Wildfire combustion and carbon stocks in the southern Canadian boreal forest: Implications for a warming world

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Abstract
Boreal wildfires are increasing in intensity, extent, and frequency, potentially intensifying carbon emissions and transitioning the region from a globally significant carbon sink to a source. The productive southern boreal forests of central Canada already experience relatively high frequencies of fire, and as such may serve as an analog of future carbon dynamics for more northern forests. Fire–carbon dynamics in southern boreal systems are relatively understudied, with limited investigation into the drivers of pre-fire carbon stocks or subsequent combustion. As part of NASA's Arctic-Boreal Vulnerability Experiment, we sampled 79 stands (47 burned, 32 unburned) throughout central Saskatchewan to characterize above- and belowground carbon stocks and combustion rates in relation to historical land use, vegetation characteristics, and geophysical attributes. We found southern boreal forests emitted an average of 3.3 ± 1.1 kg C/m² from field sites. The emissions from southern boreal stands varied as a function of stand age, fire weather conditions, ecozone, and soil moisture class. Sites affected by historical timber harvesting had greater combustion rates due to faster carbon stock recovery rates than sites recovering from wildfire events, indicating that different boreal forest land use practices can generate divergent carbon legacy effects. We estimate the 2015 fire season in Saskatchewan emitted a total of 36.3 ± 15.0 Tg C, emphasizing the importance of southern boreal fires for regional carbon budgets. Using the southern boreal as an analog, the northern boreal may undergo fundamental shifts in forest structure and carbon dynamics, becoming dominated by stands <70 years old that hold 2–7 kg C/m² less than current mature northern boreal stands. Our latitudinal approach reinforces previous studies showing that northern boreal stands are at a high risk of holding less carbon under changing disturbance conditions.

KEYWORDS
climate change, ecozone, harvesting, land use, latitudinal gradient, soil moisture, stand age

INTRODUCTION

Wildfire is a natural disturbance in the boreal forest that governs many of the biome's core properties, including carbon dynamics (Bond-Lamberty, Peckham, Ahl, & Gower, 2007; Kasischke, Christensen, & Stocks, 1995). Contemporary boreal fire regimes, however, are changing, with increases in intensity, spatial extent, and frequency of fires (Kasischke & Turetsky, 2006; Macias Fauria & Johnson, 2008; Veraverbeke et al., 2017) and associated deeper burning and
higher combustion rates (Hoy, Turetsky, & Kasischke, 2016; Turetsky et al., 2011; Walker, Baltzer, Cumming, et al., 2019). These changes in fire–carbon dynamics throughout the boreal could transition the region into a carbon source (Walker, Baltzer, Cumming, et al., 2019), reinforcing climate change. By identifying the landscape variables that govern carbon accrual and combustion in the boreal biome under a modern fire regime, we can refine projected carbon losses and their positive forcing effects on global climatic change (Walker, Rogers, et al., 2018).

A concerted research effort addressing this knowledge gap has been conducted in relatively remote northern portions of the boreal biome (e.g., Harden et al., 2000; Houle, Kane, Kasischke, Gibson, & Turetsky, 2018; Turetsky et al., 2011; Walker, Rogers, et al., 2018). However, few studies have considered the landscape factors that predict spatial heterogeneity in carbon stocks and combustion rates in the southern boreal region, despite the fact that southern forests are distinct from their northern counterparts in several key ways known to govern carbon accrual and combustion. For example, southern boreal stands occur in the most active fire centers in boreal North America with the highest annual burn rates (Héon, Arseneault, & Parisien, 2014; Rogers, Soja, Goulden, & Randerson, 2015). This is in part due to more fire-prone weather conditions and longer fire seasons in the southern boreal (Field et al., 2015; Wang et al., 2015). Consequently, southern boreal stand ages can be relatively young when they burn. As stand age corresponds directly with the amount of time carbon stocks have been accumulating following the last stand replacing disturbance, younger stands generally harbor and emit less carbon during fire (Houle et al., 2018; Hoy et al., 2016; Walker, Rogers, et al., 2018). Southern boreal stands are, however, also known to be more productive than northern stands (Beaudoin et al., 2014), potentially resulting in similar carbon combustion rates across the southern and northern boreal regions, despite the younger age structure of southern boreal stands. Southern forests also tend to have a larger proportion of broadleaf trees than northern boreal forests (Beaudoin et al., 2014). Broadleaf trees are associated with traits that reduce flammability (e.g., high-moisture leaves, smooth bark, branch shedding, relatively rapidly decomposing litter, forest floor microclimates that discourage the accumulation of mosses, and deep soil organic layers), in turn limiting fire severity and combustion levels (Rogers et al., 2015). Understanding the key drivers of carbon accumulation and combustion associated with these distinct characteristics of the southern boreal is important for predicting carbon losses from the biome, particularly as southern stands occur in a highly fire-prone region of the boreal.

The southern boreal region also has an established commercial timber harvesting industry. To minimize the impact of harvesting in southern stands, managers have widely adopted a natural disturbance management framework, which strives to minimize differences in the ecosystem structure and function between harvest- and fire-disturbed forests (Bergeron, Leduc, Harvey, & Gauthie, 2002; Gauthier et al., 2009). Several comparative studies evaluating post-disturbance carbon stock recovery at fire- versus harvest-origin sites report differences in specific carbon pools that counterbalance when combined at the ecosystem level (Hagemann, Moroni, Shaw, Kurz, & Makeschin, 2010; Seedre, Taylor, Brassard, Chen, & Jõgiste, 2014). Specifically, harvested sites initially have larger organic soils and coarse woody debris (CWD) carbon stocks but smaller aboveground vegetation carbon stocks than burned sites (Seedre et al., 2014). That said, no research has contrasted the effects of different disturbance histories (fire vs. harvest) on combustion rates during a subsequent wildfire event. Understanding this interaction between different types of disturbance will become increasingly important as timber harvesting represents an expanding portion of the landscape and wildfires continue to increase in size and frequency.

