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RESEARCH ARTICLE

Interactions among wildfire, forest type and landscape position are key determinants of boreal forest carbon stocks

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Abstract

1. Boreal forest soils contain large stocks of soil carbon (C) that may be sensitive to changes in climate and disturbance. Destablization of boreal forest soil C through changes in C inputs, belowground C pools and/or wildfire could feedback to accelerate rising atmospheric CO_2 concentration. Additionally, increasing frequency of severe fires may be changing the dominant forest types and reshaping aboveground C stocks.
2. Although controls on ecosystem C pools have received considerable attention, many studies have been limited to locations near the road system, leading to uncertainty in current and future C stocks across boreal Alaska. Here, we leveraged 545 randomly selected and spatially balanced Forest Inventory and Analysis (FIA) plots across ~13.5 million hectares in interior Alaska to examine the factors governing soil and live tree C pools.
3. Forest type mediated the effects of mean summer air temperature and the probability of near-surface permafrost on soil C. Meanwhile, forest type, stand age and aspect were the primary drivers of live tree C. Overall, plots with a known history of wildfire during the past 70 years did not have significantly different soil C stocks than plots without a known history of fire, likely due to the historical predominance of low severity fires.
4. Where wildfire likely initiated a transition to deciduous trees (19% of plots), live tree and soil C pools were reduced by 16% and 20%, respectively. Ecosystem C likely recovered over time, as maturing deciduous stands rapidly gained C in live trees. Deciduous stands without a known fire had comparatively very large live tree C stocks, suggesting a significant change in the distribution of ecosystem C following severe fire.
5. *Synthesis*. Our results highlight the nuanced interactions among wildfire, landscape position and forest type that will play important roles in shaping future boreal ecosystem C stocks.

KEYWORDS
Alaska, Alaska paper birch, aspen, black spruce, boreal, carbon, white spruce, wildfire

1 | INTRODUCTION

Boreal forest soils contain approximately 27% of the global soil organic carbon (C) stock (Jackson et al., 2017), representing one of the largest pools of terrestrial C. Climate warming at northern high latitudes is outpacing the global rate (Ballinger et al., 2020), putting this vast pool of C at risk of mobilization through decomposition of thawing permafrost (Romanovsky et al., 2010) and increasing wildfires (Coops et al., 2018; Kasischke et al., 2010; Kasischke & Turetsky, 2006), which could feedback to accelerate rising atmospheric CO_2 (Bonan, 2008; Koven et al., 2011; Loranty et al., 2018; Schuur et al., 2008, 2015). Throughout much of the boreal forest, the combination of limited aboveground productivity and cold, often anaerobic soil conditions has resulted in soil C comprising the majority of total ecosystem C (Bradshaw & Warkentin, 2015; Pattison et al., 2018). Identifying the factors contributing to vertical and spatial distributions of ecosystem C is a crucial step toward improving predictions of future C budgets.

The challenges of accessing remote parts of the boreal forest has resulted in many studies being located within close proximity to major infrastructure, where development may influence forest dynamics such as wildfire ignition and management (Calef et al., 2008). This has resulted in an uneven distribution of sample plots and likely contributed to the wide range in soil C estimates (Johnson et al., 2011; Mishra & Riley, 2012). Additionally, variation in climate and significant fine-scale topographic heterogeneity that affects soil hydrology and thermal regime (Deluca & Boisvenue, 2012; Loranty et al., 2018; Pastick et al., 2015; van Cleve et al., 1983) have a dramatic influence on soil C stocks. Much of our understanding of soil C distribution comes from analyses of black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenb) forests (Harden et al., 2012; Hollingsworth et al., 2008; Kane & Vogel, 2009; O'Donnell et al., 2011; Ping et al., 2010). While black spruce forests cover approximately 39–44% of forested land in interior Alaska (Calef et al., 2005; van Cleve et al., 1983), estimates of soil C from the remaining forests are scarce. Given the potential for biome-wide changes in community composition in response to severe fire and a warming climate (Johnstone, Hollingsworth, et al., 2010; Walker et al., 2021), quantifying live tree and soil C pools across forest types is an important step toward refining C stock estimates.

Wildfire plays an important, multifaceted role in ecosystem processes (Bond-Lamberty et al., 2007; Genet et al., 2018; Goulden et al., 2011; van Cleve et al., 1991; Veraverbeke et al., 2015; Viereck, 1983). Following an initial reduction in soil organic layer thickness and aboveground biomass (Kasischke & Johnstone, 2005), aboveground and belowground C pools usually increase with time since fire until they stabilize or, in the case of soil C, sometimes decline due to warmer soils stimulating decomposition (Alexander & Mack, 2016; Goulden et al., 2011; Kane & Vogel, 2009; Mack et al., 2008; O'Neill et al., 2003). However, the rate of recovery can be influenced by post-fire interactions among climate (Andrieux et al., 2018; Boucher et al., 2020), initial burn severity (Hoy et al., 2016; Johnstone, Hollingsworth, et al., 2010) and topo-edaphic characteristics that affect soil temperature and hydrology (Whitman et al., 2018). Fire severity, frequency and size have increased in recent decades (Coops et al., 2018; Kasischke et al., 2010) which could result in substantial direct transfer of long-held "legacy C" from deep organic layers to the atmosphere (Walker et al., 2019) and may lead to the redistribution of C to aboveground pools in severely burned sites that transition to deciduous dominance (Mack et al., 2021). Fire severity is often mediated by forest type, stand density, topography, weather and the timing of fire (Kasischke & Hoy, 2012; Turetsky et al., 2011; Veraverbeke et al., 2015; Walker et al., 2020, 2021; Whitman et al., 2018), creating a mosaic of altered ecosystem properties that can vary substantially within a single fire perimeter (Duffy et al., 2007; Ferster et al., 2016; Kasischke & Hoy, 2012; Kolden et al., 2012; Lavoie & Mack, 2012) and complicating predictions of biome-wide responses to wildfire.

Post-fire stand composition is largely influenced by fire severity due to impacts on the soil organic layer. Fires often originate in black spruce stands and can range from mild burns that partially consume trees to severe burns that result in widespread tree mortality and near total consumption of the soil organic layer, leaving behind exposed mineral soil (Boby et al., 2010). Johnstone, Chapin, et al. (2010) suggested that in the black spruce domain, the species retains dominance following low-severity fires through local reseeding and resprouting on poor quality seedbeds. The semi-serotinous cones produce a large amount of seeds that are capable of landing on suitable germination sites, even in marginal habitat (Wirth et al., 2008). Under the broadleaf domain, deciduous species benefit from severe fires that reveal high quality seedbeds on mineral soil, then maintain dominance through rapid nutrient turnover, low moss abundance and warm soils (Johnstone, Chapin, et al., 2010). These alternative domains offer a useful model for analysing post-fire ecosystem C pools when direct measurements of fire severity are not possible.

While fire effects on boreal ecosystem structure and function have been the focus of numerous studies (Balshi et al., 2007; Bonan, 2008; Ferster et al., 2016; Kasischke & Stocks, 2000), detailed ground-based observations have yet to be made from randomly selected and spatially balanced plots across a large portion of Alaska's boreal forest. In this study, we leveraged the extensive Forest Inventory and Analysis (FIA) plot network across interior Alaska to examine landscape variability in live tree and soil C stocks in relation to fire history. We had three primary objectives: (1) quantify total soil C, soil physical properties and C content in separate soil horizons in the four dominant forest communities: quaking aspen (*Populus tremuloides* Michx.), Alaska paper birch (*Betula neoalaskana* Sarg.), black spruce and white spruce (*Picea glauca* [Moench] Voss); (2) examine the relative importance of site factors (e.g. age, slope, aspect, climate, permafrost) in determining soil and live tree C stocks; (3) examine how a broad range of fire history (i.e. fire severity and time since fire) affected C stocks and the distribution of C between soil and live tree pools among forest types.

1.1 | Hypotheses

Regarding our first objective, we hypothesized (H_1) that soil C stocks would be greatest in black spruce as this species tends to grow on cool, moist-wet soils that favour organic matter accumulation, and lowest in aspen stands where well-drained, warm soils promote microbial activity. For our second objective, we examined five different site factors (stand age, slope, aspect, near-surface permafrost [NSP] and climate) and their potential interaction with forest type in determining soil and live tree C. Overall, we expected C stocks to be influenced by factors that affect temperature, as cooler soils limit microbial respiration and lead to C accumulation (Lloyd & Taylor, 1994). Specifically, we tested the following hypotheses (Figure 1):

$H_{2.1}$: Slope would have a negative effect on soil C, as well-drained soils would promote decomposition and limit organic matter accumulation. Moderate slopes with warm, better-drained soils would have a positive effect on live tree C (van Cleve et al., 1983, 1991). On very steep slopes, we expected reduced live tree C due to moisture limitation, limited soil development and/or unstable soils. We did not expect forest type to mediate the effect of slope on soil or live tree C because the underlying mechanism is primarily associated with hydrology and soils.

$H_{2.2}$: North-facing aspects, with reduced solar radiation and cooler soils (van Cleve et al., 1991), would be associated with greater soil C, due to limited decomposition. The same abiotic conditions would limit tree growth on north-facing sites, resulting in a smaller live tree C pool compared with south-facing sites. We expected this effect regardless of forest type.

