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Post-fire Recovery of Soil Organic Layer Carbon in Canadian Boreal Forests

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Abstract

Conifer forests historically have been resilient to wildfires in part due to thick organic soil layers that regulate combustion and post-fire moisture and vegetation change. However, recent shifts in fire activity in western North America may be overwhelming these resilience mechanisms with potential impacts for energy and carbon exchange. Here, we quantify the long-term recovery of the organic soil layer and its carbon pools across 511 forested plots. Our plots span ~ 140,000 km^2 across two ecozones of the Northwest Territories, Canada, and allowed us to investigate the impacts of time-after-fire, site moisture class, and dominant canopy type on soil organic layer thickness and associated carbon stocks. Despite thinner soil organic layers in xeric plots immediately after fire, these drier stands supported faster post-fire recovery of the soil organic layer than in mesic plots. Unlike xeric or mesic stands, post-fire soil carbon accumulation rates in hydric plots were negligible despite wetter forested plots having greater soil organic carbon stocks immediately post-fire compared to other stands. While permafrost and high-water tables inhibit combustion and maintain thick organic soils immediately after fire, our results suggest that these wet stands are not recovering their pre-fire carbon stocks on a century timescale. We show that canopy conversion from black spruce to jack pine or deciduous dominance could reduce organic soil carbon stocks by 60–80% depending on stand age. Our two main findings—decreasing organic soil carbon storage with increasing deciduous cover and the lack of post-fire SOL recovery in hydric sites—have implications for the turnover time of carbon stocks in the western boreal forest region and also will impact energy fluxes by controlling albedo and surface soil moisture.

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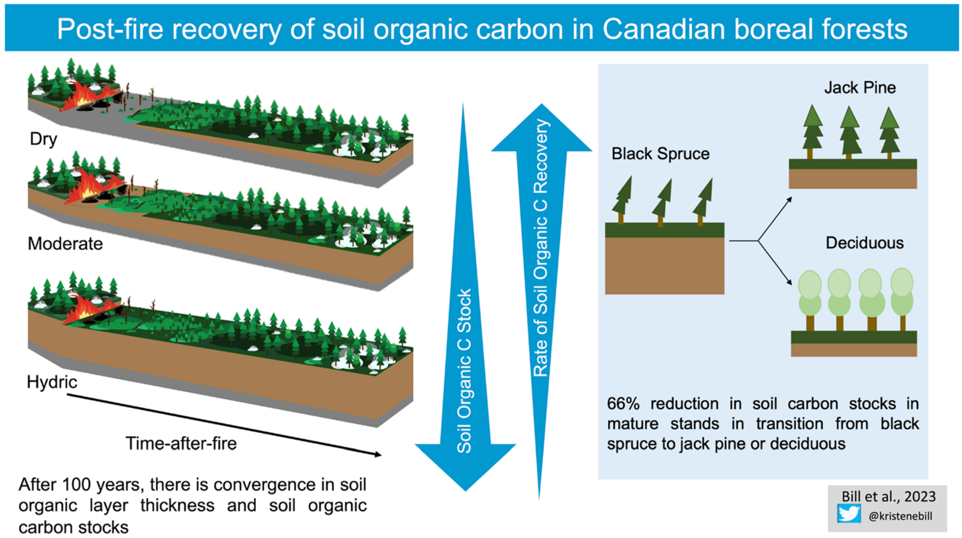
Graphical Abstract



Key words: boreal forest resilience; ecosystem carbon dynamics; post-fire recovery; soil organic layer; soil organic carbon; wildfire.

Introduction

The boreal forest biome comprises a third of the world's forested area and has globally significant stores of terrestrial carbon (C), the majority stored in soil (Brandt and others 2013; Bradshaw and others 2015; Kurz and others 2013). For several millennia, wildfire and repeated cycles of vegetation recovery in the North American boreal forest have played a key role in boreal forest resilience (Chapin and others 2010; Johnstone and others 2010a). Under moderate or typical burning conditions, black spruce (*Picea mariana*) stands in this region self-replace after fire (Johnstone and Chapin 2006; Johnstone and others 2010a). Repeated cycles of burning, followed by black spruce replacement, has led to black spruce dominance, with this species occupying approximately 44% of interior Alaskan forests (Rupp and others 2002). This pattern of black spruce self-replacement is a key aspect of contemporary boreal forest resilience to fire (Turetsky and others 2017; Johnstone and others 2016).

In recent decades, increases in fire frequency, extent, and intensity in the boreal biome are disrupting these forest resilience mechanisms (Johnstone and others 2010b; Turetsky and others 2017) primarily by increasing biomass combustion (Balshi and others 2009; Kasischke and Turetsky 2006; Kelly and others 2013). Deeper soil organic layer (SOL) combustion can break the cycle of black spruce self-replacement by changing seedbed conditions and allowing deciduous taxa (for example, *Populus* and *Betula* spp.) and jack pine (*Pinus banksiana*) species to replace black spruce (Chapin and others 2010; Hart and others 2018; Johnstone and others 2016; Johnstone and others 2010b; Kasischke and others 2010; Walker and others 2017; Whitman and others 2019). Although both empirical and modeling studies suggest that more frequent and severe fires can catalyze forest shifts from black spruce to deciduous dominance (Mekonnen and others 2019; Searle and Chen 2017), few studies have quantified the effects of a changing fire regime on long-term organic soil C recovery (Miquelajauregui and others 2019; Genet and others 2013; Rapalee and others 1998).

Fire-induced shifts from black spruce to jack pine or deciduous dominance lead to a switch from a slow to a fast soil-nutrient cycle, with broad implications for nutrient, energy, and C cycling (Mack and others 2021; Johnstone and others 2010b; Preston and others 2006). Black spruce-dominated stands have recalcitrant litter, relatively cool and wet soil conditions, and are associated with mosses that reinforce deep SOL (Johnstone and others 2010a; Mack and others 2008; Johnstone and others 2016; Walker and others 2018a). Although jack pine and deciduous stands have greater net primary productivity than black spruce stands (Alexander and Mack 2016; Amiro and others 2003; Euskirchen and others 2016; Mekonnen and others 2019), soil C sequestration is limited by readily decomposable deciduous litter and warmer and drier soil conditions. Jack pine stands also tend to have thinner, more decomposed litter layers than black spruce stands (Bhatti 2015). Overall, deciduous stands tend to have greater aboveground vegetative C stocks than conifer stands (Mack and others 2021; Alexander and Mack 2016; Preston and others 2006), whereas the opposite pattern is true for soil organic C (SOC) stocks (Walker and others 2018a). These SOL and related C stocks are associated with canopy characteristics but also site drainage and soil moisture patterns across the landscape. For example, while black spruce can dominate stands across a range of soil moisture conditions, wetter soil conditions post-fire is associated with greater moss recolonization (Jean and others 2020), which in turn contributes to regeneration of black spruce. Understanding how a changing fire regime might influence these landscape and ecosystem patterns of C storage across multiple fire cycles remains a key uncertainty, and yet is critical for predicting the future role of the boreal biome as a net C sink or source (Walker and others 2019).

