

Fire Regime and Old-Growth Boreal Forests in Central Quebec, Canada: An Ecosystem Management Perspective

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Boreal forest management in Eastern Canada has caused depletion and fragmentation of old-growth ecosystems, with growing impacts on the associated biodiversity. To mitigate impacts of management while maintaining timber supplies, ecosystem management aims to narrow the gap between natural and managed landscapes. Our study describes the fire history and associated natural old-growth forest proportions and distribution of a 5000 km² area located in the black spruce-feather moss forest of central Quebec. We reconstructed a stand-origin map using archival data, aerial photos and dendrochronology. According to survival analysis (Cox hazard model), the mean fire cycle length was 247 years for the 1734–2009 period. Age-class distribution modelling showed that old-growth forests were present on an average of 55% of the landscape over the last 275 years. The mean fire size was 10 113 ha, while most of the burned area was attributable to fires larger than 10 000 ha, leading to old-growth agglomerations of hundreds of square kilometres. In regards to our findings, we propose ecosystem management targets and strategies to preserve forest diversity and resilience.

Keywords black spruce-feather moss, fire history, ecosystem management, dendrochronology

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1 Introduction

Boreal landscapes are shaped by disturbance regimes (Van Wagner 1978, Johnson and Gutsell 1994, Wu and Loucks 1995, Angelstam and Kuuluvainen 2004). In North America, stand-initiating fires create a mosaic of forest patches which differ in their age, internal structure, and composition (Dix and Swan 1971, Rowe and Scotter 1973, Johnson 1992). Young forests form a dense and uniform canopy composed of shade-intolerant or semi-tolerant species that establish soon after a fire. With time and under the action of secondary disturbances, individuals in the canopy are replaced and the forest passes from one undergoing changes via successional processes, to one influenced by gap dynamics (Bergeron 2000, Chen and Popadiouk 2002, Angelstam and Kuuluvainen 2004). As proposed by Kneeshaw and Gauthier (2003), once die-back of the post-fire cohort is completed and the establishment of a new cohort of canopy trees has been initiated, these forests are then considered to be in the first stages of old-growth. Old-growth stands share features typically associated with gap dynamics (Pham et al. 2004, St-Denis et al. 2010), including uneven-aged structure (Kuuluvainen et al. 2002, McCarthy and Weetman 2006), horizontal and vertical heterogeneity (Kneeshaw and Bergeron 1998, Harper et al. 2002, Lecomte and Bergeron 2005), and the substantial presence and diversity of deadwood (Siitonen 2001, Ekbohm et al. 2006).

In addition to natural disturbances, forest management is an important component of forest dynamics, with consequences for landscape complexity (Östlund et al. 1997, Axelsson et al. 2002, Kuuluvainen 2009), ecological processes (Siitonen 2001, Kuuluvainen and Laiho 2004), and diversity (Berg et al. 1994, Rassi et al. 2001). In Eastern Canada, extensive management of the boreal forest started circa 1930, and intensified during the 1970's (Boucher et al. 2009). Even-aged management (clear-cutting) then became a major process, together with stand-initiating fires, by which forest succession was reinitiated. Hence, the boreal forest is now undergoing a period of transition, from a state where the forest was mainly primeval a few decades before, to a forest managed for timber production (Brassard et al. 2009).

Ecosystem-based management, which is now embedded in the Forest Act (Quebec 2011), is

a strategy that has been developed to maintain healthy and resilient ecosystems by focusing on narrowing the differences between natural and managed landscapes (Grumbine 1994, Landres et al. 1999, Gauthier et al. 2009a). The approach is based on the coarse filter principle, the rationale being that conservation of most species is assured by preserving habitat diversity (Franklin 1993, Hunter 1999, Bergeron et al. 2002). It requires a thorough understanding of ecosystem key functions and processes, including disturbance regimes (Christensen et al. 1996). Research may thus provide scientific knowledge on natural landscapes to underline the differences with the managed landscapes (Niemelä 1999, Lindenmayer et al. 2008, Gauthier et al. 2009b).

To uncover pre-industrial forest age-structure, fire regimes of the last 300 years have been studied in several regions of Eastern Canada (Grenier et al. 2005, Bergeron et al. 2006, Bouchard et al. 2008, Senici et al. 2010). It was shown that fire frequency is spatially variable, with historical burn rates varying from 0.781 (Waswanipi, Western Quebec), to <0.002 (North Shore of the St. Lawrence River) (Bouchard et al. 2008, Bergeron et al. 2006). Moreover, compared to continental Canada where high fire frequency has created a matrix of young forests within which islands of older forests are naturally isolated (Johnson et al. 1998), the lower fire frequency of Eastern Canada has allowed large expanses of forests to grow for more than 150 years (Bouchard et al. 2008). Considering old-growth forests as contributors to habitat diversity (Imbeau et al. 1999, Komonen et al. 2000, Drapeau et al. 2003, Courtois et al. 2004, St-Laurent et al. 2009), rejuvenation of the landscape by clear-cutting and the associated scarcity of old-growth attributes are major alterations of the boreal forests of Eastern Canada (Didion et al. 2007, Cyr et al. 2009, Shorohova et al. 2011).

In a context where ecosystem management is being implemented rapidly across the forests of Eastern Canada, we propose a way to bridge the gap between the scientific data that have been gathered regarding the fire regime and the establishment of simple and realistic management targets. More precisely, our objectives are 1) to estimate fire frequency over the last 300 years, together with the associated age-class distribution

of central Quebec boreal forest, where knowledge of the fire history is incomplete, 2) to describe the fire size distribution for the region, and 3) to characterise the spatial configuration of successional stages in the landscape, especially for old-growth forests. Management targets for old-growth based on historical fire regime parameters will then be proposed.

2 Methods

2.1 Study Area

The 540 300 ha study area (from 71°15' to 72°45' W, 49°36' to 50°59' N) is located in the continuous boreal forest, on the Boreal Shield geological formation (Fig. 1). Specifically, it is

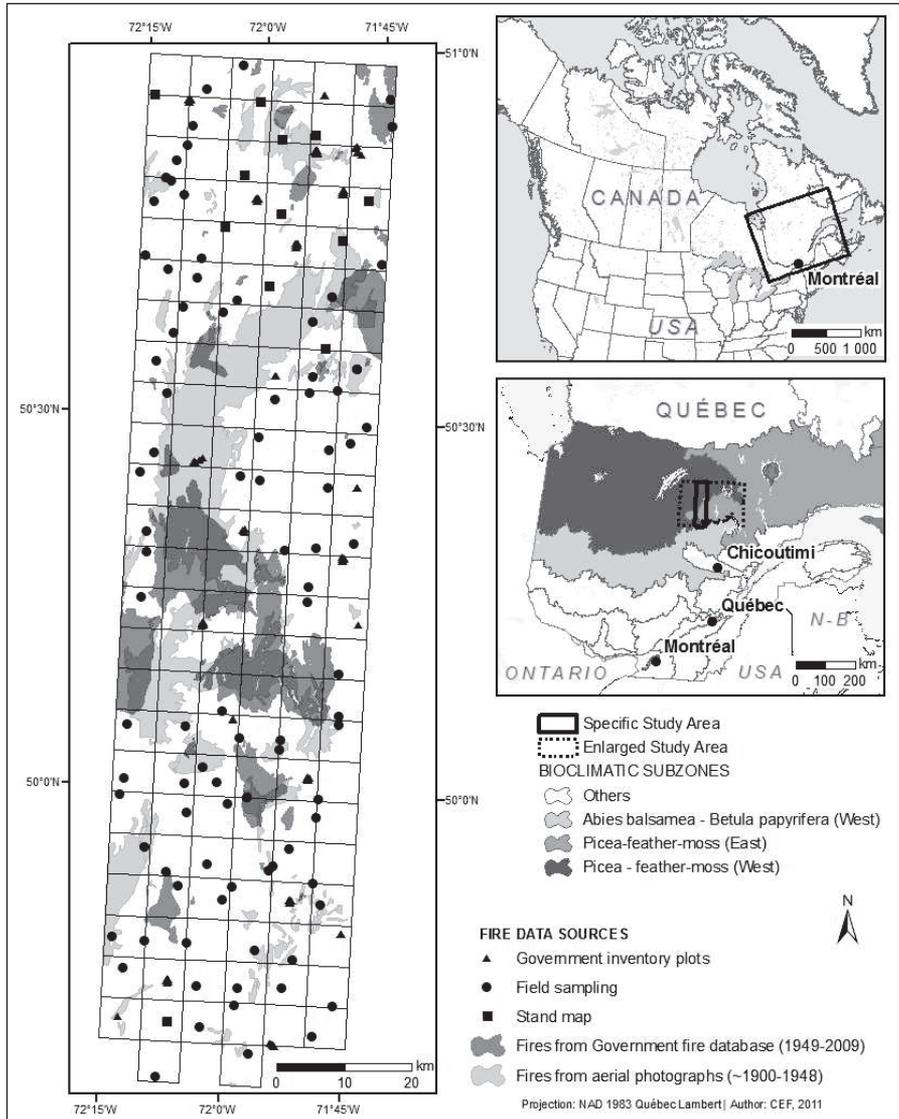


Fig. 1. Sampling design and fire map created from Government databases (1949–2009) and photointerpretation (~1900–1948). For each 3700 ha cell, a fire year (real or minimum) was attributed using different sources (points).

at the border of the western and eastern black spruce (*Picea mariana* (Mill.) BSP) bioclimatic subdomains (Saucier et al. 1998). The topography has low relief, and is composed mainly of rounded hills with surficial deposits that are dominated by mesic glacial tills. Mean elevation ranges from 339 m to 535 m. Temperature averages between 6 to 10 °C and 21 to 25 °C in July and between –29 to –25 °C and –14 to –10 °C in January (Natural Resources Canada 2011). Average annual precipitation is 900 mm to 1200 mm, with 30–35 % falling as snow (Robitaille and Saucier 1998). Knowledge of the fire history is incomplete for the study area, as it is located on the border between two zones with contrasting stand-initiating canopy fire frequencies; higher frequencies are typically west of the study area (MRNQ 2000, Cyr et al. 2007, Le Goff et al. 2007).

