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CARACTÉRISTIQUES DE LA FORÊT BOREALE DE L'EST DU QUÉBEC EN RELATION AVEC LA FAUNE AVIAIRE

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Résumé

Les objectifs de ce projet étaient, en premier lieu, de comprendre l'effet d'une perturbation naturelle (le feu) sur la disponibilité et l'abondance des arbres morts sur pied et sur les oiseaux résidant dans la forêt boréale non-aménagée de l'Est du Québec. En deuxième lieu, j'ai voulu comprendre l'effet des changements de structure et de composition des forêts boréales sur les communautés d'oiseaux en général et ce, le long de deux chronoséquences couvrant plus de 200 ans après feu. Mes résultats montrent que le taux de mortalité des arbres forme un patron en U caractérisé par une forte abondance de chicots dans les jeunes peuplements et dans les peuplements âgés. Ces peuplements sont caractérisés par un plus grand nombre de cavités et de signes d'alimentation de la part des oiseaux résidents. Toutefois, la richesse en espèces des oiseaux n'a que très peu varié en fonction des classes d'âge des peuplements, mais plusieurs espèces sont disparues et d'autres ont été recrutées en fonction des stades de succession. Cette étude souligne l'attention qu'il faut porter à tous les stades de succession de la forêt boréale, spécialement aux vieilles forêts qui procurent un environnement hétérogène requis par un grand nombre d'espèces.

Abstract

The first objective of this project was to understand the effect of natural fire disturbance on the availability and abundance of dead trees (snags) and their use by cavity-nesting birds in the northeastern part of Quebec's unmanaged boreal forest stands. Secondly, I aimed to understand the effects of the structure and composition of the boreal forest on bird species communities along two long-term chronosequences after fire (0 to >200 years postfire). Results show that tree mortality follow a U-shape pattern, with more snags in young and old-growth forests, where I also found more nest cavities and foraging signs. Although bird species richness did not vary greatly according to the different age classes, many species were lost and others recruited following succession stages. This study highlights the need to protect the forest at all stages, especially old-growth, which provides a heterogeneous environment suitable for several bird species.

Avant-propos

Ce projet de maîtrise, financé par le Fonds québécois de la recherche sur la nature et les technologies (FQRNT), s'intègre dans une vaste étude mise sur pied dans le cadre de la chaire de recherche industrielle CRSNG-Université Laval en sylviculture et faune. L'objectif principal de cette chaire consiste à acquérir les connaissances sur le fonctionnement de la forêt boréale de façon à améliorer l'aménagement durable de ces forêts et par le fait même, la conservation de la biodiversité. La présente étude suit le format d'un mémoire avec insertion d'articles. Il a été rédigé sous la codirection des Docteurs David Pothier (Université Laval) et Jean-Pierre Savard (Sciences et technologies, Environnement Canada à Québec). Les chapitres de ce mémoire, pour lesquels je suis la première auteure, seront soumis pour publication après l'accord des co-directeurs, suivant l'ordre chronologique de réalisation.

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Introduction

La forêt boréale représente l'écosystème terrestre le plus étendu de la planète, n'étant coupé le long du pôle nord que par les océans (Hammond 1994). Cette forêt représente aussi le plus grand biome ou communauté environnementale du Canada, occupant 32% de la superficie totale du pays et 77% de ses forêts. Elle fait le lien entre la toundra arctique et les forêts mixtes (ou encore les prairies). Étant donné qu'on y retrouve une très grande densité d'arbres, surtout de conifères, la forêt boréale possède aussi une grande importance économique au Canada (Larsen, 1980; Environnement Canada, 1994; Ressources Naturelles Canada, 2005).

Les arbres constituent l'élément structurel principal et le plus visible d'un écosystème forestier. La forêt boréale est dominée par un faible nombre d'espèces de résineux à aiguilles, parmi lesquelles on retrouve les épinettes, les sapins, les mélèzes et les pins. On y retrouve aussi un certain nombre d'espèces feuillues (arbres et arbustes), en particulier les bouleaux, les saules et les peupliers. Même si ces espèces se mélangent aux arbustes, mousses et lichens tout au long de l'aire de répartition des forêts boréales du pays, la densité et la diversité en espèces varient de façon importante d'est en ouest et du nord au sud (Énergie, Mines et Ressources Canada, 1993).

Les perturbations naturelles contribuent beaucoup à la diversité de la forêt boréale à l'échelle du paysage. Les épisodes fréquents de feux de forêt, d'épidémies d'insectes ravageurs (telle que la tordeuse des bourgeons de l'épinette), de maladies ou encore du chablis, se produisent à différentes périodes et à différents endroits à travers le territoire canadien (Pastor et al., 1996). Ces perturbations produisent une mosaïque de peuplements de différentes superficies, d'âges ou de stades de régénération (Dansereau et Bergeron, 1993; Hely et al., 2001). On considère le feu comme étant la perturbation naturelle la plus importante de la forêt boréale, constituant une force majeure dans la dynamique de cet écosystème (Johnson, 1992; Hejl, 1994; Hutto, 1995; Bergeron et al., 1999). La structure d'un peuplement dépend donc fortement de la récurrence des feux, phénomènes qui varient grandement d'une région à l'autre (Ruel et al., 2007). Cette structure complexe de la

mosaïque forestière est reconnue pour soutenir une importante biodiversité. Afin de comprendre la relation entre la biodiversité et les caractéristiques des peuplements soumis aux perturbations naturelles, on doit étudier une région non-aménagée dont l'historique des feux est connu. Le cycle de retour des feux peut varier de 50 à plus de 250 ans en forêt boréale (Wein et McLean, 1983; Hammond, 1994). Toutefois, il devient de plus en plus difficile d'étudier des systèmes naturels puisque l'aménagement forestier affecte les cycles de feu, ce qui fait qu'on ne retrouve que très peu de peuplements de plus de 150 ans. Toutefois, dans la forêt boréale de l'Est du Québec, le climat humide allonge cet intervalle à plus de 500 ans, ce qui fait que les vieilles forêts peuvent couvrir plus de 60% du territoire forestier qui est encore non-aménagé (Bouchard et al., 2008). Ces peuplements sont généralement caractérisés par une distribution irrégulière de la taille des arbres. Grâce à leur long cycle de retour des feux, ils peuvent donc constituer un système particulier pour étudier les patrons de mortalité des arbres et la structure de l'habitat en fonction des différents stades de succession et l'utilisation des forêts par les oiseaux sur une longue période. Enfin, une grande partie des forêts de la Côte-Nord n'a pas encore été exploitée, permettant d'étudier ce système sans l'effet de l'aménagement forestier.

Typiquement, après le passage d'un feu, plusieurs arbres morts sont laissés sur pied et le sol est noirci. De ce sol émerge des plantes adaptées à coloniser ce type de milieu, ce qui constitue la première étape de la régénération. Les feux favorisent donc la régénération de la forêt en plus de procurer une grande quantité d'arbres morts toujours sur pied (chicots) qui sont beaucoup utilisés par une variété d'organismes vivants. En effet, les chicots sont cruciaux à la biodiversité de cet écosystème en procurant des sites de nidification pour plusieurs espèces d'oiseaux (Saab et al., 2002). Ils sont aussi fortement utilisés par les insectes qui s'alimentent du bois en décomposition, ce qui, en retour, permet d'alimenter d'autres organismes tels que les pics ou d'autres espèces d'oiseaux associées aux troncs d'arbres (Machmer et Steeger, 1995; Dixon et Saab 2000; Nappi et al., 2003).

En connaissant les patrons de mortalité des arbres de la forêt boréale, on peut en connaître davantage sur l'effet multiple que peuvent avoir les cycles de feu, que ce soit à court ou à long termes. Les processus tels que la mortalité des arbres et la décomposition des débris

ligneux au sol sont maintenant reconnus comme étant vitaux au maintien du bon fonctionnement de ces forêts (Wei et al., 1997; Hagan et Grove, 1999). Plusieurs études font état de l'utilisation des forêts récemment brûlées par les oiseaux et leurs résultats soulignent l'importance de ce stade de régénération. La composition en espèces d'oiseaux de ces jeunes forêts est unique comparativement aux forêts intactes avoisinantes, certaines espèces étant restreintes à ce type d'habitat (Taylor et Barmore, 1980; Hutto, 1995; Caton, 1996; Kotliar et al., 2002; Nappi et al., 2002). De plus, comme les forêts récemment brûlées constituent aussi des milieux relativement ouverts, certaines espèces de milieux ouverts vont aussi y être observées (Hutto, 1995). Toutefois, peu de choses sont connues sur l'utilisation à long terme (plus de 200 ans après feu) des forêts par les oiseaux. Les arbres morts peuvent être plus abondants dans les vieilles forêts (Harmon et al., 1986; Spies et Franklin, 1988; Tyrrell et Crow, 1994; Clark et al., 1998), mais procurent-elles un avantage en ce qui concerne l'utilisation par les oiseaux? Les espèces d'oiseaux nichant en cavité seront-elles plus abondantes dans les vieilles forêts? Si oui, cela permettrait de confirmer l'importance des vieilles forêts dans la planification de l'aménagement forestier. Qu'en est-il de la composition des communautés d'oiseaux utilisant la forêt boréale? Les changements de structure des forêts en fonction des étapes de régénération provoquent-ils des changements de communautés d'oiseaux?

La présente étude cherchera à répondre à ces questions en examinant la quantité de chicots et les différences de structure d'habitat le long de deux chronoséquences à long terme après feu dans la forêt boréale non-aménagée de l'Est du Québec et en les reliant aux effets potentiels sur les oiseaux forestiers. Un premier volet examinera les patrons de mortalité des arbres et l'utilisation des chicots par les oiseaux nicheurs en cavités, tandis qu'un deuxième volet portera sur l'effet des changements de structure et de composition des forêts sur les communautés d'oiseaux, en tenant compte des différentes étapes de succession après feu.

