



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

X. J. Walker¹✉, B. M. Rogers¹, S. Veraverbeke¹, J. F. Johnstone^{4,5}, J. L. Baltzer⁶, K. Barrett⁷, L. Bourgeau-Chavez⁸, N. J. Day^{6,9}, W. J. de Groot¹⁰, C. M. Dieleman¹¹, S. Goetz¹², E. Hoy¹³, L. K. Jenkins^{8,14}, E. S. Kane¹⁵, M.-A. Parisien¹⁶, S. Potter¹², E. A. G. Schuur¹², M. Turetsky^{11,17}, E. Whitman¹⁶ and M. C. Mack¹

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 by 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.

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} (Fig. 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 weather^{5–7}. The Canadian Forest Fire Weather Index (FWI) System⁸ is widely used to predict fire activity and C emissions throughout the boreal forest and even globally^{9–11} and consists of six components that reflect landscape-level effects of weather on fuel moisture and fire behaviour¹². 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 with relatively low proportional combustion in the wettest landscape positions¹³. Black spruce (*Picea mariana*) forests typically have thick organic soils and 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 with 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 intermediate-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

¹Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ, USA. ²Woodwell Climate Research Center, Falmouth, MA, USA.

³Faculty of Science, Earth and Climate, Vrije Universiteit Amsterdam, Amsterdam, the Netherlands. ⁴Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada. ⁵Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, USA. ⁶Biology Department, Wilfrid Laurier University, Waterloo, Ontario, Canada. ⁷School of Geography, Geology and Environment, University of Leicester, Leicester, UK. ⁸Michigan Tech Research Institute, Michigan Technological University, Ann Arbor, MI, USA. ⁹School of Science, Auckland University of Technology, Auckland, New Zealand.

¹⁰Great Lakes Forestry Center, Canadian Forest Service, Natural Resources Canada, Sault Ste. Marie, Ontario, Canada. ¹¹Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada. ¹²School of Informatics, Computing and Cyber Systems (SICCS), Northern Arizona University, Flagstaff, AZ, USA. ¹³NASA Goddard Space Flight Center/Global Science & Technology, Inc., Greenbelt, MD, USA. ¹⁴School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA. ¹⁵College of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI, USA.

¹⁶Northern Forestry Centre, Canadian Forest Service, Natural Resources Canada, Edmonton, Alberta, Canada. ¹⁷Institute of Arctic and Alpine Research, Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO, USA. ✉e-mail: xanthe.walker@gmail.com

