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ARTICLE

Ecology of Critical Zones

Drivers of legacy soil organic matter decomposition after fire in boreal forests

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Abstract

Boreal forests harbor as much carbon (C) as the atmosphere and significant amounts of organic nitrogen (N), the nutrient most likely to limit plant productivity in high-latitude ecosystems. In the boreal biome, the primary disturbance is wildfire, which consumes plant biomass and soil material, emits greenhouse gasses, and influences long-term C and N cycling. Climate warming and drying is increasing wildfire severity and frequency and is combusting more soil organic matter (SOM). Combustion of surface SOM exposes deeper older layers of accumulated soil material that previously escaped combustion during past fires, here termed legacy SOM. Postfire SOM decomposition and nutrient availability are determined by these layers, but the drivers of legacy SOM decomposition are unknown. We collected soils from plots after the largest fire year on record in the Northwest Territories, Canada, in 2014. We used radiocarbon dating to measure $\Delta^{14}C$ (soil age index), soil extractions to quantify N pools and microbial biomass, and a 90-day laboratory incubation to measure the potential rate of element mineralization and understand patterns and drivers of legacy SOM C decomposition and N availability. We discovered that bulk soil C age predicted C decomposition, where cumulatively, older soil (approximately −450.0‰) produced 230%

less C during the incubation than younger soil (~0.0‰). Soil age also predicted C turnover times, with old soil turnover 10 times slower than young soil. We found respired C was younger than bulk soil C, indicating most C enters and leaves relatively quickly, while the older portion remains a stable C sink. Soil age and other indices were unrelated to N availability, but microbial biomass influenced N availability, with more microbial biomass immobilizing soil N pools. Our results stress the importance of legacy SOM as a stable C sink and highlight that soil age drives the pace and magnitude of soil C contributions to the atmosphere between wildfires.

KEYWORDS
carbon mineralization, laboratory incubation, nitrogen mineralization, *Picea mariana*, radiocarbon, soil age, soil decomposition, wildfire

INTRODUCTION

Boreal forests contain one third of global terrestrial carbon (C) and large amounts of organic nitrogen (N; Bradshaw & Warkentin, 2015; Korhonen et al., 2013; Näsholm et al., 1998). Both these element pools are intimately tied to the primary disturbance in boreal forests: wildfires (Bond-Lamberty et al., 2007; Gower et al., 2000; Walker et al., 2018). Wildfires emit greenhouse gases that contribute to climate warming via combustion of plant biomass, surface litter, and organic soils (Harden et al., 2002; Kasischke et al., 1992; Walker et al., 2018). For millennia, a portion of soil organic matter (SOM)—termed legacy SOM—escaped combustion during wildfires, which led to the accumulation of substantial soil C and N pools (Bond-Lamberty et al., 2007; Harden et al., 1992, 2002). Legacy SOM is defined as any SOM older than the most recent fire (Franklin, 2000; Little et al., 1997; Walker et al., 2019).

Boreal forest C and N pools are threatened as climate warms and boreal wildfire activity increases (Balshi et al., 2007; Kasischke et al., 2010), leading to greater combustion of SOM (de Groot et al., 2013). This combustion decreases soil C and N storage (Boby et al., 2010; Walker et al., 2018), increases emissions to the atmosphere (Turetsky et al., 2011), and exposes the remaining SOM to more decomposition as the insulating surface organic layer is removed (Balshi et al., 2007; Bond-Lamberty et al., 2007). Despite legacy SOM dominating processes associated with decomposition and nutrient availability during ecosystem recovery from fire, the drivers or controls that regulate the rate and/or direction of legacy SOM decomposition remain unclear.

Removal of SOM during fire alters the environmental and soil conditions that impact the decomposition of SOM. Specifically, the postfire SOM environment is typically warmer and drier than the prefire environment, which acts to change rates of decomposition (Harden et al., 2000; Kasischke & Johnstone, 2005). The remaining SOM decomposability (chemical quality) is also likely different from fresh, new SOM (Côté et al., 2000; Czimczik et al., 2006). Legacy SOM is older and may contain fire-altered black C, which is chemically resistant to decomposition (Hart & Luckai, 2013; Preston & Schmidt, 2006). Decomposition and C mineralization rates can slow as SOM decomposition progresses (Harmon et al., 2009; Lehmann et al., 2020; Mikutta et al., 2006). This is because microbes preferentially consume simple compounds and leave behind progressively more resistant compounds (Lehmann & Kleber, 2015; Schmidt et al., 2011; Sollins et al., 1996; Witzgall et al., 2021). In addition, persistent decomposition of SOM increases the proportion of microbial byproducts and other stable compounds as microorganisms die (Cotrufo et al., 2013; Reich et al., 1997; Schmidt et al., 2011). Last, nonenzymatic reactions in SOM produce decomposition-resistant compounds (Conant et al., 2011; Nannipieri et al., 2018; Schimel, 2003). Taken together, these processes, mediated by the microbial community, diminish the decomposability of nonmineral-associated SOM and ultimately curtail soil decomposition rate as soil ages. Though legacy SOM is older than fresh soil material and contains black C, the mechanisms that couple soil age to decomposition are likely similar to our current understanding of SOM decomposition, but it is unknown how much slower C will be mineralized in legacy SOM.

In addition to the decline in decomposability, C availability decreases (C:N decreases) as decomposition advances, leading to an increase in soil N availability. As C is respired by microorganisms, the amount of C available for decomposition declines (Harmon et al., 2009; Lehmann & Kleber, 2015; Witzgall et al., 2021). When microbes are C-limited, they use the C on hand for growth and maintenance and secrete N (Hicks et al., 2021; Manzoni et al., 2012). This excess N is added to the soil solution and SOM and is available for uptake by other microbes or plant roots (Fenn et al., 1998; Parton et al., 2007). Ultimately, when C is scarce, microbial net N mineralization increases N availability in the soil solution (Craine et al., 2007; Hicks et al., 2021; Sistla & Schimel, 2012). This principle generally governs N mineralization as soil ages and decomposition progresses and legacy SOM likely behaves according to these mechanisms but has not been investigated in legacy organic soils.

