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Drivers of postfire soil organic carbon accumulation in the boreal forest

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Abstract

The accumulation of soil carbon (C) is regulated by a complex interplay between abiotic and biotic factors. Our study aimed to identify the main drivers of soil C accumulation in the boreal forest of eastern North America. Ecosystem C pools were measured in 72 sites of fire origin that burned 2–314 years ago over a vast region with a range of Δ mean annual temperature of 3°C and one of Δ 500 mm total precipitation. We used a set of multivariate a priori causal hypotheses to test the influence of time since fire (TSF), climate, soil physico-chemistry and bryophyte dominance on forest soil organic C accumulation. Integrating the direct and indirect effects among abiotic and biotic variables explained as much as 50% of the full model variability. The main direct drivers of soil C stocks were: TSF >bryophyte dominance of the FH layer and metal oxide content >pH of the mineral soil. Only climate parameters related to water availability contributed significantly to explaining soil C stock variation. Importantly, climate was found to affect FH layer and mineral soil C stocks indirectly through its effects on bryophyte dominance and organo-metal complexation, respectively. Soil texture had no influence on soil C stocks. Soil C stocks increased both in the FH layer and mineral soil with TSF and this effect was linked to a decrease in pH with TSF in mineral soil. TSF thus appears to be an important factor of soil development and of C sequestration in mineral soil through its influence on soil chemistry. Overall, this work highlights that integrating the complex interplay between the main drivers of soil C stocks into mechanistic models of C dynamics could improve our ability to assess C stocks and better anticipate the response of the boreal forest to global change.

KEYWORDS

boreal forest, carbon dynamic, carbon sequestration, carbon stock, climate change, fire, soil carbon

1 | INTRODUCTION

One-third of the global forest carbon (C) is stored in boreal ecosystems (Dixon et al., 1994; Pan et al., 2011). Due to the slow rate of organic matter decomposition (Hobbie, Schimel, Trumbore, & Randerson, 2000), boreal forests accumulate C mostly in their soil (Deluca & Boisvenue, 2012). Understanding the processes involved in organic C storage in soils at high latitudes is a prerequisite to appreciate the potential of C sequestration in terrestrial sinks as a strategy to mitigate global warming (Jandl et al., 2007; Lal, 2005). Thus far, soil C pool has remained the major source of uncertainty in forest C stock predictions (Shaw et al., 2014), underlining that the complexity of soil systems is not fully pictured in models of C dynamics. By focusing on the complex interplay between climate, fire, vegetation attributes, and soil geochemistry regulating soil C pools, empirical studies should help improving the mechanistic understanding of soil C accumulation (Schmidt et al., 2011).

Climate drives forest ecosystem C stocks by affecting forest growth and decomposition processes. It also affects C stocks through changes in wildfire regime (frequency and severity). Following fire and in the absence of other major disturbance, aboveground biomass accumulates over time until it stabilizes (Bormann & Likens, 1979; Ward, Pothier, & Paré, 2014) or decreases (Wardle, Walker, & Bardgett, 2004). Similar responses have been observed in the forest floor wherein organic matter accumulates following time since disturbance (Nave, Vance, Swanston, & Curtis, 2011) until it either levels off (Ward et al., 2014) or continues to increase over time such as observed in soils undergoing paludification (Simard, Lecomte, Bergeron, Bernier, & Paré, 2007). Regarding mineral soil C stocks, the effect of time since fire (TSF) on the shape of C accumulation curves over time is not as well documented and most theoretical models simply assume a steady state or a very slow accumulation (Deluca & Boisvenue, 2012; Harden, Mark, Sundquist, & Stallard, 1992; Seedre, Shrestha, Chen, Colombo, & Jõgiste, 2011) with increasing TSF. Total ecosystem C is generally thought to reach a maximum in forest ecosystems after the living vegetation aggradation phase (Bormann & Likens, 1979; Ward et al., 2014), and possibly retrogresses (Wardle et al., 2004) in the absence of any other major disturbance event. However, it has been argued that total ecosystem C might slowly continue to accumulate in old-growth forests (Luyssaert et al., 2008), especially in dead organic matter pools (Kurz et al., 2013; Zhou et al., 2006). All such divergent patterns and conflicting ideas highlight the gaps that exist in our comprehension of the processes that regulate C dynamics in boreal forest ecosystems.

Recent findings point out climate as a secondary predictor of soil C stocks, weaker than soil geochemistry (Doetterl et al., 2015). Indeed, mineral surface reactivity has long been recognized as a strong determinant of soil C storage capacity (Castellano, Mueller, Olk, Sawyer, & Six, 2015; Six, Conant, Paul, & Paustian, 2002). In the boreal region, acidic parent material typically results in podsolization, which is characterized by organic matter accumulation in the illuvial (B) horizon, where organic matter is associated to different degrees with aluminum and iron oxides (Sanborn, Lamontagne, & Hendershot, 2011). Whereas podsolization occurs over long timescales, the changes and processes controlling mineral soil C accumulation over shorter periods of time following the years since the last fire event are poorly understood. Vegetation is another driver that can exert a profound effect on soil C cycling (Laganière, Boča, Van Miegroet, & Paré, 2017). In the boreal black spruce forest, changes in the composition of the tree canopy with TSF are limited as pure black spruce stands are typical of old-growth successional stages and are able to regenerate quickly after fire (Harper et al., 2003). Changes in the vegetation mostly occur in the understory, particularly in the moss layer (Fenton & Bergeron, 2008), where moss species dominance is known to change over time after fire disturbances. Nevertheless, simple effects of climate and vegetation on soil C stocks may prove to be difficult to disentangle as vegetation types often equilibrate within their optimal climatic envelope (Jobbagy & Jackson, 2000).

The objective of this study is to fill these knowledge gaps by quantifying changes in boreal forest C pools with TSF (from 2–314 years) and to disentangle the role played by soil physical (texture) and chemical (pH and metal oxide contents) properties, local biotic conditions (bryophyte dominance) and climate on soil C accumulation across the spruce feathermoss bioclimatic domain in eastern North America. Using a set of a priori causal hypotheses with direct and indirect effects, we addressed the following questions: (a) Does the ecosystem reach a maximum C storage after the living vegetation aggradation phase following disturbance? and (b) To which extent do interdependent relationships among TSF, climate, physical and chemical soil properties and bryophyte dominance influence soil organic C accumulation in both the FH layer and the mineral soil? Our study is framed within the state factor model of ecosystems (Amundson & Jenny, 1997). Thus, we start with the assumption that once site factors such as overstory composition, surficial deposits and soil drainage are accounted for, dynamic-ecosystem C pools (i.e., aboveground biomass, downed coarse woody debris, and FH layer) are mostly controlled by TSF (Seedre et al., 2011), whereas mineral soil C pools are mostly controlled by climate and soil chemistry (Doetterl et al., 2015).

In boreal ecosystems, the accumulation and maintenance of soil organic matter in the forest floor are driven by the primary fungal decomposition of plant residues. This humification process is governed by the incomplete decomposition of litter, notably resulting from a great biological competition for limited nitrogen, that favors an immobilization and a blockage of the nitrogen cycle (Prescott, Maynard, & Laiho, 2000). Following the Soil Classification Working Group (1998), we use the term FH layer in reference to the partially decomposed (fragmented, F) and decomposed (humified, H) soil organic matter accumulated in a thick layer at the soil surface, also defined as mor humus (Weetman, 1980), in distinction with the mineral soil layers beneath. The FH layer is equivalent to the Oi and Oe/Oa layers.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in sites distributed across the managed portion of the boreal forest of eastern Canada, a forest dominated by evergreen conifer species and located roughly between 49°N and 52°N and from 68°W to 76°W (Figure 1). In this study region, the Canadian Shield bedrock is mainly composed of igneous (granitoïds) and metamorphic (gneiss, migmatites) materials formed during the Precambrian, covered by glacial tills and localized fluvio-glacial deposits (Robitaille & Saucier, 1998). Topography is flat in the west and undulated with more pronounced slopes in the center and in the east. Regional climate is subpolar subhumid with mean annual temperatures ranging south to north from 0 to −5°C. Mean annual precipitations ranges from west to east from 800 to 1300 mm (Robitaille & Saucier, 1998), reflecting continental climate and maritime influences on the regional climate (Ecological Stratification Working Group, 1996). The landscapes are dominated by black spruce (*Picea mariana* [Mill.] B.S.P) stands associated with ericaceous understory and feathermoss ground layers. The length of fire cycles typically increases north to south and west to east (Portier, Gauthier, Leduc, Arseneault, & Bergeron, 2016). As a result, within a general matrix of black spruce, fire-resistant jack pine (*Pinus banksiana* [Lamb.]) and fire-intolerant balsam fir (*Abies balsamea* [L.] Mill.) exchange codominance across this fire gradient. In this territory where human density is very low, fires are naturally ignited by lightning strikes. Large and stand-replacing crown wildfires are common in these black spruce forests (Bergeron, Gauthier, Flannigan, & Kafka, 2004; Rogers, Soja, Goulden, & Randerson, 2015). In burnt areas, as a result of crowning most trees are left dead following fire in pure black spruce stands (Kafka, Gauthier, & Bergeron, 2001; Figure 2). The thick forest floor layer developing under the black spruce canopy can be reduced by 60% with burning (Greene et al., 2007), depending on its bulk density and its moisture content (Miyanishi & Johnson, 2002).

2.2 | Stand selection and field sampling design

Our goal was to establish sample plots across a chronosequence of time since fire (TSF). We used digital forest inventory maps produced between 1990–2000 and 2000–2010 by the ministère des Forêts, de la Faune et des Parcs du Québec (MFFPQ) to ensure that stands were as similar as possible in terms of canopy composition, surficial deposits and mesic drainage conditions. We used *ArcGIS* v10.2 to overlay these forest inventory maps with fire maps compiled by the MFFPQ and other published dendrochronological survey (Belisle, Gauthier, Cyr, Bergeron, & Morin, 2011; Bouchard, Pothier, & Gauthier, 2008; Cyr, Gauthier, & Bergeron, 2012; Frégeau, Payette, & Grondin, 2015; Le Goff, Flannigan, Bergeron, & Girardin, 2007; Portier et al., 2016) in order to implement our chronosequence. When in doubt, stand age was verified in the field by coring 2–3 dominant trees, although none of these verifications came up with ages that were significantly different from those of the digital maps. The sampling effort thus planned covered 72 sites and was carried out in 2015.

