

Title: Fuel availability not fire weather controls boreal wildfire severity and carbon emissions

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Summary

Carbon (C) emissions from wildfires are a key terrestrial-atmosphere interaction that influences global atmospheric composition and climate. Positive feedbacks between climate warming and boreal wildfires are predicted based on top-down controls of fire weather and climate, but C emissions from boreal fires may also depend on bottom-up controls of fuel availability related to edaphic controls and overstory tree composition. Here we synthesized data from 417 field sites spanning six ecoregions in the northwestern North American boreal forest and assessed the network of interactions among potential bottom-up and top-down drivers of C emissions. Our results indicate that C emissions are more strongly driven by fuel availability than fire weather, highlighting the importance of fine-scale drainage conditions, overstory tree species composition, and fuel accumulation rates for predicting total C emissions. By implication, climate change-induced modification of fuels needs to be considered for accurately predicting future C emissions from boreal wildfires.

Main Text

Climate warming and drying in parts of the boreal forest have led to heightened wildfire activity^{1,2}, with large increases in the annual area burned over recent decades^{3,4} (Figure 1). Climate influences the amount and type of fuel available to burn over long timescales. At shorter timescales, weather patterns dictate the flammability of fuels and weather parameters are expressed as percentiles relative to longer-term climate patterns. Consequently, carbon (C) emissions from boreal wildfires have been considered to be dominated by top-down controls of fire-conducive weather⁵⁻⁷. The Canadian Forest Fire Weather Index (FWI) System⁸ is broadly used to predict fire activity and C emissions throughout the boreal forest and even globally⁹⁻¹¹

and consists of six components that reflect landscape-level effects of weather on fuel moisture and fire behavior¹². However, bottom-up controls of fuel characteristics and topo-edaphic variation are also likely to be important drivers of C emissions from wildfires^{13,14}. Models of C emissions that rely on top-down drivers without including the impact of bottom-up controls may therefore inaccurately estimate C loss from boreal wildfires.

Forest age and drainage conditions that affect fuel availability for burning and plant species composition have the potential to strongly control C emissions. The fuel burned in boreal forests is a combination of belowground organic soils, dead organic matter on the soil surface, and both herbaceous and woody vegetation. In North American boreal ecosystems, fuel availability increases over time through the accumulation of above- and belowground organic matter^{15,16}. Landscape gradients in soil moisture can impact both the rate of this accumulation and the combustion of this organic matter^{13,16,17}. Combustion of organic soils dominates boreal fire C emissions, producing large C emissions per unit area^{13,16,18}. Fires can consume an equal depth of organic soils across drainage conditions, with near-complete combustion of organic soil occurring at the driest landscape positions compared to relatively low proportional combustion in the wettest landscape positions¹³. Black spruce (*Picea mariana*) forests typically have thick organic soils, extensive ladder fuels, and are highly flammable^{19,20}. They dominate in wet, poorly drained landscape positions but occur across the full gradient of drainage conditions. Jack pine (*Pinus banksiana*) and deciduous (*Populus* and *Betula* spp.) trees found in the Taiga Plains, Taiga Shield, and southern boreal ecoregions, much like deciduous trees in Alaska, are located at drier and warmer landscape positions with relatively shallow organic soils compared to black spruce forests^{20,21}. Although black spruce trees can replace jack pine or deciduous trees approximately 80-150 years after fire^{19,22}, this type of relay succession rarely has time to occur

before the next fire in northwestern North American boreal forests²³. Therefore, mixed spruce and deciduous and/or pine stands frequently occur at dry to intermediately drained landscape positions. Although drier landscape positions with a jack pine component are prone to more frequent burning, total C emissions from these stand types are generally lower due to relatively shallow organic soils^{13,24}. Similarly, mixed spruce-deciduous stands are also likely to have lower C emissions than pure black spruce stands due to the shallow depth of organic soils available for combustion. Consequently, bottom-up controls are likely to be just as important, if not more, than top-down weather and climate controls commonly used to model C emissions from fire activity.

Here we assess the dominant drivers of fire severity, measured as C combustion on a per unit area basis (g C m^{-2} ; hereafter C combustion), from boreal wildfires using a spatially extensive dataset of 417 field sites in six ecoregions of North America's western boreal forests (Figure 1 and Supplementary Table 1). We grouped ecoregions into four categories to ensure sufficient sample size for our analyses; Taiga Plains (n=141) and Taiga Shield (n=140) were left as is, but Alaska Boreal Interior and Boreal Cordillera were grouped as 'Alaska' (n=89) and the Boreal Plains and Softwood Shield were grouped as 'Saskatchewan' (n=43). This dataset captures broad gradients in stand age, drainage conditions, pre-fire ecosystem C storage, FWI System components, and C combustion from fires that burned from 2004-2015 (Figure 2, Supplementary Table 2, and Supplementary Figure 1). The top-down variables we examined (Supplementary Table 3) are at a coarser spatial resolution than the bottom-up variables. However, climate-derived FWI System components and weather patterns tend to vary at synoptic scales of several hundreds of kilometers¹¹, and the resolution of the data we used in this study captures this variability (Supplementary Figure 2). Furthermore, any fine-scale variation that does exist in

FWIs is small relative to the temporal and coarse-scale spatial variation used in this study (see ‘Sources of variation in FWIs’ section of Supplementary Information and Supplementary Table 4). Our use of coarse resolution climate data is consistent with prior work modeling fire activity and C emissions throughout the boreal forest^{9–11}. Although there are uncertainties with our measurements of pre-fire conditions, modeled estimates of C pools and C combustion, and interpolated FWI System components, the methods used to obtain these variables were comparable between ecoregions.