Human impact on the landscape has been minimal prior to the 1970s. Nomadic native communities have been present in the region for the last 3000 years at a very low density (0.005 individual/km²) (Helm 1981, Laliberté 1987, Moreau and Langevin 1991). Moreover, nothing in the ethnographic literature mentions deliberate forest fire ignition in the culture of native Innu populations from northern Quebec (Moreau, Jean-François, pers. comm.). The closest villages to our study area, which are located more than 70 km to the south, were settled between 1870 and 1930. In the 1950s, initial timber harvests in the region were limited by technology and access, being restricted to the edges of a few lakes and rivers. Their effects regarding the occurrence of large fires are generally admitted as being very low until the beginning of mechanised harvesting in the 1970s (Lefort et al. 2003). The study area, which is located on public lands, has been dedicated to timber production since 1986 (Coulombe 2004). We have therefore considered the fire regime of our study area as near-natural (Haila et al. 1997) before the beginning of mechanised logging.

2.2 Experimental Design

Several strategies have been developed to assess fire history in different ecological and scientific contexts. Charcoal collection from lake sediments (e.g. Carcaillet and Richard 2000, Carcaillet et al.

2001, Carcaillet et al. 2007, Ali et al. 2009), and the dendrochronological analysis of trees bearing multiple fire scars (e.g., Niklasson and Drakenberg 2001, Drobyshev et al. 2008, Niklasson et al. 2010) have allowed fire intervals to be recorded at a single-point in space. In contrast, stand-origin maps (Niklasson and Granström 2000, Niklasson and Drakenberg 2001, Grenier et al. 2005, Wallenius et al. 2005, Bergeron et al. 2006, Bouchard et al. 2008, Senici et al. 2010) cover a shorter time-scale, but they provide spatially explicit data and are not limited by the availability of multiple fire scars or suitable lakes for sediment collection.

The stand-origin map methodology was first described by Heinselman (1973) and improved by Johnson and Gutsell (1994). It is based on the partitioning of a landscape into a number of spatial units, or points, for which a time-since-fire, real or minimum, is attributed. When fire severity and forest type allow the presence of fire-resistant species, such as *Pinus sylvestris* (L.) in Fennoscandia and *Pinus resinosa* (Ait.) in northeastern America, time-since-fire can be precisely derived from fire scars. In the case of our study area, we were limited by a high severity fire regime and the absence of resistant species. We thus focussed our time-since-fire reconstruction on the composition and age-structure of the forest stands.

To conduct systematic random sampling (Johnson and Gutsell 1994), the study area was divided into a grid of 146 square cells, each of 3700 ha (Fig. 1). All were represented by a randomly chosen stand. The size and location of the study area were chosen to represent adequately the specific fire regime of the landscape, considering the specific fire size distribution (Johnson and Gutsell 1994) and to minimise statistical uncertainties (Cyr 2011). A time-since-fire had to be attributed to each cell. Many data sources were used to best deal with cells' specific constraints, involving fire databases and maps, archived aerial photos and field sampling.

1) For the recent fire history (1949–2009), we used the Quebec Ministry of Natural Resources and Wildlife (MRNFQ) database (*Direction de l'environnement et de la protection des forêts*), which holds fire records since 1920. Fires were precisely mapped with aerial inventories since the 1970s. Accuracy of previous fire mapping is less clear, especially for small fires, since these areas

were derived from observation tower networks (Blanchet 2003). We limited our use to data from 1949 to 2009, where the smallest fire size that had been recorded was 2 ha. However, our method was designed to ensure that any significantly sized fire that was missed in the fire records would be detected by other data sources, such as field sampling.

We overlaid the 1949–2009 fire map and the grid in a GIS (*ESRI ArcGIS 9.3*). All cells that were covered at least 50% by one or several fires were dated according to the year of the fire event. If more than one fire occurred, a random point was generated in the burned area of the 2009 fire-map. The cell was dated according to the fire year at the random point location.

- 2) To map fires that occurred before 1949, we used the photo-interpretation technique described by Lefort et al. (2003). Aerial photographs (1948) covering the entire study area were available from the National Air Photo Library of Canada (average scale is 1:35 000). Fires were recognised by their generally elliptical shape, their jagged borders, and by the presence of visible snags. We hand-mapped fires on 1:250 000 topographical maps and digitised them into *ArcGIS 9.3*. Again, when more than 50% of an undated cell of the grid was covered by a fire, the year of the fire event was attributed, this time using field sampling and dendrochronology (see information below). Overall, fire records (fire database and archived photographs) allowed us to attribute a fire year to 29 cells (about 20% of the grid). The gap between 1948 (aerial photographs) and 1970 (aerial fire mapping) is prone to fire delineation mistakes. Nonetheless, field sampling was performed in areas where no fire was recorded and validated that no large fire had been missed.
- 3) Cells where more than 50% of the surface was not occupied by fires recorded from the two previous sources (i.e. last fire occurred before ~1900; 117 cells, 80%) were attributed a date based on the age of the dominant tree-cohort. For each of these cells, a random point which had to be visited on the field was generated with *Arc GIS 9.3 (Hawth's Tools)*. To minimise bias related to fire breaks, stands located at a distance < 100 m from a water body, road, or bog were avoided. We performed field sampling to collect tree-rings data for all accessible cells (82 cells, 56%).

Thirty-five cells were inaccessible by road or had been totally harvested. We attributed a time-since-fire to these cells using the Government of Quebec's field inventory plots (1970–2000) when available. These 400 m² plots, which are organised in transects of 2 to 7 plots, were distributed over a large part of the study area. In each plot, the age of three dominant trees was derived from dating cores (taken at 1.3 m above the ground). For our purposes, the closest transect (inside the cell) from the random point was considered. Twenty-two cells (15%) were dated this way. Some uncertainties are linked to the choice of which trees were to be sampled, based on dominance status instead of apparent age. This may not be a problem for post-fire cohort stands (< 150-years-old), where all trees have approximately the same age. However, for older stands, this could have led to an under-estimation of the minimum time-since-fire compared with estimates from the field sampling we performed ourselves. A second problem with Government inventory plots is that the trees were not cored at ground level. We estimated this error to be less than 10 years, comparing data from inventory plots to data from our field sampling for a single fire polygon.

Finally, thirteen cells (9%) were impossible to reach in the field and had no inventory plots that had been sampled by the Government of Quebec.

2.3 Determination of Time Since Fire

2.3.1 Field Sampling

For all cells that had to be visited in the field, we sampled the forest stand that was both closest to the random point and accessible from the road (100 m). Cross-sections at the base of 10 dominant and co-dominant trees were collected; snags and logs, when the heartwood was still present, were also sampled (Johnson and Gutsell 1994). The trees from which we collected data were chosen according to the following criteria:

- 1) Trees bearing fire scars were selected first. They were identified by their triangular shape originating from the ground and by the presence of burned bark or wood (Molnar and McMinn 1953, Johnson and Gutsell 1994).

- 2) *Pinus banksiana* Lamb. was prioritised as well because, in a mesic context, its recruitment is limited to post-fire succession, with the majority of individuals (85%) establishing less than 20 years after a severe fire (Gauthier et al. 1993).
- 3) When *Pinus banksiana* was absent, other potential pioneer species were sampled in the following order of priority: 1. *Populus tremuloides* Michx., 2. *Betula papyrifera* Marsh., and 3. *Picea mariana* (cf. Gauthier et al. 2000, Lecomte and Bergeron 2005).
- 4) In the absence of post-fire potential species, *Abies balsamea* (L.) Mill., and *Picea glauca* (Moench) Voss were sampled.

