

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.

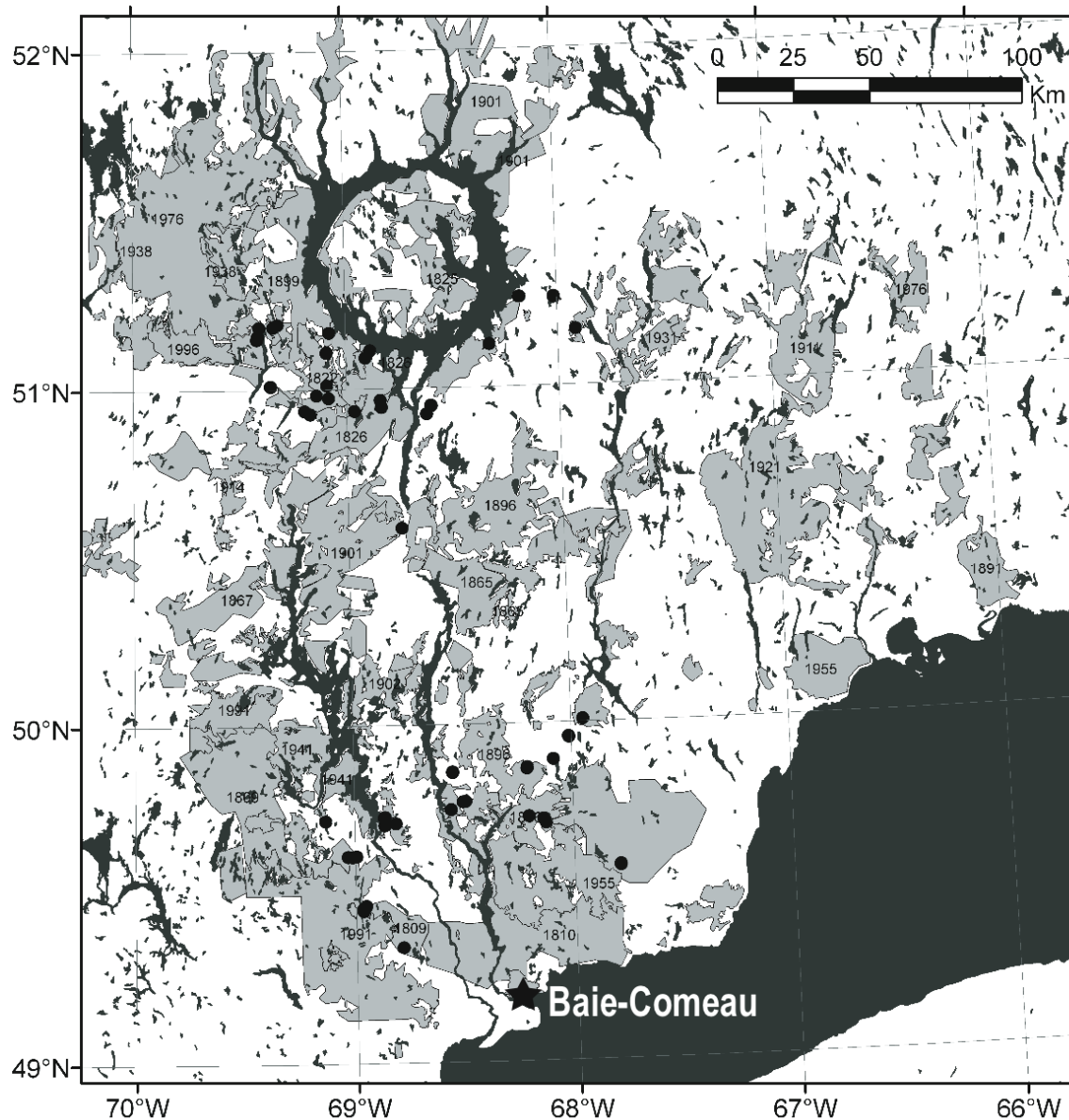


Figure 1. Location of the study area and fires mapped for the period 1800-2000. Fire dates are shown only for fires $>200 \text{ km}^2$.

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).