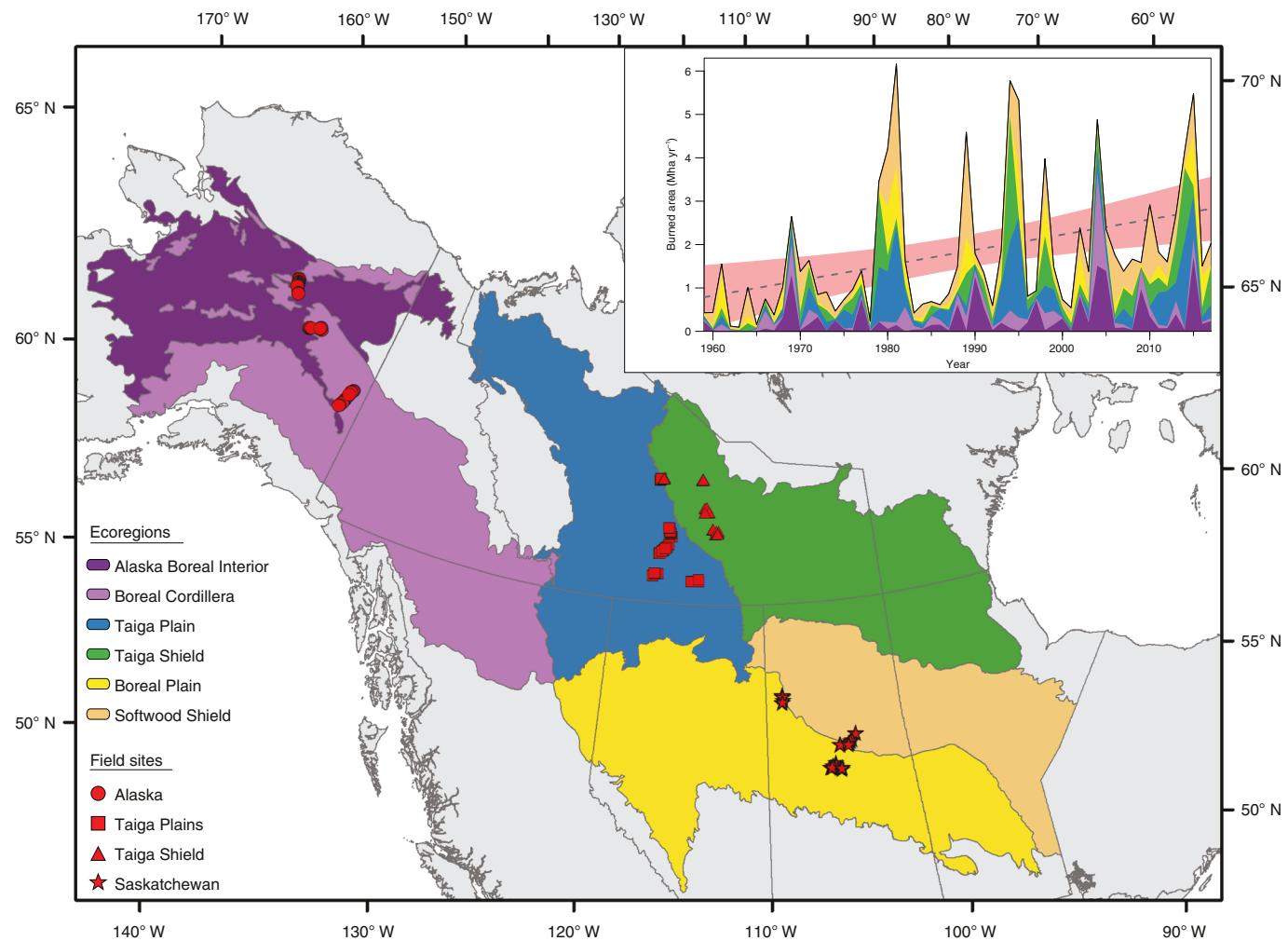


Fig. 1 | Map of studied ecoregions and field sites. Grey dotted line in the inset (showing total area burned in millions of hectares (Mha) for each ecoregion over time) represents the simple linear regression, with red shading for the 95% confidence interval, of burned area for all ecoregions combined.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

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, if not more, important 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 (gC 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 (Fig. 1 and Supplementary Table 1). We grouped the 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 to 2015 (Fig. 2, Supplementary Table 2 and Supplementary Fig. 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 kilometres¹¹, and the resolution of the data we used in this study captures this variability (Supplementary Fig. 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 modelling fire activity and C emissions throughout the boreal forest^{9–11}. Although there are uncertainties with our measurements of pre-fire conditions, modelled 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 modelling (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

