Effects of 20th-century settlement fires on landscape structure and forest composition in Eastern Québec, Canada

Running title: Effects of settlement fires on landscape structure

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Abstract

Questions

What role played historical anthropogenic disturbances in modifying the natural fire regime? To which extent have they shaped current forest? Do those have lingering impacts in present-day landscape? Are certain tree species related to former land-use?

Location

Eastern Québec, Canada.

Methods

Spatial data on landscape structure, burnt areas, settlements, and forest patches were vectorized on an archival map dating back to 1938. For each landscape class, the total area, the number of polygons, the proportion of the total landscape occupied by the largest polygon were analyzed according to elevation and to the Euclidean distance from the "settlement" polygons. An index of the spatial link between the landscape classes was calculated, based on the proportion of the perimeter of the polygons of each class shared with each of the other classes. A Kolmogorov-Smirnov test for pooled data was used to obtain the frequency distributions of landscape classes as a function of distance. The association between settlement fires and present-day vegetation, and more specifically *Populus* and *Betula* stands, was tested by superimposing the most recent ecoforest map on the 1938 land-use map. Distance bands on either side of the 1938 settlement front were delineated to calculate the proportion of each distance class occupied by present-day aspen and birch stands.

Results

Anthropogenic fires generated a recognizable landscape pattern of land-use. Burnt areas were mostly located within 2 km from a settlement. Most burnings observed on the 1938 map were human-induced, based on their spatial connection with the settled areas. Lingering impacts of these 20th-century fires on present-day forests were identified using the peculiar spatial distribution of tree species. The presence and spatial distribution of aspen in the present-day landscape is tightly associated with previously burnt areas.

Conclusions

Past land-use strongly altered the natural fires regime and associated tree species. Current land-use could potentially lead to increased degraded forest landscapes in a near future.

Keywords

Anthropogenic fires, aspen, boreal forest, land-use, North America, *Populus*, settlement, spatial landscape structure, temperate forest

Introduction

Uncovering the historical role played by anthropogenic disturbances in shaping current forests remains a crucial issue in paleoecology and forest management (Foster et al. 2003, Higgs et al. 2014, Stephens et al. 2019). Paleoecological studies relying on the abundance of charcoal in lake sediments have shown that climate was the main driver of fire regime since the onset of the Holocene at both global (Marlon et al. 2008, Power et al. 2008) and North American (Clifford and Booth 2015, Pederson et al. 2015) scales. However, anthropogenic activities have deeply modified natural fire regimes by increasing fire frequency, which in turn altered terrestrial ecosystems structure and function (Turner and Gardner 2015). This situation has been exacerbated since the industrial revolution and associated human population increase (Marlon et al. 2008, Nowacki and Abrams 2008).

Human-driven impacts on fire regimes can generally be divided in two phases in temperate and boreal biomes: a rapid and substantial increase in the frequency of anthropogenic fires during the settlement of new territories, followed by a decline, often below the pre-settlement levels. This two-phases pattern has already been documented in the boreal and temperate forests of North America (Weir and Johnson 1998, Bergeron et al. 2006, Hessl et al. 2011, Thompson et al. 2013), Eurasia (Lehtonen and Huttunen 1997, Niklasson and Granström 2000, Groven and Niklasson 2005), and Patagonia (Veblen et al. 1999). For example, during the European settlement of North America (19^{th}-20^{th} centuries), massive conversion of forests into farmlands led to a marked increase in fire frequency in surrounding forests (Weir and Johnson 1998, Weir et al. 2000, Hessl et al. 2011). The main causes of fire ignition during this period were deforestation using fire, slash-and-burn for agriculture, sparks produced by steam locomotives, and industrial forest exploitation (Blanchet 2003, Pyne 2007). Subsequently, fire frequency has dropped significantly at the wildland-urban interface due to the gradual cessation of forest conversion into farmlands, to greater and better organized efforts for fire suppression (Cardil et al. 2018), and to increased fragmentation of fuels across human-dominated landscapes (Weir and Johnson 1998, Weir et al. 2000, Lefort et al. 2003, Peter et al. 2006, Brose et al. 2013).

However, in several human-dominated landscapes, it remains difficult to identify the causes of fire ignition during the last two centuries, whether anthropogenic, climatic, or resulting from the interaction between these two drivers (Pyne 1997, Bowman et al. 2011, Boucher and Grondin 2012, Johnson and Kipfmueller 2016). This may in part result from the lack of spatially explicit data regarding the occurrence of early anthropogenic fires, which might confound our understanding of the landscape structure during the settlement phases. If anthropogenic fires accompanied some settlement episodes, then burnt areas should be spatially connected to settled areas. Indeed, previous studies have suggested that landscapes subject to anthropogenic fires display diagnostic properties that can be identified. For instance, Cochrane and Laurence (2002) reported that anthropogenic fires in Amazonia represent a typical "fish-bone" edge effect at the settlement front. In the North American and Scandinavian boreal forests, increased fire frequency has been detected directly in the vicinity of human activities during settlement phases (Weir et al. 2000, Lefort et al. 2004, Grenier et al. 2005, Wallenius et al. 2005). Similarly, dendrochronological data from Eastern European Russia (Drobyshev et al. 2004) and Patagonia (Mundo et al. 2013, Paritsis et al. 2013) have shown increased correlation between fires and settlements with decreasing distance from the nearest village. Moreover, fire-adapted forests may have subsequently developed following these settlement fires (Weir and Johnson 1998), producing a long-lasting imprint still visible in present-day landscapes in North America (Clark and Royall 1995, Nowacki and Abrams 2008, Munoz and Gajewski 2010, Danneyrolles et al. 2016), Eastern Europe (Niklasson et al. 2010), Scandinavia (Niklasson and Drakenberg 2001), and Russia (Wallenius et al. 2005). Such legacies of past fire regimes may have important consequences on the structure, composition, functioning and management options of many present-day and future landscapes (Paristis et al. 2015, Kitzberger et al. 2016, Boulanger et al. 2019).

In 1938, an aerial survey was conducted to map land-use types at the height of a European settlement episode in the Lower St. Lawrence region, within the southern boreal forest of eastern Canada. Here, we analyze an archival map produced during this survey and provide a spatially explicit reconstruction of the connection between settled and burnt areas. We also test the lingering impact of increased anthropogenic fire on the forest landscape. Specifically, we hypothesize that present-day distributions of the early-successional, fire-adapted trembling aspen (*Populus tremuloides* Michx.) (Bergeron and Charron 1994) and white birch (*Betula papyrifera* Marshall) stands reflect the occurrence of settlement fires. Both species have dramatically increased in abundance after European settlement of the North American boreal and temperate forests (Friedman and Reich 2005, Thompson et al. 2013, Dupuis et al. 2011), and anthropogenic disturbances were probably a major cause of their increase (Danneyrolles et al. 2019).

Methods

Study area

The study area covers 13,767 km^2, bordered by the St. Lawrence River to the North and by the province of New-Brunswick (Canada) and Maine (USA) to the South (Figure 1). The area belongs to the Appalachian geological formation, mainly composed of a sedimentary bedrock that forms low hills with an altitude up to 900 m (Appendix S1a). Glacial till cover the hill slopes of higher altitudes, while alteration deposits occupy the main valleys and the downslopes (Appendix S1b, Robitaille and Saucier 1998). Postglacial marine deposits from the retreat of the Goldwaith Sea characterize a narrow coastal band. The center of the study area forms a large valley that corresponds to the hydrographic basin of the Matapedia River, which flows southwards (Figure 1). Drainage is generally moderate throughout the study area (Appendix S1c).

The climate is temperate continental, with mean annual temperatures varying between -11.4°C in January and 18.3°C in July (mean 4.4°C) (Rimouski station). Mean annual precipitations reach 958.5 mm, among which 28.5% are snowfall. The growing season lasts 150 days in average and corresponds to *ca*. 1,500 degree-days above 5°C (ENRC 2019).

The study area is located in the transition zone between the temperate and the boreal zones (MRNFP 2004). The forests largely belong to the balsam fir–yellow birch bioclimatic domain, transitioning to the balsam fir–white birch domain further east (Figure 1) (Robitaille and Saucier 1998). Balsam fir (*Abies balsamea* (L.) P. Mill), yellow birch (*Betula alleghaniensis*

Britt.), white birch, trembling aspen and white spruce (*Picea glauca* (Moench).Voss) are common on mesic soil downslopes, while sugar maple (*Acer sacharum* Marsh), red maple (*Acer rubrum* L.) and yellow birch mostly occur on hilltops. Black spruce (*Picea mariana* (P.Mill.) B.S.P.) and northern white-cedar (*Thuja occidentalis* L.) are found on organic soils. Human-induced modifications of the territory have led to a generalized increase in the abundance of deciduous trees (aspen, maple, and birch) at the expense of conifers (cedar, fir, and spruces) (Boucher et al. 2006, 2009a, b, Dupuis et al. 2011, Terrail et al. 2019). Natural fires were probably uncommon before settlement, with a long rotation period estimated to 1,100 years (Lorimer 1977).