2.3.2 Dendrochronology

To estimate the age of collected trees, cross-sections were dried and sanded, and tree-rings were counted under a dissection microscope. Dead and difficult trees were cross-dated using pointer-years when evident (Yamaguchi 1991) and using chronologies when equivocal. Cross-dating accuracy was then validated with COFECHA (Grisino-Mayer 2001). To build regional chronologies for cross-dating, two radii (when possible) were measured on at least 15 trees. For evergreen species, cross-sections were scanned and tree-rings were measured using the software *Cybis CooRecorder 7.2* (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). For hardwood species, with a less defined contrast between tree-rings, tree-rings were measured using the *Velmex* measuring system (Velmex Incorporated, Bloomfield, New York, USA). Chronologies were built in the software *R* (*R Development Core Team 2010, package dplr*). Overall, 897 tree cross-sections were collected and analysed (see Table 1 for the species counts).

2.3.3 From Tree Ages to Time-Since-Fire

Fire years (real or minimum) were attributed according to the composition and age-structure of the stands. If some *P. banksiana* individuals or fire scars were present ($n=16$), the year of the fire, which was validated with the age-structure of the dominant tree cohort, was attributed. In the

Table 1. Count of individual trees collected during the field sampling campaign and analysed with dendrochronology, and counts of trees analysed from the Government inventory plots databases, selected to complete the determination of time-since-fire for all the grid cells.

Species	Field sampling	Inventory plots
<i>Picea mariana</i>	802	225
<i>Pinus banksiana</i>	62	0
<i>Betula papyrifera</i>	30	2
<i>Picea glauca</i>	2	1
<i>Abies balsamea</i>	1	38
Total	897	266

absence of this direct fire evidence, we turned to stand composition and age-structure to assign a time-since-fire. If the stand was dominated with potential post-fire species (*B. papyrifera*, *P. tremuloides*, *P. mariana*) and the age-structure was even-aged (maximum variation of 20 years), the date of origin of the oldest tree of the cohort was defined as the fire year. If the sampled stand had an uneven-aged structure, the origin year of the oldest tree was considered as the minimum fire year (or censored information, as it is referred to using survival analysis terminology) (Hosmer et al. 2008). The time-since-fire was then defined as the time elapsed between 2009 and the fire year.

The same principle was followed to date the cells with the Government inventory plots (266 trees, Table 1). According to the age-structure and composition of all sampled trees along a transect, we first determined if the dated trees originated from the post-fire cohort and, thus, if the time-since-fire should be considered as real or censored. If the approximated year of the last fire could not be found, we then systematically dated and censored the cell according to the age of the oldest tree in the second plot along the transect.

A minimum time-since-fire of 109 years (2009–1900) was attributed to the thirteen cells where no information was available, according to the time-scale covered by aerial photos (~1900 to 1948).

2.4 Fire Frequency Estimation

Fire frequency can be expressed by the fire cycle concept, which is defined as the time that is required to burn an area equal to that of the study area (Johnson and Gutsell 1994, Li 2002). It is mathematically defined as the inverse of the mean annual burn rate and fits the mean age of the forest (Johnson and Gutsell 1994). Fire cycle is not a perfect mathematical concept to estimate fire frequency, especially for point-based designs, as burn rates are generally not constant in time and space and because fire acts more like a random than a constant process (Reed 2006). However, our area-based design is suitable for burn rate calculations, and consequently, for fire cycle estimation (Li 2002).

Moreover, the fire cycle concept can be compared with that of stand rotation and allows a simple bridge to be built between natural and anthropogenic disturbance regimes. In a theoretical landscape where the fire cycle equals 100 years, 1% of the landscape burns every year. Assuming that the fire hazard is independent of stand-age, after 100 years, a portion of the landscape will have burned once, a portion will have burned more than once, and a portion will have not burned at all. The process leading to old-growth depletion in managed landscapes can be understood by comparing the concepts of fire cycle and stand rotation. Again, in a theoretical managed landscape with a stand rotation of 100 years, 1% of the landscape would be harvested every year. Nevertheless, after 100 years, the whole landscape will have been harvested once and only once. Thus, for two stand-initiating disturbance regimes with a same annual rate, i.e., fires and harvests, the first will release space for some forests to grow for a time longer than the fire cycle, while the second will not allow forests to grow for longer than the stand-rotation time.

To derive the fire cycle directly from the burned area, we would need a complete fire record. In the present case, we were unable to date the last fire for 44% of the area. Thus, we used survival analysis, a statistical technique that has been adapted to deal with censored data such as the minimum time-since-fire. Cox proportional-hazards is a semiparametric survival model that does not assume survival to fit a parametric distribution

(negative exponential or Weibull) (Cox 1972, Hosmer et al. 2008). We applied the Cox model using R software (Survival package, *R Development Core Team, 2010*) and the function *coxph*. The baseline hazard function was then extracted using *basehaz*. The fire cycle was calculated by dividing the time-since-fire associated with the maximum cumulated hazard by this maximum hazard (Therneau 2011). A 95% confidence interval on the fire cycle was calculated by bootstrapping (1000 resamplings with replacement from the original dataset, $n = 146$).

To estimate the influence of human activities on the fire frequency, we compared the fire cycle prior to 1948, a period for which no sign of human activity was noticeable on the aerial photos, and the recent fire cycle (1949–2009), which was calculated by inverting the mean annual burn rate for this period.

2.5 Fire Size

The fire size analysis required more fires than were available in the study area. Hence, we used an enlarged study area (Fig. 1) of 28 931 km², including 176 fires (1949–2009) that were selected to maintain the proportions of the Eastern and Western *Picea mariana*-feather moss bioclimatic sub-domains. We first analysed the size distribution and frequencies of fires that were considered as having their ignition point inside the boundaries of the enlarged study area. For the burned area analysis, all fires that intersected the enlarged study area were considered, although only the area contained inside the limit of our enlarged study area was integrated.

We calculated the mean fire size and estimated the 95% confidence interval with bootstrapping (1000 resamplings with replacement from the original dataset, $n = 176$) on the log-transformed fire size distribution. We then back-transformed the mean and confidence intervals to their original scale.

2.6 Age-Class Distribution and Management Targets

The age-structure of a forest landscape can be mathematically derived from the fire cycle (Van

Wagner 1978). In a theoretical landscape where fire occurs randomly and its probability is independent of stand age, the time-since-fire distribution follows a negative exponential distribution (see Eq. 1) (Johnson and Wagner 1984). This model which has the advantage of integrating the variability of the last 300 years, was used to calculate the historical mean age-class distribution for our study area.

$$A(T) = e^{-(t/b)} \quad (1)$$

where $A(T)$ is the proportion of the landscape that escaped fire during a time T with a fire cycle b .

Fire hazard may be influenced by local factors (Mansuy et al. 2010), although these are poorly documented and only partly understood. We judged appropriate to make no assumptions regarding their effects and consider that model validity is not compromised. In addition, we know that large scale factors, such as weather, influence fire hazard and behaviour to a greater degree than the fuel when the landscape is dominated by conifers (Bessie and Johnson 1995).

To make some concrete and simple management targets, four age-classes were defined according to the succession models described for the neighboring regions of the black spruce-feather moss forest. Forests from 0–30 years after a fire were considered to be in the regeneration phase, 31–80 years post-fire were considered as young, 81–150 as mature (Harper et al. 2002), and > 150 as old-growth (Harper et al. 2003, Lecomte and Bergeron 2005). The mean proportions of each successional stage in the landscape were calculated by running Eq. 1 with the corresponding time intervals. The confidence intervals on the successional stage proportions were calculated by running Eq. 1 with the limits of the fire cycle 95% confidence interval.

3 Results

Between 1949 and 2009, 12.5% of the landscape was encompassed by stand-replacing fires. Moreover, for 20.7% of the area, fire boundaries could be drawn from the aerial photographs of 1948,

where the earliest fire that could be mapped was dated to 1892, as confirmed by our field sampling. Overall, 27.6% of our study area burned at least once between ~1890 and 2009.

Fires from ~1900 to 2009 were mapped and dated either directly from the archives (1949–2009) or with field sampling. Regarding the period prior to 1949, the fire perimeter data come from our interpretation of aerial photos. The accuracy of delineating fire boundaries decreased with increasing time-since-fire; some fires may have been missed in the initial fire map, especially the old and small ones. However, these earlier fires were detected by the systematic field sampling design. Overall, we are confident that all fires of a significant size for our purposes (i.e. > 2 ha) were recorded from ~1890 to 2009.

Fire and tree-ring data were analysed for each of the 146 cells (3700 ha) of the grid and a time-since-fire, real or minimum, was assigned. For 82 cells (56%), we were able to assign a time-since-fire with an accuracy of about 10 years. However, for the 64 other cells (43%), only a minimum-time-since-fire (censored) was assigned because there was no clear sign of a post-fire cohort, ($n=36$) or because of the impossibility of reaching the site in the field ($n=28$).