Recently, the Northwest Territories, Canada, experienced the region's largest fire year, providing an opportunity to examine legacy SOM decomposition controls and consequences. In 2014, 2.85 million ha of land burned and released as much C as 50% of the annual C uptake of Canada's terrestrial ecosystems (Canadian Interagency Forest Fire Center, 2014; Walker et al., 2018). Here, we assess the drivers of legacy SOM decomposition and how they impact C mineralization and N availability after fire. We use "soil age" as an index to include the physical and chemical characteristics of legacy SOM related to decomposability. We hypothesized that soil age, C:N, and microbial biomass would drive legacy SOM C mineralization and N availability. Specifically, older legacy SOM, with lower C:N ratios and microbial biomass, would mineralize C more slowly and release more N than younger soil with higher C:N ratios and microbial biomass. To identify the characteristics and consequences of legacy SOM decomposition, we used a laboratory incubation to measure the potential rates of C and net N mineralization, radiocarbon dating to estimate soil age, and soil extractions to quantify nutrients and microbial biomass. Our results highlight the critical role of legacy SOM in C and N cycling and how soil age contributes to the functions of boreal forest after fire.

MATERIALS AND METHODS

Site and plot description

To better understand the decomposition dynamics of legacy SOM, we collected soils near Yellowknife, Canada, after the record-setting fire year of 2014. The mean annual temperature in this region is −4.3C with an average annual precipitation of 290 mm (1980–2010; Environment Canada, 2014). The study sites were in two ecozones (Taiga Plains and Taiga Shield), underlain by discontinuous permafrost, and located across seven independent fire scars that burned between June and August 2014. Within each fire scar, we selected independent sites (78 total sites) that consisted of three plots per site (211 total plots), according to a stratified random sampling design (Walker et al., 2018). Each plot was sampled along two parallel 30-m transects spaced 2 m apart. Study plots were dominated by black spruce (Pinus mariana) and jack pine (Pinus banksiana) prior to burning. We measured stand characteristics at each plot, including prefire tree density and soil moisture class, among others (Table 1). Assignment of soil moisture consisted of a six-point scale based on topography-controlled drainage and adjusted for soil texture and permafrost presence (Johnstone et al., 2008). We used standard dendrochronological techniques to determine stand age by collecting basal tree disks in each plot (Cook & Kairiukštis, 1990).

Soil profile selection

We selected a subset of soil profiles from our study area to represent the complex spatial and landscape dynamics of boreal forests in this region. We began the selection process by ensuring soils originated from both ecozones, all seven fire scars, and mature (>70 years) black spruce-dominated stands. To have enough soil material for experimentation, it was necessary for the postfire residual SOM depth to exceed 10 cm. Because the residual SOM of the driest moisture classes is nearly completely combusted during fire, the two driest moisture classes were excluded. From those remaining, we selected soil from across all moisture classes. We then identified soil profiles from a single plot per site to represent the largest spatial area. This selection procedure resulted in 74 intact soil profiles from 41 plots within 41 sites that met our experimental criteria.

Soil core description

At each of the 41 plots, we collected one to three soil cores (5 cm × 10 cm × variable depth) that consisted of all residual organic matter above the mineral soil or frozen ground. Cores were wrapped in aluminum foil and kept frozen at −4C until further processing. In the laboratory, soil samples were thawed and split lengthwise with a serrated knife, and one section was archived. From the remaining section, we cut a 1-cm organic basal increment located just above the organic–mineral interface. With the remaining profile material, we cut a 10-cm section that began at the organic–mineral interface. We used the material from the 10-cm section and pooled all cores from a plot for incubation and soil analysis. We then weighed the material and obtained a subsample for field soil moisture, bulk density, and C and N analyses. We removed all rocks and roots >2 mm in diameter and homogenized all

TABLE 1 Summary of legacy soil organic matter response and measured variables in soils collected after fire from the Northwest Territories, Canada.

Type	Variable	Units	Mean ± SE	Range
Response	Total C lost	CO_2-C g C^{-1}	53.6 ± 6.7	6.1–178.6
	Respired C age	$\Delta^{14}C$	−60.9 ± 26.1	−368.0 to 114.1
	Turnover time	years	582.5 ± 200.6	4214.2–30.5
	Net N mineralization	g N g N^{-1}	−0.07 ± 0.07	−1.33 to 2.12
Mixed model fixed	Bulk soil age	$\Delta^{14}C$	−164.7 ± 20.2	−460 to 42.2
	C:N	ratio	29.3 ± 1.6	14.1–60.5
	Microbial biomass	μg C g C^{-1}	13.6 ± 0.1	3.6–24.8
Random forest fixed	Carbon	%	41 ± 1.0	25.3–51.3
	Carbon density	g m^{-2}	8.3 ± 0.5	3.2–19.7
	Nitrogen	%	1.5 ± 0.05	0.7–2.2
	Nitrogen density	g m^{-2}	0.3 ± 0.03	0.06–1.09
	Bulk density	g cm^{-3}	0.2 ± 0.02	0.07–0.78
	Moisture	%	72.0 ± 1.6	50.1–89.0
	Microbial biomass	μg C	569.6 ± 43.6	141.8–1124.5
	Microbial biomass C:N	ratio	10.4 ± 0.7	4.4–21.2
	Elevation	m asl	269.7 ± 9.6	190.8–384.4
	Slope	radians	0.6 ± 0.4	0.0–14.0
	Stand age	years	113.9 ± 6.7	71.0–220.0
	Prefire organic layer depth	cm	24.4 ± 2.1	5.7–65.5
	Black spruce density	stems m^{-2}	0.8 ± 0.1	0.1–2.9
	Soil ash	%	20.0 ± 5.2	7.0–42.0

Note: Response variables are used for both mixed model and random forest analysis.

profiles from one plot into a single sample. Using a Costech elemental analyzer (Costech Analytical, Los Angeles, CA, USA), we determined C and N concentrations. Carbon concentration had to be >20% to be considered organic. All soils used in our analysis were greater than 20% (μ = 41%; Table 1). Soil ash (%) of samples, a proxy for mineral-associated C, was unrelated to total C lost and soil age (Table 1), indicating that mineral association likely played a minor role in decomposition rates.