$H_{2.3}$: Stand age would have a positive effect on soil and live tree C that varied across forest types, reflecting differences in tree growth, moss accumulation, litter inputs and root turnover among the dominant tree species (Alexander & Mack, 2016; Mack et al., 2021).

$H_{2.4}$: Near-surface permafrost (NSP) would interact with the forest type to affect soil and live tree C, as tree species range in their tolerance of permafrost (Viereck et al., 1983). Specifically, we expected the strongest positive effect of NSP on soil C in black spruce forests which are more tolerant of permafrost. In contrast, we predicted the strongest negative effects of NSP in aspen and birch, which grow poorly and are often incapable of germinating on permafrost-associated soils (Perala, 1990; van Cleve et al., 1983).

$H_{2.5}$: Sites with warmer summer air temperature would have less soil C due to warmer soils promoting decomposition (Kane & Vogel, 2009), and this effect would vary among forest types. We predicted that forest type would mediate the effect of summer temperature on live tree C, reflecting differences in optimal temperature and ideal habitat among tree species (Nicklen et al., 2016; Sullivan et al., 2017). We expected a stronger negative effect of summer temperature on live tree C in black spruce and white spruce than in aspen and birch, similar to patterns shown previously in tree-ring analyses of these species (Cahoon et al., 2018).

Regarding our third objective, we hypothesized (H_3) that plots with a known history of fire would have smaller C stocks in both live trees and soil across all forest types, compared to plots without a history of fire since 1947. More specifically, we hypothesized that severely burned plots, which transitioned from coniferous to deciduous dominance, would have smaller C stocks, particularly in the soil,

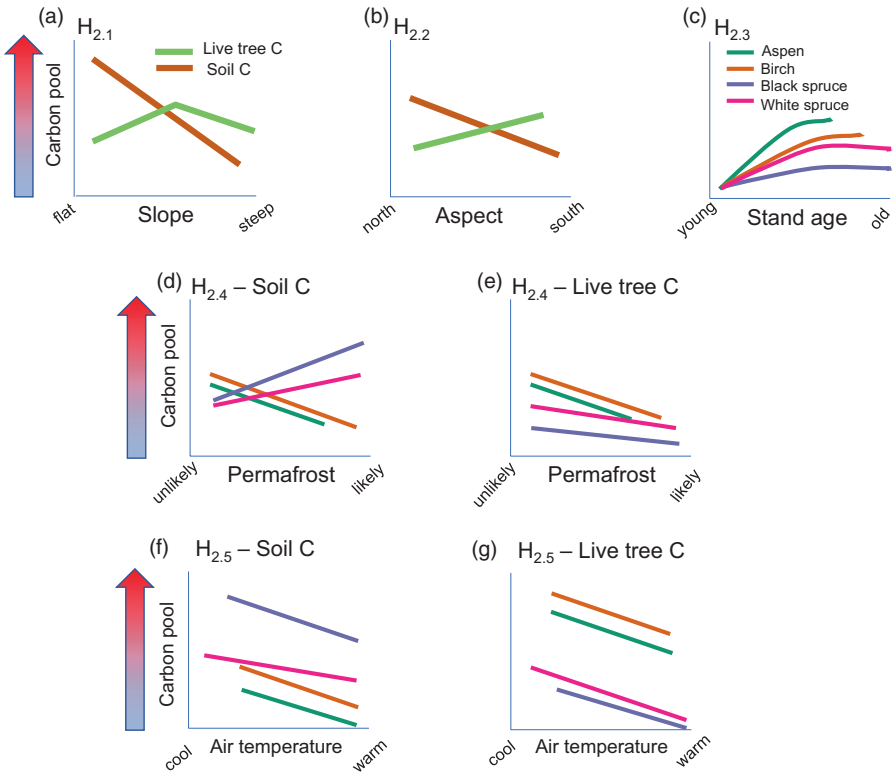


FIGURE 1 Graphical representation of our hypotheses to explain spatial variation in soil and live tree C. In each panel, larger C pools are represented higher on the vertical axis. We did not expect a strong interaction between forest type and slope ($H_{2.1}$), and forest type and aspect ($H_{2.2}$). In contrast, differences among forest types in $H_{2.3}$ – $H_{2.5}$ are depicted as different coloured lines. Variation in line lengths represent relative differences in observed site conditions among forest types described in Table S3. See Hypotheses section in main text for details.

than plots without a known fire history and those that remained coniferous after wildfire.

2 | MATERIALS AND METHODS

2.1 | Inventory description and plot design

The Tanana Inventory Unit (8.4 million forested hectares; Cahoon et al., 2022) is one of six units in interior Alaska identified by the FIA program to inventory and monitor Alaska's boreal forest (Figure 2). The region experiences a continental climate and largely overlaps with the Southeast Interior climate division (Bieniek et al., 2014). The landscape is characterized by broad river valleys with forests comprised mainly of black spruce, white spruce, Alaska paper birch and quaking aspen. The underlying geology consists mostly of young volcanic rock and unconsolidated surficial deposits from the Quaternary and Tertiary Periods (Wilson et al., 2015). Plots were distributed throughout a hexagonal grid, with one plot randomly located within each 12,141 ha polygon (Bechtold & Patterson, 2005). Plots were arranged according to standard FIA procedures consisting of four 168 m^2 subplots 36.5 m apart. For this study, a total of 545 plots were visited during the growing seasons (May–September) of 2014 and 2016–2018.

2.2 | Soil sampling

Soils were sampled at every plot according to the FIA protocol for interior Alaska (USDA, 2018). At every plot, up to three cores were collected (one each from subplots 2–4) using a power drill and a steel corer approximately 35 cm in length with an internal diameter of 5.4 cm. Each core was separated into five discrete layers when present: green moss/lichen, identifiable plant parts (hereafter ID parts), unidentifiable plant parts (hereafter, un-ID parts) and mineral soil. Although these layer definitions differ from NRCS soils classification (e.g. Schoeneberger et al., 2012), the ID parts layer is roughly equivalent to the Oi layer of slightly decomposed compacted litter and other identifiable plant parts, and the Un-ID parts layer is similar to the Oe and Oa layers of moderately and highly decomposed organic materials. The thickness of each layer was measured in the field, then sent to the lab for analysis. Prior to soil core extraction, litter layer thickness was measured at the four cardinal directions within a 30.5 cm diameter frame placed directly over the centre of the soil core.

2.3 | Live tree, standing dead and down woody material sampling

Tree inventory methods consisted of recording tree species, height, status (live or dead) and any damage noted on trees larger than 12.7 cm in diameter at breast height (DBH; 1.37 m height) on each subplot. The same methods were used on smaller trees (<12.7 and >2.5 cm DBH) on a microplot (26.9 m^2) located within each subplot. Allometric equations within the FIA database were then used to estimate tree-level biomass (Woodall et al., 2011). Carbon in live trees was assumed to be 50% of biomass (Chapin et al., 2002). Down woody material (DWM) data were collected using line-intersect sampling from two 7.32 m transects that originated at the center of each subplot. For each piece of DWM, the diameter, species (when identifiable) and decay class were recorded. Species-specific allometric equations were used to estimate subplot-level biomass, with a decay-reduction constant applied to each piece (Woodall & Monleon, 2010). Forest type was defined by the species that comprised a plurality of live trees on

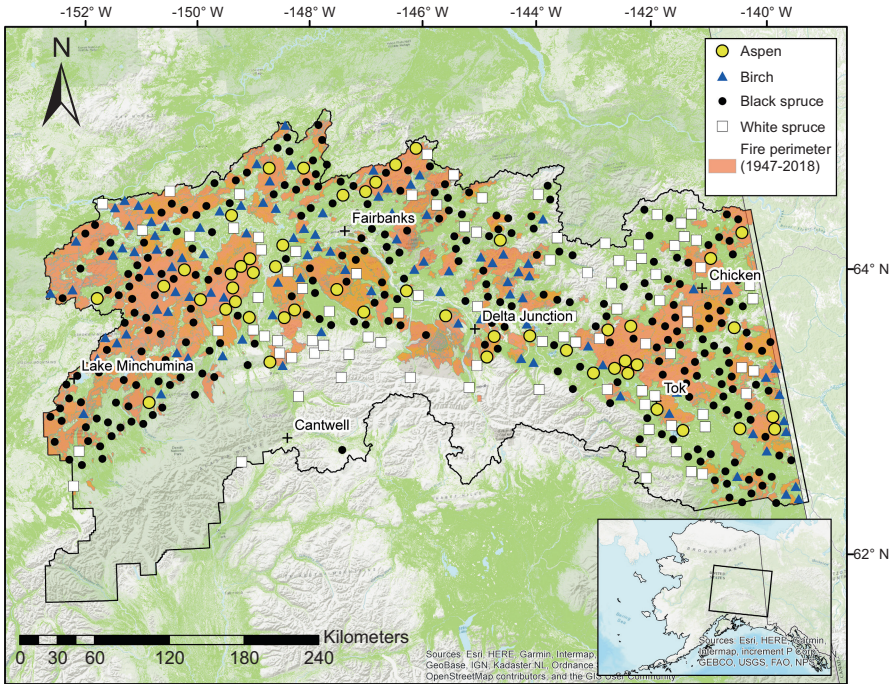


FIGURE 2 Approximate locations of FIA plots listed by forest type in the Tanana inventory unit in interior Alaska. The solid line is the approximate location of the inventory unit boundary and the green background is the forested portion of the land (NLCD; Dewitz 2019). Fire perimeter data are shown in orange and gathered from the Alaska Interagency Coordination Center (AICC; https://fire.ak.blm.gov).

the plot (≥2.54 cm, DBH; USDA, 2018). On plots where all live trees were less than 2.54 cm DBH, forest type was determined by counting all live seedlings >30 cm tall by species within the microplot.