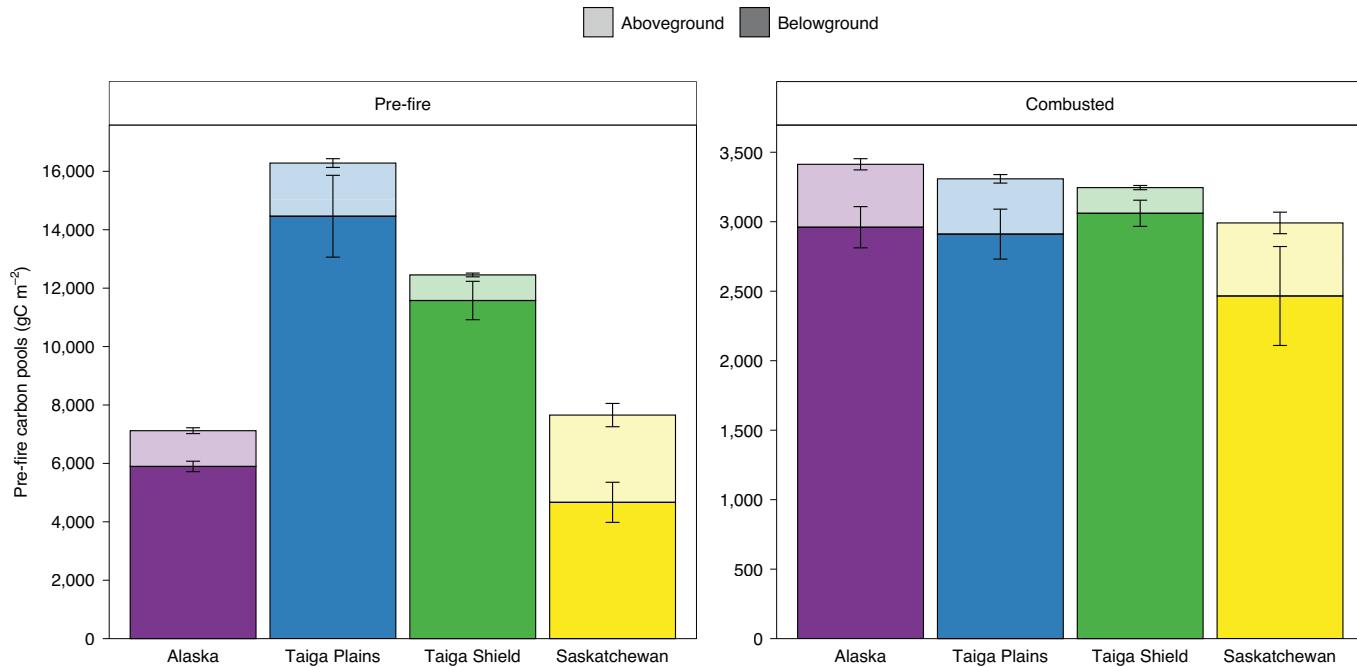


Fig. 2 | Average above- and belowground pre-fire and combusted carbon (C) pools for each ecoregion group. Pre-fire C pools (left panel) and C combusted (right panel) are divided into aboveground (top bars in lighter colours) and belowground (bottom bars in darker colours) components for each ecoregion 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).

related to fuel availability and evaluated the consistency of these networks among ecoregions. We hypothesized (Fig. 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 with 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 (Fig. 2 and Supplementary Table 6). In all ecoregions, the 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 $C_{18}=28.40$, $P=0.06$; Fig. 3b) and explained 43% of the variation in C combustion (marginal $R^2=0.43$, conditional $R^2=0.72$). Note that, for Fischer's C-statistic,

Table 1 | Results of variance partitioning for total C combustion (gC m⁻²) in relation to top-down and bottom-up variables for all sites combined, Alaska, Taiga Plains, Taiga Shield and Saskatchewan

	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

Values represent adjusted R^2 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. * $P < 0.05$.

the subscript numbers represent the degrees of freedom, and a P -value of >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 ($C_{22}=23.75$, $P=0.36$; Fig. 3c), Taiga Plains ($C_{16}=18.45$, $P=0.30$; Fig. 3d), Taiga Shield ($C_{18}=18.41$, $P=0.43$; Fig. 3e) and Saskatchewan ($C_{24}=33.12$, $P=0.10$; Fig. 3f) were generally better than the SEM fit on all sites and showed some ecoregion specificity in important drivers and feedbacks.