Fig. 2 presents the stand-origin year distribution in the 2009 landscape (without considering harvests). We observed that a few fire-decades (1820, 1860, 1920 and 2000) strongly influenced the age-class abundances over the study area (30% of the grid cells). Considering the censored data, for which we were unable to find sufficient evidence to determine a time-since-fire, we noted that their distribution exhibited two peaks, i.e., the decades 1900 and 1750. We explained this pattern respectively, by the minimum age available according to aerial photos, which led to many cells being censored in 1900, and by the apparent longevity of black spruce (~250 years).

By grouping time-since-fire into the successional stages presented in the methodology, we can draw a portrait of the 2009 landscape age structure (excluding the effect of harvesting). Roughly, forests in regeneration (0–30 yr) represented 10% of the landscape, while young forests (31–80 yr) were less than 1%. Including stands for which only a minimum age is known, mature forests (81–150 yr) accounted for a maximum of 38% of the landscape,

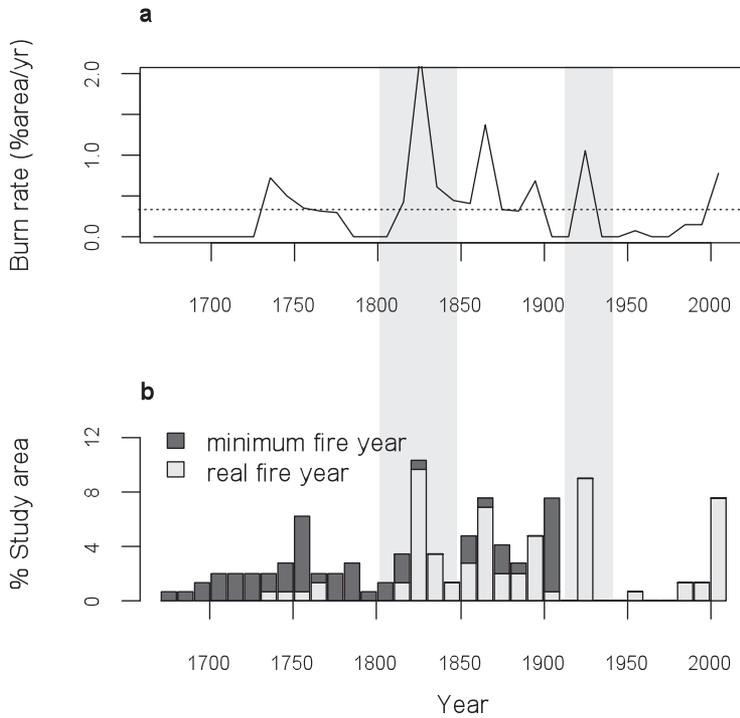


Fig. 2. a) Fire hazard variation from 1734 to 2009 grouped into 10 year classes, estimated by the Cox regression model. The dotted line represents the mean burned area per year (0.4%), or the inverse of the fire cycle (247 yr). Peaks over this line indicate high fire frequency decades while troughs indicate low fire frequency decades. b) For the distribution of stand initiation (or fire) year, real or minimum, each cell of the grid presented in Fig. 1 accounts for one unit of the landscape ($n = 146$). The shaded rectangles were identified by Girardin et al. (2006) as periods where the occurrence of years with fire-prone weather patterns was high.

while over-mature forests (> 150 yr) represented at least 51% of the landscape.

Survival analysis (Cox regression model) led to the estimation of a fire cycle of 247 years for the period from 1734 to 2009. The 95% confidence interval about this mean ranged from 187 to 309 years. Fig. 2 presents the Cox fire hazard variations over time. As noted in the age-class distribution, fire hazard peaked in the decades 2000, 1920, 1860 and 1820, and was low between 1930 and 2000. Because the effect of settlement on fire frequency remains ambiguous, we calculated the fire cycle before and after settlement (Table 2). The fire cycle after settlement (375 yrs) was significantly longer than before settlement (209 yrs), according to confidence intervals calculated for the pre-settlement fire cycle.

Table 2. Fire cycles of the entire period covered (1734–2009), the pre-management period (1734–1948), and the management period (1949–2009). Fire cycles were calculated with the Cox regression model when involving censored data and using the inverse of the burn rate when complete fire records were available. The 95% confidence intervals were then calculated by bootstrapping. Fire cycle for 1949–2009 was derived from the effective burned area and, hence, does not have a confidence interval.

Period	2.5%	Fire cycle	97.5%
1734–2009	187	247	309
1734–1948	157	209	273
1949–2009	-	375	-

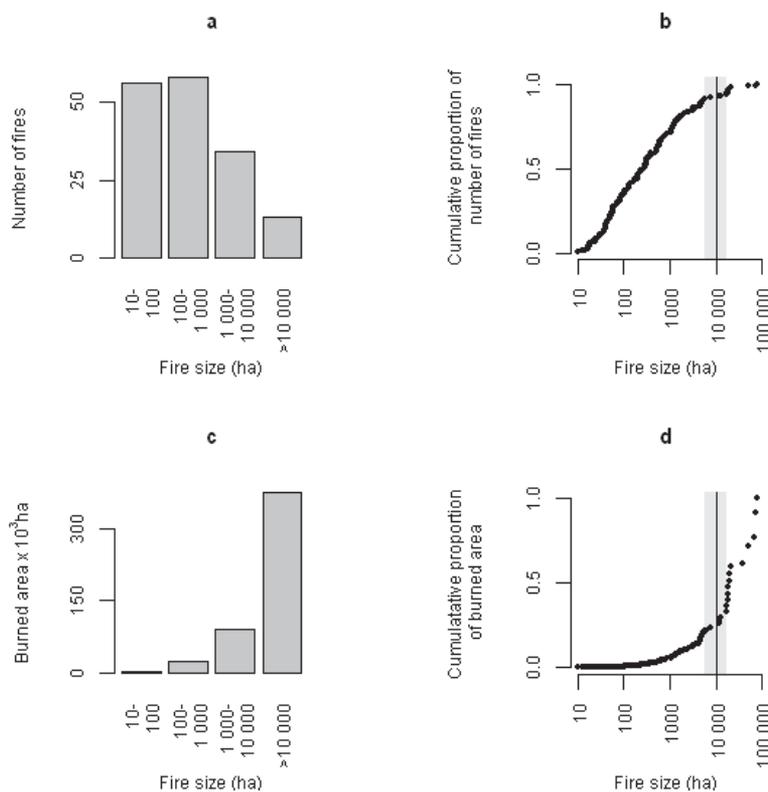


Fig. 3. Fire size distribution (>2 ha), from fire data recorded by the Government of Quebec between 1949 and 2009. For the a) absolute and b) cumulative relative frequencies, only fires for which the ignition point was located inside the enlarged study area were considered ($n=161$). For the c) absolute and d) cumulative relative burned areas, the size of all fires that intersect the enlarged study area was considered, but the associated burned area was limited to the boundaries of the enlarged study area ($n=176$). For b) and d), the mean fire size (10,113 ha) is represented by the vertical lines and the 95% confidence intervals by the shaded areas.

The fire size analysis for the original study area showed that large fires were responsible for most of the burned area. From all fires mapped ~1900 to 2009, those that were more than 3800 ha in area, which roughly fits the cell size of the grid (3700 ha), were responsible for 77% of the burned area (8 fire years: ~1871, ~1924, ~1927, ~1948, 1986, 1991, 2005, and 2007). The maximum fire size was 75 231 ha (~1924) and was responsible for 42% of the total burned area.

Fig. 3 depicts fire size frequency and distribution, and associated burned areas for the enlarged study area. Overall, mean fire size was estimated at 10 113 ha, with a 95% confidence interval

ranging from 5796 ha to 17 530 ha. The fire size distribution followed a negative exponential shape (Fig. 3b). This meant that the number of fires decreased with size (except for small fires) on a log-scale (Fig. 3a). Otherwise, regarding the burned area on Figs. 3c and 3d, the relation is inverted, where large fires (>10 000 ha), even if infrequent, were responsible for 74.7% of the burned area.

