats for a large variety of liverworts, mosses, and vascular plants like Mylia anomala, Vaccinium oxycoccos, Polytrichum strictum, and, to a

TABLE I. Ombrotrophic plant species with a relative frequency (F_{re}) significantly influenced by forest cover in peatlands of the Bas-Saint-Laurent region, southeastern Québec. Bold: species restricted to bogs in the study area (according to Blouin & Grandtner, 1971).

Scientific name	Z^1
Chamaedaphne calyculata	-3.59**
Kalmia angustifolia	-4.38**
Kalmia polifolia	-3.41**
Maianthemum trifolium	-2.46*
Mylia anomala	-4.61**
Picea mariana	2.93*
Pohlia nutans	-3.93**
Polytrichum strictum	-4.19**
Rhododendron groenlandicum	-5.57**
Rubus chamaemorus	-2.36*
Sphagnum capillifolium	-2.75*
Sphagnum fuscum	-2.47*
Vaccinium angustifolium	-3.03**
Vaccinium oxycoccos	-5.29**

* 0.01 < P < 0.05.

¹A high value indicates a strong relationship with forest cover while the sign indicates the direction (+: species favoured by forest expansion; -: species impeded by forest expansion).

TABLE II. Most frequent nesting avian species sampled in 16 peatlands, Bas-Saint-Laurent region, southeastern Québec. Results of the logistic regression with the intensity and direction (Z-score) as well as the significance of the relationship between species frequency and forest cover are shown. Bold: species considered as bog specialists according to Calmé, Desrochers and Savard (2002). Species sorted by decreasing association with forest cover.

English name	Scientific name	Z^1	Р
Winter wren	Troglodytes troglodytes	2.26	0.02
Yellow-rumped warbler	Dendroica coronata	2.13	0.03
American goldfinch	Carduelis tristis	1.47	0.14
Magnolia warbler	Dendroica magnolia	1.42	0.16
Ruby-crowned kinglet	Regulus calendula	1.09	0.27
Nashville warbler	Vermivora ruficapilla	0.54	0.59
Palm warbler	Dendroica palmarum	0.36	0.72
Swainson's thrush	Catharus ustulatus	0.10	0.92
Hermit thrush	Catharus guttatus	0.03	0.98
Boreal chickadee	Parus hudsonicus	-0.01	0.99
Golden-crowned kinglet	Regulus satrapa	-0.09	0.93
American robin	Turdus migratorius	-0.70	0.48
White-throated sparrow	Zonotrichia albicollis	-1.61	0.11
Common yellowthroat	Geothlypis trichas	-2.07	0.04
Lincoln's sparrow	Melospiza lincolnii	-4.93	< 0.01

¹ A high value indicates a strong relationship with forest cover while the sign indicates the direction (+: species favoured by forest expansion; -: species impeded by forest expansion).

lesser extent, Pohlia nutans (Gauthier, 1967; 1980; Jacquemart, 1997).

Most of the species affected by an increase in the forest cover but not associated with the microhabitat structure created by Sphagnum fuscum appear particularly light sensitive. Chamaedaphne calyculata, Kalmia polifolia, Rubus chamaemorus, and Vaccinium angustifolium have a strong association with open Sphagnum bogs (Gauthier, 1967; Hoefs & Shay, 1981; Lapointe & Rochefort, 1997; Dyck & Shay, 1999; Jean & Lapointe, 2001). Under controlled conditions, shading significantly reduces the growth of Sphagnum capillifolium (Hayward & Clymo, 1983).

Afforestation probably influences Kalmia angustifolia and Rhododendron groenlandicum through a combination of effects. Kalmia angustifolia prefers dry habitats (Gauthier, 1967), but is more vigorous in open canopy black spruce forests (Mallik, 1994). Therefore, only a dense tree cover would significantly impede its growth. The fact that this species is affected by tree cover in this study indicates the intensity of the afforestation process. On the other hand, Rhododendron groenlandicum prefers a denser canopy and a wetter habitat than Kalmia angustifolia (Gauthier, 1967; Dyck & Shay, 1999). The negative influence of increasing black spruce cover on the frequency of Rhododendron groenlandicum suggests that the detrimental effect of water-table drawdown caused by a dense tree cover (Prévost, Plamondon & Roy, 2001; Van Seters & Price, 2001; 2002; Girard, Lavoie & Thériault, 2002) negates the positive influence of the canopy closure.