In 2014, the Northwest Territories (NWT), Canada, experienced an annual burn area (3.41 ± 0.21 Mha) eight times greater than average, presenting a unique opportunity to understand patterns of succession and potential losses of forest resilience after a severe fire year (Walker and others 2018b). The 2014 fires released 94.3 Tg C to the atmosphere (Walker and others 2018b) and under some conditions (well- and moderately drained areas) released legacy C that had survived historical fires (Walker and others 2019). Following the 2014 fires, shifts in initial tree species dominance also occurred in response to deep burning, with declines in black spruce and increases in jack pine or trembling aspen (*Populus tremuloides,* deciduous) in the Taiga Plains ecozone, and birch (*Betula papyrifera,* deciduous) in the Taiga Shield ecozone (Day and others 2020; Reid 2017; Whitman and others 2018). To explore variation in post-fire soil C recovery across various successional trajectories, we used a network of 511 forested and wetland plots within the Taiga Plains and Taiga Shield ecozones in the NWT, Canada, to quantify controls on SOC and SOL thickness with time-after-fire. Many chronosequence designs attempt to control for site conditions or ecosystem state factors by selecting sites that vary in time-following-disturbance only (or as much as possible), thus limiting the space-for-time substitution to a narrow set of ecological conditions. Instead, our large plot network allowed us to include landscape-level variation in canopy and ground-layer vegetation, moisture class, and soil development in our analyses as covariates along with time-after-fire. More information on our plot selection and network design is found in the Supplemental Material and Walker and others (2018a), Day and others (2020).

Given the importance of the SOL not only to post-fire soil C recovery but also overall vegetation stand resilience to fire (Chapin and others 2010; Hart and others 2018; Johnstone and others 2016; Johnstone and others 2010b; Kasischke and others 2010; Walker and others 2017; Whitman and others 2019), this study tests two main hypotheses related to SOL thickness and soil organic C stocks across our extensive plot network in the NWT:

1) Recovery of the SOL and its C stock will be predominantly influenced by moisture class, given that moisture governs both canopy tree and nonvascular plant community structure. We hypothesized that SOL and SOC recovery would occur faster in poorly drained (wetter) areas than in well-drained (drier) plots due to slower anaerobic decomposition and the dominance of plants that produce recalcitrant biomass, such as black spruce and *Sphagnum* moss.

2) Because productivity and litter quality are not always co-associated with soil moisture in these stands, dominant canopy type will influence SOL and SOC recovery. We hypothesized that, independent of moisture class, jack pine- and deciduous-dominated plots would be associated with smaller SOC stocks compared to black spruce across time-after-fire, but would have higher rates of faster post-fire soil C accumulation due to greater net primary productivity in these stands.

Methods

Study Region

The study area covers $\sim$140,000 km^2 across the Taiga Plains (hereafter Plains) and Taiga Shield (hereafter Shield) ecozones of the North and South Slave regions in the NWT, Canada (Figure 1). Sedimentary rock deposits of limestone and shale characterize the Plains, whereas sandstone creates its rolling uplands and lowlands (Ecosystem Clas-

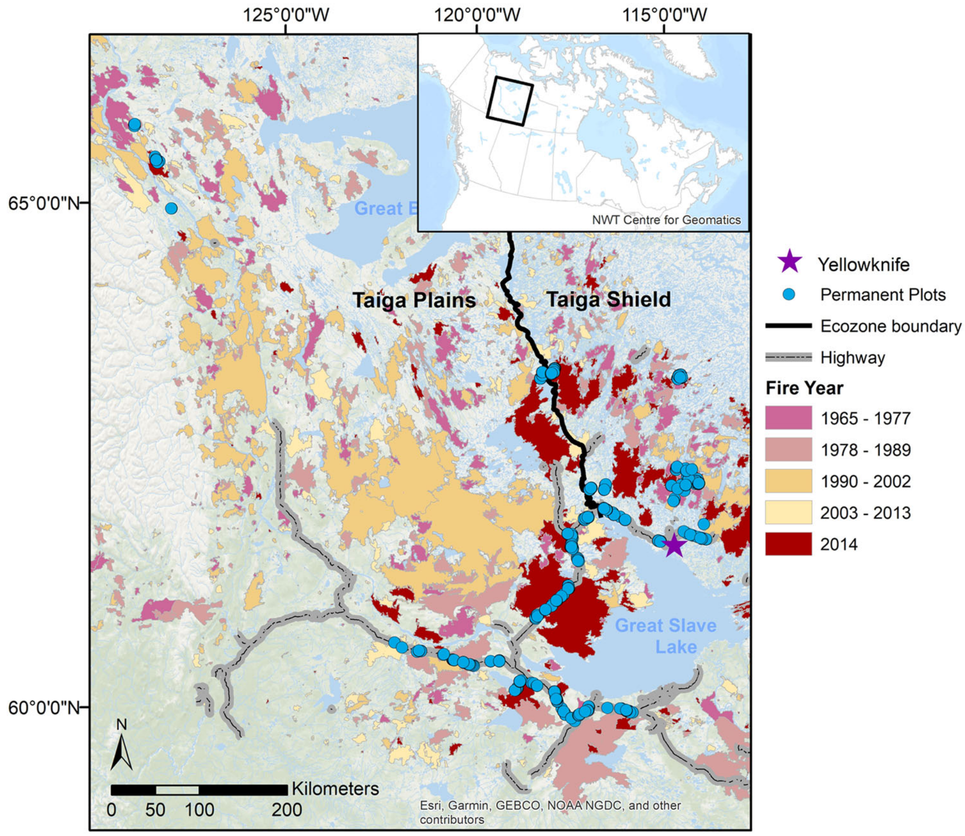


Figure 1. Locations of a chronosequence of plots ($n=511$) in the Northwest Territories, Canada, where soil organic layer thickness and total carbon stocks were measured. Plots were sampled along a chronosequence of time-after-fire, stratified by ecozone, and constrained by accessibility. Fire history from 1965 to 2014 was determined from the fire year associated with mapped fire scars (NWT Centre for Geomatics 2012). For plots not within any recorded fire, time-after-fire was determined by tree ring analysis.

sification Group 2009). The Shield is characterized by exposed granite bedrock and peatland (Ecosystem Classification Group 2008). Mean annual temperature for Yellowknife, NWT, is −4 °C (1958–2012), with growing season precipitation for this area ranging from 28 to 40 mm (1981–2010; Environment and Climate Change Canada 2019). Forests in our study region are generally dominated by black spruce. The Plains also has mixed-coniferous plots comprised mainly of jack pine, larch (*Larix laricina*), and/or white spruce (*Picea glauca*). In the Shield, mixed-coniferous plots have jack pine, paper birch (*Betula papyrifera* and *Betula neoalaskana*), white spruce, and trembling aspen (*Populus tremuloides*), listed in descending order of dominance.

