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Fire and canopy species composition in the Great Lakes-St. Lawrence forest of Témiscamingue, Québec

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Abstract

Large severe fires are typically rare in the northern hardwood forests of eastern North America, with estimated return intervals as high as 1400–4500 years. We investigated the history of large severe fires in western Québec, Canada, where sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), and eastern hemlock ((*Tsuga canadensis* (L.) Carr.) dominate a landscape at northern limit of the Great Lakes-St. Lawrence forest region. Using a combination of provincial archives of fire data, interpretation of historic air photos and dendrochronological sampling, we estimated fire frequency in a 179,300 ha landscape and tested the hypothesis that time-since-fire is a principal determinant of canopy species composition. Our results indicated that despite its proximity to the boreal mixedwood forest, fires have been relatively infrequent in this landscape, with over 60% of the landscape remaining unburned during the 413 year period of study. The overall fire cycle, an estimate of the time required to burn an area of equivalent size to the study area, was 494 year (95% CI: 373–694). This estimate showed strong temporal partitioning, with an elevated frequency that coincided with the period of pioneering settlement beginning in 1880, and spatial partitioning according to surficial deposits, pine dominance and ecological site type. Multivariate analyses elucidated both (i) distinct assemblages of canopy species that differed in their association with time-since-fire and (ii) the relative importance of environmental variables affecting canopy species composition, where time-since-fire explained the largest amount of variation. This time-since-fire effect suggested an important role for secondary disturbances in influencing composition of the canopy. Given the current long fire cycles, it is likely this landscape will experience an increasing dominance of fire-avoiding species such as sugar maple and eastern hemlock, with consequences for fire-adapted tree species and fire-dependent communities.

Keywords: Fire cycle; Canopy species composition; Time-since-fire; *Acer saccharum*; *Betula alleghaniensis*; Pine; Late-seral species; Fire-adapted species; Great Lakes-St. Lawrence forest region

1. Introduction

Large severe fires have important consequences for the spatial patterning of different stand types, composition and age-class structure of temperate forests (Turner and Romme, 1994). However, large severe fires, i.e. fires that destroy most or all of the overstory and understory, are typically rare events in the northern hardwood forests of eastern North America. For example, in the Great Lakes forests of Michigan, estimates of the return interval for large severe fires range between 1400 and 4500 years (Whitney, 1986; Frelich and Lorimer, 1991). Several factors provide forests dominated by deciduous trees such as sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) with structural attributes and fuel loadings of low flammability as compared to conifer-dominated forests; these include their high foliar moisture content, low amounts of flammable resins and oils, fuel discontinuity between tree crowns and the forest floor, high decomposition rates of coarse woody debris, and relatively fire-retardant fine leaf litter (Mutch, 1970; Philpot, 1970; Bessie and Johnson, 1995; Hély et al., 2001; Frelich, 2002). However, at the northerly limit of their distribution in western Québec, Canada,

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northern hardwood forests are adjacent to the boreal mixed-woods, where fire is a common and extensive influence on forest composition and structure (Grenier et al., 2005; Bergeron et al., 2001). In other 'near boreal' forests, such as the red and white pine forests of the Boundary Waters Canoe Area in Minnesota or pine–aspen forests of Algonquin Park in Ontario, large severe fires are relatively more frequent – between 175 and 300 years – than in the Michigan landscapes (Heinselman, 1973; Cwynar, 1977).

We conducted a landscape-scale assessment of the history of large severe fires for a forested landscape in Témiscamingue, Québec. We calculated the fire cycle, an estimate of the time required to burn an area of equivalent size to the study area (Johnson and Van Wagner, 1985), examined its spatial and temporal variability, and tested hypotheses regarding the role of time elapsed since large severe fire on species composition in the canopy. We tested the hypotheses that (i) European settlement increased the frequency of large severe fire and (ii) spatial partitioning of fire frequency exists in this landscape, where fire frequency increases in coarse surficial deposits and pine-dominated stands and decreases in deciduous-dominated ecological site types.

In addition, we addressed some fundamental questions regarding the role of fire in determining canopy species composition. We asked: are there distinct stand types comprised of contrasting assemblages of canopy tree species related to time-since-fire (TSF)? If so, what are these assemblages? We also examined the extent to which variation in the presence or absence of canopy species can be explained by TSF relative to environmental and site history variables such as aspect, slope or frequency of partial harvesting. We tested the hypothesis that TSF is the principal determinant explaining variation in canopy species composition in this landscape.

2. Methods

2.1. Study area

The study area (~46°40′N; 78°45′W) covers 179,300 ha (Fig. 1). The Ottawa River is its western limit; the remaining boundaries correspond to the limits of 'ecological districts' i.e.

