

Strong gradients in forest sensitivity to climate change revealed by dynamics of forest fire cycles in the post Little Ice Age era

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Abstract

The length of the fire cycle is a critical factor affecting the vegetation cover in boreal and temperate regions. However, its responses to climate change remain poorly understood. We re-analysed data from earlier studies of forest age structures at the landscape level, in order to map the evolution of regional fire cycles across Eastern North American boreal and temperate forests, following the termination of the Little Ice Age (LIA). We demonstrated a well-defined spatial pattern of post-LIA changes in the length of fire cycles towards lower fire activity during the 1800s and 1900s. The western section of Eastern North America (west of 77 °W) experienced a decline in fire activity as early as the first half of the 1800s. By contrast, the eastern section showed these declines as late as the early 1900s. During a regionally fire prone period of the 1910s-1920s, forests in the western section of Eastern boreal North America burned more than forests in the eastern section. The climate appeared to dominate over vegetation composition and human impacts in shaping the geographical pattern of the post-LIA change in fire activity. Changes in the atmospheric circulation patterns following the termination of the LIA, specifically changes in Arctic Oscillation and the strengthening of the Continental Polar Trough, were likely drivers of the regional fire dynamics.

Key points

1. The onset of longer fire cycles, following the cessation of the LIA, exhibited a strong spatial pattern over Eastern boreal and temperate North America.
2. Large-scale features of atmospheric circulation over the boreal forest influenced the spatial variability in fire activity.
3. Climate appeared to dominate over vegetation composition and human impacts in shaping the geographical pattern of the post-LIA change in fire activity.

Index terms

0426, 0439, 0468

Keywords

forest fires / natural disturbances / dendrochronology / climate forcing / boreal biome / forest resilience / regime shift / fire regimes

1. Introduction

Fire is one of the primary disturbance agents across the boreal and temperate biomes (Conard et al., 2002; Stocks et al., 2002; Flannigan et al., 2005). Therefore, understanding its spatiotemporal features is crucial for projecting future ecosystem dynamics. Climatically-induced changes in fire activity impact the functioning of the boreal ecosystem by affecting tree regeneration, growth conditions, forest composition and its successional pathways (Payette et al., 1989; Bergeron et al., 2004; Johnstone et al., 2010). Across boreal North America, fire activity increases towards the west, with an average fire returning interval decreasing from above 500 years in the North Shore region of Quebec (Bouchard et al., 2008) to 100-200 years in interior Alaska (Kasischke et al., 2010). Nevertheless, the regional impacts of fires can be significant already in Quebec with up to 2.1 million ha burning annually (Stocks et al., 2002).

In Eastern North America, the length of the fire cycle, which is the time required to burn the equivalent of a specified area, has been shown to have an important control on regional vegetation cover dynamics. The fire cycle shapes the northern distribution limits of canopy dominants (Senici et al., 2013) and defines successional pathways (McIntire et al., 2005).

Ultimately, fire cycle variability controls the transitions between temperate and boreal forests (Bergeron et al., 2004) and from closed to open canopy boreal forests (Blarquez et al. 2015; Gauthier et al. 2015). At the regional level, fire dynamics interacts and possibly overrides the direct effects of climate on forest vegetation (Drobyshev et al., 2014b; Zhang et al., 2015). Similarly, paleochronological evidence has pointed to a correlation between fire-conducive weather and regional species abundance. For example, a higher abundance of white cedar (*Thuja occidentalis* L.) and a lower abundance of serotinous jack pine (*Pinus banksiana* Lamb) has been noted in boreal South-Eastern North America around 6000 BP, which was a wetter and warmer Holocene period with reduced fire activity (Carcaillet et al., 2010).

Synoptic-scale atmospheric circulation anomalies define the geographical and temporal extent of fire-conducive periods (Schroeder, 1964; Skinner et al., 2002; Fauria and Johnson, 2008). High-pressure anomalies during the fire season promote the drying of forest fuels and increase fire hazards and annually burned areas. By contrast, low-pressure air masses bring precipitation and decrease fire activity (Skinner et al., 1999). It is becoming evident that the global climate system exerts a significant influence on fire activity in Canada through its effect on regional atmospheric circulation. In eastern Canada, positive phases of Arctic Oscillation (AO) are associated with summer ridging and eastward shifts of the Canadian Polar Trough (CPT) (Skinner et al., 1999; Skinner et al., 2002), leading to an increase in burned areas (Fauria and Johnson, 2006). Furthermore, the atmospheric response to sea surface temperature anomalies in the equatorial Pacific ultimately affects the large-scale atmospheric circulation over lands and fire weather and climate conditions across Canada (Skinner et al., 2006).

There is a general consensus that human-caused global warming will lead to an increase in fire activity during the 21st century in boreal Canada (Flannigan et al., 2009; Bergeron et al., 2010; Boulanger et al., 2013). However, considerable uncertainty remains concerning both the scale and the geographical pattern of the historical and future fire dynamics in this biome. Temporal trends in fire activity vary among different sections of the boreal domain as well as along the latitudinal gradient covered by this biome (Girardin et al., 2013; Drobyshev et al., 2014a). Dendrochronological drought reconstructions have suggested high variability in the year-to-year and decade-to-decade drought severity across the boreal forest of eastern to central Canada (Girardin et al., 2006a). For example, although multi-year droughts have always covered vast land areas, prolonged drought conditions have been virtually absent in eastern Canada since the 1850s (except during the 1910-1920s, Girardin et al., 2006a). It has been suggested that increasing cyclonic activity (deeper troughing) in eastern Canada and the incursion of moist air masses may have favoured climate conditions that were less suitable to fires (Girardin et al., 2006a).