Snag characteristics and use by cavity-nesting birds in the unmanaged post-fire Québec eastern boreal forest

Abstract

We studied the availability of snags and their use by cavity-nesting birds in the northeastern part of the Canadian boreal forest. We built up two long-term (>200 years) chronosequences following time elapsed since the last fire of the unmanaged stands in the boreal forest of northeastern Québec, which is characterized by long fire cycles (up to 500 years). We then sampled and characterized snags and live trees in 30 stands from each of these two chronosequences. We also looked for nest cavities and foraging signs on all sampled snags, and performed complete bird inventories by point counts. Results show that tree mortality follow a U-shape pattern, with more snags in young (<50 years) and in old (>200 years) forests. A greater proportion of snags with large diameter (>20 cm DBH) was found in old forests, where we also found more nest cavities and foraging signs. Although primary cavity-nesters (excavating species) were not more abundant in any age class, secondary cavity-nesters (using cavities already available) tend to be more numerous in older forests. Our results highlight the capacity for old-growth forests to provide quality habitat for species that are dependent on large snags. Proper forest management should maintain a mosaic of mature forest stands, including snags, to promote biodiversity and provide important resources for resident bird species.

Résumé

Nous avons étudié la disponibilité des arbres morts (chicots) et leur utilisation par les oiseaux nicheurs en cavité dans la forêt boréale non-aménagée de l'Est du Québec. Grâce à de longs intervalles de retour des feux (jusqu'à 500 ans), on y retrouve les conditions idéales pour étudier la mortalité des arbres et les communautés d'oiseaux. Nous avons sélectionné des peuplements formant deux chronoséquences à long terme après feu (>200 ans) formées chacune de 30 parcelles dans lesquelles nous avons échantillonné et caractérisé les chicots et les arbres vivants. Dans ces parcelles, nous avons aussi recensé les cavités et les signes d'alimentation sur les chicots, ainsi qu'inventorié les oiseaux présents dans les parcelles grâce à la méthode des points d'écoute. Les résultats démontrent que le taux de mortalité des arbres forme un patron en U, où il y a une plus forte abondance de chicots dans les jeunes peuplements (<50 ans) et dans les vieux peuplements (>200 ans). Ces peuplements sont aussi caractérisés par une plus grande proportion de chicots à gros diamètre (>20 cm DHP) et un plus grand nombre de cavités et de signes d'alimentation. Même si l'abondance des oiseaux nicheurs en cavité primaire (espèces qui creusent les cavités) ne varie pas selon les classes d'âge de peuplement, les oiseaux nicheurs en cavité secondaire (espèces qui utilisent les cavités seulement) ont tendance à être plus abondant dans les vieilles forêts. Ces résultats montrent donc la forte capacité des vieilles forêts à fournir un habitat adéquat aux espèces dépendantes des arbres morts à gros diamètre, ce qui était jusqu'à maintenant peu documenté. Un aménagement forestier adéquat permettrait donc de conserver une mosaïque forestière riche en biodiversité et de protéger les ressources nécessaires aux espèces d'oiseaux résidents.

1.1. Introduction

In boreal forest ecosystems, snags (dead standing trees or dying trees) contribute to many physical, chemical, and biological functions and provide valuable habitats for the conservation or enhancement of wildlife (e.g. Black-backed Woodpecker; Bate et al., 1999). They are used by a wealth of invertebrate, vertebrate, and plant species. Furthermore, organisms such as fungi and insects that are found in dead trees greatly enhance the value of snags for other wildlife. For example, decomposers invade dead or dying trees, and weaken and soften them, facilitating their use by primary cavity-nesters (i.e. woodpeckers) and secondary cavity-nesters (species that use cavities excavated by primary cavity-nesters or natural cavities created by decay; Thomas et al., 1979; Bull, 1983; Drapeau et al., 2000).

Snag abundance along a chronosequence following fire typically follows a well-defined “U-shaped” pattern: the volume of snags in young stands is usually high right after fire; as the forest grows back, few snags are produced; and after maturity is attained, many dominant trees become senescent and snag production increases to reach a steady-state, becoming constant (e.g., Harmon et al., 1986; Spies and Franklin, 1988; Tyrrell and Crow, 1994; Clark et al., 1998). In the course of this long-term stand development, other forest attributes may change, including species composition and tree size distribution. In boreal forests, bird communities may thus be affected by ecosystem changes as time since fire increases, especially birds that directly depend on snags for nesting and foraging. However, it is often difficult to monitor these changes over time, especially during the steady-state phase (see Bormann and Likens, 1979), because harvesting often occurs when forests are at a younger age and because fire cycles are generally short (< 150 years for the most part of the boreal forests in Canada, Bergeron et al., 2001).

In the eastern part of the Québec boreal forest, the humid climate lengthens the fire cycle up to 500 years (Bouchard et al., 2008), resulting in old-growth stands covering approximately 60 % of the unmanaged forest territory (Boucher et al., 2003). These old-growth stands are characterized by an uneven age structure and may play an important role

for birds through high snag abundance and availability. Some studies on bird abundance, species richness, and diversity have compared succession changes originating from fire and logging (Imbeau et al., 1999; Le Blanc, 2009), but few have investigated continuous changes in bird communities along a long-term gradient in unmanaged forests. Fire has an immediate positive impact on woodpecker breeding and foraging because of the high number of snags produced (Nappi et al., 2003). However, little data are available concerning the rate of tree mortality and the use of snags by cavity-nesters along the entire gradient from fire to old growth in unmanaged boreal forests. In addition, little is known about the capacity of mature forests to provide adequate habitat for bird species associated with large snags. By exploring these issues, we might be able to provide better recommendations and rationales to help protect habitats for cavity-nesting birds in the boreal forests of eastern Canada.

In the boreal forests of Québec's North Shore region, old-growth predominates with patches of even-aged stands originating from relatively recent fires. Hence, the presence/absence of avian species might not only be related to forest characteristics at the stand level, but also to the forest age structure and composition at the landscape level. The general objective of this study was to determine if there is variation in habitat quality for cavity-nesting birds along two chronosequences after fire, and to relate any variation to avian species richness and abundance. First, we quantified snag abundance (basal area) and availability (e.g. size classes) as well as tree mortality rate along chronosequences following fire. Second, we characterized snags actively used for nesting and foraging by birds. Finally, we evaluated the effect of tree size and wood degradation levels on snag use by birds.

1.2. Methods

1.2.1. 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%), with a maximum recorded altitude of 700 m and a cold maritime climate (Robitaille and Saucier, 1998). According to the nearest meteorological station in Baie-Comeau, average annual temperatures fluctuate between -2.5 and 0.0 °C and annual precipitation between 1100 and 1130 mm, 35% of which falls as snow (Anonymous, 2002).

Surveys were carried out in two regions of the study area: the southern region (49°42'N, 68°51'W) located a few km north of Baie-Comeau, and the northern region (50°57'N, 68°50'W) located south of the Manic 5 reservoir (Fig.1). 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 (*Abies balsamea* (L.) Mill) characterizes the former, with black spruce (*Picea mariana* (Mill.) BSP) dominating stands in poorer sites (MNRF, 2003). As latitude increases (shifting to the northern sub-domain), forest stands are increasingly dominated by black spruce. Dominant species found in the region include balsam fir and black spruce, with minor components of white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb), white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.). 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). The region is known for outbreaks of spruce budworm (*Archips fumiferana* (Clemens)), especially in the southern part of the study area (near Baie-Comeau) between 1974 and 1985 (Bouchard and Pothier, 2010). However, in the northern part of the study area, these outbreaks resulted in very little tree mortality (Bouchard and Pothier, 2010). Although the southern part was also used for logging, numerous fragments of unmanaged stands in the forest still remain today (Bouchard et al., 2008) and were used in this study.

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.1). 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 (class 4). We also selected ten mature stands for which the time since fire (from here on TSF) was not determined, but was greater than 200 years (class 5). Overall, we sampled 60 stands (2 chronosequences of 30 stands per chronosequence); we then established two types of inventory plots within each stand.