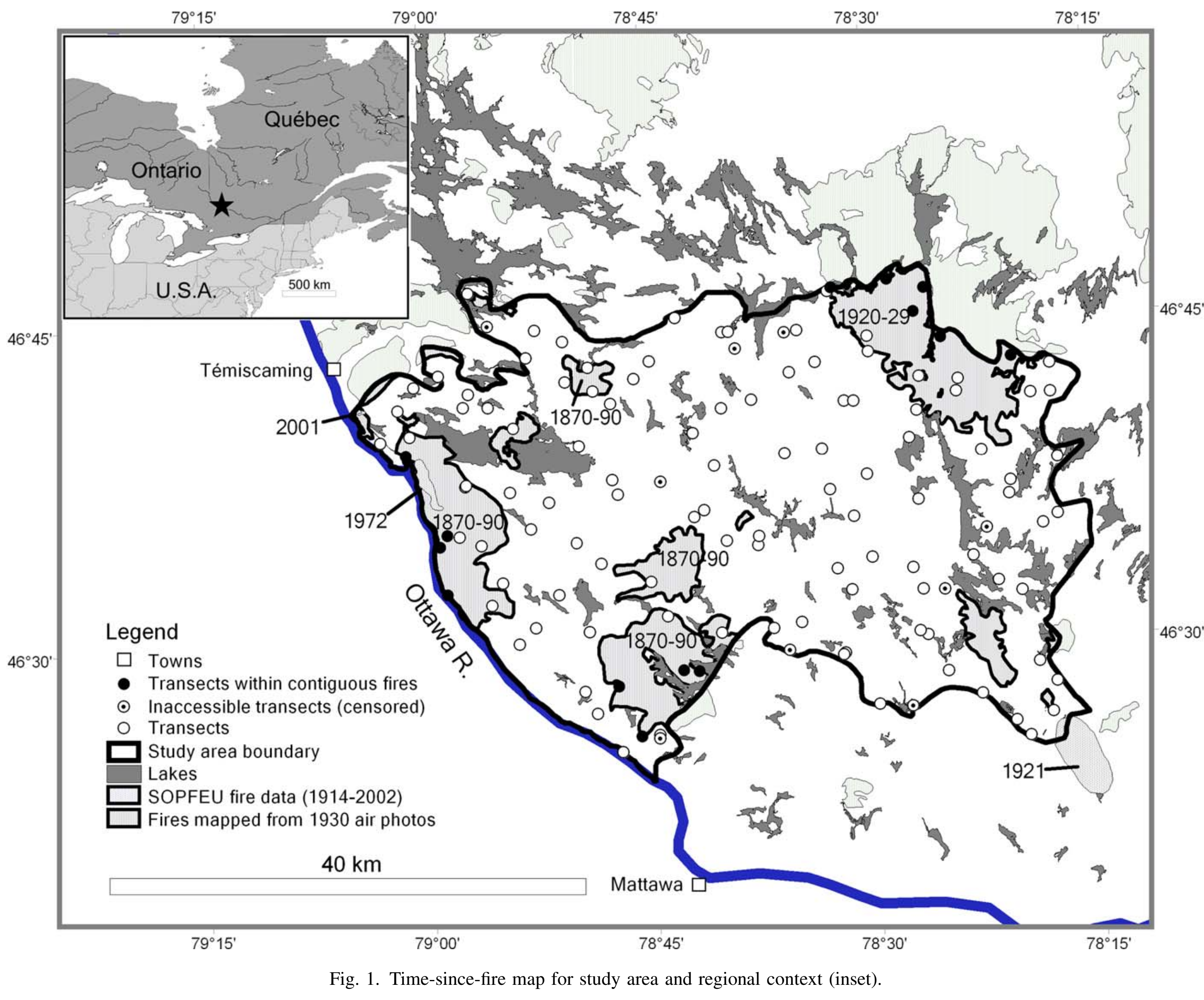

Fig. 1. Time-since-fire map for study area and regional context (inset).

relatively homogeneous units based on topography, elevation, surficial deposits, parent materials, and hydrology (Robitaille and Saucier, 1998). The climate is subpolar continental with cold winters and warm summers. Based on the nearest meteorological station, Barrage Témiscamingue ($46^\circ 42'$N, $79^\circ 6'$W, 181 m above sea level), the mean annual temperature is 4.4 $^\circ$C (Environment Canada, 2005). Mean annual precipitation is 963 mm, with 226 mm (23%) falling as snow. Average snow depth is 13 cm. Growing degree days above 5 $^\circ$C range between 1350 and 1550 while the growing season is typically 180 days long (Robitaille and Saucier, 1998; Richard, 2003).

The topography is characterized by gentle to moderately steep hills, with rounded and sometimes rocky summits. The study area is on the Grenville geological province of the Canadian Shield and its surficial deposits are principally undifferentiated or rocky glacial tills. Parent materials are metamorphic or sedimentary, almost exclusively gneissic or paragneissic and acidic (Brown, 1981). Soils are principally humo-ferric podzols (Brown, 1981). Mean elevation is 311 m above sea level. Mean slope is 9%. Forests cover almost the entire land surface while lakes, rivers and other water bodies cover about 20% of the total area.

The landscape is within the sugar maple–yellow birch bioclimatic domain for western Québec (Robitaille and Saucier, 1998) and, more generally, the Great Lakes-St. Lawrence forest region (Rowe, 1972). Sugar maple and yellow birch, often with a subdominant component of white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.), typically dominate the canopy. Such stands comprise 70,141 ha (40% of study area). Eighty-three percent of the landscape is considered mesic, with the potential tree vegetation on midslope mesic sites being sugar maple and yellow birch (Robitaille and Saucier, 1998).

Other common tree species include eastern hemlock (*Tsuga canadensis* (L.) Carr.), white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), large tooth aspen (*Populus grandidentata* Michx.), red pine (*Pinus resinosa* Ait.) and white pine (*Pinus strobus* L.). Stands of red and white pine occur throughout the study area while stands dominated principally by red pine are abundant on dry sites, shores and rocky outcrops, especially adjacent to the Ottawa River. Pines are the dominant or codominant canopy species across 17,372 ha (10% of the study area).

Forest management by Europeans in Témiscamingue began about 1800 with the targeted extraction of large-diameter white pine, red pine and white spruce (Vincent, 1995). However, it was not until after 1874 when forestry concessions were assigned and saw mills built that industrial logging began on a large scale (Vincent, 1995). Settlement followed in the 1880s, greatly enhanced by the completion of a railway in 1890 and the 1916 completion of a pulp and paper mill in the town of Témiskaming. The role of aboriginal burning for berry or ungulate management is unknown.

2.2. Fire history reconstruction

The interpretation of historic air photos, dendrochronological analyses and archival records from the provincial forest agency were used to determine the cumulative TSF distribution for the study area. A preliminary TSF map was created in ARCVIEW 3.2a (ESRI, 1996) by combining georeferenced information of large fires from provincial fire archives (1914–2002) with an assessment of 1930 air photos (B&W; 1:30,000) (Fig. 1). The boundaries of recent past fires (i.e. since $\sim$1900) were identified and digitized from the air photos based on tonal, shape, pattern and textural attributes characteristic of post-fire patches. Air photos from 1950 were also examined, but no large fires were detected.