We examined bivariate relationships of all the variables associated with bottom-up and top-down drivers that we hypothesized could influence C combustion (Supplementary Table 5) and completed a variance partitioning analysis to determine the relative influence of these variables in predicting C combustion. Based on the bivariate relationships and our understanding of the system, we used piecewise structural equation modeling (SEM) to test a hypothesized network of interactions among the top-down controls on C combustion represented by fire weather indices and bottom-up controls related to fuel availability and evaluated the consistency of these networks among ecoregions. We hypothesized (Figure 3a) that C combustion would increase with increases in fuel availability represented by aboveground fuels (including coarse woody debris), belowground fuels, and the proportion of highly flammable black spruce in a forest. We expected that as forests aged, fuels available for combustion would accumulate and black spruce trees would increase in proportion relative to other tree species. We also hypothesized that moisture class, based on topography-controlled drainage and adjusted for soil texture and presence of permafrost, would impact C combustion through its effects on fuel availability. Specifically, we expected that wet sites would have greater belowground C pools due to deeper organic soils but lower aboveground C pools through the presence of less productive black

spruce compared to jack pine or deciduous broadleaf species. We also hypothesized that C combustion would be impacted by top-down controls of severe fire weather and late-season drying of deep organic soil layers and coarse woody debris. The generality of these predictions may be affected by interactions between top-down and bottom-up controls and differences between ecoregions in climate and soils.

Carbon combustion was not significantly different among ecoregions and, as expected, the majority of C combustion originated from the burning of organic soils rather than aboveground C pools (Figure 2 and Supplementary Table 6). In all ecoregions, variance in C combustion associated with top-down variables of fire weather was not significant (Table 1). In contrast, bottom-up variables were always significant and the shared variance between top-down and bottom-up variables was consistently much less than bottom-up alone (Table 1).

The SEM for all sites combined aligned with our original hypothesized model (Fischer's $C_{18}=28.40$, $p=0.06$, Figure 3b) and explained 43% of the variation in C combustion (marginal $R^2=0.43$, conditional $R^2=0.72$). Note that for the Fischer's C-statistic the subscript numbers represent the degrees of freedom, and a $p\text{-value}>0.05$ indicates that the model represents the data well and that there are no missing paths based on Shipley's test of d-separation (see Methods). Correlations between exogenous variables were either weak or non-significant (Table 2). Model fit and explained variance for sites in Alaska ($C_{22}=23.75$, $p=0.36$, Figure 3c), Taiga Plains ($C_{16}=18.45$, $p=0.30$, Figure 3d), Taiga Shield ($C_{18}=18.41$, $p=0.43$, Figure 3e), and Saskatchewan ($C_{24}=33.12$, $p=0.10$, Figure 3f) were generally better than the SEM fit on all sites and showed some ecoregion specificity in important drivers and feedbacks.

The strongest predictor of C combustion across all ecoregions was belowground C pools, which were always greatest in poorly drained landscapes. Belowground C pools generally

increased with age (Figure 3 and Table 2), but large heterogeneity in total belowground C pools and organic soil accumulation rates across topo-edaphic moisture gradients^{13,25} can conceal this relationship. In landscape positions with poor drainage, such as those underlain by permafrost or a shallow water table, belowground C pools are too wet for combustion and result in a decrease in C combustion associated with increasing moisture. We observed this non-linear response of moisture impacting C combustion through a positive indirect effect, where increasing moisture increases fuels, and through a direct negative effect where too much moisture directly decreases C combustion.

In support of our hypothesis, C combustion generally increased with the presence of black spruce (Figure 3 and Table 2) but not in Alaska, where all sites were dominated by black spruce trees (>80% of stems) or in Saskatchewan, where black spruce was absent from 37% of the sites. Black spruce dominance generally increased with site moisture but only increased with age when the full range of black spruce and jack pine mixing ratios were present (Taiga Plains and Saskatchewan), suggesting that either a successional change from jack pine to black spruce occurs or black spruce in wetter areas experience less frequent burning than jack pine in drier landscape positions.

We also found that C combustion generally increased with higher pre-fire aboveground C pools. These aboveground C pools increased with age and decreased in association with increasing moisture, highlighting the importance of time since last fire and local drainage conditions on tree productivity (Figure 3 and Table 2). Given that the vast majority of C combustion came from belowground and not aboveground, the increase in C combustion in response to higher pre-fire aboveground C pools is also likely a function of these higher biomass sites burning more intensely and facilitating the combustion of organic soils.