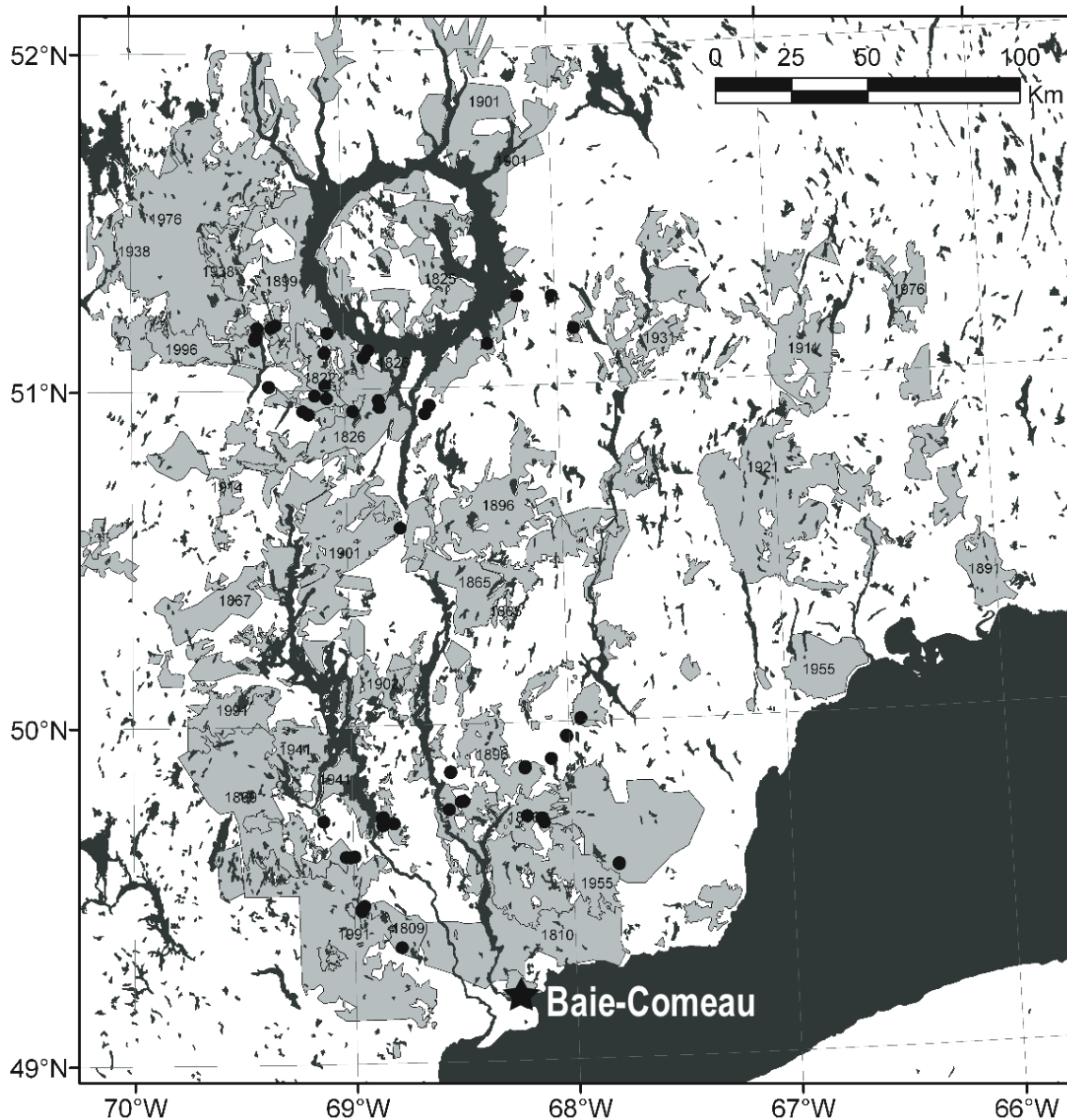


Figure 1. Location of the study area and fires mapped for the period 1800-2000. Fire dates are shown only for fires $>200 \text{ km}^2$.

1.2.2. Standard inventory plots

In each selected stand, we established a standard inventory plot to characterize stand composition and tree 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. The state of decomposition of each snag was categorized following Hunter's classification (decay stages, 2 declining to 7 decomposed; Fig. 10.1 in Hunter 1990). In addition, 20 subplots of 4 m² were systematically established in the 400 m² 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 m² plots were established to count the number of tree seedlings.

1.2.3. Characteristics and use of snags

To quantify snag decomposition, 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 all snags to increase sample size because standard inventory plots (400 m²) were too small to accurately determine the number of snags available to birds.

For each snag, we determined height (± 0.1 m), DBH (± 1 cm), and the state of decomposition. 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).

To collect evidence of woodpecker-foraging on snags, we looked for the presence of flaked bark and foraging excavations (Nappi et al., 2003), independently from the woodpecker species. These signs correspond to different foraging techniques woodpeckers use to extract beetles under the bark or in the wood (Hutto, 1995; Murphy and Lehnhausen, 1998; Imbeau and Desrochers, 2002; Gagné et al., 2007). Because we did not follow woodpeckers and record directly the trees they used for foraging, there were no direct measures of when the foraging signs were made (either the snags were used recently (past year) or they were used in previous years; Mannan et al., 1980). This is important since the snag characteristics for which foraging occurred in previous years might have been different. Therefore we

distinguished recent foraging from that of previous years by the presence and color of wood chips at the base of the tree and the wood color from the foraging cavities or flaked bark. Chips from recent excavating and the wood in the excavation and under flaked barks are brighter and lighter in color than older ones which tend to be duller or grayer (modified from Bull et al., 1990). We ranked trees from 0 (no foraging signs) to 4 (surface largely covered with signs). The classification was as follows: flaked bark (F) or excavations (E); 0 (no foraging signs), 1 (1-25% of bark surface covered with signs), 2 (26-50%), 3 (51-75%), and 4 (> 76%). These measures were recorded for each of the following tree sections: 0-5 m high, 5-10 m, 10-15 m, and > 15 m when available. A list of woodpecker species present in the study area can be found in Table 2.

We also measured crown condition which is defined by the remaining quantity of twigs and branches on the snag (1: some or all foliage lost; 2: no foliage, up to 50% of twigs lost; 3: no foliage or twigs, up to 50% of branches lost; 4: most branches gone, some branch stubs remaining; 5: no branches, some branch stubs; and 6: no branches or stubs). Finally, we measured bark retention, which was defined by the proportion of bark still present on the trunk surface (1: all bark present; 2: < 5% lost; 3: 5-25% lost; 4: 26-50% lost; 5: 51-75% lost; 6: 76-99% lost; and 7: no bark). These characteristics are considered useful for describing the general deterioration condition of each snag.

1.2.4. Permanent sample plots

A network of permanent sample plots (PSPs) established in 1970 by the Ministère des Ressources Naturelles et de la Faune du Québec (MRNFQ) was also used in this study. We overlapped these georeferenced PSPs to the fire map of Bouchard et al. (2008), to determine the time elapsed since the last fire for each of the 460 PSPs corresponding to the territory covered by the fire map. The inventory taken in each 400 m² circular PSP consisted of measuring the DBH (1.3 m, DBH \pm 1 mm) of each tree (live and dead) larger than 9.0 cm. Also, the age and height (\pm 0.1 m) of at least three live dominant tree species

were recorded (Pothier and Mailly, 2006). Data from 1970 until summer 2007 were available for this study. Periodic measurements of each PSP allowed us to quantify the rate of mortality as a function of time since fire and to relate this rate of mortality to stand characteristics.

1.2.5. 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.

1.2.6. Bird nest cavity searching

We considered a cavity nest to be a hollowed-out opening in the trunk of a tree, either found naturally in snags or purposely made by birds such as woodpeckers. Other examples of cavity-nesting birds include chickadees, nuthatches, and creepers (Hunter, 1999). We also included brown creepers' nests, built between the trunk and a loose piece of bark, since they are found mostly on dead or dying trees (Hejl et al., 2002). A list of the cavity-nesting species found in the study area can be found in Table 2. From mid-May to July 2007, in addition to dead trees inventories, all 60 stands were surveyed for the presence of cavities in each snag located in the 50 x 20 m plots. Each cavity (active or recently active) was characterized according to the following: bird species using the cavity (when identifiable),

height (distance in cm from the ground to the cavity), orientation (cavity orientation north, north-east, etc.), form (shape: round, square, oval, bark; natural or excavated cavity), condition (cavity entrance appearance fresh or old), diameter (cavity entrance size in centimetres). These data allowed us to describe cavity use by resident (e.g. chickadees) and migratory bird species (e.g. swallows) and provided information on primary cavity nesters (excavators), secondary cavity users and characteristics of trees supporting cavities. Moreover, we determined nest activity by finding cavities directly and by observing subsequent activities, such as following adult birds to their nests or hearing young in the nest. Recently used cavities may also be recognized by the presence of fresh wood chips at the base of the tree (Bull et al., 1990).

1.2.7. Point counts

To estimate species richness and bird abundance, we used the point count method (Reynolds et al., 1980; Hutto et al., 1986). One point was located at the center of each standard inventory plot established in the 60 stands from the two chronosequences. All points 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. Up to three trained observers performed independently the point counts.

Two visits (replicates) were conducted at each point 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 distance classes from the center of the point: 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 to each stand were made by a different person to minimize observer bias. 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 the standard time procedure for boreal forest bird communities when one wants to relate bird richness and abundance with the vegetation characteristics of the area around the point (Drapeau et al., 2000; Drapeau et al., 2002).

1.2.8. Statistical Analyses

We weighted the number of snags per plot so that each plot contributed to only one degree of freedom in the model (Desrochers, 1992). This technique allows the use of all observations while avoiding pseudo-replication (Machlis et al., 1985). An analysis of variance (ANOVA) was used to compare mean snag density and rate of tree mortality 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 value for plots with TSF >200 years (class 5) from the available fire map (Bouchard et al., 2008). When the ANOVA detected a significant difference for one of the factors, we compared the means of this factor using a Waller-Duncan comparison test. For all analyses of point count data, we used the maximum number of individuals for each species recorded (residents vs. migrants, primary vs. secondary cavity nesters) at each plot for the two visits.

On the basis of presence/absence of cavities and foraging signs, we used a logistic regression with a stepwise procedure (proposed by Hosmer and Lemeshow, 2000) to determine which set of explanatory variables best predicted snag use by cavity nesters and foraging woodpeckers (the species for whom we can actually observe foraging traces on

snags). For this, we used the Wald test that calculates a z statistic, which represents a chi-square distribution (Harrell, 2006). We included the following independent variables in the model: time since fire, tree species, snag DBH, height, decomposition condition, crown condition, bark retention, stand composition at the plot level, basal area and volume. 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. All analyses were performed with the software SAS (SAS Institute 2008), using a significance level of 0.05.

1.3. Results

1.3.1. Snag basal area and tree mortality rate

A total of 1,740 snags were measured from 60 stands (30 per chronosequence) covering five TSF classes. Significant differences in snag basal area were observed between the two chronosequences, with a higher value observed in the southern chronosequence (Fig. 2).