We implemented a stratified random sampling design to estimate the TSF distribution ($n = 129$). (Johnson and Gutsell, 1994). We first overlaid a rectangular grid of approximately 1800-ha cells over the study area and located a potential sampling site within each cell using the random point utility in ARCVIEW 3.2a. During the summers of 2003 and 2004, we sampled 106 transects, each 20-m wide by 250-m long, and assessed percent slope, aspect, elevation, evidence of past fires (i.e. charcoal or burnt seeds in the mineral soil, burned stumps, charred logs or snags, etc.), tree species composition (presence or absence) in the canopy stratum, and evidence of harvesting (i.e. presence and condition of cut stumps, machine ruts, skid roads, etc.). Evidence of windthrow (toppled, snapped or bent trees, abundant pit-mounds, aligned woody debris) was also noted when present. Our study focused on productive sites, so extreme conditions such as hydric conifer forest or rocky, xeric pine ridges were not sampled.

For dendrochronological sampling ($n = 106$), we obtained disks or increment cores at approximately 30–50 cm above the ground from five to 15 large living trees at each site, preferably of post-fire pioneer species. From first to last, selection priority was: white birch > aspen spp. > red pine > white pine > yel-yellow birch. For sites where a cohort of these species was not present and there was only weak evidence of recent past fires, we sampled for the oldest living tree to ascertain an estimate of minimum TSF.

The increment cores and disks were mounted, dried and sanded with progressively finer sandpaper. Sample age was then determined by counting annual rings using a dissection stereomicroscope (on two radii for the disks). For cores where the pith was not traversed, we used pith locators to estimate the missing years based on ring curvature and growth rate (Applequist, 1958). Visual cross-dating using diagnostic rings (i.e., narrow, light, and frost rings) was performed across cores and disks of the same species to confirm age determinations (Yamaguchi, 1991).

For dendrochronological sites, a TSF estimate was determined using a sliding temporal window to detect a cohort containing at least 60% of the sampled trees that established within the same 30-year period. In these cases, the TSF estimate corresponded to the age of the oldest tree in the cohort. When such a cohort was not present, a minimum TSF was assigned to the site according to the establishment date of the oldest sampled tree (Bergeron and Dubuc, 1989; Johnson and Gutsell, 1994). Minimum TSF estimates consider that the last fire burned some time before the establishment date of the present stand; they are deemed censored in further survival analyses (see Statistical analyses for details) (Allison, 1995).

Several sites ($n = 14$) that fell within the fire boundaries of the initial TSF map were assigned the same TSF estimated from other examined sites within the same fire. Nine other sites located outside the fires mapped from 1930 air photos that proved inaccessible in the field were assigned a censored, minimum TSF corresponding to 1900; this was done to complete aerial coverage of the study area. An estimate of fire date was possible for 49 (38%) sites, whereas the remaining 80 (62%) sites provided censored, minimum TSF estimates. Due to the lack of precision in estimating fire date, data in the stand-age distribution are presented in bi-decadal age classes. This method does not have the resolution necessary to detect small or low-severity fires that did not initiate succession.

2.3. Statistical analyses

2.3.1. Fire cycle

To estimate the fire cycle, we used established fire frequency methods in combination with survival statistics (Johnson and Gutsell, 1994; Bergeron et al., 2004b). This involved fitting the following negative exponential model of survivorship to TSF estimates ($n = 129$):

$$A(t) = \exp\left[-\left(\frac{t}{b}\right)^{c}\right] \quad (1)$$

where $A(t)$ is the cumulative proportion of the landscape surviving longer than time t; b, the scale parameter, is an estimate of the fire cycle; and, c, the shape parameter, is equal to one. The key assumption of the negative exponential model is that the hazard of burning is constant with time, i.e. forest age does not influence the instantaneous probability of burning (Johnson and Gutsell, 1994). This assumption is supported by research showing most large and severe fires burn when fire weather is extreme (Stocks, 1991; Johnson et al., 1998); during such periods, fuel loads and stand age become less important than weather characteristics such as wind speed and direction in determining the size and severity of fires (Bessie and Johnson, 1995; Hély et al., 2001).

2.3.2. Survival statistics

We estimated the fire cycle using survival analysis by fitting our TSF estimates to the exponential model. We used the PROC LIFEREG procedure in SAS 8.2 (SAS Institute, 1999) to compare cumulative TSF distributions and assess whether the fire cycle varied as a function of spatial and temporal variables. For each model, a Lagrange multiplier χ^2 test determined whether its hazard function was constant over time. Another χ^2 test evaluated whether the fire cycle estimates of different groups (pine-dominated stands, surficial deposits, etc.) were significantly different (Allison, 1995).

To examine for temporal partitioning in fire cycle, we split the data set into different periods and calculated the fire cycle for each period. To study settlement effects, we partitioned the data set into three periods: pre-settlement (before 1880), settlement (1880–1924) and post-settlement (after 1924). A different analysis involved splitting the entire data set into two periods, before and after the end of the Little Ice Age (1850), to examine whether the fire cycle changed when a regional climatic shift impacted fire regimes throughout eastern Canada (Girardin et al., 2004; Bergeron et al., 2004b). For the post-settlement period, the portion of the study area that had burned before 1924 was considered censured at 79 years; for the settlement period, the portion that had burned before 1880 or after 1924 were censured; and for the pre-settlement period, the portion that had burned before 1880 was censured. A similar process was implemented relative to 1850. This process allowed inter-period comparisons by treating each period distinctly but simultaneously (cf. Bergeron et al., 2004b).

To understand whether spatial partitioning exists in how fire burns the Témiscamingue forest, we estimated the fire cycle for sites that differed in surficial deposits (glacial, fluvioglacial or other), canopy species dominance (pine species or other), and ecological type. Ecological type is a site-scale category of ecosystem classification determined by a combination of potential vegetation and local physical characteristics such as topographic position, drainage and surface deposit (Gosselin, 2002). We examined the following ecological types:

- Sugar maple–yellow birch on shallow to deep deposits of moderate texture and mesic drainage (FE32, $n = 32$)
- Yellow birch–balsam fir–sugar maple on very shallow to deep deposits of varied texture and xeric to hydric drainage (MJ1, $n = 52$).
- Balsam fir–yellow birch on shallow to deep deposits, of moderate to coarse texture and xeric to subhydric drainage (MJ2, $n = 25$).
- Pine or balsam fir on very shallow to deep deposits of varied texture and xeric to subhydric drainage (RP1, $n = 20$).