Fire weather indices commonly used to project and model future boreal C emissions^{6,9,26} were generally poor predictors of C combustion, and the direction of these effects was not always as expected (Figure 3 and Table 2). Day of burn (DOB), which is the Julian calendar day of the year, is considered an important predictor of C combustion because longer exposure to drying can lead to greater fuel vulnerability to combustion later in the fire season^{16,27}, but this metric was a weak or unimportant driver of C combustion across ecoregions. Drought Code (DC), which represents the drying of deep organic soils and coarse woody debris⁸, increased with DOB but had relatively weak or non-significant effects on C combustion in all ecoregions. Although these top-down controls had little effect on C combustion across fuel types, we did find evidence of C combustion increasing with higher DC in black spruce-dominated sites with large pre-fire belowground C pools in the Taiga Shield but not in other fuel types or ecoregions (see ‘DC interactions with fuel type’ section of Supplementary Information and Supplementary Figures 3 and 4). Given the unexpected inability for these top-down controls to capture variation in C combustion, we obtained DOB and DC from numerous different data sources at different spatial resolutions to assess how data source impacts our results and conclusions (see ‘Impacts of DOB and FWI data sources’ section of Supplementary Information). We found that the nature of the relationships between DOB, DC, and C combustion varied between data sources for some ecoregions (see ‘Impacts of DOB and FWI data sources’ section of Supplementary Information and Supplementary Table 7 and 8). However, regardless of the datasets used, the overall SEM fits did not improve and DOB and DC contributed very little explanation to the variation in C combustion relative to bottom-up controls. These results suggest that FWI System components derived from daily fire weather are not capturing the smoldering of deep organic soils that can take place for weeks to months after fire initiation and contribute substantially to C emissions.

The majority of sites we examined (368 out of 417) burned in particularly large fire complexes (2004 in Alaska, USA, 2014 in the Northwest Territories, Canada, and 2015 in Saskatchewan, Canada; Supplementary Table 1), yet spanned a wide range of FWI System components measurements and DOB (June 6th to August 28th). We also compiled a broader dataset of burn depth alone (no direct estimates of C emissions) from almost 850 sites (see ‘Effects of DC and DOB on burn depth’ section of Supplementary Information and Supplementary Table 9) that included an even larger range in DOB (May 7th to September 4th), FWI System components, and fires sizes. We found no significant relationships between depth of burn (which strongly correlates to C combustion in all ecoregions – Supplementary Figure 5) and DOB or DC in this larger dataset or when excluding large fire years (Supplementary Figure 6). These results, in combination with our variance partitioning analyses and SEMs, highlight the greater importance of fine-scale drainage conditions, overstory tree species, and fuel availability compared to fire weather conditions in predicting C combustion.

Although our field-based measurements span a broad geographic area and capture a large amount of variability in C combustion and top-down and bottom-up predictors, they have a relatively small footprint compared to the extent of the North American boreal forest. Based on sampling design, our sites are representative of burned boreal forests in these regions, but lack replication of a few ecosystem types that are less prone to burning such as deciduous forests, fens, and bogs²⁸. Another conceivable limitation of our study is that the top-down predictors we used, regardless of their spatial resolution (see ‘Impacts of DOB and FWI data sources’ section of Supplementary Information), were always at a coarser resolution compared to field-based measurements of C combustion and bottom-up predictors. Although climate variables, particularly precipitation, can vary over relatively fine spatial scales, weather patterns and

climate-derived FWI System components tend to vary at synoptic scales of several hundreds of kilometers (Supplementary Figure 2). Any fine-scale spatial variability that does exist in the FWIs is small relative to the temporal and coarse-scale spatial variability used in this study (see ‘Sources of variation in FWIs’ section of Supplementary Information and Supplementary Table 4). However, in topographically diverse regions, like interior Alaska, the data we used may not resolve microclimatic effects that could influence C combustion. Although the weather variables of temperature and precipitation, which are used with DOB to retrieve the DC, are at a coarse spatial scale, the resolution for DOB (1 km MODIS or 375 m VIIRS) is at a scale comparable to the minimum distance among our study plots (>500 m). DOB is often considered to be one of the primary top-down drivers of C emissions in boreal forests due to the drying out of organic soils over the fire season¹⁶. Our data captured large variation in DOB and FWIs among sites both within and between individual fire scars and ecoregions, often exceeding the variation we observed in bottom-up predictors.