The unique disturbance regimes, forest structures, and resource management of southern boreal stands may be representative of the future of northern boreal forests. For example, lightning ignitions have been increasing by approximately 2%–5% per year throughout the Northwest Territories and interior Alaska since 1975 (Veraverbeke et al., 2017), approaching those currently observed in the southern boreal forest. More frequent northern boreal fires combined with warmer temperatures may promote the proliferation of broadleaf species in historically coniferous stands (Hoy et al., 2016; Johnstone et al., 2010), potentially generating forests with a similar composition to southern stands. Commercial timber harvesting is also projected to intensify and expand northward in response to an ever-increasing demand for wood-based products (Burton, Messier, Adamowicz, & Kuuluvainen, 2006), introducing a common southern boreal forest disturbance into the northern boreal forest. Thus, the contemporary high-frequency fire regime of the southern boreal combined with its established commercial timber industry may serve as an analog for the future of northern boreal stands.

In 2015, the southern boreal forest of Saskatchewan, Canada, experienced its third largest fire season on record, with 1.41 million ha burned (Fraser, Li, & Cihlar, 2000; Stocks et al., 2003). These fires affected stands with diverse disturbance histories and landscape conditions. As such, this large fire year provided an opportunity to address persistent knowledge gaps associated with fire and carbon cycling in the southern boreal forest. Our study had four main goals: (a) discern drivers of carbon stocks and combustion rates in southern boreal forests, (b) identify the legacy effects of historical timber harvests on contemporary wildfire carbon combustion rates, (c) consider southern boreal carbon stocks and combustion rates as a potential analog for the future of northern boreal stands; and (d) estimate the variability and total carbon emissions across the 2015 Saskatchewan fire complex. As stand age, stand composition, fire weather conditions, and soil moisture govern fuel production and flammability, we predicted these factors would be important controls on carbon stocks and carbon combustion rates associated with biomass burning. As carbon accrues over time, we expected carbon stocks to be maximized at older stands with cool, wet soils that limit decomposition, while carbon combustion rates would be greatest at older stands, dominated by fire promoting tree species (i.e., *Picea mariana*, *Pinus banksiana*; Rogers et al., 2015; Wirth, 2005) on drier soils under fire weather conditions that increase fire danger. We further hypothesized that harvest- and fire-disturbed sites would have
similar rates of post-fire carbon recovery at the ecosystem level, and as a result would have comparable carbon combustion rates during a subsequent burn event. Finally, due to the higher frequency fire regime in the southern boreal region, we expected that southern boreal stands would have lower average carbon stocks and emissions than those commonly reported in northern stands.

2 | MATERIALS AND METHODS

2.1 | Study region

Between May 30 and June 15, 2016, we sampled 79 study sites (47 burned and 32 unburned) in central Saskatchewan, focusing on stands surrounding La Ronge, Weyakwin, and Clearwater River Provincial Park (Figure 1). The sites were located within three major fire events from 2015: the Egg, Philion, and Brady fires. These three fires accounted for roughly one quarter of the total area burned in Saskatchewan that year (1.41 Mha), which was the third largest fire year recorded for Saskatchewan since 1959 (Stocks et al., 2003). Our selected fires burned within two ecozones, the Boreal Shield and the Boreal Plains. Study sites in the Boreal Shield were characterized by expanses of granitic bedrock outcroppings paired with thin Humo-Ferric Podzol soils (Ecological Stratification Working Group, 1995), while Boreal Plains sites contained thick glacial till deposits with predominantly fine-textured Luvisolic soils underlain by Cretaceous shales (Ecological Stratification Working Group, 1995). The broader forested Saskatchewan region experiences continental climate conditions with a mean annual air temperature of 0.2°C and mean annual precipitation of 486 mm (Environment Canada, 2018). The tree stands we sampled were characteristic of central Saskatchewan, largely dominated by either black spruce or jack pine, with a presence of trembling aspen (Populus tremuloides), paper birch (Betula papyrifera), green alder (Alnus viridis), white spruce (Picea glauca), tamarack (Larix laricina), and willow species (Salix spp.).

Our sites were selected using a stratified random sampling design to represent potential important dimensions of carbon stock variation in the southern Canadian boreal: ecozone, stand age, stand origin (previous fire- or harvest-initiated stand development), dominant tree species, and site moisture. To do so, we first pre-selected a pool of potential 30 m × 30 m sites by randomly choosing burned sites within each fire scar that were within 1 km of roads, stratified by ecozone, stand age, and stand origin. We were not able to pre-select sites by dominant tree species or moisture class due to the lack of appropriate geospatial layers. For every pre-selected potential burned site, we randomly selected a corresponding 30 m × 30 m unburned site within a subsample surrounding each fire scar for those that had similar tree cover (±3% based on Hansen et al., 2013), slope (±0.5°), and the same aspect quadrant (N, E, S, W, or flat) according to the Canadian Digital Elevation Model (Government of Canada, 2016). We derived ecozone from the Ecological Framework of Canada (Ecological Stratification Working Group, 1995), historical fire perimeters since 1945 from the Canadian National Fire Database (Stocks et al., 2003), and harvest polygons since 1967 from Saskatchewan Forestry Harvest Data v1.1 (Saskatchewan Ministry of Environment, 2015). Harvesting occurred on the landscape prior to 1967, but the spatial data on these activities
are of lower quality. To be conservative, our analysis of stand-origin effects only includes sites that experienced stand-replacing disturbances in the past 50 years.

In the field, we sampled 47 random burned sites chosen from our pre-selected site pool, prioritizing sites for adequate coverage of ecozone, stand age, and stand origin to ensure we were able to test our hypotheses. We also chose 32 unburned sites in the field from our pre-selected pool to best match conditions at sampled burned sites, particularly considering dominant tree species and site moisture class that we were unable to account for during the site pre-selection process. The raw site level data from this effort are available online (Dieleman et al., 2019) and summarized in Table S1.

2.2 Field measurements

At all sites, we established a 30 m × 30 m quadrant with a 2 m × 30 m belt transect oriented from north to south intersecting the site’s centroid, following the design of Boby, Schuur, Mack, Verbyla, and Johnstone (2010) and Rogers et al. (2014). At each site’s center, we used a high-precision GPS receiver (GeoExplorer 6000 series GeoXH GPS device, Trimble; 0.3–1.4 m horizontal and 0.5–1.7 m vertical errors at our sites) to record latitude, longitude, elevation, and aspect, and a clinometer to determine slope. We classified site moisture class according to a six-point scale defined by Johnstone, Hollingsworth, and Chapin (2008), using site-level observations of topographic position, permafrost prevalence, and soil texture. We then condensed these soil moisture classes into three categories: xeric (xeric + subxeric), mesic (subxeric to mesic + mesic), and subhygric (mesic to subhygric + subhygric).