2.3.3. Canopy species composition

Two analyses were performed to examine variation of species composition in the canopy: K-means partitioning, a non-hierarchical, iterative clustering method based on a least-squares partitioning technique (MacQueen, 1967; Legendre and Legendre, 1998), followed by Correspondence Analysis (CA), an indirect, unimodal ordination method that preserves the χ^2 distance between objects (Legendre and Legendre, 1998). We first performed the K-means technique (1000 permutations; 2–10 groups) to examine how the sites we field sampled cluster according to canopy species composition ($n = 106$). With a CA, we then characterized how variation in species composition is partitioned at the different sites. To circumvent the double-zero problem inherent to species abundance or presence/absence data, i.e. non-sensical interpretation of the absence of species from two different sites (Legendre and Legendre, 1998), we first calculated an asymmetrical similarity coefficient among the sites. We then calculated a distance coefficient, ran a Principal Coordinate Analysis and finally the K-means procedure on the table of principal coordinates (Legendre and Legendre, 1998). These analyses were performed using Progiciel R (Casgrain and Legendre, 2001).

2.3.4. Canopy species composition, TSF, and environmental and site history variables

We examined the relative role of TSF in explaining variation in canopy species composition with a ReDundancy Analysis (RDA). RDA is a multivariate ordination technique that allows the simultaneous comparison of a matrix of response variables (**Y**) and of a matrix of explanatory variables (**X**) while structuring of information by separating systematic variation from variation that is not important (ter Braak and Verdonschot, 1995). CANOCO – the program used to perform the canonical analyses – allows the user to determine the importance of individual environmental variables in explaining the variance in **Y** through the use of forward selection of variables (ter Braak and Smilauer, 1998). During the selection process, we used CANOCO to test statistical significance by 1000 Monte Carlo random permutations using the full model with all variables. Since rare species can greatly influence the results of RDA (Legendre and Gallagher, 2001), we excluded species present at five sample sites or less.

The matrix of explanatory variables contained six environmental and two site history variables. The environmental variables were: percent slope, aspect, elevation, surficial deposit type, latitude, and longitude. We coded aspect as a semi-quantitative variable by using two variables that calculate the cosine and sine values for each of eight cardinal directions, thereby presenting aspect as a circular rather than linear variable (P. Legendre, Université de Montréal, *pers. comm.*). Elevation (meters above sea level), surficial deposit type (coarse fluvioglacial, fine fluvioglacial, glacial till, rocky glacial till, glaciolacustrine, rocky), and latitude and longitude (meters from origin of MTM 83 Zone 10 mapping projection) were obtained from the 1996 provincial digital forest inventory (Ministère des ressources naturelles et de la faune du Québec, 2004).

The examined site history variables were TSF and harvesting history. TSF is a quantitative variable measured, as described above, in years before 2004. Harvesting history is a semi-quantitative variable reflecting the frequency of partial cuttings, determined from provincial harvesting records corroborated with field observations. Since 1970, harvesting in the deciduous stands of Témiscamingue has been principally single-tree and group selection or diameter-limit cut. Previous to 1970, logging consisted principally of selective cutting of yellow birch and dominant conifers such as white pine, red pine and white spruce (Vincent, 1995).

We conducted a Hellinger transformation on the species data to deal with the double-zero problem mentioned above (Legendre and Legendre, 1998; Legendre and Gallagher, 2001). The environmental variables were standardized automatically by CANOCO (ter Braak and Smilauer, 1998) to remove the scale effects of the physical dimensions of variables and thereby allow comparisons of the regression coefficients with each other (Legendre and Legendre, 1998). Significance was set at p-value ≤ 0.05.

3. Results

3.1. Fire history reconstruction

The TSF map shows that, within the recent past, large severe fires represent only a fraction of the total area, roughly 20% (Fig. 1). No large fires (>200 ha) were detected since the mid-1920s, with the exception of a 384-ha fire in 1972 that burned in the northwest section of the landscape (Fig. 1). Most of the fires (18,504 ha in total) occurred between 1870 and 1890. The largest fire (11,035 ha), in the northeast of the study area, was contiguous with a much larger fire dated to 1921 (Grenier et al., 2005). This pattern was reflected in the forest age distribution, which shows a peak of stand initiation beginning about 1880 (Fig. 2a).

This paucity of large severe fire was corroborated by the cumulative TSF distribution (Fig. 2b). The survival probability was very close to 100% for the first 76 years and only decreased to 58% by the end of the 413-year period of study, meaning the majority of the landscape remained unburned by large severe fires. The rate of burning, as indicated by the slope of the fitted line, was low up to 150 year ago, increased at the turn of the century, and decreased to its very low level at present from