History of the study area

Indigenous peoples in the study region were mainly nomadic (*i.e.* Algonquians), by contrast with the Iroquoians peoples living closer to current Québec and Montréal cities, who were mainly sedentary (Michaud 2015, Miller 2018). Little is known, however, about the extant of their territory and their land-use. First Europeans settled at the end of the 17th century, although the population actually increased only after 1830, alongside the development of industrial forest exploitation. Before 1860, colonists essentially settled in seigniories established before 1760 under the French regime along the St. Lawrence River (Fortin et al. 1993). The construction of roads and railways, growth of forest industry, and demographic pressure from more densely populated territories westwards led to the spread of agriculture inland and, more specifically, into the Matapedia River valley after 1880 (Roy 1992). Many settlement campaigns occurred after 1895, especially in the 1930s, leading to rapid expansion of land clearing and cultivation. Agricultural expansion and population density of the hinterland (including the Matapedia River valley) peaked around 1940, before the abandonment of several farmlands and the population exodus to urbanized areas along the coast (Fortin et al. 1993). In the 19th century, the forest industry practiced selective logging of the largest trees near watercourses used for timber floating (Boucher et al. 2009a, b, 2014). With the growth of the pulp and paper industry at the beginning of the 20th century, clearcutting extended inland and intensified in the 1940s owing to mechanization.

The 1938 landscape map

The steps of our analysis and associated geodata layers and time steps are conceptualized in the Appendix S2. The 1938 map was produced during a series of aerial surveys carried out in June and July, as part of an inventory of the natural resources in the Lower St. Lawrence region (Hébert 1938). In addition to rivers and lakes, the original document included four landscape classes: "old forest", "young forest", "agriculture", and "burnt". According to the report accompanying the map, these classes corresponded to ≥ 60-year-old forests, 10- to 35-year-old forests, agricultural areas, and burnt areas of less than 10 years, respectively (Hébert 1938). A series of 85 oblique aerial photographs taken concurrently, as well as early land survey records of public lands conducted prior to 1940 (Dupuis et al. 2011, Terrail et al. 2019), allowed us to determine the origin of 80% of the "young forest" polygons. Because these polygons consistently correspond to burned areas, with typical unburned islands and irregular contours on aerial photographs (Appendix S3), we reclassified all "young forest" as "ancient fire" and changed the "burnt" class to "recent fire". This reclassification is supported by "fire" and "old fire" mentions in early land surveys from the 1900-1940 period as well as by a governmental database of ancient fires dated by fire scars (https://www.donneesquebec.ca/recherche/fr/dataset/feux-de-foret/resource/8ce4f503-94f8-4041-a395-959c5ade950c). We then combined our "recent fire" and "ancient fire" classes into a more general "total fire" class. Similarly, we replaced the "agriculture" class as "settlement" because we found that it also included cities, villages and other urban structures. In the original conception of the map (Hébert 1938), this "settlement" class was systematically drawn above the "fire" polygons, thus partially masking and spuriously fragmenting these into several smaller polygons. Hence, the total area of the "fire" polygons is likely underestimated (*i.e.* masked by settled areas) and their number overestimated. No procedure has allowed for satisfactory reconstruction of the original "fire" polygons.

Landscape structure

The map was scanned using 70-m × 70-m pixels (Figure 1b), then georeferenced by using permanent reference lines (e.g. township and provincial borders) and vectorized all polygons of the different landscape classes (ARCGIS 10, ESRI 2011). We first described landscape structure by measuring, for each landscape class, the total area, the number of polygons, the proportion of the total area of the class occupied by the largest polygon, and the proportion of the total landscape occupied by the largest polygon. Elevation was an important factor influencing the spread of the settlement front from the coastal terraces (Fortin et al. 1993). We thus calculated the relative abundance of landscape classes within 100-m elevation bands, between 0 m and 700 m altitude. We generated elevation bands by using the digital hypsometric maps provided by the Québec Ministry of Natural Resources (scale 1: 20,000 with 10-m isolines, MRNQ 2000b).

The spatial connection between the "settlement" and "fire" polygons was studied by creating 100-m-wide land bands up to 30 km away from all "settlement" polygons. We then examined how the "fire" and "forest" areas were distributed according to the distance to the "settlement" class, and measured the shortest Euclidean distance separating each "fire" polygon from the nearest "settlement" polygon. Finally, we evaluated how the "fire" polygons and their cumulative area were distributed on the landscape according to the shortest distance separating each "fire" polygon from a "settlement" polygon. As an index of the spatial link between the landscape classes, we measured P_{ij}, the proportion of the perimeter of the polygons of each class i ("settlement", "total fire", "ancient fire", "recent fire", and "forest"), shared with each of the other classes j:

$$P_{ij} = [(p_{ij} / p_i) \times 100] \text{ (eq. 1)}$$

where p_{ij} is the total perimeter length shared between polygons of classes i and j in the entire map, and pi is the total perimeter length of class i. We used a Kolmogorov-Smirnov test for pooled data (Zar 1999) to test the frequency distributions of landscape classes as a function of distance.

Association between settlement fires and present-day vegetation

In order to assess whether present-day fire-adapted forest stands (*i.e.* aspen and white birch stands) are a legacy of settlement and fire patterns at the peak of settlement, we superimposed the ecoforest map of the Third Decennial Inventory conducted by the Québec Ministry of Natural Resources (1991-2003, MRNQ 2000a) on the 1938 land-use map. Ecoforest mapping of extant *Populus* and *Betula* stands relied on the photo-interpretation of aerial photographs (1:15,000), based on taxa dominance and co-dominance in the forest cover (MRNFQ 2009). Because it was not possible to distinguish trees beyond the genus level from these map data, we validated the forest composition from 1,251 temporary sampling plots inventoried by the Québec Ministry. This analysis indicated that poplar and birch stands were dominated by trembling aspen and white birch, respectively (Appendix S4).

Considering that the maximal extent of agricultural territory was reached around 1940 (Fortin and Lechasseur 1999), we assessed whether present-day abundance of aspen and birch stands reflects the location and the spatial configuration of the settlement front mapped in 1938. We first positioned the 1938 settlement front at the interface between the largest forest polygon not fragmented by human activities and the reunion of "settlement" and "fire" polygons directly connected with the early settled coastal sector. We then delineated distance bands (of increasing width from 500 m to 5 km) ranging from 500 m to 20 km on either side of the 1938 settlement front to calculate the proportion of each distance class occupied by present-day aspen and birch stands.

Aspen and birch stands were superimposed on the 1938 map to test more specifically whether pre-1938 fires and settlement directly influenced the present-day distribution of these forest stands. Because more recent fires may also have contributed to the forest dynamics, we added 1940-2007 "fire" polygons contained in the database of the Forest Fire Protection Agency (SOPFEU, 2018). Note, however, that the older the time period, the less complete and accurate the polygons outline becomes. Similarly, we also added fires older than those mapped in 1938, as reconstructed from early land surveys conducted between the 1820s and the 1930s. We calculated the frequency of fire observations (number fires mentioned by a surveyor divided by the total number of surveyors' observations) in each 2-km × 2-km cell throughout the surveyed territory. The two-km unit was the smallest land unit we could use for this analysis given that land surveys were conducted along range lines spaced by 1.6 km (*i.e.* a mile). Settlers later established their farms along these rage lines (Appendix S5). We then conducted a permutation test in order to verify the null hypothesis that aspen and birch stands are randomly distributed relative to the "total fire" (including cells with surveyor's fire mentions), the "settlement", and the union of total fire and settlement landscape classes. The number of stands expected in each of these classes under the assumption of random aspen or birch stands distributions were estimated from 1,000 random permutations of the stand centroids within the study area. The confidence intervals of the expected values were determined from the corresponding 2.5th and 97.5th percentiles of the permutations and were compared to the corresponding observed values. This analysis was repeated after excluding the "young forest" class to confirm that our conclusions are not influenced by the reclassification of "young forest" into "ancient fire" (Appendix S6).