The belt transect was used to characterize both the soil environment and vegetation community. We measured organic soil depth approximately every 3 m along the transect (6–10 equally spaced measures per site) by carefully excavating to the surface of the mineral soil and noting the pit depth at three locations. To determine percent soil carbon, a subset of 58 soil subsamples was processed on an elemental analyzer (630-100-100 TruSpec CN Analzyer, LECO Corporation). These 58 subsamples spanned the range of organic soil types and LOI values observed in this study. A linear relationship was built between the percent carbon and LOI values observed in this study. A linear relationship was built between the percent carbon and LOI values observed in this study. A linear relationship was built between the percent carbon and LOI values observed in this study. A linear relationship was built between the percent carbon and LOI values observed in this study.

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statistical analyses were conducted in R statistical software version 3.4.2 (R Core Development Team, 2017). Soil carbon content (kg C/m²) was determined by multiplying sample bulk density by its percent carbon and depth. Samples from the same soil profile were then summed together to determine cumulative organic soil carbon stocks.

Pre-fire soil depths were estimated using two approaches: (a) adventitious root height at sites with spruce trees and (b) a mixed effects model for sites without spruce species (19 of the 47 burned stands). For sites with spruce trees, we followed the methods of Bobby et al. (2010), Rogers et al. (2014), and Walker, Baltzer, et al. (2018) developing a linear regression model relating the average organic soil depth at unburned sites to their respective average adventitious root height above the mineral soil (pre-fire organic soil depth = 1.080 \times \text{adventitious root height above mineral} + 0.956; R² = .94; p < .001). For stands without spruce species (19 of the 47 burned stands), we calculated pre-fire organic soil depth using a mixed effects model relating the average organic soil depth at unburned sites to predictive landscape variables. Nine predictors were tested for collinearity and removed if a significant relationship was found (Spearman’s p < .05). The six remaining variables were used as fixed effects in the full model (see Table 1), with site ID as a random effect, using the R “nlme” package (Mazerolle & Mazerolle, 2017), where a decrease in AICc by 2 units or more and maximized AICc model weights indicated a superior model. In doing so, percent broadleaf trees, stand age, and soil moisture class were identified as key predictors pre-fire organic soil depths from both approaches were then used to determine depth of burn, calculated as the difference between pre- and post-fire organic soil depth. Negative values were treated as non-detectable depth of burn.

Post-fire organic soil carbon stocks were calculated for each site by averaging the carbon stocks from the three to five cores collected within each burned site. Combusted organic soil carbon values were determined via a mixed effects model, considering ecozone, transformed soil depth, soil moisture class, and stand dominance type—employing an approach similar to Walker, Rogers, et al. (2018). Model reduction was completed as described above, retaining transformed soil depth and soil moisture class as predictors of transformed, cumulative soil carbon stocks at unburned stands (Table S2), with soil core ID nested in site ID as random effects (Table 1). Depth of burn of the organic soil layer was then input to the resultant model in place of soil depth to calculate combusted carbon emitted from the organic soil layer. Pre-fire carbon stocks at burned sites were calculated as

<table>
<thead>
<tr>
<th>Modeled variable</th>
<th>Model</th>
<th>Fixed effects</th>
<th>K</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>AICcwt</th>
<th>R²m</th>
<th>R²c</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-fire organic soil depth</td>
<td>Full</td>
<td>Ecozone, elevation, percent broadleaf trees, soil moisture class, stand age, vegetation abundance principle component scores</td>
<td>13</td>
<td>1,571.86</td>
<td>5.24</td>
<td>0.03</td>
<td>.61</td>
<td>.70</td>
</tr>
<tr>
<td>Final</td>
<td>Percent broadleaf trees, stand age, soil moisture class</td>
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<td>1,566.62</td>
<td>0.00</td>
<td>0.35</td>
<td>.60</td>
<td>.70</td>
<td></td>
</tr>
<tr>
<td>Pre-fire organic soil carbon content</td>
<td>Full</td>
<td>Ecozone, soil depth, soil moisture class, stand dominance type</td>
<td>13</td>
<td>-851.02</td>
<td>6.21</td>
<td>0.03</td>
<td>.75</td>
<td>.91</td>
</tr>
<tr>
<td>Final</td>
<td>Soil depth, soil moisture class</td>
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<td>-857.23</td>
<td>0.00</td>
<td>0.65</td>
<td>.75</td>
<td>.91</td>
<td></td>
</tr>
<tr>
<td>Pre-fire total carbon stocks</td>
<td>Full</td>
<td>Ecozone, origin, stand age, slope, stand dominance type, condensed soil moisture class</td>
<td>9</td>
<td>-252.82</td>
<td>9.63</td>
<td>0.00</td>
<td>.48</td>
<td>–</td>
</tr>
<tr>
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<td>0.00</td>
<td>0.39</td>
<td>.49</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>Total carbon combustion</td>
<td>Full</td>
<td>Ecozone, origin, stand age, slope, stand dominance type, condensed soil moisture class, fire weather index (FWI)</td>
<td>11</td>
<td>-249.72</td>
<td>16.02</td>
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<td>Ecozone, condensed soil moisture class, stand age, FWI</td>
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<td>0.00</td>
<td>0.57</td>
<td>.70</td>
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</table>

Abbreviations: ΔAIC, Change in AICc between a given model and the final model; AICcwt, AICc weights, indicating the probability a given model is the most parsimonious among candidate models; R²m, marginal R² for mixed effects models, and multiple R² for general linear models; R²c, conditional R² for mixed effects mode.
the sum of post-fire and combusted organic carbon stocks. For simplicity, we refer to organic soil carbon as “belowground” carbon.

2.4 | Vegetation processing and analysis

To quantify stand age, tree cores and disks were processed using standard dendrochronology techniques. Samples were sanded and mounted before being analyzed using WinDENDRO™ Reg 2009b software to enumerate tree rings. The oldest representative tree age from each stand was compared with digital spatial records of historical fire and harvest events. When both tree age and the historical records were within 10% of each other, we used the ages from the historical records (23 of the 79 sites). When the biological and historical records did not coincide, or historical records did not exist, the oldest tree core that was representative of the stand was used to age the site (41 of the 79 sites). Finally, historical records were used to age the stand when tree cores could not be collected, or those collected were exceptionally poor quality (15 of the 79 sites).