2.4 | Laboratory analysis and data processing

Soils were analysed for elemental concentration at the University of Alaska Fairbanks Forest Soils Lab. Samples were oven dried at 65°C for at least 48 hours and soil C and N concentration (%) were determined by combustion using a LECO CN628 Elemental Analyser. Soil C data were calculated for each layer as:

$$SC = \%C \times BD \times T \times 100, \quad (1)$$

where SC is soil C in Mg ha^{-1}, %C is the fraction of C in the sample (expressed as a proportion), BD is bulk density (g cm^{-3}) and T is the thickness of the layer (cm). As we did not test for the presence of inorganic C, we refer to our data as soil C rather than soil organic C (SOC). Mineral soil samples varied in thickness based on the presence of seasonally frozen soils or other obstructions. For comparisons among forest types and layers, we standardized mineral soil C to a common sample thickness by setting T in Equation 1 to the mean mineral soil thickness sampled for each forest type. Total soil C was then summed across all layers for every core. We also compared soil C density (g cm^{-3}) among forest types and soil layers to examine differences in C per unit soil volume. Mineral soil C was not standardized when comparing soil C density or in hypotheses testing and prediction.

To address the sampling limitations imposed by a frozen active layer early in the growing season, we limited our analyses to soil cores that were deep enough to contain a sample of mineral soil at the bottom of the core. Out of a total 1991 cores, 1345 contained mineral soil. Of the cores that were excluded, only 13 were from locations where thaw depth exceeded 1 m and mineral soil was not sampled. The remainder of the excluded cores were sampled early in the summer when frozen ground was encountered near the surface. Overall, compaction was minor as the average difference between the hole depth and the total soil core length was 2.4 cm. In total, our sample included 1291 soil cores and 8750 live trees sampled across 545 plots (USDA, 2020).

2.5 | Landscape and climate variables

Plot attributes and downscaled climate data were obtained for each plot. Slope and aspect were measured at each subplot; aspect was linearized for analysis between −1 (due south) and 1 (due north). Plots were considered neutral when slope was less than three degrees. Stand age was estimated based on increment cores collected at breast height of dominant or sub-dominant trees on or near the plot, or by intersecting plot locations with fire history polygons obtained from the Alaska Interagency Coordination Center (AICC; https://fire.ak.blm.gov), which provides statewide fire data dating to 1939. When the tree core age exceeded that of the most recent fire, stand age was set to the fire year since FIA tree core collection methods often seek survivors and may not always represent the most recent disturbance. If a plot experienced two fires, stand age was set to the most recent fire. We elected to use AICC fire perimeter data instead of satellite-based methods (i.e. the Monitoring trends in Burn Severity dataset) to maximize the time series of wildfire in Alaska and incorporate small (<405 ha) fires that may have affected C pools in our study region. However, we caution that AICC fire perimeter data might overestimate area burned (Kasischke et al., 2010) and, thus, are simply used here as a guide to regions with a history of fire.

We obtained estimates of the probability of near-surface permafrost (NSP; within 1 m of the ground surface, 30 m pixels) at plot locations from the model by Pastick et al. (2015). Downscaled average monthly temperature (1 km pixels) was obtained from the Scenarios Network for Alaska and Arctic Planning (SNAP; www.snap.uaf.edu). Monthly climate data for each location were aggregated to the 30-year normal period (1981–2010). We further subset the data to the growing season months of June–August (JJAtmp). Although biological activity occurs year-round in boreal forests (Kim et al., 2007; Sullivan et al., 2008; Winston et al., 1997), we focused on the summer months because production and decomposition are greatest during the growing season (Vogel et al., 2005).

2.6 | Statistical analyses

We tested for differences in soil characteristics among forest types for each layer, total soil C and live tree C with linear mixed-effects models (LMEMs) in the LME4 package (Bates et al., 2015) in R v. 4.0.2 (R Core Team, 2020), where plot was considered a random effect. Pairwise comparisons were considered significant if $p < 0.05$ using Tukey's Honest Significant Difference (HSD).

We used a series of LMEMs to test our hypotheses regarding the relative importance of various site factors in determining soil and live tree C. First, we constructed a full model that included all five variables (age, slope, northness, NSP, JJAtmp) and the interactions of forest type with northness, NSP and JJAtmp, then tested our hypotheses by removing the variable in question (Table 1). We then compared each reduced model with the full model using a likelihood ratio test and rejected hypotheses where the full model and the reduced model were not significantly different ($p > 0.05$). Each soil C model included sample depth ($\log_{10}$-transformed), and the intercept was forced through 0, as there should be no soil C when the coring depth was 0. Collinearity among predictors was low, with a maximum Pearson correlation of $r = -0.30$ between slope and JJAtmp. Each model was fit using the NLME package (Pinheiro et al., 2021). Total soil C and live tree C were $\log_{10}$-transformed to meet the assumptions of normality. To account for spatial autocorrelation among subplots, we included plot as a random effect and a spatial correlation term with a Gaussian distribution. All predictors were centred and scaled to have a mean of 0 and standard deviation of 1 to facilitate comparison of coefficients across predictor variables. We tested for normality of

TABLE 1 Summary of linear mixed effects models used to test our five hypotheses ($H_{2.1}$ – $H_{2.5}$) describing variation in soil C and live tree C. Each hypothesis was tested by removing the relevant predictor variable from the model. Significance ($p < 0.05$) was determined using a likelihood ratio test of the reduced model versus the full model. Each model included plot as a random effect and all predictor variables were centred and standardized to have a mean of 0 and standard deviation of 1.

Model	Model formula	df	Log likelihood	χ^2	*p*
Soil C (Mg ha^{-1})					
Full model	0 + log(D) + slope + northness + (age + NSP + JJAtmp) * fortyp	22	−737		
$H_{2.1}$: slope	0 + log(D) + northness + (age + NSP + JJAtmp) * fortyp	21	−740	7.01	**0.008**
$H_{2.2}$: northness	0 + log(D) + slope + (age + NSP + JJAtmp) * fortyp	21	−737	6.92	**<0.001**
$H_{2.3}$: age	0 + log(D) + slope + northness + (NSP + JJAtmp) * fortyp	18	−738	2.50	0.4748
$H_{2.4}$: NSP	0 + log(D) + slope + northness + (age + JJAtmp) * fortyp	18	−742	9.04	**<0.001**
$H_{2.5}$: JJAtmp	0 + log(D) + slope + northness + (age + NSP) * fortyp	18	−740	4.60	**<0.001**
Live tree C (Mg ha^{-1})					
Full model	slope + northness + (age + NSP + JJAtmp) * fortyp	21	−1157		
$H_{2.1}$: slope	northness + (age + NSP + JJAtmp) * fortyp	20	−1157	0.0	0.97
$H_{2.2}$: northness	slope + (age + NSP + JJAtmp) * fortyp	20	−1161	8.0	**<0.001**
$H_{2.3}$: age	slope + northness + (NSP + JJAtmp) * fortyp	17	−1223	123.6	**<0.001**
$H_{2.4}$: NSP	slope + northness + (age + JJAtmp) * fortyp	17	−1163	119.5	**<0.001**
$H_{2.5}$: JJAtmp	slope + northness + (age + NSP) * fortyp	17	−1168	9.7	**<0.001**

Abbreviations: D, sample depth (cm); slope, plot slope; northness, aspect, linearized; age, stand age; NSP, near-surface permafrost; JJAtmp, mean summer (June–August) temperature (1981–2010). fortyp, forest type. See Methods for detailed description of predictor variables.

model residuals using Lilliefors test (Lilliefors, 1967). The live tree C model met the assumption of normality ($p = 0.124$), however the soil C model violated the null hypothesis ($p < 0.01$). The significant Lilliefors test result in the soil C model may be attributed to the test's high sensitivity to minor deviations from normality, particularly in a multi-level model with variable sample sizes among groups (Razali & Wah, 2011). Indeed, after visually inspecting histograms of model conditional raw residuals and plots of residuals versus fitted values, as suggested for LMEMs by Zuur et al. (2010), we did not detect obvious trends in variance, nor were there clear deviations from normality (Figure S1). Therefore, we are confident that our models were consistent with their underlying assumptions and are suitable for deriving inference from our data.