Field inventory and soil sampling mostly followed Canada's National Forest Inventory ground plot guidelines (NFI (2016); Supporting information Figure S1). In each stand, we established a single 314 m^2 circular plot (10 m radius) for biophysical descriptions and soil sampling. Slope was measured from the center of the plot with

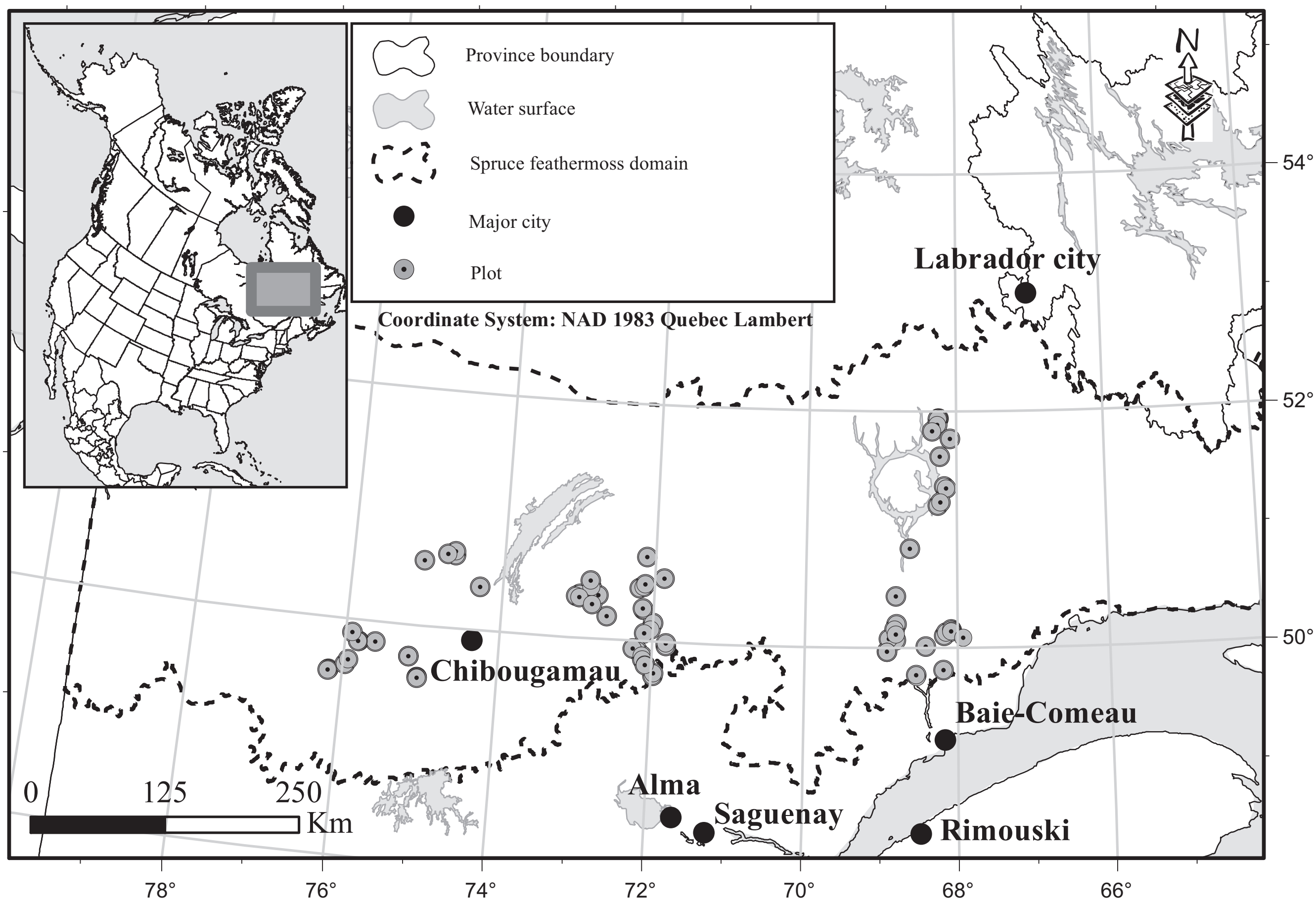

FIGURE 1 Map of the study area showing the spatial distribution of the sample plots (N = 72)

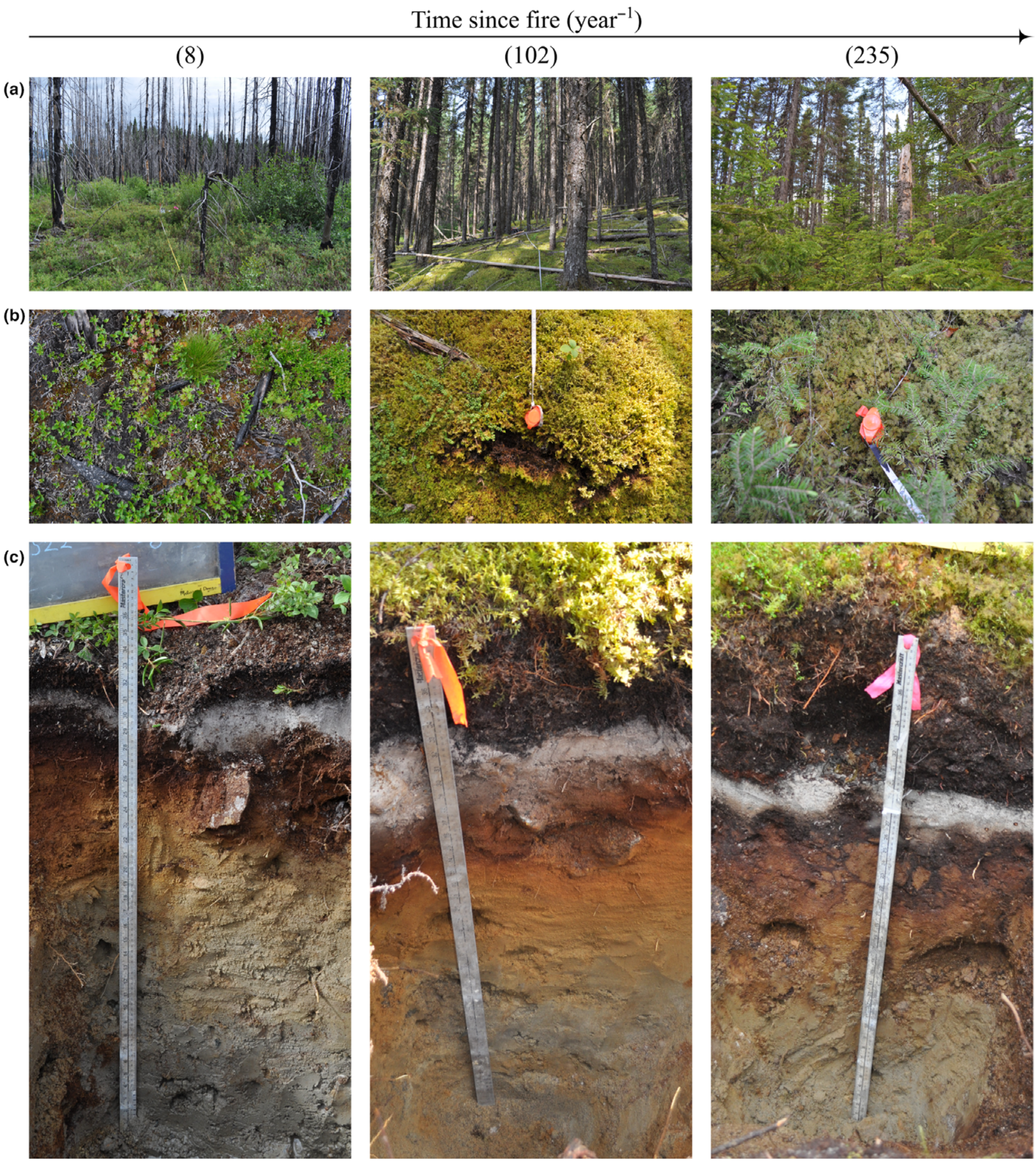

FIGURE 2 Set of field photos. Horizontal overall plan of the stand from the plot center (a) shows the transition from dead trees to single age structure toward a more complex age-class structure with several cohorts and senescent trees when the stand gets older. View from above (b) captured the ground layers, with charred twigs and mosses after fire toward a dense moss carpet in mature stands, with seedlings benefiting from canopy opening in older stands. Soil pits (c) exhibit the organic layer depth and the podzolized mineral soil horizons (scale = 1 m)

a clinometer, aspect with a compass, and stand basal area using a factor-2 prism. FH layer depth was measured every 2 m with a soil auger along two orthogonal transects following main cardinal directions, for a total of 20 measurements per plot. At the same point locations where FH layer depth was recorded, we identified the dominant moss at the genus level using 400 cm^2 microplots, for a total of 20 microplots per 314 m^2. We also recorded tree species, diameter and decay class of all downed coarse woody debris ($\geq$3 cm in diameter) crossing the two orthogonal transects. For the FH layer sampling, we selected three 400 cm^2 microplots, each separated by a minimum distance of 15 m. In these microplots, we first gathered the litter and the green living mosses layer separately. We then collected volumetric samples of the FH layer down to the mineral soil (Preston, Bhatti, Flanagan, & Norris, 2006). After FH layer was carefully extracted, we sampled the mineral soil (top 15 cm) using volumetric samples with a metallic cylinder (height = 15 cm, inner diameter = 4.7 cm) in each of the three microplots. Finally, a soil pit was dug down to the illuvial (B) horizon or to the bedrock when possible. One wall of the pit was cleaned and the entire soil profile was described. Then, we collected samples from 15 to 35 cm under the FH layer-mineral soil boundary and in the illuvial horizon (top 15 cm) using volumetric samples with a metallic cylinder (inner diameter = 4.7 cm). Because of the stoniness in one site, we could not sample the mineral soil. Thereafter, this site was discarded from the analyses of soil C stocks. Soil samples were maintained at 2°C in a cooler before processing for analyses.