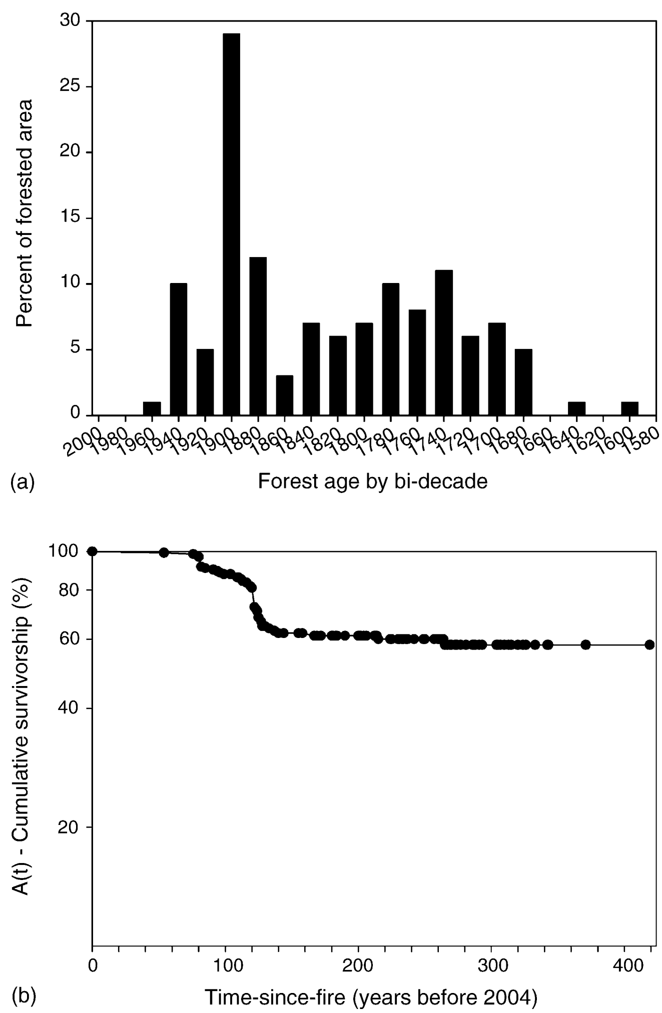

Fig. 2. (a) Forest age distribution and (b) cumulative survivorship distribution for southern Témiscamingue, QC.

Table 1
Temporal partitioning of fire cycle in relation to European settlement and the Little Ice Age in Témiscamingue, QC

Period	n	Number of detected fires	Fire cycle[a] (years)	Survival analysis ($p > \chi^2$)	Lagrange statistic ($p > \chi^2$)
Overall (1591–2004)	129	49	494 (373–694)	<0.001	<0.001
Pre-settlement (<1880)	83	13	909 (489–1690)	<0.001	0.020
Settlement (1880–1924)	127	33	153 (108–218)	<0.001	0.624
Post-settlement (>1924)	129	2	5081 (3593–20318)	<0.001	n\a
Little Ice Age (<1850)	71	3	2322 (748–7199)	0.013	0.9491
Post-Little Ice Age (>1850)	129	46	375 (281–501)	0.013	n\a

[a] Lower and upper 95% CI in parentheses.

approximately 1928–1950. Overall, the fire cycle estimated by the negative exponential distribution was 494 years (95% CI: 373–694) (Table 1). The mean TSF, an estimate biased downwards by censored data, was 213 ± 8 years ($\pm$S.E.).

Most of the fires detected and dated coincided with the settlement period in Témiscamingue. Two sharp breaks evident in the cumulative TSF distribution indicated a sudden drop in survivorship, one beginning in 1922 (TSF = 82 years before 2004) and the other in 1884 (TSF = 120 years) (Fig. 2b). Partitioning the temporal record into three periods (pre-settlement, settlement, and post-settlement) indicated a long pre-settlement fire cycle, an elevated fire cycle during settlement, and then a return to a long fire cycle since the mid-1920s (Table 1). A similar partitioning relative to the end of the Little Ice Age indicated a longer fire cycle before 1850 than afterwards (Table 1).

In terms of spatial partitioning, the fire cycle was shorter on pine-dominated sites than sites dominated by other species (Table 2). Moreover, the fire cycle was shorter on sites with surficial deposits of fluvioglacial origin than on sites with glacial deposits. In terms of ecological type, sugar maple-dominated stands (FE32) showed the longest fire cycle, pine and balsam fir-dominated sites (RP2) showed the shortest fire cycle while yellow birch–balsam fir stands (MJ1, MJ2) were intermediate (Table 2).

3.2. TSF and canopy species composition

At least two distinct assemblages of canopy tree species are present in this landscape. The best partition detected by K-means clustering, in the least squares sense, was for two types of sites. This partitioning had the highest Calinski–Harabasz pseudo-F-statistic (Calinski and Harabasz, 1974; Casgrain and Legendre, 2001). As indicated in the CA ordination by the position of various species along the abscissa (canonical axis 1), canopy species composition varies primarily between sites composed of late-seral, shade-tolerant, thin-barked and fire-avoiding species (i.e. sugar maple, yellow birch, American beech (*Fagus grandifolia* Ehrh.), eastern hemlock, eastern white cedar) versus sites composed of early-seral, fire-adapted species (i.e. red pine, white birch, trembling aspen, large tooth aspen) on the other (Fig. 3).

The environmental and site history variables significantly explained about 35% of the variation in canopy species composition (Trace = 0.347, F-ratio = 3.810, p-value = 0.001). The first two canonical axes (the abscissa and ordinate on Fig. 4) captured 79% of the cumulative percent variance of the species–environment relationship. In terms of specific environmental and site history variables, TSF explained the largest amount of the variation in species composition of the canopy (Table 3). Several other environmental variables also

Table 2
Spatial partitioning of fire cycle in relation to pine canopy dominance, surficial deposits and ecological type in Témiscamingue, QC

Strata	n	Number of detected fires	Strata effects ($p > \chi^2$)	Fire cycle[a] (years)	Survival analysis ($p > \chi^2$)	Lagrange statistic ($p > \chi^2$)
Canopy dominance						
Pine spp.	18	15	<0.001	165 (100–274)	<0.001	<0.001
Other spp.	111	34		640 (210–1948)	<0.001	
Surficial deposits						
Fluvioglacial	14	4	0.018	216 (48–965)	0.114	<0.001
Glacial	90	29		610 (160–815)	0.368	
Other	25	16		438 (236–815)	<0.001	
Ecological type[b]						
FE32	32	4	0.004	918 (292–2887)	<0.001	<0.0001
MJ1	52	20		362 (156–836)	0.066	
MJ2	25	13		259 (108–621)	0.683	
RP1	20	12		233 (161–336)	<0.001	

[a] Lower and upper 95% CI in parentheses.
[b] See Section 2 for descriptions of ecological types.