Site Selection

Permanent plots (n=511) were established during 2015–2018 across 41 wildfire scars and unburned areas (no burn history prior to 1965; see Text S1), with 317 plots in the Plains and 194 plots in the Shield (Figure 1; Table S1). Fire scars were selected based on post-1965 fire history polygon data because this is when fire records began (NWT Centre for Geomatics, 2012). All plots were established at least 500 m from roadways and greater than 100 m from trails or any visible evidence of past resource extraction such as small-scale logging or quarries. Within fire scars, the first plot within a site complex was selected based on random stratified methods and sampled within land cover classes (vegetation and abiotic characteristics) proportional to class abundance within the fire scar (Latifovic and others 2008) and constrained to within 1 km of access point (Text S1). One or two additional plots were established within a few hundred meters of the initial plot to capture local variation in soil moisture regime (see Supplementary Material: Site Design and Field Measurements). Plots were assigned to a moisture class (xeric, mesic, or hydric) in the field, using methods of Johnstone and others (2008) considering topography, drainage, soil texture, and presence of surface water and the frost table. Our sampling did not always capture the entire soil organic layer in hydric plots, particularly when sampling occurred in June or July when seasonal ice was still present, limiting our access to deeper organic soils.

Plot Design and Field Measurements

At each plot, two adjacent 30-m transects were established 2 m apart, running north from the plot origin. SOL depth (cm) was measured every 3 m and the mean was taken from these 10 measures to calculate a plot-level SOL thickness. Three soil organic layer profiles were destructively sampled at 0, 12, and 24 m using a 5×30 cm or 7.7×52 cm corer that was custom-designed for NWT soils and consisted of a metal core barrel with a sharpened bottom edge. We hand-inserted the metal corer into the ground surface, which resulted in minimal compaction. Soil cores with more than 2–3 cm of surface compaction were rejected. Soil cores captured the organic layer to either surface mineral soil or the permafrost table. When coring was not possible, due to rocks for example, samples were carefully excavated from the soil matrix in 5×10 cm blocks using large knives and shears. Soil samples collected with the corer were gently extracted into protective plastic sheaths, whereas excavated samples were wrapped in aluminum foil. All soil samples were frozen on the day of collection.

Within the 60 m^2 transects, all stems above diameter at breast height (DBH: 1.37 m) were identified to species to calculate tree density (stems/m^2). Where stems were < DBH, total basal diameter (cm^2/m^2) was measured at the base of the tree and used to calculate tree density. Mean stand age was derived using standard dendrochronology techniques to represent the timing of the last fire (Walker and others 2018a) from basal tree disks or cores ($n=5$ per plot). Nonvascular plant percent cover was identified to functional group at five, 1 m^2 quadrats spaced 6 m apart along the belt transect. The plot-level mean nonvascular plant percent cover was calculated by taking the mean of the five quadrats.

Soil Organic Carbon Stock Estimation

Soil samples (n = 1803) were shipped frozen, on ice from Yellowknife, NWT, Canada, to the University of Guelph (UoG), Ontario, Canada, or Northern Arizona University (NAU), Arizona, USA (see Walker and others 2018b) where they were stored at approximately 4 °C until removed individually for further sub-sectioning. Prior to sub-sectioning samples at the UoG, we identified and measured the thickness of the organic soil horizons within each intact soil core, classifying them as ground layer, dead moss, fibric (USDA soil classification: Oi), mesic (Oe), or humic (Oa) layers based on composition (that is, amount of fine roots and decomposed plant material), and degree of decomposition (Canadian Agricultural Services Coordinating Committee 1998). To isolate the various soil horizons and estimate C for each, organic profiles were sectioned into ~5 cm increments, without cutting through visible horizons. For samples collected in 2015 and 2016 (NAU), the monoliths were cut vertically for archiving (see Walker and others 2018b) and the remaining half was handled as follows. For both the samples at the UoG and the remaining half from NAU, the mean of length, width, and height of each increment were measured; the coarse fraction (> 2 mm) was removed and recorded to calculate the volume for each sample. Each increment was then oven-dried at 65 °C until achieving a stable mass to determine soil bulk density (g cm^{-3}; Text S2) and ground to homogenize.

A subset of 2067 of 5137 total increments from 1803 profiles from 421 plots were analyzed for total % C using a CHN analyzer (PerkinElmer 2400 CHNS analyzer or Costech Elemental Analyzer at Wilfrid Laurier University). Total % C was assumed to be equivalent to organic C as there is seldom inorganic C present in samples of this type (Santín and others 2016). Relationships between soil bulk density and measured total % C were modeled to estimate SOC stocks (kg C m^{-2}) (Text S3). Soil increments were classified as organic soil where total % C was greater than 20% (Hossain and others 2007; Ražauskaitė and others 2020). Samples with less than 20% total C were classified as mineral soil and excluded from SOC calculations. The C content of organic soil increments was calculated from the product of increment volume, bulk density, and % C. Profile total SOC content was calculated by summing over the profile's organic soil increments. Plot-level SOC stocks (kg C m^{-2}) were estimated as the mean profile C content of three soil cores, scaled to the profile surface areas.

Plot-level Statistical Analysis

Ecozone was identified as a categorical variable (Taiga Plains and Taiga Shield), derived from the Ecological Framework of Canada (Ecological Stratification Working Group 1995). Time-after-

Table 1. Results of Sample-size Corrected Akaike Information Criterion (AICc)-Based Model Selection Among a Suite of A priori Alternate Linear Mixed-Effects Models of Soil Organic Layer (SOL) Thickness (cm) and Total Soil Organic C (SOC) Stock (kg C m^{-2}), Measured Along a Chronosequence of Plots in the Northwest Territories, Canada