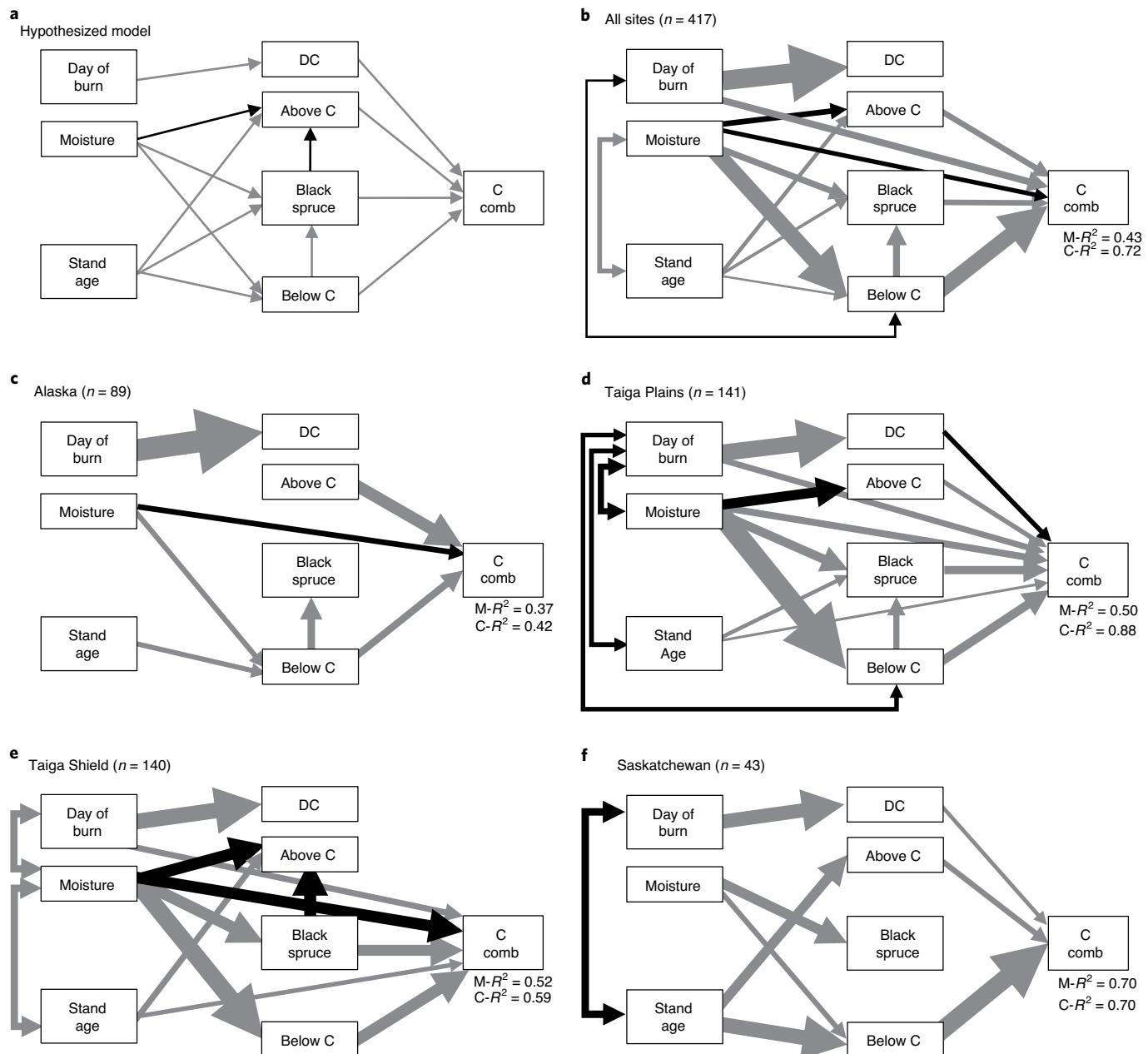


Fig. 3 | SEM results testing a hypothesized network of top-down and bottom-up controls on C combustion. a-f, SEMs hypothesized (a) and fit for all sites combined (b), Alaska (c), Taiga Plains (d), Taiga Shield (e) and Saskatchewan (f). Grey arrows represent positive effects, and black arrows represent 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 sub-hygric (6); Stand age, age of stand at time of fire (years); DC, Drought Code; Above C, aboveground C combusted (gC m^{-2}); Black spruce, proportion of black spruce in a stand based on density (0–1); Below C, belowground C combusted (gC m^{-2}); C comb, C combusted (gC m^{-2}).

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 (Fig. 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 (Fig. 3 and Table 2) but not in

Table 2 | Piecewise SEM results showing the standardized estimates of paths from predictor variables to response variables

	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

NA indicates that the relationship was not included in the structural equation model. These effect sizes were used to scale the arrows in Fig. 3. * $P < 0.05$.

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 (Fig. 3 and Table 2). Given that the vast majority of C combustion came from below-ground 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 (Fig. 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 Figs. 3 and 4). Given the unexpected inability of 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 Tables 7 and 8). However, regardless of the data source 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 smouldering 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 (in 2004 in Alaska, USA, in 2014 in the Northwest Territories, Canada and in 2015 in Saskatchewan, Canada; Supplementary Table 1) yet spanned a wide range of FWI System components measurements and DOB (6 June to 28 August). 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 (7 May to 4 September), FWI System components and fire sizes. We found no significant relationships between depth of burn (which strongly correlates to C combustion in all ecoregions—Supplementary Fig. 5) and DOB or DC in this larger dataset or when excluding large fire years (Supplementary Fig. 6). These results, in combination with our variance partitioning analyses and SEM, highlight the greater importance of fine-scale drainage conditions, overstory tree species and fuel availability compared with 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 with the extent of the North American boreal forest. Based on the 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 with 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 kilometres (Supplementary Fig. 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, such as 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 for the Moderate Resolution Imaging Spectroradiometer (MODIS) or 375 m for Visible Infrared Imaging Radiometer Suite (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 modelled 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 patterns of fuel availability. Climate warming and drying of boreal forests in association with changes to the fire regime can alter successional trajectories³², and a switch from black spruce to deciduous or jack pine dominance could decrease C combustion from fires as a result of lower fuel accumulation. As the climate continues to warm, permafrost degradation and drying of soils could act to increase the belowground C pools available for combustion. However if fires continue to increase in frequency, these organic soils are unlikely to re-accumulate in the between-fire interval³³ and therefore would reduce combustion. Our study highlights that the magnitude of C emissions per unit area burned is more controlled by fuel availability than by fire weather conditions. It is these self-regulating feedbacks between fire and vegetation that can stabilize or destabilize regional fire regimes³⁴ and ultimately determine the direction of the feedback between increasing wildfire emissions and climate warming.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-020-00920-8>.