Results

Landscape structure

The 1938 landscape reflected the rapid advance of a settlement front inland and along the Matapedia River valley (Figure 1). The "forest" class was dominant, covering 67% of the total landscape area, while the "settlement" and "total fire" classes accounted for 19% and 13%, respectively (Table 1). The "settlement" class dominated along the coast and "forest" was inland, whereas the "fire" class was located at the interface between "settlement" and "forest" classes (Figure 1). Forests were still highly connected, with the largest "forest" polygon occupying 59% of the total landscape area and 87% of the total forest area.

The spatial structuring of the landscape also depended on altitude (Figure 2a and b). The "settlement" class occupied the lowest altitudes, with a relative abundance reaching *ca*. 70% in the 0-100 m elevation band, and decreasing steadily to a relative abundance < 1% above 400 m in elevation. By contrast, the relative abundance of the "forest" class increased from *ca*. 30% below 100 m, to almost 100% higher than 600 m. The "ancient fire" and “recent fire” classes occupied an intermediate position, with a maximum relative abundance reaching 20% between 200 m and 300 m (Appendix S1). The "settlement" class disappeared completely along with the "recent fire" class above 600 m.

The proportion of polygon perimeter shared between the various landscape classes pairs (P_{ij} index) illustrates the diagnostic position of the fire polygons at the interface between the "settlement" and "forest" classes (Table 2). Indeed, "total fire" had almost as much perimeter in common with "settlement" (42%) as with "forest" (50%). "Ancient fire" shared a greater perimeter with "settlement" (59%) than with "forest" (28%), whereas "recent fire" had a greater perimeter in common with "forest" (61%) than with "settlement" (31%). Hence, the "ancient fire" class is found at lower altitude and closer to the St. Lawrence River compared to the "recent fire" class.

In 1938, fires were strongly connected to settled areas (Figure 1). More than 70% of the total burnt area ("ancient fire" plus "recent fire" polygons) was located within 2 km from a "settlement" polygon (Figure 2c). In comparison, only 42% of the "forest" area occurred within 4 km from the nearest "settlement" polygon. In addition, more than 80% of all "fire" polygons were located (at the shortest distance) within 2 km from a "settlement" (Figure 2d), and more than 95% of the total burnt area was included in polygons whose shortest distance to a "settlement" polygon was less than 2 km (Figure 2e). While "ancient fire" and "recent fire" polygons had a similar frequency distribution according to their shortest distance to a "settlement" polygon ($D_{\text{Kolmogorov–Smirnov}} = 0.20$, $P = 0.28$), "recent fire" distribution was skewed inland compared to "ancient fire" (Figures 1 and 2d).

Association between settlement fires and present-day vegetation

The present-day distribution of aspen and birch stands in the landscape was strongly shaped by the 1938 settlement front and associated fire polygons (Appendix S6). The position of the settlement front in 1938 strikingly delineates the zones of highest abundance for aspen and birch stands, respectively (Figure 2f; Figure 3). The transition between the relative abundance of the two stand types across the landscape corresponds precisely to the position of the settlement front in 1938 (Figure 2f). Aspen stands are more abundant towards the coast, behind the settlement front (Figure 3a), whereas birch stands are rather found inland, ahead of the settlement front

(Figure 3b). Permutation tests indicated that centroids of aspen stands are more frequently located inside fire polygons than expected from 1,000 random simulations (Figure 3c) whereas birch stands centroids are less often found within fire polygons than expected from the null distribution (Figure 3d). The fire-aspen connection remains strong, even when considering only the "recent fire" class (Appendix S6) or the reunion of all 19th century and 20th century fire polygons and fire mentions (Appendix S7). Indeed, 44% of all aspen stands were present in areas that have burnt since the mid-19th century, whereas these burnt areas covered less than 13% of the total landscape. The high frequency of aspen stands in the seignories settled during the first half of the 19th century in the coastal sector along the St. Lawrence River (Appendix S6) suggests that these forest stands can persist for more than 150 years.

Discussion

Connection between settlements and fires

Several studies have documented a general increase in fire frequency triggered by the expansion of human activities following European settlement in North America (Pyne 2007). This phenomenon was exacerbated during agricultural expansion in the southern boreal and temperate zones, as previously reported at the margin of the boreal zone in central Canada (Weir and Johnson 1998). Such increase in fire frequency was generally inferred from historical documents (e.g. early land survey archives, early maps and aerial photos) (e.g. Lorimer 1977, 2001, Schulte and Mladenoff 2005, Boucher et al. 2014, 2017, Danneyrolles et al. 2016) and empirical data from field observations (e.g. fire scars) (Drobyshev et al., 2008a, b, Hessl et al., 2011). These sources of information are often fragmentary and seldom allow for a systematic location or an accurate contour of fires related to European colonization over large geographic areas, thus hindering any attempt at inferring a cause-and-effect relationship between the human presence and fire activity. Interestingly, the archival map used in the present study rigorously shows the extent of fires relative to other landscape classes from a large area of eastern Canada in 1938, at the peak of agricultural expansion and reveals a strong spatial connection between the "settlement" and "fire" landscape classes. We inferred that increasing European settlement during the early 20th century has modified fire activity and landscape structure. Furthermore, we demonstrated that this increase in anthropogenic fires has altered forests and left a lingering imprint on present-day landscape.

The spatial connection between European settlement and fires in 1938 likely resulted from burning by the settlers to prepare land for agriculture. During the 19th century and the first half of the 20th century, early settlers cleared the forest for their establishment and usually burnt the logging waste (Blanchet 2003). The presence of smoke plumes on the oblique photos (Appendix S5) and the report of their high prevalence during the 1938 aerial survey (Hébert 1938) are additional indications of the historical widespread use of slash fires in the study region. Moreover, the government inventory report of 1938 strongly emphasized that settlers used fire inconsequentially, and that poorly controlled slash fires regularly escaped to the surrounding forest (Guay 1942). In addition, for all inhabited areas in Québec during the 1906-1941 period, only 5.5% of the reported fires were associated with lightning strikes, whereas 66.5% were of human origin (SOPFEU 1909-1941). The deep incisions of the settled land within the forest, following the cadastral plan at the settlement front (Figure 1), probably increased the contact area between settled and forest areas, which, in turn, increased the probability of anthropogenic fires to spread into the remaining forest matrix. The construction of a railway through the Matapedia

River valley between 1871 and 1876 is an additional factor for the occurrence of anthropogenic fires in the late 19th and early 20th centuries (SOPFEU 1909-1941, Blanchet 2003). The steam locomotives let out sparks that ignited fires along the railway by burning the available fuels. This source of ignition, however, would have become negligible after 1914, due to the introduction of locomotives inspections, to improvement of spark arresters, and to a reduction of forest fuel close to the railways (Blanchet 2003).

The spatial arrangement of the landscape in 1938 also reflected the progression of the settlement along the elevation gradient from the coast. The fires were mainly located at intermediate altitudes, between the coastal and lowland settled areas along the St. Lawrence River and in the Matapedia River valley, and the forests at higher altitudes in the hinterland. The gradual expansion of settlement, from the seigniories established in the 18th century along the shore of the St. Lawrence to the Matapedia valley, as well as the greater agricultural potential of the soils along the St. Lawrence and in the Matapedia valley in comparison with those of the highlands, could explain this peculiar pattern. The "ancient fire" polygons probably indicate the position of the settlement front around 1900-1925. Their location at lower elevation and at a shorter distance from the coast, compared to the "recent fire" class, indicate a rapid progression of the settlement front to the hinterland between 1900 and 1938. Conversely, the virtual absence of both "ancient fire" and "recent fire" classes within the coastal seigniories probably reflect the much older occupation and forest fuel exhaustion of this territory, as well as the slower progress of the settlement before the beginning of the 20th century (Fortin et al. 1993).

Settlement as an ignition agent

In the transition zone between the boreal and mixedwood forests of northeastern North America, the pre-settlement disturbance regime was likely dominated by secondary disturbances such as insect outbreaks and windthrow, with a long fire cycle estimated to more than 1,100 years (Lorimer 1977). Consequently, the presettlement forest was strongly dominated by shade-tolerant conifer tree species typical of late successional stages, such as fir, spruces, and cedar, with relatively low occurrence of fire-adapted species, such as aspen and pines (Boucher et al., 2009a, 2009b, 2017, Dupuis et al 2011, Thompson et al. 2013, Danneyrolles et al. 2016).