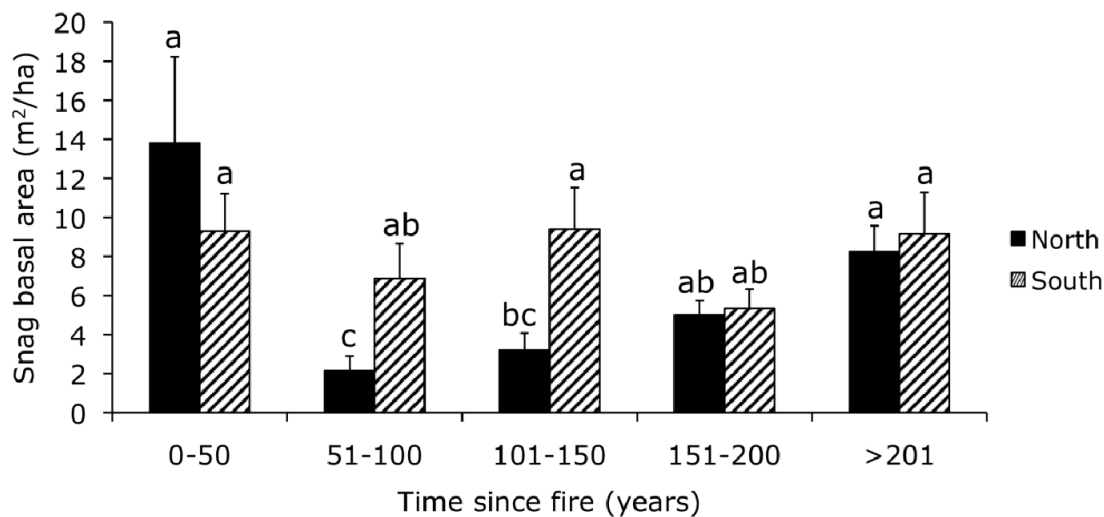


Figure 2. Snag basal area of all snags measured in the study area according to the time since last fire. Significant differences ($P < 0.05$) for means values (\pm S.E; $n = 30$) among years are indicated by different letters.

Snag availability changed significantly among TSF classes ($F_{9,50} = 3.33$, $P = 0.003$). These differences were more structured in the northern than southern chronosequence, the former showing a defined “U-shape pattern” of abundance. Snag basal area was larger in TSF classes 0-50 and >201 years because of a higher presence of large sized trees.

Tree mortality rate differed among TSF classes ($F_{4,455} = 5.92$, $P = 0.0001$) and tended to increase with TSF (Fig. 3). The average mortality rate was twice as large in the two oldest plots (>151 years, rate ≈ 0.40) compared to the two younger ones (<100 years, ≈ 0.18). For TSF over 200 years, however, the mortality rate tended to decrease, suggesting a sort of stabilization or steady state.

Tree mortality rates also differed among TSF classes and tree species groups (Fig. 3). For instance, mortality rates of black spruce increased with TSF, while those of intolerant hardwoods (mostly composed of paper birch, and trembling aspen) were highest in TSF classes between 51 and 200 years. Mortality rates of balsam fir remained relatively constant versus TSF except in the 51-100 class, within which mortality rates were low. No

difference in mortality rates were observed in the other species groups dominated by white spruce, tamarack, and jack pine.

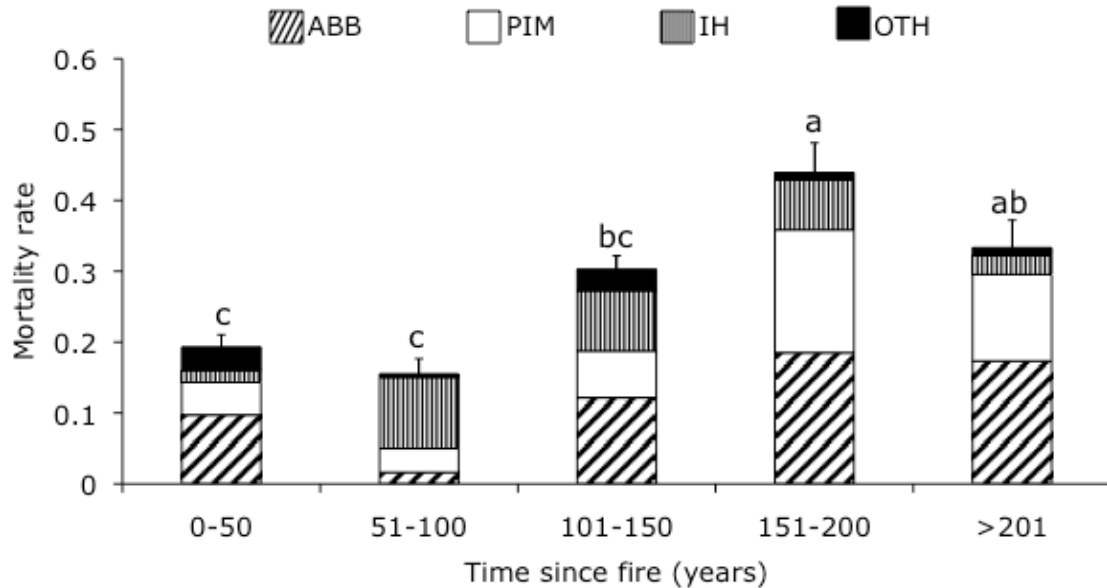


Figure 3. Annual tree mortality rates (%) calculated on a basal area basis for each time since fire (TSF) classes and for four tree species groups. Species groups are balsam fir (ABB), black spruce (PIM), intolerant hardwoods (IH) and the other remaining species (OTH).

1.3.2. Snag use

A total of 71 cavities were found in 50 snags, representing 2.87% of all snags tallied in this study (1740). The number of cavities per hectare did not differ significantly among TSF classes, but young stands (0-50 years) and those older than 200 years tended to contain more cavities (Fig. 4a). When snags were in a more advanced stage of decomposition, they seemed to be increasingly used by birds for nesting (Fig. 4b) although the result is not significant. Also, a greater proportion of trees with cavities were observed in snags larger than 20 cm DBH compared to smaller snags (8.2% and 1.2% respectively) (Fig. 4c). The number of cavities present in snags larger than 30 cm DBH seemed to be relatively low

because such trees were rare on our study sites. The mean number of large snags (>20 cm) per hectare was significantly different among TSF classes ($F_{9,404} = 2.83$, $P = 0.0031$; Fig. 4d). Snags >20 cm DBH were generally more abundant in young (0-50 years) and older stands (> 100 and > 150 years for the southern and the northern chronosequence respectively), compared to those of intermediate ages.

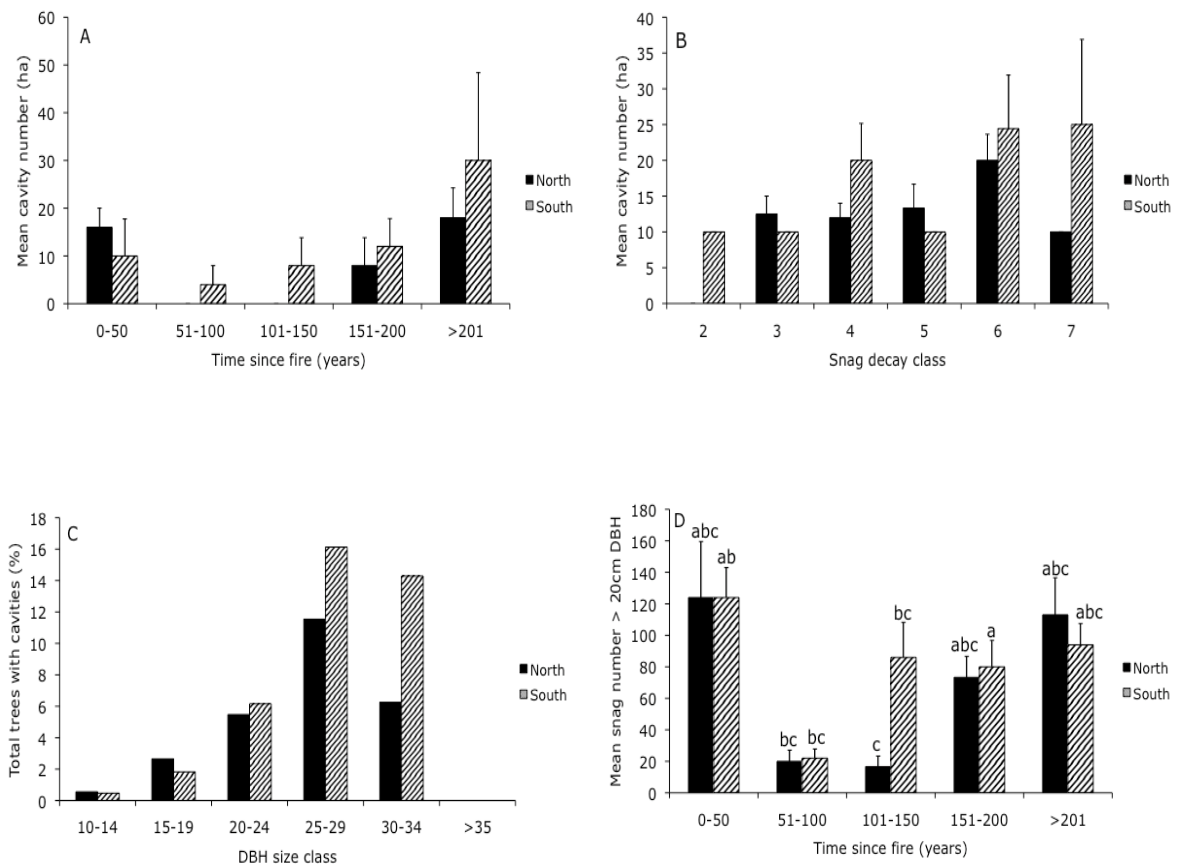


Figure 4. Snag availability and cavity numbers following the two chronosequences. The four diagrams show (A) average number of cavities according to the time since fire; (B) total number of cavities by state of snag decomposition; (C) proportion of trees holding cavities by DBH class; and (D) average number of snags >20 cm DBH per ha according to time since fire.