2.3 | Laboratory analyses

For soil analyses, we used mean composite samples for each of the 72 sample plots where soil materials obtained from every microplot were pooled and mixed by plot and soil layer (FH layer or top 15 cm of mineral soil). FH layer was sieved at 6 mm and oven dried (60°C), whereas mineral soil samples were air dried and sieved through a 2-mm mesh. Dried samples were weighted to estimate bulk density before processing for physicochemical analyses.

All samples were finely ground (0.5 mm) for C content or Fe and Al (illuvial horizon only) determination. Carbon concentration was analyzed by dry combustion (Skjemstad & Baldock, 2007) using a Leco TruMac (Leco Corp., St. Joseph, MI, USA). Organically complexed Fe and Al (Mpy), hereafter defined as metal oxides, were extracted with a tetrasodium pyrosphosphate solution ($Na_4P_2O_7$ 0.1N) and analyzed by inductively coupled plasma atomic emission spectroscopy (Courchesne & Turmel, 2007) with an Optima 7300 DV (Perkin Elmer Inc., Waltham, MA, USA). FH layer and mineral soil potential of hydrogen (pH) was determined in a soil:water solution of 1:10 and 1:2 (Hendershot & Lalande, 2007), respectively, with a pH meter (Orion 2 Star) and soil texture was assessed by a standard hydrometer method (Kroetsch & Wang, 2007). Because bedrocks are acidic and soil pH is low ($3.3 <$ FH layer pH < 4.2; $4.4 <$ illuvial horizon pH < 5.7), we did not expect any carbonates in soil samples, and total C is considered here as organic C (Strand, Callesen, Dalsgaard, & de Wit, 2016).

All laboratory analyses were carried out at the Laurentain Forestry Center in Québec, QC, Canada.

2.4 | Carbon pool calculations

We calculated C stock in aboveground tree biomass separately for each plot using basal area field measurements and the allometric equation of Paré et al. (2013), assuming half C in the total biomass:

$$C_{\mathrm{ABG}} = \frac{1}{2}\sum\left(a \times B_S^b \times B_T^c\right)$$

where C_{ABG} is the aboveground C density (MgC/ha), B_S is the basal area for a species S (m^2/ha), B_T is the total basal area (m^2/ha), and a, b, and c are parameters whose values are species-specific.

We calculated C stock in coarse woody debris according to the line intersect method of Van Wagner (1968) assuming total biomass contains half C (C. Wang, Bond-Lamberty, & Gower, 2003), as follows:

$$C_{\mathrm{CWD}} = \left(\frac{\pi^2 \sum\left(d^2 D_{\mathrm{WS}}\right)}{8L}\right) \times 0.5$$

where C_{CWD} is the C density in coarse woody debris (kgC/ha), d is piece diameter (cm), D_{WS} is the wood density (kg/m^3) for a species S and for a given decay class (unpublished internal database: National Forest Inventory Project Office), and L is the total measured transect length (m).

We calculated soil C content for each sample by multiplying its C concentration with its respective bulk density and depth (here, equals to mean depth based on 20 measurements for the FH layer), assuming there were no coarse fragments in FH layer, and corrected for coarse fragments (>2 mm) in the mineral soil horizons.

Because of some very stony mineral soils, some samples (samples 15–35 cm, $n = 8$; samples 0–15 cm in the illuvial horizon, $n = 5$) had to be extracted in a nonvolumetric manner. Based on the other samples of our database, we estimated their bulk density using a nonlinear organic density model developed by Federer, Turcotte, and Smith (1993) and successfully used by Périé and Ouimet (2008) in soils of eastern North America:

$$D_b = \frac{D_{\mathrm{bm}}\, D_{\mathrm{bo}}}{\left(F_o\, D_{\mathrm{bm}}\right) + \left(1 - F_o\right)\, D_{\mathrm{bo}}}$$

where D_b is the bulk density, D_{bm} is the bulk density of "pure" mineral soil material (i.e., soil without any organic fraction), D_{bo} is the bulk density of "pure" organic soil (i.e., soil without any mineral fraction), and F_o is the organic mass fraction of the sample. Whereas only C concentration was analyzed here, we assumed a conversion factor of 2 (Pribyl, 2010) to estimate the value of F_o.

Mineral soil C stocks were summed across horizons (top 15 cm and 15–35 cm deep) and other mineral soil explanatory variables were transformed with a weighted mean by depth for subsequent statistical analysis. For this study, we did not use the litter plus green living mosses carbon pool because this C reservoir was very small (Taylor, Seedre, Brassard, & Chen, 2014). All C stocks are reported in tons per hectare (MgC/ha) hereafter.

2.5 | Climatic data

Climatic data were generated using BioSIM v10.3.2 (Régnière, Saint-Amant, & Béchard, 2013). Based on current knowledge and a priori hypotheses, we selected mean annual temperature (MAT), mean annual precipitation (MAP), annual growing degree-days above 5°C (GDD5), and water balance (WB, i.e., annual precipitation minus potential evapotranspiration) as the main possible climatic drivers of soil C stocks in our analyses. We used the 1981–2010 climate normals (http://climat.meteo.gc.ca/) to interpolate these climatic drivers at the plot level from the eight nearest surrounding weather stations, considering local field-measured slope attributes as correcting factors (for more details, see Régnière (1996)). The Canadian climate normals used in this study are meteorological daily records of weather stations across the national territory. Following the World Meteorological Organization standards, normals are computed with the arithmetic mean for each month within a year, over a 30-year period.

2.6 | Ground layer dominance

To discriminate the importance of *Sphagnum* spp. from that of feathermoss species holding different ecophysiological characteristics (Bisbee, Gower, Norman, & Nordheim, 2001), we calculated an index of moss dominance (IMD) inspired by Nalder and Wein (1999) as follows:

$$\mathrm{IMD} = \frac{O_{\mathrm{sph}}}{O_{\mathrm{sph}} + O_{\mathrm{pl}} + O_h + O_{\mathrm{pt}}}$$

where O is the sum of occurrence for a species in the 20 (20 × 20 cm^2) microplots, *sph*: *Sphagnum* spp., *pl*: *Pleurozium schreberi* (Brid.) Mitt., *h*: *Hylocomium splendens* (Hedw.) Schimp., and *pt*: *Ptilium crista-castrensis* (Hedw.).

When the IMD tends toward 1, the moss stratum is dominated by *Sphagnum* spp., whereas when the IMD tends toward 0, other moss species dominate the moss stratum. For plots where fire was recent and no moss species were observed (n = 5), the IMD was set to 0. We detected no significant changes in the results when excluding or including these plots in our analyses.

2.7 | Ecological a priori hypotheses

The chronosequence approach used in our study implies the existence of a single successional trajectory (Kenkel, Walker, Watson, Caners, & Lastra, 1997). In black spruce-dominated forests of eastern North America, Frégeau et al. (2015) inferred from paleological data that the local vegetation has developed under recurrent dynamics (i.e., the cyclic return to a black spruce dominance after fire) for several millennia. Thus, we assumed there were no changes in canopy composition with time and that the current vegetation has developed from similar vegetation. Also, the low vegetation diversity in the study area together with the single and cyclic successional trajectory makes space-for-time inferences suitable (Walker, Wardle, Bardgett, & Clarkson, 2010).

The following environmental variables were considered as important drivers of soil C storage within boreal forest ecosystems and were included in our analyses: climate (temperature and water supply), soil texture, TSF, dominance of the moss functional type, soil pH, and concentration in metal oxides. Based on our overall dataset, preliminary results showed that carbon stocks in the FH layer and in the mineral horizons were uncorrelated (Supporting information Figure S2). Moreover, numerous studies have already shown that C storage patterns in the FH layer and mineral soil are often governed by different processes (Fierer, Allen, Schimel, & Holden, 2003; Salomé, Nunan, Pouteau, Lerch, & Chenu, 2010; Ziegler et al., 2017). We therefore built, for each of these two C pools, separate sets of a priori ecological hypotheses using direct acyclic graphs (DAGs) representing different causal relationships among environmental variables and C stocks (Figure 3). This led us to test the validity of six competing a priori ecological hypotheses, each being represented by a DAG. We used a hypothetico-deductive approach in which each a priori hypothesis was coherent with ecological knowledge and represented an alternative causal explanation that could be falsified as regards the underlying mechanisms of soil C storage in the two main C pools. The first two hypotheses, one for each C pool (hypothesis FH0 and B0 in Figure 3), assume direct relationships between variables and C stocks, as well as statistical independence among variables. These two hypotheses were used as baseline for comparisons since they mirror the dominant approach with only direct effects used in the literature to assess the effect of environmental variables on soil C stocks (for example, see Marty, Houle, and Gagnon (2015); Nalder and Wein (1999); Strand et al. (2016)), which uses Jenny's factor model of soil formation (Jenny, 1994). We also formulated a set of a priori competing hypotheses involving indirect effects among variables and C stocks (hypotheses FH1, FH2, B1 and B2 in Figure 3). Ecological justification for each a priori hypothesis represented by a different DAG (Figure 3) is given below:

2.7.1 | Baseline hypothesis for the FH layer, FH0

In this hypothesis, fire directly affects FH layer pool size through direct combustion and FH layer buildup with TSF (Harden et al., 2012; Knicker, 2007). Climatic conditions and pH both have direct effects on C accumulation because they are key determinants of the decomposition process (Prescott et al., 2000; Zhang, Hui, Luo, & Zhou, 2008). Climate and pH also are important drivers of the substrate use efficiency of soil microbes (Cotrufo, Wallenstein, Boot, Denef, & Paul, 2013), but their relative contributions remain unknown. Several studies have reported that the dominance of the ground layer vegetation also influences C accumulation processes (Bisbee et al., 2001; Bona, Fyles, Shaw, & Kurz, 2013). Feathermosses have a higher decomposability (Fenton, Bergeron, & Paré, 2010; Lang et al., 2009) and lesser productivity (Bisbee et al., 2001) than sphagna, so we expected more C accumulation in the FH layer with the increasing dominance of sphagna. Finally, waterlogged conditions are known to promote anoxic environment impeding microbial decomposition, so rapid draining on coarse-textured soils may favor faster soil organic matter decomposition (Bauhus, Paré, & Côté, 1998; Trumbore & Harden, 1997).