Received: 17 September 2019; Accepted: 3 September 2020;
Published online: 12 October 2020

References

1. Balshi, M. S. et al. Assessing the response of area burned to changing climate in western boreal North America using a multivariate adaptive regression splines (MARS) approach. *Glob. Change Biol.* **15**, 578–600 (2009).
2. Flannigan, M. D., Krawchuk, M. A., de Groot, W. J., Wotton, B. M. & Gowman, L. M. Implications of changing climate for global wildland fire. *Int. J. Wildland Fire* **18**, 483–507 (2009).
3. Calef, M. P., Varvak, A., McGuire, A. D., Chapin, F. S. & Reinhold, K. B. Recent changes in annual area burned in interior Alaska: the impact of fire management. *Earth Interact.* **19**, 5 (2015).
4. Hanes, C. C. et al. Fire-regime changes in Canada over the last half century. *Can. J. For. Res.* **49**, 256–269 (2018).
5. Flannigan, M. D., Logan, K. A., Amiro, B. D., Skinner, W. R. & Stocks, B. J. Future area burned in Canada. *Climatic Change* **72**, 1–16 (2005).
6. Amiro, B. D., Cantin, A., Flannigan, M. D. & de Groot, W. J. Future emissions from Canadian boreal forest fires. *Can. J. Res.* **39**, 383–395 (2009).
7. Young, A. M., Higuera, P. E., Duffy, P. A. & Hu, F. S. Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. *Ecography* **40**, 606–617 (2017).
8. Van Wagner, C. E. *Development and structure of the Canadian Forest Fire Weather Index System*, vol. 35 (Canadian Forest Service, 1987).
9. de Groot, W. J., Pritchard, J. M. & Lynham, T. J. Forest floor fuel consumption and carbon emissions in Canadian boreal forest fires. *Can. J. Res.* **39**, 367–382 (2009).
10. Flannigan, M. et al. Global wildland fire season severity in the 21st century. *Ecol. Manag.* **294**, 54–61 (2013).
11. Field, R. D. et al. Development of a global fire weather database. *Nat. Hazards Earth Syst. Sci.* **15**, 1407–1423 (2015).
12. Stocks, B. J. et al. Canadian forest fire danger rating system: an overview. *For. Chron.* **65**, 258–265 (1989).
13. Walker, X. J. et al. Cross-scale controls on carbon emissions from boreal forest megafires. *Glob. Change Biol.* **24**, 4251–4265 (2018).
14. Parisien, M.-A. et al. Contributions of ignitions, fuels, and weather to the spatial patterns of burn probability of a boreal landscape. *Ecosystems* **14**, 1141–1155 (2011).
15. Thompson, D. K., Simpson, B. N. & Beaudoin, A. Using forest structure to predict the distribution of treed boreal peatlands in Canada. *Ecol. Manag.* **372**, 19–27 (2016).
16. Turetsky, M. R. et al. Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. *Nat. Geosci.* **4**, 27–31 (2011).
17. Whitman, E. et al. Variability and drivers of burn severity in the northwestern Canadian boreal forest. *Ecosphere* **9**, e02128 (2018).