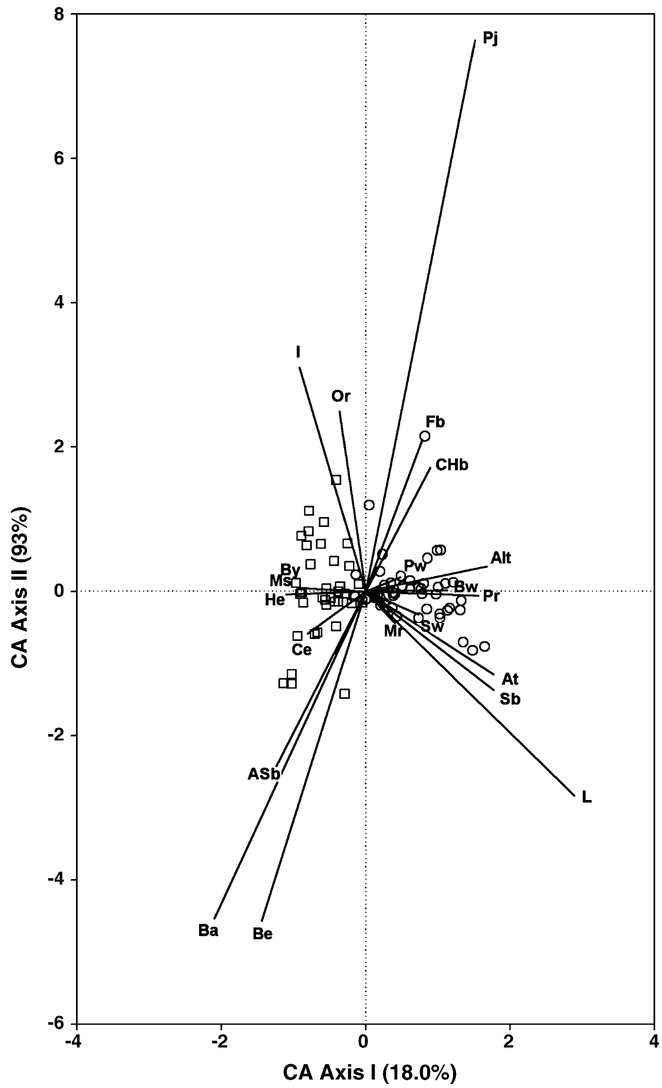

Fig. 3. K-means clustering and correspondence analysis (CA) according to canopy species composition ($n = 106$). Type 1 scaling type was used to illustrate the differences among sites. The circles and squares denote the two site types detected by K-means. Species codes are: ASb, black ash (*Fraxinus nigra*); Ba, basswood (*Tilia americana*); Be, American beech (*Fagus grandifolia*); Bw, white birch (*Betula papyrifera*); By, yellow birch (*Betula alleghaniensis*); CHb, black cherry (*Prunus serotina*); Ce, eastern whitecedar. (*Thuja occidentalis*); Fb, Balsam fir (*Abies balsamea*); He, eastern hemlock (*Tsuga canadensis*); I, ironwood (*Ostrya virginiana*); L, tamarack (*Larix laricina*); Ms, sugar maple (*Acer saccharum*); Mr, red maple (*Acer rubrum*); Or, red oak (*Quercus rubra*); Alt, large tooth aspen (*Populus grandidentata*); Pj, jack pine (*Pinus banksiana*); Pr, red pine (*Pinus resinosa*); At, trembling aspen (*Populus tremuloides*); Pw, eastern white pine (*Pinus strobus*); Sb, black spruce (*Picea mariana*); and Sw, white spruce (*Picea glauca*).

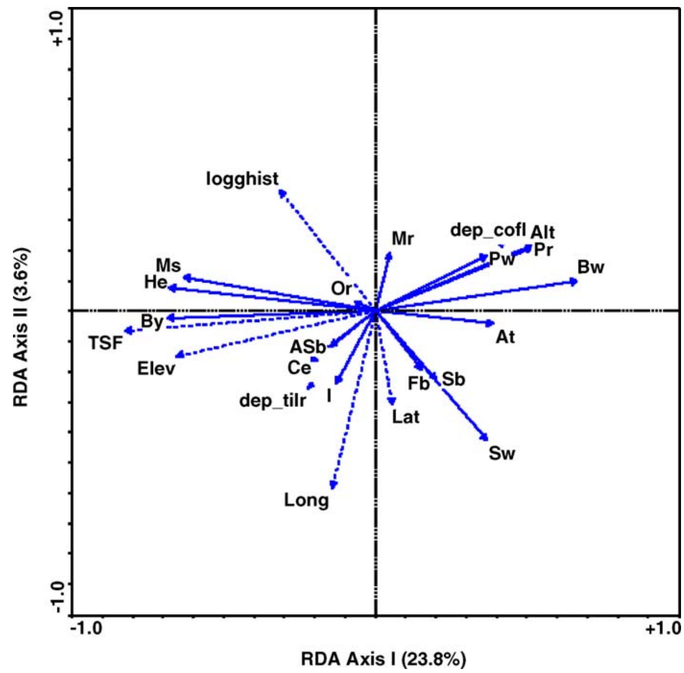

Fig. 4. Bi-plot of redundancy analysis (RDA) of canopy species composition ($n = 106$) with significant environmental and site history variables. Type 2 scaling was used to highlight differences among the species. The environmental and site history variables are elevation (Elev), longitude (Long), latitude (Lat), presence of coarse fluvioglacial deposits (dep_cofl), presence of undifferentiated rocky glacial tills (dep_tilr), time-since-fire (TSF) and logging history (logghist). Species codes as per Fig. 3.

Table 3
Results for redundancy analyses (with forward selection of variables) for significant environmental variables influencing canopy species composition in southern Témiscamingue, QC

Environmental variable	Variance explained	*F*-Ratio	*p*-Value
Time-since-fire (TSF)	0.17	20.95	0.0010
Elevation (Elev)	0.04	5.83	0.0010
Longitude (Long)	0.02	2.84	0.0080
Latitude (Lat)	0.02	2.29	0.0120
Coarse fluvioglacial deposits (dep_cofl)	0.02	3.36	0.0020
Logging history (logghist)	0.02	3.22	0.0030
Undifferentiated rocky glacial tills (dep_tilr)	0.01	1.85	0.0320

significantly explained smaller amounts of the variation in canopy species composition: elevation, longitude, latitude, logging history, presence of coarse fluvioglacial deposits (dep_cofl) and presence of undifferentiated rocky glacial tills (dep_tilr) (Table 3). Sugar maple, yellow birch and eastern hemlock are positively associated with sites of longer TSF and higher elevation, and, to a lesser extent, with finer textured, unsorted tills put in place without major intervention by glacial meltwaters (Fig. 4). In contrast, red and white pine, white birch and aspen species are positively associated short TSF, lower elevation and sandy to gravelly, coarse-textured, sorted, well-to excessively drained soils originating from glacial meltwaters (Fig. 4).