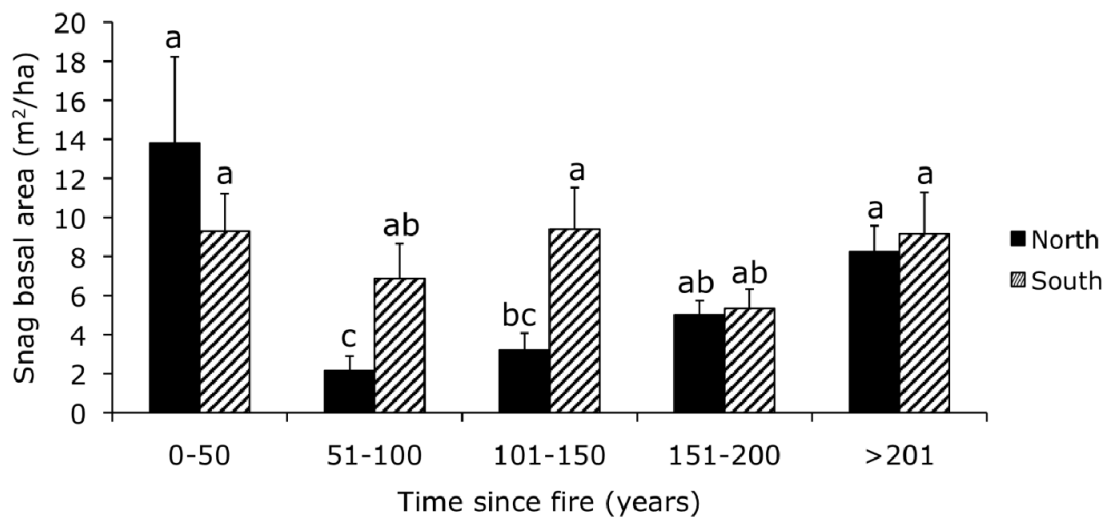


Figure 2. Snag basal area of all snags measured in the study area according to the time since last fire. Significant differences ($P < 0.05$) for means values (\pm S.E; $n = 30$) among years are indicated by different letters.

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.

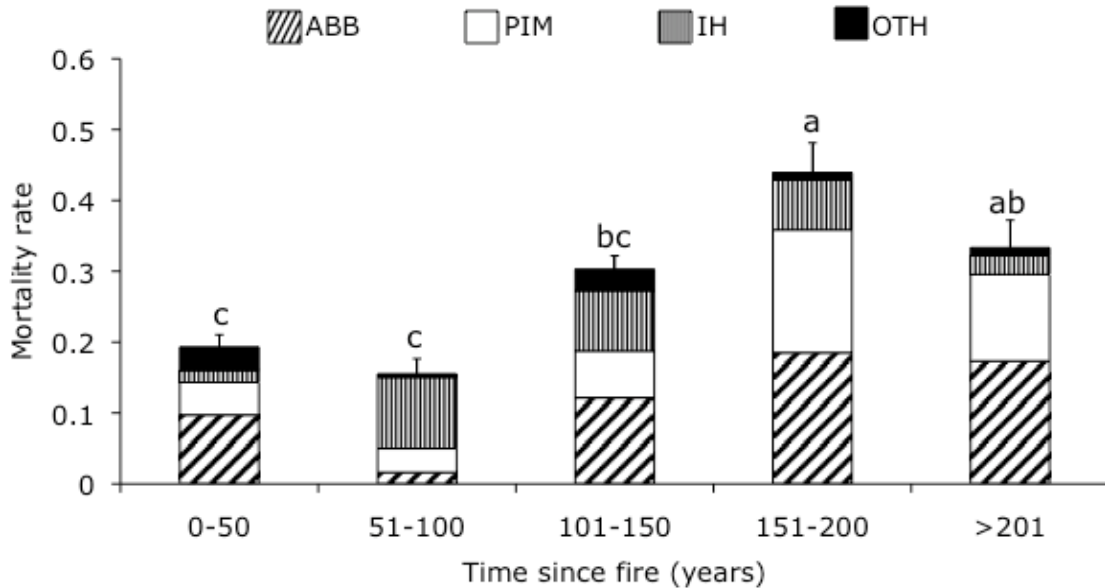


Figure 3. Annual tree mortality rates (%) calculated on a basal area basis for each time since fire (TSF) classes and for four tree species groups. Species groups are balsam fir (ABB), black spruce (PIM), intolerant hardwoods (IH) and the other remaining species (OTH).

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.