In a separate analysis designed to maximize the predictive power of our fixed variables, we used the *dredge* function in the MUMIN R package (Barton, 2022). Each sub-model used the same dataset and included plot as a random effect and the same autocorrelation structure as the hypotheses models, but variables were left on their original scale. Models were considered similar to one another if the difference in Akaike's Information Criteria (AIC) values was <4 (Table S1). Parameter estimates for the top models were then averaged (Burnham et al., 2002) and the predictions of soil and live tree C were made using the GGEFFECTS package (Lüdecke, 2018).

2.7 | Fire history effects on ecosystem C pools

We examined the effect of fire on live tree and soil C pools by comparing plots that fell within a fire perimeter with those located beyond fire polygons. While it is likely that all plots experienced fire at some point in history, we used fire history data beginning in 1939 as an indicator of plots with a "recent" history of wildfire. Within each forest type, we tested for differences in live tree C, total soil C, organic soil C, mineral soil C, organic layer thickness and bulk density with separate LMEMs that treated fire history as a categorical fixed effect (i.e. fire, no fire) and plot as a random effect. Additionally, we examined the effects of fire on the structure of soil horizons by comparing individual layer thickness and bulk density between burned and unburned sites within each forest type. In a space-for-time analysis, we selected only those plots with a known history of fire and used simple linear regression models to examine the relationship between time since fire and live tree and soil C.

Our final analysis of fire effects on ecosystem C pools consisted of grouping our data by functional group and fire history. We grouped black and white spruce into the coniferous functional group, while aspen and birch plots comprised the deciduous functional group. Each plot was assigned to one of four categories: coniferous, no fire history; coniferous, history of fire; deciduous, no fire history; deciduous, history of fire. Our goal was to compare ecosystem C pools between potential successional pathways following high or low severity fire. This analysis relies on the assumptions that (i) pre-fire stands were conifer-dominated, as pure deciduous stands rarely burn (Krawchuk et al., 2006), (ii) severe fires consume the soil organic layer and result in replacement by deciduous species and (iii) mild to moderate fires allow for conifer regeneration in a relatively intact soil organic layer. These assumptions are based on a broad set of previous studies that have illustrated the importance of fire severity on

post-fire stand composition (Baltzer et al., 2021; Boby et al., 2010; Johnstone et al., 2020; Johnstone, Chapin, et al., 2010; Johnstone, Hollingsworth, et al., 2010; Walker et al., 2021). Thus, plots classified as deciduous at the time of the inventory that intersected with fire polygons were assumed to have experienced severe fire, whereas plots classified as coniferous that intersected with fire polygons were assumed to have experienced low severity fire. For each category, we calculated mean live tree C, total soil C, organic layer C, mineral soil C, organic layer thickness and bulk density. In total, 566 soil cores were sampled from 228 plots dispersed across 114 separate fires ranging in size from approximately 65 to 217,989 hectares (see Table S2). Although fire records extend to 1939, our plots intersected with fires that originated between 1947 and 2018.

Although we lacked direct assessments of fire severity for each plot, we used inventories of coniferous snags and coniferous DWM to corroborate our assumption that plots within known fire perimeters that are currently classified as deciduous were coniferous stands prior to wildfire. We calculated the mean conifer snag and DWM biomass (Mg ha^{-1}) and its proportion to total snag and DWM biomass for each category of burn severity and forest type. We expected that dead coniferous biomass (snags and DWM) would be greatest on plots classified as deciduous with a history of fire.

3 | RESULTS

3.1 | Site characteristics

The FIA plot grid represents a broad range of landscape positions within and among forest types, which captured ecological niches unique to the focal species (Figure 2, Table S3). Live tree basal area was greatest among the productive white spruce stands (mean: 12.8 m^2 ha^{-1}), followed by birch (9.9 m^2 ha^{-1}), aspen (8.1 m^2 ha^{-1}) and lowest in black spruce stands (7.3 m^2 ha^{-1}). Aspen and birch stands were generally younger (30.7 and 38.9 years old, respectively) than black spruce and white spruce stands (68.6 and 94.6 years old, respectively). White spruce stands were generally higher in elevation, as this species often forms the altitudinal treeline in interior Alaska (Lloyd & Fastie, 2003), likely coinciding with cooler summer temperature compared with the other forest types.

3.2 | Soil physical and chemical properties

There were substantial differences in soil horizon structure, %C and C content (Mg ha^{-1}) among and within forest types. Within the organic layer, the thickest horizon was ID parts in black spruce, which also had the lowest bulk density among forest types (Figures S2–S6). The green moss/lichen horizon was thicker and less dense in coniferous forests than in aspen and birch forests, but had higher %C, such that C content (Mg ha^{-1}) was similar among forest types. All forest types displayed increasing soil C content (Mg ha^{-1}) with depth through the soil profile, with significant differences among horizons arising within each forest type (Figure 3a–d). Soil C density (g cm^{-3}) was significantly greater in organic than in mineral soil in each forest type (Figure 3e), likely driven by the notably denser C pool in the un-ID layer (Figure S6). When pooled across organic horizons, C density did not differ among forest types. Mineral soil C was densest in black spruce forest types, but similar among the remaining forest types (Figure 3e).

3.3 | Distribution of soil and live tree carbon among forest types

When summed across all soil layers, with mineral horizon thickness held at the mean for each forest type, black spruce soil C was greater than other forest types (91.88 ± 2.7 Mg ha^{-1}; mean ± 1 SE), but was not significantly different from birch (81.92 ± 3.9 Mg ha^{-1}). Soil C in white spruce forests (76.24 ± 3.4 Mg ha^{-1}) was not significantly different than in birch, whereas soil C in aspen forests (57.53 ± 5.8 Mg ha^{-1}) was significantly lower than all other forest types (Figure 3f). Carbon in live trees was greatest in birch forests (21.77 ± 2.3 Mg ha^{-1}), followed by white spruce (18.27 ± 2.1 Mg ha^{-1}), aspen (17.94 ± 3.4 Mg ha^{-1}) and least in black spruce (7.84 ± 0.5 Mg ha^{-1}). Overall, belowground C accounted for 76%, 79%, 92% and 81% of total C (soil C + live tree C) in aspen, birch, black spruce, and white spruce, respectively. Deeper sampling and a more complete accounting of mineral soil C stocks would yield an increase in these estimates that would be offset somewhat by inclusion of aboveground C in understory plants.

3.4 | Environmental determinants of soil carbon

The five LMEMs used to test our hypotheses of determinants of spatial variation in soil C (Table 1) confirmed our hypotheses that slope and aspect would affect soil C, and that NSP and JJAtmp would interact with forest type ($H_{2.1}$, $H_{2.2}$, $H_{2.4}$, $H_{2.5}$, respectively), as removal of those variables led to significantly weaker (e.g. lower log-likelihood) models than the full model. However, models that omitted the interaction between forest type and stand age ($H_{2.3}$) were not significantly different from the full model. After including all possible interactions with forest type and averaging over similar models, significant fixed effects included slope, forest type, and the interaction between NSP and black spruce, while the interaction between JJAtmp and black spruce was nearly significant ($p = 0.085$; Table S4). After holding all other predictor variables at their mean, the predicted values of soil C in response to NSP showed an increase in black spruce, while there was a decline in birch and aspen forests with increasing probability of NSP (Figure 4a). Soil C in black spruce increased significantly with warmer JJAtmp, while birch and white