4. Discussion

4.1. Temporal trends in fire frequency

Our results provide evidence that in southern Témiscamingue, as in other areas of eastern Canada, European settlement during the latter half of the 19th century profoundly accelerated fire frequency. Fires originating from burning of logging slash, railroad sparks, land clearing and mineral prospecting created an era of elevated disturbance that affected hundreds of square kilometres in this landscape. It is, however, not possible to discern from our data whether the pronounced shortening of fire cycle was due to heightened human activity alone or some combination of human activity and climate, since settlement coincides with a period of frequent extreme fire weather and severe drought described for the boreal forest of western Québec (Bergeron and Archambault, 1993; Bergeron et al., 2004a; Girardin et al., 2004).

We found the fire cycle was shorter after the end of the Little Ice Age than before. This finding is inconsistent with other studies in western Québec indicating a lengthening of fire cycles since the onset of the wetter and warmer period following the Little Ice Age (Bergeron and Archambault, 1993; Bergeron et al., 2004a). This inconsistency may be due to settlement fires overwhelming the fire record and obscuring a climate effect. It is also plausible that a longer lag exists in deciduous-dominated landscapes, relative to the boreal, for the fire regime to reflect climatic changes. Since deciduous-dominated landscapes are less likely to burn (Hély et al., 2001, Cleland et al., 2004), the regime of large severe fire may depend on extreme weather conditions that occur relatively less frequently than those conducive to such fires in the boreal forest. If this is the case, then our temporal record may not be long enough to detect climate-induced changes in fire regime.

Since European settlement ended, the landscape has experienced a longer fire cycle. This elongation is possibly due to an improvement in the efficacy of fire suppression through improved road access, detection networks, and fire-fighting technology as well as a consequence of climate change since the end of the Little Ice Age, during which a gradual increase in average annual temperatures has meant an increase in summertime precipitation and lowered risk of catastrophic fire in the region (Bergeron and Archambault, 1993; Bergeron et al., 2001).

4.2. Hazard of burning

Our use of the negative exponential model to estimate fire cycle assumes a constant hazard of burning and that large severe fires burn irrespective of fuel conditions or stand age (Van Wagner, 1978). This assumption is not without debate in the fire ecology literature, where at least two hypotheses have been proposed to characterize how fires burn forests: the *weather hypothesis* (large severe fires are a function of extreme fire weather and burn irrespective of fuel conditions) and the *fuels hypothesis* (variation in fuel types affects fire spread or severity) (Cumming, 2001).

Evidence for the weather hypothesis includes work showing surface fire intensity and crown fire initiation are strongly related to fire weather and weakly related to fuel conditions (Bessie and Johnson, 1995; Johnson et al., 1998). Alternatively, several researchers report that the hazard of burning– as determined by ignition potential or fire spread – increases with stand age, distance to natural firebreaks such as lakes, and conifer dominance of stand composition in the boreal forest of Scandinavia and western North America (Schimmel and Granstrom, 1997; Cumming, 2001; Hellberg et al., 2004; Tanskanen et al., 2005); in other words, as assumed by the use of the Weibull function when estimating fire cycle (Johnson and Van Wagner, 1985). These Scandinavian and western North American forests experience surface fire dynamics that are strongly linked to changes in understory fuels—a phenomenon of reduced importance in crown fire-regulated boreal forests where the hazard of burning is less dependent on understory fuel dynamics (Johnson et al., 2001). In the northern hardwood forests of Témiscamingue, the hazard of burning on some sites may actually decrease with time as a shift occurs in the absence of fire from pine-dominated stands towards dominance of shade-tolerant, late-seral, and relatively less flammable hardwoods.

4.3. Canopy species composition, TSF, and environmental variables

Our results support the hypothesis that fire absence, as measured by TSF, is the most significant influence on the composition of dominant tree species in the mesic forests of Témiscamingue. TSF significantly explained the variation in canopy species composition that occurs as stands age and their early successional component changes to late seral species. TSF essentially tracks succession, with early seral species in sites with short TSF and late seral species in sites with long TSF (Fig. 3). This finding, in combination with the important part of the variation in composition remaining unexplained by redundancy analysis, alludes to the role of local, secondary natural disturbances in determining canopy species composition. Windthrow, low intensity surface fire, spruce budworm (*Choristoneura fumiferana* Clemens), white pine blister rust (*Cronartium ribicola* J.C. Fisch.), forest tent caterpillar (*Malacosoma disstria* Hubner) and other disturbances, acting singly or in combination, enhance compositional heterogeneity by providing opportunities for gap-phase establishment, growth and release of early seral species in old stands and vice versa (Runkle, 1982; Sousa, 1984; Canham, 1989).

Several studies (e.g. Frelich and Reich, 1995; Davis et al., 1998; Carleton, 2003) describe how the distribution of tree species in northern hardwood forest depends on time since catastrophic disturbance. For instance, red pine and white birch, in combination with shade intolerant hardwoods such as aspen are associated with short TSF, whereas eastern hemlock along with shade-tolerant hardwoods such as yellow birch and sugar maple are associated with long TSF. These assemblages, elucidated by the ordination and clustering procedure (Fig. 3), may represent different relationships between fire and vegetation. Fire both perpetuates and is perpetuated by species such as red pine and white birch. Alternatively, species associated with long TSF may persist because the probability of fire decreases dramatically once the transition to shade-tolerant species, in particular tolerant hardwoods, has occurred (Frelich, 2002).

Elevation also explained an important component of the variation in canopy species composition, as evidenced by its position along the primary axis in Fig. 4. Cold air ponding in the low-elevation valley bottoms of Témiscamingue can create relatively unfavourable conditions for hardwood species because of the impacts of more frequent freeze–thaw events on their growth (Burke et al., 1976; Brown, 1981). Therefore, coniferous species such as white spruce, balsam fir, and eastern white cedar that are better cold-adapted tend to occur at lower elevations while hardwoods typically dominate upper slopes and mesic ridges (Brown, 1981).

