Changes in bird community along two fire chronosequences in the Québec eastern boreal forest

Abstract

Different vegetation compositions and structures are generally observed through post-fire succession stages and these changes should affect bird communities. Nevertheless, little is available on long-term changes in bird community following fire in the unmanaged stands of the boreal forest. In this study, we evaluated and compared bird species communities along two long-term chronosequences after fire (0 to >200 years post fire) in the Quebec eastern boreal forest, where long fire return intervals are known to occur. By characterizing forest habitat in stands of different ages (time since fire), we were able to model species richness and bird community characteristics in three habitat types: mature forests, forest-edge and open-forests. Although bird species richness did not vary greatly, many species were lost and others recruited following succession stages. The calculation of a bird community index indicates differences in species composition and the number of species sensitive to habitat modifications. Our study highlights the need to protect the forest at all stages, especially old-growth, which provides a heterogeneous environment suitable for several species. Keeping a mosaic composed of all-age, fire-disturbed forests should help conserve bird diversity in the eastern boreal forest.

Résumé

Des différences de structure et de composition de la végétation sont généralement observées entre les étapes de succession après feu. Par conséquent, on s'attend à ce que ces changements affectent aussi les communautés d'oiseaux. Toutefois, on en connait très peu sur les changements à long terme des communautés d'oiseaux à la suite de feux en forêt boréale non-aménagée. Dans la présente étude, nous avons évalué et comparé les communautés d'oiseaux le long de deux chronoséquences après feu (0 à >200 ans) dans la forêt boréale de l'Est du Québec, où le cycle de retour des feux est long. Grâce à la caractérisation de l'habitat forestier à l'intérieur de ces chronoséquences, nous avons pu modéliser la richesse et la composition en espèces d'oiseaux pour trois types d'habitat : forêt mature, forêt de bordure et forêt ouverte. Même si la richesse en espèces n'a que très peu varié en fonction des classes d'âge des parcelles, plusieurs espèces sont disparues et d'autres ont été recrutées suivant les étapes de succession. Le calcul d'un indice de communauté d'oiseau m'a permis d'observer une différence de composition d'espèces et du nombre d'espèces jugées sensibles aux changements apportés à l'habitat. Cette étude souligne la nécessité de protéger les différents stades de succession de la forêt boréale, particulièrement les vieilles forêts qui procurent un environnement hétérogène requis par un grand nombre d'espèces. En conservant une mosaïque de peuplements de tous les âges, la forêt naturellement perturbée par les feux permettrait de sauvegarder la diversité aviaire de la forêt boréale de l'Est.

2.1. Introduction

Fire is the most important natural disturbance in the boreal forest (Wein, 1993) as it structures the vegetation mosaic that governs the development and function of most deciduous, coniferous, and mixed forest types (White, 1979; Heinselman, 1981; Pickett and White, 1985; Bergeron, 1991; Gauthier et al., 1996; Frost, 1998; Johnson et al., 1998). Vegetation structure and composition are key factors determining habitat selection by birds (MacArthur and MacArthur, 1961; Karr and Roth, 1971; Cody, 1981) and succession changes in habitats through time result in corresponding changes in bird communities (Wiens and Rotenberry, 1981; James and Wamer, 1982)

Long fire return intervals, such as those observed in eastern boreal forests, lead to patches of forests in various stages of succession creating a complex landscape mosaic (Drapeau et al., 1999; Imbeau et al., 2001; Morissette et al., 2002). Early stages of forest succession are characterized by plant species with high colonization abilities and later stages by shade-tolerant species that can compete for light resources and have poor dispersal abilities. This phenomenon is observed in the Eastern Quebec's boreal forest where fire usually leads to the establishment of stands dominated by black spruce (*Picea mariana* (Mill) BSP), shade-intolerant hardwoods (white birch, *Betula papyrifera* Marsh. and trembling aspen, *Populus tremuloides* Michx.), or mixed cover of black spruce with hardwood species (De Grandpré et al., 2000). Such early stage of succession often include dense shrub cover of fast growing species which cannot survive under canopy (Bergeron and Dubuc, 1989). Later on, forest succession in these sites leads to dominance by *P. mariana* or to a shared dominance with balsam fir (*Abies balsamea* (L) Mill.) towards old-growth stages (De Grandpré et al., 2000). These shade-tolerant species will eventually affect shrub density, which will be replaced by species adapted to moist humus and rotten woods on the forest floor (Bergeron and Dubuc, 1989). These developments towards an old-growth stage are typical of the relatively species-poor boreal forests, where changes in forest vertical structure towards old-growth stages are more important than changes in species composition (Harper et al., 2002; Aakala et al., 2007).

In a landscape where fire is the predominant disturbance, many plant and animal species have likely adapted to each habitat type associated with each succession stage after fire (Morissette et al., 2002). For example, in recently burned areas, wood boring beetles and species such as the Black-backed Woodpecker (*Picoides arcticus*) are frequently found due to the predominance of dead standing trees (Hutto, 1995; Murphy and Lehnhausen, 1998; Morissette et al., 2002). Ecological changes resulting from fire disturbances thus produce habitat for specific birds (Hobson and Schieck, 1999; Imbeau et al., 1999). Unique bird community assemblages can be found in recently burned areas and this, even if fire occurs in different boreal habitats such as boreal mixedwoods (Hobson and Schieck, 1999) and black spruce forests (Imbeau et al., 1999; Morissette et al., 2002; Saab et al., 2005). Although most studies have focused on bird species responses to early post-fire stages, changes in bird community assemblages can be expected in later succession stages as well (Saab et al., 2005). For example, by about 25 years post-fire, the shrubby understory is well developed and shrub-breeding species are expected to increase following increase in free-flying arthropods, loss of residual snags and decline of wood-boring beetles (Raphael et al., 1987; Saab et al., 2005). Few studies provide such detailed changes in bird species communities through long-term succession stages (up to 200 years and over). In view of the important changes reported in early succession stages, important community changes might also occur on the longer term. Such information could be crucial in our understanding of boreal forest ecosystems, particularly for the conservation and the management of late succession stages such as old-growth forests.

In this study, we evaluated and compared bird species communities along two long-term chronosequences after fire (0 to >200 years post-fire) in the Quebec eastern boreal forests, where long fire return intervals are known to occur. First, we determined the major habitat characteristics related to bird communities along these chronosequences. Second, we developed different statistical models to explain the presence of bird species in three different habitat types: mature-forest, forest-edge and open-forest. Finally we looked at variation patterns in species richness, bird community and species loss and recruitment, based on time since fire (TSF) to evaluate the changes along the chronosequences.