Fig. 4 illustrates the spatial distribution of the stand-origin years and associated successional stages in 2009. Regenerating, young, mature, and old-growth forests are grouped in large tracts (>2 cells of 3700 ha), forming vast areas of the same

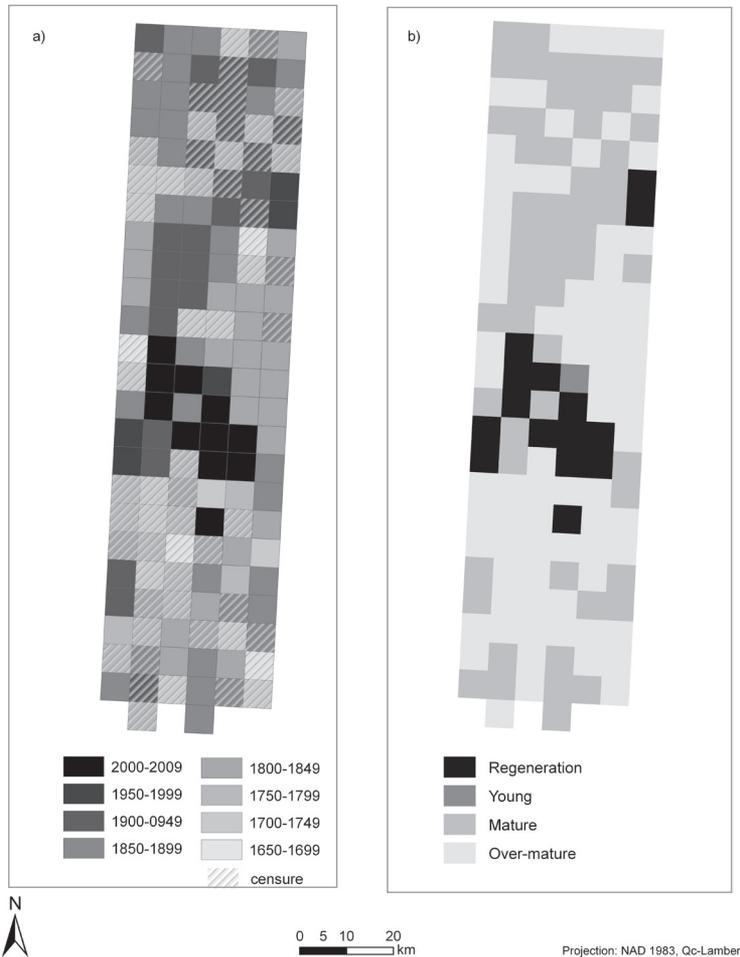


Fig. 4. a) Spatial distribution of stand origin years, grouped in 50-year classes. Fire years were determined with a precision of about 10 years and are illustrated by the fully colored squares, while the minimum time-since-fires are represented by the hatched cells. The same grid is presented in b) but time-since-fire is grouped into structural age-classes: regeneration (0–30 yr), young (31–80 yr), mature (81–150) and over-mature (>150 yr). 1 cell=3700 ha.

successional stage. Moreover, censored data, for which we could solely attribute a minimum time-since-fire, seem to be agglomerated within the landscape.

The mean proportions of successional stages in the landscape between 1734 and 2009 are presented in Table 3. According to the negative exponential model, old-growth forests (>150 after a fire) represented the most important group (45% to 61% of the landscape). We noted that only 1%

of young forests were observed in the 2009 representation of the un-managed landscape, which is outside of the range defined by the confidence interval of our model. We attribute this gap to low fire activity observed between 1930 and 2000 and to the age-class lower limit (80 yr), which fits with the transition between high and low fire activity periods (~1930).

Table 3. Theoretical age-class distribution in the landscape (% of the landscape), modelled with the negative exponential distribution associated with a fire cycle of 247 years and its 95% confidence interval (CI) i.e., 187 yrs to 309 yrs. Values for 2009 would represent the age-class distribution if the territory had remained un-managed.

Tsf	2.5% (CI) %	FC =247yr %	97.5% (CI) %	In 2009 %
0–30	9.2	11.4	14.8	10
31–80	13.5	16.2	20.0	1
81–150	15.6	17.9	20.3	<38
>150	44.9	54.5	61.6	>51

Note: Tsf=time-since-fire, CI= Confidence interval limit

4 Discussion

4.1 Historical Fire Regime

4.1.1 Fire Cycle

The 247-year historical fire cycle that we calculated for the black-spruce-feather moss forest of Central Quebec is consistent with the fire cycle gradient observed between western (128, 189, 141 yr; Bergeron et al. 2004, Le Goff et al. 2007) and eastern (281 yr, 270 yr, >500 yrs, Cyr et al. 2007, Bouchard et al. 2008) neighbouring regions of Quebec. In addition, the observations for our study area seem more similar to the situation in the East, associated with a lower fire frequency, although the 95% confidence intervals (187–309 yr) are broad. The fire cycle value involves important temporal variability at the century- and decade-scales. Our results show a fire hazard peak around 1825 and a general decrease thereafter. Such long-term trends are not uncommon for boreal forests. In some regions, changes around 1850 have been attributed to the end of the Little-Ice-Age (Bergeron and Archambault 1993, Bergeron et al. 2004), an era characterised by dryer decades (Girardin et al. 2004). On a shorter time-scale, a few fire-decades have strongly influenced the age-class distribution in 2009 (1820, 1860, 1920, and 2000). As Girardin et al. (2006) indicated 1920–1940 and 1800–1850 as periods of enhanced occurrence of a high drought index

over the Boreal Shield, we may at least partly attribute these fire decades to similar dry conditions. Overall, as elsewhere in the boreal forest of North America, it appears that temporal variation in fire frequency is mainly driven by climate (Bergeron and Archambault 1993, Larsen 1996, Gillett et al. 2004, Le Goff et al. 2007, Flannigan et al. 2009).

The fire cycle that was calculated after 1949, from the beginning of industrial human activities in our region, is significantly longer than the fire cycle prior to settlement (1734–1948). The impact of land-use changes on the fire regime is probably not the main reason for this trend, notably when the only activity in the area was logging (Lefort et al. 2003). This period also corresponds with the beginning of active fire control in Quebec, which started around 1930 (Blanchet 2003). Although fire control may have had some effect on the observed low fire frequency, the effectiveness of control strategies on the occurrence of large fires is questionable (Bridge et al. 2005), especially regarding the large fires that occurred in 2005 and 2007 and despite having much more advanced technology. As unfavorable climate trends for fire occurred during the second half of the 20th C in the region (Lefort et al. 2003, Girardin et al. 2006, Girardin and Wotton 2009), it is probable that the low fire frequency is attributable to a period where the climate was not conducive to large fires.

The fire frequency variation previously described is partly responsible for the broad confidence interval associated with fire cycle calculation (187–309 years). A portion is also attributable to the gradual loss of information that is caused by aging of the forest, when traces of the initial post-fire cohort gradually disappear, making it impossible to date the last fire event from within-stand age-structure. Moreover, in the context of high fire severity and in the absence of fire-resistant species, re-burning of some areas erases the traces of past events.

4.1.2 Fire Size

The fire size distribution roughly fitted a truncated negative exponential curve (e.g., Cumming 2001). However, Fig. 3a showed that small fires (10–100

ha) should be more frequent to perfectly fit the distribution. We suspect underestimation of this size class, either because of the lower efficiency of detection techniques for small fires, or because of human influence on the fire size distribution. Regarding the burned area, most of it was attributable to fires larger than 10 000 ha.

The fire size distribution was of the same order of magnitude as those for other black spruce-feather moss regions in Quebec (Belleau et al., 2007). Otherwise, while size distribution followed a curve similar to that found for Western Canada (Cumming 2001), it is 10 times lower in magnitude.

4.1.3 Fire Regime and Old-Growth Forests

At the time of the study, in 2009, regardless of harvests, the study area was mainly represented by forests older than 150 years (more than 51%), followed by a maximum of 38% for mature forests (81–150 years). Young forests and regeneration accounted for 11% of the landscape. However, as shown in Fig. 2a, the study was conducted following a period of low fire activity (1930–2000), which explains the quasi-absence of young forests (31–80 years). The associated age-class spatial configuration of the landscape is characterised by large areas of contiguous forests that differ in their successional stage. A few fire events (~1820, ~1860, 1924, 2005, 2007) have successively created large areas of regeneration forests. Moreover, their spatial contingency has resulted in old-growth agglomerations of hundreds of square kilometres.

Although our portrayal of 2009 is an example of a realisation of the fire regime that has occurred over the last three centuries, it is not accurate for describing the historical variability of age-class proportions in the landscape (Armstrong 1999). Therefore, we turned to the fire cycle, which includes the variability of the last 300 years. Average proportions of each age-class that are associated with a fire cycle of 247 years and its confidence interval (187–309 years) have been calculated for the entire 1734–2009 period. After modelling, old-growth forests still represent most of the study area with an average of 55% of the landscape.

Given the importance of providing clear numerical targets for ecosystem-based management (Angelstam 1998, Lindenmayer et al. 2008), the question arises: *how much old-growth is enough?* We found that fire hazard has been variable over the last 300 years, as has the proportion of old-growth forests. Despite this evidence of important natural variability, we propose a single-value target of 55% of the landscape that should be managed to maintain the specific composition and structure of old-growth stands. We used this average value being aware that extreme events (e.g., fires of the 1920's) are an important part of the natural variability that can drive a natural landscape outside the management target described here. Three main reasons justify our decision to present targets based on average mean values. First, unlike in Fennoscandia where fires have been practically excluded, such extreme events are still occurring in eastern North America (for example, the great fires of 2005 and 2007), and even more considering climate changes (Amiro et al. 2009, Flannigan et al. 2009, Girardin et al. 2010). As successive disturbances such as fires, insect outbreaks, and harvesting lead to loss of ecosystem resilience (Payette and Delwaide 2003, Girard et al. 2008), we argue that, even if large fire events are an important part of natural variability, ecosystem management should avoid going to these extremes. Second, for socio-economic concerns, forest-dependent communities need a constant timber-supply. Finally, if the emulation of extreme-natural-events could be justified by ecosystem management, the occurrence of extreme-management-events may be prone to happening simultaneously over extended regions, following market fluctuations. Such regional standardisation of the boreal forest may be desirable for neither diversity nor resilience of the forest.