Based on the stepwise, logistic regression, three of fifteen variables were significant predictors of the presence of cavities in snags: DBH (Wald test chi-square distribution, $z = 32.66$, $P < 0.0001$), snag decomposition condition ($z = 29.87$, $P < 0.0001$) and time since fire ($z = 5.3$, $P = 0.0213$). Thus, a snag with a large diameter, at an advanced stage of decomposition and within an old stand is more likely to be used by primary and secondary cavity-nesters.

Signs of recent foraging by woodpeckers (presence/absence of flaked bark or foraging excavations) were observed in 1205 snags (69.3% of snags found). According to a logistic regression, nine variables were significant predictors. The presence of foraging signs was positively correlated with: bark retention (Wald test chi-square distribution, $z = 127.2$, $P < 0.0001$), crown condition ($z = 32.33$, $P < 0.0001$), mean TSF in a 50 ha buffer ($z = 14.20$, $P = 0.0002$), DBH ($z = 11.92$, $P = 0.0006$), snag decomposition ($z = 18.25$, $P = 0.0027$), mean height ($z = 6.95$, $P = 0.0084$), mean basal area of live hardwood trees in standard inventory plots ($z = 6.88$, $P = 0.0087$), TSF at the plot level ($z = 33.21$, $P = 0.0103$) and proportion of coniferous trees at 100 ha buffer size ($z = 3.84$, $P = 0.0498$). In general, trees with a large diameter, which were partially decomposed, within older stands, and with certain bark retention and for which the crown is relatively intact were more likely to provide foraging opportunities for birds. Also, foraging signs positively increased with mean TSF in 50 ha buffer zones, a lower presence of live hardwood trees, and an increasing number of coniferous trees. Table 1 provides the details (e.g., means, standard deviation) for the predictor variables used in the analysis.

Table 1. Details on predictor variables used for the presence of cavities in snags and foraging signs analyses.

Predictor variables	Mean	Standard deviation	Minimum	Maximum
DBH (cm)	16.32	5.46	10	50
Time since fire (years)	137.74	93.39	2	250
Bark retention (%)	75.53	20.27	0	100
Crown condition (%)	25.32	30.02	0	100
Mean TSF in a 50 ha buffer	165.02	64.60	25	225
Mean basal area of live hardwood (%)	87.58	22.18	0	100
Proportion of coniferous at 100 ha buffer size (%)	67.17	23.91	0	100

1.3.3. Cavity-nesting birds

There was an interaction between TSF and chronosequence that influenced the species richness of cavity-nesting birds ($F_{9,50} = 2.39$, $P = 0.0246$), as young forests (age class: 0-50 years) were associated with fewer cavity-nesters than other TSF classes in the southern chronosequence but not in the northern one (Fig. 5). Apart from these young stands, no other significant differences were observed between cavity-nesters and TSF.

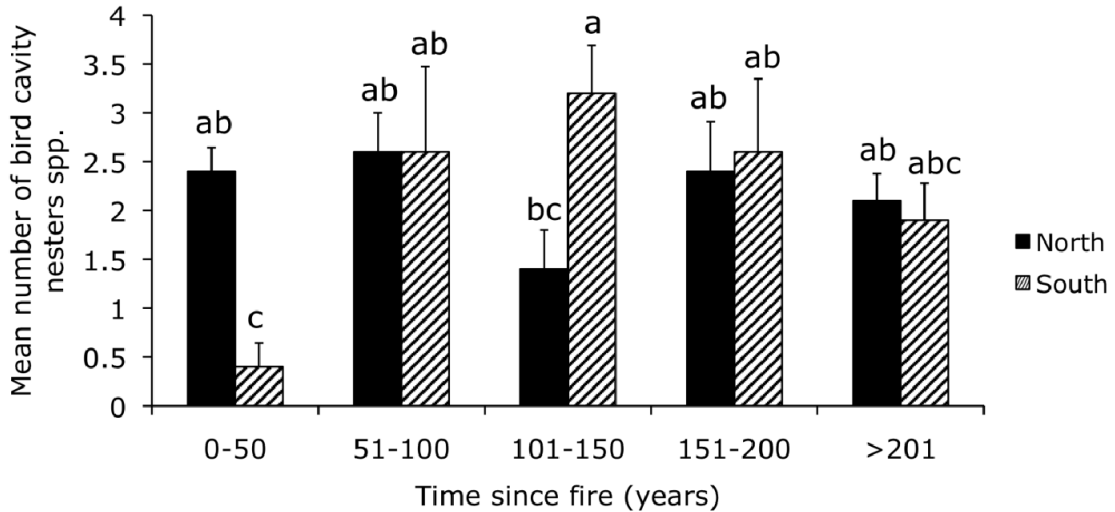


Figure 5. Average number of bird species using cavities per plot according to the time since last fire (TSF). Significant differences ($P < 0.05$) among mean values (\pm S.E.; $n = 30$) of TSF classes are indicated by different letters.

Relative abundance (averaged for all point counts) of primary cavity-nesters did not vary among age classes. However, secondary nesters seemed to be more abundant in older forests (>101 years). These included the Boreal Chickadee and Brown Creeper (Fig. 6). A list of the English, French and scientific names of all cavity-nesting birds observed in this study can be found in Table 2 (see also Appendix 1).

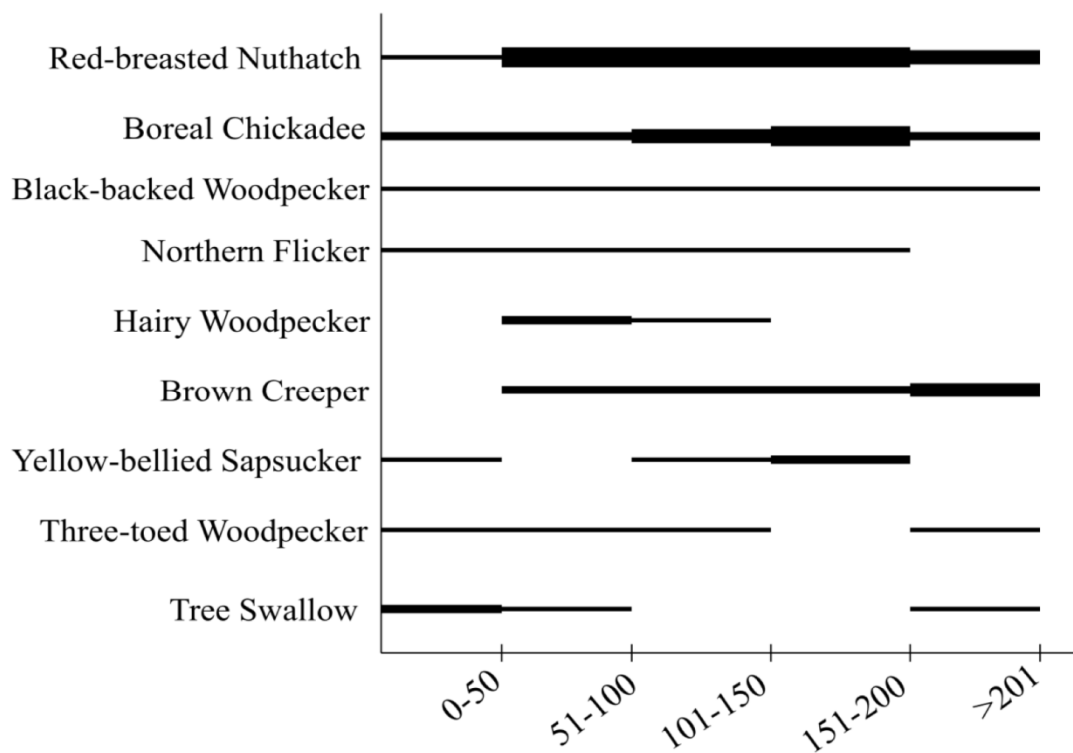


Figure 6. Presence of cavity-nesters according to time since fire. For each species, line width corresponds to the relative abundance of these birds during point counts (2 visits in June). Within each TSF class, no line means 0 birds per point count, the thinner black line represents a density of ≤ 0.2 bird/point count whereas the thickest black line corresponds to a density of ≥ 0.8 bird/point count. Scientific names for the species listed can be found in Table 1.

Table 2. List of cavity-nesting bird species found in the study area.

Species name (English)	Species name (French)	Scientific name
Brown Creeper	Grimpereau brun	<i>Certhia americana</i>
Tree Swallow	Hirondelle bicolor	<i>Tachycineta bicolor</i>
Boreal Chickadee	Mésange à tête brune	<i>Parus hudsonicus</i>
Hairy Woodpecker	Pic chevelu	<i>Picoides villosus</i>
Black-backed Woodpecker	Pic à dos noir	<i>Picoides arcticus</i>
Northern Flicker	Pic flamboyant	<i>Colaptes auratus</i>
Yellow-bellied Sapsucker	Pic maculé	<i>Sphyrapicus varius</i>
Three-toed Woodpecker	Pic à dos rayé (tridactyle)	<i>Picoides tridactylus</i>
Red-breasted Nuthatch	Sitelle à poitrine rousse	<i>Sitta canadensis</i>

1.4. Discussion

Snag availability changed with time elapsed since the last fire in the two chronosequences (Fig. 2). In general, our results for the northern chronosequence agree with the typical mortality rate for boreal forests, characterized by the U-shaped pattern that represents an early, high level of mortality, a subsequent transition phase with little mortality, and then, a later increase in mortality once a forest matures, followed finally by a steady-state where large canopy trees are continuously dying (Harmon et al., 1986; Peet and Christensen, 1987; Clark et al., 1998). In the southern chronosequence, this pattern was not observed: rather, during the 101-150 year period, we found an increase in the overall mean basal area for dead trees. This might be explained by the random sampling of some dense plots in the southern chronosequence in which we observed a high rate of natural mortality, perhaps resulting from competition for light, nutrients or space. This phenomenon, referred to as self-thinning mortality (Adler, 1996), is known to occur once a closed canopy has formed. An intense competition takes place among trees of the initial cohort, leaving very little space for suppressed trees, which die as survivors get larger (Peet and Christensen, 1987).