Fire regimes are largely controlled by a combination of fuel availability, climate, and ignition sources over broad temporal and spatial gradients. However, boreal wildfire occurrence, spread, and C combustion are often modeled based on fire weather conditions^{6,9,26}. Similar to studies conducted in different forest types in the western United States^{29–31}, we found that C combustion per unit area was strongly influenced by topography and fuel availability. Models of C combustion from boreal wildfires that rely on top-down controls without considering the importance of bottom-up drivers will likely inaccurately estimate combustion and fail to capture important complexities associated with the spatial and temporal variation of emissions. In predicting future fire occurrence and C combustion, it is therefore important to consider how environmental changes will affect the bottom-up controls on C combustion through altered

247 patterns of fuel availability. Climate warming and drying of boreal forests in association with
248 changes to the fire regime can alter successional trajectories³² and a switch from black spruce to
249 deciduous or jack pine dominance could decrease C combustion from fires as a result of lower
250 fuel accumulation. As the climate continues to warm, permafrost degradation and drying of soils
251 could act to increase the belowground C pools available for combustion. However if fires
252 continue to increase in frequency, these organic soils are unlikely to re-accumulate in the
253 between-fire interval³³ and therefore would reduce combustion. Our study highlights that the
254 magnitude of C emissions per unit area burned is more controlled by fuel availability than fire
255 weather conditions. It is these self-regulating feedbacks between fire and vegetation that can
256 stabilize or destabilize regional fire regimes³⁴ and ultimately determine the direction of the
257 feedback between increasing wildfire emissions and climate warming.

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Author Contributions:

MCM and XJW conceived the study with help from BMR and SV. Field data was contributed by LB-C, WdG, CMD, EH, ESK, BMR, MCM, XJW, and EW. Additional data was contributed by BMR, EH, LJ, SP, and SV. XJW combined the datasets and analyzed the data with help from MCM, BMR, and SV. XJW led the writing in collaboration with MCM, JFJ, BMR, and SV. All authors read and edited this manuscript.

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Competing interests:

The authors declare no competing interests.

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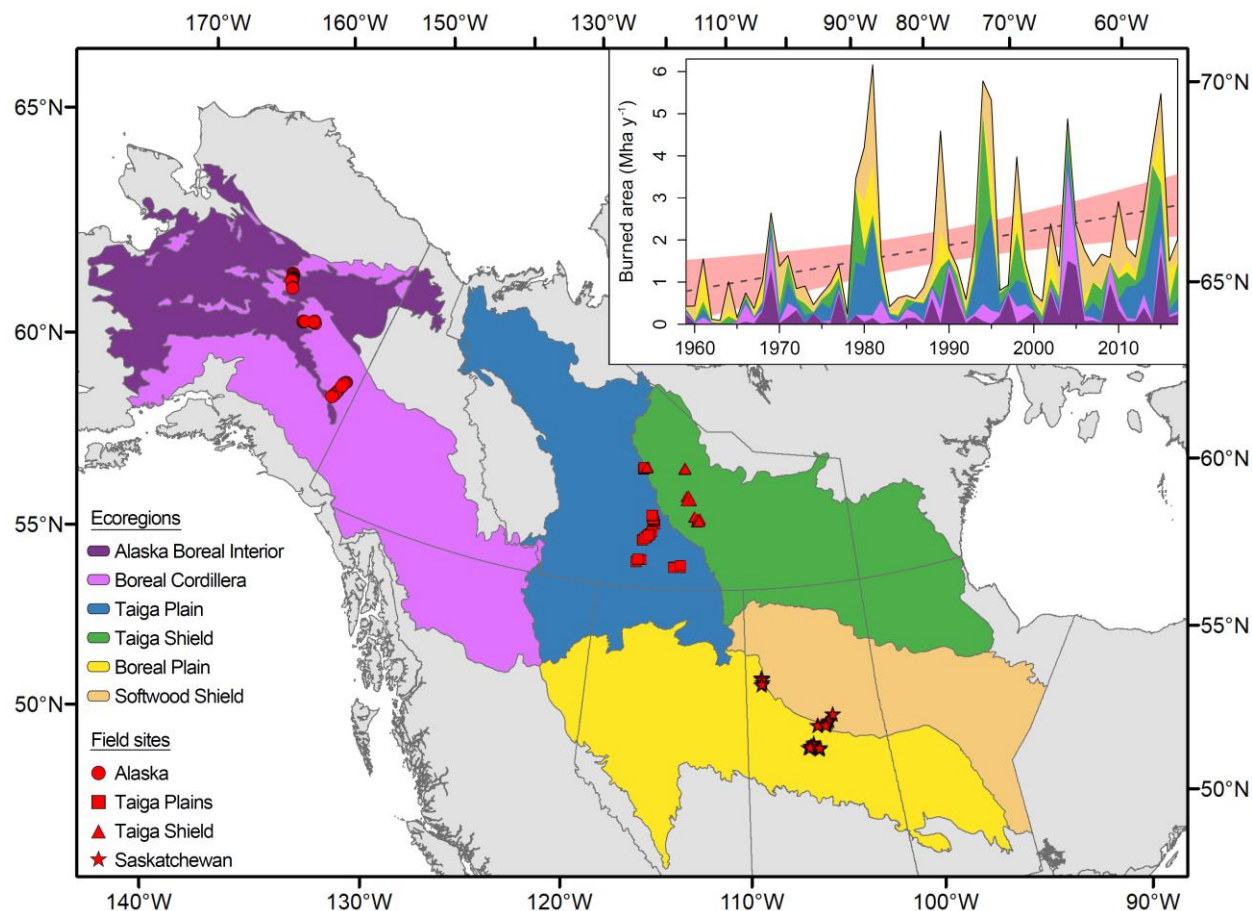