To better understand past and future impacts of climate change on regional forest fire regimes we studied the response of fire cycles, a spatial metric of forest fire regimes, to climate forcing across boreal and temperate biomes of Eastern North America over decadal and century long time scales. We put forward the following hypotheses: (1) there is a detectable spatial pattern in the onset of longer fire cycles over Eastern North America in the post-LIA era; (2) the sensitivity of fire cycles to climatic forcing positively correlates with climate continentality, reflecting generally higher drought levels under a more continental climate, and (3) the geographical pattern of changes in fire cycles over Eastern North America reflects changes in the location of the dominant upper atmosphere pattern across the Canadian boreal forest during the summer months. We tested the first and the second hypotheses by re-analysing and mapping results from stand initiation studies that are available for Eastern

North America. For the second hypothesis, we also evaluated the amount of area disturbed during 1910s-1920s, a regionally fire-prone period, across the climate continentality gradient in our study region. To provide an independent line of evidence for the spatial pattern in climate change during the fire season, we analysed growth synchronicity across a network of tree-ring chronologies independently sampled across latitudinal and longitudinal gradients in Quebec. The comparison of these chronologies was assumed to provide the means to evaluate climate homogeneity within our study region. Finally, we tested the third hypothesis by comparing the geographical pattern of modern fire activity with the indices of atmospheric circulation, focusing primarily on the Arctic Oscillation (AO) index. AO provides a measure of the jet stream southwards migration and, at the same time, the degree of meridional vs. zonal flow across Canada (Ambaum et al., 2001). Since both of these elements demonstrated considerable post-LIA dynamics, we related them in a spatially-explicit way to the pattern of modern fire activity.

2. Methods

2.1. Study area

We re-analysed stand initiation maps that were developed for the region of Eastern North America, within 47.37 - 50.29°N and 79.53 - 65.79°W (SI Table 1, Fig. 1). This region covers a range of biogeographical zones, stretching from spruce-lichen domain in the north down to the sugar maple - yellow birch domain in the south (Saucier et al., 2003). Although the current fire activity is currently much higher in the northern and western sections of the study area (Le Goff et al., 2008), fire has been shown to be a crucial and temporally varying factor of forest dynamics over the entire study area during the Holocene period (Blarquez et

al., 2015), which warranted the inclusion in the analysis of the areas outside of the boreal domain.

2.2. Analysis of stand initiation maps

Stand age structure within a landscape is assumed to result from periodic stand replacing disturbances, serving as a quantitative proxy of historic disturbance rates (Van Wagner, 1978).

The analysis of stand initiation maps seems particularly suited for the boreal Eastern North America, where fire history reconstructions at annual resolution is a challenging task, due to the stand-replacing nature of fire events (Brassard and Chen, 2006; Belisle et al., 2011). This leaves few surviving trees whose fire scar records could extend over several centuries.

Independently reconstructed forest age structures at the landscape scale, have previously been used to evaluate fire activity changes in Eastern North America, following the termination of the Little Ice Age (LIA) (Bergeron and Archambault, 1993; Bergeron et al., 2001; Girardin et al., 2013).

The stand initiation map represents an outcome of dendrochronological dating of cohort establishment dates over an area considerably exceeding the size of single disturbance events ($> 10^{3-4}$ ha and above) (Van Wagner, 1978; Cyr et al., 2016). The resulting stand age distribution can be viewed as a distribution of time passed since the last stand replacing fire.

The parameters of these time-since-fire distributions are obtained by fitting them to Weibull or negative exponential functions (Heinselman, 1973; Johnson and Gutsell, 1994). The conversion of age data into a metric of fire activity is based on the concept of fire cycle (FC).

This is a spatially-explicit parameter of fire regime, which is the time required to burn the area the size of the studied landscape (Johnson and Gutsell, 1994). FC is defined as

$$FC = \int_0^{\infty} A(t)dt \quad (1)$$

where $A(t)$ is the cumulative time-since-fire distribution. Since these distributions typically cover several centuries, it is logical to assume its multi-modal nature, i.e. the initial distributions are a mixture of more than one homogenous distribution with their own parameters:

$$A(t) = p_1 A_1(t) + \dots + p_i A_i(t) \quad (2)$$

Where p_i is the proportion of the i distribution in the initial distribution.

To define parameters of the stand age distributions within each study area, we relied on an over-dispersed survival model, i.e. a model with variability exceeding the one predicted from a given statistical model. To account for the spatial nature of fire activity (the so-called contagion effect), we used a model based quasi likelihood (Q) (Reed et al., 1998):

$$Q = \frac{1}{\sigma^2} \sum_{j=1}^m y_j \log(\theta_j) \quad (3)$$

where σ is the over-dispersion parameter, m is the number of time-since-fire classes, θ is the probability of the spatial unit belonging to class j , and y_j is the proportional area in class j , calculated as

$$y_j = \frac{A_j}{\sum_{j=1}^m A_j} \quad (4)$$

To test for the changes in fire cycles within each study area, we analysed the complete set of possible combinations of the change points by calculating Bayes Information Criterion (BIC) operating on the complete set of possible combinations of break points. Following the logic presented in (Reed, 2001), we considered up to six potential break points for each landscape.