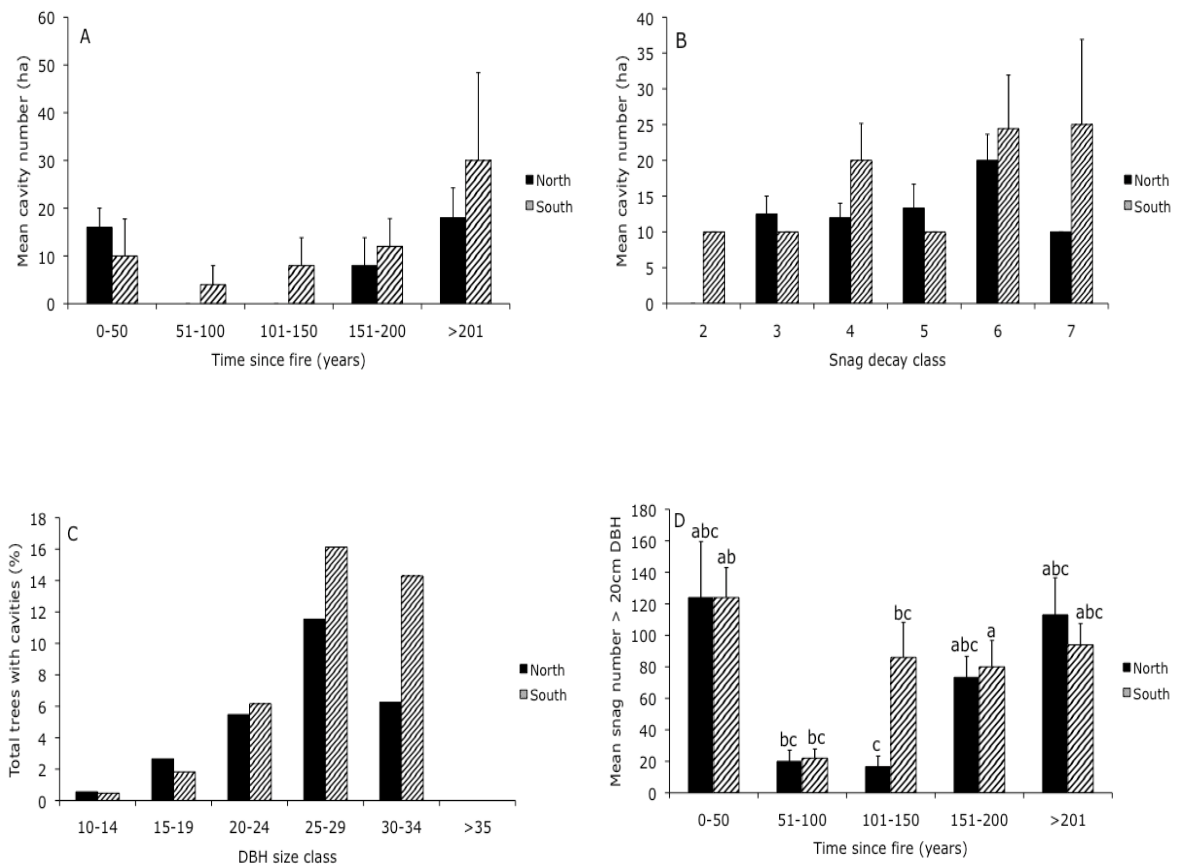


Figure 4. Snag availability and cavity numbers following the two chronosequences. The four diagrams show (A) average number of cavities according to the time since fire; (B) total number of cavities by state of snag decomposition; (C) proportion of trees holding cavities by DBH class; and (D) average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