Regarding spatial configuration of successional stages, Fig. 4 shows that, as a consequence of a regime of large fires, burned areas are to a great extent contiguous, and so are the old-growth forests. The ability of old-growth forests to meet their ecological functions is closely linked to their size and their connectivity (Harris 1984, Saunders et al. 1991, Lindenmayer et al. 2008). Yet remnant forests, as provided in traditional management plans, tend to be left as strips or islets (Doucet et al. 2009); they are highly susceptible

to wind-throw, further decreasing the amount of interior forest (Ruel et al. 2001). To respect the landscape pattern that originates from the natural fire regime, ecosystem management should plan to include large contiguous areas of old-growth forests. Fig. 4b provides an order of magnitude of the target sizes, where three contiguous cells correspond to patches $> 100 \text{ km}^2$.

4.2 Management Strategies

To reach the objective of maintaining diversity and resilience associated with old-growth forests, ecosystem management strategies should be oriented towards both natural processes and feature conservation and restoration (Lahde et al. 1999, Franklin et al. 2002, Vanha-Majamaa et al. 2007). We propose a brief overview of four complementary strategies to reach the 55% of old-growth's objective.

- 1) Extending rotation time: Currently, stand rotations truncate the succession process that leads to the natural development of old-growth stands. Simply extending the rotation-time, as described by Burton et al. (1999), would allow stands to reach an old-growth stage before they get harvested. Taken this strategy alone, according to the fire regime of our study area, rotation time should be extended over 300 years, which may be hardly reconcilable with industrial and economic requirements. Alternatively, Seymour and Hunter (1999) proposed adopting variable rotation lengths for the same landscape. For example, some stands would be harvested every 100 years, while others were allowed to grow for 300 years before being harvested, in order to re-create an age-structure similar to the natural one generated by fires. In all cases, extending the rotation time in our study area as elsewhere in the eastern boreal forest, to be efficient and realistic, may be used in addition to other strategies.
- 2) Integral conservation: Along with the idea of preserving succession and gap formation processes, the integral conservation of some key areas may be an effective way of preserving a part of the primeval landscape. In parallel, Bengtsson et al. (2003) introduced the concept of spatially and temporally dynamic reserves. These could be selected according to specific old-growth features

(Timonen et al. 2011) and moved in time and space to make sure they keep their specific ecological functions. Dynamic reserves are already being implemented for a woodland caribou preservation strategy (Équipe de rétablissement du caribou forestier du Québec 2008).

- 3) Cohort management: Along with these process-oriented strategies, feature-oriented strategies focus on preserving or restoring old-growth attributes (composition, structure). They involve greater alteration of ecosystems but reduced costs in relation to timber supply (Harvey et al. 2002). For example, partial cuttings that are designed to emulate secondary disturbances such as spruce-budworm outbreaks and wind-throw have proved effective in emulating old-growth structure and composition (Harvey et al. 2002, Harvey and Brais 2007, Kneeshaw et al. 2011), especially when improved by special attention being paid to deadwood supply (Harmon 1986, Siitonen 2001, Harvey et al. 2002).
- 4) Landscape deployment: Ecosystem management addresses the problem of forest fragmentation (Fahrig 2003) by creating harvest agglomerations (adjacent cutovers aggregated over a 5–15 year period) rather than dividing them sporadically in space and time through the landscape (Belleau et al. 2007), which better mimics the spatial pattern generated by the natural fire regime. Aggregated harvests can thus minimise habitat fragmentation provided that large tracks of mature and over-mature forest (managed or natural) are interspersed among them (Perron et al. 2009).

5 Conclusion

We conclude from our results that 1) old-growth forests ($> 150 \text{ yr}$) represented an average of 55% of the study area during the last 300 yrs. 2) Because of the regime of large fires, the spatial pattern of these forests is organised into large patches of several hundred square kilometres. 3) In order to preserve diversity associated with old-growth forests, a critical portion of the landscape should be dedicated to preservation/restoration of old-growth structure and composition, with a focus on connectivity. Considering the variability of fire frequencies throughout the boreal forest,

the data should not be extrapolated to neighbouring regions as a whole but should contribute to specifying the spatial variation of fire frequency in the Eastern boreal forest of North America.

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References

- Ali, A.A., Carcaillet, C. & Bergeron, Y. 2009. Long term fire frequency variability in the eastern Canadian boreal forest: the influences of climate vs. local factors. *Global Change Biology* 15(5): 1230–1241.
- Amiro, B., Cantin, A., Flannigan, M. & De Groot, W. 2009. Future emissions from Canadian boreal forest fires. *Canadian Journal of Forest Research* 39(2): 383–395.
- Angelstam, P. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science* 9(4): 593–602.
- & Kuuluvainen, T. 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures – a European perspective. *Ecological Bulletins* 51: 117–136.
- Armstrong, G.W. 1999. A stochastic characterisation of the natural disturbance regime of the boreal mixedwood forest with implications for sustainable forest management. *Canadian Journal of Forest Research* 29(4): 424–433.
- Axelsson, A.L., Östlund, L. & Hellberg, E. 2002. Changes in mixed deciduous forests of boreal Sweden 1866–1999 based on interpretation of historical records. *Landscape Ecology* 17(5): 403–418.
- Belleau, A., Bergeron, Y., Leduc, A., Gauthier, S. & Fall, A. 2007. Using spatially explicit simulations to explore size distribution and spacing of regenerating areas produced by wildfires: recommendations for designing harvest agglomerations for the Canadian Boreal forest. *Forestry Chronicle* 83(1): 72–83.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. & Nyström, M. 2003. Reserves, resilience and dynamic landscapes. *Ambio* 32(6): 389–396.
- Bergeron, Y. 1993. Decreasing frequency of forest fires in the southern boreal zone of Québec and its relation to global warming since the end of the «Little Ice Age.» *The Holocene* 3(3): 255–259.
- 2000. Species and stand dynamic in the mixed woods of Québec's southern boreal forest. *Ecology* 81(6): 1500–1516.
- , Cyr, D., Drever, C.R., Flannigan, M., Gauthier, S., Kneeshaw, D., Lauzon, È., Leduc, A., Goff, H.L., Lesieur, D. & Logan, K. 2006. Past, current, and future fire frequencies in Québec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. *Canadian Journal of Forest Research* 36: 2737–2744.
- , Flannigan, M., Gauthier, S., Leduc, A. & Lefort, P. 2004. Past, current and future fire frequency in the Canadian boreal forest: Implications for sustainable forest management. *Ambio* 33(6): 356–360.
- , Leduc, A., Harvey, B.D. & Gauthier, S. 2002. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. *Silva Fennica* 36(1): 81–95.