Model	Predictor variables	SOL							SOC						
		K	AIC_c	$_i$	w_i	LogL	R^2_m	R^2_c	K	AIC_c	$_i$	w_i	LogL	R^2_m	R^2_c
Ecosystem	Time-after-fire × Moisture Class × Ecozone+Stand Dominance+Nonvascular Functional Group+Jack Pine Proportion+ Deciduous Proportion	27	492.1	0	1	−217.454	0.73	0.8	20	308.65	0	1	−125.12	0.64	0.68
Drainage Interaction	Time-after-fire × Moisture Class × Ecozone	15	569.2	77.14	0	−269.113	0.67	0.75	9	569.20	260.55	0	−269.11	0.67	0.75
Drainage	Time-after-fire+Moisture Class+Ecozone	8	595.2	103.19	0	−289.479	0.65	0.72	7	344.18	35.54	0	−163.89	0.56	0.6
Vegetation	Time-after-fire+Stand Dominance+Nonvascular Functional Group+Jack Pine Proportion+Deciduous Proportion	17	789.2	297.17	0	−376.985	0.51	0.58	19	469.34	160.69	0	−216.8	0.40	0.48
Vegetation Interaction	Time-after-fire x Stand Dominance+Nonvascular Functional Group+Jack Pine Proportion+Deciduous Proportion	20	791.6	299.57	0	−374.947	0.51	0.59	16	473.68	165.03	0	−215.64	0.40	0.49
Time-after-fire	Time-after-fire	5	1099.6	607.53	0	−544.732	0.03	0.23	5	604.03	295.38	0	−296.93	0.04	0.25
Null	Intercept	4	1100.8	608.79	0	−546.380	0	0.23	4	606.1	297.45	0	−298.99	0	0.24

All models included random effects of site nested within fire scar (see Methods for sample design). SOC was measured only for the soil organic layer. For each model, number of parameters (K), sample size-corrected AIC score (AIC_c), increase in AIC_c relative to the best model ($^{\Delta i}\Delta AIC_c$), model weight (w_i), model log-likelihood (LogL), marginal R^2 (R^2m), and conditional R^2 (R^2c) are shown.

fire was established using fire history records and for older plots where no-known fire history is recorded, tree age was used because as most fires in boreal North America are stand replacing and trees tend to establish rapidly post-burn (Viereck 1983; Greene and Johnson 1999). To determine tree age, cores or basal cookies were taken just above the root collar from five trees of the (co)dominant conifer species within each plot, representing the dominant size class (see also Figure 1). Samples were sanded with increasingly finer grits before being scanned to a resolution of 4800 dpi and their rings counted using dendrochronology software (see Walker and others 2018a). The proportion of jack pine and deciduous trees (mix of paper birch and trembling aspen) was calculated using the density of stems that contributed to the canopy (> 5 cm at DBH), divided by the total number of stems of all canopy trees. To classify stand dominance, we considered plots to be black spruce- (n=286), jack pine- (n=83), or deciduous-dominated (n=39) when proportion of stems of each species were greater than 50% of the stand (Walker and others 2018a). We classified plots as mixed where no one species was > 0.5 in proportion (n=103). Dominant nonvascular functional group was determined using the mean nonvascular plant percent cover (> 50%). All statistical analyses were performed with R statistical software (v. 4.0.1; R Core Development Team 2020).

We needed to constrain our dataset for analyses in two ways. First, in a subset of plots the full organic profile was not captured due to frozen soils, which burned more than 100 years ago. Thus, we excluded these older stands (n=57) from subsequent analyses, limiting our analyses to stands that burned in the past 100 years (n=543). Second, in a small portion of our 159 permafrost plots, we were not able to measure the entire SOL because our plot sampling occurred before maximum seasonal thaw depth. Because of this, we excluded 32 permafrost plots with incomplete SOL from our analyses, leaving 127 permafrost plots in our dataset. Based on these two constraints, 511 plots were retained for these analyses.

A candidate model approach and Akaike information criterion (AICc) were used to understand post-fire recovery of SOL thickness and SOC stocks. Hierarchical, linear mixed-effect models were created based on a priori hypotheses to assess vegetation and moisture controls using the R package: *nlme* (Pinheiro and others 2020) (Table 1). We designed the candidate models to represent predominant hypotheses on factors controlling post-fire recovery in depth of SOL and SOC stocks with

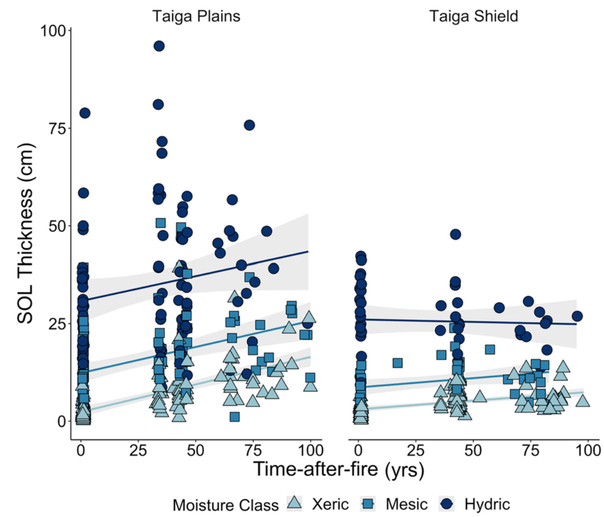


Figure 2. Scatter plots of measured soil organic layer thickness (SOL cm) against time-after-fire (in years) stratified by moisture class within ecozone. Relationships with strata are summarized by univariate linear models plotted as color-coded lines with 95% prediction intervals in light gray.

first- and second-order interactions. These candidate models were denoted as null, time-after-fire, drainage, drainage interaction, vegetation, vegetation interaction, and ecosystem (Table 1). Explanatory variables for SOL thickness and SOC stocks that were highly correlated with each other were removed using Spearman's rho correlation coefficient matrix; this included proportion of black spruce (based on stem density), basal area of black spruce, jack pine, and deciduous trees (R package: *PerformanceAnalytics*, Table S2). The response variables for both SOL and SOC stock models were cube-root-transformed to meet model assumptions (i.e., normality of residuals, homogeneity of variance). Multicollinearity between predictor variables was assessed using the variance inflation factor in the R package: *car*; however, a priori modeling enables us to explore relationships between the response and fixed effects without excluding variables as a result of ecological complexity (Graham 2003). We tested for differences among moisture classes, stand dominance class categories (black spruce, jack pine, deciduous and mixed), and ecozones using Tukey–Kramer *post hoc* analyses for multiple comparisons (R package: *emmeans*) (Lenth 2021). Because vegetation (that is, landcover type, stand dominance) varied between ecozones, the selected models were also examined separately for each ecozone. As sites were nested within unburned areas or burned (fire scar), these were used as random effect terms to account for

Table 2. Summary of Fixed Effects for Best Supported Models (Table 1) of Soil Organic Layer (SOL) Thickness (cm) and Soil Organic C (SOC) Stock (kg C m^{-2})) Measured at Chronosequences of Plots Within the Northwest Territories, Canada