Computationally, BIC is presented as

$$BIC \approx \hat{D} - (m - 2r - 2) \log \left(\frac{\sum_{j=1}^{m-1} s_{j-1}}{\hat{\sigma}^2} \right), \quad (5)$$

where \hat{D} is the minimum scaled quasi deviance for a given model and $\hat{\sigma}^2$ is the Pearson estimate of the over-dispersion parameter (Reed 2000). In contrast to the original protocol (Reed 2000), we did not supply the algorithm with a list of a priori selected locations of the breakpoints. Instead, we considered all possible combinations with $n \leq 6$. The rationale for this decision was based on the hypothesized dependency of the onsets of longer fire cycles on the geographical position of a studied area. Testing a hypothesis with a predefined set of breakpoints would then necessitate multiple and site-specific assumptions on the location of breakpoints, which would compromise its objective testing.

We compiled a database of areas with forest age structures reconstructed at the landscape scale (10^3 - 10^4 km², SI Table 1, Fig. 1). For the analysis of onsets of fire cycle changes, we only selected studies that provided data for the period starting in 1780 AD or earlier. The purpose of this cut-off, which resulted in the exclusion of one site (LAV, SI Table 1), was to only consider sites with the coverage extending into the Little Ice Age period. To test the presence of spatial patterns over the period with instrumental observations, we considered the 1910s-1920s, a regionally fire prone period in Eastern North America (Lefort et al., 2003; Drobyshev et al., 2012; Vijayakumar et al., 2015). For this analysis, we added an earlier excluded site (LAV) whose cohort age data only extended back to 1810 AD. The size of single inventoried landscapes ranged from $1.8 \cdot 10^3$ to $14.1 \cdot 10^3$ km² (SI Table 1). We characterized the age structure of each landscape using 20-year intervals, which reflected the temporal resolution of the largest of the time units (10 or 20 years) used in the initial age reconstructions. For the sensitivity tests of the size of the time frames we refer to SI Fig. 3. It is important to note that analyses based on stand initiation maps assume: (a) a certain skill in

locating the oldest tree within the defined, typically randomly sampled spatial unit, and (b) the interpretation of that date as the origin date for the whole spatial unit. Both assumptions introduce uncertainty into the estimation of historical disturbance rates. It makes this method less precise than analyses that are based on observational records or networks of sites with fire scar dates.

We were aware of the possibility of a bias associated with the censored observations in the oldest period of the landscape age structure. The potential bias is a product of the accumulation of censored observations in the oldest classes. It would lead to a decrease in the fire cycle early in the period that is covered by the landscape age structure. We did not have access to initial raw data to circumvent the problem, using survivorship analysis (Cox, 1972). To assess the potential bias associated with censored observations, we analysed the timing of the onset of the fire cycle change in relation to the oldest age class in studied landscapes. We also studied the relationship between the age of the oldest classes and the landscape geographical position to evaluate any potential bias due to differences in maximum age classes across the study region.

2.3. Analysis of growth synchronicity in tree-ring chronologies

The analysis of teleconnections (spatial synchronicity) among tree ring-width chronologies, provided an independent line of evidence to verify the homogeneity of the summer climate in the studied region. Anticipating the presence of both latitudinal and longitudinal gradients in the offset of longer fire cycles, we used a network of chronologies developed along these gradients (Ols et al., 2016) to evaluate the temporal dynamics of the teleconnections in growth. We assumed that high levels of correlations among sites along the gradient would be indicative of the annual synchronicity in the regional climate conditions, which would, in turn,

point to the similarity in the origin of air masses dominating the studied locations. By contrast, the lack of teleconnections would suggest a climatic non-homogeneity, i.e. the presence of different climate systems resulting in the lack of region-wide growth synchronicity. The idea behind this assumption has been used extensively in dendrochronological research, especially for development of continent-wide drought reconstructions (Cook et al., 2007; Li et al., 2014; Cook et al., 2016).

To test for the temporal variability in the growth synchronicity, we used a network of black spruce (*Picea mariana*) chronologies, each representing trees from 4 to 10 sites and stretching from 53 to 49.5 ° N and from 77.50 to 72 °W (Fig. 1) (Ols et al., 2016). To study the temporal variability in the growth synchronicity along the latitude, we aggregated the data over five of the most northern and southern sites on the western transect to produce North and a South chronologies (n = 56 and 46 trees, respectively). For the longitudinal gradient, we used the eastern chronology and southern half of the western chronology (n = 147 and 74 trees, respectively). All sites were located in the spruce - moss forest bioclimatic domain.

The dataset represented dominant and healthy looking trees growing in unmanaged old black spruce forests (>100 years) on well-drained soils (Ols et al., 2016). We were aware that pine chronologies are generally superior to spruce chronologies in capturing fire-related climate signals. However, in the studied region, the availability of long pine chronologies was limited. The primary reasons for this were the forest use history in the south and a short fire cycle in the north. Both of these factors removed older trees from the landscape, and resulted in the increasingly rare occurrence of pine stands towards the eastern section of the study area.

Initial tree-ring chronologies were detrended with a spline function with a 50% frequency cut-off at 24 years. To remove temporal autocorrelation in growth patterns, each tree-ring curve was modelled as an autoregressive process with the order selected by the first-

minimum Akaike Information Criterion (Akaike, 1974). Both treatments enhanced the high-frequency variability in the records.