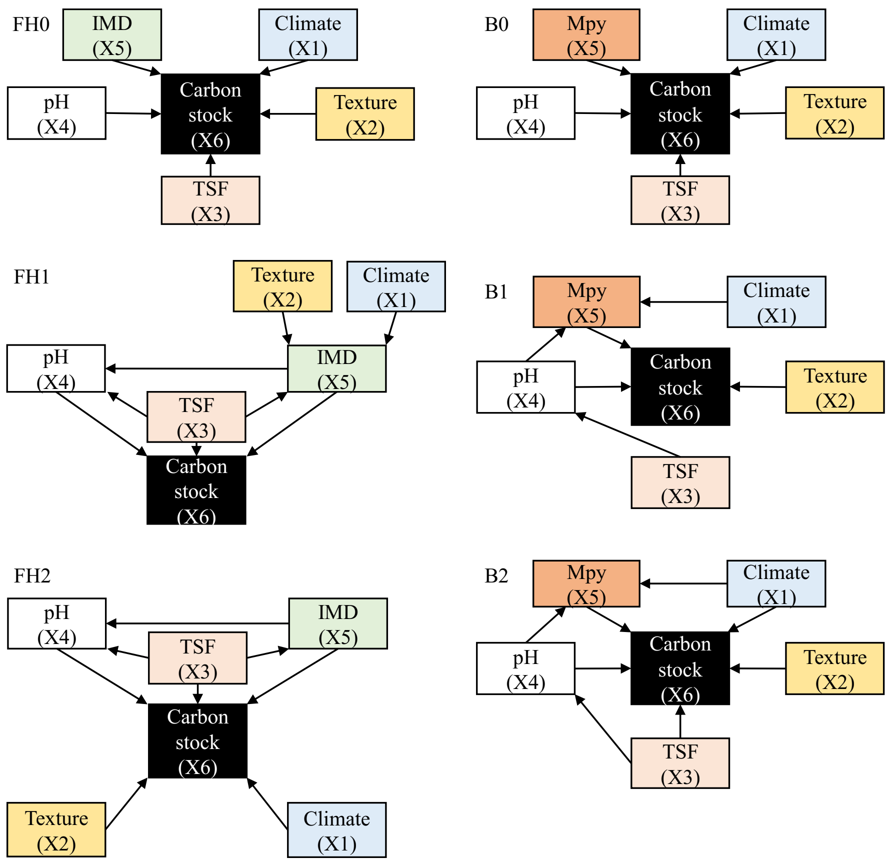

FIGURE 3 Path models for multivariate causal hypotheses testing FH layer C stocks (FH0, FH1 and FH2) and illuvial horizon C stocks (B0, B1 and B2). Arrows indicate direct causal effects. *Climate*: climate variable; *Texture*: texture of the mineral soil (top 35 cm); *TSF*: time since fire; *pH*: potential of hydrogen in the FH layer (FH models) or illuvial horizon (B models); *IMD*: index of moss dominance; *Mpy*: pyrophosphate extractable metals in the illuvial horizon

2.7.2 | Alternative hypothesis for the FH layer, FH1

In this hypothesis, as in hypothesis FH0, fire has a direct effect on C stocks through changes in FH layer pool size with TSF. However, contrary to hypothesis FH0, hypothesis FH1 postulates that TSF also has indirect effects on C stocks through direct effects on pH conditions and on the moss dominance, as supported by empirical studies (Simard et al., 2007; Ward et al., 2014). FH1 hypothesis also postulates that climate conditions and soil texture influence C stocks only indirectly through their direct and synergic effects on the change of dominance in the ground layer from feathermosses to sphagnum species. Fire can modify soil pH through organic acid denaturation and neutralization of acidity by base-saturated ash materials (Certini, 2005; Gonzalez-Perez, Gonzalez-Vila, Almendros, & Knicker, 2004; Knicker, 2007). In addition, FH layer pH has been shown to decrease with TSF in the mesic black spruce forests of eastern Quebec (Ward et al., 2014), as well as in most aggrading forests, due to the imbalance of charge in nutrient uptake (Driscoll & Likens, 1982). More specifically, protons are exchanged by roots when cations are taken up by growing vegetation in excess compared to anions. When the vegetation maintains physiological electroneutrality, it leads to soil acidification. Simard et al. (2007) reported a shift in ground layer dominance with TSF on poorly drained fine textured soil, suggesting that under these conditions, an increasing dominance of sphagnum species may be expected in the ground layer with increasing TSF. The IMD may have a direct effect on pH because sphagnum mosses have distinct physiological characteristics (release of polyuronic, humic and fulvic acids during decomposition, and hyaline cells retaining water) involved in the acidification of their environment relative to feathermosses (Lavoie, Paré, Fenton, Groot, & Taylor, 2005) and the drawing of water from the water table (Bisbee et al., 2001), which create conditions that favor the maintenance and spread of sphagnum colonies. Hence, contrary to hypothesis FH0, hypothesis FH1 postulates that climate has a direct effect on the IMD because we expected that feathermosses would be more dependent on water availability than sphagna.

2.7.3 | Alternative hypothesis for the FH layer, FH2

This hypothesis is a combination of FH0 and FH1. In this hypothesis, TSF is predicted to have both direct and indirect effects on C stocks according to the same causal relationships as in hypothesis FH1. However, hypothesis FH2 differs from hypothesis FH1 in that climate conditions and soil texture only have direct effects on C stocks, irrespective of the dominance of feathermoss versus sphagnum species. Sphagnum spp. occurrence is mostly related to local hydraulic parameters and available light (Bisbee et al., 2001), and because we controlled for drainage conditions in our study, we could expect ground layer dominance to be independent of soil texture and climate.

2.7.4 | Baseline hypothesis for the illuvial horizon, B0

In this hypothesis, variables are assumed to have only direct and independent effects on C stocks in the illuvial horizon. Metal oxides and fine mineral particles are known to bind C in mineral soils (organometallic complexation and adsorption) (Kaiser, Eusterhues, Rumpel, Guggenberger, & Kögel-Knabner, 2002; Rumpel & Kögel-Knabner, 2011; Soucémarianadin, Quideau, & MacKenzie, 2014). This suggests that C stocks in the mineral soil will increase with concentrations of metal oxides or fine mineral particles. Acidity slows the activity of decomposers (see hypothesis FH0), whereas a wetter and a warmer climate enhances C accumulation in the mineral soil (Buurman & Jongmans, 2005; Liski & Westman, 1997; Sanborn et al., 2011; Strand et al., 2016). This is supposedly due to an above- and belowground litter production that is imbalanced with the activity of decomposers in well-drained soils (Callesen et al., 2003), which allows for larger organic matter inputs to the mineral soil that can potentially be stabilized through complexation and adsorption on the inorganic mineral phase. The effect of fire on C stocks in the mineral soil is still ambiguous in the literature and is often assumed to be negligible (Deluca & Boisvenue, 2012; Knicker, 2007; Seedre et al., 2011). Nevertheless, we assumed a direct effect of TSF on C stocks in the illuvial horizon as some studies have shown that C stocks in the mineral soil were larger in old forests compared with adjacent burnt stands (Smith, Coyea, & Munson, 2000), or that they accumulated slightly with TSF (Johnson & Curtis, 2001; Pregitzer & Euskirchen, 2004).

2.7.5 | Alternative hypothesis for the illuvial horizon, B1

In this hypothesis, climate exerts an indirect control only on C stocks (Doetterl et al., 2015) through its direct effect on mineral weathering and on the amounts of metal oxides leached from the upper horizons (Egli et al., 2009). Soil pH is hypothesized to have both a direct effect on C stocks through changes brought to the decomposition process and an indirect effect on C stocks through changes occurring in the creation of organometallic complexes (Buurman & Jongmans, 2005; Porras, Hicks Pries, McFarlane, Hanson, & Torn, 2017). Time since fire exerts an indirect effect on C stocks by influencing soil pH through the liming effect within the first few years after fire (see FH1), whereas over the long-term, mineral soil acidifies through a charge imbalance in the nutrient uptake with vegetation growth (Driscoll & Likens, 1982).

2.7.6 | Alternative hypothesis for the illuvial horizon, B2

This hypothesis is a combination of B0 and B1. In this hypothesis, climate and TSF are predicted to have both direct and indirect effects on C stocks according to the same causal relationships as in hypotheses B0 and B1. The direct effect of TSF on illuvial horizon C stocks arises from the slow incorporation of charcoal and hydrophobic organic matter into the mineral soil following fire (Johnson & Curtis, 2001). The indirect effect of TSF on illuvial horizon C stocks is attributed to changes in the mineral soil pH with TSF (see FH1). Climate has a direct effect on illuvial horizon C stocks through its direct effect on litter inputs and on the decomposition process (see B0). Climate also has an indirect effect on illuvial horizon C stocks through its direct effect on mineral weathering and leaching (see B1).