Fixed effect	SOL thickness				SOC stock			
	df	Error df	*F*	*p*	df	Error	*F* value	*p value*
Time-after-fire	1	257	49.13	< 0.0001	1	152	20.07	< 0.0001
Moisture class	2	257	598.67	< 0.0001	2	152	275.29	< 0.0001
Ecozone	1	209	29.88	< 0.0001	1	149	42.73	< 0.0001
Stand dominance	3	257	10.58	< 0.0001	3	152	2.31	0.08
Nonvascular functional group	7	257	6.39	< 0.0001	7	152	1.25	0.28
Jack pine proportion	1	257	19.76	< 0.0001	1	152	12.86	0.0005
Deciduous proportion	1	257	16.76	< 0.0001	1	152	10.36	0.0016
Time-after-fire × Moisture	2	257	14.98	< 0.0001	2	152	12.98	< 0.0001
Time-after-fire × Ecozone	1	257	1.56	0.212	1	152	1.31	0.25
Moisture × Ecozone	2	257	2.24	0.108	2	152	6.31	0.0023
Time-after-fire × Moisture × Ecozone	2	257	0.34	0.710	2	152	0.62	0.54

Effect (df) and residual degrees of freedom (Error df), test statistic (F) and significance (p). Parameter estimates for (the two best models/for all models?) are reported in Table S5.

non-independence. Recovery of SOL and SOC was assessed using the estimated marginal means of linear trends for both most parsimonious models.

Post-fire SOC recovery for each stand dominance class was assessed for each moisture class using mixed-effect models with time-after-fire as a fixed effect and site nested within unburned or burn areas as random effects (Walker and others 2018b). A mixed-effect model and estimated marginal means were used with second-order interactions between time-after-fire, moisture, and stand dominance class to examine the differences in post-fire recovery of SOC among the successional trajectories in each moisture class ($p < 0.05$).

Results

Post-fire Changes in the Soil Organic Layer

A mix of abiotic and biotic factors influenced post-fire changes in the SOL, resulting in the Ecosystem Model being weighted the highest of the set of candidate models (most parsimonious) (Table 1). Averaged across all other predictor variables, the thickest SOL occurred in hydric plots (37.0 ± 1.0 cm, mean ± SEM) with decreasing thicknesses with progressively drier moisture conditions (mesic = 14.0 ± 1.0, xeric = 6.0 ± 0.5 cm).

An interaction between moisture class and ecozone significantly influenced post-fire changes in SOL thickness (Figs. 2 and S1). Plots in the Plains had thicker SOL than in the Shield, and this was particularly true for hydric plots (Plains-hydric plots: 27.3 ± 0.07 cm, Shield-hydric plots: 22.2 ± 0.09 cm). In contrast, ecozone differences were less apparent in mesic (Plains: 13.65 ± 0.07 cm; Shield: 9.7 ± 0.09 cm) and xeric (Plains: 7.08 ± 0.07 cm; Shield: 6.23 ± 0.08 cm) plots. Despite generally thicker SOL in hydric plots, the SOL in xeric plots accumulated twice as fast (0.15 ± 0.02 cm $decade^{-1}$) as mesic (0.07 ± 0.02 cm $decade^{-1}$) or hydric (0.06 ± 0.02 cm $decade^{-1}$) plots within the Plains ecozone (Figure 2; Table S4). Within the Shield ecozone, xeric (0.08 ± 0.02 cm $decade^{-1}$) and mesic (0.08 ± 0.02 cm $decade^{-1}$) plots changed an order of magnitude faster than in hydric plots (0.008 ± 0.02 cm $decade^{-1}$).

Changes in the SOL post-fire also depended on several biotic variables, including the proportion of jack pine and deciduous trees, stand dominance class, and dominant nonvascular functional group (Table 2). SOL was thickest in black spruce- and mixed-species-dominated plots where the proportions of deciduous taxa and jack pine were low (Figure S2). Averaged across moisture, ecozone, and dominant nonvascular function group, SOL varied with stand dominance class, with black spruce and mixed plots having significantly thicker SOLs than jack pine or deciduous plots (Figure 3). Nonvascular group dominance also explained variation in SOL, with the thickest organic soils found at *Sphagnum*-dominated plots (Figure S3).

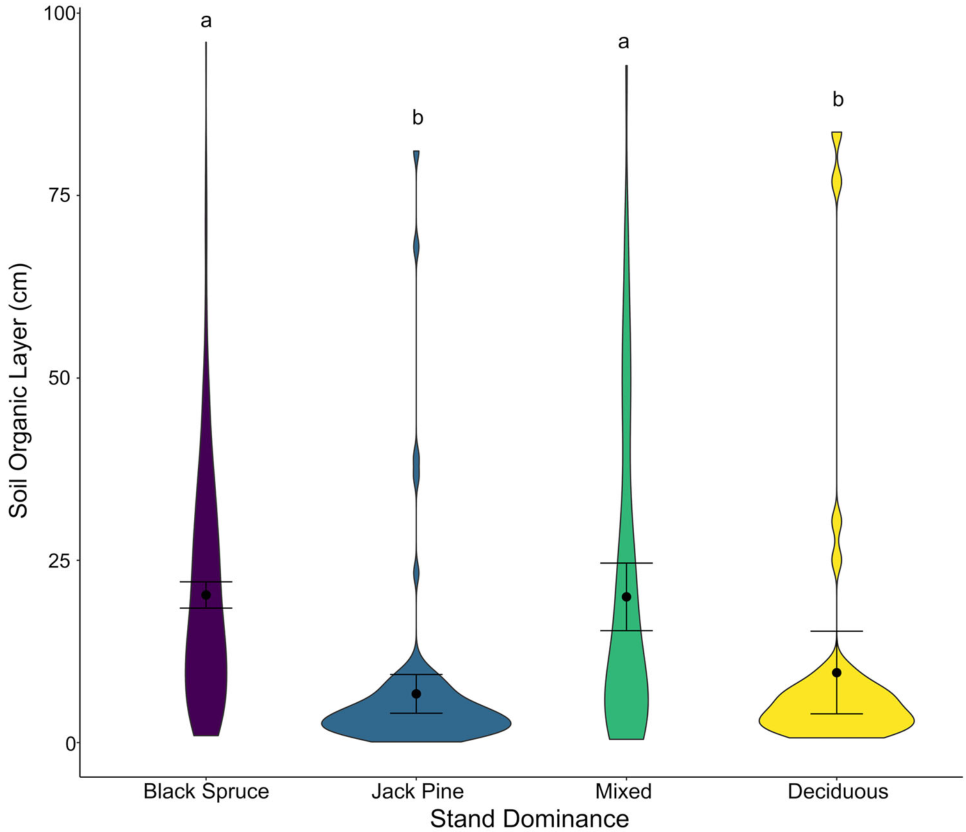


Figure 3. Distributions of plot soil organic layer thickness (cm) by stand dominance classes violin plots with means and standard error. Data are averaged across ecozones. Nonsignificant differences are based on Tukey–Kramer post hoc tests of multiple comparisons and are denoted by same letter superscripts above each stand dominance class. Black spruce and mixed stands had thicker soil organic layers than jack pine and deciduous stands.