For each analysis, we ran correlations between a focal chronology, the most northerly located chronology in the latitudinal analysis and the most easterly located chronology in the longitudinal analysis, and two other chronologies (the southern and western chronologies, respectively) using a partly overlapping 20-year moving window with 10-year shifts. The significance of correlation coefficients was assessed through bootstrapping ($n = 1000$). Based on data availability, we limited the analysed period in the latitudinal transect to between 1830 and 2006.

To further evaluate the influence of large-scale atmospheric patterns on fire activity, we used modern fire statistics to obtain the area burned in Canada within 80° and 70° W between 1972 and 2013. This is the period with the most reliable fire data in Quebec province (<http://cwfis.cfs.nrcan.gc.ca/ha/nfdb>). We examined the relationship between fire activity and the main indices of atmospheric circulation: Arctic Oscillation (AO), North-Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO), Atlantic Meridional Oscillation (AMO), and Southern Oscillation index (SOI). The indices were extracted from the Climate Prediction Centre database (National Oceanic and Atmospheric Administration (NOAA), 2016). For AO, we also compared the spatial distribution of burned areas along a latitudinal gradient during the five years with the highest and lowest values of AO indices. Areas burned during these years were binned into 0.25° latitudinal degree intervals. The resulting distributions were compared by a two-sided Wilcoxon rank sum test. For all indices, we also ran superimposed epoch analyses with the five most fire-prone years identified for each $3 \times 3^{\circ}$ grid cell over the 1972-2013 period.

3. Results

3.1. Forest fire cycles in post-Little Ice Age era

The analysis of forest age distribution revealed a strong and region-wide increase in the length of fire cycles, reflecting a decline in fire activity from the early 1800s through the present day (Fig. 1B). The only exception from this pattern was site WAS, where the length of the fire cycle first increased from 100 years (prior to 1940) to 1165 (during 1940-1980) and then decreased again to 100 years during the 1980-2000 period. Analyses of the onset of longer fire cycles identified two periods: one in the late 1700s-early 1800s, and another at the turn of the 20th century. Five out of the 12 sites (38%) had more than one change in fire cycle, and one site did not present any change in fire cycle (CLS). The first change correlated with the sites' latitude and longitude (Fig. 1C-E). The linear regression was significant between latitude and time, at $p = 0.025$ ($R^2 = 42.2\%$), and marginally non-significant between longitude and time, at $p=0.085$ ($R^2 = 24.0\%$).

Two lines of evidence suggested that possible bias related to censored observations of the oldest age classes can be ignored in our case. First, the changes in fire cycles, identified within single landscapes, were "located" between 50 and 270 years (average 181 years) from the start of the record. This is at least four 10-year classes and, on average, 18 10-year classes from the start of the record. Second, the analyses revealed no trend in the start of the landscape-specific records (age structures) along latitudinal-longitudinal gradients (SI Fig. 1), which could potentially contribute to the creation of a geographical pattern in fire cycle changes. Both observations indicated that the geographical trends in fire activity were unlikely to be a result of methodological biases.

The 1910 and 1920 decades were a fire prone period in Eastern North America, with the proportion of landscapes originating at that time ranging from 3 to 30% (Fig. 1F and

references in the SI Table 1). The highest proportion was observed in the south-western section of the study area, while the relatively less affected landscapes tended to be located in the north-eastern section. Regression analysis between that proportion and the landscape geographical location, showed significance of longitudinal gradient ($p = 0.019$, $R^2 = 44.1\%$), but not of latitudinal gradient ($p = 0.993$, $R^2 < 1.0\%$).

3.2. Gradients in forest sensitivity to climate change

Tree growth across geographical gradients in the study area revealed a generally high degree of synchronicity ($r \sim 0.4-0.8$), which was interrupted between 1850-1910 and 1870-1890 for the latitudinal and longitudinal gradients, respectively (Fig. 3A and SI Fig. 3). During these periods, the correlation between chronologies representing the respective geographical gradient became insignificant. For the latitudinal transect, this desynchronicity immediately preceded the fire prone 1910s-1920s period (Fig. 1). The analyzed tree ring chronologies tended to correlate with AO dynamics, supporting their use as another proxy for synchronicity in fire weather in the study region (see the end of this section). In particular, both the northern and southern chronologies significantly correlated with spring-summer AO (Pearson $r = -0.31$ and -0.29 , $p = 0.023$ and 0.017 , respectively). The western and eastern chronologies correlated with AO at $r = -0.23$ and -0.25 ($p = 0.074$ and 0.057 , respectively). Furthermore, direct correlation of tree-ring chronologies with modern fire activity, as revealed by superimposed epoch analysis (SI Fig. 2), indicated that these chronologies contained signals representing conditions conducive to regional fire activity. Specifically, spruce growth tended to be significantly lower during the five largest fire years estimated for each cell.

Comparison of spatial patterns of fire activity between years with the highest and the lowest AO indices, revealed a migration of the region with the highest fire activity along the latitudinal gradient between years with contrasting AO conditions (Fig. 4). During the years

with the highest AO index values, which is indicative of a more northerly location of the polar vortex and a stronger polar low, fire activity was concentrated around 50 and 53° N. In contrast, during the years of the lowest AO values (corresponding to the expansion of the polar vortex southwards), the zone with the most fire activity was centred between 48 and 58° N, shifting towards lower latitudes. Differences in distributions between these two groups of years, tested by the two-sided Wilcoxon rank sum test were significant at $p < 0.001$.