Figure 1. Map of studied ecoregions and field sites with inset showing total area burned (millions of hectares; Mha) for each ecoregion over time. Grey dotted line in the inset represents the simple linear regression, with red shading for the 95% confidence intervals, of burned area for all ecoregions combined. Analyses were completed using four ecoregion groups based on field sites, located within the six ecoregions described by the United States EPA (Environmental Protection Agency) Level II Ecoregions of North America³⁵. Fire data was obtained from point version of the Alaska Large Fire Database (ALFD)³⁶ and the Canadian National Fire Database (CNFD)³⁷.

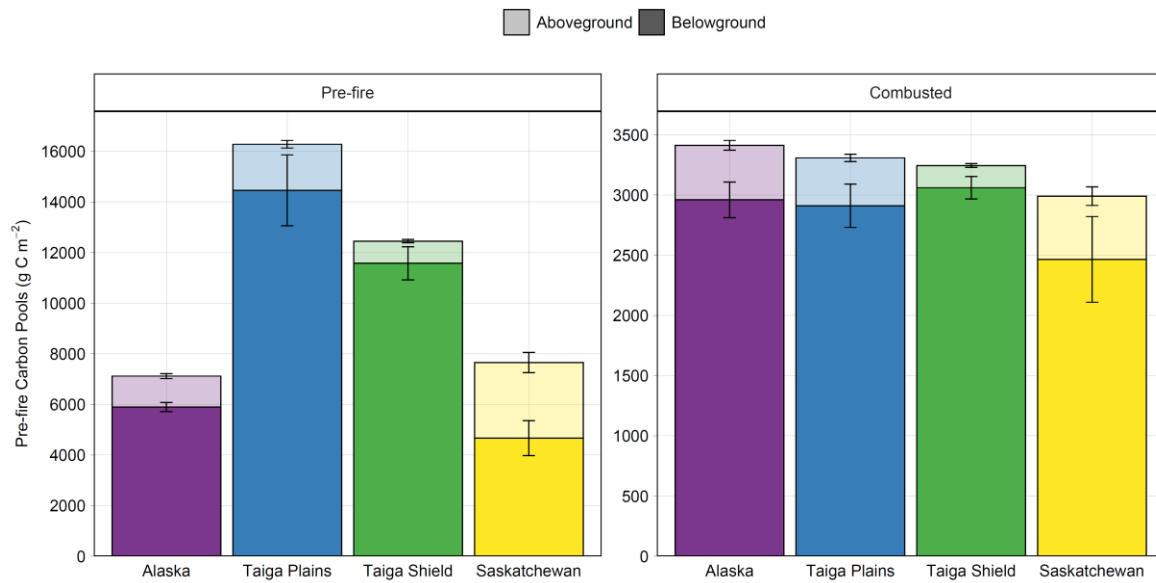


Figure 2. Average above- and belowground pre-fire and combusted carbon (C) pools for each ecoregion group. Pre-fire C pools in the left panel and C combusted in the right panel are divided into aboveground (top bars in lighter colors) and belowground (bottom bars in darker colors) components for each ecoregion group. Note differences in the y-axis scale between panels. Error bars represent standard error of the mean, but do not account for random effects. See Supplementary Table 7 for model fits. There were no significant differences between ecoregion groups in above- or belowground C pools in the pre-fire stand or combusted based on linear mixed effects models with random effects of projects and individual fires nested within projects (Supplementary Table 6).

Table 1. Results of variance partitioning for total C combustion (g C m⁻²) in relation to top-down and bottom-up variables for all sites combined, Alaska, Taiga Plains, Taiga Shield, and Saskatchewan. Values represent adjusted R² values for the unique variation explained by top-down and bottom-up variables and the shared variance between these groups. Note that the significance of shared variation cannot be tested and that a negative shared variation occurs when there is no relationship between the response variable and one of the explanatory groups.

	Top-down	Bottom-up	Shared	Residual
All sites (n=417)	0.05	0.33*	0.02	0.60
Alaska (n=89)	0.01	0.42*	-0.05	0.62
Taiga Plains (n=141)	0.07	0.46*	0.13	0.34
Taiga Shield (n=140)	0.03	0.34*	0.07	0.56
Saskatchewan (n=43)	0.22	0.51*	0.15	0.12