AFFORESTATION AND BIRD DIVERSITY

Afforestation influenced bird species by changing the vegetation structure of bogs (fewer mosses and shrubs, more trees) and by homogenizing the spatial distribution of plant communities (open patches progressively replaced by forested patches). Previous studies have shown the importance of both factors for bird distribution (Rotenberry, 1985; Stockwell, 1994; Calmé & Desrochers, 2000). In bogs of the Bas-Saint-Laurent region, recent changes in the spatial distribution of open and forested patches probably explain the main patterns in bird distribution, since the distributions of three of the four bird species significantly affected by afforestation (common vellowthroat, Lincoln's sparrow, and winter wren) apparently relate to ecotones. Common yellowthroat and Lincoln's sparrow were negatively affected by an increase in the forest cover because, in peatlands, they usually nest in copses of black spruce localized in transition areas (ecotones) between forested edges and open areas (Gauthier & Aubry, 1995; Desrochers, 2001). A decrease in the extent of open areas therefore affects those birds since it reduces the area occupied by ecotones. On the other hand, yellow-rumped warbler and winter wren, two coniferous forest species (Gauthier & Aubry, 1995; Anthony et al., 1996), benefit from an increase in the forest cover. However, the positive influence of afforestation may only be a temporary situation for winter wren since in our study sites this bird species mainly prefers young copses of black spruce.

During the nesting period, palm warbler is strongly and almost exclusively associated with peatlands, at least in temperate regions where coniferous forests are scarce and mainly restricted to bogs (Wilson, Zierzow & Savage, 1998; Calmé & Desrochers, 1999; Desrochers, 2001). This species is usually associated with small copses of black spruce surrounded by open areas, a situation that is somewhat intermediate between open and closed canopy. Palm warbler typically nests on the ground and uses the tallest tree of the copse for surveillance and as a song post (Welsh, 1971). Therefore, it is somewhat puzzling that palm warbler is not significantly affected by an increase in the forest cover. It is hypothesized that an increase in the number of black spruce copses in open areas temporarily compensates for the loss of area occupied by open patches and that the palm warbler will eventually find itself impeded by forest expansion.

AFFORESTATION AS A THREAT TO REGIONAL BIODIVERSITY

Among ombrotrophic plant species significantly affected by an increase in the forest cover, five are exclusively restricted to bogs in the Bas-Saint-Laurent region (Blouin & Grandtner, 1971). These five species are also associated with plant communities typical of pristine open bogs (Lachance & Lavoie, 2004). However, considering that 154 plant species were found in the 16 bogs that were studied, the loss of only five species (3% of the total) may appear negligible, especially because none of these species is rare in Québec. Furthermore, it is likely that some open patches will remain in the next decades, especially in larger, less disturbed bogs. Such patches will constitute refuges for typical bog species.

Afforestation is mainly due to black spruce expansion, and peatlands will remain coniferous islands providing appropriate habitats for many passerine bird species like yellow-rumped warbler, magnolia warbler, and hermit thrush. However, it is unlikely that peatlands will remain refuges for specialist birds in the near future. It is indeed doubtful that species like Lincoln's sparrow and palm warbler will maintain viable populations in the region, since these birds require large open bog areas that are slowly disappearing.

In summary, there is a clear trend toward a homogenization of the landscape. There are fewer and fewer bogs in the Bas-Saint-Laurent region because of industrial (peat extraction) and agricultural activities, and remaining sites are being progressively transformed into forested stands with a vegetation structure very different from that of typical, pristine open bogs. Peatlands of the Bas-Saint-Laurent region remain islands of boreal vegetation in a matrix of deciduous forests and agricultural fields, but the diversity of their habitats is progressively reduced because of the afforestation process. This phenomenon does not imperil plant or bird species across their entire range, but it does contribute to the impoverishing the regional diversity. Protecting the remaining bogs in this region, especially the largest ones, from anthropogenic disturbances (Lachance & Lavoie, 2004) would probably slow the afforestation process and ensure that at least some refuges will remain available for typical bog plant and bird species.