2.2. Methods

2.2.1. Study Area

Our study was conducted in the Québec North Shore region, in the northeastern part of the Canadian boreal forest. The topography is characterized by hills and moderate slopes (16-30%), the maximum altitude recorded is 700 m and the climate is cold maritime (Robitaille and Saucier, 1998). According to the nearest meteorological station located in Baie-Comeau, average annual temperatures fluctuate between -2.5 and 0.0 °C and annual precipitations between 1100 and 1130 mm, 35% of which falling as snow (Anonymous, 2002).

Surveys were carried out in two regions of the study area: the southern region (49°42'N, 68°51W), located a few kilometers north of Baie-Comeau and the northern region (50°57'N, 68°50'W), located south of the Manic 5 reservoir (Fig. 7). These regions overlap two bioclimatic sub-domains of the boreal zone: the balsam fir-white birch domain (southern region) and the spruce-mosses domain (northern region). Balsam fir characterizes the former, with black spruce dominating stands in poorer sites (MNRF, 2003). As latitude increases (changing to the latter sub-domain), forest stands are increasingly dominated by black spruce. Dominant species found in the study area include balsam fir, black spruce, white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb), white birch and trembling aspen. With time elapsed since the last fire, the size structure of live trees becomes more irregular which is generally accompanied by a gradual increase in balsam fir abundance (De Grandpré et al., 2000).

Fire history has been reconstructed over the area by (Bouchard et al., 2008) who mapped burned stands larger than 10 hectares and up to 200 years since last fire. In each of the two regions, 30 stands were identified to form a chronosequence after fire (Fig.7). For each chronosequence, five stands were selected in each of the following age classes: from 0 to 50 years since last fire (class 1), 51 to 100 years (class 2), 101 to 150 years (class 3) and 151 to 200 years (class 4). Moreover, we selected ten mature stands for which the time

since fire (TSF) was not determined, but was greater than 200 years (class 5). Overall, we sampled 60 stands (2 chronosequences of 30 stands per chronosequence) within which we established two types of inventory plots.
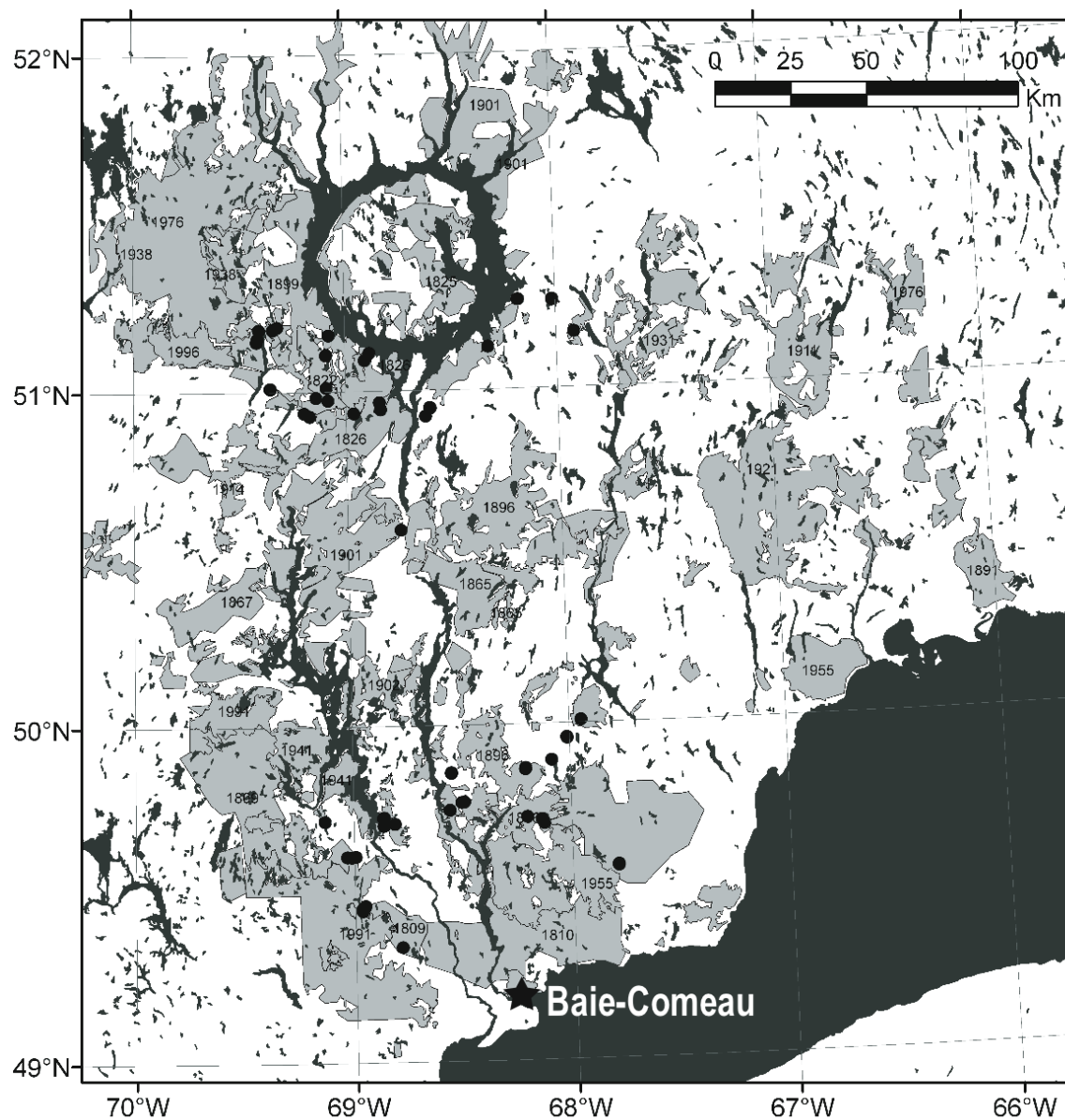

Figure 7. Location of the study area and of fires mapped for the 1800-2000 period. Fire dates are shown on the map only for fires > 200 km^2.

2.2.2. Forest stand inventory

In each selected stand, we established a standard inventory plot to characterize stand composition and diameter distribution. These circular plots covered 400 m^2 with a fixed radius of 11.28 m and were established from May until August 2007. In each plot, all snags and live trees were identified, along with their diameter at breast height (DBH) for trees larger than 9.1 cm. In addition, 20 subplots of 4 m^2 were systematically established in the 400 m^2 plots, five per cardinal points. In those subplots, all live and dead saplings (trees from 1 to 9.1 cm DBH) were recorded by species and size. Finally, four additional 1 m^2 plots were established to count the number of tree seedlings.