- Bessie, W.C. & Johnson, E.A. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology* 76(3): 747–762.
- Blanchet, P. 2003. Feux de forêt, l'histoire d'une guerre. Éditions trait d'union and Patrick Blanchet, Montréal.
- Bouchard, M., Pothier, D. & Gauthier, S. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. *Canadian Journal of Forest Research* 38: 1621–1633.
- Boucher, Y., Arseneault, D., Sirois, L. & Blais, L. 2009. Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. *Landscape Ecology* 24(2): 171–184.
- Brassard, F., Bouchard, A. R., Boisjoly, D., Poisson, F., Bazoge, A., Bouchard, M.-A., Lavoie, G., Tardif, B., Bergeron, M., Perron, J., Balej, R. & Blais, D. 2009. Portrait du réseau d'aires protégées au Québec – 2002–2009. Ministère du développement et des Parcs du Québec (ed.). Québec. 39 p.
- Bridge, S.R.J., Miyamishi, K. & Johnson, E.A. 2005. A critical evaluation of fire suppression effects in the boreal forest of Ontario. *Forest Science* 51(1): 41–50.
- Burton, P.J., Kneeshaw, D.D. & Coates, K.D. 1999. Managing forest harvesting to maintain old growth in boreal and sub-boreal forests. *Forestry Chronicle* 75(4): 623–631.
- Carcaillet, C., Bergeron, Y., Richard, P.J.H., Fréchette, B., Gauthier, S. & Prairie, Y.T. 2001. Change of fire frequency in the eastern Canadian boreal forests during the Holocene: Does vegetation composition or climate trigger the fire regime? *Journal of Ecology* 89: 930–946.
- , Bergman, I., Delorme, S., Hornberg, G. & Zackrisson, O. 2007. Long-term fire frequency not linked to prehistoric occupations in northern Swedish boreal forest. *Ecology* 88(2): 465–477.
- & Richard, P.J.H. 2000. Holocene changes in seasonal precipitation highlighted by fire incidence in eastern Canada. *Climate Dynamics* 16: 549–559.
- Chen, H.Y.H. & Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. *Environmental Reviews* 10: 137–166.
- Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F. & Parsons, D.J. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. *Ecological Applications* 6(3): 665–691.
- Coulombe, G. 2004. Commission d'étude sur la gestion de la forêt publique québécoise.
- Courtois, R., Ouellet, J.-P., Dussault, C. & Gingras, A. 2004. Forest management guidelines for forest-dwelling caribou in Quebec. *Forestry Chronicle* 80(5): 598–607.
- Cox, D.R. 1972. Regression models and life-tables. *Journal of the Royal Statistical Society. Series B (Methodological)* 34(2): 187–220.
- Cumming, S. 2001. A parametric model of the fire-size distribution. *Canadian Journal of Forest Research* 31(8): 1297–1303.
- Cyr, D. 2011. Cycle des feux, vieilles forêts et aménagement en forêt boréale de l'est du Canada. Ph.D. thesis, Université du Québec à Montréal, Montréal, QC.
- , Gauthier, S. & Bergeron, Y. 2007. Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada. *Landscape Ecology* 22(9): 1325–1339.
- , Gauthier, S., Bergeron, Y. & Carcaillet, C. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. *Frontiers in Ecology and the Environment* 7(10): 519–524.
- Didion, M., Fortin, M.J. & Fall, A. 2007. Forest age structure as indicator of boreal forest sustainability under alternative management and fire regimes: a landscape level sensitivity analysis. *Ecological Modelling* 200(1–2): 45–58.
- Dix, R.L. & Swan, J.M.A. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. *Canadian Journal of Botany* 49: 657–676.
- Doucet, R., Jutras, S., Lessard, G., Pineau, M.P., Guy, Ruel, J.-C. & Thiffault, N. 2009. Sylviculture appliquée. In: É. MultiMonde (ed.). Manuel de foresterie. p. 1147–1186.
- Drapeau, P., Leduc, A., Bergeron, Y., Gauthier, S. & Savard, J.-P.L. 2003. Bird communities of old spruce-moss forests in the Clay Belt region: problems and solutions in forest management. *Forestry Chronicle* 79(3): 531–540.
- Drobyshev, I., Goebel, P.C., Hix, D.M., Corace, R.G. & Semko-Duncan, M.E. 2008. Pre- and post-European settlement fire history of red pine-dominated forest ecosystems of Seney National Wildlife Refuge, Upper Michigan. *Canadian Journal of*

- Forest Research 38(9): 2497–2514.
- Ekbohm, B., Schroeder, L.M. & Larsson, S. 2006. Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. *Forest Ecology & Management* 221(1–3): 2–12.
- Équipe de rétablissement du caribou forestier du Québec. 2008. Plan de rétablissement du caribou forestier (*Rangifer tarandus*) au Québec – 2005–2012. Ministère des Ressources naturelles et de la Faune, Faune Québec & Direction de l'expertise sur la faune et des habitats (eds.). 78 p. Québec.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution & Systematics* 34: 487–515.
- Flannigan, M., Stocks, B., Turetsky, M. & Wotton, M. 2009. Impacts of climate change on fire activity and fire management in the circumboreal forest. *Global Change Biology* 15(3): 549–560.
- Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems or landscapes? *Ecological Applications* 3(2): 202–205.
- , Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K. & Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology & Management* 155(1–3): 399–423.
- Gauthier, S., Bergeron, Y. & Simon, J.-P. 1993. Cone serotiny in jack pine: ontogenetic, positional, and environmental effects. *Canadian Journal of Forest Research* 23(3): 394–401.
- , De Grandpré, L. & Bergeron, Y. 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. *Journal of Vegetation Science* 11: 781–790.
- , Vaillancourt, M.-A., Kneeshaw, D.D., Drapeau, P., De Grandpre, L., Claveau, Y. & Pare, D. 2009a. Forest ecosystem management: Origins and foundations. In: S. Gauthier, M.A. Vaillancourt, A. Leduc, L. De Grandpre, D.D. Kneeshaw, H. Morin, P. Drapeau & Y. Bergeron (eds.). *Ecosystem management in the boreal forest*. Les Presses de l'Université du Québec. p. 13–38.
- , Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D.D., Morin, H., Drapeau, P. & Bergeron, Y. 2009b. *Ecosystem management in the boreal forest*. Québec: Presses de l'Université du Québec.
- Gillett, N., Weaver, A., Zwiers, F. & Flannigan, M. 2004. Detecting the effect of climate change on Canadian forest fires. *Geophysical Research Letters* 31(18): L18211.
- Girard, F., Payette, S. & Gagnon, R. 2008. Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. *Journal of Biogeography* 35: 529–537.
- Girardin, M.P. & Wotton, B.M. 2009. Summer moisture and wildfire risks across Canada. *Journal of Applied Meteorology and Climatology* 48(3): 517–533.
- , Tardif, J., Flannigan, M.D., Wotton, B.M. & Bergeron, Y. 2004. Trends and periodicities in the Canadian Drought Code and their relationships with atmospheric circulation for the southern Canadian boreal forest. *Canadian Journal of Forest Research* 34(1): 103–119.
- , Bergeron, Y., Tardif, J.C., Gauthier, S., Flannigan, M.D. & Mudelsee, M. 2006. A 229-year dendroclimatic-inferred record of forest fire activity for the Boreal Shield of Canada. *International Journal of Wildland Fire* 15(3): 375–388.
- , Ali, A.A. & Hély, C. 2010. Wildfires in boreal ecosystems: Past, present and some emerging trends. *International Journal of Wildland Fire* 19(8): 991–995.
- Grenier, D.J., Bergeron, Y., Kneeshaw, D. & Gauthier, S. 2005. Fire frequency for the transitional mixed-wood forest of Timiskaming, Quebec, Canada. *Canadian Journal of Forest Research* 35(3): 656–666.
- Grissino-Mayer, H.D. 2001. Research report evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57(2): 205–221.
- Grumbine, R.E. 1994. What is ecosystem management? *Conservation Biology* 8(1): 27–38.
- Haila, Y., Comer, P.J., Hunter, M., Samways, M.J., Hambler, C., Speight, M.R., Hendricks, P., Herrero, S., Dobson, F.S. & Smith, A.T. 1997. A natural «benchmark» for ecosystem function. *Conservation Biology* 11(2): 300–307.
- Harmon, M.E. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133–302.
- Harper, K.A., Bergeron, Y., Gauthier, S. & Drapeau, P. 2002. Post-fire development of canopy structure and composition in black spruce forests of Abitibi,

- Québec: a landscape scale investigation. *Silva Fennica* 36(1): 249–263.
- , Boudreault, C., De Grandpre, L., Drapeau, P., Gauthier, S. & Bergeron, Y. 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. *Environmental Reviews* 11(1 Suppl.): S79–S98.
- Harris, L.D. 1984. *The fragmented forest: island biogeography theory and the preservation of biotic diversity*: University of Chicago Press, Chicago, IL.
- Harvey, B. & Brais, S. 2007. Partial cutting as an analogue to stem exclusion and dieback in trembling aspen (*Populus tremuloides*) dominated boreal mixedwoods: implications for deadwood dynamics. *Canadian Journal of Forest Research* 37: 1525–1533.
- , Leduc, A., Gauthier, S. & Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. *Forest Ecology & Management* 155(1–3): 369–385.
- Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3(3): 329–382.
- Helm, J. (ed.). 1981. *Handbook of North American Indians*. Vol. 6, Subarctic. Smithsonian Institution Press, Washington, DC.
- Hosmer, D.W., Lemeshow, S. & May, S. 2008. *Applied survival analysis: regression modeling of time-to-event data*. Wiley-Interscience, Hoboken, NJ.
- Hunter, M.L. 1999. *Maintaining biodiversity in forest ecosystems*. Cambridge University Press, Cambridge, UK. 698 pp.
- Imbeau, L., Savard, J.-P.L. & Gagnon, R. 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. *Canadian Journal of Zoology* 77(12): 1850–1860.
- Johnson, E.A. 1992. *Fire and vegetation dynamics: Studies from the North American boreal forest*. Cambridge University Press, Cambridge, UK.
- & Gutsell, S.L. 1994. Fire frequency models, Methods and interpretation. *Advances in Ecological Research* 25: 239–287.
- & Van Wagner, C.E. 1984. The theory and use of two fire history models. *Canadian Journal of Forest Research* 15: 214–220.
- , Miyanishi, K. & Weir, J.M.H. 1998. Wildfires in the western Canadian boreal forest: Landscape patterns and ecosystem management. *Journal of Vegetation Science* 9(4): 603–610.
- Kafka, V., Gauthier, S. & Bergeron, Y. 2001. Fire impacts and crowning in the boreal forest: study of a large wildfire in western Quebec. *International Journal of Wildland Fire* 10: 119–127.
- Kneeshaw, D.D. & Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the boreal southeastern boreal forest. *Ecology* 79(3): 783–794.
- , Harvey, B.D., Reyes, G.P., Caron, M.N. & Barlow, S. 2011. Spruce budworm, windthrow and partial cutting: Do different partial disturbances produce different forest structures? *Forest Ecology & Management* 262(3): 482–490.
- Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos* 90(1): 119–126.
- Kuuluvainen, T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: the complexity challenge. *AMBIO* 38(6): 309–315.
- & Laiho, R. 2004. Long-term forest utilization can decrease forest floor microhabitat diversity: Evidence from boreal Fennoscandia. *Canadian Journal of Forest Research* 34(2): 303–309.
- , Mäki, J., Karjalainen, L. & Lehtonen, H. 2002. Tree age distributions in old-growth forest sites in Vienansalo wilderness, eastern Fennoscandia. *Silva Fennica* 36: 169–184.
- Lahde, E., Laiho, O. & Norokorpi, Y. 1999. Diversity-oriented silviculture in the Boreal Zone of Europe. *Forest Ecology & Management* 118: 223–243.
- Laliberté, M. 1987. Sur la piste des toukouamis. *Saguenayensia* 29(4): 2–10.
- Landres, P.B., Morgan, P. & Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9(4): 1179–1188.
- Larsen, C.P.S. 1996. Fire and climate dynamics in the boreal forest of northern Alberta, Canada, from AD 1850 to 1989. *The Holocene*, 6(4): 449–456.
- Le Goff, H., Flannigan, M.D., Bergeron, Y. & Girardin, M.P. 2007. Historical fire regime shifts related to climate teleconnections in the Waswanipi area, central Quebec, Canada. *International Journal of Wildland Fire* 16: 607–618.
- Lecomte, N. & Bergeron, Y. 2005. Successional pathways on different surficial deposits in the coniferous boreal forest of the Quebec Clay Belt. *Canadian*