2.8 | Statistical analyses

First, we evaluated postfire C dynamics using linear regression of C pools with TSF. When a curvature in the relationship was observed, we used a piecewise regression with the R package '*segmented*' (Muggeo, 2008) to extract breakpoint coordinates. Second, we used confirmatory path analysis with directional separation tests (*d-separation* or *d-sep*; Shipley (2000a)) to quantify direct and indirect causal relationships between variables and C stocks according to the set of alternative a priori ecological hypotheses described above (Figure 3). We used path analysis together with Fisher's C test (Shipley, 2000b) as a simultaneous test of independence for a model basis set (i.e., all nonadjacent pairs of variables defined as claims of independence) in order to assess how each hypothetical DAG was supported by our data and to identify which hypothesis could be rejected or not based on a robust statistical test (Shipley, 2009). Fisher's C statistic was compared to a chi-squared distribution with 2k degrees of freedom (where k is the number of independence claims in a model basis set). We chose the significance level of 0.05 to decide when to reject a causal model (rejected when $p < 0.05$). All variables were standardized (i.e., centered on the mean and divided by the standard deviation) prior to analyses to quantify their relative contributions to C stocks variability.

We compared the fit of each DAG within each C pool using a model selection approach (Shipley, 2013) together with the second order Akaike's information criterion (AICc) in order to account for finite sample size ($N = 71$). Model selection was based on relative AICc difference with the 'best model' or relative weight (Symonds & Moussalli, 2010). As we had no a priori knowledge about which specific climate and texture variables should be used for testing the validity of each hypothesis/DAG, we used the cross-product of four climatic (MAT, MAP, GDD and WB) and three soil texture (sand %, silt %, and clay %) variables, which yielded a total of 12 model combinations to be tested for each hypothesis/DAG. As we had three different hypotheses in both C pools, the model selection procedure resulted in the comparison of 36 candidate DAG models for each C pool. We calculated model-averaged estimates by multiplying each estimate within each model by the corresponding Akaike weight and by summing the resulting values across all models. By doing so, we avoided making arbitrary decisions about which model should be considered by allowing all models to influence model-averaged estimates. Path analyses were conducted using the '*ggm*' package (Marchetti, Drton, & Sadeghi, 2015) and all calculations and statistical analyses were made with *R* software version 3.0.2 (R Core Team, 2017). All data presented in this paper can be retrieved online for free (Andrieux, Beguin, Bergeron, Grondin, & Paré, 2018).

3 | RESULTS

3.1 | Postfire carbon dynamics

Across our plots, carbon (C) accumulated with increasing time since fire (TSF), but the shape of this accumulation varied by pool (Figure 4). Total ecosystem C stock tended to increase linearly (Figure 4a), ranging from 83 to 356 MgC/ha for TSF values of 2 years and 283 years, respectively. Aboveground tree C stock (Figure 4b) was negligible in the first decades after fire, peaked at 90 ± 9 years, and showed a significant ($p = 0.02$) but minor decrease in older stands. The maximum observed aboveground tree C stock was 105 MgC/ha in a 91-year-old stand. The C stock in coarse woody debris first decreased until 51 ± 11 years, and then increased until TSF reached 237 ± 25 years. The maximum observed C stock in coarse woody debris was 19 MgC/ha in a 10-year-old stand. Values of C stocks in coarse woody debris were negligible for values of TSF between 48 and 91 years. Coarse woody debris was found to be the smallest of all ecosystem C pools (Figure 4c). FH layer C stock generally increased linearly with TSF, but showed a very high variability around this trend. The lowest and highest values of 26 and 217 MgC/ha were found in plots with TSF values of 102 and 91 years, respectively (Figure 4d). Mineral soil (top 35 cm) C stock also increased linearly with TSF and also showed a high variability in measured values. The lowest and highest values of 19 and 159 MgC/ha were found in plots with TSF values of 171 and 314 years, respectively (Figure 4e).

The simple linear functions using TSF as sole explanatory variable explained 40% (for ecosystem), 61% (for aboveground tree biomass), 27% (for coarse woody debris), 9% (for FH layer) and 11% (for mineral soil) of C stock variability. According to these simple linear models, the ecosystem accumulated 0.44 MgC ha^{-1} $year^{-1}$ ($p < 0.001$) (Table 1). In the first 90 ± 9 years following fire, aboveground tree showed the greatest C accumulation rate, followed by FH layer and mineral soil (Table 1).

3.2 | FH layer path analysis and model selection

The first hypothesis (FH0) testing for direct effects of variables on FH layer C stocks was rejected based on Fisher's *C* statistic ($p < 0.01$), whereas most models related to FH1 and FH2 were not (Table 2). According to the model selection procedure, the two competing path models that best explained the data (ΔAICc < 2; Table 2), both belonged to hypothesis FH1 with water availability (MAP or WB) as climate variable and clay content as texture variable. Together, these two path models accounted for 74% of the Akaike weight and explained 44% and 46% of the variation between covariables and FH layer C stocks (FH1 with WB and clay % and FH1 with MAP and clay %, respectively; Figure 5 and Supporting information Table S1). We therefore concentrated our analyses on these two FH1-based path models.

Overall, in the FH1 hypothesis, TSF showed the greatest direct effect on FH layer C stocks (standardized path coefficient, pc = 0.37, $p < 0.01$), followed by moss layer dominance (pc = 0.31, $p < 0.01$). The value of pH decreased with TSF (pc = –0.32, $p < 0.01$), but increased with IMD (pc = 0.31, $p < 0.01$). The index of moss dominance significantly decreased with increasing values of WB or MAP (pc = –0.27, $p < 0.05$ or pc = –0.33, $p < 0.01$, respectively), suggesting that either WB or MAP have an indirect effect on FH layer C accumulation (indirect path coefficient, $pc_i = -0.08$ or $pc_i = -0.10$) through their influence on moss dominance. When accounting for the effect of other variables, the direct effects of pH on FH layer C stocks, of TSF on moss dominance, and of clay content on moss dominance all became nonsignificant in the FH1 hypothesis ($p > 0.05$).

When averaging path coefficients (Supporting information Table S1), the most important variables exerting a direct control on FH layer C stocks were found to be, in decreasing order of importance, TSF (model-averaged estimator, $pc_{avg} = 0.37$) and moss dominance ($pc_{avg} = 0.32$). Direct effects of pH ($pc_{avg} = 0.13$), climate ($pc_{avg} = 0$), and soil texture ($pc_{avg} = -0.01$) were either nonsignificant or negligible.

3.3 | Mineral soil path analysis and model selection

The first hypothesis (B0) testing for direct effects of variables on illuvial horizon carbon stocks was rejected based on Fisher's *C* statistic ($p < 0.01$), whereas most models related to B1 and B2 hypotheses were not (Table 3). Six path models best explained the data (ΔAICc < 2; Table 3) and all included clay content as texture variable. For climate variables, the two best path models belonging to hypothesis B1 had WB or MAT as the best climate explanatory variables. The four other best path models belonging to hypothesis B2 had GDD5 and MAP in addition to WB and MAT as the best climate explanatory variables. Together, those six path models accounted for 83% of the Akaike weight.

The best DAG under hypotheses B1 and B2 explained 56% and 61% of the variation between covariates and illuvial horizon C stocks, respectively (Figure 6 and Supporting information Table S2). Carbon stocks were correlated positively with Mpy ($0.37 \le pc \le 0.41$, $p < 0.01$), but negatively with pH ($-0.32 \le pc \le -0.23$, $p < 0.05$, except for B2 with MAP and clay content where $p = 0.053$). Pyrophosphate extractable metals (Mpy) were found to depend on WB (pc = 0.25, $p < 0.05$) and MAP (pc = 0.23, $p < 0.05$) but not on other climate variables ($p > 0.05$), and were negatively correlated with pH ($-0.52 \le pc \le -0.46$, $p < 0.001$), which was itself found to be negatively correlated with TSF (pc = –0.28,