Our results suggest that this low incidence of natural fires mainly resulted from unsuitable conditions for fire ignition. Indeed, the occurrence of multiple large fires directly connected to the settlement front combined with a virtual absence of fires distant to the settlement front, indicate that fires were not limited by fuel type or weather conditions, but rather by a low frequency of ignition events. The increase in anthropogenic ignitions at the edge of the settled areas resulted in extremely high burn rates at the peak of colonization. According to the 1938 regional forest inventory, fires annually burnt 5% of the territory. Although this estimate is limited to a short time period, it is similar to the highest values ever reported for the most fire-prone boreal regions (Weir and Johnson 1998, Héon et al. 2014). This did not preclude interactions between weather conditions and anthropogenic ignitions. Weather has probably influenced the spread of fires ignited by settlers in the study area at the beginning of the 20th century, because this period was particularly prone to large fires across both the commercial and non-commercial eastern Canadian boreal forest (Bergeron et al. 2004, Erni et al. 2017). Nevertheless, human ignition in regions were natural fires are uncommon, is a widespread phenomenon already described from the tropics (Cochrane and Laurence 2002, Morin-Rivat et al. 2016) to temperate (Balch et al. 2017) and boreal environments (Achard et al. 2007). Moreover, the low fire incidence following the settlement peak in our study area may be attributed to a decrease in human ignitions, along with organized fire suppression (Cardil et al. 2018), and possibly the increasing abundance of aspen stands, a fuel type which tends to be avoided by fire (Bernier et al. 2016).

Several studies assessing burn rates in the temperate and southern boreal forests have highlighted the difficulty to discriminate between the relative contributions of natural and anthropogenic fires (Bergeron et al. 2004). Our results indicate that studying spatial landscape structure at the time of the settlement could provide useful insights regarding the imprint of anthropogenic fires. The overwhelming proportion of fires connected to the "settlement" polygons (more than 80%) lend credence to the critical role of past anthropogenic fires in shaping present-day landscapes.

Lingering impacts of anthropogenic fires on present-day forest structure and composition

Our results demonstrate that the high occurrence of anthropogenic fires in the early 20th century has altered the forest composition of present-day landscape. However, the trends differed markedly between aspen and white birch. These two light-demanding species have high reproductive output and growth rate and are often reported to increase in abundance following ecological disturbance (Zasada et al. 1992, Bergeron and Charron 1994, Thompson et al. 2013, Boucher et al. 2017). Hence, we initially hypothesized that they would react in a similar way to increasing settlement fires. By contrast, our results strikingly demonstrate that aspen and birch stands display opposite patterns of abundance on either side of the 1938 settlement front (Figure 2f; Figure 3a and b).

The contrasted patterns of current abundance might reflect different responses of each species according to their respective abundance patterns in the 19th century. Reconstruction of the 19th-century forest composition based on early land survey records, indicated that trembling aspen was rare, while white birch was widespread as a companion species throughout the study area (Dupuis et al. 2011, Terrail et al. 2019). This assertion is supported by forest maps of the early 20th century (Boucher et al. 2009a, 2009b) and the land survey archives from neighboring Maine (Lorimer 1977, Thompson et al. 2013). That said, comparing historical data with the modern forest inventories indicates that white birch and especially aspen are more common in today's landscape than in the 19th century (Dupuis et al. 2011, Terrail et al. 2019). This trend has also been reported in southern boreal (Brown and Simmerman 1986, Bergeron 2000, Boucher et al. 2014, 2017, Danneyrolles et al. 2016) and northern temperate forests (Foster et al. 1998) throughout North America. Aspen-dominated stands are common today behind the settlement front, but virtually absent beyond. We thus infer that aspen frequency increased as a consequence of anthropogenic fires behind the front, but that it could not significantly establish beyond the front in the absence of fires. Conversely, birch stands are now mainly confined beyond the settlement front. We conclude that birch frequency decreased behind the front, while increasing within the forested area ahead of colonization.

This contrasted pattern of species abundance probably reflects the faster postfire establishment of aspen thanks to its sprouting and clonal multiplication, that is its greater competitiveness compared to birch on burnt areas (*i.e.* behind the settlement front). Trembling aspen benefits from the occurrence of fires across its entire distribution range (Bergeron 2000, Bergeron et al. 2001, Kulakowski et al. 2004). Aspen regeneration by suckering allows this species to establish massively and aggressively after fire (Burns and Honkala 1990). Increased ground temperature induced by fire strongly influences nutrient remobilization in soils (Heinselman 1981), while litter removal also creates favorable conditions for suckers growth (Weir and Johnson 1998). The new suitable environments created by anthropogenic fires probably prompted a rapid and massive post-fire aspen establishment, likely excluding birch and other taxa. The rapid expansion of aspen behind the settlement front suggests that at least some individuals were already present, although they needed not be dominant. Indeed, aspen produces abundant wind-dispersed seeds that can travel over great distances and readily germinate on burnt substrates (Bergeron 2000).

White birch regional abundance has increased since the 19th century (e.g. Dupuis et al. 2011, Terrail et al. 2019). Birch-dominated stands are now concentrated in the forested area ahead of the 1938 settlement front. These stands may have been favored by logging activities and spruce budworm (*Choristoneura fumiferana* [Clem.]) outbreaks, two major drivers of forest disturbance beyond the settlement front. Logging of mature trees creates canopy openings allowing light penetration and ground warming, thus favoring white birch regeneration by seeding. (Burns and Honkala 1990). At least three spruce budworm outbreaks occurred across the study area over the past century (Boulanger and Arseneault 2004). While birch benefits from regular canopy gaps created by spruce budworm, the small forest openings associated with insect outbreaks are inappropriate for massive aspen establishment (Kneeshaw and Bergeron 1999, Bergeron 2000).

Mitigating expected deleterious effects of global climate warming on ecosystems is now a worldwide endeavor (IPCC 2018). Understanding how ecosystems will respond to ongoing climate change requires a sound comprehension of the complex interplay between climate, disturbance regimes, and associated biotic responses. For example, our study exemplifies how human activities since the 19th century have deeply altered natural disturbance regimes and associated ecosystems. Based on aspen persistence in the early settled coastal seignories of our study area, as well as in the early settled regions elsewhere in the province of Québec (Danneyrolles et al. 2019), we anticipate a long-lasting impact of these legacies. These and other anthropogenic land-use changes such as landscape fragmentation along with forest homogenization, both in terms of structure and composition, could modify ecosystem responses to future global warming (Millar et al. 2007, Wang et al. 2015, García-Valdés et al. 2015, Danneyrolles et al. 2019) and complicate efforts to manage forest ecosystems sustainably (Boulanger et al. 2019).

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Author contributions

RF, DA and MJF conceived the research idea; RF and DA collected data and performed the analyses. RF, with contributions of DA and MJF, wrote the original version of the manuscript; JMR, with contributions of GdL and DA, translated, updated and corrected the manuscript and followed up the submission process; all authors discussed the results and commented on the manuscript.

Data accessibility

Primary data and datasets are stored at Département de biologie, chimie et géographie, Université du Québec à Rimouski, Rimouski, Canada, and could be accessed by following the link: https://doi.org/10.6084/m9.figshare.9992336.v1.

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Table 1. Metrics of the 1938 landscape.

Class	Proportion of the total landscape (%)	Perimeter (km)	Area (km^2)	Nb of polygons	Proportion of the largest polygon	
					% of the class area	% of the total landscape
Settlement	19	4987	2605	143	74	14
Ancient fire	4	1222	590	109	22	2
Recent fire	9	2047	1153	89	21	1
Total fire	13	3127	1729	199	15	2
Forest	67	6230	9189	423	87	59
River/lake	2	1372	228	489	8	0
Total	100	15716	13751	1452		

Table 2. Perimeter in common (P_{ij} index) among the 1938 landscape classes in the study area.

	j class							
i class (%)	Settlement	Fire			Forest	Lake	Shore	Outer limits
		Ancient	Recent	Total				
Settlement	-	14	13	27	65	4	3	1
Total fire	42	-	-	-	50	5	0	3
Ancient fire	59	-	-	-	28	8	0	0
Recent fire	31	-	-	-	61	3	0	1
Forest	52	5	20	25	-	16	1	6