Superimposed epoch analyses done on the five most fire-prone years identified for each 3° x 3° grid cell, revealed an association between these years and positive phases of AO (Fig. 3D) and NAO (SI Fig. 4). The area of statistically significant effects was concentrated in the western section of the study region. PDO dynamics showed a similar but largely non-significant effect of the same sign (SI Fig. 4). For AMO and SOI, we did not observe a significant pattern, except for one grid cell in eastern Quebec (SI Fig. 4).

4. Discussion

In this study, we provided the first spatially explicit and cohort based reconstruction of changes in forest fire cycles in boreal and temperate Eastern North America, following the cessation of the LIA. By revealing a well-defined region-wide trend towards longer fire cycles during the 1800s and 1900s, we demonstrated differences in boreal forest sensitivity to historical climate changes. We argue that the large-scale features of atmospheric circulation over the Eastern Canadian boreal and temperate forest, and particularly the Canadian Polar Trough, influenced the long-term variability in fire cycles. Assuming the temporal consistency of these features over century-long periods, we propose that they will likely shape the pattern of forest response to future environmental variability.

4.1. Geographical pattern in fire cycle changes

The onset of a longer fire cycle, following the cessation of the LIA, exhibited a strong spatial pattern in boreal Eastern North America. In particular, the western section of the region (west of 77 °W) experienced a decline in fire activity as early as the first half of the 1800s, whereas the more easterly located sections showed changes in their fire cycles as late as in the early 1900s (Fig. 3C). Climate has likely been the main driving force of this lengthening in the fire cycle (Parisien et al., 2016). We observed consistency between the onset of the decline in fire activity and tree growth synchronicity along both latitudinal and longitudinal gradients (Fig. 3A, B). We interpret the mid-1880s and late 1800s drop in growth synchronicity along latitudinal and longitudinal gradient, respectively (Fig. 3A, B), as an indication that during the late 1800s, the summer climate was dominated by warmer and wetter conditions in the south-western segment, while dryer and colder air masses likely prevailed in the north-east. The recovery of the growth synchronicity in the early 1900s, was likely associated with the summer climate becoming more homogenous and increasingly dominated by warmer and wetter air masses originating from the subtropical North Atlantic, while cold and dry polar air retreated northwards. The pattern of modern fire activity is consistent with this interpretation. During years of the highest AO, and therefore, strongest northward jet stream migration, the fire activity was more than one order of magnitude stronger and concentrated at higher latitudes, as compared to years with lowest AO values, i.e. years with a southerly displaced jet stream (Fig. 4).

Spatiotemporal changes in regional fire activity, and in particular, the temporal longitudinal gradient in the onset of the longer fire cycle, were likely modulated by one of the main zonal features of atmospheric circulation over the Canadian boreal forest, the CPT located around 72-67° W (Ahrens, 2003). The presence of CPT might have lowered the long-term variability in fire activity in the past, since it limited the inflow of dry Arctic air during periods of increased fire hazard (such as during the LIA). The strength of the CPT has been shown to be

strongly correlated with the temperatures of the Labrador Sea (Shabbar et al., 1997). This suggests that during cold periods, the strength of the CPT increased, making it an even more important mechanism counteracting the increase in fire activity during cold periods. Both the strength of the CPT and the position of the polar front may, therefore, control the regional fire hazard by influencing the frequency of periods with persistent high pressure systems (Fauria and Johnson, 2008). Therefore, the increase in the Labrador Sea temperatures as a result of global warming, may lead to the weakening of the CPT and make the regional fire activity more sensitive to climatic changes. The observed longitudinal gradient in the dynamics of the fire cycles across Ontario and Quebec boreal forests, is likely part of a larger zonal gradient in the variability of summer drought conditions, shown earlier for the Canadian boreal zone (Girardin et al 2006).

The 1910s-1920s period was a climatically fire-prone period in boreal Eastern North America (Lefort et al., 2003; Drobyshev et al., 2012; Vijayakumar et al., 2015) and the proportion of the forest area affected by fires during that period, could be viewed as another proxy of forest sensitivity to regionally fire-prone periods. Our data suggested a strong longitudinal gradient in fire impact during that period. In particular, the area in the section of the study region west of 72 °W was affected at least twice as much as the area east of that longitude (Fig. 1F). This pattern closely resembled the one of the onset towards generally longer fire cycles during the 1800s and 1900s (Fig. 1C). This implies that parts of the regions exhibiting delays in fire cycle change were also less affected by fire during the regionally fire-prone periods.

Changes in the atmospheric circulation patterns following the termination of the LIA, specifically changes in AO regimes and the strengthening of the CPT, were likely drivers of regional fire dynamics. Periods with strongly positive AO, associated with increased ridging in central Canada and expansion of the high pressure systems across the mid-latitudes (Fauria and Johnson, 2009), have been shown to lead to increased fire activity across most of the

Canadian boreal forest (Fauria and Johnson, 2006; Girardin, 2007). Expansion and the westward migration of the CPT were likely important in this respect. Reconstruction studies have suggested that both Canadian Continental Ridge and CPT were weaker during the 1700s and 1800s (Girardin et al., 2006b). This pattern likely promoted zonal flow across the continent and suppressed the moisture-bearing systems of Eastern boreal Canada, which originated south of the boreal zone. Consistent with this explanation, a dendrochronological reconstruction of the AO index (D'Arrigo et al., 2003) has suggested that there was a generally higher AO index during the fire-prone LIA (Bergeron and Archambault, 1993; Bergeron et al., 2001; Girardin et al., 2013). Our results also indicate that since the 1970s, higher AO indices have been associated with an increased fire hazard in the northernmost regions (Figs. 2D and 3).