To calculate carbon stocks and combustion values associated with trees and CWD, we used a suite of diameter-based allometric equations to estimate vegetative biomass and assumed a mean carbon fraction of 0.50 (see Supplementary Methods and Table S3 for details). For simplicity, we refer to the combined carbon associated with the CWD and tree pools as “aboveground” carbon.

2.5 | Pan-regional analyses

We compared our carbon stocks and combustion values with northern boreal studies conducted in Alaska, USA and the Northwest Territories, Canada. We accessed a novel, pan-regional synthesis dataset that coalesced field measurements of fire–carbon data from central and western boreal North America (Walker, Baltzer, Bourgeau-Chavez, et al., 2019). We then selected datasets from each target region that used comparable field, laboratory, and statistical approaches to our own study. This resulted in 238 stands in the Northwest Territories and 90 stands in Saskatchewan that had a correlation coefficient greater than 0.6, the variable with a significant relationship was found (excluded variables included latitude, elevation, stand density, percent cover for each individual tree species, percent cover of coniferous species, percent cover of broadleaf species, vegetation biomass, CBI, and burn date). Carbon response variables were transformed using Tukey Ladder of Powers (Table S2) to address model assumptions. Forward model selection was then conducted using AICc values, with stand age, condensed soil moisture class, ecozone, origin, stand dominance type, and slope as potential fixed effects (Table 1). The Canadian Forest Fire Weather Index (FWI; Table S4) was included in the model selection process for combustion rates. Forward model selection was employed to test for significant interactions among variables whenever the addition of a variable improved the overall model. Simple linear regressions were conducted to determine the relationship between quantify carbon pools and stand age as well as FWI. We tested for differences in total carbon stocks across ecozones using Tukey-HSD post-hoc tests in the “lsmean” package (Lenth, 2016). The same statistical approach was used to test for differences in total carbon combustion rates across soil moisture classes and ecozones.

To test for an effect of historical timber harvesting on contemporary carbon stocks and combustion rates across all carbon pools measured, we used a targeted general linear model, which included historical disturbance and stand age (Table 2). Only stands 50 years old or younger were included in this model as historical records of anthropogenic land use prior to 1967 decrease incrementally in reliability (L. Gelhorn; personal communication). Prior to analysis, subsetted carbon stocks and combustion rates were transformed using Tukey Ladder of Powers to address model assumptions (Table S2). Simple linear regressions were conducted following model testing to further define the relationship between carbon stocks and combustion rates, stand age, and historical land use.

Finally, we used generalized least square (GLS) models via the “nlme” package (Pinheiro et al., 2017) to consider the effects of stand age class and boreal study region (i.e., Saskatchewan, Northwest Territories, Alaska) on stand age, as well as on measures of carbon stocks and combustion rates. A GLS modeling approach was selected to address unequal variances within our dataset. Prior to analysis, stand age, carbon stocks, and carbon combustion rates were transformed using the Tukey Ladder of Powers to address model assumptions (Table S2). We then tested for differences in the aforementioned target variables using Tukey-HSD post-hoc tests in the “lsmean” package.

2.7 | Spatial modeling

To spatially extrapolate our estimates of combustion to all 2015 fires in Saskatchewan, we developed a predictive model that was trained using only geospatial predictors. We acquired 47 initial predictors that were associated with environmental conditions such as soil type, topography, and fire weather (Table S4). We then implemented a multicollinearity analysis based on the absolute values of pair-wise Pearson correlations between all predictors. For any two variables that had a correlation coefficient greater than 0.6, the variable with
a larger mean absolute correlation compared across all other predictors was removed. This resulted in a final predictor set of 20. These final 20 predictors were re-gridded to 30 m on a Canadian Albers Equal Area Conic projection within all 2015 fire scars using nearest neighbor for categorical variables (ecoregion and land cover) and bilinear interpolation for continuous variables. We used fire scars from the Canadian National Burned Area Composite (Fraser et al., 2000), which indicated a total burned area of 1.41 Mha. The performance of several spatial models was tested in selecting our final model, where \( R^2 \) values were maximized between observed predicted combustion rates (see Supplementary Methods). The raw data associated with this upscaling effort are available online (Potter, Rogers, & Dieleman, 2020).

### RESULTS

#### 3.1 Southern boreal carbon stocks and combustion rates: Patterns and drivers

Prior to the 2015 wildfires, total carbon stocks in the sampled southern boreal stands of Saskatchewan, Canada averaged 7.9 ± 1.2 kg C/m².

![Table 2](image)

<table>
<thead>
<tr>
<th>Hypothesis testing</th>
<th>Variable modeled</th>
<th>Fixed effect</th>
<th>df</th>
<th>Error</th>
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<td>.0366</td>
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Note: Aboveground—Vegetation and coarse woody debris located above the soil surface.
Belowground—Organic soil layer.
Total—Aboveground and belowground measures summed.
ranging from 2.0 to 29.4 kg C/m². Approximately 50% of these stocks were contained within the organic soils, while the remainder was comprised of aboveground vegetation and CWD (Table S1). Stand age was the strongest predictor of total carbon stocks, with stocks increasing linearly by 0.10 ± 0.01 kg C m⁻² year⁻¹ (Table 1; Figure 2). Both aboveground vegetation and belowground carbon stocks reflected these overarching trends, increasing linearly with time (Figure S3). Only aboveground CWD values differed, maintaining relatively consistent values through time. Total carbon stocks also differed between ecozones, with 40% greater mean carbon stocks in the Boreal Plains versus the Boreal Shield. This corresponded with higher carbon accumulation rates at Boreal Plains sites; however, there was no significant difference in these rates between the two ecozones (F₁,75 = 0.61; p = .4384).