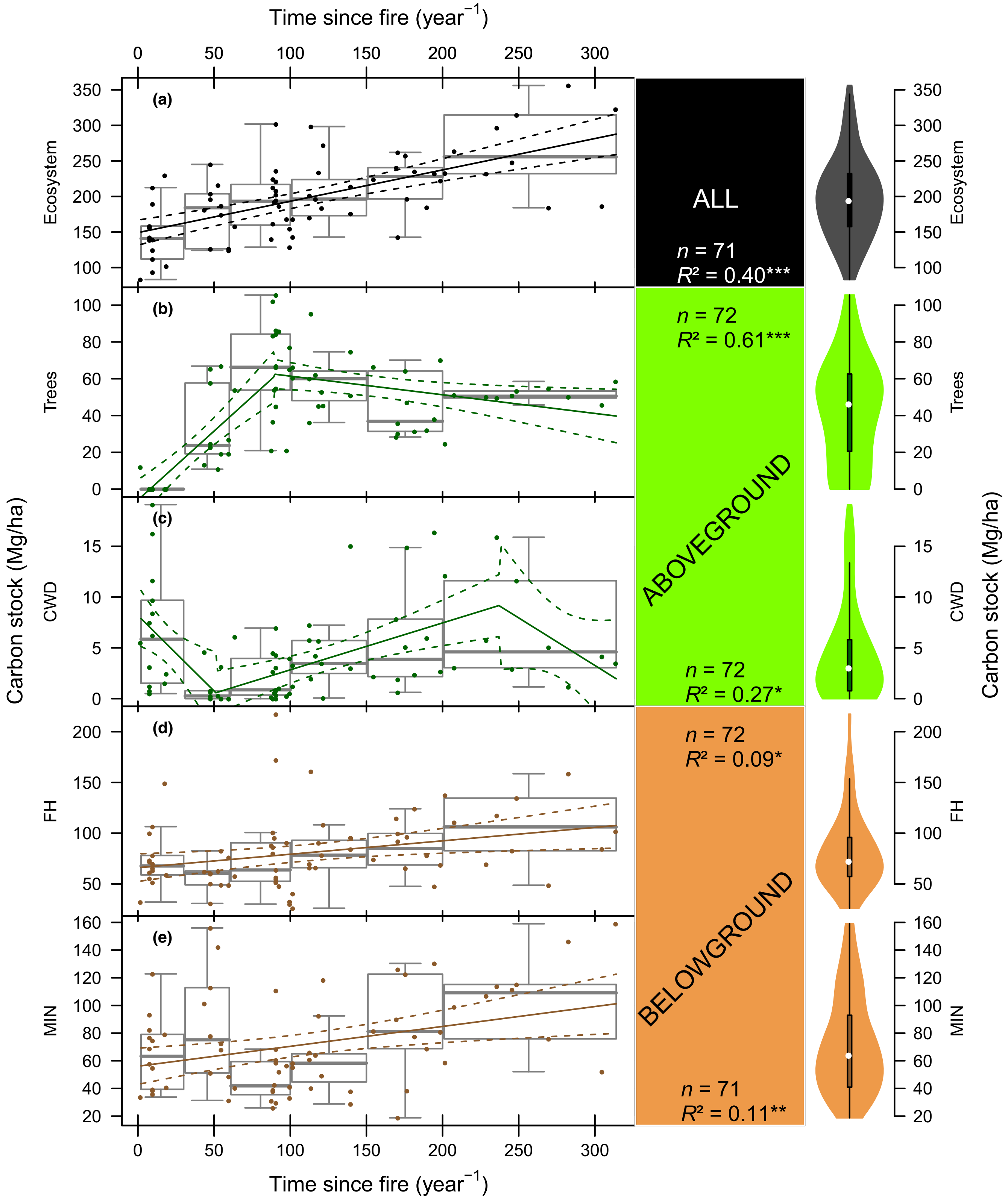

FIGURE 4 Observed (points) and predicted (plain lines) postfire carbon stocks with 95% confidence interval (dashed lines) as a function of time since fire and the type of aboveground (green) or belowground (maroon) carbon pool, with boxplots representing age-class carbon stock distribution (limits at 2, 30, 60, 100, 150, 200, and 314 years; see Supporting information Figure S3 for the number of plots per age-class) (left panel). Violin plots show the kernel density of observed carbon stocks within each carbon pool (right panel). *Ecosystem* (a): sum of all carbon pools; *Trees* (b): aboveground trees; *CWD* (c): lying coarse woody debris; *FH* (d): FH layer; *MIN* (e): top 35 cm of mineral soil. *$p \le 0.05$; **$p \le 0.01$; ***$p \le 0.001$

TABLE 1 Equation parameters and statistics in linear trends of carbon stocks (MgC/ha) changes with time since fire (yr^{-1}) for the main ecosystem carbon pools

Carbon pool (MgC/ha)	Number of breakpoints	Breakpoint (years ± *SD*)	Equation before breakpoint	Equation after breakpoint	R^2	*p*-value
Ecosystem	0	–	149.20 + 0.44 (TSF)	–	0.40	<0.001
Aboveground trees	1	90 ± 9	−5.93 + 0.75 (TSF)	71.57–0.10 (TSF)	0.61	<0.001
Coarse woody debris	2	51 ± 12	8.17–0.15 (TSF)	−1.78 + 0.05 (TSF)	0.27	0.012
		237 ± 25	−1.78 + 0.05 (TSF)	31.94–0.10 (TSF)		
FH layer	0	–	66.00 + 0.13 (TSF)	–	0.09	0.011
Mineral soil (top 35 cm)	0	–	56.05 + 0.14 (TSF)	–	0.11	0.004

$p < 0.05$). Accounting for the effects of other variables, the direct effects of both clay content and TSF on illuvial horizon C stocks became nonsignificant ($p > 0.05$). Nevertheless, climate (WB and MAP variables only) was found to affect illuvial horizon C stocks through its effect on Mpy (indirect path coefficient, $pc_i = 0.1$ for hypotheses B1 and B2 with WB and clay content, and $pc_i = 0.09$ for hypothesis B2 with MAP and clay content). Also, TSF was found to be indirectly linked to illuvial horizon C stocks through its effect on pH, considering the effects of pH on C stock, of pH on Mpy, and of Mpy on C stock ($0.12 < pc_i < 0.15$).

When averaging path coefficients (Supporting information Table S2), the most important variables exerting a direct control on illuvial horizon C stocks were Mpy (model-averaged estimator, $pc_{avg} = 0.39$) followed by pH ($pc_{avg} = -0.26$). The direct effect of TSF ($pc_{avg} = 0.19$) was not significant and direct effects of climate ($pc_{avg} = -0.1$) and texture ($pc_{avg} = -0.02$) were either not significant or negligible.

4 | DISCUSSION

Our results show that time since fire (TSF) is an important driver of the most dynamic ecosystem carbon (C) pools (Figure 4). Carbon stocks in live aboveground biomass (Figure 4b) and in coarse woody debris (Figure 4c) varied predictably with TSF in agreement with aggradation and stabilization patterns (Bormann & Likens, 1979; Sturtevant, Bissonette, Long, & Roberts, 1997; Ward et al., 2014), whereas C stocks in the FH layer increased linearly with TSF (Czimczik, Schmidt, & Schulze, 2005; Nalder & Wein, 1999) in agreement with our hypothesis (see the description of FH0), although the latter relationship was weak. Contrary to our expectations, we also found a significant but weak positive correlation between TSF and mineral soil C stocks. Together, these results indicate that the net C accumulation phase in the terrestrial pools of these forests goes beyond the aboveground aggradation phase, which is in agreement with Luyssaert et al. (2008) and Zhou et al. (2006), but in contradiction with Bormann and Likens (1979), Wardle et al. (2004), and Gao et al. (2017). Soil C pools (FH layer and top 35 cm of mineral soil) were found to represent as much as 77% of total ecosystem C stocks (Figure 4), whereas still not accounting for deeper soil stocks (Jobbagy & Jackson, 2000). This percentage clearly indicates that better predictions of changes in boreal forest C stocks can only be achieved through a better understanding of the processes involved in soil C accumulation (Shaw et al., 2014), in particular with respect to changes in disturbance patterns (Buma, Poore, & Wessman, 2014; Fu et al., 2017) or climate.

4.1 | Soil C stock predictability

When quantifying explicitly direct and indirect relationships among fire, climate, local biotic and abiotic variables involved in soil C storage, our study demonstrates that the overall model explained variability (i.e., accounted for all causal relationships among variables, and between variables and soil C stocks) increases from 28% (model assumes only direct relationships between variables) to 46% (model with indirect relationships), and from 40% to 60% for FH layer and illuvial horizon, respectively (Supporting information Table S1, Table S2). In our study, the rejection of all hypotheses that assumed only direct relationships between environmental variables and soil C stocks supports the claim that the assumption of direct relationships associated with the dominant modeling approaches such as ANOVA, multiple regressions or machine learning algorithms may be an important limitation and a source of uncertainty in current soil organic C predictions. This result agrees with recent findings showing that complex direct and indirect relationships between climate, soil properties, C inputs, and C pools regulate soil organic C dynamics in agricultural landscapes (Luo, Feng, Luo, Baldock, & Wang, 2017). Our study goes a step further by using a confirmatory approach with a set of a priori hypotheses and a low number of variables (climate, soil texture, TSF, pH, moss dominance, and metal oxide concentrations) that are readily interpretable from an ecological point of view and readily comparable in terms of their relative contribution. With only five variables, our best path models explained as much as 46% and 61% of the overall variation among environmental variables and C stocks in the FH layer and illuvial horizon, respectively.

4.2 | Climate is an indirect driver of soil C stocks

When accounting explicitly for direct and indirect relationships between climate and C stocks, our results indicate that the influence of water availability—i.e., the main climatic predictor in our study—

TABLE 2 Model comparisons for alternative a priori hypotheses, each testing for different causal relationships among variables and carbon stocks in the FH layer of the boreal forest of eastern North America (see Figure 3 for details about the Directed Acyclic Graph (DAG) associated with each hypothesis)

Hypothesis	Climate	Texture	C statistic (*df*, *p*)	K	AICc	ΔAICc	W
FH1	**WB**	**Clay %**	**8.956 (14, 0.83)**	**11**	**35.43**	**0**	**0.40**
FH1	**MAP**	**Clay %**	**9.294 (14, 0.81)**	**11**	**35.77**	**0.34**	**0.34**
FH1	GDD5	Clay %	11.996 (14, 0.61)	11	38.47	3.04	0.09
FH1	GDD5	Silt %	14.009 (14, 0.45)	11	40.48	5.05	0.03
FH2	WB	Clay %	14.643 (14, 0.40)	11	41.12	5.69	0.02
FH2	GDD5	Clay %	15.103 (14, 0.37)	11	41.58	6.15	0.02
FH1	MAT	Clay %	15.248 (14, 0.36)	11	41.72	6.29	0.02
FH1	WB	Sand %	15.416 (14, 0.35)	11	41.89	6.46	0.02
FH1	GDD5	Sand %	15.422 (14, 0.35)	11	41.90	6.47	0.02
FH2	GDD5	Silt %	16.357 (14, 0.29)	11	42.83	7.40	0.01
FH2	GDD5	Sand %	16.629 (14, 0.28)	11	43.10	7.67	0.01
FH1	WB	Silt %	16.710 (14, 0.27)	11	43.18	7.75	0.01
FH2	MAP	Clay %	17.517 (14, 0.23)	11	43.99	8.56	0.01
FH1	MAP	Sand %	18.166 (14, 0.20)	11	44.64	9.21	0
FH1	MAT	Silt %	18.572 (14, 0.18)	11	45.05	9.62	0
FH2	MAT	Clay %	18.874 (14, 0.17)	11	45.35	9.92	0
FH1	MAP	Silt %	19.175 (14, 0.16)	11	45.65	10.22	0
FH2	WB	Sand %	19.202 (14, 0.16)	11	45.68	10.25	0
FH1	MAT	Sand %	19.214 (14, 0.16)	11	45.69	10.26	0
FH2	MAT	Sand %	20.939 (14, 0.10)	11	47.41	11.98	0
FH2	MAT	Silt %	21.438 (14, 0.09)	11	47.91	12.48	0
FH2	WB	Silt %	21.637 (14, 0.09)	11	48.11	12.68	0
FH2	MAP	Sand %	24.487 (14, 0.04)	11	50.96	15.53	0
FH0	GDD5	Clay %	37.746 (20, 0.01)	6	51.06	15.63	0
FH0	WB	Clay %	38.410 (20, 0.01)	6	51.72	16.29	0
FH0	GDD5	Silt %	39.458 (20, 0.01)	6	52.77	17.34	0
FH0	GDD5	Sand %	39.727 (20, 0.01)	6	53.04	17.61	0
FH2	MAP	Silt %	26.637 (14, 0.02)	11	53.11	17.68	0
FH0	MAP	Clay %	42.112 (20, <0.01)	6	55.42	19.99	0
FH0	WB	Sand %	43.425 (20, <0.01)	6	56.74	21.31	0
FH0	MAT	Clay %	43.895 (20, <0.01)	6	57.21	21.78	0
FH0	WB	Silt %	45.863 (20, <0.01)	6	59.18	23.75	0
FH0	MAT	Sand %	46.416 (20, <0.01)	6	59.73	24.30	0
FH0	MAT	Silt %	46.917 (20, <0.01)	6	60.23	24.80	0
FH0	MAP	Sand %	49.539 (20, <0.01)	6	62.85	27.42	0
FH0	MAP	Silt %	51.691 (20, <0.01)	6	65.00	29.57	0