We used common soil characteristics to describe legacy SOM properties (Table 1). We determined bulk density by dividing oven dry soil mass by total soil sample volume. Soil water content was calculated by subtracting the mass of oven-dried soil from the soil wet mass and then dividing it by the wet mass of soil. To calculate soil C stocks, we multiplied the C concentration by the bulk density and depth.

Incubation and CO_2 measurements

To prepare soils for incubation, we first divided each pooled organic sample into eight replicate 10-g subsamples. Separating soil into replicates was necessary for destructive sampling over the course of the incubation period for extractions. Subsamples were wrapped in perforated aluminum foil and placed in vials with glass beads at the bottom to allow excess water to drain and maintain field moisture throughout the incubation. Soil samples received deionized water every 10 days. Next, we placed each soil sample into a 1-L mason jar for incubation. Samples were preincubated for 9 days at 15C to ensure laboratory preparation and disturbance were not captured in the early flux measurements (Schädel et al., 2020). Last, we connected jars of soil samples to an automated soil incubation system (ASIS; Bracho et al., 2016).

To measure the rate of soil C mineralization, we incubated each soil sample on ASIS for 90 days. For the first two weeks, we measured CO_2 flux daily, and then for the next two weeks we measured CO_2 flux every third day and once a week for the remainder of the incubation. ASIS measures CO_2 concentration with an infrared gas analyzer at 0.9 L min^{-1} (Li-820 Licor, Lincoln, Nebraska) and records the pressure in each jar sequentially in a closed-loop system. For an 8.5-h cycle, each jar is measured every 3 s for 8 min. We calculated CO_2 concentration as the rate of CO_2 increased inside the jar for a total of three to five cycles. More details on the ASIS and CO_2 measurements are available in Bracho et al. (2016).

Nutrient and microbial biomass extractions

We performed soil extractions on subsamples from the incubation to measure N availability and microbial biomass. Dissolved organic nitrogen (DON) and dissolved inorganic nitrogen (DIN) extractions were performed on vials from each sample jar at four time points of the incubation: days 1, 30, 45, and 90 (Salmon et al., 2018). Soils were extracted using 2 M KCl at a 1:5 ratio of soil mass to volume. Soil slurries were agitated for 4 h on a shaker table, and then vacuum filtered through Whatman GF/A filters. We analyzed colorimetrically for ammonium and nitrate concentrations on a discrete autoanalyzer (SmartChem, Salem, OR, USA). Using the nonpurgeable organic method on a Shimadzu TOC-L analyzer (Shimadzu, Kyoto, Japan), we determined DOC and total N and used it as part of the microbial biomass calculations. From these extractions, we also measured microbial biomass C using the chloroform slurry method (Fierer & Schimel, 2003). We added 0.04 g of chloroform to lyse microbial cell membranes, and sparged extracts for 30 min to volatize remaining chloroform. They were then analyzed for DOC and total N as above. Microbial biomass C and N were calculated as the difference between total C or N in the unfumigated and chloroform-fumigated extractants.

Radiocarbon dating

To determine the age of bulk SOM, we measured $\Delta^{14}C$ (as parts-per-mil difference between ^{14}C and ^{12}C) on soil basal increments collected from the bottom of each organic soil profile. At each plot, one soil profile from up to three profiles was chosen for $\Delta^{14}C$ analysis. We obtained the $\Delta^{14}C$ value of each basal increment by isolating organic particulates. This segregates the "biologically available" C from mineral-sorbed C and prevents older-age bias (Trumbore et al., 2016). Isolation of particulates began by adding 400 mL of nanopure water to the bulk soil and shaking the soil solution on a table shaker for 2 h. We then filtered the shaken solution through a 250-μm sieve and vacuum-filtered the solution with a glass microfilter. We then dried the glass microfilter at 60C for 24 h. We added 3 mg of the dried isolated organic fraction to a quartz tube, with 0.1 g of cupric oxide. After vacuum sealing, we heated each tube in a muffle furnace at 900C for 2 h. Heating the quartz tube produced CO_2 that was cryogenically purified under vacuum, and subsampled (0.5–1.0 mg) for graphitization. Each subsample was converted to graphite with an iron catalyst in a hydrogen atmosphere at 550C. We used NIST oxalic acid II as our primary standard, FIRI-D and FIRI-G as secondary standards, and anthracite coal as our blank. The WM Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory of University of California, Irvine determined the ^{14}C content (±1%) of each graphite sample.

In addition to bulk soil age, we also measured the age of respired CO_2-C for 20 of 41 jars. Jars were chosen to represent all soil moisture classes and a range (low to high) in daily CO_2 flux rates. On incubation day 15, we scrubbed the headspace of each jar with soda lime to remove background atmospheric CO_2. We then allowed 0.5–1.0 g of C to accumulate in the headspace and collected the CO_2 in zeolite molecular sieve traps (Alltech 13X; Alltech Associates, Deerfield, IL, USA; Hardie et al., 2005). Each sieve trap was baked at 650C to desorb CO_2 (Bauer et al., 1992) and then reduced to graphite with identical methods as the isolated organic particulates above. Graphite was shipped to University of California, Irvine for $\Delta^{14}C$ measurement.