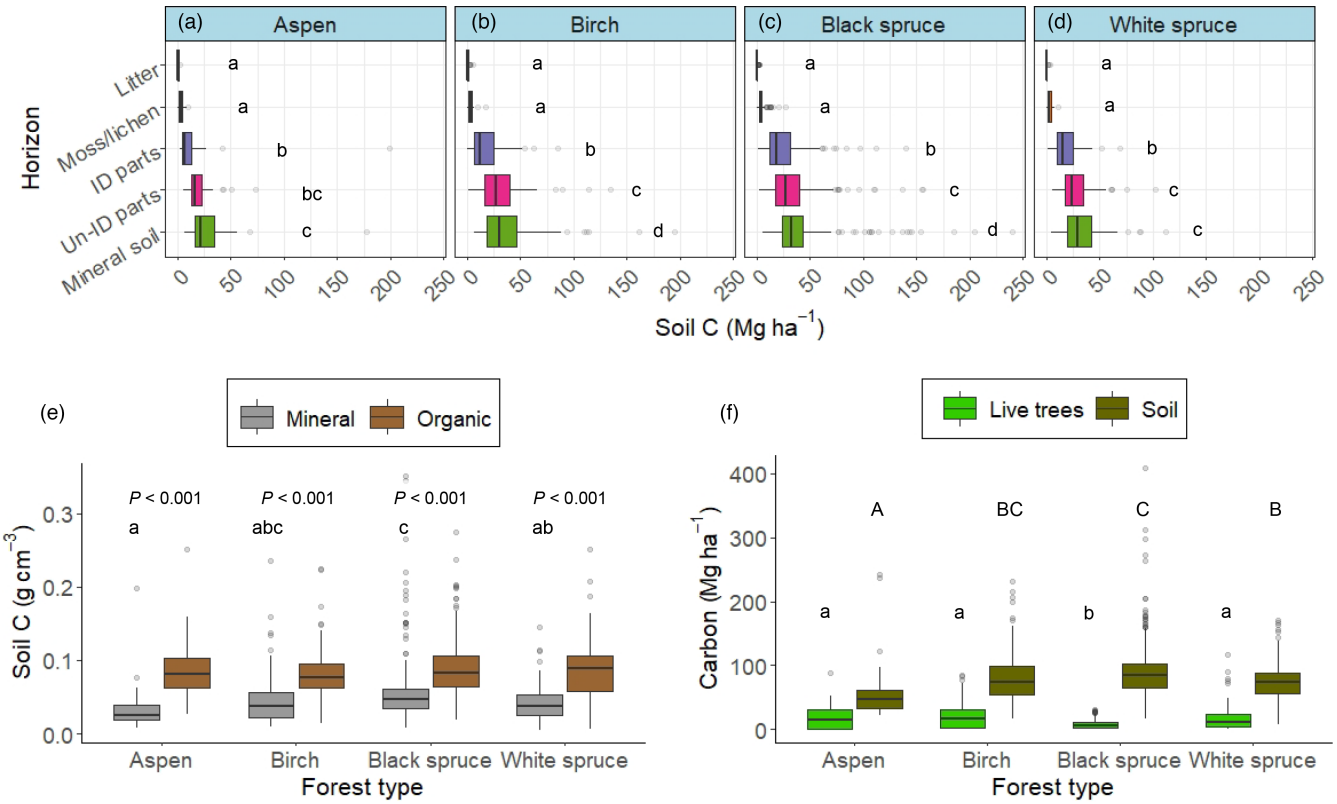


FIGURE 3 Boxplots showing the distribution of soil carbon content (Mg ha^{-1}) across layers in four forest types in the Tanana unit, Alaska (a–d). (e) Shows soil carbon density (g cm^{-3}) in mineral and organic portions of the soil profile for each forest type. Organic soil consists of litter, green moss/lichen, ID parts and Un-ID parts layers. (f) Shows the distribution of soil and live tree C (Mg ha^{-1}) among forest types Tukey's HSD pairwise comparisons were made among horizons within each forest type in panels a–d, and among forest types for mineral soil carbon density in (e). Letters were omitted from organic soil C density because differences did not arise among forest types. Comparisons among forest types were made for soil (lowercase letters) and live tree C (uppercase letters) in panel f. Bars that share a letter were not significantly different ($p > 0.05$).

spruce showed little change over the same range and aspen soil C declined (Figure 4b).

3.5 | Environmental determinants of carbon in live trees

For live tree C, only the model that omitted slope ($H_{2.1}$) was not statistically different ($p = 0.97$) from the full model (Table 1). The models representing our remaining hypotheses ($H_{2.2}$-$H_{2.5}$) were significantly different from the full model, pointing to the importance of northness and the interactions between forest type and stand age, NSP and summer temperature as determinants of live tree C stocks. After fitting all possible LMEMs to the live tree C data and averaging over the top models, NSP had a significant negative effect overall. There were also significant interactions between stand age and all forest types, and the interaction between northness and black spruce approached significance ($p = 0.067$; Table S5). Predicted values from this model indicated that C in live trees in aspen forests accumulated at a faster rate with increasing stand age than in the other forest types (Figure 4c) while northness had a negative effect on live tree C in black spruce (Figure 4b).

3.6 | Fire history effects on live tree and soil C

Carbon content (Mg ha^{-1}) in live trees was greatest in birch forests without a known recent fire history (31.87 ± 3.5 Mg ha^{-1}; mean ± 1 SE) and least in plots with a known fire history that are currently dominated by aspen (4.02 ± 1.4 Mg ha^{-1}; Figure 5). Total soil C did not significantly differ between plots with and without a known fire history when comparisons were made within forest types, while only organic soils in birch stands contained significantly less C in burned plots (Figure 5c). When analysed by layer, burned plots had significantly thinner moss/lichen layers in aspen, birch and black spruce forest types, and thinner ID-parts layers in birch and black spruce forests (Figure 6). In contrast, soil bulk density in plots with a history of fire was greater in moss/lichen layers in birch and black spruce, and in the mineral soil horizon of aspen, birch and black spruce forest types. Our space-for-time analysis of burned plots indicated that aspen forests accumulated C in live trees at a faster rate post-fire (0.58 Mg C ha^{-1} year^{-1}) than birch forests (0.49 Mg C ha^{-1} year^{-1}), and much faster than white spruce (0.05 Mg C ha^{-1} year^{-1}) and black spruce (0.01 Mg C ha^{-1} year^{-1}; Figure 7a). In contrast, soil C in birch forests showed a significant negative relationship with time since fire (Figure 7b), with an annual net loss of 0.72 Mg C ha^{-1}.

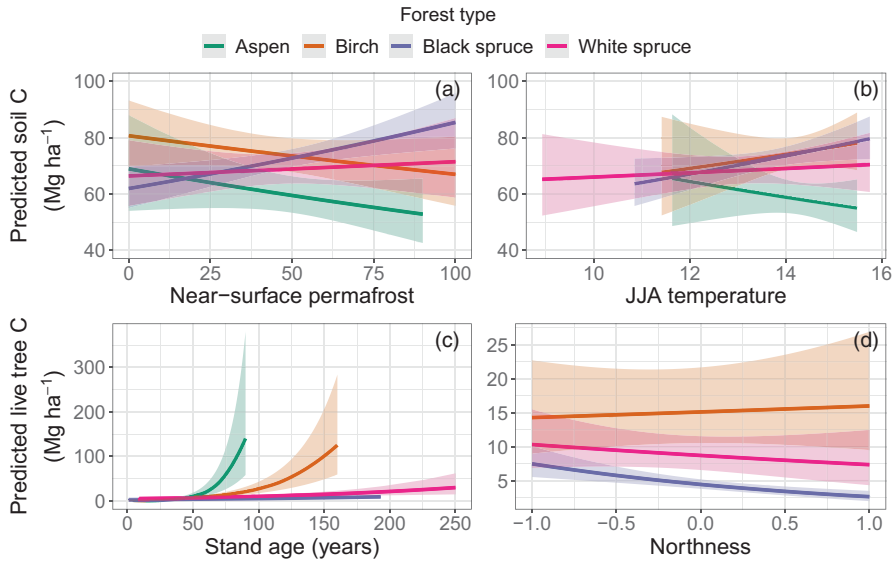


FIGURE 4 Predicted values of soil C (Mg ha^{-1}) in response to the interaction between forest type and probability of near-surface permafrost (NSP, a), and forest type and June–August mean temperature (JJA temperature; b) from the linear mixed-effects model with the lowest AICc value (see Table S4). Panels c and d represent the predicted values of live tree C (Mg ha^{-1}) in response to the interaction between forest type and stand age (c), and the interaction between forest type and northness (d) from the linear mixed-effects model with the lowest AICc value (see Table S5). Aspen was excluded from (d) to emphasize the effect of aspect on the other forest types, particularly black spruce. For a version with all four forest types, see Figure S7. Other variables in each model were held at their mean value. Shading represents the 95% confidence interval based on the variance of fixed effects.