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Species	Family	Trophic regime	Species	Family	Trophic regin
Mosses			Cladonia deformis	Cladoniaceae	m
Aulacomnium androgynum	Aulacomniaceae	unknown	Cladonia fimbriata	Cladoniaceae	m
Aulacomnium palustre	Aulacomniaceae	0	Cladonia gracilis	Cladoniaceae	0
Brachythecium reflexum	Brachytheciaceae	m	Cladonia humilis	Cladoniaceae	m
Brachythecium salebrosum	Brachytheciaceae	unknown	Cladonia macilenta	Cladoniaceae	m
Callicladium haldanianum	Hypnaceae	unknown	Cladonia peziziformis	Cladoniaceae	m
Campylium chrysophyllum	Amblystegiaceae	unknown	Cladonia phyllophora	Cladoniaceae	m
Campylium stellatum	Amblystegiaceae	m	Cladonia rei	Cladoniaceae	m-o
Dicranum fuscescens	Dicranaceae	m	Cladonia squamosa	Cladoniaceae	0
Dicranum majus	Dicranaceae	m-o	HERBACEOUS PLANTS		
Dicranum montanum	Dicranaceae	m	Aralia nudicaulis	Araliaceae	m
Dicranum polysetum	Dicranaceae	m-o	Aralia racemosa	Araliaceae	m
Dicranum scoparium	Dicranaceae	m-o	Aster acuminatus	Compositae	m
Dicranum undulatum	Dicranaceae	0	Aster radula	Compositae	m
Funaria hygrometrica	Fumariaceae	unknown	Calamagrostis canadensis	Poaceae	m
Herzogiella turfacea	Hypnaceae	unknown	Carex canescens	Cyperaceae	m
Hylocomium splendens	Hylocomiaceae	0	Carex disperma	Cyperaceae	m
Hypnum fertile	Hypnaceae	unknown	Carex echinata	Cyperaceae	m
Hypnum pallescens	Hypnaceae	unknown	Carex hirtifolia	Cyperaceae	
Isopterygiopsis pulchella	Plagiotheciaceae	unknown	Carex oligosperma	Cyperaceae	m m
Limprichtia revolvens	Amblystegiaceae	m-o		* 1	
Plagiothecium cavifolium	Plagiotheciaceae	unknown	Carex trisperma	Cyperaceae Liliaceae	m
Pleurozium schreberi	Hylocomiaceae	m-o	Clintonia borealis		m
Pohlia nutans	Bryaceae	0	Coptis trifolia	Ranunculaceae	m
Polytrichum commune	Polytrichaceae		Cornus canadensis	Cornaceae	m
5	•	m-o	Cypripedium acaule	Orchidaceae	m-o
Polytrichum strictum	Polytrichaceae	0	Drosera rotundifolia	Droseraceae	0
Pseudotaxiphyllum elegans	Plagiotheciaceae	unknown	Dryopteris campyloptera	Dryopteridaceae	m
Ptilium crista-castrensis	Hypnaceae	m	Dryopteris carthusiana	Dryopteridaceae	m
Sanionia uncinata	Amblystegiaceae	m-o	Dryopteris intermedia	Dryopteridaceae	m
Sphagnum angustifolium	Sphagnaceae	0	Elytrigia repens	Poaceae	m
Sphagnum capillifolium	Sphagnaceae	0	Epilobium angustifolium	Onagraceae	m
Sphagnum centrale	Sphagnaceae	m	Equisetum arvense	Equisetaceae	m
Sphagnum fallax	Sphagnaceae	m-o	Equisetum sylvaticum	Equisetaceae	m
Sphagnum fimbriatum	Sphagnaceae	m	Eriophorum vaginatum		
Sphagnum fuscum	Sphagnaceae	0	ssp. spissum	Cyperaceae	0
Sphagnum girgensohnii	Sphagnaceae	m	Iris versicolor	Iridaceae	m
Sphagnum magellanicum	Sphagnaceae	0	Lythrum salicaria	Lythraceae	m
Sphagnum papillosum	Sphagnaceae	m	Maianthemum canadense	Liliaceae	m
Sphagnum rubellum	Sphagnaceae	0	Maianthemum trifolium	Liliaceae	0
Sphagnum russowii	Sphagnaceae	m-o	Melampyrum lineare	Scrophulariaceae	m-o
Sphagnum squarrosum	Sphagnaceae	m	Monotropa uniflora	Pyrolaceae	m
Sphagnum wulfianum	Sphagnaceae	m	Osmunda cinnamomea	Osmundaceae	m-o
Warnstorfia exannulata	Amblystegiaceae	m	Osmunda claytoniana	Osmundaceae	m
Warnstorfia fluitans	Amblystegiaceae	m	Pteridium aquilinum	Dennstaedtiaceae	m-o
			Ribes glandulosum	Saxifragaceae	m
IVERWORTS			Rubus chamaemorus	Rosaceae	0
Bazzania trilobata	Lepidoziaceae	m-o	Rubus idaeus	Rosaceae	m
Calypogeja sphagnicola	Calypogejaceae	0	Rubus pubescens	Rosaceae	m
Cephalozia bicuspidata	Cephaloziaceae	unknown	Sanguisorba canadensis	Rosaceae	m
Cephalozia connivens	Cephaloziaceae	0	Solidago rugosa	Compositae	m
Cephalozia lunulifolia	Cephaloziaceae	unknown	Thalictrum pubescens	Ranunculaceae	m
Cephalozia pleniceps	Cephaloziaceae	0	Trientalis borealis	Primulaceae	m
Cladopodiella fluitans	Cephaloziaceae	0	C		
Lophocolea heterophylla	Geocalycaceae	m-o	Shrubs	D 1	
Lophozia ventricosa	Jungermanniaceae	unknown	Alnus crispa	Betulaceae	m
Mylia anomala	Jungermanniaceae	0	Alnus incana ssp. rugosa	Betulaceae	m
Ptilidium ciliare	Ptilidiaceae	0	Amelanchier bartramiana	Rosaceae	m-o
Ptilidium pulcherrimum	Ptilidiaceae	m	Aronia melanocarpa	Rosaceae	m-o
*			Chamaedaphne calyculata	Ericaceae	0
ICHENS	01 1		Cornus stolonifera	Cornaceae	m
Cladina mitis	Cladoniaceae	0	Empetrum nigrum	Empetraceae	0
Cladina rangiferina	Cladoniaceae	0	Gaultheria hispidula	Ericaceae	m-o
Cladina stellaris	Cladoniaceae	0	Kalmia angustifolia	Ericaceae	0
Cladonia bacilliformis	Cladoniaceae	m	Kalmia polifolia	Ericaceae	0
Cladonia cenotea	Cladoniaceae	m	Linnaea borealis	Caprifoliaceae	m
Cladonia chlorophaea	Cladoniaceae	m	Myrica gale	Myricaceae	m
Cladonia coniocraea	Cladoniaceae	0	Nemopanthus mucronatus	Aquifoliaceae	m-o
Cladonia conista	Cladoniaceae	m	Rhododendron canadense	Ericaceae	0
Cladonia crispata	Cladoniaceae	0	Rhododendron groenlandicum	Ericaceae	0
*	Cladoniaceae		Salix discolor	Salicaceae	