Statistical analysis

Soil properties and age

We performed all statistical analyses using R version 4.0.3 (R Development Core Team, 2020). To examine how the properties of legacy SOM change with age, we used linear mixed-effects modeling in the "lme4" package (Bates et al., 2015). We tested the relationship between fixed-effect soil age and several soil properties as response variables (%C, %N, C:N, soil water content, bulk density, and C stock), with fire name/ID as random effect to account for spatial nonindependence of plots located within fire events. We used Akaike information criterion (AIC) as the selection criterion, and we tested soil age against the null model. We log-transformed when normality and homoscedasticity assumptions were unmet. When soil age was a significant predictor of the soil property, we calculated marginal and conditional R^2 values (R^2_m, R^2_c, respectively) using the "MuMIn" package function "r.squaredGLMM" (Barton, 2020). This general procedure was performed on all subsequent linear mixed model analyses.

C decomposition and N mineralization

We derived several metrics to assess the drivers of legacy SOM C decomposition and N availability (Table 1). To encompass the entire amount of C respired over the incubation, we used total C lost as our metric of C mineralization. For each soil sample, we calculated the total C lost with the area under the curve (AUC) function using the "spline" method in base R. The AUC function sums CO_2 measurements from each day for 90 days and interpolates daily missing data. We calculated C turnover time as C pool/C flux using a two-pool model (Trumbore, 1997). Boreal forest organic soil accumulates vertically through time and combustion propagates from the top down during fire, likely resulting in the combustion of the fast C pool (Harden et al., 2000; Trumbore et al., 2016). Assuming most of the fast C pool was combusted during the fire, the slow and passive pools remained and were measured in our experiment. We estimated that soil in our samples had a 3:1 slow to passive pool ratio (Trumbore, 1997). We first multiplied averaged daily respired C (over the entire incubation) by the slow and passive pool constituents and added them together for flux. We then divided the total C mass by the proportioned flux for each sample for turnover time. To represent the change in N availability over time, we calculated net N mineralization as the difference between DIN (NH_4^+ and NO_3^-) in the initial soil sample (day 1) and in the final sample (day 90). We calculated microbial biomass C as the C difference between unfumigated and fumigated extractants.

To assess the relationships between C and N mineralization with soil age, microbial biomass, and soil C:N, we used linear mixed-effects models. We built a model for each response variable (total CO_2 lost, respiration $\Delta^{14}C$, net N mineralization, and turnover time). In each model, we tested the fixed effects of soil age, microbial biomass, and C:N and their first-order interactions with fire name/ID as the random effect. We performed backward model selection, testing the full model against the reduced models using AIC as the selection criterion. After model selection, we visually inspected residual plots for normality and homoscedasticity and log-transformed data when assumptions were not met.

Additional C and N predictors

We used random forest algorithms to test 14 potential predictors, in addition to our three hypothesized variables of legacy SOM C and N cycling. We conducted a random forest analysis on each response variable (total CO_2 lost, respiration age, turnover time, and N mineralization). We first identified predictor variables that are most important at "threshold, interpretation, and prediction" steps of analysis using the variable selection using random forests (VSURF) package (Genuer et al., 2015). Each VSURF model began with predictor variables of soil age ($\Delta^{14}C$), %C, %N, C:N, microbial biomass C (in grams of carbon), microbial biomass C (in grams of soil), microbial C:N, latitude, longitude, ecoregion, elevation, slope, moisture class, organic layer thickness, black spruce stem density, and stand age. We used VSRUF to identify variables to remove from the model because either they did not predict any variability in the first model run or were collinear to other predictors. We executed five averaged runs of random forest on each response variable with 10,000 decision trees using the randomForest package (Breiman et al., 2018). The four most important predictor variables from the five averaged random forest runs were used for interpretation.

RESULTS

Soil properties

We found several significant relationships between soil age and legacy SOM properties (Figure 1; Table 2). Soil C concentration decreased, but bulk density and C stocks increased from younger more enriched ^{14}C values to older more depleted ^{14}C values. In other words, as soil aged, C concentration decreased while bulk density and C stock increased. As soil aged, water content, %N, and C:N tended to decrease, but this was not statistically significant.

Carbon decomposition

Across fire scars and plots, soil age was highly correlated to C decomposition in legacy SOM (Figure 2; Table 3). Soil age predicted both total CO_2 lost over the entire incubation period (R^2_c = 0.64; Figure 2a) and respired $\Delta^{14}C$ (R^2_c = 0.74; Figure 2b). There was a log-linear ($\ln x$) relationship between soil age and total CO_2 lost. As soil became younger and more ^{14}C enriched, the amount of C respired increased. Younger soil respired (~0.0‰; ~175.0 mg C g C^{-1}) 230% more CO_2 than the oldest soil (approximately −450.0‰; ~17.5 mg C g C^{-1}) over the 90-day incubation. Like total respired CO_2, soil age had a positive linear relationship with respired $\Delta^{14}C$. When the soil source was old, old C was respired, and when source soil was young, new C was respired. Although soil age explained the amount and age of respired CO_2, soil age also showed a positive correlation with microbial biomass C (R^2 = 0.39; Appendix S1: Figure S1). Prefire organic layer depth is also correlated to soil age (R^2 = 0.43; Appendix S1: Figure S2). C:N did not predict C mineralization.