Notes. The two competing path models that best explain the data (ΔAICc ≤ 2) are in bold font. *MAT*: mean annual temperature; *MAP*: mean annual precipitation; *GDD5*: growing degree-days above 5°C; WB: water balance; *C statistic* (df: degree of freedom; *p*: probability of compliance of the basis set with the conditions of independence testing the hypothesized causal structure of the DAG); *K*: number of free parameters; *AICc*: second order Akaike's information criterion; *ΔAICc*: relative AICc difference with the 'best model'; *W*: Akaike weight.

on soil C stocks is only indirect through changes in vegetation dominance (i.e., moss layer composition, which, when dead, is the primary source of FH layer mass in our study system) or through changes in metal oxide contents (illuvial horizon). This result is in agreement with previous findings showing that accounting for sphagnum- and feathermoss-derived C reduces errors in black spruce C stock estimates (Bona et al., 2013). Relationships between climate and bryophyte vegetation justify the use of climate parameters to predict moss species distribution at the landscape scale (Gignac, 2001). Our results indicate that water availability is more important than temperature in explaining moss layer dominance, as bryophyte species often tolerate a wide range of temperatures and are dependent on

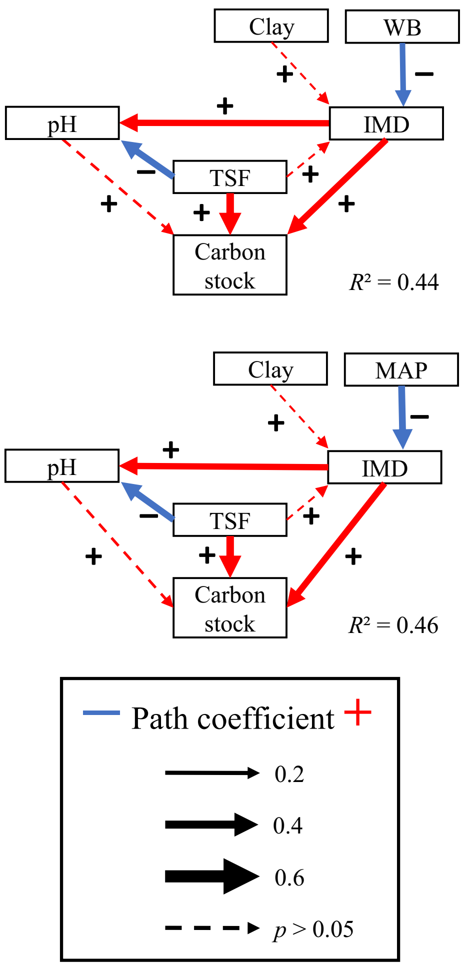

FIGURE 5 The two minimum adequate path models based on the FH1 hypothesis that best fit the data to explain FH layer carbon stock variability. Arrows indicate direct causal relationships between variables. Arrow widths are proportional to path coefficients. Red or blue arrows show positive or negative path coefficients, respectively. Plain or dashed arrows depict significant ($p \le 0.05$) or nonsignificant ($p > 0.05$) causal relationships between variables, respectively. *WB*, water balance; *MAP*, mean annual precipitation; *Clay*, mineral soil (top 35 cm) clay content; *TSF*, time since fire; *pH*, FH layer potential of hydrogen; *IMD*, index of moss dominance

the water content of their habitat (Gignac, 2001). The index of moss dominance used in our study is a gross index that discriminates between Sphagnum spp. and feathermosses and that does not account for all the diversity of species or functional traits in the ground layer vegetation. Nevertheless, the indirect effect of climate on soil C stocks through changes in bryophyte dominance indicates that considering water availability (i.e., bryophyte dominance)—FH layer C stock relationships should improve our ability to predict soil C stocks with changes in climate.

In our study, metal oxide content exerted a primary control on illuvial horizon C stocks, indicating that binding of organic matter on the mineral phase is a major direct process of C sequestration (Kramer, Sanderman, Chadwick, Chorover, & Vitousek, 2012; Mikutta, Kleber, Torn, & Jahn, 2006; Porras et al., 2017). Doetterl et al. (2015) argue that over a wide climatic gradient soil C stocks primarily evolve with climate-driven mineral weathering and release of reactive mineral surfaces. In our study, we also found an indirect control of climate on illuvial horizon C stocks through metal oxide contents rather than a direct relationship between climate and illuvial horizon C stocks. Our findings corroborate the view that climate-mediated mineral weathering is important for C sequestration. Indeed, the faster podsolization process favored by increased eluviation (Sanborn et al., 2011) has been shown to occur under wetter and warmer climate compared with a dryer and colder one (Egli et al., 2009; Protz, Shipitalo, Ross, & Terasmae, 1988).

At the global scale, soil C stocks have been shown to decrease with rising temperatures (Crowther et al., 2016). In our study, it is noteworthy that temperature factors (MAT and GDD5) did not significantly contribute to soil C stocks once direct and indirect relationships with other biotic and abiotic factors were accounted for. Our data encompass a range of mean annual temperatures of about 3.5°C (Supporting information Figure S4), which could be insufficient to detect a temperature gradient effect. Moreover, we used the most recent 30-year climate data that do not span the range of the TSF studied here (314 years). This evidently brings some uncertainties in interpreting the role played by climate in soil C accumulation. Nevertheless, our results suggest that contrary to water availability, soil C stocks do not vary quantitatively with temperature, which implies that under a raise of mean annual temperature of 2°C, global warming would be unlikely to have a net direct effect on boreal soil C stocks at the scale of our study area. Increasing temperature at the regional scale has been showed to accelerate boreal forest ecosystem C fluxes without changing soil C stocks (Ziegler et al., 2017).

4.3 | Distinct mechanisms of C stock changes with TSF in FH layer and in mineral soil

Our results support previous findings that TSF is an important direct driver of C stocks in the organic layer (Czimczik et al., 2005; Harden et al., 2012; Nalder & Wein, 1999; Pellegrini et al., 2018). Indeed, the organic layer is consumed in part or in whole during fire (Greene et al., 2007; Harden et al., 2012), depending on fire severity (Lecomte, Simard, Fenton, & Bergeron, 2006) and prefire organic layer depth (Kane, Kasischke, Valentine, Turetsky, & McGuire, 2007). However, in the illuvial horizon, our results demonstrate that TSF is mostly an indirect driver that alters pH conditions, which in turn influence both C stocks directly or indirectly through changes in metal oxide contents. To our knowledge, this study is the first to simultaneously document and quantify these complex relationships among TSF, pH, metal oxides and C stocks in the illuvial horizon of forest ecosystems; previous studies mainly focused on separate elements of these complex relationships. Interestingly, we found that pH was the strongest driver of metal oxide contents, and that metal oxides increased when pH decreased. This result supports the view that organo-metal complexation reactions in acidic environments depend on soil pH

TABLE 3 Model comparisons for alternative a priori hypotheses, each testing for different causal relationships among variables and carbon stocks in the illuvial (B) horizon of the boreal forest of eastern North America (see Figure 3 for details about the Directed Acyclic Graph (DAG) associated with each hypothesis)