Latitude and longitude significantly explain a minor component of the variation in canopy species composition. In this transitional landscape, a north–south gradient exists from northerly coniferous boreal species adapted to cold temperatures, a short growing season, and frequent fire to southern deciduous species such as American beech, ironwood (*Ostrya virginiana* (Mill.) K. Koch), and American basswood (*Tilia americana* L.) that are favoured by longer growing seasons (Rowe, 1972; Currie and Paquin, 1987). The longitudinal gradient may reflect distributional variation of surficial deposits; fluvial scouring by the paleo, Ottawa River exposed large areas of bedrock and left in place expanses of glacial deposits with boulders in the west of the study area while relatively finer tills and organic deposits are more common in the east (Brown, 1981).

4.4. Fire frequency and the role of site variables and ecological types

We present evidence for spatial partitioning of fire frequency in this landscape according to surficial deposits, pine-dominance and ecological site type. Surficial deposits influenced both fire cycle and canopy species composition. These deposits affect the drainage and texture of the growing substrate and influence species composition by the total and seasonal availability of soil moisture and nutrients (Hack and Goodlett, 1960; Whitney, 1986). For example, coarse fluvioglacial deposits are positively associated with pines, white birch and aspen species (Fig. 4). Therefore, it seems pines, white birch and aspen species are associated with short TSF and fire cycle not only because these species are present on coarse deposits but also because they are abundant after fire on more intermediate sites where sugar maple will eventually dominate the old-growth stages.

Sites on fluvioglacial deposits, of the pine–fir ecological type or dominated by pine showed a shorter fire cycle than sites on undifferentiated glacial tills, of the maple–birch ecological type or dominated by species other than pine. Together, these findings illustrate the mutually-reinforcing and interdependent relationships between soils, tree cover and fire (Schulte et al., 2005). For example, finer-textured soils less prone to seasonal moisture deficits favor the development of fire-avoiding tolerant hardwoods whereas coarser, well-drained soils favor the development of pines and early seral hardwoods that depend on and propagate fire. These inter-relationships suggest that although TSF is an important determinant of stand composition, its role depends on the influence of physiographic setting on fire. In other words, it appears that at least two different fire frequencies exist as a function of physiography and that TSF has a different effect in each of two distinct successional pathways. Generally, a short fire cycle on coarse-deposit sites maintains pines and other fire-dependent species whereas fine-deposit sites more easily allow a long TSF and succession to shade-tolerant species of low flammability.

4.5. Logging history

The frequency of partial cutting is positively associated with the maple–birch–hemlock assemblage and negatively associated with relatively less merchantable, boreal conifers such as white spruce and balsam fir (Fig. 4). These results are consistent with several studies that indicate selective and partial cutting treatments in hardwood forests favour a preponderance of sugar maple and other shade-tolerant species (Schuler, 2004; Brisson et al., 1988; Bouchard et al., 1989; Smith and Miller, 1987). At the landscape scale, Jackson et al. (2000) documented an increase in abundance, as compared to pre-settlement composition, of sugar maple and its associates in the Great Lakes-St. Lawrence hardwood forests of central Ontario, attributing this trend to the historical dominance of partial cutting since the onset of commercial harvesting in this region. We therefore suggest partial logging advances succession and acts to ‘fire proof’ the landscape by promoting the development of deciduous assemblages at the expense of fire-adapted assemblages and, possibly, by removing structural features such as supra-overstory white pines that may attract lightning strikes. Moreover, pine removal by logging may entrain a shift in fire regime by altering the structural and compositional aspects of stands that are conducive to the frequent, low-intensity ground fires that maintain pine-dominated stands (Engstrom and Mann, 1991; Ryan, 2002).

Selective logging of pines and spruce may have removed evidence of fire on some sites. If these species previously had a wider distribution in this area, the fire cycle of southern Témiscamingue may have been shorter than our pre-settlement estimate of 909 years (Table 1). For example, Whitney (1986, 1987) reports that pure and mixed stands of pine covered 45% of the area in a pre-industrial northern Michigan landscape and had a cycle of 129–258 years for large severe fire, while the entire landscape had a fire cycle of 205–411 years. It seems unlikely that partial cutting affected the TSF estimates on sites where we relied on the oldest living tree; these silvicultural treatments, as implemented in Témiscamingue, often retain the full range of tree ages found before harvest.

5. Conclusion

Currently the landscape is experiencing a longer fire cycle relative to historical rates. The lack of fire may be diminishing the competitive advantage that pines and other fire-adapted species have over dominant deciduous trees; this diminution may be especially relevant in intermediate sites where the physiographic factors or microclimatic conditions do not overwhelmingly favour one suite of species over another and allow a wide variety of species assemblages. In other words, the fire-dependence of coarse-deposit sites dominated by pines, in combination with their high timber value, makes them more vulnerable to permanent change than sugar maple–yellow birch sites. Therefore, our prognosis for landscape development is for increasing dominance of fire-avoiding species and decreasing abundance of fire-maintained pine stands and their associated floral and faunal communities. Such a decrease in the abundance of white and red pine communities has already been documented throughout their range (Noss et al., 1995; Radeloff et al., 1999; Zhang et al., 1999; Thompson et al., 2006) and suggests these sites should be a conservation focus in maintaining the historical diversity of stand types.

The above prognosis has several management implications. Current harvesting regulations mandate the exclusive use of single-tree selection in the hardwood forests of Québec. Under a natural disturbance-based approach to forest management (Hunter, 1993; Bergeron et al., 1999), this silvicultural system is appropriate over most of the landscape given the dominance of late-seral stands and gap-phase dynamics in this forest type. However, large and severe fires were previously important disturbances in this landscape. We therefore recommend a diversification of forest practices to include some low to mid-retention silvicultural systems that resemble the size, pattern, frequency, and within-burn legacies of large severe fires, thereby more closely emulating the full range of natural disturbances. Moreover, these silvicultural systems are suitable for the regeneration of drought-tolerant species like red and white pine, red maple, and red oak and may enhance landscape resilience to possible increases in summertime drought resulting from climate change (Boer et al., 2000).

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