This may happen fairly late in stand development (between 100 and 150 years old), depending on the type of forest involved (see Franklin et al., 1987). This phenomenon was not observed in the northern chronosequence, likely because dense stands are less frequent than in the southern region.

At the species level, our results agree with the pattern of tree succession observed after fire in the study area (Bouchard et al., 2008). The progressive increase in balsam fir abundance from 50 to 175 years after fire (Bouchard et al., 2008) was followed by a proportional increase in balsam fir mortality, especially from 100 years onwards. Black spruce basal area normally increases until 90 years and then slowly declines as dominant trees become senescent (Garet et al., 2009), while our results indicate an increase in mortality from 100 onwards.

Early post-fire forests are key habitats for snag recruitment (Fig. 2) because trees killed by fire are a major source of new snags (Wein and MacLean, 1983; Gauthier et al., 2001). At the other end of the chronosequence spectrum, old-growth forests provide a large number of snags, mostly with large DBH, at varying stages of decomposition. These large-diameter snags are more valuable for wildlife than smaller ones because they persist longer (lower falling rate, see Saab and Dudley, 1998). Indeed, large diameter snags resulted in an increased number of nests and foraging signs, and cavity-nesters such as woodpeckers are known to prefer these trees (Swallow et al., 1986; Drapeau et al., 2002; Nappi et al., 2003; Smith et al., 2008). Our results for predictors of foraging signs are concordant with those from a study on Black-backed Woodpeckers (Nappi et al., 2003) where more foraging signs were observed on slightly decomposed trees, with many dead branches, and with bark still remaining (see also Drapeau et al., 1999). Our study provides further predictors of foraging signs such as the presence of large trees (which are more frequent in old-growth forests) and the larger proportion of coniferous stands at the landscape scale (100 ha). The latter result underscores the importance of bigger landscape scales needed to encompass the large home range sizes of species included in this study (e.g. Black-backed Woodpecker; Dixon and Saab, 2000; Hoyt and Hannon, 2002). This reflects the value of studying resident habitat specialists (such as the woodpecker; Imbeau et al., 1999) with large home range

requirements; these species are likely to be most sensitive to habitat changes or alterations (Hunter, 1992; Wiens, 1994).

Studies of the occurrence of primary and secondary cavity-nesters have found that some species are more common in recently-burned forests and old-growth stands (Imbeau et al., 1999; Drapeau et al., 2002). In our study, Black-backed Woodpeckers were not more numerous in the recently-burned or over-mature forests, but rather were found in all TSF classes. Due to our low detection of this and the other species, it is difficult to provide abundance estimates by TSF class. Most studies have shown that high productivity in terms of burn use by this woodpeckers occurs only 1 to 3 years following a burn (Dixon and Saab, 2000; Nappi et al., 2003), but our 1-50 year TSF class includes only one such recent fire. This explains why the woodpecker population may not dominate as much as it does in other studies that may have included the period right after fire. Moreover, in the southern chronosequence, dead tree abundance was not found only in young and old TSF classes, but also in the 101-150 years (Fig. 2). This might explain why Black-backed or Three-toed woodpeckers were not necessarily more abundant in any age class (Fig. 6). Our study described cavity-nesters distribution in long-term chronosequences; finer age-class separations, especially in the 1-50 year TSF class might provide more details of woodpecker distribution according to stand age post fire. Nevertheless, similar to the findings of Drapeau et al. (2000; 2002) in the boreal forests of western Québec, cavity-nesters such as the Red-breasted Nuthatch, Boreal Chickadee and Brown Creeper were all more abundant in mature and old-growth forests than in younger stands. The high quantity of live and dead trees >20 cm DBH might explain their abundance in these forests as they provide higher opportunities for nesting and for foraging.

1.5. Implications for management

The boreal forest of eastern Québec is characterized by long fire-return intervals (Bouchard et al., 2008) that lead to the dominance of old-growth forest stands. These stands are

characterized by, among other factors, a high level of deadwood, which has a significant ecological function in the ecosystem (Hunter, 1999; Imbeau et al., 2001; Bergeron et al., 2006). Our study shows the importance of proper management and silvicultural practices in exploited old-growth forests (>150 year) in order to retain structural elements essential to the maintenance of biological diversity, such as snags throughout the regeneration cycle. This would maintain nesting and foraging opportunities for cavity-nesters, whereas secondary nesters will also benefit from such management. Our results therefore highlight the strong capacity for old-growth forests to provide quality habitat for species dependent on large snags.

Snags are important to a variety of cavity-nesters and foragers, mainly because of their decaying structure which attracts a multitude of insect species (Bull, 1983; Bunnell et al., 1999). The availability of these organisms as food items likely affects bird foraging behavior and home ranges. Similar studies have provided diverse recommendations as to the size of mature forests stands that should be preserved. Here, we recommend a minimum size of 100 ha, enough to protect species with large home-range requirements, those most sensitive to habitat alteration. Proper forest management should therefore maintain a mosaic of forest stands of at least that size. This should promote biodiversity and provide important resources for resident bird species.

1.6. Acknowledgments

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**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 connaît 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°51'W), 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.

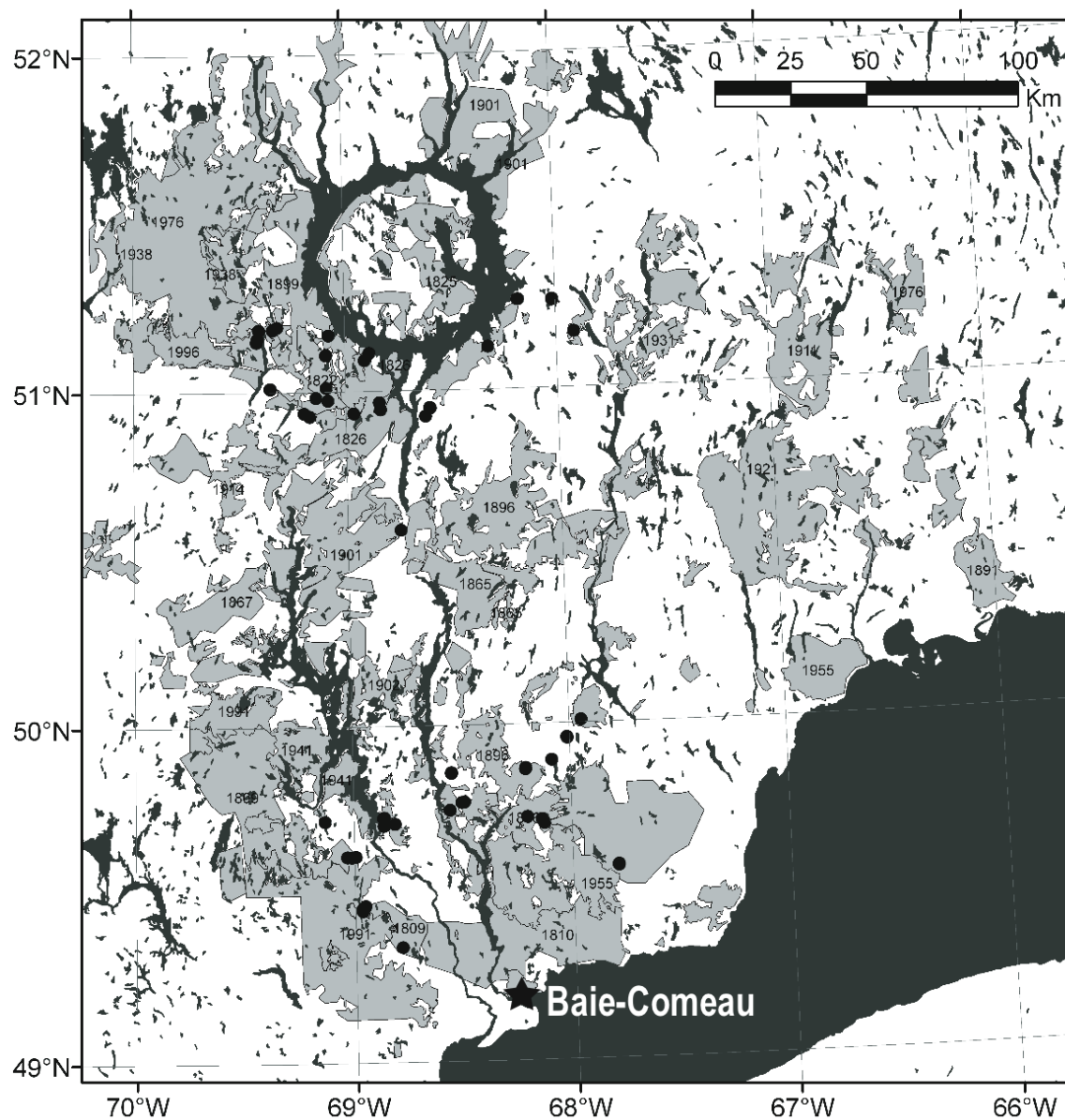


Figure 7. Location of the study area and of fires mapped for the 1800-2000 period. Fire dates are shown on the map only for fires $> 200 \text{ km}^2$.