* p-value <0.05

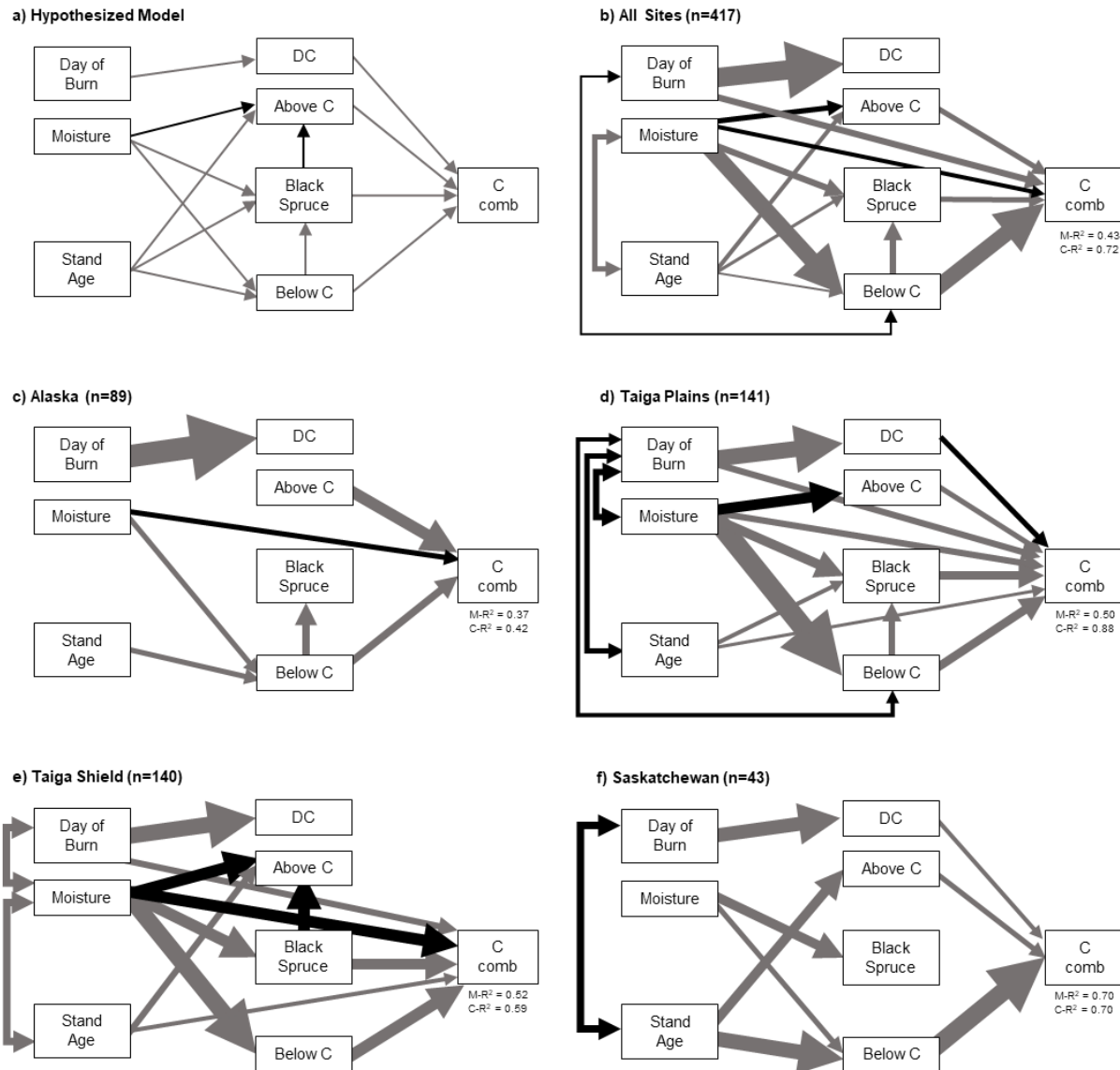


Figure 3. Structural equation modeling results testing a hypothesized network of top-down and bottom-up controls on C combustion. Structural equation models hypothesized (a) and fitted for all sites combined (b), Alaska (c), Taiga Plains (d), Taiga Shield (e), and Saskatchewan (f). Grey lines represent positive effects and black lines represent negative effects. Single-headed arrows represent direction of causal relationships. Double-headed arrows represent non-causal relationships or correlations between exogenous variables. Only significant ($p < 0.05$) lines are shown and they are scaled to the effect size. See Table 2 for effect sizes. Marginal R^2 ($M-R^2$) represents the variation explained by the fixed effects only and conditional R^2 ($C-R^2$) is a measure of the variation explained by both the fixed and random effects. Day of Burn = calendar day of burn; Moisture = moisture class on a six-point scale ranging from xeric (1) to subhygric (6); Stand Age = age of stand at time of fire (years); DC = Drought Code; Above C = aboveground C combusted (g C m^{-2}); Black Spruce = proportion of black spruce in a stand based on density (0-1); Below C = belowground C combusted (g C m^{-2}); C comb = C combusted (g C m^{-2}).

Table 2. Piecewise structural equation model results showing the standardized estimates of paths from predictor variables to response variables. Shaded cells represent significant effects (p-value<0.05) with light grey representing positive effects and dark grey representing negative effects. NAs indicate that the relationship was not included in the structural equation model. These effect sizes were used to scale the arrows in Figure 3.