- Journal of Forest Research 35: 1984–1995.
- Lefort, P., Gauthier, S. & Bergeron, Y. 2003. The influence of fire weather and land use on the fire activity of the lake Abitibi area, eastern Canada. *Forest Science* 49(4): 509–521.
- Li, C. 2002. Estimation of fire frequency and fire cycle: A computational perspective. *Ecological Modelling* 154(1–2): 103–120.
- Lindenmayer, D., Hobbs, R.J., Montague-Drake, R., Alexandra, J., Bennett, A., Burgman, M., Cale, P., Calhoun, A., Cramer, V., Cullen, P., Driscoll, D., Fahrig, L., Fischer, J., Franklin, J., Haila, Y., Hunter, M., Gibbons, P., Lake, S., Luck, G., MacGregor, C., McIntyre, S., Mac Nally, R., Manning, A., Miller, J., Mooney, H., Noss, R., Possingham, H., Saunders, D., Schmiegelow, F., Scott, M., Simberloff, D., Sisk, T., Tabor, G., Walker, B., Wiens, J., Woinarski, J. & Zavaleta, E. 2008. A checklist for ecological management of landscapes for conservation. *Ecology Letters* 11(1): 78–91.
- Mansuy, N., Gauthier, S., Robitaille, A. & Bergeron, Y. 2010. The effects of surficial deposit-drainage combinations on spatial variations of fire cycles in the boreal forest of eastern Canada. *International Journal of Wildland Fire* 19(8): 1083–1098.
- McCarthy, J.W. & Weetman, G. 2006. Age and size structure of gap-dynamic, old-growth boreal forest stands in Newfoundland. *Silva Fennica* 40(2): 209–230.
- MRNQ (Ministère des Ressources Naturelles du Québec). 2000. La limite nordique des forêts attribuables, rapport final du comité. Québec.
- Molnar, A.C. & McMinn, R.G. 1953. The origin of basal scars in the British Columbia interior white pine type. *Forestry Chronicle* 36: 50–60.
- Moreau, J.-F. & Langevin, É. 1991. Les premières occupations de la Grande-Décharge du Pékouagami. *Saguenayensia* 33(4): 7–14.
- Natural resources Canada 2011. [Internet site]. The Atlas of Canada. Available at: <http://atlas.nrcan.gc.ca/auth/english/index.html>. [Cited 19 Oct 2011]
- Niemelä, J. 1999. Management in relation to disturbance in the boreal forest. *Forest Ecology & Management* 115(2–3): 127–134.
- Niklasson, M. & Drakenberg, B. 2001. A 600-year tree-ring fire history from Norra Kvills National Park, southern Sweden: Implications for conservation strategies in the hemiboreal zone. *Biological Conservation* 101(1): 63–71.
- & Granström, A. 2000. Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology* 81(6): 1484–1499.
- , Zin, E., Zielonka, T., Feijen, M., Korczyk, A.F., Churski, M., Samojlik, T., JeDrzejewska, B., Gutowski, J.M. & Brzeziecki, B. 2010. A 350-year tree-ring fire record from Białowieza Primeval Forest, Poland: implications for Central European lowland fire history. *Journal of Ecology* 98(6): 1319–1329.
- Ostlund, L., Zackrisson, O. & Axelsson, A.L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research* 27(8): 1198–1206.
- Payette, S. & Delwaide, A. 2003. Shift of conifer boreal forest to lichen-heath parkland caused by successive stand disturbances. *Ecosystems* 6: 540–550.
- Perron, N., Belanger, L. & Vaillancourt, M.-A. 2009. Spatial structure of forest stands and remnants under fire and timber harvesting regimes. In S. Gauthier, M. A. Vaillancourt, A. Leduc, L. De Grandpre, D. D. Kneeshaw, H. Morin, P. Drapeau & Y. Bergeron (eds.). *Ecosystem management in the boreal forest*. Les Presses de l'Université du Québec. p. 103–128.
- Pham, A.T., De Grandpre, L., Gauthier, S. & Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. *Canadian Journal of Forest Research* 34(2): 353–364.
- Quebec. 2011. Loi sur l'aménagement durable du territoire forestier.
- Reed, W.J. 2006. A note on fire frequency concepts and definitions. *Canadian Journal of Forest Research* 36(7): 1884–1888.
- Robitaille, A. & Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Gouvernement du Québec, Québec.
- Rowe, J.S. & Scotter, G.W. 1973. Fire in the boreal forest. *Quaternary Research* 3(3): 444–464.
- Ruel, J.C., Pin, D. & Cooper, K. 2001. Windthrow in riparian buffer strips: effect of wind exposure, thinning and strip width. *Forest Ecology & Management* 143(1–3): 105–113.
- Saucier, J.-P., Bergeron, J.-F., Grondin, P. & Robitaille, A. 1998. Les régions écologiques du Québec méridional (3e version): un des éléments du système hiérarchique de classification écologique du territoire mis au point par le ministère des Ressources

- naturelles du Québec. Ministère des ressources naturelles du Québec, Québec.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5(1): 18–32.
- Senici, D., Chen, H.Y.H., Bergeron, Y. & Cyr, D. 2010. Spatiotemporal variations of fire frequency in central boreal forest. *Ecosystems* 13(8): 1227–1238.
- Seymour, R. & Hunter, M.L. 1999. Principles of ecological forestry. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, UK. p. 22–61.
- Shorohova, E., Kneeshaw, D., Kuuluvainen, T. & Gauthier, S. 2011. Variability and dynamics of old-growth forests in the circumboreal zone: implications for conservation, restoration and management. *Silva Fennica* 45(5). (Current issue).
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* 49: 11–41.
- St-Denis, A., Kneeshaw, D. & Bergeron, Y. 2010. The role of gaps and tree regeneration in the transition from dense to open black spruce stands. *Forest Ecology & Management* 259(3): 469–476.
- St-Laurent, M.-H., Dussault, C., Ferron, J. & Gagnon, R. 2009. Dissecting habitat loss and fragmentation effects following logging in boreal forest: conservation perspectives from landscape simulations. *Biological Conservation* 142: 2240–2249.
- Therneau, T. 2011. Survival analysis, including penalised likelihood. In: CRAN (ed.). Documentation for package ‘survival’ version 2.36-9.
- Timonen, J., Gustafsson, L., Kotiaho, J.S. & Mönkkönen, M. 2011. Hotspots in cold climate: conservation value of woodland key habitats in boreal forests. *Biological Conservation* 144(8): 2061–2067.
- Van Wagner, C.E. 1978. Age-class distribution and the forest fire cycle. *Canadian Journal of Forest Research* 8: 220–227.
- Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T. & Kuuluvainen, T. 2007. Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: the EVO experiment. *Forest Ecology & Management* 250(1–2): 77–88.
- Wallenius, T.H., Pitkänen, A., Kuuluvainen, T., Penanen, J. & Karttunen, H. 2005. Fire history and forest age distribution of an unmanaged *Picea abies* dominated landscape. *Canadian Journal of Forest Research* 35(7): 1540–1552.
- Wu, J. & Loucks, O.L. 1995. From balance-of-nature to hierarchical patch dynamics: a paradigm shift in ecology. *Quarterly Review of Biology* 70: 439–466.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* 21(3): 414–416.

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