Field-sampled Saskatchewan stands that burned in 2015 emitted an average of 3.3 ± 1.1 kg C/m² (range 0.3–14.2 kg C/m²). Approximately 70% of this mean carbon emission was attributable...
to organic soil combustion (Table S1). Numerous sites (10 of the 47 burned stands) had 75% or more of the organic soil stocks consumed by fire. As a result, aboveground residual carbon comprised ~60% of the total residual carbon while belowground pools only comprised the remaining ~40%—a shift from the 50:50 ratio of aboveground and belowground stocks found on average in control sites and estimated to be found at burned sites prior to the fire. Rates of combustion were best predicted by stand age and the fire weather conditions as described by FWI, as well as the interaction between soil moisture class and ecozone (Tables 1 and 2). As with total carbon stocks, rates of combustion increased linearly with stand age, as stands lost an additional 0.05 ± 0.01 kg C/m$^2$ for every 1-year increase in stand age (Figure 3a). Carbon losses also increased with FWI values, with stands losing more carbon under increasing fire weather severity (Figure 3b). The least-squares mean combustion losses were greatest at stands within the Boreal Shield with

**FIGURE 4** The interactive effects of stand origin and stand age on (a) total carbon stocks, (b) aboveground vegetation carbon stocks, and (c) aboveground coarse woody debris (CWD) carbon stocks, (d) belowground carbon stocks, (e) total carbon combustion rates, (f) aboveground vegetation carbon combustion rates, (g) aboveground CWD carbon combustion rates, and (h) belowground carbon combustion rates for sites that experienced a stand-replacing disturbance in the past 50 years (see Table 2 for statistics). The dotted trend line is associated with harvest origin stands, while the solid trend line is associated with forest origin stands. Shaded regions represent the 95% confidence interval associated with each linear relationship. All data here are the simple regression results for illustrative purposes, see Figure S6 for transformed modeled results.
**TABLE 3** Pan-regional comparison of southern (SK, Canada) and northern boreal (NT, Canada, AK, USA) stand age, as well as carbon emissions and carbon stocks as standardized by stand age class. Unique symbols indicate a Tukey-HSD determined significant difference among stand ages, while unique lower- and uppercase letters indicated differences within a given row among carbon emission measures and carbon stock measures respectively. No letters are presented for the aboveground combustion rates as values did not significantly differ among regions when standardized by stand age (see Table 4). Errors are reported as standard errors, and numbers in brackets indicate the sample size.

<table>
<thead>
<tr>
<th>Stand age class</th>
<th>Young (0–69 years)</th>
<th>Intermediate (70–99 years)</th>
<th>Mature (100+ years)</th>
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<tbody>
<tr>
<td></td>
<td>SK, Canada</td>
<td>NT, Canada</td>
<td>AK, USA</td>
</tr>
<tr>
<td>Mean stand age (years)</td>
<td>26 ± 3 (57)</td>
<td>49 ± 2 (46)</td>
<td>52 ± 5 (12)</td>
</tr>
<tr>
<td>Total carbon combustion (kg C/m²)</td>
<td>1.89 ± 0.22 (31)</td>
<td>2.03 ± 0.27 (39)</td>
<td>3.24 ± 0.34 (12)</td>
</tr>
<tr>
<td>Aboveground carbon combustion (kg C/m²)</td>
<td>0.75 ± 0.10 (31)</td>
<td>0.15 ± 0.03 (39)</td>
<td>0.22 ± 0.04 (12)</td>
</tr>
<tr>
<td>Belowground carbon combustion (kg C/m²)</td>
<td>1.14 ± 0.22 (31)</td>
<td>2.03 ± 0.27 (36)</td>
<td>3.03 ± 0.35 (12)</td>
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<tr>
<td>Total carbon stocks (kg C/m²)</td>
<td>5.53 ± 0.34 (57)</td>
<td>6.51 ± 1.08 (AB) (39)</td>
<td>5.95 ± 0.46 (ABC) (12)</td>
</tr>
<tr>
<td>Aboveground carbon stocks (kg C/m²)</td>
<td>3.11 ± 0.26 (C) (57)</td>
<td>0.97 ± 0.14 (A) (39)</td>
<td>0.69 ± 0.10 (A) (12)</td>
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<tr>
<td>Belowground carbon stocks (kg C/m²)</td>
<td>2.41 ± 0.24 (A) (57)</td>
<td>6.00 ± 1.15 (AB) (36)</td>
<td>5.26 ± 0.44 (BC) (12)</td>
</tr>
</tbody>
</table>

**Note:** Aboveground—Vegetation and coarse woody debris located above the soil surface. Belowground—Organic soil layer. Total—Aboveground and belowground measures summed.

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**Note:** Aboveground—Vegetation and coarse woody debris located above the soil surface. Belowground—Organic soil layer. Total—Aboveground and belowground measures summed.
mesic soil moisture conditions and lowest within the Boreal Shield at stands with subhygric moisture conditions, when differences in stand age and fire weather conditions between ecozones were accounted for (Figure 3c).

### 3.2 | Legacy effects of historic timber harvesting

Historic timber extraction increased total carbon stock recovery with stand age (Table 2; Figure 4a). Carbon recovery was driven by aboveground vegetation (Figure 4b), as we found no effect of stand origin on aboveground CWD or belowground carbon recovery (Figure 4c,d). As a product of increased carbon stocks, combustion rates were elevated at sites with historical timber extraction. Combustion rates increased by $0.04 \pm 0.03$ kg C/m$^2$ for every year of post-timber harvest recovery (Figure 4e). In contrast, when sites were impacted by a previous fire in the past 50 years, rates of combustion did not vary with stand age. Instead, these stands emitted approximately $1.7 \pm 0.29$ kg C/m$^2$ regardless of their stand age when they burned. This trend was consistent for combustion of aboveground vegetation and belowground carbon pools (Figure 4f,h). In contrast with other carbon pools, the combustion rates of aboveground CWD had no significant relationship with stand origin but did significantly decline with stand age (Figure 4g).