The post-LIA period was characterized by an eastward progression in fire cycle change towards lower fire activity, which is indicative of the western origin of the observed changes. This trend was probably associated with a decrease in the frequency of positive 500 mPa anomalies during the fire season (Skinner et al., 1999). The eastward progression in the fire cycle towards lower fire activity (i.e. longer fire cycles) implies that regional fire activity in more continentally located sectors of the Canadian boreal zone, was more sensitive to changes in water balance. This was likely due to a stronger control of forest fuel conditions by the eastbound jet stream, as compared to the areas under CPT, which are under the influence of moisture-bearing systems from the south. This interpretation also suggests that apart from the latitudinal shift in the position of the jet stream at the end of the LIA, as implied by AO reconstruction (D'Arrigo et al., 2003), jet stream dynamics also contributed to a strong longitudinal pattern in fire activity.

AO and NAO were the only indices significantly connected to regional fire activity in superposed epoch analyses (Fig. 3D and SI Fig. 4), reflecting an important role of the polar

vortex in shaping summer drought conditions. Since these analyses specifically target patterns in the high-frequency (annual) domain, the lack of the pattern for other indices may not necessarily indicate an absence of the relationship at longer temporal scales. Interactions between modes (e.g. PDO and AO) has previously been suggested as factors bringing a specific signal in Canadian regional fire activity (Fauria and Johnson, 2006).

4.2. Importance of non-climatic factors

Climatic influence on fire activity might interact with human effects. However, we consider these interactions to be of a minor importance in the study region. In theory, human effects might be realized through changes in the probability of ignition and an increase in the landscape fragmentation. The presence of humans may both increase and decrease ignition probability (Granström and Niklasson, 2008). The decrease in ignition probability is due to fire suppression. Landscape fragmentation leads to reduced fuel continuity and lower fire activity, which can be considered as passive fire suppression. Neither of these mechanisms are consistent with the timing of the observed change and the rate of its propagation across the region. The early 1800s was still a pre-European period in the study region (Lefort et al., 2003; Boucher et al., 2014), which excluded the possibility of active fire suppression or an impact on fire activity driven by forest fragmentation. The change in fire activity towards lower fire cycles occurred at the eastern fringes of the study area in the second half of the 1800s. At that time, eastern Quebec remained largely un-colonized by European settlers, maintaining its natural vegetation cover (Riopel, 2002; Danneyrolles et al., 2016).

Vegetation composition did not appear to be an important factor in shaping the geographical pattern of the fire activity change. The fast propagation of the change in fire activity, which spread over the studied region in just over two decades, is inconsistent with the vegetation composition having a driving role in controlling fire activity, as suggested by previous studies (Girardin et al., 2004; Drever et al., 2008b). A synchronous onset of a change in fire cycles in

western Quebec might present another line of evidence supporting the limited importance of vegetation composition. Indeed, this region exhibits a large variability in the amount of deciduous vegetation (Saucier et al., 2003), which would lead to large differences in fire regime given vegetation was an critical factor in shaping fire dynamics. Nevertheless, a higher abundance of deciduous species might act as a secondary factor facilitating the change towards longer fire cycles due to the generally lower flammability of deciduous vegetation, compared to coniferous forests (Drever et al., 2008a; Terrier et al., 2013).

4.3. Future of fire activity in the boreal forests of Eastern North America

The spatially complex pattern of decline in regional fire activity revealed in this study, may be reversed in the future towards more fires in the Canadian boreal forest, as consistently predicted by climate models (Bergeron et al., 2010). This study and other studies indicate that changes in fire activity will likely be spatially heterogeneous (Girardin et al., 2009; Boulanger et al., 2013), with variability in fire cycles positively correlated with the degree of the jet stream meridional flow (Girardin et al., 2006b). In the case of boreal Eastern North America, this heterogeneity will be, in part, a result of the magnitude of CPT. It will likely buffer the rapid changes in atmospheric circulation, leading to an increase in the regional drought. We hypothesize that the changes towards high fire activity will occur first in the areas not located under the CPT. Limited empirical support for this view comes from the fact that the only site in our dataset (WAS, Fig. 1B) recording an increase in fire activity (also visible in modern fire records, Portier et al., 2016), was located in the western portion of the study area, outside of the areas under the direct influence of CPT.

An increase in future fire hazard will likely reflect changes in the atmospheric circulation patterns, as suggested by retrospective studies analysing teleconnections between fire activity and the states of the climate systems over the North American, Pacific and Atlantic regions (Skinner et al., 1999). There is a possibility that the frequency of the episodes with humid and

warm air reaching the study region from the subtropical sections of Eastern North America will decline, while the frequency of dry and warm air masses of more westerly origin will rise. This shift may lead to a regional decline in precipitation which, together with the projected increase in fire season temperatures, will drive an increase in fire activity. Therefore, teleconnections and feedback mechanisms between the regional climate and the elements of the global climate system may become particularly important. Although we did not observe a clear pattern linking modern fire activity with PDO or SOI dynamics (Fig. 3D), earlier analyses of the modern datasets have linked the longitudinal positions of CPT to the PDO and ENSO dynamics (Skinner et al., 2006) and ocean temperatures (Shabbar and Skinner, 2004; Shabbar et al., 2011). There is a strong correlation between CPT strength and Labrador Sea temperatures (Shabbar et al., 1997) and an earlier demonstrated effect of forest proximity to the Atlantic Ocean on fire activity (Cyr et al., 2007). This suggests that a continuing warming of the Labrador Sea may reduce the role of CTP in buffering fire activity and accelerate changes in fire activity in the areas under the CTP influence.