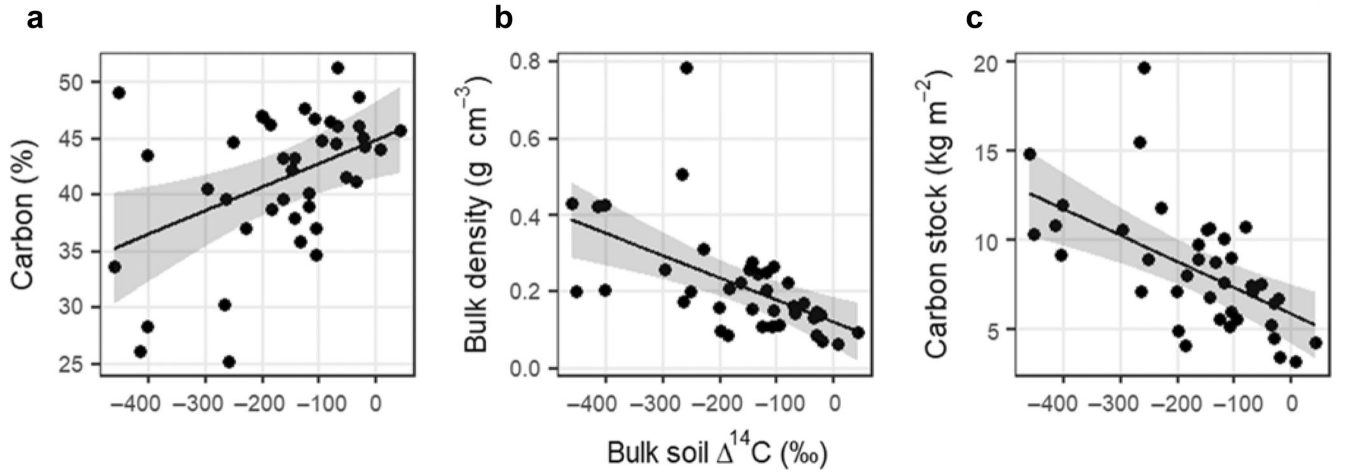

FIGURE 1 Bulk soil Δ^{14}C effect on legacy soil organic matter properties (%C, bulk density, and C stock) in soils collected after fire from the Northwest Territories, Canada. Black line represents linear mixed model results with 95% CI shaded.

TABLE 2 Final reduced linear mixed model results of soil age impact on soil properties (only significant properties are shown).

Response	Variable	Estimate	SE	Z or t value	R^2_m; R^2_c
Carbon concentration	Intercept	44.92	1.68	26.69	0.18; 0.32
	Soil age	0.02	0.01	2.97	
Bulk density	Intercept	0.12	0.03	3.67	0.29; 0.38
	Soil age	−0.001	0.00	−4.02	
Carbon stock	Intercept	5.81	0.82	7.08	0.32; 0.46
	Soil age	−0.01	0.00	−4.36	

Note: The full model included soil age as fixed effect and fire scar ID as random effect. Marginal R^2 (R^2_m) provides the variance explained by fixed effects and conditional R^2 (R^2_c) provides the variance explained entire model.

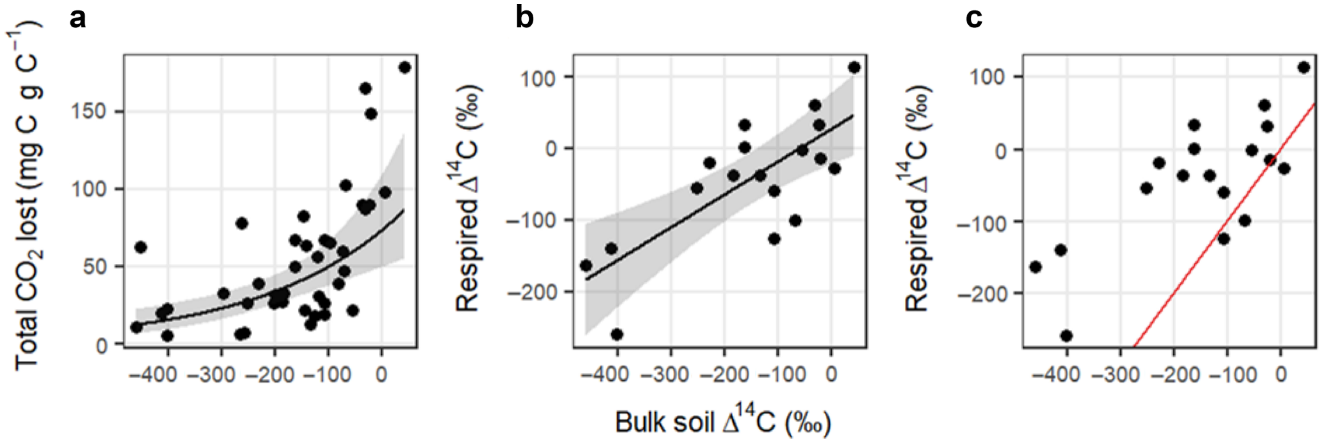

FIGURE 2 Bulk soil Δ^{14}C effect on (a) total CO_2 lost, and (b) respired Δ^{14}C in incubated soils collected after fire from the Northwest Territories, Canada. Black line represents linear mixed model results with 95% CI shaded. Results are similar on a per C and per dry soil basis. (c) Adapted from Sierra et al. (2018) comparing the relationship between bulk soil Δ^{14}C and respired Δ^{14}C. The red line is 1:1.

To investigate the drivers of C mineralization not explained by our hypothesized predictors, we performed a random forest analysis with 14 additional predictor variables (Table 1). The random forest conclusions were similar to the mixed models. Soil age and microbial biomass C were the two most important predictors of C

TABLE 3 Final reduced linear mixed model results for each response variable (total CO_2 lost, respired $\Delta^{14}C$, turnover time, and net N mineralization).

Response	Variable	Estimate	SE	Z or t value	R^2_m; R^2_c
Total C lost	Intercept	73.51	1.24	22.23	0.53; 0.64
	Soil age	1.00	0.01	4.37	
Respired C age	Intercept	27.83	23.42	1.169	0.67; 0.74
	Soil age	0.45	0.10	4.36	
Turnover time	Intercept	6.36	0.49	12.81	0.47; 0.50
	Soil age	−0.01	0.01	−4.03	
	C:N	−0.04	0.01	−3.01	
Net N mineralization	Intercept	0.23	0.15	1.99	0.22; 0.22
	Microbial biomass C	−0.02	0.01	−3.35	

Note: The full model included soil age, C:N, microbial biomass C, and all interactions as fixed effects with fire scar ID as random effect. Marginal R^2 (R^2_m) provides the variance explained by fixed effects and conditional R^2 (R^2_c) provides the variance explained by the entire model.

respiration (Table 4). Soil age and microbial biomass C predicted total CO_2 lost ($R^2 = 0.61$) and respired $\Delta^{14}C$ ($R^2 = 0.52$).