### 3.3 | Pan-regional stand ages, carbon stocks, and combustion rates

Within each stand age class, Saskatchewan stands were either equal to or younger than those stands sampled in the NT and AK ($F_{4,335} = 9.62; p < .0001$; Table 3). As a result, Saskatchewan stands within the young age class stored and subsequently released less total carbon during a fire event than northern boreal stands in the same age class (Tables 3 and 4). When southern boreal stands reached intermediate to mature ages, their total carbon stocks were comparable to those in the Northwest Territories and exceeded those in Alaska by approximately 50% (Table 3). Total carbon stocks in the south were consistently bolstered by significantly greater aboveground carbon stores, with intermediate and mature Saskatchewan sites holding approximately fivefold the aboveground carbon found in corresponding Alaskan stands. Higher total carbon stocks in older southern stands corresponded to significantly higher total carbon emissions, with mature southern boreal stands releasing on average 2.5 and 3.2 kg C/m$^2$.
**FIGURE 5** Proposed governing mechanisms of soil moisture and timber harvesting on carbon dynamics, contextualized by contrasting stand age and moisture conditions in southern and northern boreal stands. Specifically, we suggest that southern boreal xeric stands have limited carbon stocks and combustion rates due to frequent fires that consume the majority of the relatively thin organic soils found at these sites. This sustains environmental conditions that promote broadleaf tree species (Johnstone et al., 2010; i.e., “non-fire promoting species”) that facilitate low-severity fires (Rogers et al., 2015). In contrast, subhygric stands have substantial carbon stocks as their wet conditions inhibit most stand-replacing fires, despite the dominance of fire promoting tree species. Mesic stands represent intermediate conditions, where severe fires occur more commonly as fire adapted species are widely prevalent, but carbon stocks are not as well protected by soil moisture conditions. Timber harvesting overlays these soil moisture controls, promoting the rapid recovery of aboveground carbon stocks via reforestation from retention forestry techniques; however, aboveground carbon stocks are highly susceptible to subsequent wildfire combustion. This framework implies if future northern boreal stands develop an age and moisture structure akin to the southern boreal (younger, less subhygric), paired with increased timber harvesting, their total carbon stores will likely be reduced [Colour figure can be viewed at wileyonlinelibrary.com]

**FIGURE 6** Spatial estimates of total combustion at 30 m across the 2015 fire perimeters in Saskatchewan (a) and our sampled fires (b, c, d). The spatial extents of our sampled fires are shown as blue rectangles in (a) [Colour figure can be viewed at wileyonlinelibrary.com]
more than mature stands in the Northwest Territories and Alaska, respectively. That said, young stands comprise approximately 70% of Saskatchewan’s southern boreal forests, indicating most stands in the region do not reach intermediate to mature ages (Figure 5).

3.4 | Spatial modeling

Although all models tested for spatial extrapolation performed relatively well, radial support vector machines explained the most variance across all field sites ($R^2 = .73$). Our cross-validation procedure indicated this was not the result of over-fitting (Figure S7). The final spatial model indicated a mean pixel-level combustion across all 2015 Saskatchewan fires of $2.5 \pm 1.1$ kg C/m$^2$. This was notably lower than the mean site-level combustion estimate of $3.3 \pm 1.1$ kg C/m$^2$, although the ranges of combustion values were similar between the two (Table S5) and our spatial model struggled to predict the highest combustion rates (Figure S7b). Modeled carbon emissions displayed substantial spatial variability across and within fire scars (Figure 6). The model also indicated an overarching pattern of higher carbon emissions in the southern and western portions of the domain (i.e., the Boreal Plains ecozone). Uncertainty in total combustion also tended to be highest in these regions (Figure S8). Aggregated across all 2015 fire scars in Saskatchewan, and accounting for missing imagery, total domain-wide emissions were estimated to be $36.3 \pm 15.0$ Tg C.

4 | DISCUSSION

4.1 | Landscape predictors of southern boreal carbon stocks and combustion rates

Stand age was consistently an important driver of both carbon stocks and combustion rates. Young stands tended to have relatively low carbon stocks, which in turn limited their combustion rates during a subsequent fire event. This is because stand age represents the length of time fuel has been accumulating since the last stand replacing disturbance (Harden, O’Neil, Trumbore, Veldhuis, & Stocks, 1997; Seedre et al., 2014). In our study, sites accumulated approximately 0.10 kg C m$^{-2}$ year$^{-1}$, which is faster than the 0.02–0.05 kg C m$^{-2}$ year$^{-1}$ range reported in other boreal studies (Andrieux, Beguin, Bergeron, Grondin, & Paré, 2018; Harden et al., 2012), most likely reflective of the high productivity that characterizes the southern boreal region as a whole (Beaudoin et al., 2014). Given the mean 2015 wildfire combustion rate, we estimate that it will take on average 47 years of post-fire succession for a southern boreal stand to recover back to its initial pre-fire carbon stocks.

In northern boreal stands, carbon stocks and rates of combustion often vary with soil moisture conditions (Turetsky et al., 2011; Walker, Rogers, et al., 2018). This relationship is primarily attributed to differing decomposition rates, where well-drained soils support the rapid decomposition of carbon stocks, while the anoxic conditions of poorly drained soils slow decomposition rates to allow carbon to accumulate over time (Fenner & Freeman, 2011). However, models indicate that well-drained sites can burn at three times the frequency of wetter sites, resulting in an order of magnitude less carbon stocks (Harden et al., 2000)—suggesting the relationship between soil moisture and fire history is equally if not more important in governing northern boreal ecosystem carbon dynamics. Our results empirically support this framework, indicating carbon stocks and combustion rates in southern boreal stands are governed by feedbacks between soil moisture class and fire frequency (inferred from stand age), as well as stand dominance (see Figure 5)–as we originally hypothesized in this study. Specifically, we found xeric stands were predominantly young (<70 years) with four times the number of broadleaf trees as subhygric stands (e.g., P. tremuloides, B. papyrifera), with the lowest average carbon stocks and combustion rates. Subhygric sites were predominately mature (>100 years) stands populated by fire-promoting conifer species (e.g., P. mariana) and had the highest carbon stocks, presumably because organic soils were protected from both frequent and severe burning historically (Whitman, Parisien, Thompson, & Flannigan, 2019). Finally, mesic sites were still dominated by fire-promoting conifer species but lacked the poorly drained conditions that inhibit severe burning, and as a result had the largest carbon combustion rates. This indicates that hypothesized fire history and soil moisture relationships found in northern boreal stands are not only maintained in southern boreal stands but further reinforced by feedbacks from stand dominance.