Table 3. Rates of Combustion of Soil Organic C (SOC) and Ecosystem C (SOC+Aboveground Carbon Stock) in kg C m^{-2} From Walker and others (2019) Across Different Combinations of Stand Dominance and Moisture Class

Stand dominance	Moisture class	Soil C combusted (kg C m^{-2})	Ecosystem C combusted (kg C m^{-2})	Time to recover combusted SOC (y)	Time to recover combusted ecosystem C (y)
Black spruce	Xeric	2.46±0.24	2.89±0.23	29±1.0	15±0.1
	Mesic	3.83±0.21	4.40±0.23	65±1.2	72±0.02
	Hydric	4.23±0.25	4.56±0.26	NA	NA
Jack pine	Xeric	0.49±0.01	0.84±0.7	14±1.9	25±0.02
Deciduous	Xeric	1.56±0.37	1.69±0.36	21.5±0.4	27±0.03
Mixed	Xeric	1.56±0.37	1.69±0.36	53.5±0.2	33.5±0.04
	Mesic	5.14±2.41	5.42±2.28	104±6.5	34±0.04
	Hydric	2.56±0.39	2.68±0.35	NA	NA

We used changes in SOC stocks (this study) and AG stocks (Todd-Brown and others in review) with time-after-fire to calculate the amount of time required to recover these C stocks lost during combustion. Models described all include a random effect of site nested within fire scar ID (R package nlme). Because our data showed that hydric plots did not correspond to significant increases in SOC stocks with time-after-fire, we did not calculate recovery times for these conditions.

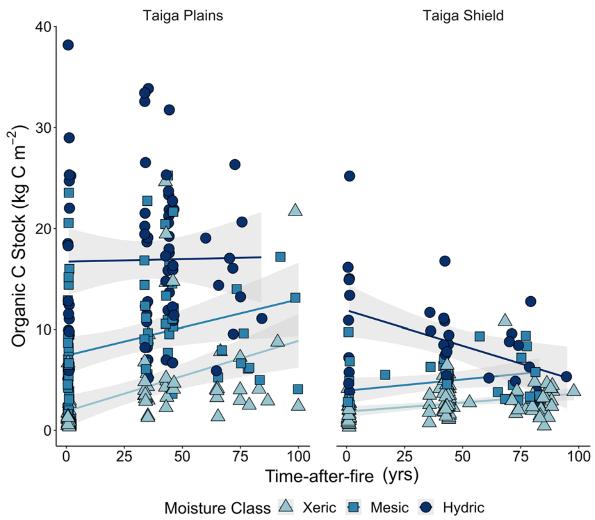


Figure 4. Scatter plots of measured soil organic carbon stock (SOC kg C m^{-2}) against time-after-fire stratified by moisture class within ecozone. Relationships within strata are summarized by univariate linear models plotted as color-coded lines with 95% prediction intervals in light gray.

Post-fire Changes in Soil Organic Carbon Stocks

Soil organic C stocks (kg C m^{-2}) were influenced by an interaction between time-after-fire, moisture class, and ecozone (Table 2). When SOC stocks were examined separately within each ecozone, the most parsimonious model also included the interaction between time-after-fire and moisture (Table 1). The results from estimated marginal means indicate that changes in SOC stocks varied among moisture classes and ecozone (Table 3). Below, we describe trends in the results based on estimated marginal means.

SOC stocks were greater overall in the Plains than in the Shield, but the trend was dependent on moisture class. Mesic and hydric plots in the Plains ecozone (mesic: 9.5±0.07 kg C m^{-2}, hydric: 18.2±0.07 kg C m^{-2}) held 45% more soil C than the equivalent moisture class in the Shield (mesic: 5.3±0.09 kg C m^{-2}, hydric: 9.9±0.09 kg C m^{-2}, Table S4). In contrast, C stocks in xeric plots did not vary between ecozones averaging 4.2±0.08 kg C m^{-2}. SOC stocks increased with time-after-fire at a similar rate among all moisture classes in the Plains ecozone. In the Shield, however, xeric (310±20 g C m^{-2} decade^{-1}) and mesic (380±30 g C m^{-2} decade^{-1}) plots corresponded to faster increases in SOC stocks than hydric plots, which showed no evidence of increasing SOC with time-after-fire (−560±30 g C m^{-2} decade^{-1}; Figs. 4 and S5). Despite these differences among moistures classes, SOC accumulated at a similar rate at all xeric plots regardless of ecozone, averaging 444±159 g C m^{-2} decade^{-1}. After 100 years of post-fire succession, xeric SOC stocks remained consistent at an average of 6±1 kg C m^{-2}.

There were no differences in SOC stocks across stand dominance class or nonvascular functional types, whereas there was a negative relationship between SOC stock and proportion of jack pine and deciduous trees (%) (Table 2, Figure S2). We found no correlations between dominant stand type and time-after-fire, suggesting that post-fire recovery of soil C is not influenced by canopy structure in terms of stand dominance class when factors of moisture class, ecozone, and dominant nonvascular functional group are taken into account. When analyzed separately within each ecozone, vegetation components of the plot (stand dominance class, nonvascular functional group dominance, and proportion of jack pine and deciduous) drop out as important predictors of SOC stocks. This result reinforces our interpretation that moisture and ecozone variation were more important drivers of post-fire SOC recovery than biotic variables.

Variation in the thickness, bulk density, or C concentration of individual organic soil horizons caused divergences in the relationship between SOL thickness and SOC stock across a subset of our plots (Figure S4). In some cases, comparatively thick SOL contained relatively small SOC stocks due to both low bulk density and C concentration values.

Change in SOC Stocks with Stand Dominance Class

Post-fire accumulation of SOC stocks (kg C m^{-2}) varied among moisture class for black spruce-, jack pine-, deciduous-, and mixed-species-dominated stands (Figure 5; Table S4). Separate models were assessed to understand the interaction between stand dominance class and moisture class due to an unbalanced design. Black spruce-dominated plots accumulated SOC at a rate of 860±240 g C m^{-2} decade^{-1} in xeric and 570±300 g C m^{-2} decade^{-1} in mesic plots. Black spruce-hydric plots lost 450±380 g C m^{-2} decade^{-1}. Mixed-species plots accumulated SOC at a rate of 290±230 g C m^{-2} decade^{-1} in xeric plots, 500±490 g C m^{-2} decade^{-1} in mesic plots, and showed no recovery (30±960 g C m^{-2} decade^{-1}) in hydric plots. Jack pine and deciduous plots, which were confined to xeric moisture conditions, accumulated 340±160 g C m^{-2} decade^{-1} and 230±130 g C m^{-2} decade^{-1}, respectively. There were no statistically significant differences in the post-fire recovery of SOC accumulation rates between stand dominance classes.