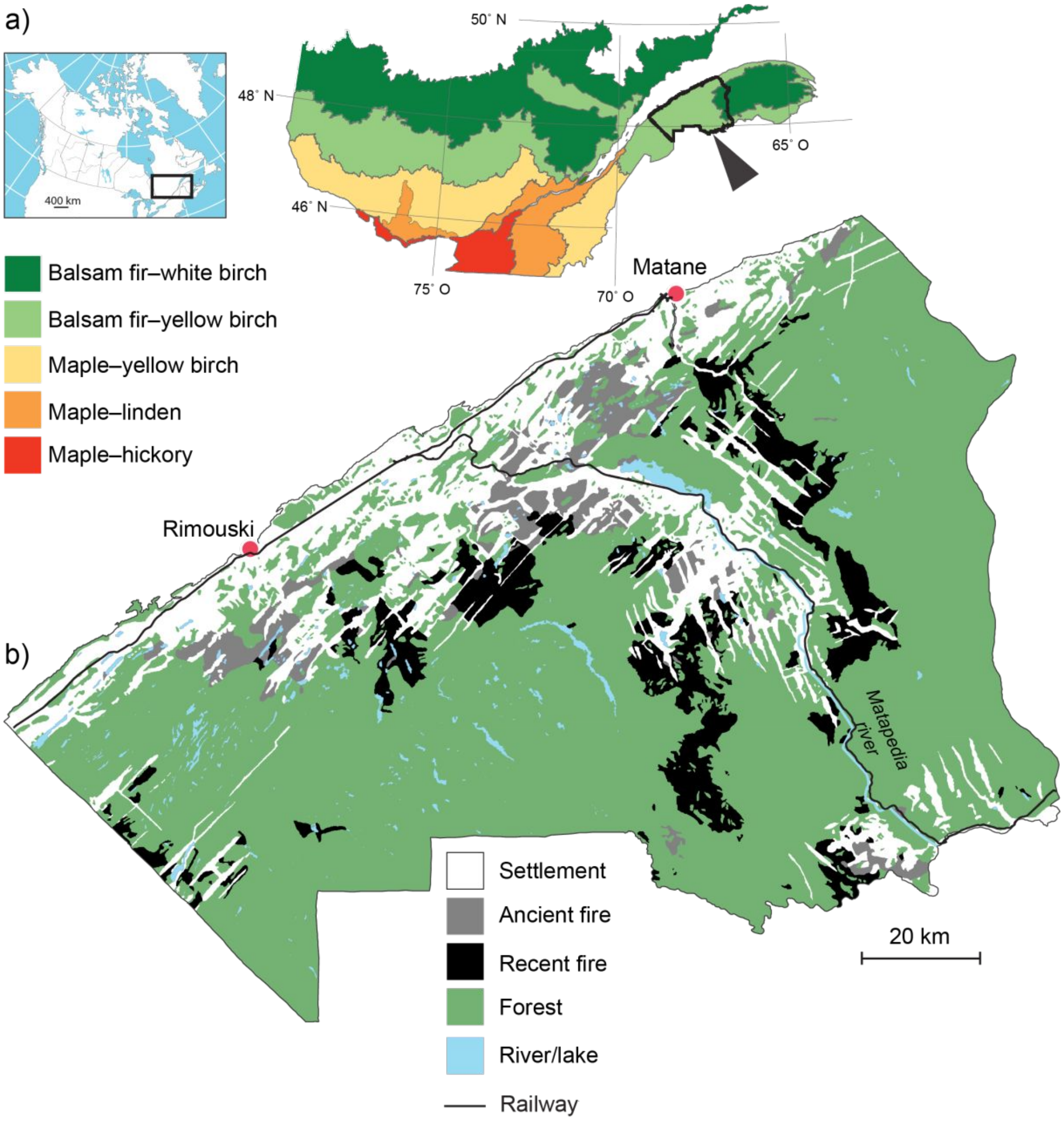


Figure 1. Location of the study area in the Lower St. Lawrence region in eastern Québec: (a) the bioclimatic zones in Southern Québec; (b) Land-use types based on the 1938 archival map (Bibliothèque et Archives nationales du Québec, ref. ANQ-A16-P5_1938). "Ancient fire" correspond to 10- to 35-year-old forests (1903-1928) and "recent fire” to burnt areas of less than 10 years (1928-1938).

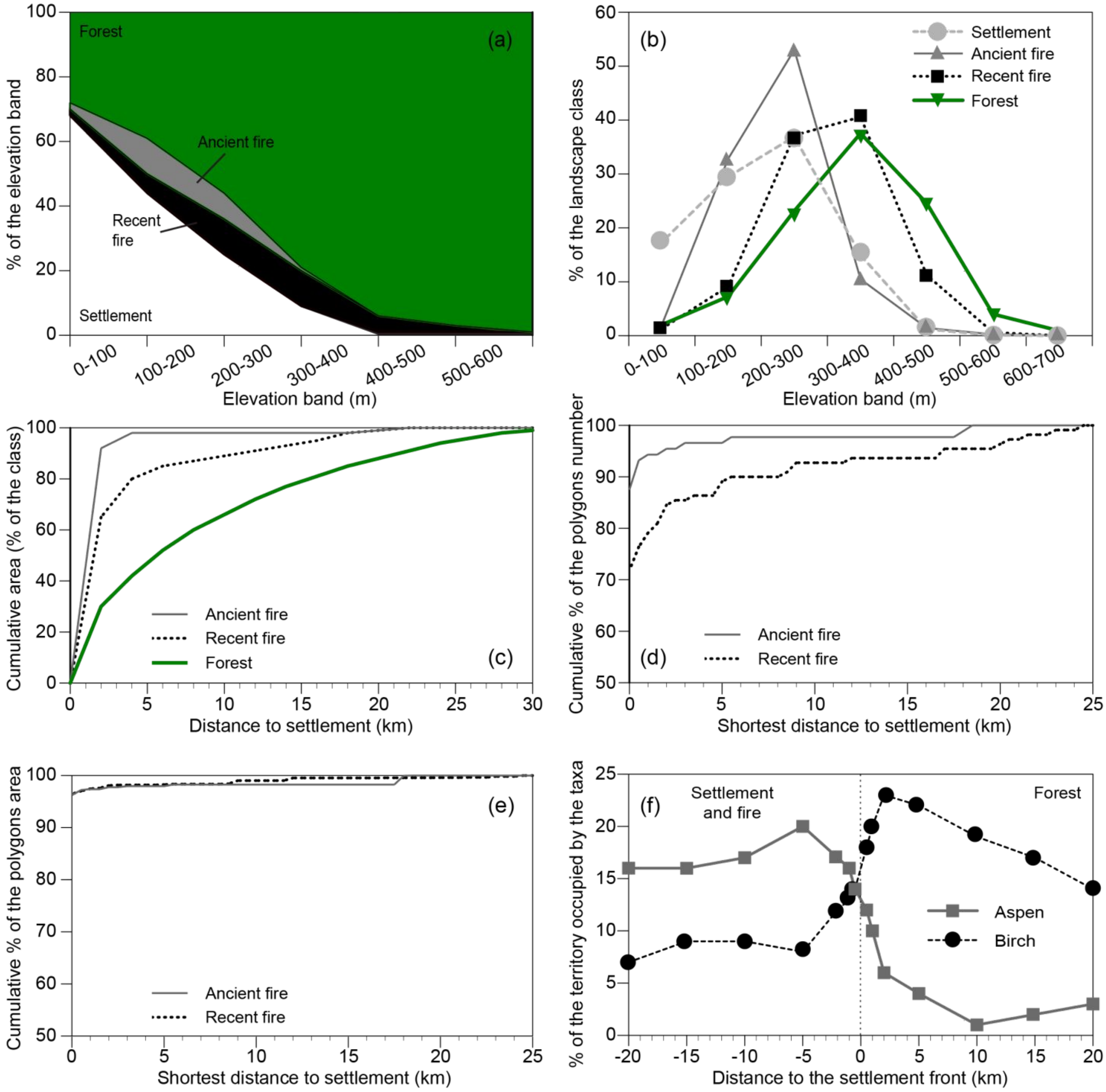


Figure 2. The spatial structure of the Lower St. Lawrence landscape in 1938 and its association with explanatory variables. (a) Proportion of each elevation band occupied by each landscape class. (b) Proportion of the total area of each landscape class occupying each elevation band. (c) Cumulative area of the "fire" and "forest" classes in successive 100-m-wide bands surrounding each "settlement" polygon. (d) Cumulative proportion of the total number of "fire" polygons at increasing shortest distance to a "settlement" polygon, and (e) cumulative proportion of total area of "fire" polygons at increasing shortest distance to a "settlement" polygon. (f) Spatial distribution of present-day aspen and birch stands as a function of the distance to the 1938 settlement front.