During the 2015 wildfires, antecedent environmental and fuel conditions were an important driver of carbon combustion rates in the southern boreal, as hypothesized. The FWI encapsulates trends in recent temperature, humidity, vapor pressure deficit, and wind speed at a given time point to indicate the ease of ignition and expected fire intensity (Van Wagner, 1987). We found emissions increased with FWI, observing ~130% increase in mean carbon losses under very high to extreme FWI conditions (20+) in comparison with low conditions (0–5). These trends reflect increasing fuel flammability as driven by spatially and temporally local weather conditions (de Groot, Pritchard, & Lynham, 2009), and emphasizes the modulating role of fire weather on fire severity (Whitman et al., 2018). However, FWI was only one component of our larger model. Key stand traits like stand age are required to anticipate wildfire carbon losses in the southern boreal and should be considered alongside more readily accessible datasets like FWI.

4.2 | Upscaled carbon combustion rates

Based on field measurements and mechanistic drivers, our upscaled spatial model of combustion performed notably better than similar past efforts. Total variance explained was substantially larger than previous combustion modeling in Alaska and the Northwest Territories (Our study: $R^2 = .73$; Veravebeke, Rogers, & Randerson, 2015: belowground combustion $R^2 = .29$, aboveground combustion $R^2 = .53$; Walker, Rogers, et al., 2018: $R^2 = .23$).
while our mean residual error was substantially smaller or approximately equal (Our study: 0.13 kg C/m²; Veraverbeke et al., 2015: belowground combustion 1.18 kg C/m², aboveground combustion 0.12 kg C/m²; Walker, Rogers, et al., 2018: 1.39 kg C/m²).

Several factors likely contribute to this improved model performance. The relative contribution of aboveground combustion to total combustion was higher in our study domain compared with past efforts in the northern boreal, making it easier to capture the combustion signature using remote sensing-based predictors (Rogers et al., 2014; Veraverbeke et al., 2015). Stand age was also highly influential in the southern boreal and was captured well by available spatial layers. Finally, we were able to leverage a high-resolution and regional vegetation layer, which was not available in past efforts. Still, we found greater uncertainty in our overall estimates of domain-wide mean combustion and total emissions compared with these past efforts (Our study: 1.1 kg C/m²; Veraverbeke et al., 2015: 0.5 kg C/m²; Walker, Rogers, et al., 2018: 0.3 kg C/m²), most likely reflecting differences in samples sizes (Our study: n = 47; Veraverbeke et al., 2015: n = 126; Walker, Rogers, et al., 2018: n = 211). These differences in model performance suggest that accounting for fire emissions in southern boreal forests is feasible and accurate at large scales, given appropriate field data for calibration.

Our spatial model indicated a general pattern of higher combustion levels in the southern and western part of the domain, coinciding with more productive stands in the Boreal Plains ecoregion. This at least partially explains why the mean combustion from our spatial model across all of 2015 Saskatchewan fires (2.5 ± 1.1 kg C/m²) was lower than the mean at field sites (3.3 ± 1.1 kg C/m²), which tended to be more concentrated in the southern portion of the domain. Our spatial model also tended to underestimate higher combustion levels (>6 kg C/m²; Figure S7), perhaps indicating a bias toward lower emission levels overall. Nonetheless, mean combustion across the 2015 Saskatchewan fire complex was within the range of uncertainty of mean spatially extrapolated combustion values from previous efforts for the Northwest Territories (Walker, Rogers, et al., 2018: 3.3 ± 0.3 kg C/m²) and Alaska (Veraverbeke et al., 2015: 2.5 ± 0.5 kg C/m²), confirming results from our pan-regional analysis based solely on field measurements and considering all stand ages.

Based on our spatial modeling efforts, we estimated the 2015 wildfire season in Saskatchewan emitted a total of 36.3 ± 15.0 Tg C. These total carbon emissions represent approximately half of the upscaled, direct combustive losses from similar megafire seasons in Alaska and Northwest Territories, reflecting differences in the domain considered, total area burned, and fire severity among these megafire years (Veraverbeke et al., 2015; Walker, Rogers, et al., 2018). Still, these upscaled combustion rates from 2015 alone account for approximately 75% of the annual mean wildfire carbon combustive losses across all of Canada, and represent approximately threefold the annual mean carbon emissions from wildfires in Alaska (Chen, Hayes, & McGuire, 2017). Considering this result applies only to the province of Saskatchewan, it emphasizes the importance of considering southern boreal fire dynamics in regional and continental carbon budget estimates.

### 4.3 Legacy effects of human land use on contemporary carbon dynamics

Anthropogenic disturbances on the landscape are expected to intensify in the northern boreal as the demand for wood-based products continues to increase with population growth (Burton et al., 2006). The southern boreal forest is already experiencing this anthropogenic stressor, providing a unique opportunity to study the effects of commercial harvesting on carbon combustion rates from subsequent wildfires. The increase in combustion rates from harvest-origin sites during the 2015 fires was largely due to a rapid recovery in combustible stocks, particularly aboveground carbon stocks. In fact, total carbon stocks at fire-origin sites decreased by 0.07 ± 0.04 kg C m⁻¹ year⁻¹ following the fire, reflecting a limited recovery in aboveground vegetation carbon stocks, paired with enhanced decomposition of CWD and belowground organic soil carbon stocks in the first 50 years following disturbance. In contrast, total carbon stocks at harvest-origin stands increased by 0.09 ± 0.05 kg C m⁻¹ year⁻¹, with aboveground vegetation stocks alone recovering 0.13 ± 0.02 kg C m⁻¹ year⁻¹. As harvesting efforts actively target more productive stands, harvested sites may naturally recover from stand replacing disturbances at a faster rate. However, a rapid rebound in aboveground carbon stocks following harvest is commonly attributed to reforestation practices like active planting and retention forestry (Hagemann et al., 2010; Seedre et al., 2014). Retention forestry involves clear-cutting a designated area but retaining an intact sub-population of adult trees and understory vegetation to promote regeneration of the forest's structure and function following harvest (Gustafsson et al., 2012). This management technique, as mandated in our study region and observed at our study sites, employed historical fire pattern analysis to determine the target amount (Andison & McClearly, 2014) and spatial arrangement (Andison, 2012) of retention under a high-frequency/low severity fire regime. In contrast, severe wildfire, as observed in our study sites, is often a stand-replacing event, killing all local adult trees and understory vegetation, in turn slowing stand regeneration and the recovery of the aboveground carbon pool (Hagemann et al., 2010). As such, reforestation practices in our study appear to be successful at rapidly re-establishing aboveground carbon stocks due to higher carbon accumulation rates.