Relationship between respired $\Delta^{14}C$ and bulk soil $\Delta^{14}C$

By comparing bulk soil $\Delta^{14}C$ and respired $\Delta^{14}C$ (Figure 2c), we found that a majority (78%) of legacy SOM fell above the 1:1 line, where bulk soil was older than the respired ^{14}C. Overall, bulk soil C was centuries older (μ difference = 95.5 ± 113‰) than respired C leaving the profile as CO_2. This relationship indicates that most C entered and exited the soil profile relatively quickly. However, the C that remained in the bulk soil resided for a long time and was relatively stable.

Turnover time

Soil age and C:N predicted the turnover time (total pool/flux) of legacy SOM C after fire ($R^2_c = 0.50$; Figure 3; Table 3). Turnover times exponentially increased as soils aged and C:N decreased. Several millennia (max = 4, 214 years) elapsed before C in older soils (approximately −450.0‰) left the soil profile. In contrast, in younger soils (~0.0‰), only several decades (min = 30 years) elapsed before C exited the soil profile. Microbial biomass did not predict C turnover time. The random forest analysis came to a similar conclusion that C:N was an important predictor of turnover time ($R^2 = 0.64$; Table 4). However, in the random forest framework, soil age was not a predictor of turnover time. The most important predictor, by a large margin, was soil C concentration (%C).

Nitrogen availability

Net N mineralized decreased with microbial biomass C, but the relationship was relatively weak ($R^2_c = 0.22$; Figure 4; Table 3). As microbial biomass C increased, N became increasingly more immobilized and presumably less available for plant uptake. In general, across soils, N availability was low (<0.27 μg N g N^{-1}), but the greatest immobilization occurred when microbial biomass C was greater than 10 μg C g C^{-1}. Soil age and C:N did not predict nitrogen availability. Additionally, random forest results were inconsistent with the mixed model results (Table 4). No variables predicted N availability ($R^2 = 0.049$; Table 4).

DISCUSSION

The extensive aging of legacy SOM combined with C production rates gives clarity to the speed and magnitude of C decomposition in boreal forest soils. This indicates that legacy SOM C production rate decreases exponentially as soils get older. As a result, older legacy SOM constrains C decomposition and sustains a stable C sink. In recently formed legacy SOM, a decade difference in soil age, from changing fire regimes, could have profound impacts on C storage in boreal soils. While our findings resolve soil age and C mobilization, uncertainty remains surrounding the influences of soil age on N availability in boreal forest organic soils.

We show that legacy SOM age strongly influences C decomposition and turnover times. Older soil slowed C flux from the soil and increased turnover time. With average turnover times of several centuries, legacy SOM can preserve C from decomposition after a fire for several fire cycles into the future. We found most C enters and

TABLE 4 Four most important predictors ranked by score for each response variable (total CO_2 lost, respired $\Delta^{14}C$, turnover time, and net N mineralization) from random forest analysis on incubated soils collected after fire from the Northwest Territories, Canada.

Response	Rank	Predictor	μ variable importance score	R^2
Total C lost	1	Microbial biomass	186.1	0.62
	2	Soil age	139.4	
	3	%C	123.2	
	4	C:N	44.6	
Respired C age	1	Soil age	79.3	0.20
	2	Microbial biomass g C	43.7	
	3	Tree density	32.9	
	4	Organic layer depth	21.5	
Turnover time	1	%C	331.9	0.67
	2	C:N	65.3	
	3	Stand age	31.4	
	4	%N	1.4	
Net N mineralization	1	Soil age	114.8	0.04
	2	Microbial biomass	72.5	
	3	Organic layer depth	68.1	
	4	Microbial biomass g C	45.6	

Note: Scores from the top four predictors were averaged across five iterations of random forest model. R^2 was calculated for the model that included only the top four predictors listed here.

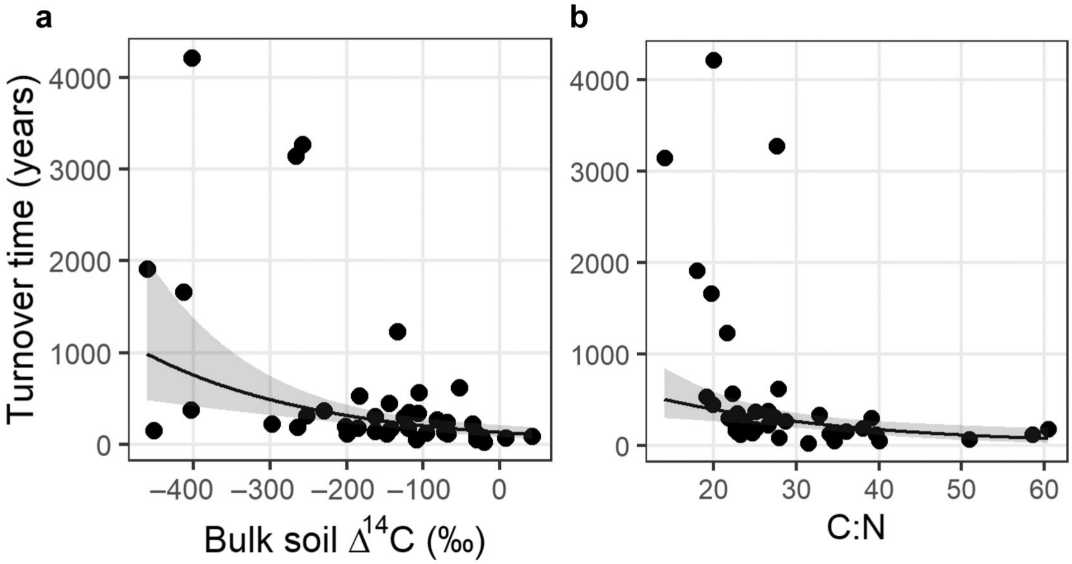

FIGURE 3 Turnover time response as a function of bulk soil $\Delta^{14}C$ and C:N in incubated soils collected after fire from the Northwest Territories, Canada. The black line represents linear mixed model results with 95% CI shaded.

leaves the system quickly while the oldest C remains protected from decomposition. Though soil age was not related to N availability, more N immobilization occurred with increased microbial biomass C. These results are the first investigation into the properties and process of legacy SOM and highlight the importance of soil age as fire regimes change in boreal forests.