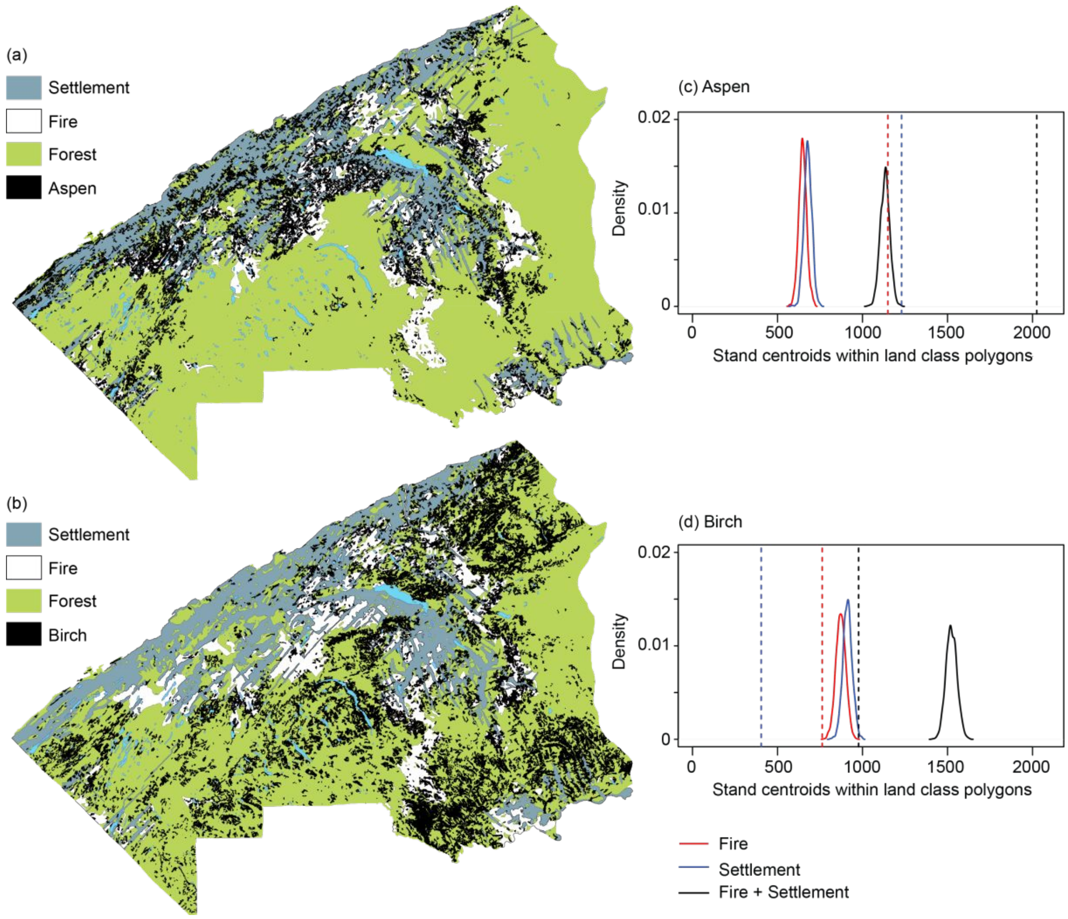


Figure 3. (a, b) Distribution of (a) aspen and (b) birch stands (ecoforest maps from the Ministry of Natural Resources, MRNQ 2000a) in relation with the landscape structure classes of the 1938 map. (c, d) Simulated and observed number of aspen (c) and birch (d) stands centroids tallied within land class polygons (fire, settlement). Frequency distributions indicate the number of stand centroids for aspen (n = 3,586) and birch (n = 4,822) stands falling within each land class polygon over 1,000 random permutations. Vertical dotted lines indicate the number of observed stands actually recorded within each land class polygon.

List of appendices

Appendix S1. Maps of altitude (a), surficial deposits (b) and drainage classes (c) across the study area.

Appendix S2. Diagram showing the temporal and conceptual relationships between the georeferenced layers used in this study.

Appendix S3. Archive photo illustrating the landscape classes mapped from the 1938 aerial survey in the hinterland of the Lower St. Lawrence region (Québec, Canada).

Appendix S4. Validation of the mapped ecoforest polygons dominated by *Populus* and *Betula* taxa from the associated field plots of the Third Decennial Inventory of the Québec Ministry of Natural Resources.

Appendix S5. Archive photos illustrating typical slash fires during the settlement in the hinterland of the St. Lawrence region (Québec, Canada): (a) oblique aerial photograph taken at the time of the mapping of the study area in 1938 (Bibliothèque et Archives nationales du Québec, E21, P112).

Appendix S6. Comparison of simulated and observed numbers of aspen stand centroids tallied within all fire polygons (as shown in Fig 3c; blue curve) with the number tallied when considering only the "recent fire" class.

Appendix S7. The spatial distribution of fire, aspen and birch in the Lower St. Lawrence region (Québec, Canada) (ecoforest maps from the Ministry of Natural Resources, MRNQ 2000a) in relation with the landscape structure classes of the 1938 map.

Summary for the expanding entries

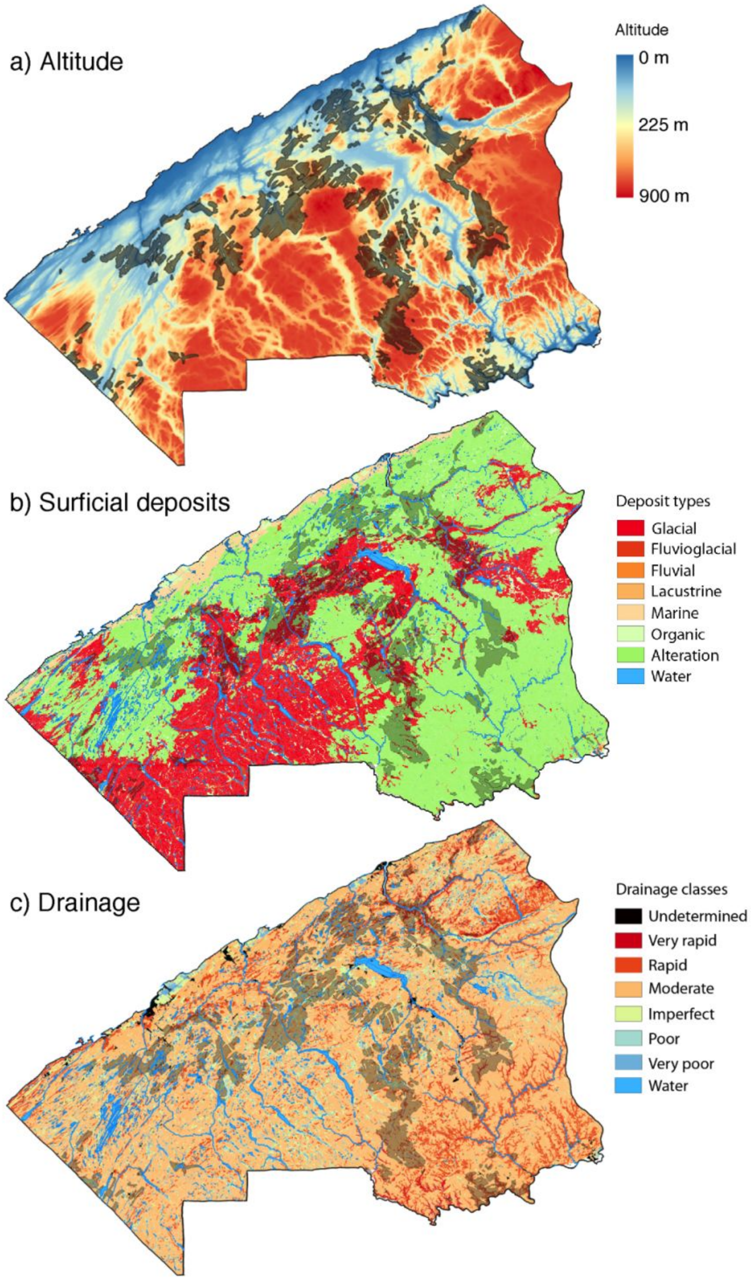
Using an archival map dated to 1938 and other spatial data, this study showed that anthropogenic fires generated a recognizable landscape pattern of land-use in Eastern Québec, Canada. Lingering impacts of 20th-century fires on present-day forests were identified using the peculiar spatial distribution of tree species. Specifically, the presence and spatial distribution of aspen on present-day landscape is tightly associated with previously burnt areas.

Chosen image for the expanding entries

Figure 1 (1938 map).

Supporting information to the paper

Terrail, R. et al. Effects of 20th-century settlement fires on landscape structure and forest composition in Eastern Québec, Canada. *Journal of Vegetation Science*



Appendix S1. Maps of altitude (a), surficial deposits (b) and drainage classes (c) across the study area. Shaded gray areas correspond to all fires (ancient plus recent).