APPENDIX I. Trophic regime of plant species sampled in 16 peatlands of the Bas-Saint-Laurent region, southeastern Québec: m: minerotrophic; m-o: minerotrophic; o: ombrotrophic.

APPENDIX I. Continued.

Species	Family	Trophic regime	Species	Family	Trophic regime
Salix humilis	Salicaceae	m	Betula cordifolia	Betulaceae	m-o
Salix pyrifolia	Salicaceae	m	Betula papyrifera	Betulaceae	m
Spiraea latifolia	Rosaceae	m	Betula populifolia	Betulaceae	m-o
Vaccinium angustifolium	Ericaceae	0	Larix laricina	Pinaceae	m-o
Vaccinium myrtilloides	Ericaceae	0	Picea glauca	Pinaceae	m
Vaccinium oxycoccos	Ericaceae	0	Picea mariana	Pinaceae	0
Vaccinium vitis-idaea	Ericaceae	0	Picea rubens	Pinaceae	m
Viburnum nudum	Elledeede	0	Pinus banksiana	Pinaceae	m
var. cassinoides	Betulaceae	m	Populus tremuloides	Salicaceae	m
val. cussinoides Betulaceae	111	Prunus pensylvanica	Rosaceae	m	
TREES			Sorbus americana	Rosaceae	m
Abies balsamea	Pinaceae	m	Sorbus decora	Rosaceae	m
Acer rubrum	Aceraceae	m	Thuja occidentalis	Cupressaceae	m-o