Hypothesis	Climate	Texture	C statistic (df, *p*)	K	AICc	ΔAIC	W
B2	**WB**	**Clay %**	**14.554 (14, 0.41)**	**12**	**43.93**	**0**	**0.18**
B1	**MAT**	**Clay %**	**20.528 (18, 0.30)**	**10**	**44.19**	**0.26**	**0.16**
B2	**MAT**	**Clay %**	**14.918 (14, 0.38)**	**12**	**44.30**	**0.37**	**0.15**
B1	**WB**	**Clay %**	**20.684 (18, 0.30)**	**10**	**44.35**	**0.42**	**0.14**
B2	**GDD5**	**Clay %**	**15.585 (14, 0.34)**	**12**	**44.96**	**1.03**	**0.11**
B2	**MAP**	**Clay %**	**15.944 (14, 0.32)**	**12**	**45.32**	**1.39**	**0.09**
B1	GDD5	Clay %	22.766 (18, 0.20)	10	46.43	2.50	0.05
B1	MAP	Clay %	22.885 (18, 0.20)	10	46.55	2.62	0.05
B1	MAT	Sand %	25.143 (18, 0.12)	10	48.81	4.88	0.02
B2	MAT	Sand %	19.461 (14, 0.15)	12	48.84	4.91	0.02
B2	GDD5	Sand %	19.498 (14, 0.15)	12	48.88	4.95	0.01
B2	WB	Sand %	20.663 (14, 0.11)	12	50.04	6.11	0.01
B1	WB	Sand %	26.579 (18, 0.09)	10	50.25	6.32	0.01
B1	GDD5	Sand %	26.859 (18, 0.08)	10	50.53	6.60	0.01
B2	GDD5	Silt %	21.884 (14, 0.08)	12	51.26	7.33	0
B1	MAT	Silt %	28.406 (18, 0.06)	10	52.07	8.14	0
B2	MAT	Silt %	22.731 (14, 0.06)	12	52.11	8.18	0
B1	GDD5	Silt %	29.308 (18, 0.04)	10	52.98	9.05	0
B2	MAP	Sand %	24.802 (14, 0.04)	12	54.18	10.25	0
B1	MAP	Sand %	31.568 (18, 0.02)	10	55.23	11.30	0
B2	WB	Silt %	26.506 (14, 0.02)	12	55.89	11.96	0
B1	WB	Silt %	32.376 (18, 0.02)	10	56.04	12.11	0
B2	MAP	Silt %	30.479 (14, 0.01)	12	59.86	15.93	0
B1	MAP	Silt %	37.245 (18, <0.01)	10	60.91	16.98	0
B0	MAT	Clay %	49.722 (20, <0.01)	7	65.50	21.57	0
B0	GDD5	Clay %	50.158 (20, <0.01)	7	65.94	22.01	0
B0	WB	Clay %	50.597 (20, <0.01)	7	66.37	22.44	0
B0	MAP	Clay %	50.809 (20, <0.01)	7	66.59	22.66	0
B0	GDD5	Sand %	52.583 (20, <0.01)	7	68.36	24.43	0
B0	MAT	Sand %	52.686 (20, <0.01)	7	68.46	24.53	0
B0	WB	Sand %	56.056 (20, <0.01)	7	71.83	27.90	0
B0	GDD5	Silt %	56.902 (20, <0.01)	7	72.68	28.75	0
B0	MAT	Silt %	57.776 (20, <0.01)	7	73.55	29.62	0
B0	MAP	Sand %	58.680 (20, <0.01)	7	74.46	30.53	0
B0	WB	Silt %	63.082 (20, <0.01)	7	78.86	34.93	0
B0	MAP	Silt %	65.421 (20, <0.01)	7	81.20	37.27	0

Notes.. The six competing path models that best explain the data (ΔAICc ≤2) are in bold font. *MAT*: mean annual temperature; *MAP*: mean annual precipitation; *GDD5*: growing degree-days above 5°C; *WB*: water balance; *C statistic* (df: degree of freedom; *p*: probability of compliance of the basis set with the conditions of independence testing the hypothesized causal structure of the DAG); *K*: number of free parameters; *AICc*: second order Akaike's information criterion; *ΔAICc*: relative AICc difference with the 'best model'; *W*: Akaike weight.

(Heckman, Welty-Bernard, Rasmussen, & Schwartz, 2009; Porras et al., 2017). In addition, soil pH largely controls the weathering of minerals (Drever, 1994; Drever & Stillings, 1997); thus, we assume that enhanced organo-metal complexation could arise from the increased availability of metal ions released by mineral weathering when pH decreases (Porras et al., 2017). In other words, the potential of organo-metal complex formation at the scale of our study could reflect the synergistic effect of soil pH with microbial decomposition process and mineral weathering. As the soil substrate becomes more acidic, greater amounts of undecomposed organic materials can bind to the overload of metal ions released from enhanced weathering.

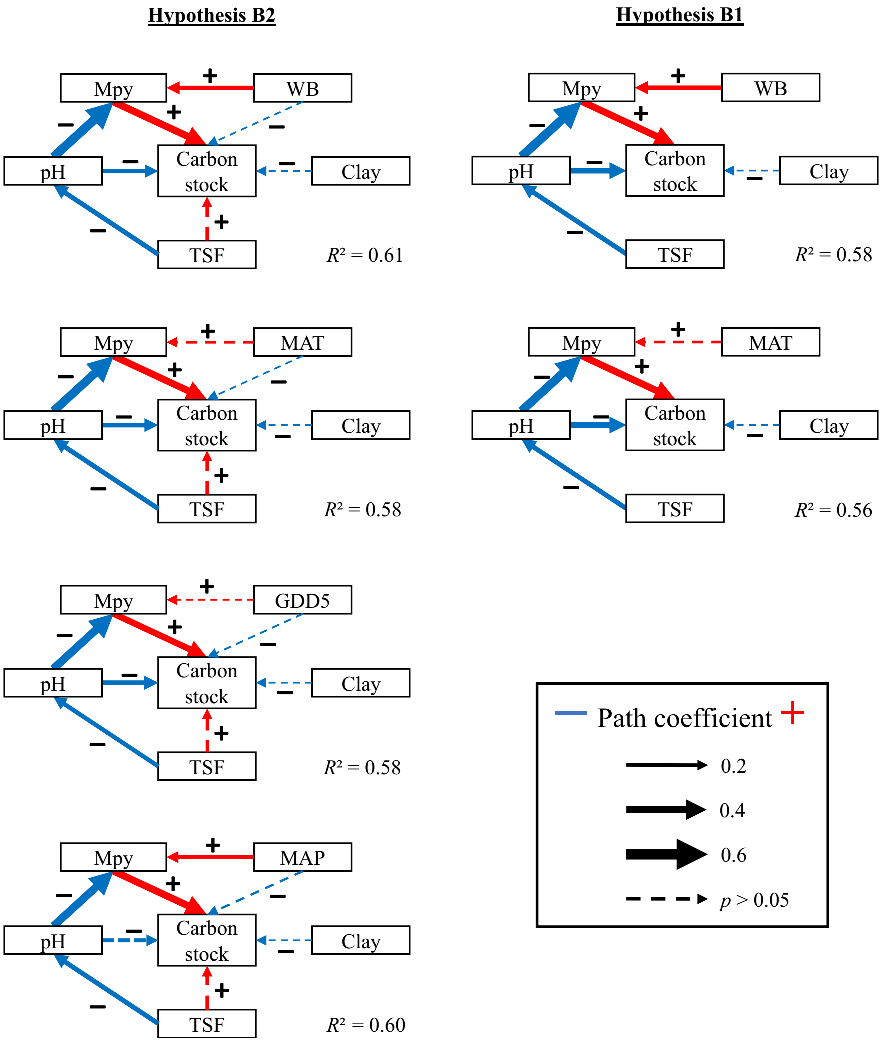

FIGURE 6 The five minimum adequate path models that best fit the data to explain illuvial (B) horizon carbon stock variability. Arrows indicate direct causal relationships between variables. Arrow widths are proportional to path coefficients. Red or blue arrows show positive or negative path coefficients, respectively. Plain or dashed arrows depict significant ($p \leq 0.05$) or nonsignificant ($p > 0.05$) causal relationships between variables, respectively. *WB*, water balance; *MAT*, mean annual temperature; *Clay*, mineral soil (top 35 cm) clay content; *TSF*, time since fire; *pH*, illuvial horizon potential of hydrogen; *Mpy*, pyrophosphate extractable metals in the illuvial horizon

4.4 | Insignificant role of soil texture

Surprisingly, we found no direct or indirect effect of soil texture on both FH layer and illuvial horizon C stocks, indicating that once the effects of other factors are controlled, soil texture does not contribute quantitatively to C sequestration. This result contrasts with the wide use of soil texture in models of soil organic matter (Six et al., 2002; Soucémarianadin et al., 2014). One explanation could lie in the low Nordic soil data availability. Indeed, most of our knowledge on the control of soil C stocks by soil texture comes from warm agricultural regions (Rasmussen et al., 2018). Also, it is possible that the weathering of the granitic bedrock of the Canadian Shield did not produce reactive surface silt and clay particles considering that the studied soils are young and have been developing since the end of the last glaciation (<10k years; Minasny, McBratney, and Salvador-Blanes (2008)). It is also possible that our results are limited to the short range of mineral soil clay content contained in these boreal soils (Supporting information Figure S5), and that on fine textured boreal soils, silt and clay contents could have a significant influence on soil C stocks.

4.5 | Research avenues

In this study, TSF and climate only had indirect effects on mineral soil C stocks. This finding brings some important implications. First, it may help solving discrepancies found in the literature where mineral soil C stocks either decrease, increase, or do not change with TSF (Johnson & Curtis, 2001; Knicker, 2007; Nave et al., 2011; Pregitzer & Euskirchen, 2004; Seedre et al., 2011). Indeed, the effects of TSF on mineral soil C stocks in these studies may be the reflection of unevaluated complex interrelationships between local site conditions defined by conditions such as pH and metal oxide content. The second main implication about the prevalence of indirect climatic and fire-mediated effects on mineral C stocks is that it questions the underlying assumption of forecasting exercises projecting the effect of global changes on future soil C stocks, and especially how forecast models account for the important role played by local variation in vegetation and chemical soil properties. Eastern North America is projected to receive about 10% more precipitation by the end of this century (IPCC, 2013). According to our results, increasing the water supply through greater amounts of precipitation could increase mineral soil C stocks through enhanced mineral weathering and leaching, releasing metal oxides that can bind to organic matter (Doetterl et al., 2015; Mikutta et al., 2006; Porras et al., 2017; Rumpel & Kögel-Knabner, 2011). Otherwise, the projected increase in fire frequency suggested by models (Kloster & Lasslop, 2017; Wang et al., 2017; Wotton, Flannigan, & Marshall, 2017) could weaken the C capture function of boreal forests (Genet et al., 2018; Pan et al., 2011). Integrating direct and indirect effects of abiotic and biotic factors on C storage processes, as presented here through mechanistic models of C dynamics in boreal forest ecosystems, could improve our ability to account for C stocks and anticipate the response of boreal forests to global change. Assessing the sensitivity of global change forecast models to local variation in biotic and abiotic conditions is a key challenge that will need to be addressed and integrated in future studies.

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