18. Boby, L. A., Schuur, E. A., Mack, M. C., Verbyla, D. & Johnstone, J. F. Quantifying fire severity, carbon, and nitrogen emissions in Alaska's boreal forest. *Ecol. Appl.* **20**, 1633–1647 (2010).
19. Ott, L. A. V. R. A., Mann, P. C. A. D. & Van Cleve, K. *Successional Processes in the Alaskan Boreal Forest* (Oxford Univ. Press, 2006).
20. Johnson, E. A. *Fire and Vegetation Dynamics* (Cambridge Univ. Press, 1992).
21. Hély, C., Bergeron, Y. & Flannigan, M. D. Effects of stand composition on fire hazard in mixed-wood Canadian boreal forest. *J. Veg. Sci.* **11**, 813–824 (2000).
22. Rogers, B. M., Randerson, J. T. & Bonan, G. B. High-latitude cooling associated with landscape changes from North American boreal forest fires. *Biogeosciences* **10**, 699–718 (2013).
23. Johnstone, J. F. et al. Fire, climate change, and forest resilience in interior alaska. *Can. J. Res.* **40**, 1302–1312 (2010).
24. Walker, X. J. et al. Soil organic layer combustion in boreal black spruce and jack pine stands of the Northwest Territories, Canada. *Int. J. Wildland Fire* **27**, 125–134 (2018).
25. Tarnocai, C. et al. Soil organic carbon pools in the northern circumpolar permafrost region. *Glob. Biogeochem. Cycles* **23**, GB2023 (2009).
26. Flannigan, M. D. et al. Fuel moisture sensitivity to temperature and precipitation: climate change implications. *Climatic Change* **134**, 59–71 (2016).
27. Veraverbeke, S., Rogers, B. M. & Randerson, J. T. Daily burned area and carbon emissions from boreal fires in Alaska. *Biogeosciences* **12**, 3579–3601 (2015).
28. Bernier, P. Y. et al. Mapping local effects of forest properties on fire risk across Canada. *Forests* **7**, 157 (2016).
29. Birch, D. S. et al. Vegetation, topography and daily weather influenced burn severity in central Idaho and western Montana forests. *Ecosphere* **6**, art7 (2015).
30. Dillon, G. K. et al. Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. *Ecosphere* **2**, art130 (2011).
31. Parks, S. A. et al. High-severity fire: evaluating its key drivers and mapping its probability across western US forests. *Environ. Res. Lett.* **13**, 044037 (2018).
32. Johnstone, J. F., Hollingsworth, T. N., Chapin, F. S. & Mack, M. C. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Glob. Change Biol.* **16**, 1281–1295 (2010).
33. Walker, X. J. et al. Increasing wildfires threaten historic carbon sink of boreal forest soils. *Nature* **572**, 520–523 (2019).
34. Kelly, R. et al. Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. *Proc. Natl Acad. Sci. USA* **110**, 13055–13060 (2013).
35. US EPA. *Ecoregions of North America* <https://www.epa.gov/eco-research/ecoregions-north-america> (2015).
36. Kasischke, E. S., Williams, D. & Barry, D. Analysis of the patterns of large fires in the boreal forest region of Alaska. *Int. J. Wildland Fire* **11**, 131–144 (2002).
37. Stocks, B. J. et al. Large forest fires in Canada, 1959–1997. *J. Geophys. Res. Atmos.* **107**, FFR 5-1–FFR 5-12 (2002).

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s), under exclusive licence to Springer Nature Limited 2020

Methods

Study areas and data acquisition. We obtained data from 1,019 burned and 152 control (that is, 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 (Fig. 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, 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 sub-hygric³⁹. 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 (that is, 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 of stems per m³), basal area (m² ha⁻¹), aboveground biomass (g dry matter per m³) and aboveground C content (gC m⁻²). Tree combustion estimates of either total percent burned or combustion of structural classes (that is, foliage, fine branches, large branches and bark) were then used to quantify the amount of aboveground C combusted. Residual soil organic layer (SOL) depth was measured at 5 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 (gC 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 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⁻¹), relative humidity (%) and 24-h accumulated precipitation (mm) from GFWED. The FWI System components are calculated from these daily weather conditions and include three fuel moisture codes and three fire behaviour 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 3.5.1 (ref. ⁴⁰). 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 (gC m⁻²) as a function of ecoregion group (4 levels), we fitted 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 (gC 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 $P < 0.05$. 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 whether 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 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 Tables 2 and 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 fitted 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 -value of > 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/ORNLDAC/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.