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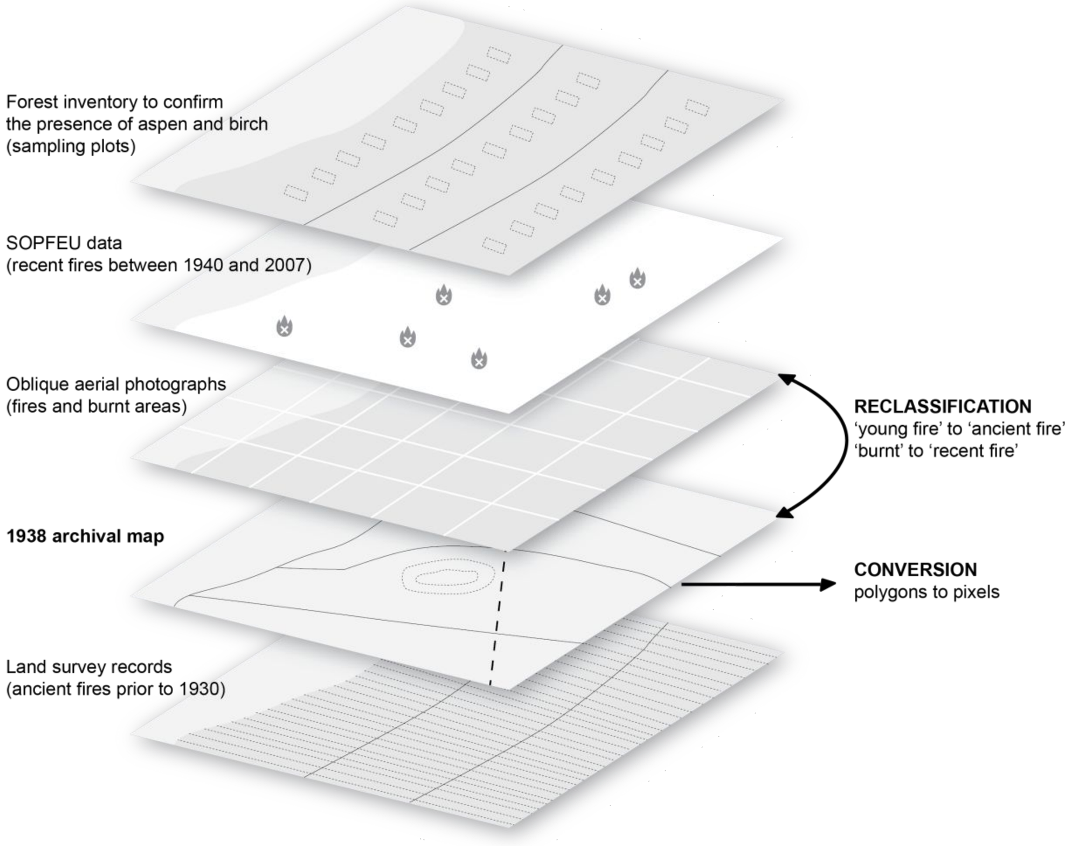
Terrail, R. et al. Effects of 20th-century settlement fires on landscape structure and forest composition in Eastern Québec, Canada. *Journal of Vegetation Science*



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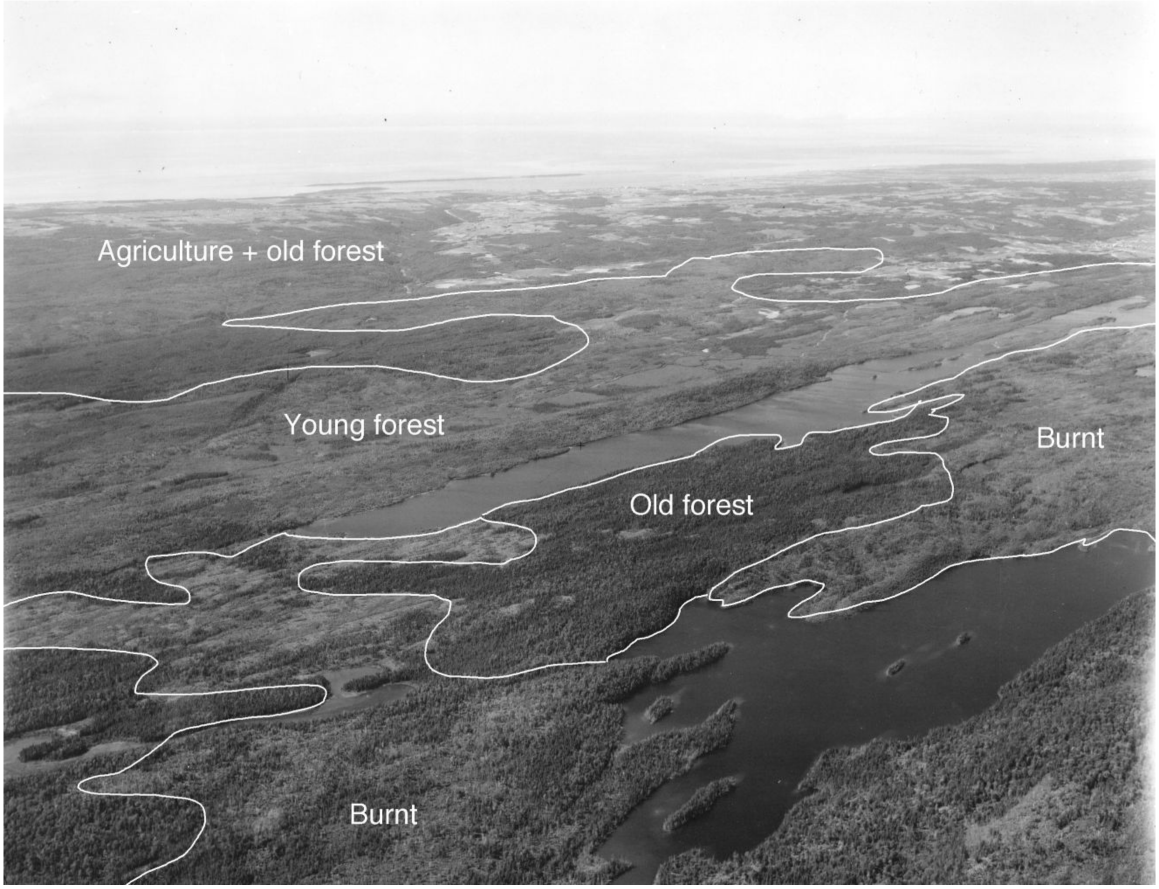
5

6 **Appendix S2.** Diagram showing the temporal and conceptual relationships between the georeferenced layers used in

7 this study.

Supporting information to the paper

Terrail, R. et al. Effects of 20th-century settlement fires on landscape structure and forest composition in Eastern Québec, Canada. *Journal of Vegetation Science*



Appendix S3. Archive photo illustrating the landscape classes mapped from the 1938 aerial survey in the hinterland of the Lower St. Lawrence region (Québec, Canada). "Young forest" polygons consistently correspond to fires with very similar appearance and age as "burnt" polygons, with typical unburned islands and irregular contours. In fact, the "burnt" and "young forest" areas displayed in the photo burned during the same fire event in 1923. The St. Lawrence River is in the background. The oblique photo was taken during the aerial survey and was then used to validate the mapping of landscape classes (Bibliothèque et Archives nationales du Québec, E21, P96).

Supporting information to the paper

Terrail, R. et al. Effects of 20th-century settlement fires on landscape structure and forest composition in Eastern Québec, Canada. *Journal of Vegetation Science*

Appendix S4. Validation of the mapped ecoforest polygons dominated by *Populus* and *Betula* taxa from the associated field plots of the Third Decennial Inventory of the Québec Ministry of Natural Resources. Plots are circular units covering surfaces of 0.4 ha (MRNFQ 2007). Frequency: number (percent) of plots containing the corresponding species for each polygon category. Mean stem density is averaged across all plots containing a given species.