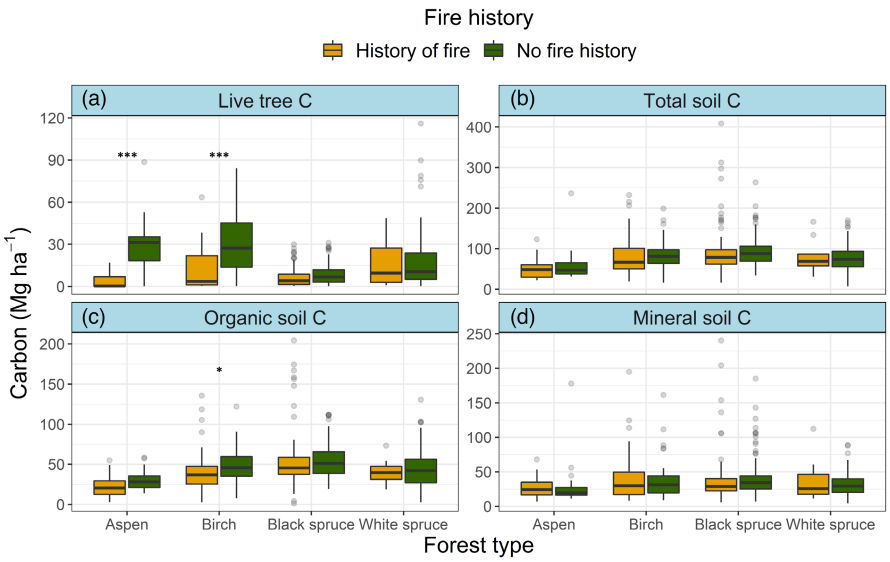


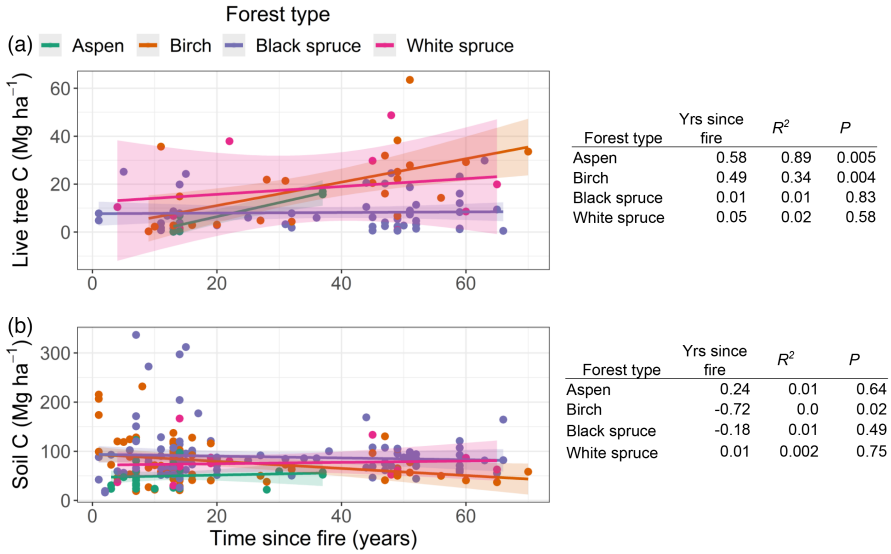
FIGURE 5 Boxplots showing the distribution of C (Mg ha^{-1}) in live trees (a), total soil (b), organic soil (c), and mineral soil (d) among forest types with and without a history of fire. Differences in C between burned and unburned plots within each forest type were tested using a linear mixed-effects model. Tukey's HSD was used for pairwise comparisons between burned and unburned plots where significance is symbolized as: $^{*}p < 0.05$, $^{***}p < 0.001$. Bars without a symbol did not differ ($p > 0.05$).

Coniferous DWM and coniferous snag biomass were significantly greater in plots dominated by deciduous species with a history of fire than deciduous plots with no known fire history (Figure 8). Deciduous stands assumed to have a history of severe fire comprised 19% of our dataset and had the least C in all pools (live tree, total soil, organic soil and mineral soil), and the thinnest organic layer compared with the other categories (Figure 9; Table S6). Meanwhile, 23% of our plots were assumed to have experienced relatively low severity fire and maintained coniferous dominance. These sites had approximately 30% lower live tree C and thinner organic layers, but were similar to coniferous plots without a known fire history (47% of plots) in total soil C, organic soil C and mineral soil C. Deciduous stands with no known fire history (12% of plots) had the largest live tree C pool. Soil organic layers in these forests were thicker and soil bulk density was greater than in deciduous stands with fire history.

4 | DISCUSSION

Boreal forests soils hold large stocks of C that may be vulnerable to changes in climate and/or wildfire regimes (Deluca & Boisvenue, 2012; Genet et al., 2018; Kasischke et al., 2010; Walker et al., 2019). One of our most notable findings is the overall lack of wildfire effect on soil C due to the historical predominance of low

FIGURE 6 Boxplots showing the distribution in horizon thickness (cm; a–d) and bulk density (g cm^{-3}; e–h) among forest types with and without a history of fire. Orange bars represent plots that intersected with fire history polygons, while green bars represent plots that fell outside fire perimeters. Tukey's HSD was used for pairwise comparisons between burned and unburned soil characteristics where significance is symbolized as: $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$. Bars without a symbol did not differ ($p>0.05$).



Forest type	Yrs since fire	R^2	P
Aspen	0.58	0.89	0.005
Birch	0.49	0.34	0.004
Black spruce	0.01	0.01	0.83
White spruce	0.05	0.02	0.58

Forest type	Yrs since fire	R^2	P
Aspen	0.24	0.01	0.64
Birch	-0.72	0.0	0.02
Black spruce	-0.18	0.01	0.49
White spruce	0.01	0.002	0.75

FIGURE 7 Relationship between time since fire and live tree C (a) and soil C (b) among plots that experienced fire between 1947 and 2018. Each dot represents an individual plot, characterized by forest type. Linear regression analyses were performed for each forest type across all plots. Shading represents 95% confidence interval. Regression statistics for each forest type are shown at right.

severity fires. However, severe fires that led to a change in forest type from coniferous to deciduous likely had a profound effect on ecosystem C pools, reducing soil and live tree C by 20% and 16%, respectively, at least initially. Deciduous stands without a known history of fire held the largest stocks of live tree C, while deciduous stands with a known history of fire accumulated C with increasing stand age faster than other forest types. These findings are consistent with recent work suggesting that rapid accumulation of live tree C following severe wildfire that initiates a transition from coniferous to deciduous dominance may at least partially offset soil C losses to combustion (Mack et al., 2021).

4.1 | Distribution of soil C within and among forests

One of the main goals of our study was to compare soil C among forest types in interior Alaska and gain better understanding of variability in soil C pools. The FIA plot network provides an unbiased sample of forested locations that captures spatial heterogeneity across a large scale, as demonstrated by the broad range of landscape conditions (Figure 2, Table S3). As expected, black spruce contained much greater total soil C and higher C content in the component soil horizons than the other forest types. The significant differences in soil C between layers and among forest types may have important implications for future C budgets. Across all forest types, soil C content was greatest in the two deepest horizons: the un-ID parts and mineral layers. This result is consistent with previous studies that have noted the vast amount of C in mineral soils throughout the permafrost zone and boreal forest (Hugelius et al., 2014; Johnson et al., 2011; Jorgenson et al., 2013; Mishra & Riley, 2012; Ping et al., 2015; Tarnocai et al., 2009). Cryoturbation in permafrost soils can redistribute relatively poorly decomposed organic matter deeper in the soil profile, particularly in poorly drained locations (Bockheim, 2007). Our results suggest that warming-induced mineralization of deep

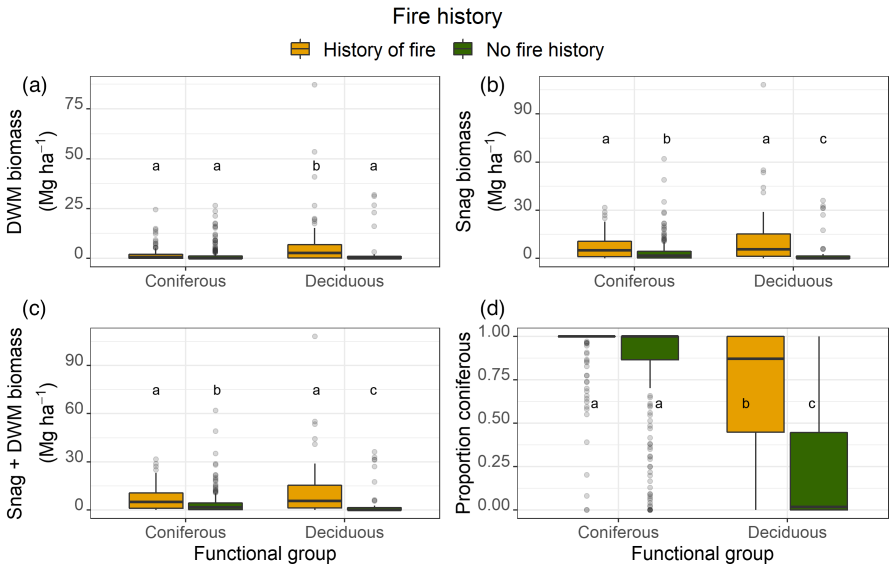


FIGURE 8 Boxplots showing average coniferous down woody material (DWM) biomass (a), coniferous snag (standing dead) biomass (b), coniferous snag + DWM biomass (c), and the proportion of coniferous biomass in snag and DWM relative to total snag and DWM biomass (d) among plots currently dominated by coniferous (i.e. black or white spruce) and deciduous (i.e. aspen or birch) functional groups with and without a history of fire since 1947. Post-hoc pairwise comparisons among functional group-fire history categories were made using Tukey's HSD on log-transformed data to meet the assumptions of normality. Categories that share a letter were not significantly different ($p > 0.05$) from one another.

soil C will be spatially heterogeneous as C stocks in deep humified and mineral layers varied across forest types and with slope. This detail could improve projections of soil C cycle dynamics that sometimes assume belowground C to be a relatively homogenous pool.

4.2 | Environmental determinants of soil carbon

Testing for interactive effects of forest type and site factors on soil and live tree C pools was another goal of this research, which we addressed with a series of LMEMs. Our results confirmed part one of our second hypothesis ($H_{2.1}$; Figure 1a) that slope would have an important impact on soil C, which is similar to previous work noting less soil C in relatively well-drained black spruce forests across a broad range of site conditions (Ping et al., 2015). Our results extend that finding to other forest types and indicate that steeper, better-drained sites have lower soil C stocks, regardless of forest community. The significantly poorer performance of models that omitted northness and NSP ($H_{2.2}$, $H_{2.4}$) supports our hypotheses that landscape positions that foster cooler soil conditions would lead to greater soil C pools due to more limited microbial activity (Kane & Vogel, 2009; van Cleve et al., 1983). Although we expected stand age to have a positive effect on soil C ($H_{2.3}$), removing this variable did not result in a significantly inferior model. Hollingsworth et al. (2008) also found a weak relationship between stand age and soil C among black spruce stands, while other studies have found C pools following fire to vary with landscape position and drainage (Rapalee et al., 1998; Trumbore & Harden, 1997).