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 m² 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 m² were systematically established in the 400 m² 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 m² 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-m² inventory plots were too small to accurately determine the amount of snags available to birds. For each snag, we determined height (± 0.1 m), and DBH (± 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 (AIC_c) 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 Δ AIC > 10 indicates that the model is very unlikely (Burnham and Anderson, 2002). As described by Burnham and Anderson (2002), Δ AIC is defined as a measure of each model relative to the best model. When several models compete for the best ranking (Δ AIC_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:

$$CI = \ln (F+1) - \ln (E+O+1) \quad [1]$$

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

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

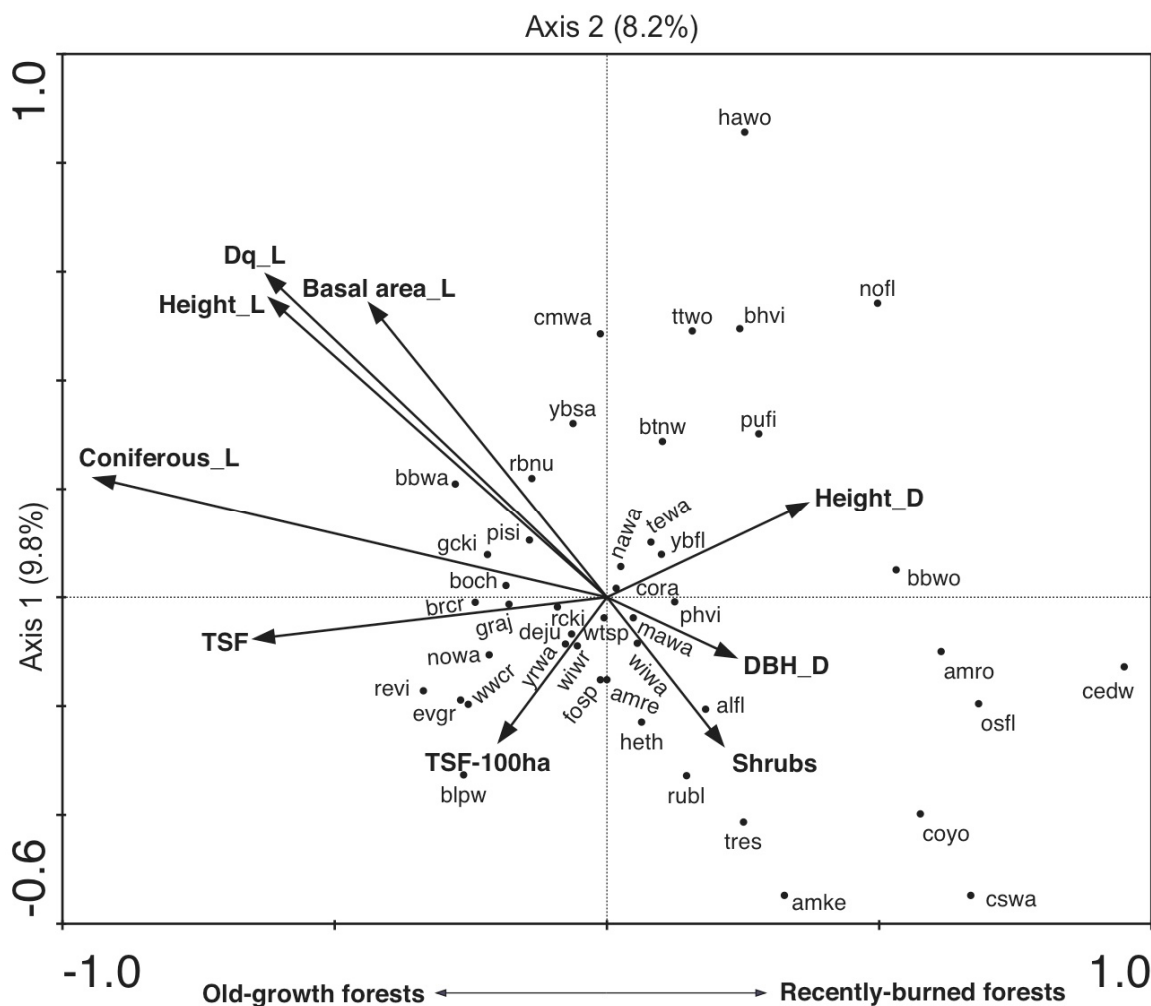


Figure 8. Canonical correspondence analysis axes one and two, showing the association of bird species and environmental variables. Axis 1 represents a gradient ranging from recently-burned forests (right) to old-growth forest (left); while Axis 2 represents a gradient from low stand density (down) to 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 ($\Delta\text{AICc} = 0$) to least plausible (only model with $\Delta\text{AICc} > 7$ 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 – 4.16coniferous100ha – 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 ($\Delta\text{AICc} = 0$) to least plausible (only model with $\Delta\text{AICc} > 7$ 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)	R²
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 + 2.17mixedwoods100ha - 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 ($\Delta\text{AIC}_c = 0$) to least plausible (only model with $\Delta\text{AIC}_c > 7$ 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)	R²
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 $\Delta\text{AIC}_c < 2$; 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 ($\Delta AIC_c = 0$) to least plausible (only model with $\Delta AIC_c > 7$ 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)	R²
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 mixedwoods 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.

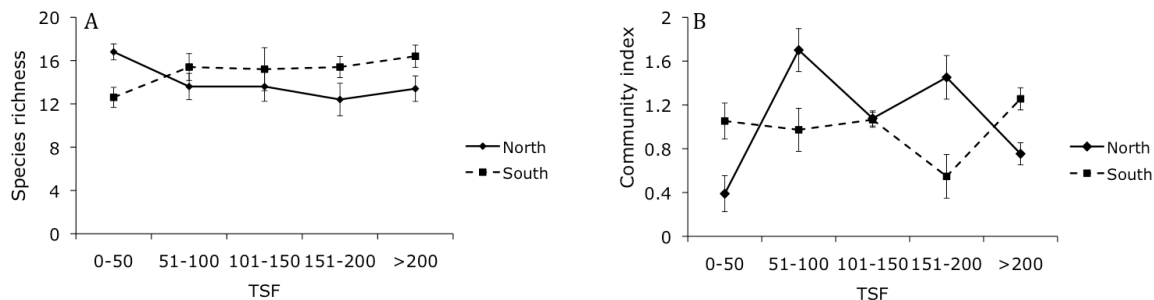


Figure 9. Mean number (\pm S.E.; $n = 30$) of species and community index along the two chronosequences. The two diagrams show (A) average number of bird species and (B) average value of bird community index, both according to time since fire (TSF).

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).

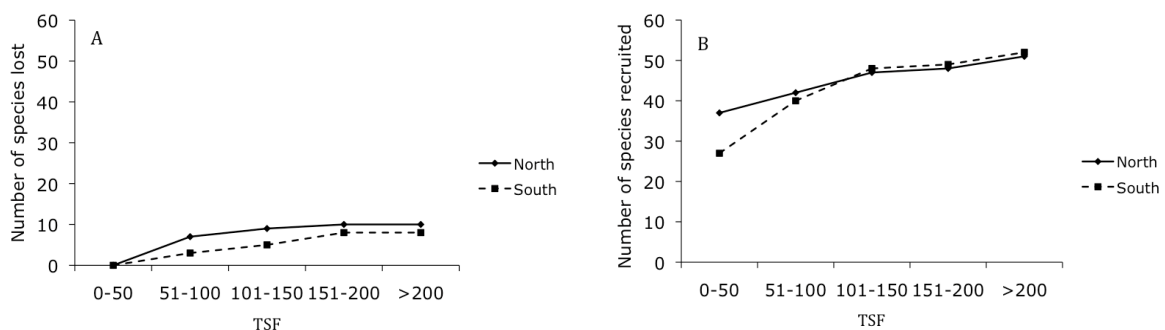


Figure 10. Cumulative number of bird species lost and recruited in the two chronosequences. The two diagrams present (A) the cumulative number of bird species lost and (B) the cumulative number of bird species recruited, both according to time since fire (TSF).

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 m²), 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.

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Conclusion

Les perturbations naturelles altèrent grandement le paysage forestier et le feu représente une de ces perturbations qui contribuent à la diversité écologique (Pringle, 1979; White 1979; Heinselman, 1981; Brawn et al., 2001) de la forêt boréale (Wein, 1993; Drapeau et al., 2000; Bouchard et al., 2008). Les feux de forêt produisent souvent une riche régénération et divisent le paysage forestier en une mosaïque de peuplements d'âges différents. La structure et la composition des arbres vivants varient de façon importante selon les différentes étapes de succession après feu, ce qui engendre un paysage fortement hétérogène, apte à procurer un habitat adéquat pour plusieurs espèces (McElhinny et al., 2005).

Une des caractéristiques des forêts procurant l'habitat requis par plusieurs espèces d'oiseaux est la présence d'arbres morts. Les résultats de la présente étude indiquent qu'en forêt boréale, les arbres morts sur pied (chicots) constituent un facteur important pour la nidification et l'alimentation de plusieurs espèces d'oiseaux, principalement des espèces résidentes à l'année. En fonction du patron de mortalité des arbres en forme de U, on remarque que les chicots sont importants pour plusieurs organismes non seulement dans les forêts récemment brûlées (Wein et MacLean, 1983; Imbeau et al., 1999, Gauthier et al., 2001), mais aussi dans les vieilles forêts où le processus de mortalité est plus graduel et stable. Cette étude démontre bien la forte abondance des chicots de gros diamètres dans les forêts de plus de 200 ans après feu. On y retrouve un grand nombre de cavités utilisées par les oiseaux nicheurs primaires et secondaires et aussi un grand nombre de signes d'alimentation. Ces arbres morts constituent donc un apport important pour les oiseaux, ce qui contribue à la survie de leur population. Il devient donc important de considérer ces vieilles forêts pour la conservation de la biodiversité des milieux boréaux. L'élimination des vieilles forêts pourrait avoir une forte influence négative sur les oiseaux qui ont besoin de ces peuplements à l'année. Il est donc vital de considérer un aménagement forestier adéquat qui permettrait de conserver ces forêts.