To estimate snag abundance, we established one 50 x 20 m plot adjacent to the standard inventory plot in each of the 60 stands selected from the two chronosequences. In each plot, we tallied solely snags to increase sample size because the 400-m^2 inventory plots were too small to accurately determine the amount of snags available to birds. For each snag, we determined height ($\pm$ 0.1 m), and DBH ($\pm$ 1 cm). For the purpose of this study, only snags with DBH >9.1 cm and a minimum height of 1.3 m were considered. These characteristics are considered minimal conditions for nesting or foraging birds (Thomas et al., 1979).

2.2.3. Landscape variables

We evaluated the effect of forest composition around the 60 plots at three buffer size scales (1, 50, and 100 ha, according to the home range of various birds species), by noting the proportion of area covered by each of the following forest compositions as determined from forest maps: hardwoods, mixedwoods, coniferous and non-forested land types (e.g., lakes, transmission lines, gravel pits). We used ArcGIS® to calculate the buffer areas for the whole study area. This analysis allows to look at landscape scale effects on the different species' home ranges (Wiens, 1994). We also evaluated the relative proportion of the extent of stand-types based on time elapsed since the last fire at the three buffers size scales.

2.2.4. Bird survey

To estimate species richness and bird abundance, we used the point count method (Reynolds et al., 1980; Hutto et al., 1986). Each point count was located at the center of each standard inventory plot established in the 60 stands from the two chronosequences. All point counts were at least 200 m from each other and 100 m from the edge of a burned site. At each point, an observer recorded the site name, stand age, plot number, replicate number, date, and time.

Two visits (replicates) were realized at each point count during the breeding period (late May to late June 2007), to allow detection of a maximal number of species during their peak of singing activity. Observers recorded the number of individuals of each bird species detected by sight or sound for each of the following class distance from the center of the point count: from 0 - 30 m, 30 - 50 m, 50 - 75 m, and 75 - 100 m. In this study, we used the number of species detected in both visits of each point count to a maximum radius of 100 m.

Observers were familiar with bird vocalizations. However, if identification was doubtful, they recorded the bird song using a digital tape recorder with a directional microphone. The two visits made to each stand were realized by a different observer to eliminate biases. Similarly, we varied the time we visited each point count (e.g.: early vs. later in the morning) to maximize detection probabilities of each species present. At each visit, birds (seen or heard) were recorded at 10-min intervals for a 20-min period. This is a standard time procedure for boreal forest bird communities when one wants to relate bird richness and abundance with the vegetative characteristics of the point count (Drapeau et al., 2002).

2.2.5. Statistical Analyses

Multivariate analyses were used to detect differences in bird communities along a long-term forest habitat gradient based on time since fire. A direct gradient analysis approach allowed us to determine relationships between forest bird species and environmental variables (Lepš and Šmilauer, 2003). Our analyses include environmental measurements at the local and landscape scales. At the local scale, we used: time since fire (TSF), latitude, longitude, proportion of black spruce, balsam fir, overall coniferous species, hardwoods, sphagnum and shrubs, basal area, height, DBH, and quadratic mean diameter (Dq) of live and dead trees. Dq corresponds to the average basal area relative to the density of trees within the stand or the stand volume (West, 2009). At the landscape scale, we used the forest composition around the 60 plots at three buffer sizes (1, 50 and 100 ha) each representing the area proportion of hardwoods, mixedwoods, coniferous and non-forested land types, as determined from forest maps. For the same three buffer sizes, we also used the proportion of the extent of stands based on TSF.

Canonical correspondence analysis (CCA) was based on binary data (presence-absence) suitable for unimodal methods (ter Braak and Šmilauer, 2002). Only species observed at >5% of sampling locations were considered for this analysis. Indirect gradient analyses were performed and consisted in, first, a detrended correspondence (DCA) which indicates the relation among bird species and orders sampling sites along an environmental axis (showing a unimodal species response along an ordination axis) (Drapeau et al., 2000; Lee and Rotenberry, 2005). Second, a principal component analysis (PCA) was performed with the environmental data, allowing the use of variables that are not measured in the same measure units. Finally we used a Monte-Carlo Permutation from CCA test to evaluate the statistical significance on the relation between bird communities and environmental variables. Monte-Carlo tests of significance were conducted on the first canonical eigenvalues and independently on all canonical eigenvalues based on 1,000 permutations to determine the statistical significance of the first and all canonical eigenvalues respectively

(ter Braak and Šmilauer, 2002). All multivariate analyses were performed using the CANOCO software program.

We classified the number of bird species observed in each plot into three habitat assemblages (see Table 3): mature-forest species (F), forest-edge species (E) and open-forest species (O). As discussed by Imbeau et al. (2003), true edge species are rare if existent at all in boreal forests, therefore we consider forest-edge species as being more associated with shrubs and areas where early successional characteristics can be found; open-forest species are basically associated with open areas (e.g. American Kestrel). This classification is based on habitat associations found in recent species description (Gauthier and Aubry, 1996; see also Canterbury et al., 2000). Based on this classification, we performed multiple regressions (generalized linear models) using the GLIMMIX procedure (SAS Institute 2008) for model comparisons. The response variable is continuous (number of bird species per habitat assemblages or overall species richness) and we assumed normal distribution. We modeled, first, the environmental variables present in each assemblages that can explain the number of bird species and second, the possible variation in total species richness per point count as a function of a combination of vegetation variables. In order to determine the strongest variables that were used in the GLIMMIX procedure and the model comparisons, all variables selected were tallied using PROC REG (SAS Institute 2008). Furthermore, we included the variable TSF in the model comparisons to verify its potential effect on our data. The Akaike's Information criterion (AICc) was then used to select the best model among all predetermined models compared (Burnham and Anderson, 2002; Johnson and Omland, 2004). As generally considered, a Delta (Δ) AIC < 2 suggests substantial evidence for the model, values between 4 and 7 indicate that the model has considerably less support, whereas a ΔAIC > 10 indicates that the model is very unlikely (Burnham and Anderson, 2002). As described by Burnham and Anderson (2002), ΔAIC is defined as a measure of each model relative to the best model. When several models compete for the best ranking (ΔAIC$_c$ < 2 or equivalent), we recomputed the parameter estimates found in the subset models to obtain a model-averaging and unconditional standard errors. Finally, we used the estimates of each parameter for every model to evaluate their positive or negative effects.

The three habitat assemblages were used to calculate a bird community index that provides a direct measure of the status of the bird community in each plot (Canterbury et al., 2000). We modified the equation described in Canterbury et al. (2000) to better express variations in forest bird community from our study area. These three habitat assemblages were grouped as disturbance-sensitive species represented by birds associated with mature forest assemblage (F) and disturbance-tolerant bird species (E + O). Using these groups, the bird community index (CI) expresses variations in forest bird community associated with habitat disturbance calculated with the following equation:

$$CI = \ln (F+1) - \ln (E+O+1) \qquad [\mathbf{1}]$$

A positive bird community index indicates that the local bird assemblage is dominated by disturbance-sensitive species, whereas a negative index specifies that the assemblage is dominated by disturbance-tolerant species.