Belowground carbon stocks and combustion rates can also be impacted by stand disturbance histories. Differences in belowground carbon stocks have commonly been reported in stands with contrasting origins, as boreal fires primarily combust belowground carbon stocks, while harvesting primarily targets aboveground stocks (Hagemann et al., 2010; Kishchuk, Lorente, Quideau, Keddy, & Sidders, 2015). Nevertheless, we observed similar belowground carbon stocks among the two stand origin types. This trend may be due to the quantity and quality of fuel available to historic fires,
potentially preventing severe combustion of the organic horizon and limiting belowground carbon stock losses at fire-origin sites. Alternatively, these trends may be due to common boreal post-harvesting practices, which can also reduce belowground stocks by actively relocating or removing post-harvest organic soils (Colombo, Parker, Luckai, Dang, & Cai, 2005; Frey, Lieffers, Munson, & Blenis, 2003). Site preparation techniques remove surface soils from the forest floor at large to limit competition from less profitable species, while generating microclimate conditions that can enhance the productivity of target tree species (Frey et al., 2003). Harvesting disturbances can also limit or change the character of belowground carbon stocks by altering microclimate conditions to stimulate microbial decomposition (e.g., warmer soils due to reduced shading). These conditions would further limit belowground carbon stocks at harvest-origin sites (Colombo et al., 2005). Taken together, our findings demonstrate that, contrary to our predictions, differing recovery pathways prompted by disturbance can have legacy effects on both above- and belowground carbon stocks and resultant emissions during subsequent wildfire events.

The implications of a harvest legacy on carbon dynamics are pertinent to boreal forest management at large, particularly in regions that employ natural disturbance-based harvesting. This management technique strives to minimize differences in structure and function between naturally and anthropogenically disturbed stands to maintain resilient forests (Bergeron et al., 2002; Gauthier et al., 2009). As boreal forests have been a globally significant carbon reservoir over the past epoch, their future management will have important ramifications on the carbon-climate change feedback (Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepasschenko, 2015). Our research demonstrates that historically harvested sites can rapidly cycle carbon during the first 50 years after disturbance when subsequent fire events are considered. It is important to note that if these sites were subsequently harvested, their rapidly amassed aboveground carbon stores would avoid combustion, potentially allowing them to persist as a carbon store within the anthropogenic commercial sector. This depends greatly on the decay rate of harvested wood products, as fire-combusted dead standing trees and woody debris have been estimated to be longer-lived than most sawn timber products (Keith et al., 2014). Moreover, these harvested sites support biogeochemical cycling rates not observed at contemporary fire-origin sites. As these legacy effects are a departure from natural systems, they need to be acknowledged and addressed as part of a cohesive management plan for the boreal region.

4.4 Southern boreal as an analog for the northern boreal forest

The northern boreal region is a relatively pristine and intact contiguous region of the boreal forest; however, the frequency of both natural and anthropogenic disturbances is expected to increase throughout the north in the coming century (Brandt, Flannigan, Maynard, Thompson, & Volney, 2013; Erdozain et al., 2019; Flannigan, Logan, Amiro, Skinner, & Stocks, 2005). The southern boreal region already experiences a high frequency fire regime and commercial timber harvesting predicted to affect the northern boreal in the future. Likely, as a consequence of its disturbance regime, approximately 70% of southern boreal stands across the Saskatchewan region are classified as young (<70 years). As we hypothesized, these young southern stands have smaller carbon stocks and combustion levels than northern boreal stands of the same age class. When southern stands are able to reach intermediate or mature ages, their stocks and combustion rates are similar to, or exceed those of northern stands. For example, intermediate and mature stands in Saskatchewan and the Northwest Territories have similar carbon stocks, although the southern boreal stands of Saskatchewan combust almost double that of Northwest Territories stands—most likely reflecting the permafrost protected soils found predominantly in the northern boreal (Biskaborn et al., 2019; Genet et al., 2013). Because mature or even intermediate-aged stands are relatively rare throughout the southern boreal landscape, young stands in this region should be used as a potential analog for the future of the northern boreal region (see Figure 5). Accordingly, we anticipate an increased prevalence across the North American boreal region of young-aged stands with relatively low total carbon stocks and combustion levels per fire cycle.

The distribution of carbon stores within a stand also varies by boreal region. Southern stands hold approximately 50% of total carbon stores within the aboveground pool, contrasting with northern stands that only hold approximately 10%–20% of their total carbon aboveground. This regional contrast most likely reflects the warmer climatic conditions in the southern boreal that both stimulate heterotrophic respiration and primary productivity, and are expanding northward (Sulla-Menashe, Woodcock, & Friedl, 2018). Despite higher aboveground stores, the majority of the carbon combusted in southern stands was still sourced belowground, following patterns commonly reported in the northern boreal (Walker, Rogers, et al., 2018). Nonetheless, these findings indicate that future boreal stands in North America may have carbon recovery trajectories distinct from historical patterns, with a larger component of the carbon store held aboveground.

4.5 Implications

Boreal fire dynamics are changing rapidly with the potential to transition this biome into a globally relevant carbon source. Understanding the factors that govern carbon accrual and combustion losses across the boreal region are important for predicting future radiative forcing effects on the climate system. This study shows that stand age, fire weather, and soil moisture dynamics are key controls on fire–carbon relationships, though the nature of these relationships can vary between boreal ecoregions. Historical land use practices are also an important factor in southern boreal carbon dynamics, as they create legacy effects that influence future carbon combustion
rates and post-fire carbon recovery. When these trends in carbon combustion rates were upscaled, we found southern boreal stands in Saskatchewan during the 2015 fire season accounted for 75% of the mean annual wildfire carbon emissions from all of Canada (Chen et al., 2017), emphasizing the importance of southern boreal wildfire carbon dynamics in regional carbon budget estimates. Finally, considering southern boreal stands as a future analog for the north, we predict increases in the prevalence of young forests (<70 years), which store ~2–7 kg C/m² less on average than in mature northern boreal stands. Our study reinforces other empirical work suggesting boreal forests are at a high risk of holding less carbon under a changing climate.

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DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in Oak Ridge National Laboratory Distributed Active Archive Center at https://doi.org/10.3334/ORNLDAAC/1740 as well as https://doi.org/10.3334/ORNLDAAC/1787.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.