Discussion

Factors Controlling Changes in Post-fire Soil Organic C Stocks

Using an extensive network of field plots varying in time-after-fire and dominant tree type, we show that trends in SOL thickness and SOC stocks with time-after-fire are most strongly influenced by moisture class. Immediately post-fire, xeric plots had thin residual organic soils with small C stocks, indicative of greater proportional combustion in drier plots—a trend broadly observed in the North American boreal forest (Genet and others 2013; Senici and others 2013). However, SOL and SOC accumulation rates were faster in xeric plots post-fire, likely because of larger aboveground C pools and faster litterfall (Mack and others 2021; Johnstone and others 2010a; Senici and others 2013; Holden and others 2015; Thompson and others 2017) relative to the other moisture classes. Because of this trend, despite immediate post-fire differences, SOL and SOC stocks in xeric and mesic plots converged after a century of post-fire recovery.

Across all stages of post-fire recovery, wetter (mesic and hydric) plots had thicker SOL and greater SOC stocks than xeric plots. Historically, deeper organic layers commonly observed in wetter portions of the landscape have been attributed to slow decomposition (Harden and others 2000; Hobbie and others 2000), anaerobic conditions (Hobbie and others 2000; Hollingsworth and others 2008), and recalcitrant litter (Hollingsworth and others 2008; Johnstone and others 2016; Mack and others 2008). More recently, Walker and others (2019) found that wetter plots in our study region had organic soils with legacy C that had escaped combustion during previous fires. Our study demonstrates that these wetter locations have much slower rates of post-fire SOC recovery. Together, these results point to the importance of moisture-driven differences in fuel combustion across multiple fire cycles perpetuating landscape-level variation in SOC stocks.

Although it is beyond the scope of this study, we suspect that our results demonstrating little-to-no SOC recovery in hydric plots are due to active layer thickening and enhanced mineralization of surface permafrost (Herndon and others 2020) that is not compensated by net primary productivity. Projections for a shorter fire return interval in this region suggest that these hydric soil regions will store less C into the future (Miquelajauregui and others 2019). Given the current range of fire return interval (70–130 years) in North American boreal forests (Johnstone and others 2010a; Wang and others 2015), we estimate that under a shorter fire return interval of 70 years, hydric plot C stocks would be reduced by 50% in three fire cycles equivalent to a loss of soil C of 25 kg C m^{-2} (assuming loss of 990 ± 1620 g C m^{-2} $decade^{-1}$ between fires reflecting the average across all hydric plots).

While our results highlight the importance of abiotic controls on post-fire changes in SOL and SOC stocks, there were several important examples of biotic controls. First, post-fire SOL and SOC accumulation rates did not differ across dominant stand types. These taxa often outcompete black spruce during seedling establishment when the SOL is thin following severe wildfire events (Day and others 2020; Moore and others 2006). Once matured, deciduous and jack pine litter have lower lignin-nitrogen ratios than black spruce litter, which support faster soil-nutrient turnover and shade out mosses—likely limiting SOL and SOC accumulation (Jean and others 2020; Johnstone and others 2010a; Moore and others 1999; Fujii and others 2020). Second, *Sphagnum* moss presence was associated with the thickest organic soils in our study. *Sphagnum* mosses tend to be found in wetter habitats such as peatlands and permafrost forests (90% of *Sphagnum*-dominant plots were hydric in our study). Not only do *Sphagnum* thrive under hydric soil conditions, but they also contribute to soil wetting through traits such as high-water retention and upward wicking of water (Turetsky and others 2012) and thus contribute to resistance to deep burning (Granath and others 2016; Shetler and others 2008).

Consequences of Canopy State Changes for Soil C Stocks

Boreal vegetation is changing with increasing fire severity (Day and others 2020; Alexander and Mack 2016; Johnstone and others 2010c; Kishchuk and others 2016; Mann and others 2012). More severe burning and increased fire frequency (including more reburning of young conifer stands) lead to increases in deciduous cover and jack pine (Alonzo and others 2017; Brown and Johnstone 2012; Gibson and others 2016; Hart and others 2018; Johnstone and others 2011; Walker and others 2019; Whitman and others 2018; Boulanger

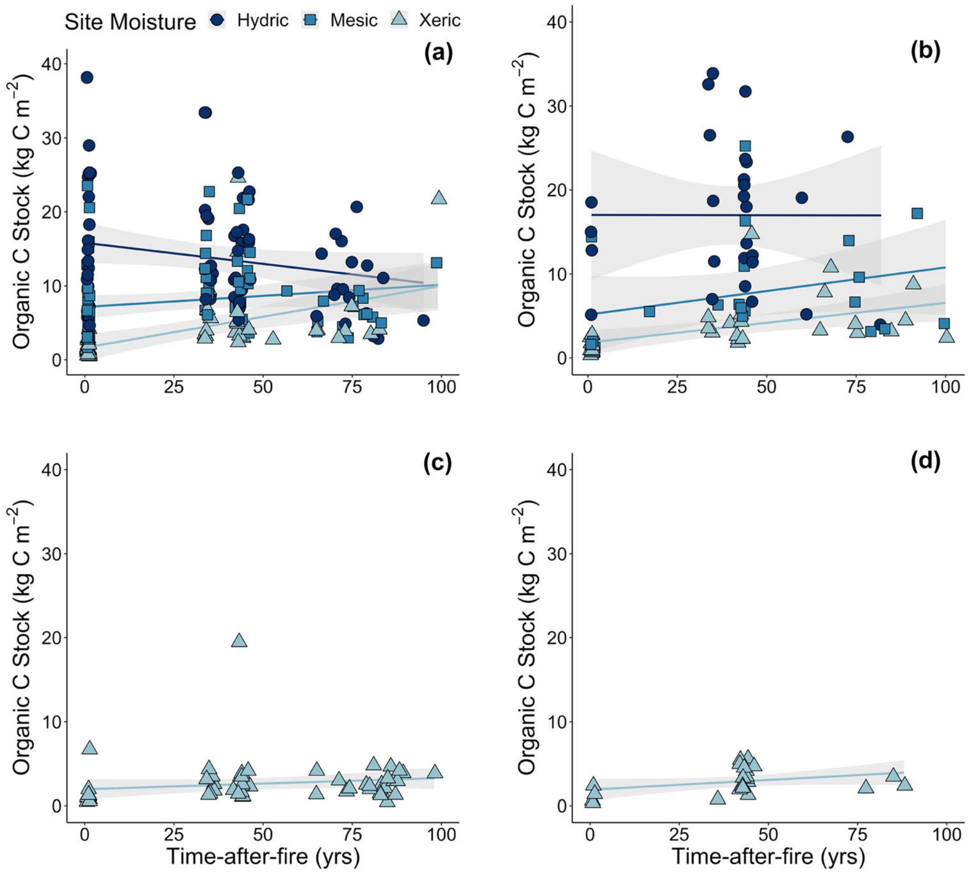


Figure 5. Scatter plots of soil organic carbon stock (SOC kg C m^{-2}) against time-after-fire stratified by stand dominance: **A** black spruce, **B** mixed, **C** jack pine, **D** deciduous and by moisture class within stand dominance where sample sizes permit. Relationships within strata are summarized by univariate linear models plotted as color-coded lines with 95% prediction intervals in light gray.