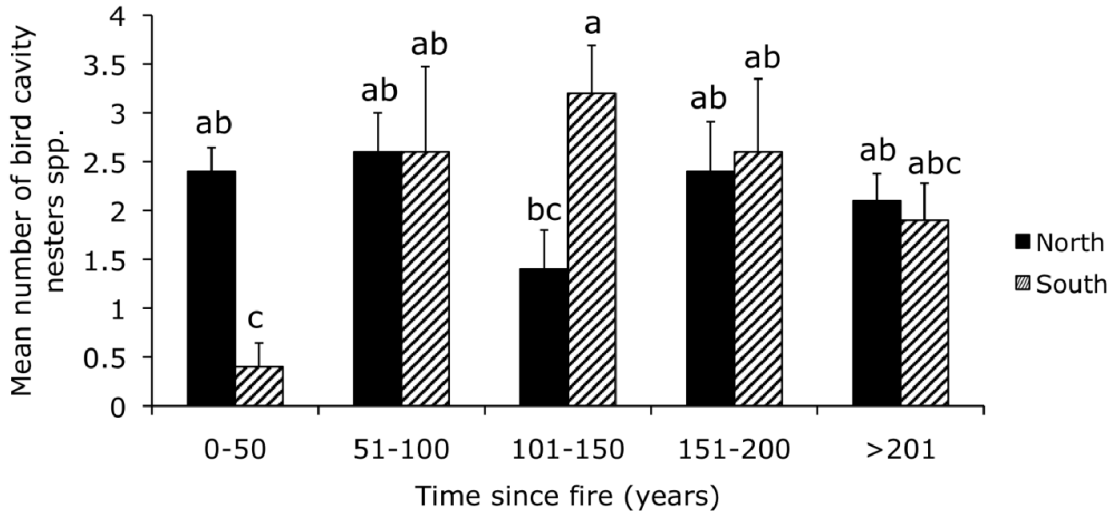


Figure 5. Average number of bird species using cavities per plot according to the time since last fire (TSF). Significant differences ($P < 0.05$) among mean values (\pm S.E.; $n = 30$) of TSF classes are indicated by different letters.

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).

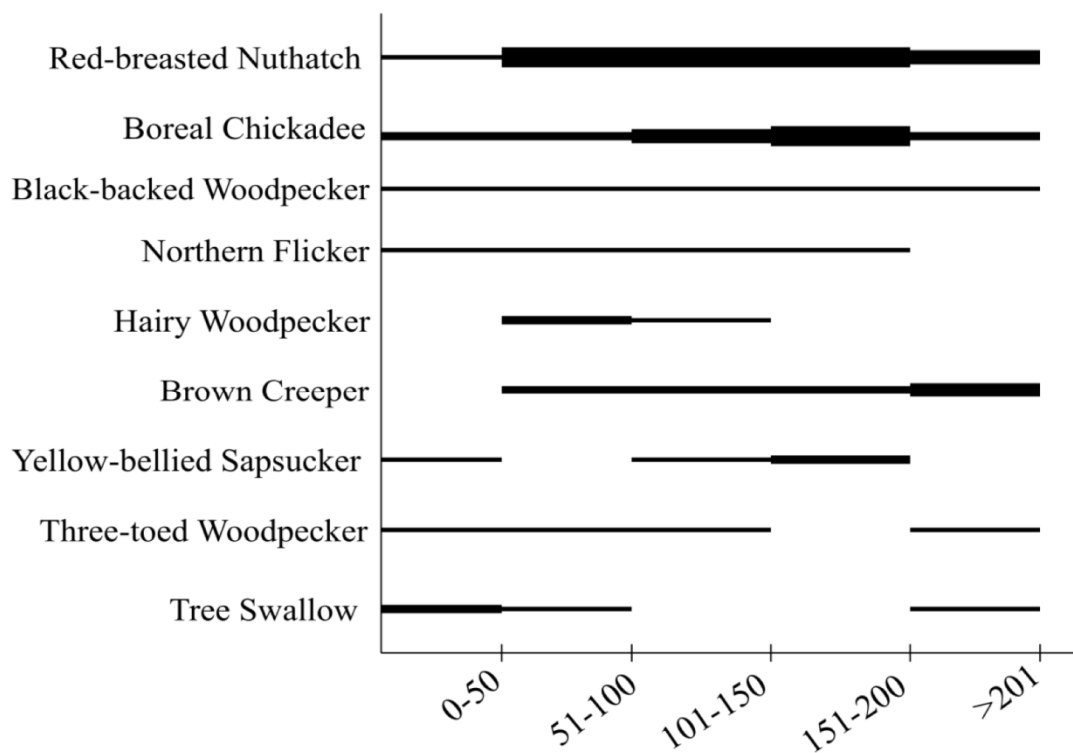


Figure 6. Presence of cavity-nesters according to time since fire. For each species, line width corresponds to the relative abundance of these birds during point counts (2 visits in June). Within each TSF class, no line means 0 birds per point count, the thinner black line represents a density of ≤ 0.2 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.

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