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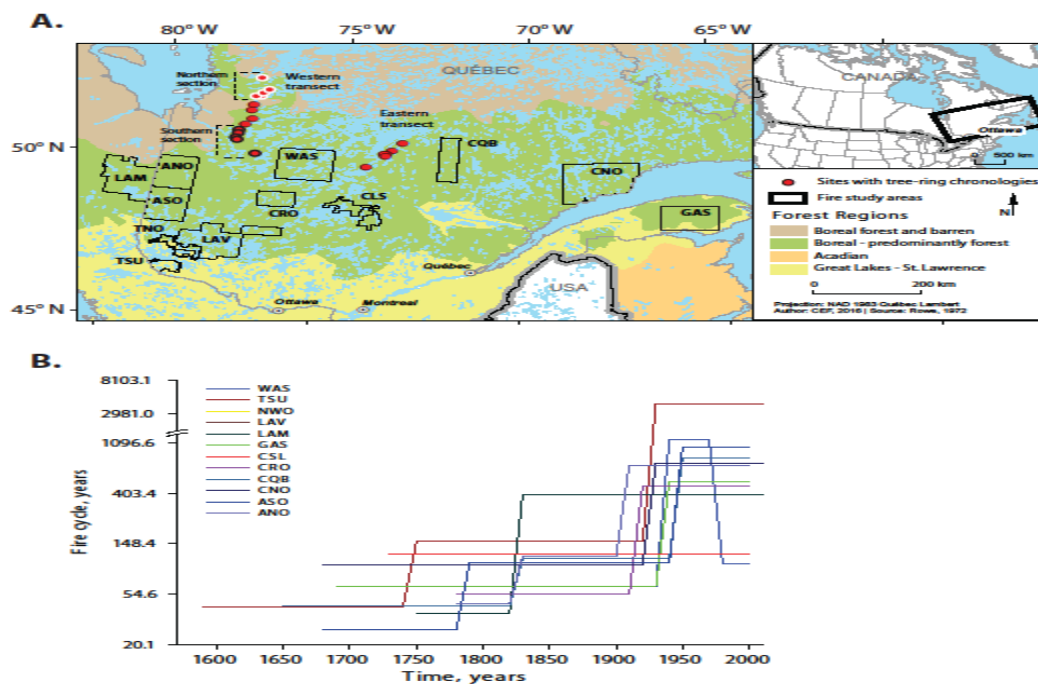


Fig. 1.

Location of the studied landscapes (A) and trends in the change of fire cycles in Eastern North American boreal and temperate forests (B). For A, black lines delimit the areas analyzed for changes in fire cycles (SI Table 1). Red circles indicate the locations of sites that provided black spruce tree-ring chronologies. The five northernmost and southernmost sites on the western transect, indicated with white and thick black circle borders, respectively, were used to analyze growth synchronicity along the North-South gradient. B - Site-specific changes in fire cycles. Each line represents a single study area, where the time-since-fire distribution was analyzed to detect epochs with constant hazard of burning (horizontal line segments). Changes in fire cycle, i.e. changes in the time required to burn the area of the studied landscape, are identified by Bayes Information Criterion and are shown as vertical

line segments. Note the break of the scale on the vertical axis was introduced to accommodate a dramatic increase in the fire cycle for one site (TSU) around 1900.

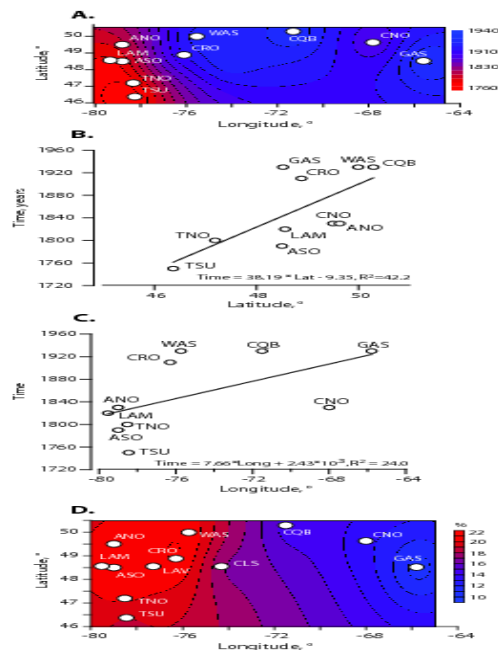


Fig. 2.

Geographical patterns in fire cycles. A: Onset of the trend towards a longer fire cycle and location of the areas studied. The colour gradient reflects the timing of the onset of a longer fire cycle in the studied region. B and C: Latitudinal (B) and longitudinal (C) trends in the timing of the onset. Regression equations and respective R^2 are presented at the bottom of each graph. Sites CLS and LAV were not used for graphs (B) through (D) since there were no fire cycle changes detected in the record (CLS) and the chronology was too short (LAV). D: Percentage of area burned during the 1900s-1920s period. This was a period with an increased level of fire activity across boreal Eastern North America. The colour gradient reflects the gridded percentage of forest stands that originated in the 1910s-1920s. The site codes from all graphs are explained in SI Table 1. White circles in A and D represent the geographical position of the centre of each of the studied landscapes.