An analysis of variance (ANOVA) was used to compare mean bird species richness and mean bird community index between the two chronosequences and among TSF classes. We used TSF as a classification variable rather than as a continuous variable in the statistical analyses because we were not able to determine the exact TSF for plots >200 years (class 5) according to the information provided by the available fire map (Bouchard et al., 2008). Also based on TSF classes, we evaluated (1) the total number of bird species and (2) the total number of bird species lost and recruited from one TSF class to all other classes, for the two chronosequences. To avoid differences in sample size (class 5 having 10 sites instead of five for the other classes) we randomly chose 5 sites out of 10 and evaluated species lost and recruited for these sites. We ran this procedure 100 times for each chronosequence (method described as bootstrapping, see Sokal and Rohlf, 1995; Magurran, 2004). These analyses were performed using SAS (SAS Institute 2008), with a significance level of 0.05.

Table 3. List of bird species, habitat association: mature-forest (F), forest-edge (E) and open-forest (O); and percentage of occupied stations detected on the study area.

Species name	Scientific name	Code	Habitat assemblage	Detection %
White-throated Sparrow	*Zonotrichia albicollis*	wtsp	E	96.66
Ruby-crowned Kinglet	*Regulus calendula*	rcki	F	93.33
Swainson's Thrush	*Catharus ustulatus*	swth	F	85.00
Magnolia Warbler	*Dendroica magnolia*	mawa	E	80.00
Winter Wren	*Troglodytes troglodytes*	wiwr	F	80.00
Yellow-rumped Warbler	*Dendroica coronata*	yrwa	F	73.33
Dark-eyed Junco	*Junco hyemalis*	deju	F	71.66
Nashville Warbler	*Vermivora ruficapilla*	nawa	F	71.66
Red-breasted Nuthatch	*Sitta canadensis*	rbnu	F	60.00
Tennessee Warbler	*Vermivora peregrina*	tewa	F	50.00
Boreal Chickadee	*Parus hudsonicus*	boch	F	45.00
Gray Jay	*Perisoreus canadensis*	graj	F	43.33
Yellow-bellied Flycatcher	*Empidonax flaviventris*	ybfl	F	41.66
Golden-crowned Kinglet	*Regulus satrapa*	gcki	F	41.66
Pine Siskin	*Carduelis pinus*	pisi	F	41.66
Hermit Thrush	*Catharus guttatus*	heth	F	40.00
Brown Creeper	*Certhia americana*	brcr	F	35.00
White-winged Crossbill	*Loxia leucoptera*	wwcr	F	33.33
American Robin	*Turdus migratorius*	amro	O	25.00
Alder Flycatcher	*Empidonax alnorum*	alfl	E	25.00
Wilson's Warbler	*Wilsonia pusilla*	wiwa	E	25.00
Blue-headed Vireo	*Vireo solitarius*	bhvi	F	25.00
Purple Finch	*Carpodacus purpureus*	pufi	F	16.66
Fox Sparrow	*Passerella iliaca*	fosp	E	15.00
Black-backed Woodpecker	*Picoides arcticus*	bbwo	F	13.33
Philadelphia Vireo	*Vireo philadelphicus*	phvi	F	13.33
Tree Swallow	*Tachycineta bicolor*	tres	O	11.66
Bay-breasted Warbler	*Dendroica castanea*	bbwa	F	11.66
Cape May Warbler	*Dendroica tigrina*	cmwa	F	11.66
Northern Flicker	*Colaptes auratus*	nofl	E	11.66
Yellow-bellied Sapsucker	*Sphyrapicus varius*	ybsa	F	11.66

Evening Grosbeak	*Hesperiphona vespertina*	evgr	F	10.00
Blackpoll Warbler	*Dendroica striata*	blpw	F	10.00
Northern Waterthrush	*Seiurus noveboracensis*	nowa	F	10.00
American Kestrel	*Falco sparverius*	amke	O	8.33
Common Raven	*Corvus corax*	cora	E	8.33
American Redstart	*Setophaga ruticilla*	amre	F	8.33
Black-throated Green Warbler	*Dendroica virens*	btnw	F	8.33
Three-toed Woodpecker	*Picoides tridactylus*	ttwo	F	8.33
Cedar Waxwing	*Bombycilla cedrorum*	cedw	O	6.66
Olive-sided Flycatcher	*Contipus cooperi*	osfl	E	6.66
Chestnut-sided Warbler	*Dendroica pensylvanica*	cswa	E	6.66
Common Yellowthroat	*Geothlypis trichas*	coyo	E	6.66
Hairy Woodpecker	*Picoides villosus*	hawo	F	6.66
Rusty Blackbird	*Euphagus carolinus*	rubl	E	6.66
Red-eyed Vireo	*Vireo olivaceus*	revi	F	6.66
Red-tailed Hawk	*Buteo jamaicensis*	rthk	O	5.00
Pine Grosbeak	*Pinicola enucleator*	pigr	F	5.00
Downy Woodpecker	*Picoides pubescens*	dowo	F	5.00
Lincoln's Sparrow	*Melospiza lincolnii*	lisp	E	3.33
Common Nighthawk	*Chordeiles minor*	conh	O	3.33
American Bittern	*Botaurus lentiginosus*	ambi	O	1.66
Sharp-shinned Hawk	*Accipiter Striatus*	sshk	F	1.66
Ruffed Grouse	*Bonasa umbellus*	rugr	F	1.66
Gray-cheeked Thrush	*Catharus minimus*	gcth	F	1.66
Blackburnian Warbler	*Dendroica fusca*	blwa	F	1.66
Mourning Warbler	*Oporornis philadelphia*	mowa	E	1.66
Spruce Grouse	*Falcipennis canadensis*	spgr	F	1.66