Our multi-model averaging approach indicated that the effect of NSP on soil C varied among forest types and confirmed part four of our second hypothesis ($H_{2.4}$). The deciduous species in this region tend to be more productive on well-drained sites (van Cleve et al., 1983) where permafrost is less common. In these locations, greater aboveground productivity with high litter inputs may have resulted in greater soil C accumulation (Melvin et al., 2015). Meanwhile, aspen and birch stands associated with greater probability of NSP may be growing at the margins of their tolerance of cooler and wetter soils that hamper aboveground growth and limit litter inputs, resulting in relatively lower soil C accumulation. Omitting NSP resulted in a significantly poorer live tree C model (Table 1), providing support for the link between aboveground growth and soil conditions. In contrast, NSP had a positive effect on soil C in black spruce where permafrost creates a barrier to soil water drainage, resulting in cold, saturated soils that limit organic matter decomposition. Of the four tree species, black spruce is better adapted to survive and maintain productivity on cold and wet soils (Nicklen et al., 2021; van Cleve et al., 1983). The positive relationship between NSP and black spruce soil C highlights the vulnerability of black spruce forest soil C to permafrost thaw.

While the interaction between JJAtmp and black spruce in our multi-model comparison approached statistical significance ($p = 0.085$), removing JJAtmp resulted in a significantly weaker model than the full version, thus confirming our hypothesis that summer temperature is an ecologically important driver of soil C ($H_{2.5}$). The

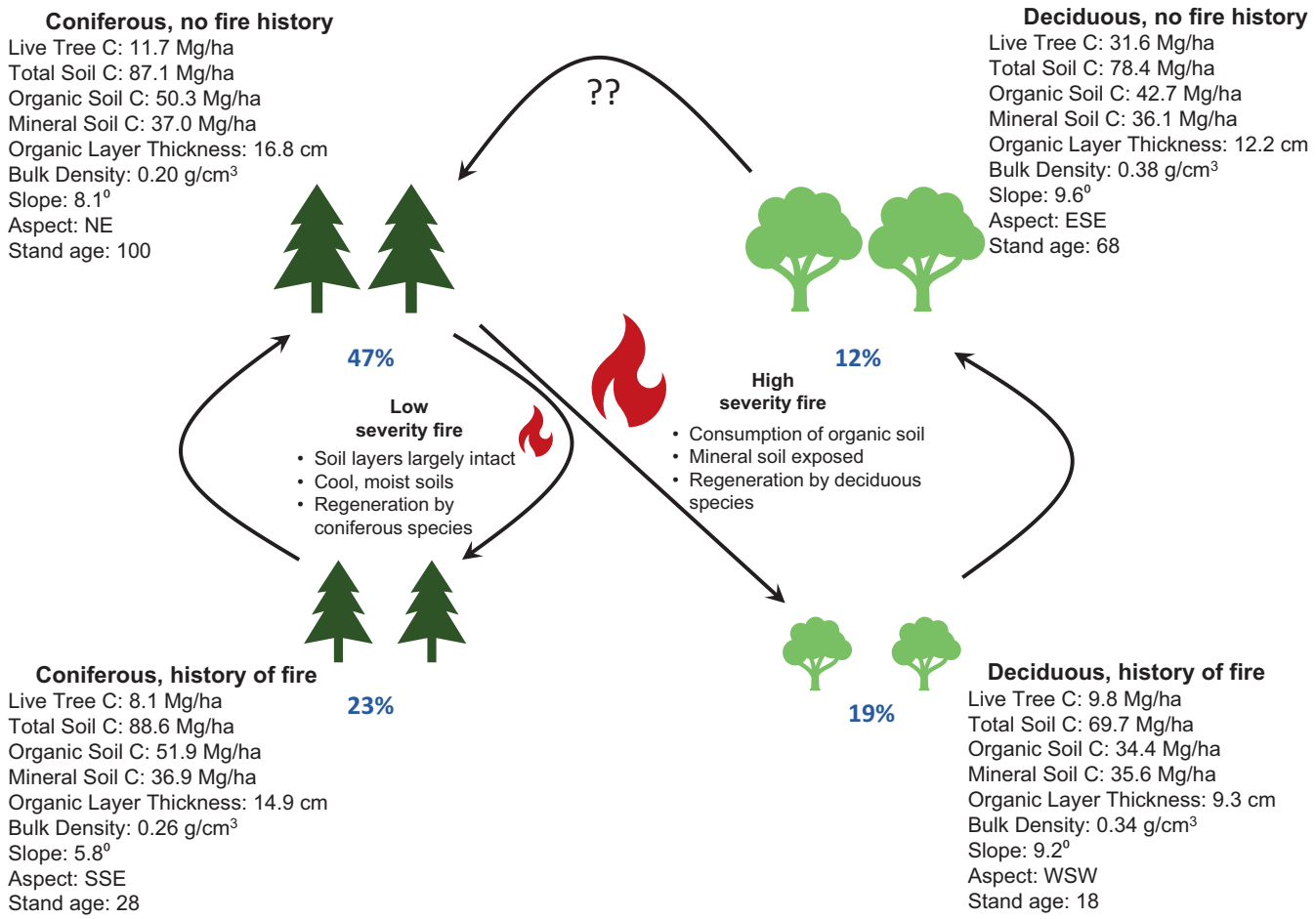


FIGURE 9 Conceptual diagram showing the distribution of soil and live tree C pools and soil characteristics following potential succession scenarios after low and high severity fires. In both cases, it is assumed that the pre-fire stand was dominated by coniferous species. Deciduous stands were classified as either aspen or birch forest types, whereas coniferous stands consisted of either black spruce or white spruce. The effects of each fire severity scenario are described and based on the alternative stability domains concept presented by Johnstone, Chapin, et al. (2010). Values in blue represent the percentage of plots in the Tanana FIA database that fell under each category. Values of each C pool, organic layer thickness and bulk density are the mean of all plots within each category. Average slope and the mode of plot aspect, binned into 16 secondary intercardinal directions, are provided for each category. For standard error and Tukey comparisons, see Table S6.

positive effect of JJAtmp on soil C in black spruce stands may be driven by greater aboveground growth at the warmer sites, resulting in greater litter inputs (after holding NSP at the mean). If those sites also have permafrost, the combination of warmer air temperature stimulating growth and cooler, wetter soils limiting microbial activity and promoting moss growth (Bisbee et al., 2001) could explain this trend. In fact, when we examined the occurrence of forest types in different topographic categories along a continuum of summer temperature (Figure S8), we found a relatively high proportion of black spruce stands occurred at topographic positions where drainage was poor (lower hillslopes, or wet, flat areas) *and* experienced warm summer temperature. Positive effects of both summer air temperature and NSP on soil C in black spruce forests points to the potential importance of locations on the landscape that are warm enough to promote black spruce growth and stimulate litter inputs, but cool enough to preserve permafrost and create conditions that limit organic matter decomposition, resulting in relatively high soil C stocks.

4.3 | Environmental determinants of live tree carbon

After averaging over the top live tree C LMEMs, our results indicate that aspect and stand age are important in determining the distribution of live tree C, partially supporting $H_{2.2}$ and $H_{2.3}$ hypotheses (Table 1). The most rapid increase in live tree C with stand age occurred in aspen and birch, similar to previous research showing aboveground net primary productivity (ANPP) in deciduous stands can be 5–7 times greater than that in coniferous forests (Alexander & Mack, 2016). Greater ANPP in aspen stands was likely driven by the synergistic effects of younger, faster growing individuals, preference for well-drained and warmer sites, and greater soil nutrient availability (van Cleve et al., 1991). Indeed, litter and green moss/lichen C:N ratios were much lower in aspen and birch compared with black spruce (Figure S5), which likely contributed to greater soil nutrient availability in these stands. With more recalcitrant litter

(Hobbie et al., 2000) and biophysical traits that regulate soil microclimate and nutrient turnover (Turetsky et al., 2010), mosses in black spruce stands exert a strong effect on element cycling which we suspect reduced nutrient availability and contributed to lower black spruce live tree C pools.

Removing northness resulted in a significantly weaker model, while the interaction between northness and black spruce approached statistical significance ($p = 0.067$), pointing to the strong effect of landscape position in regulating growing conditions. At north-facing sites, we suspect a combination of lower solar input (van Cleve et al., 1991), cooler soils, and shorter growing seasons (Nicklen et al., 2016; Wolken et al., 2016), are the primary mechanisms responsible for limiting tree growth and a smaller live tree C pool. Spring drought stress may also be exacerbated on north-facing sites, where soil water is locked in frozen ground or beneath deep snow for a longer period at a time when atmospheric demand is high (Walker et al., 2015). The significance of northness in our models suggests aspect may play a relatively larger role in the spatial distribution of C in live black spruce trees than other forest types.

4.4 | The effects of fire on ecosystem C stocks and distribution

Our analysis of the effects of wildfire showed that birch and aspen stands with a known fire history contained less than half the amount of live tree C than plots without a known fire history. The large difference between burned and unburned plots in deciduous stands is a snapshot in time of sites that burned since 1947, and now consist of young and intermediate aged aspen and birch that are still rapidly accumulating C in live trees, whereas stands that have not experienced fire since the middle of the 20th century are dominated by older, mature individuals with a majority of ecosystem C in live trees, representing the culmination of growth over an extended fire-free period.