and others 2017). Increases in deciduous dominance following severe burning are likely to reduce flammability, which could serve to dampen the climate sensitivity of boreal fire regimes (Cumming 2001; Lynch and others 2004). Shifts away from black spruce self-replacement toward deciduous or jack pine expansion may result in long-term changes in soil C accumulation, which we investigated in this study. Surprisingly, we found that SOC stocks in black spruce-dominated plots were not greater on average than in other canopy types. This is likely because of the wide range of environmental conditions associated with black spruce plots in this region (Kasischke and Johnstone 2005; Walker and others 2019). However, with increasing deciduous and jack pine canopy fraction, SOL thickness and SOC stock both decline (Figure S2). Soon after fire, we found that black spruce plots store 80% and 85% more SOC than jack pine and deciduous plots, respectively. After 70 years of post-fire succession, black spruce plots gain approximately 10 kg SOC m^{-2}, while mature jack pine and deciduous plots gained about 3 kg SOC m^{-2}. Overall, these results suggest that severe fire activity in the NWT that converts black spruce to jack pine or deciduous-dominated stands will reduce SOC stocks by 60–80% across stages of post-fire succession (that is, 1–100 years).

We used SOC combustion rates from the 2014 fires (Walker and others 2018b), along with changes in SOC stocks (this study) to calculate the amount of time required to re-accumulate what was lost immediately during fire with combustion (turnover rate (year)=combustion (kg C m^{-2})/annual C accumulation (kg C m^{-2} year^{-1}). Recovery of the combusted SOC pool was fastest in xeric plots (ranging from 14 to 29 years depending on stand dominance; Figure 5; Table 3). Recovery of the SOC combusted stock was slower in mesic plots, averaging 104 years ± 6.48 to recover to pre-fire SOC stock in mixed-dominance plots and 65 years ± 1.23 in black spruce-dominated plots. Because our data showed little evidence of significant increases in SOC in hydric plots, we assumed no recovery of the SOC combusted pool over the timeframe investigated in this study.

Stands dominated by jack pine and deciduous species are expected to store less SOC, instead storing more C in aboveground biomass relative to black spruce (Mack and others 2021; Alexander and Mack 2016; Gibson and others 2016; Laganière and others 2013). These aboveground C stores can help to offset soil C losses; however, these aboveground stocks are more vulnerable to burning during subsequent fire compared to soil carbon stocks (Walker and others 2020). We used aboveground vegetation carbon combustion rates (Walker and others 2018b) and changes in aboveground vegetation carbon stocks with time-after-fire (Todd-Brown and others Unpublished Manuscript, in review) to ask how the recovery times reported above would be altered if based on total ecosystem C (SOC plus aboveground vegetation stocks). Given that fuel combustion is dominated by SOC burning during fire (Walker and others 2018b), the differences between total ecosystem and SOC recovery rates would be driven by changes in vegetation carbon stocks with time-after-fire. In xeric mixed- and jack pine-dominated stands, the time to recover combusted SOC was faster than the time to recover total combusted ecosystem C, despite including post-fire recovery of aboveground biomass (Table 3). However, the opposite pattern was observed for xeric deciduous- or black spruce-dominated stands, where inclusion of vegetation C in our estimates led to faster recovery rates. These differences also were observed in mesic plots. For mesic black spruce plots, there were no substantial differences in the amount of time to recover combusted SOC versus combusted total ecosystem C pools. However, including aboveground vegetation C in our estimates greatly reduced recovery times in mesic mixed-dominance stands (Table 3). While these recovery estimates are quite variable, overall, these calculations provided little evidence that greater productivity post-fire of deciduous species would be able to compensate for the soil C losses associated with fire or fire-induced vegetation state changes documented in this study.

There are two main sources of uncertainty in this study worth acknowledging. First, while our statistical models explored how landscape, vegetation, and ecozone characteristics potentially interacted with time-after-fire, our design was not able to address variation in burn severity across our sites. We recognize this is a weakness of our approach, given significant variation in burn severity observed in recently burned plots (Walker and others 2018a). That said, our study explicitly captures variation in eco-topographical conditions that are known to govern combustion rates, such as soil moisture class. Thus, despite the limitations of the chronosequence design, our study allowed us to explore dominant patterns influencing post-fire changes in soil C stocks across a range of abiotic and biotic conditions that hold true even if historical burn severity variation also governs changes in soil C. Second, we used a modeled relationship between organic matter and C concentrations on a subset of measured samples to estimate data across our entire population of samples. We ensured that the measured subset represented a range of soil horizon and plot-level variation; however, we did not propagate the error from this relationship throughout subsequent analyses. Although this is a source of uncertainty, there is no evidence that it would bias our conclusions regarding plot type or behavior with time-after-fire.

Conclusions

Overall, our results suggest that a century of post-fire succession tends to minimize spatial variation in SOL layers across moisture classes likely caused by deeper burning in mesic moisture classes (Walker and others 2018a). While we observed more rapid rates of SOC accumulation post-fire in xeric and mesic sites, our results showed negligible recovery of SOC stocks with time-after-fire in the wettest boreal forest sites, possibly associated with ongoing rates of permafrost thaw. This has implications for regional C accumulation under an intensified fire regime, as wetter parts of the landscape are hotspots for thick carbon-rich peat or organic soil layers but are expected to dry and burn more frequently in the future. If this pattern of minimal recovery holds true for other poorly drained conifer forests, including the forested peatlands that are abundant in this region, the western boreal forest region could be poised to lose one of its most dominant and persistent carbon sinks. Our results also point to the implications of increasing deciduous cover as a consequence of intensified boreal forest fire regimes. Increasing jack pine and deciduous cover at the expense of black spruce stands will translate to thinner soil organic layers but perhaps more C stored in aboveground biomass. This shift has implications for the turnover time of carbon stocks on the landscape and also will impact energy fluxes by controlling albedo and surface soil moisture.

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DATA AVAILABILITY

The data are archieved with ORNL DAAC: https://doi.org/10.3334/ORNLDAAC/2235.

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