Soil age and soil properties

Determining the relationship between commonly measured soil properties and soil age is an important link in understanding essential soil processes and is currently understudied in boreal forest. We found legacy SOM age relates to soil bulk density and C stocks. As legacy SOM

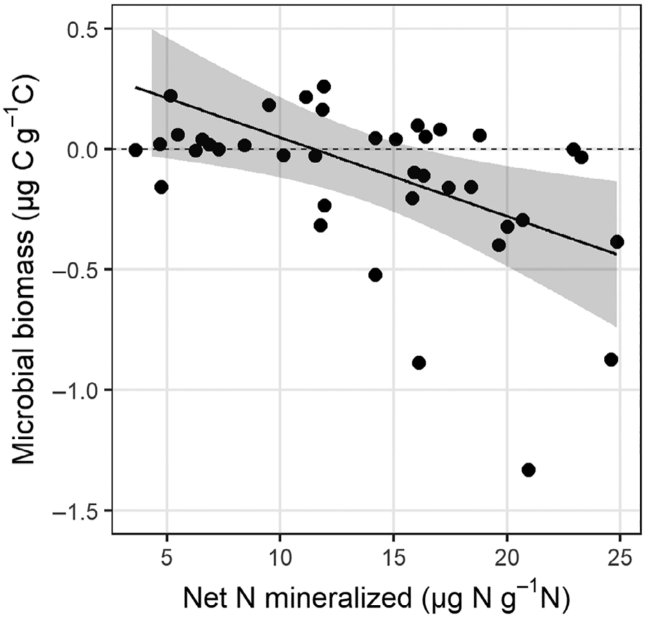

FIGURE 4 Microbial biomass effect on net N mineralization in incubated soils collected after fire from the Northwest Territories, Canada. Black line represents linear mixed model results with 95% CI shaded. Results are similar on a per N and per dry soil basis. Above the dotted line at 0 is net N mineralization; below the dotted line is microbial immobilization.

gets older, the amount of C it sequesters per unit volume increases due to increases in bulk density. This translates into more terrestrial C storage with increased age. Soil radiocarbon age and C stock are rarely investigated in boreal forests (Wickland et al., 2018); however, knowing the relationship between soil age and C stock can be used to understand the mechanisms that contribute to SOM persistence across biomes and environments.

C mineralization

Soil age was the most important driver of legacy SOM C mineralization, which agrees with our hypothesis. There is still considerable debate about the primary mechanisms of soil C (de)stabilization (Bhatnagar et al., 2018; Kleber et al., 2011; Lehmann & Kleber, 2015). However, it is clear that a combination of soil chemical qualities, physical attributes, and environmental interactions contributes to the rate of C decomposition (Conant et al., 2011; Lavallee et al., 2020; Lehmann et al., 2020; Schmidt et al., 2011). Here we found that the basal layer bulk soil Δ^{14}C predicted the total amount of CO_2 lost, the age of respired CO_2, and the turnover time of C in legacy SOM. It is likely that with increasing soil age, the compounds in legacy SOM become more resistant to degradation, thereby slowing decomposition. However, it is also likely that legacy SOM C′s long residence time is due to mechanisms related to physical protection and interactions in the environmental matrix (Hemingway et al., 2019; Witzgall et al., 2021). We measured the first three months of decomposition, which is primarily determined by chemical quality and likely did not capture long-term mechanisms of destabilization. Other short-term incubations concluded that the chemical quality of organic matter was the primary control regulating the initial decomposition rate of soil C (Andrieux et al., 2020; Knorr et al., 2005; Lee et al., 2012). While mineral-associated SOM often impacts C decomposition, in our study, soil ash content (proxy for mineral-associated SOM) was unrelated to soil age and C decomposition rate. Though understanding that soil age predicts legacy SOM mineralization is important, this finding also emphasizes the need to measure how chemical composition and physical attributes change with age and contribute to soil stabilization. Continued research should focus on describing the stabilization characteristics that impact legacy SOM decomposition rate.

In addition to physical protection and chemical quality, black or pyrogenic C concentration also influences soil C decomposition (J. Wang et al., 2016). Black C impact is particularly relevant in boreal forests that experience numerous wildfires (Hart & Luckai, 2013; Preston & Schmidt, 2006). Our soil C was often several centuries old, likely experienced many fire events, and therefore was composed, in part, of pyrolyzed biomass from fire events. Although we did not directly examine black C and its resistance to decay, it is likely that its presence played a role in the decomposition rate of C in our soils.

In support of our hypothesis, we found that older legacy SOM released C more slowly than younger legacy SOM. As legacy SOM ages, its contribution to atmospheric C concentration decreases and its time in the soil profile increases. Thus, older legacy SOM is more resistant to decomposition. In contrast, younger legacy SOM respires C at a higher rate and is below ground for a shorter amount of time. Because a large proportion of boreal forest soil C is composed of slow decomposing material, a small change in the C cycling of such a large pool could have profound effects on C-climate feedback. If older legacy SOM is lost to increases in fire activity through combustion and is then replaced with younger soil as it recovers, the contribution of C to the atmosphere will be greater, therefore diminishing boreal forest C sink strength over multiple fire cycles and changing the C sequestration dynamics of boreal forests.