2.3. Results

2.3.1. Patterns of bird community assemblage

A total of 58 bird species were detected in the 60 stands (30 stands per chronosequence) covering the five TSF (time since fire) classes. Of these, 53 were detected in the northern chronosequence, while 54 were detected in the south. Species composition analyses were conducted on 46 species, which were present in more than 5% of the point count stations (Table 3). Canonical correspondence analysis identified the nine environmental variables most strongly related to bird community composition: snag height and DBH, live trees height, basal area, Dq, proportion of conifers and shrubs, TSF and the relative proportion of the extent of stands based on TSF for a buffer size of 100 ha (Fig. 8). The first and second canonical axes summarized approximately 9.8% and 8.2% of the variation, respectively, in species composition. A Monte-Carlo permutation test indicates that the first axis was significantly related to species-environmental variables (F=2.466, $P = 0.0018$) and that all canonical axes (including the first and all others) significantly summarized the relationships between bird species and environmental variables (F=1.438, $P = 0.0001$). The first canonical axis represents a gradient ranging from recently-burned forests (right, Fig. 8) to old-growth forest (left), whereas the second axis represents a gradient from low stand density (down) to high stand density (up) (close association to measures of Basal area and Dq of live trees). The position of bird species along the axes or the environmental variables represents their association to their habitat. Bird species near the center of the CCA ordination (e.g., Ruby-crowned Kinglet, rcki; Magnolia Warbler, mawa) are considered common and found ubiquitously in most habitats. On the contrary, the Black-backed Woodpecker (bbwo) is strongly associated with recently burned forests (proximity to the first axis) and tall snags (proximity to the Height_D variable), and other species such as the American Kestrel (amke) and the Chestnut-sided Warbler (cswa) are associated with low stand density (open areas) and early succession forests respectively.
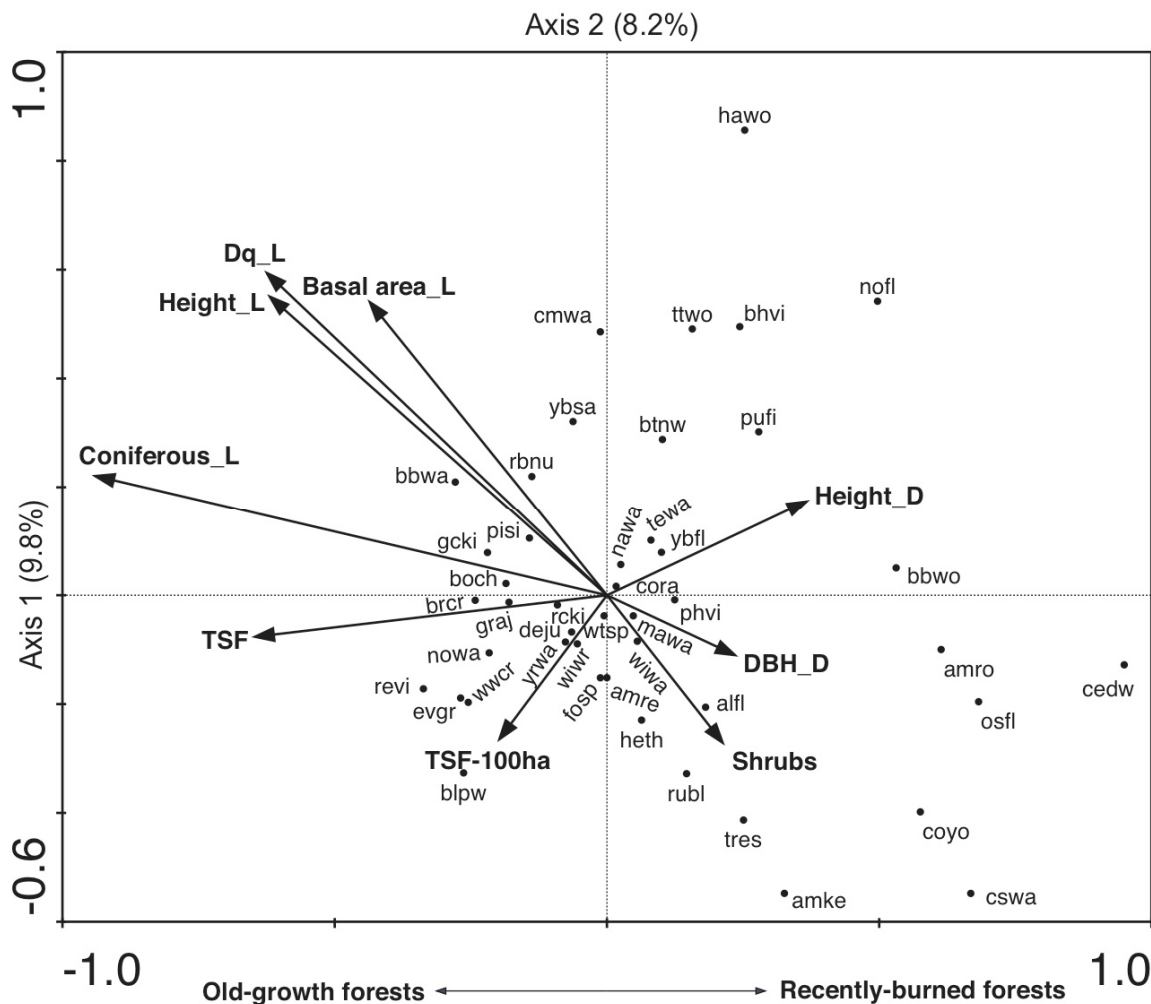
Axis 2 (8.2%)

1.0

hawo

Dq_L

Basal area_L

Height_L

nofl

cmwa   ttwo   bhvi

ybsa   btnw   pufi

Coniferous_L   rbnu

bbwa

Height_D

gcki   pisi   nawa   tewa   ybfl

boch   cora   bbwo

brcr   phvi

TSF   graj   rcki   wtsp   mawa

deju   DBH_D

nowa   yrwa   wiwr   wiwa   amro   cedw

revi   wwcr   fosp   amre   alfl   osfl

evgr

TSF-100ha   heth   Shrubs

blpw   rubl

tres   coyo

amke   cswa

-0.6

Axis 1 (9.8%)

-1.0   1.0

Old-growth forests ◄———————► Recently-burned forests

Figure 8. Canonical correspondence analysis axes one and two, showing the association of bird species and environmental variables. Axis 1 represents a gradient ranging from recently-burned forests (right) to old-growth forest (left); while Axis 2 represents a gradient from low stand density (down) to high stand density (up). Points represent bird species and arrows represent environmental variables. The letter D or L in the environmental variables indicates dead or live trees. The length of an arrow reflects the importance of the environmental variable and the angles between arrows signifies the correlation between variables. See Methods for variables descriptions and Table 3 for species names related to the four letter codes.

2.3.2. Bird species and habitat association models

Mature forest bird species

The best models explaining the presence of birds associated with mature-forest are summarized in Table 4. The best model includes the following variables: the proportion of non forested land types within a 50-ha buffer (non-forested 50 ha, negative effect), the proportion of coniferous trees within a 100-ha buffer (coniferous 100 ha, negative effect), and the proportion of black spruce at the plot scale (PIM, negative effect). The second best model, which is also highly probable (very low delta AIC=0.29), indicates that the proportion of black spruce is not a predictor as strong as the two first variables of the best model. Other variables such as TSF and the relative proportion of the extent of stands based on TSF within a buffer size of 100 ha might affect the occurrence of bird species in mature forests, but were not retained in our best models. These models indicate that forest-bird species are not all coniferous forest specialists, some being associated with deciduous trees and tend to avoid the presence of other land-use type on a mid-scale (such as lakes, transmission lines, or gravel pit).