	"*Populus*" polygon		"*Betula*" polygon	
	Frequency	Stem density (N/ha)	Frequency	Stem density (N/ha)
All species	444	1069 ± 470	807	920 ± 457
Populus tremuloides	354 (79.7%)	366 ± 335	123 (15.2%)	135 ± 168
Populus balsamea	65 (14.6%)	332 ± 423	10 (1.2%)	90 ± 65
Betula papyrifera	331 (74.5%)	181 ± 206	651(80.7%)	259 ± 257
Betula alleghaniensis	53 (11.9%)	80 ± 61	482(49.8%)	102 ± 86

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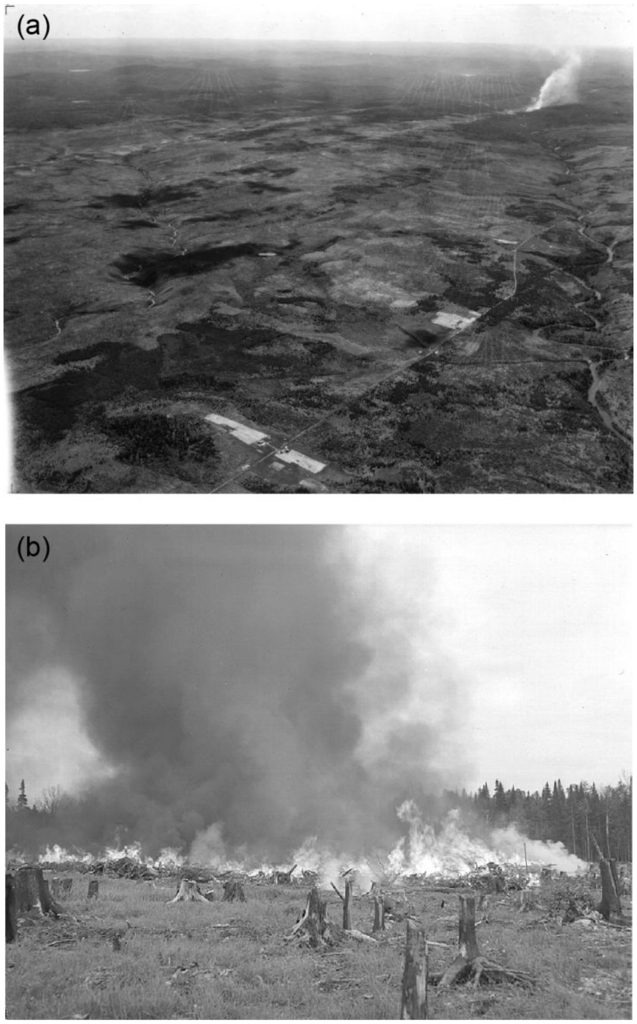
Terrail, R. et al. Effects of 20th-century settlement fires on landscape structure and forest composition in Eastern Québec, Canada. *Journal of Vegetation Science*



Appendix S5. Archive photos illustrating typical slash fires during the settlement in the hinterland of the St. Lawrence region (Québec, Canada): (a) oblique aerial photograph taken at the time of the mapping of the study area in 1938 (Bibliothèque et Archives nationales du Québec, E21, P112). Note the establishment of ribbon farms along two range lines (front and background of the photo). The land between the two ranges were almost completely burnt shortly before the photograph. An active slash fire is visible on the top-right; (b) slash fire in 1944 at Saint-Marcellin (photo by Paul Carpentier, Bibliothèque et Archives nationales du Québec, E6, S7, SSl, P21326).

Supporting information to the paper

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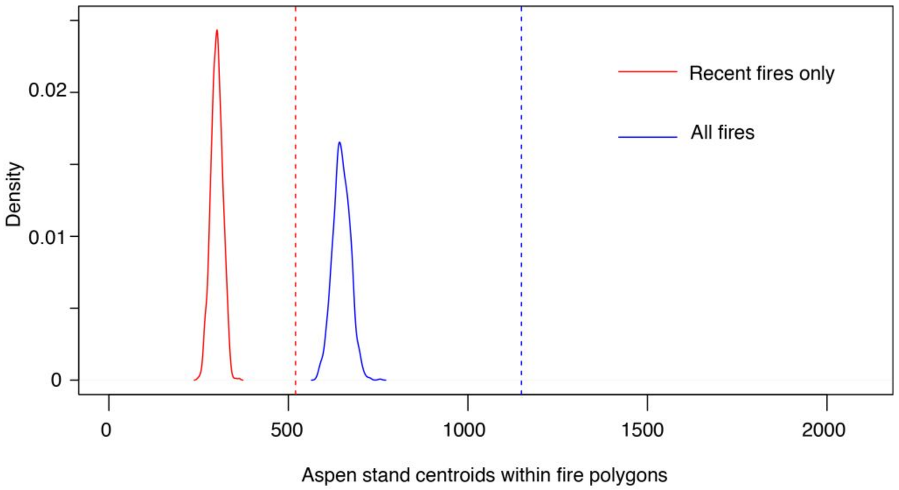

Appendix S6. Comparison of simulated and observed numbers of aspen stand centroids tallied within all fire polygons (as shown in Fig 3c; blue curve) with the number tallied when considering only the "recent fire" class. Frequency distributions indicate the number of aspen stand centroids (n = 3,586) included within fire polygons over 1,000 random permutations. Vertical dotted lines refer to the number of stands actually recorded within each fire polygon dataset, which are far greater than the numbers observed during each of the 1000 random permutations. The conclusion of a strong connection between aspen stands and fire polygons thus holds whatever the fire dataset considered.

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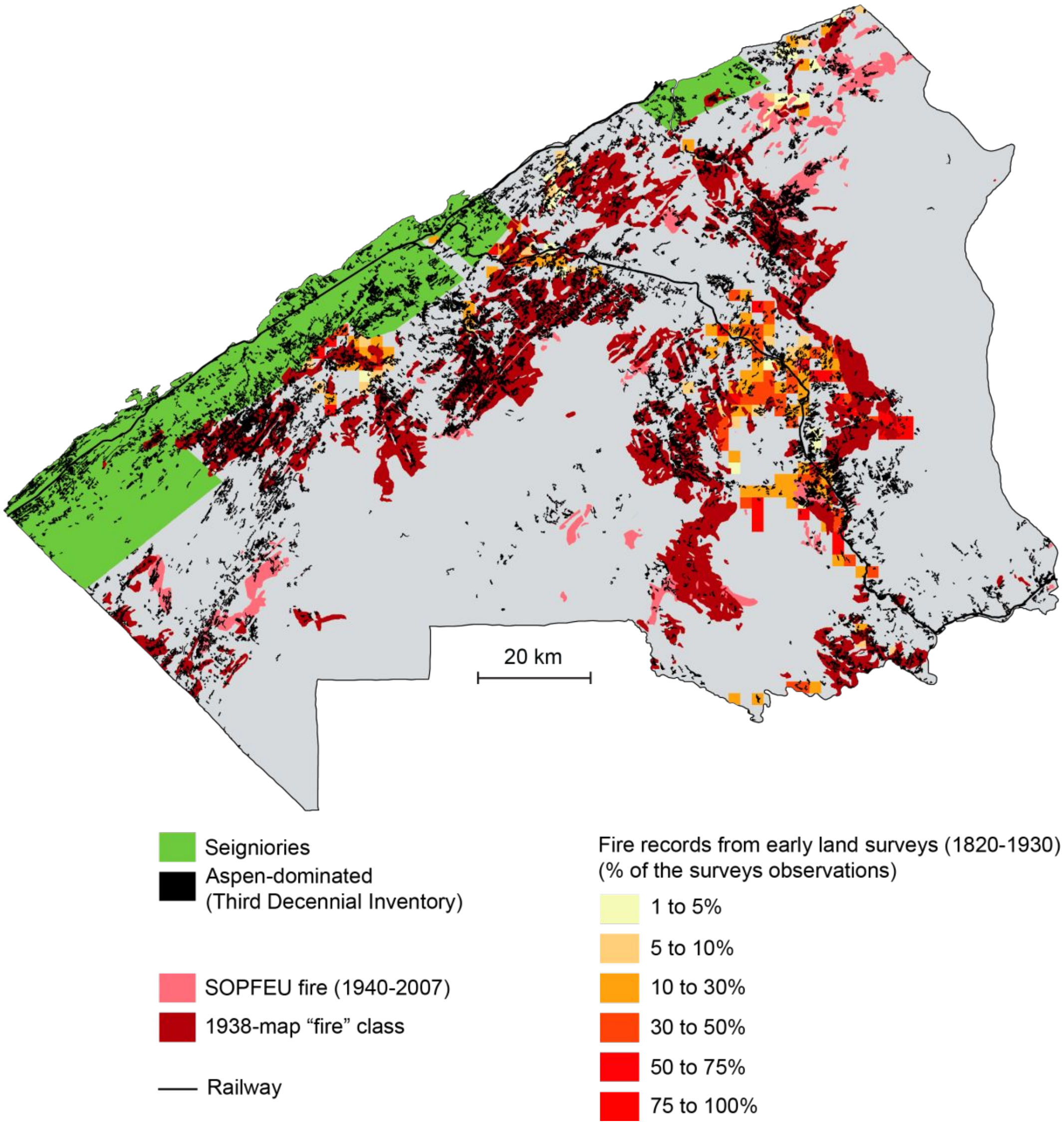

Appendix S7. The spatial distribution of fire, aspen and birch in the Lower St. Lawrence region (Québec, Canada) (ecoforest maps from the Ministry of Natural Resources, MRNQ 2000a) in relation with the landscape structure classes of the 1938 map.