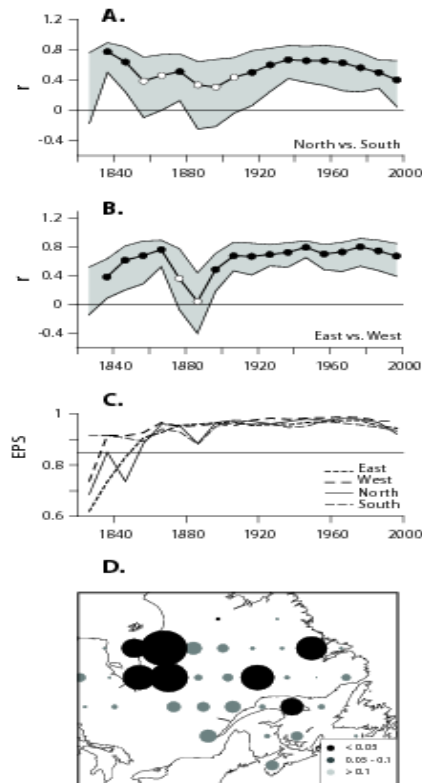


Fig. 3. Growth teleconnection patterns along latitudinal (A) and longitudinal (B) gradients in the studied region, expressed as a correlation between a pair of chronologies (Northern vs. Southern chronology in A, and Eastern vs. Western chronology in B) along a sliding 20-year window. Correlation significance ($p < 0.05$) is indicated by filled circles centred on respective periods; white circles indicate non-significant correlations. C - Expressed population signal (EPS) for all chronologies. The horizontal line indicates a 0.85 EPS threshold. D - The relationship between summer (June through August) AO atmospheric circulation and fire activity in Eastern Canada. Results of superimposed epoch analyses (SEA) with the five the most fire-prone years identified for each cell in $3 \times 3^\circ$ grid over the 1972-2013 period. The size of circles represents the absolute value of departure of the respective index and its shading represents the significance level (black - $p < 0.05$, grey $0.05 \leq p < 0.10$ and light grey $p \geq 0.10$). In all cases, significant departures were observed for the positive values of the indices. The results for the other circulation indices can be found in SI Fig 4.

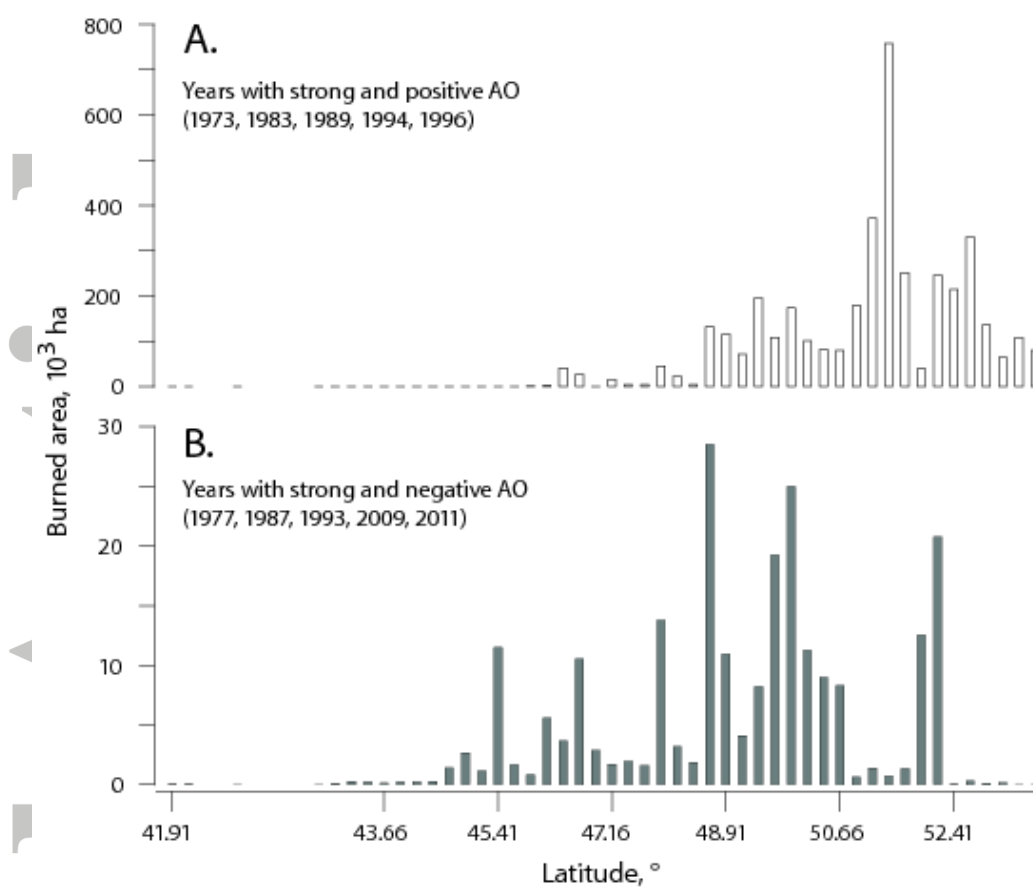


Fig. 4.

Latitudinal distribution of fire activity during years with contrasting Arctic Oscillation conditions. Data - forest area burned in Canada (Natural Resource Canada, <http://cwfis.cfs.nrcan.gc.ca/ha/nfdb>), within 80° and 70° W, binned in 0.25° classes, between 1972 and 2013, during the five years with the highest (A) and the lowest (B) summer AO index.