Table 4. Model selection explaining the presence of mature-forest bird species. Models are ranked from most plausible (ΔAICc = 0) to least plausible (only model with ΔAICc >7 are included). The Akaike weights (w_i) indicate the plausibility of the best-fitting model compared to other models. R^2 indicates the variance explained by each model. Models are presented as the equation from the generalized linear model, including the intercept and the parameter estimates associated with each variable. See Methods for description of variables.

Model ID	Model	AIC_c	Delta AIC (Δ_i)	Akaike weight (w_i)	R^2
1	16.44 − 10.27nonforested50ha − 4.43coniferous100ha − 0.94PIM	283.80	0	0.421	0.2708
2	15.65 − 9.65nonforested50ha − 4.21coniferous100ha	284.09	0.29	0.364	0.2571
3	16.56 − 10.38nonforested50ha − 4.37coniferous100ha − 0.95PIM − 0.0009TSF	287.25	3.45	0.075	0.2709
4	15.74 − 9.72nonforested50ha − 4.16 coniferous100ha − 0.0007TSF	287.42	3.62	0.069	0.2572
5	12.17 − 6.15nonforested50ha	289.37	5.57	0.026	0.1985
6	12.63 − 6.49nonforested50ha − 0.72PIM	289.39	5.59	0.026	0.2065

Forest-edge bird species

The model that best explains the presence of birds associated with forest-edge (Table 5), includes variables such as proportion of black spruce (negative effect), proportion of mixedwoods (positive effect), proportion of sphagnum (positive effect) and snag basal area (positive effect). Bird species commonly associated with forest edges thus seem to avoid black spruce, prefer mixed forests and benefit from lower stand density (where sphagnum can be found) and sparse snags.

Table 5. Model selection explaining the presence of forest-edge bird species. Models are ranked from most plausible (ΔAICc = 0) to least plausible (only model with ΔAICc >7 are included). The Akaike weights (w_i) indicate the plausibility of the best-fitting model compared to other models. R^2 indicates the variance explained by each model. Models are presented as the equation from the generalized linear model, including the intercept and the parameter estimates associated with each variable. See Methods for description of variables.

Model ID	Model	AIC_c	Delta AIC (Δ_i)	Akaike weight (w_i)	R^2
1	2.70 + 2.26sphagnum + 2.18mixedwoods100ha − 1.47PIM + 0.09basal area_D	184.36	0	0.8399	0.4621
2	3.02 + 2.04mixedwoods100ha − 1.42PIM + 0.07 basal area_D	189.76	5.4	0.0564	0.3971
3	2.77 + 2.30sphagnum + 2.17mixedwoods 100ha − 1.47PIM + 0.09basal area_D − 0.0005TSF	190.0	5.64	0.0501	0.4626
4	3.99 − 1.91PIM	190.32	5.96	0.0427	0.2998

Open-forest bird species

To help explain the presence of birds associated with open-forested habitat (Table 6), two models came out as probable (model 2 has a delta AIC=1.85). The proportion of conifers at the plot level (negative effect) and, to a lesser extent, the proportion of conifers in a buffer of 50 ha (positive effect) affected bird species associated with open-forest habitats. These bird species thus mainly use forest patches characterized by low basal area in conifers.

Table 6. Model selection explaining the presence of open-forest birds. Models are ranked from most plausible (ΔAICc = 0) to least plausible (only model with ΔAICc >7 are included). The Akaike weights (w_1) indicate the plausibility of the best-fitting model compared to other models. R^2 indicates the variance explained by each model. Models are presented as the equation from the generalized linear model, including the intercept and the parameter estimates associated with each variable. See Methods for variables description of variables.

Model ID	Model	AIC_c	Delta AIC (Δ_i)	Akaike weight (w_i)	R^2
1	1.77 − 1.39coniferous	120.32	0	0.6783	0.3614
2	1.65 − 1.49coniferous + 0.30coniferous50ha	122.17	1.85	0.2690	0.3704
3	1.77 − 1.38coniferous − 0.00002TSF	126.16	5.84	0.0366	0.3614

Overall species richness

Our AIC comparison for species richness indicates that 5 of the 9 models shown may explain the number of bird species in the entire study region (Table 7). The first model includes variables such as the proportion of mixedwoods within a 100-ha buffer, the percent cover of sphagnum, and height of live trees which all have positive effects whereas the proportion of black spruce at the plot level has a negative effect. Models 2 through 5 include a combination of these variables, with the addition of TSF and snag basal area (both having very little effect, see Table 7). In our comparison, 5 models obtained $\Delta AIC_c <$ 2; in order to provide more details on the ranking of these models, we performed the model-averaging using the parameter estimates of the mixedwoods 100ha variable, present in all these models (see Table 8). This variable's estimate is different from 0 (95 % C.I. for the model-averaged estimate being between 1.84 and 12.18); therefore indicating that overall species richness is strongly influenced by the presence of mixedwood at 100ha scale. Finally, Table 9 provides with the information related to each variables used for the models, including means and standard deviations.

Table 7. Model selection explaining the overall species richness. Models are ranked from most plausible (ΔAICc = 0) to least plausible (only model with ΔAICc >7 are included). The Akaike weights (w_i) indicate the plausibility of the best-fitting model compared to other models. R^2 indicates the variance explained by each model. Models are presented as the equation from the generalized linear model, including the intercept and the parameter estimates associated with each variable. See Methods for variables description of variables.