Un autre résultat important de cette étude est que les changements de structure et de composition de l'habitat forestier en milieu boréal vont aussi fortement influencer la communauté d'oiseaux dans son ensemble. Ce résultat n'est pas complètement nouveau (MacArthur and MacArthur, 1961; Karr and Roth, 1971; Wiens and Rotenberry, 1981; James and Wamer, 1982; Saab et al., 2005), toutefois, peu d'études en ont fait état sur une aussi longue période et ce, dans un contexte de forêts non-aménagées. Cette étude confirme que les jeunes forêts sont importantes pour des espèces spécialistes comme le pic à dos noir (Nappi et al., 2003) à cause de la forte abondance de nouveaux chicots, mais aussi pour une variété d'espèces adaptées aux milieux ouverts. Toutefois, mon étude démontre aussi que les changements structurels à long terme à la suite d'un feu sont suivis par des changements de communautés d'oiseaux. Certaines espèces disparaissent lorsque la forêt devient dominée par des espèces de conifères (qui remplacent les arbustes intolérants à l'ombre), tandis que d'autres sont recrutées. Certaines espèces d'oiseaux, plus sensibles aux changements apportés à la forêt, seront plus abondantes aux étapes de succession précédant la maturité des peuplements. Cela indique que chaque stade de succession peut représenter l'habitat unique de certaines espèces, qui sont importantes à conserver. Il devient donc impératif de préserver cette mosaïque de peuplements d'âges différents, à partir du moment où la forêt est brûlée jusqu'à l'obtention d'une vieille forêt « stable » du point de vue de la biodiversité.

De façon à préserver les patrons et les processus responsables de l'hétérogénéité de l'habitat, il est crucial de maintenir les régimes de perturbations naturelles telles que les feux et ce, à différentes échelles, fréquences et intensités. À l'échelle locale, on doit maintenir les perturbations de petite envergure comme, par exemple, la mortalité d'arbres individuels afin d'accroître la diversité des micro-habitats. Une attention particulière doit être portée aux éléments structurels caractéristiques des vieilles forêts comme, par exemple, les chicots, les arbustes et les arbres vivants. Ces éléments structurels procurent des refuges à court terme pour un grand nombre d'organismes qui sont influencés par les différents stades de succession et les changements subis au paysage après feu jusqu'à l'obtention d'une vieille forêt « stable ». À l'échelle du paysage, les perturbations comme les feux de forêts contribuent au maintien d'une mosaïque naturelle et fonctionnelle d'habitats en

régénération et de peuplements de différents âges. Le côtoiement de différents types de peuplements et leur connectivité influencent aussi les communautés d'oiseaux présentes dans un peuplement particulier. Le feu maintient donc un paysage hétérogène particulièrement adéquat pour les espèces utilisant les forêts à tous les stades de succession. Il est donc impératif d'aménager la forêt boréale canadienne de façon à respecter les patrons spatio-temporaux des feux de forêts qui ont une influence cruciale sur la biodiversité.

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Annexe

Annexe 1. Liste complète des espèces d'oiseaux observées dans la forêt boréale non-aménagée de l'Est du Québec durant l'été 2007, incluant les noms français, anglais et scientifiques.

Nom français	Code	Nom anglais	Code	Nom scientifique
Bec-croisé bifascié	bcbi	White-winged Crossbill	wwcr	<i>Loxia leucoptera</i>
Bruant à gorge blanche	brgb	White-throated Sparrow	wtsp	<i>Zonotrichia albicollis</i>
Bruant de Lincoln	brli	Lincoln's Sparrow	lisp	<i>Melospiza lincolnii</i>
Bruant fauve	brfv	Fox Sparrow	fosp	<i>Passerella iliaca</i>
Buse à queue rousse	buqr	Red-tailed Hawk	rthk	<i>Buteo jamaicensis</i>
Butor d'Amérique	buam	American Bittern	ambi	<i>Botaurus lentiginosus</i>
Crécerelle d'Amérique	cram	American Kestrel	amke	<i>Falco sparverius</i>
Durbec des sapins	dusa	Pine Grosbeak	pigr	<i>Pinicola enucleator</i>
Engoulevent d'Amérique	enam	Common Nighthawk	conh	<i>Chordeiles minor</i>
Épervier brun	epbr	Sharp-shinned Hawk	sshk	<i>Accipiter Striatus</i>
Gélinotte huppée	gehu	Ruffed Grouse	rugr	<i>Bonasa umbellus</i>
Grand corbeau	grco	Common Raven	cora	<i>Corvus corax</i>
Grimpereau brun	grbr	Brown Creeper	brcr	<i>Certhia americana</i>
Grive à dos olive	grdo	Swainson's Thrush	swth	<i>Catharus ustulatus</i>
Grive à joues grises	grjg	Gray-cheeked Thrush	gcth	<i>Catharus minimus</i>
Grive solitaire	grso	Hermit Thrush	heth	<i>Catharus guttatus</i>
Gros-bec errant	gber	Evening Grosbeak	evgr	<i>Hesperiphona vespertina</i>
Hirondelle bicolore	hibi	Tree Swallow	tres	<i>Tachycineta bicolor</i>
Jaseur d'Amérique	jaam	Cedar Waxwing	cedw	<i>Bombycilla cedrorum</i>
Junco ardoisé	juar	Dark-eyed Junco	deju	<i>Junco hyemalis</i>
Merle d'Amérique	meam	American Robin	amro	<i>Turdus migratorius</i>
Mésange à tête brune	metb	Boreal Chickadee	boch	<i>Parus hudsonicus</i>
Mésangeai du Canada	meca	Gray Jay	graj	<i>Perisoreus canadensis</i>
Moucherolle à côtés olive	moco	Olive-sided Flycatcher	osfl	<i>Contopus cooperi</i>
Moucherolle à ventre jaune	movj	Yellow-bellied Flycatcher	ybfl	<i>Empidonax flaviventris</i>
Moucherolle des aulnes	moau	Alder Flycatcher	alfl	<i>Empidonax alnorum</i>
Paruline à calotte noire	pacn	Wilson's Warbler	wiwa	<i>Wilsonia pusilla</i>
Paruline à croupion jaune	pacj	Yellow-rumped Warbler	yrwa	<i>Dendroica coronata</i>
Paruline à flanc marron	pafm	Chestnut-sided Warbler	cswa	<i>Dendroica pensylvanica</i>
Paruline à gorge noire	pagn	Black-throated Green Warbler	btnw	<i>Dendroica virens</i>
Paruline à gorge orangée	pago	Blackburnian Warbler	blwa	<i>Dendroica fusca</i>
Paruline à joues grises	pajg	Nashville Warbler	nawa	<i>Vermivora ruficapilla</i>
Paruline à poitrine baie	papb	Bay-breasted Warbler	bbwa	<i>Dendroica castanea</i>
Paruline à tête cendrée	patc	Magnolia Warbler	mawa	<i>Dendroica magnolia</i>

Paruline des ruisseaux	paru	Northern Waterthrush	nowa	<i>Seiurus noveboracensis</i>
Paruline flamboyante	pafl	American Redstart	amre	<i>Setophaga ruticilla</i>
Paruline masquée	pama	Common Yellowthroat	coyo	<i>Geothlypis trichas</i>
Paruline obscure	paob	Tennessee Warbler	tewa	<i>Vermivora peregrina</i>
Paruline rayée	para	Blackpoll Warbler	blpw	<i>Dendroica striata</i>
Paruline tigrée	pati	Cape May Warbler	cmwa	<i>Dendroica tigrina</i>
Paruline triste	patr	Mourning Warbler	mowa	<i>Oporornis philadelphia</i>
Pic à dos noir	pidn	Black-backed Woodpecker	bbwo	<i>Picoides arcticus</i>
Pic à dos rayé (tridactyle)	pittr	Three-toed Woodpecker	ttwo	<i>Picoides tridactylus</i>
Pic chevelu	pich	Hairy Woodpecker	hawo	<i>Picoides villosus</i>
Pic flamboyant	pifl	Northern Flicker	nofl	<i>Colaptes auratus</i>
Pic maculé	pima	Yellow-bellied Sapsucker	ybsa	<i>Sphyrapicus varius</i>
Pic mineur	pimi	Downy Woodpecker	dowo	<i>Picoides pubescens</i>
Quiscale rouilleux	quro	Rusty Blackbird	rubl	<i>Euphagus carolinus</i>
Roitelet à couronne dorée	rocd	Golden-crowned Kinglet	gcki	<i>Regulus satrapa</i>
Roitelet à couronne rubis	rocr	Ruby-crowned Kinglet	rcki	<i>Regulus calendula</i>
Roselin pourpré	ropo	Purple Finch	pufi	<i>Carpodacus purpureus</i>
Sitelle à poitrine rousse	sipr	Red-breasted Nuthatch	rbnu	<i>Sitta canadensis</i>
Tarin des pins	tapi	Pine Siskin	psis	<i>Carduelis pinus</i>
Tétras du Canada	teca	Spruce Grouse	spgr	<i>Falcapennis canadensis</i>
Troglodyte mignon	trmi	Winter Wren	wiwr	<i>Troglodytes troglodytes</i>
Viréo de Philadelphie	viph	Philadelphia Vireo	phvi	<i>Vireo philadelphicus</i>
Viréo tête bleue	vitb	Blue-headed Vireo	bhvi	<i>Vireo solitarius</i>
Viréo yeux rouge	viyr	Red-eyed Vireo	revi	<i>Vireo olivaceus</i>