Along with soil C decomposition mechanisms, defining soil C (de)stabilization is also contentious (Lehmann & Kleber, 2015; Schmidt et al., 2011). Another way to think about decomposition, as opposed to C mineralization, is with turnover time, which is the average time an atom remains in a pool. Like decomposition rate, soil age also governed the turnover time of legacy SOM C in our study. The older soils had turnover times several centuries longer than the youngest soils. Turnover time is important because it offers an estimate of how long C will stay in the soil pool and out of the atmosphere. Our average turnover time of the organic biologically available C pools is the better part of a millennium (582 ± 150 years). This is in line with other boreal forest turnover time estimates (Trumbore, 2000; Trumbore & Harden, 1997) and highlights the importance of legacy SOM age in boreal C cycling.

Relationship between soil age and CO_2 age

A comparison between the C pool age and flux age gives important information about how C is cycled in legacy SOM (Sierra et al., 2018). Consistent with our hypothesis, the age of the bulk soil C was centuries older than the C respired during decomposition. This indicates that most C enters the soil profile and is emitted relatively quickly through respiration. It also suggests another portion of the C is stable and remains in the soil profile, out of the atmosphere, for a long time. This is in line with the idea that most CO_2 produced by heterotrophic respiration is derived from short-lived components and does not represent the pool of SOM, which is much older C (Trumbore, 2000). In the case of legacy SOM, that pool remains in the soil profile and functions as a reliable long-term C sink. This insight suggests that long-term soil C sequestration relies on protecting these older layers of legacy SOM, and fire management in boreal forests should consider techniques to conserve legacy SOM.

Nitrogen availability

We found microbial biomass C is related to N availability. In agreement with our hypothesis, less microbial biomass C translated to increased N availability in the soil. Globally, microbial biomass is a crucial determinant of N mineralization and governs many ecosystem processes (Cao et al., 2021; Cotrufo et al., 2013; Li et al., 2019). Microorganisms are the conduit through which climate, soil properties, and soil substrates alter N availability (Parton et al., 2007). Through extracellular enzymes and consumption of SOM, microorganisms transform organic N into inorganic plant available nutrients (Billings & Ballantyne, 2012; Li et al., 2019; Nannipieri et al., 2018). Our results suggest that microbial biomass C is correlated with legacy SOM N availability where more microbial biomass C diminishes the soil N pool.

Over the course of our 90-day incubation, which approximates the growing season length, legacy SOM immobilized soil N. Our hypothesis that older soil would lead to greater N availability was not supported and soil age did not impact net N mineralization. However, the generally low rates of net N mineralization across samples do suggest that legacy SOM has low chemical quality. That is because SOM quality primarily determines microbial net N mineralization (Cao et al., 2021; Y. Wang et al., 2019). As discussed above, legacy SOM is old and difficult to decompose, leading to low chemical quality and likely inducing low N availability (Aerts, 1997; Berg, 2014; McClaugherty et al., 1985).

The uncertainty of N availability controls in legacy SOM is highlighted by the relatively weak correlation between N availability and our measured variables along with the disagreement between the mixed model and random forest analyses. Net N mineralization is the difference between two large soil N pools that move in opposition to one another. While mineralization and immobilization occur simultaneously in soil, net N mineralization measurements can mask the synthesis of N taken up immediately by microbes (Cui et al., 2022; Fenn et al., 1998; Mooshammer et al., 2014). The parameters included in this study explained little about legacy N availability, which suggests that variables not measured could influence legacy N availability. It is likely that climate characteristics prior to our experiment, like temperature and precipitation, play a large role in legacy N availability (Aerts, 1997; Parton et al., 2007). However, our findings emphasize the uncertainty of N availability controls in boreal forests (Kohl et al., 2018; Sierra et al., 2017). Further understanding of N availability drivers is important for plant productivity, decomposition, and ecosystem C balance.

CONCLUSIONS

Boreal forest resilience to wildfire is determined by legacy materials that promote the retention of their fundamental structure and function after fire (Franklin, 2000; Johnstone, Chapin, et al., 2010). Changes in disturbance regimes that modify legacies can cause ecosystem reorganization (Johnstone et al., 2016; Johnstone, Hollingsworth, et al., 2010). A fundamental component of legacy SOM is that old soil releases C slower than young soil. If legacy SOM is lost, not only does less C reside in the soil profile, but boreal forest C decomposition rates will increase as younger soil replaces old stable C.

If increases in fire activity lead to greater combustion of young soil organic material, legacy SOM will likely dominate where SOM decomposition and plant nutrient availability originate after fire. Legacy SOM age is critical to C decomposition and mineralization and will therefore play a central role in determining the modifications of boreal forest C with increased wildfire activity. Specifically, the chemical characteristics of older legacy SOM constrain C decomposition and maintain a reliable C sink in boreal soils. Therefore, increased loss or exposure of legacy SOM with increased fire activity will likely destabilize a critical component of long-term C storage in boreal forests.

AUTHOR CONTRIBUTIONS

Brian Izbicki was responsible for conceptualization, methodology, validation, formal analysis, investigation, data curation, writing—original manuscript, visualization, and administration. Xanthe J. Walker was involved in conceptualization, methodology, validation, investigation, resources, writing—review and editing, supervision, and data curation. Jennifer L. Baltzer and Jill F. Johnstone contributed to conceptualization, methodology, resource management, writing—review and editing, and played a key role in securing project funding. Nicola J. Day participated in conceptualization, methodology, and writing—review and editing. Christopher Ebert conducted investigation and contributed to writing—review and editing. Elaine Pegoraro's contributions encompassed conceptualization, methodology, investigation, data curation, and writing—review and editing. Edward A. G. Schuur provided resources and participated in writing—review and editing. Merritt R. Turetsky had significant involvement in conceptualization, methodology, resource management, and writing—review and editing. Michelle C. Mack contributed to conceptualization, methodology, validation, resources, writing—review and editing, supervision, project administration, and funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Incubation data and code (Izbicki, 2023) are available from Zenodo: https://doi.org/10.5281/zenodo.8034712. Stand and plot-level data are available from NASA ABoVE: https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=1664.

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SUPPORTING INFORMATION

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