	All sites	Alaska	Taiga Plains	Taiga Shield	Saskatchewan
Day of burn					
Drought Code (DC)	0.882	0.993	0.743	0.715	0.629
Pre-fire belowground C pool (Below C)					
Moisture	0.720	0.237	0.930	0.782	0.238
Stand Age	0.077	0.230	0.031	0.041	0.674
Proportion of Black Spruce (Black Spruce)					
Moisture	0.290	0.130	0.413	0.526	0.449
Stand Age	0.143	0.130	0.183	0.032	0.403
Pre-fire belowground C pool (Below C)	0.309	0.325	0.267	0.111	0.170
Pre-fire aboveground C pool (Above C)					
Moisture	-0.244	0.009	-0.459	-0.503	-0.158
Stand Age	0.185	0.078	0.145	0.272	0.439
Proportion of Black Spruce (Black Spruce)	0.072	-0.211	0.103	0.535	0.236
Carbon combustion (C comb)					
Moisture	-0.204	-0.255	0.310	-0.461	NA
Stand Age	NA	NA	0.124	0.210	NA
Pre-fire belowground C pool (Below C)	0.720	0.316	0.390	0.527	0.814
Proportion of Black Spruce (Black Spruce)	0.262	-0.049	0.372	0.515	-0.167
Pre-fire aboveground C pool (Above C)	0.295	0.546	0.219	0.032	0.251
Day of burn (DOB)	0.311	NA	0.261	0.264	NA
Drought Code (DC)	-0.186	0.149	-0.225	-0.139	0.187
Non-directional relationships					
Below C ~ ~ DOB	-0.093	NA	-0.207	NA	NA
Exogenous correlations					
Stand Age ~ DOB	0.020	-0.125	-0.219	-0.009	-0.339
Stand Age ~ Moisture	0.219	0.069	-0.007	0.297	0.261
DOB ~ Moisture	0.094	0.204	-0.273	0.187	-0.183

Methods

Study areas and data acquisition

We obtained data from 1019 burned and 152 control (i.e., no recorded history of fire) sites (Supplementary Table 9). Based on the data collected from each of these sites, we were able to use 417 burned sites that span six different ecoregions in the boreal forest of northwestern North America where the area burned has increased in recent decades (Figure 1 and Supplementary Table 1). Study sites were located in the ecoregions of Interior Boreal Alaska, Boreal Cordillera, Taiga Plains, Taiga Shield, Softwood Shield, and Boreal Plains, which differ in their geologic history, soil development and parent materials, and mean annual temperatures and precipitation³⁸. Site selection and sampling methods differed between studies (see references within Supplementary Table 1 for additional details) but were chosen to be representative of burned forests within each ecoregion by remote sensing imagery and fire history records or by a combination of drainage conditions and fire severity. We obtained field-collected data related to pre-fire tree species composition, stand age, topography, and pre- and post-fire above- and belowground C pools. Across all studies, calculations largely followed the methods described in Walker et al.¹³. Briefly, each site was assigned a moisture class based on topography-controlled drainage and adjusted for soil texture and presence of permafrost, on a six-point scale, ranging from xeric to subhygric³⁹. Stand age, or time since establishment from previous disturbance, was based on tree ring counts from five to ten dominant trees per site using standard dendrochronology techniques. All stems within a plot, including snags (i.e., coarse woody debris), were counted, and a diameter at breast height measurement along with study- and species-specific allometric equations were used to calculate tree density (number stems m⁻²), basal area (m² ha⁻¹), aboveground biomass (g dry matter m⁻²), and aboveground C content (g C

m⁻²). Tree combustion estimates of either total percent burned or combustion of structural classes (i.e., foliage, fine branches, large branches, bark) were then used to quantify the amount of aboveground C combusted. Residual soil organic layer (SOL) depth was measured at five to 20 points per site and a site-level burn depth was estimated based on the height of adventitious roots above the residual SOL or by moisture class specific comparisons with control sites. Pre-fire SOL depth was calculated as the sum of the residual SOL and the SOL burn depth. We also compiled site-level estimates of residual SOL C, pre-fire SOL C, and belowground C combusted. Using these variables, we then calculated total C combustion (g C m⁻²) as the sum of above and belowground C emissions, proportion of pre-fire C combusted as total C combusted divided by the total pre-fire C, and proportional of total C combusted attributed to the belowground C pool as belowground C combustion divided by total C combusted.