Our space-for-time analysis of burned plots partially confirmed our original hypothesis that live tree C would accumulate faster in deciduous stands compared with coniferous forests and aligns with our LMEMs. However, the lack of positive relationship between time since fire and soil C contradicts part of our hypothesis ($H_{2.3}$). In fact, we detected a weak, but significant negative relationship between soil C and time since fire in plots currently dominated by birch, suggesting these sites may be losing soil C over time. Similarly, Alexander and Mack (2016) detected a (non-significant) decline in belowground C in post-fire stands dominated by birch, and a significant decline in belowground C in aspen stands, which they attributed to differential rates of decomposition associated with aspect and soil conditions. It is possible that a decline in soil C with time since fire in birch forests reflects the post-fire transition from black spruce-dominated to birch-dominated stands. Greater input of labile birch litter may have impeded moss growth (Jean et al., 2020), thus altering the chemical composition and soil microclimate, resulting in accelerated decomposition of legacy black spruce soil C over time.

When fire effects were examined within forest types (i.e. when fire did not initiate a change in forest type), we found limited effects on soil C. These non-stand changing fires occurred on 23% of our plots and were likely of low severity, although there is a possibility that plots were occasionally established on unburned islands within fire perimeters. The prevalence of low severity fires in our dataset is reflected in fire effects on soil layer thickness. The largest differences in layer thickness occurred in the moss/lichen and ID parts horizons, not the deeper un-ID parts (Figure 6). The lack of significant difference in layer thickness in the un-ID parts horizon suggests that the low severity fires captured in our sample did not consume much of the deepest soil organic layers. Since this is where much of the total soil C is located (Figure 3a–d), the overall effect on soil C pools was minor. Nevertheless, reduced soil organic layer thickness reveals an important subtlety of fire effects that may have implications for long-term C cycle dynamics. Thinner organic layers tend to be warmer following fire (Harden et al., 2006) and can cause permafrost thaw for decades (Pastick et al., 2017; Yoshikawa et al., 2002) and accelerate decomposition of deep, old organic matter, resulting in substantial CO_2 losses (Estop-Aragonés et al., 2018; Gibson et al., 2019). Moreover, as fire return intervals shorten (Buma et al., 2022), the threat to deeper soil C pools is much greater in dry sites (Walker et al., 2020) or areas with thinner organic layers (Hoy et al., 2016), even in response to low severity fires, which could result in significant atmospheric CO_2 emissions.

Due to unexpected similarities in soil C between burned and unburned plots within each forest type, and the well-documented effects of severe fire on boreal soil C (Boby et al., 2010; Genet et al., 2013; Kasischke et al., 2010; Loranty et al., 2018; Turetsky et al., 2011), we leveraged our observations of current forest type in conjunction with known fire perimeters to make inferences about the prevalence of severe fires—which lead to a change in forest type—and their effects on ecosystem C stocks. Although we lack data on pre-fire forest type, our analysis broadly aligns with the alternative stability domains outlined by (Johnstone, Chapin, et al., 2010). Our assumption that current deciduous plots within a fire perimeter likely experienced a severe wildfire, is supported by the DWM and snag biomass on these plots, where nearly 70% of the dead biomass (DWM + snag) was coniferous (Figure 8). Moreover, deciduous stands within a fire perimeter had reduced organic layer thickness, consistent with severe fire, while sites that retained coniferous dominance had a much thicker organic layer, consistent with low severity fire. Notably, our inference that 19% of our plots experienced severe fires that led to a shift from coniferous to deciduous dominance agrees very closely with the recent findings of Baltzer et al. (2021), that approximately 20% of black spruce forests across boreal North America failed to achieve dominance or experienced decreased density following wildfire.

Severe wildfire and altered forest type led to notable changes in ecosystem C pools. For example, live tree C in unburned deciduous stands was more than three times greater than in burned deciduous stands, consistent with the rapid live tree C accumulation noted in our LMEM and univariate analyses. Our analysis

indicates that, on average, plots that experienced severe fires had at least 19.3 Mg ha^{-1} less C in soil and live trees, while low severity fires resulted in a reduction of 2.1 Mg ha^{-1} compared with unburned coniferous stands. Our estimates of C lost to high and low severity fires fall within the range of emissions for interior Alaska produced by Kasischke and Hoy (2012), who estimated C lost from fires between 2004 and 2008 ranged from 1.67 to 30.1 Mg ha^{-1}. However, Turetsky et al. (2011) calculated C losses of 21.5 to 82.9 Mg C ha^{-1}, depending on the timing of fire activity. The lower values presented here are likely because our estimates represent a range in regrowth following fire as we included all fires dating to 1947, whereas other studies examined more recent fires. Although our sample size of multiple-burn plots was relatively small (17 plots), we did not detect a significant difference in soil C ($F = 0.184$, $p = 0.854$) nor live tree C ($F = 0.05$, $p = 0.961$) between plots that had experienced a single fire or multiple fires. However, multiple burns over short intervals (<20 years between fires) may become more frequent in the future (Buma et al., 2022), leading to shifts in species composition (Hayes & Buma, 2021) and reduced ecosystem C (Hoy et al., 2016). Future investigations of multiple burns across the FIA network may elucidate further details of this phenomenon at a broad spatial scale.

Coniferous stands without a history of fire since 1947 comprised nearly half of the plots in the FIA network, representing a large portion of the landscape that may experience fire in the near future. Our analysis shows that if these stands experience severe fire and shift to the broadleaf domain, soil C stocks could be substantially reduced. However, the rapid growth of aspen and birch could lead to accelerated C accumulation in live trees, potentially offsetting soil C losses over time (Mack et al., 2021). If stands experience low severity fires that reinforce black spruce regeneration, the immediate effect on soil C could be relatively minor. What remains unclear, however, is what portion of mature deciduous stands will transition back to conifer dominance, or to a different vegetation type altogether, following deciduous tree mortality. Several studies have suggested that deciduous species maintain their dominance due to high nutrient turnover on warmer soils and their presumed tolerance of a warmer, drier climate (Hansen et al., 2021; Johnstone, Chapin, et al., 2010; Johnstone, Hollingsworth, et al., 2010). However, aspen experienced a widespread growth decline from the aspen leaf miner (*Phyllocnistis populiella* Cham.; Wagner & Doak, 2013, Cahoon et al., 2018, Boyd et al., 2021) and mortality from a fungal pathogen (*Neodothiora populina* Crous; Ruess et al., 2021). Meanwhile, birch gas exchange physiology and growth may be more limited under warm and dry conditions than white spruce (Sullivan et al., 2021). Thus, the phase of rapid C accumulation in deciduous stands following severe wildfire may be somewhat tenuous under warmer and drier conditions. It is unknown how ecosystem C stocks may change following death of the relatively short-lived deciduous tree species, particularly if coniferous trees are not present in the understory or are unable to establish following deciduous tree mortality.

Our results suggest changes in fire severity may be more important in altering boreal ecosystem C pools, than simply wildfire itself. That a larger percentage of our plots experienced low severity fire and appear to have regenerated as coniferous stands compared with high severity fires, seems to indicate a relatively high degree of resilience among coniferous forests in the region, at least historically. Baltzer et al. (2021) found that the majority of black spruce stands surveyed in boreal North America (62%) were able to regenerate following recent fire, but concluded that this resilience may be challenged by future moisture deficits. Fine-scale factors such as pre-fire stand density and fuels (Walker et al., 2020, 2021), soil drainage (Whitman et al., 2018), and the timing of fire ignition (Kasischke & Hoy, 2012; Turetsky et al., 2011) affect organic layer combustion and fire severity in boreal forests. Remote sensing tools capable of capturing drivers of within-fire variation in fire severity (e.g. Holsinger et al., 2021) will be key to improving estimates of fire-derived C emissions and advancing predictions of post-fire effects on ecosystem dynamics.

Our finding that low severity fire has had a relatively minor impact on soil C demonstrates the importance of sampling from a wide range of fire size, age, severity and landscape positions, and sheds new light on the cumulative impacts of wildfire over space and time. While larger and more severe fires have impacted vast stretches of interior Alaska and the boreal biome, the impacts to above- and belowground C pools should be placed in the context of within- and among-fire variability. Low severity fires that did not initiate changes in forest type comprised a greater proportion of plots in our data than high severity fires and had minor effects on soil C pools, overall. Meanwhile, severely burned areas that become dominated by deciduous trees may compensate for initial C losses from combustion due to the rapid growth and accumulation of C in aboveground biomass. Whether these live tree C pools can be sustained over the long-term is uncertain due to the short life span of boreal deciduous tree species and their susceptibility to moisture limitation, insect outbreaks and fungal infection.

AUTHOR CONTRIBUTIONS

S.M.P.C. and A.N.G. analysed the data with input from P.F.S. S.M.P.C. wrote the manuscript with input from P.F.S. and A.N.G.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at https://www.fs.usda.gov/pnw/tools/pnw-fiadb-forest-inventory-and-analysis-databases.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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