Model ID	Model	AIC$_c$	Delta AIC (Δ_i)	Akaike weight (w_i)	R^2
1	13.55 + 7.16mixedwoods100ha − 3.97 PIM + 3.34sphagnum + 0.20height_L	296.66	0	0.2698	0.3409
2	12.82 + 8.36mixedwoods100ha + 4.55sphagnum − 1.61PIM + 0.20basal area_D	297.54	0.88	0.1738	0.2963
3	15.20 + 8.00mixedwoods 100ha + 3.14sphagnum − 2.98PIM	297.57	0.91	0.1712	0.2119
4	12.65 + 8.40mixedwoods100ha + 4.47sphagnum − 1.61PIM + 0.20basal area_D + 0.0011TSF	297.63	0.97	0.1661	0.4014
5	11.43 + 7.55mixedwoods100ha + 4.65sphagnum − 2.61PIM + 0.19height_L + 0.18basal area_D	298.38	1.72	0.1142	0.3574
6	15.35 + 7.84mixedwoods 100ha − 2.72PIM	300.39	3.73	0.0418	0.1974
7	12.65 + 8.39mixedwoods100ha + 4.47sphagnum − 1.61PIM + 0.20basal area_D + 0.0011TSF	300.99	4.33	0.031	0.2988
8	13.45 + 8.07mixedwoods 100ha − 1.49PIM + 0.16basal area_D	302.02	5.36	0.0185	0.2521
9	12.23 + 8.03mixedwoods 100ha + 0.21basal area_D	303.38	6.72	0.0094	0.2300

Table 8. Akaike weight and associated measures recomputed to obtain the model-averaging estimate and precision (unconditional SE) of the mixedwoods 100ha variable for the first five (5) models from the selection explaining the overall species richness.

Model ID	Model	AIC$_c$	Delta AIC (Δ_i)	Akaike weight (w_i)	Regression estimate of mixedwoods 100ha	SE of estimate of mixewoods 100ha
1	mixedwoods100ha PIM sphagnum height_L	296.66	0	0.2698	7.16	2.79
2	mixedwoods100ha sphagnum PIM basal area_D	297.54	0.88	0.1738	8.36	2.76
3	mixedwoods 100ha sphagnum PIM	297.57	0.91	0.1712	8.00	2.87
4	mixedwoods100ha sphagnum PIM basal area_D TSF	297.63	0.97	0.1661	8.40	2.79
5	mixedwoods100ha sphagnum PIM height_L basal area_D	298.38	1.72	0.1142	7.55	2.69
	Model-averaged estimate				**7.011**	
	Unconditional SE					**2.638**

Table 9. Details on predictor variables used for the model comparison (mature forests, forest-edge, open forests and overall species richness). See Methods for details.

Predictor variables	Mean	Standard deviation	Minimum	Maximum
Basal area_D	7.48	5.52	0.53	24.9
Coniferous %	0.83	0.33	22.53	100
Coniferous 100ha %	0.67	0.24	9.44	100
Coniferous 50ha %	0.69	0.26	7.84	100
Height_L	11.23	6.64	1.46	27.6
Mixedwoods 100ha %	0.08	0.13	0	58.2
Non-forested 50ha %	0.18	0.21	0	92.2
PIM %	0.55	0.38	5.01	100
Sphagnum %	0.09	0.15	0	72.36
TSF -100ha	160.19	62.71	25	225
TSF	149.68	87.38	2	250

2.3.3. Bird species and conservation criteria

The mean number of species remained significantly constant ($F_{9,50}$ = 0.18, P = 0.9460) among TSF classes for both chronosequences (Fig. 9A). However, the bird community index in the two chronosequences (Fig. 9B) differed significantly among TSF classes ($F_{9,50}$ = 9.92, P = <0.0001). All community index values were low but positive, indicating that bird communities of all stands were dominated by disturbance-sensitive species (mature-forest species). In recently burned forests (0-50 years), there were fewer disturbance-sensitive species and the index value increased thereafter until a slight decline occurring at >200 years for the north chronosequence. In the south chronosequence, the pattern showed less variation across TSF classes, and ended up at >200 years with a little more disturbance-sensitive species than in younger forests.
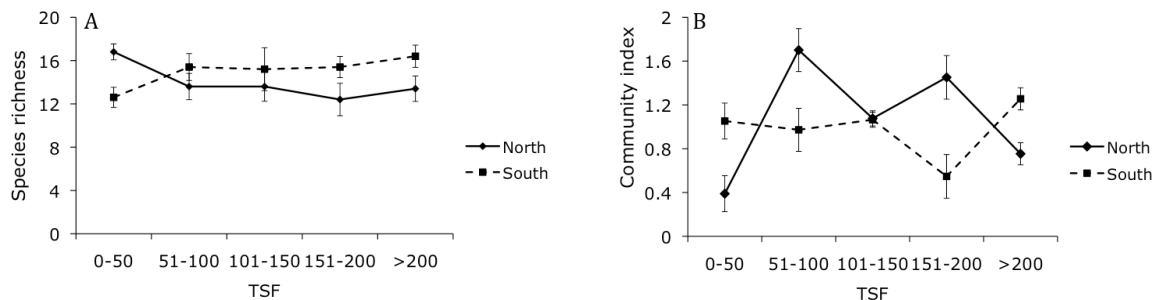
Figure 9. Mean number (± S.E.; n = 30) of species and community index along the two chronosequences. The two diagrams show (A) average number of bird species and (B) average value of bird community index, both according to time since fire (TSF).

Both chronosequences were associated with similar trends, each tend to reach lower levels of species loss and recruitment toward older forests (cumulative loss of bird species with increasing TSF classes, Fig. 10A; cumulative recruitment of bird species with increasing TSF classes; Fig. 10B). Total recruited species added up to 51 and 52 species for the north and south chronosequence respectively (instead of 53 and 54 species) due to the difference in sample size for the TSF class >200 years (for which we did bootstrapping, see Methods).
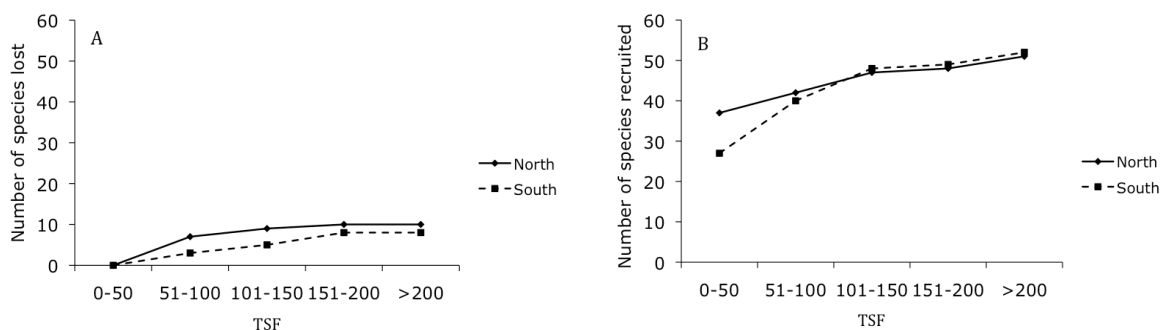
Figure 10. Cumulative number of bird species lost and recruited in the two chronosequences. The two diagrams present (A) the cumulative number of bird species lost and (B) the cumulative number of bird species recruited, both according to time since fire (TSF).