We obtained Fire Weather Index (FWI) System components for each site based on the plot location, year of burn, and a dynamic start-up date from the global fire weather database (GFWED), gridded to a spatial resolution of 0.5° latitude by 0.667° longitude, using input variables from the Modern-Era Retrospective Analysis for Research and Application version 2 (MERRA-2)¹¹. Day of burn (DOB; local solar time) for each of our study sites was extracted from the Global Monthly Fire Location Product (MCD14ML), which contains geographic location and time for each fire pixel detected by the Moderate Resolution Imaging Spectroradiometer (MODIS; 1 km spatial resolution) on Terra (launched in December 1999) and Aqua (launched in May 2002). We assigned DOB based on the nearest MODIS observation, which outperforms interpolating between multiple MODIS observations in Veraverbeke et al.²⁷. Using DOB we also obtained daily weather conditions of air temperature (°C), wind speed (m/s), relative humidity (%), and 24-hour accumulated precipitation (mm) from GFWED. The FWI

System's components are calculated from these daily weather conditions and include three fuel moisture codes and three fire behavior indices⁸. The three codes, the Fine Fuel Moisture Code (FFMC), Duff Moisture Code (DMC), and Drought Code (DC) represent the fuel moisture or the drying out of the surface, intermediate, and deep soil layers, respectively. The Initial Spread Index (ISI) is a wind-based indicator of fire danger, whereas the Buildup Index (BUI) is chiefly drought based. The Fire Weather Index (FWI) is an integrated indicator of overall fire danger computed from the ISI and BUI. We also obtained the daily severity ranking (DSR) which represents the expected difficulty of controlling a fire.

Statistical analyses

All statistical analyses were performed using R statistical software version 3.5.1⁴⁰. We grouped ecoregions into four large areas to ensure sufficient sample sizes. Taiga Plains (n=141) and Taiga Shield (n=140) were left as is, but Alaska Boreal Interior and Boreal Cordillera were grouped as 'Alaska' (n=89) and the Boreal Plains and Softwood Shield were grouped as 'Saskatchewan' (n=43).

To model above- and belowground C pools and C combustion (g C m^{-2}) as a function of ecoregion group (4 levels), we fit generalized linear mixed effects models with hierarchical random effects of projects (4 levels) and individual fires nested within projects (18 levels) using the package 'nlme'⁴¹. These random effects allow for varying intercepts and account for the non-independence of C combustion estimates from individual research projects and the spatial non-independence of sample sites within fire scars. The significance of fixed effects was assessed using likelihood ratio tests of the full models against reduced models and verified using Akaike information criterion (AIC)⁴². We verified that the statistical assumptions of homogeneity of variance and independence were not violated by visually inspecting residual versus fitted values,

ecoregion groups, and each grouping level of the random intercepts⁴². We tested for differences in effect sizes among ecoregions using Tukey–Kramer post hoc analysis for multiple comparisons in the package ‘emmeans’⁴³ (Supplementary Table 6).

To estimate the covariation of potential top-down and bottom-up drivers (Supplementary Table 2) with total C combustion (g C m^{-2}), we first used a variance partitioning analysis by partial regression in the package ‘vegan’⁴⁴ to estimate the variation in combustion explained by bottom-up and top-down variables. This analysis does not require the removal of collinear variables, allowing for the use of all collected variables. The significance of unique variation (controlling for variation explained by the other explanatory matrix) for both bottom-up and top-down matrices was assessed using adjusted R^2 and $p\text{-value} < 0.05$. We conducted five separate variance partitioning analyses, one model using all the sites and then one for each of the four ecoregion groups, to assess if the factors explaining C combustion are consistent among ecoregions.

Based on our expectation that there would be a complex network of interactions among the factors impacting combustion, we conducted piecewise structural equation modeling (SEM) in the R package ‘piecewiseSEM’⁴⁵. Piecewise SEM combines multiple linear models, which can incorporate random structures, into a single causal network⁴⁶. We conducted five separate SEMs; one model using all the sites and then one for each of the four ecoregion groups. We included variables associated with fuel availability and fire weather indices based on our knowledge of the system with support from the published literature and by examining bivariate relationships of all the variables associated with environmental, stand, and fire characteristics that could influence combustion (Supplementary Table 2 and Supplementary Table 5). The bivariate relationships were assessed by simple linear regressions between C combustion and

each of the collected variables (Supplementary Table 5). We converted the six-point moisture classification into an ordinal variable. Each component of the SEM was fit with a linear mixed effects model. For the all sites model, we used hierarchical random effects of ecoregions, projects nested within ecoregions, and individual fires nested within projects and ecoregions. Random effects of projects and individual fires nested within projects were used for the Taiga Plains and Taiga Shield SEMs and random effects of ecoregions and individual fires nested within ecoregions were used for the Alaska and Saskatchewan SEMs. Missing paths were assessed using a Shipley's test of d-separation (d-sep) based on the χ^2 distributed Fisher's C statistic, where degrees of freedom are equal to two times the number of pairs in the basis set⁴⁶. We then included missing paths identified by tests of d-sep into the hypothesized SEMs to obtain an accurate interpretation of the overall model. Overall fit was assessed based on d-sep, where a $p\text{-value} > 0.05$ indicates that the model represents the data well and no paths are missing⁴⁶. Coefficients were scaled by means and standard deviations for comparisons of effects across covariates with different units.

Data availability

The data used in this manuscript are archived at the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC). <https://doi.org/10.3334/ORNLDAAC/1744>.

Code availability

No custom code or mathematical algorithms were used in the analyses of these data. The R code for our statistical analyses is available from the authors upon request and each of the R packages used is referenced in the methods.

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