2.4. Discussion

The analysis of bird species composition (as revealed by the CCA, Fig. 8) provided information about how bird assemblages changed following local and landscape characteristics, which are generally driven by the long-term succession stages according to the time elapsed since the last fire. Even though few studies have examined the time elapsed since the last fire in relation to bird communities (but see Helle, 1985), most agree on the important changes that occur in bird species composition and abundance following changes in habitat structure during succession stages (MacArthur and MacArthur, 1961; Karr and Roth, 1971; Wiens and Rotenberry, 1981; James and Wamer, 1982; Imbeau et al., 1999; Saab et al., 2005). In this study, recently burned forests were associated with a large quantity of dead standing trees and high shrub cover, all of which attract specific wildlife species (Drapeau et al., 2000; Nappi et al., 2004). On the other hand, old-growth forests had a complex structure mainly composed of conifers with large live trees, which are usually considered as key habitats for wildlife (Raphael and White, 1984; Probst et al., 1992). Our results therefore provide a first look at the changes in bird community, species composition

and distribution along two long-term chronosequences with increasing forest structure along succession stages.

Patterns of bird distribution found in this study are consistent with results about specific habitat preferences (Smith, 1993; Hutto, 1995; Saab and Dudley, 1998; Nappi et al., 2003). Distinct species composition during the years following fire can be explained by the presence of more open, accessible forests that attract generalist species (such as the American Robin), while other species, such as the Black-backed Woodpecker, may benefit from particular niche requirements such as the abundance of wood-boring beetles on recently burned trees (Evans, 1966; Hutto, 1995; Morissette et al., 2002). On the other hand, species constantly requiring tree cover and foliage for nesting or foraging remained associated with older forests, providing a more stable bird community (Drapeau et al., 2002; Morissette et al., 2002). For example, Brown Creepers, Boreal Chickadees and Red-breasted Nuthatches are present in mature to over-mature forests due to the higher density of large live trees with few large snags (Drapeau et al., 2002; Chapter 1). Results also highlight the importance of deciduous vegetation as a factor affecting species composition, especially within a context of forests dominated by conifers. This factor appears to be even more important than time since fire. This is not totally unexpected considering that few species are adapted equally to deciduous and coniferous vegetation (Girard et al., 2004) and those heterogeneous habitats usually sustain a greater diversity of species.

Bird species richness was higher in stands not purely coniferous, i.e. with presence of hardwoods. Hardwood presence in coniferous stands may provide an abundant insect fauna, numerous cavity sites and greater vertebrate richness than purely conifer stands (James and Wamer, 1982; Bruce et al., 1985). In British Columbia, Bunnell et al. (1999) observed that more than two-thirds of bird nests were located in mixedwoods. In the Quebec province, as in other parts of North America, bird species richness overall is higher in mixed forests than in coniferous forests (James and Wamer, 1982; Gauthier and Aubry, 1996). Our results indicate that forest characteristics can affect bird communities not only at the local scale (plot level; 400 m^2), but also at the landscape level (50 and 100 ha). Specific associations between bird communities belonging to general habitat assemblages (forest,

edge, open) and the forest characteristics of these habitats generally agree with the various reports available on these species-groups. For example, bird species in forest-edge habitat seem to benefit from the areas of lower stand density within forests (all our point counts were located in forests), where we recorded a higher abundance of sphagnum (Fenton and Bergeron, 2006). Even though our point count data came from mostly forested areas, our models for open-forest and forest edge provide interesting insight on how little habitat change within forested habitat may explain variation in species richness and composition in boreal forests.

The number of years elapsed since the last fire affected species composition more than species richness in the study area (Fig. 9). Helle (1985) and Smucker et al. (2005) obtained similar results but on mid to shorter-term chronosequences respectively. Imbeau et al. (1999) also noticed that bird assemblages "did not increase uniformly" towards mature forest. This might be characteristic of northern boreal forests (Imbeau et al., 1999). The changes appear to occur through changes in habitat structure and composition but may also occur through changes in food supply, abundance of competitors and/or predators (Rotenberry et al., 1995). There is considerable variation in the pattern of response by forest birds during long-term successions. The boreal forest is a very dynamic ecosystem, where snags only follow long-term cycles, which in turn affect cavity-nesting birds (Chapter 1). Live conifer and hardwood species of the boreal forest also go through a shift in dominant species with increasing TSF (James and Wamer, 1982; Bouchard et al., 2008), which can also affect the bird species community. Nevertheless, little consensus has emerged on exactly how bird communities vary with succession stages (Helle and Mönkkönen, 1990). In our study, species richness and community index provided a broad-based indicator of the extent to which the bird community had been affected by forest disturbances like fire (see also Angermeier and Karr, 1994; Canterbury et al., 2000). Although bird species richness did not vary greatly in our study, species were lost and other recruited following the successions (Fig. 10). Variability was high throughout age classes with high recruitment especially in young forests; as forest stands matured, we observed fewer species lost and fewer species recruited, indicating a stabilizing community structure (species composition) in old-growth forests. In addition, substantial differences were

observed in the bird community index, indicating differences in species composition and the number of species sensitive to habitat modifications. The latter substantiate the need to protect forests at all ages because sensitive species were numerous in mid-aged stands. Helle (1985) similarly found specialist species in several age classes, including recently burned forests and mid-aged stands (up to 150 years after fire). Recently burned stands provide not only habitat for new-coming species, attracted to the new openings, but also attract species with specific habitat requirements (e.g., bbwo). As forest age increases (following fire), changes in habitat structure towards mature stands carry more changes to the bird community, bringing species requiring the key habitats found only in old-growth stands. Future studies should focus on smaller scale age-class periods in order to improve the detection in bird community variations across long-term chronosequences. Although, in our study, we were able to detect certain changes using 50-years increments, a more thorough study using shorter increments might describe even further the changes in bird communities and habitat characteristics, especially in the light of the important changes occurring between 0 and 50 years post fire (Raphael et al., 1987; Hobson and Schieck, 1999; Imbeau et al., 1999; Smucker et al., 2005).

Time since fire reflects habitat structural changes at different scales and thus changes in the bird species community. This study provides further evidence that this is particularly true when looked upon long-term data from two chronosequences. Changes (species lost and recruitment) observed along TSF need to be taken into account in the context of forest management. Species come and go following the different succession stages and sensitive species might be present at any succession stages of forest development. Our study confirms the need to increase the value of recently burned boreal forests for a unique bird diversity (Helle, 1985), but also highlight the need to protect the forest at all stages, including old-growth with its associated well-defined species composition. These stages provide heterogeneous environments required by several species (Drapeau et al., 2000; Saab et al., 2005). By keeping a mosaic of fire naturally-disturbed forests, we keep intact these succession stages and its associated avifauna.

2.5. Acknowledgments