References

38. Wang, T., Hamann, A., Spittlehouse, D. & Carroll, C. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE* **11**, e0156720 (2016).
39. Johnstone, J. F., Hollingsworth, T. N. & Chapin, F. S., III. *A key for predicting postfire successional trajectories in black spruce stands of interior Alaska, general technical report* (USDA Forest Service, 2008).
40. R Development Core Team. R: a language and environment for statistical computing (2018).
41. Pinheiro, J. et al. Package 'nlme'. Linear nonlinear mixed effects models version 3-1 (2017).
42. Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. *Mixed effects models and extensions in ecology with R* (Springer Science & Business Media, 2009).
43. Lenth, R., Singmann, H., Love, J., Buerkner, P. & Herve, M. Package 'emmeans: estimated marginal means, aka least-squares means' (2019).
44. Oksanen, J. et al. Package vegan: community ecology package (2013).
45. Lefcheck, J., Byrnes, J. & Grace, J. Package piecewiseSEM: piecewise structural equation modeling (2018).
46. Shipley, B. Confirmatory path analysis in a generalized multilevel context. *Ecology* **90**, 363–368 (2009).

Acknowledgements

This synthesis work for this project was supported by funding from the NASA Arctic Boreal and Vulnerability Experiment (ABoVE) Legacy Carbon grant NNX15AT71A

awarded to M.C.M. The original field studies were supported by funding in the United States from NSF DEB RAPID grant no. 1542150 to M.C.M., NASA ABove grant NNX15AT83A to L.B.-C., NASA ABove grant NNX15AU56A to B.M.R., S.V. and M.T., Joint Fire Science Program grant 05-1-2-06 to J.F.J., NSF grant 0445458 to M.C.M., NSF support to the Bonanza Creek LTER (DEB-0423442); and in Canada from NSERC Discovery Grant funding to J.F.J. and M.R.T.; Government of the Northwest Territories Cumulative Impacts Monitoring Program Funding project #170 to J.L.B.; NSERC PDFs to N.J.D. and C.M.D.; GNWT logistical and financial support through the Laurier-GNWT Partnership Agreement; Polar Knowledge Canada's Northern Science Training Program funding awarded to Canadian field assistants; S.V. acknowledges Vidi grant support from the Netherlands Organization for Scientific Research (NWO).

Author contributions

M.C.M. and X.J.W. conceived the study with help from B.M.R. and S.V. Field data were contributed by L.B.-C., W.J.d.G., C.M.D., E.H., E.S.K., B.M.R., M.C.M., X.J.W. and E.W. Additional data were contributed by B.M.R., E.H., L.K.J., S.P., and S.V. X.J.W. combined

the datasets and analysed the data with help from M.C.M., B.M.R. and S.V. X.J.W. led the writing in collaboration with M.C.M., J.F.J., B.M.R. and S.V. All authors read and edited this manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41558-020-00920-8>.

Correspondence and requests for materials should be addressed to X.J.W.

Peer review information *Nature Climate Change* thanks Gregory Dillon, Matthew Hurteau, Rachel Loehman and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

Terms and Conditions

Springer Nature journal content, brought to you courtesy of Springer Nature Customer Service Center GmbH (“Springer Nature”).

Springer Nature supports a reasonable amount of sharing of research papers by authors, subscribers and authorised users (“Users”), for small-scale personal, non-commercial use provided that all copyright, trade and service marks and other proprietary notices are maintained. By accessing, sharing, receiving or otherwise using the Springer Nature journal content you agree to these terms of use (“Terms”). For these purposes, Springer Nature considers academic use (by researchers and students) to be non-commercial.

These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the relevant terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). For Creative Commons-licensed articles, the terms of the Creative Commons license used will apply.

We collect and use personal data to provide access to the Springer Nature journal content. We may also use these personal data internally within ResearchGate and Springer Nature and as agreed share it, in an anonymised way, for purposes of tracking, analysis and reporting. We will not otherwise disclose your personal data outside the ResearchGate or the Springer Nature group of companies unless we have your permission as detailed in the Privacy Policy.

While Users may use the Springer Nature journal content for small scale, personal non-commercial use, it is important to note that Users may not:

1. use such content for the purpose of providing other users with access on a regular or large scale basis or as a means to circumvent access control;
2. use such content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
3. falsely or misleadingly imply or suggest endorsement, approval, sponsorship, or association unless explicitly agreed to by Springer Nature in writing;
4. use bots or other automated methods to access the content or redirect messages
5. override any security feature or exclusionary protocol; or
6. share the content in order to create substitute for Springer Nature products or services or a systematic database of Springer Nature journal content.

In line with the restriction against commercial use, Springer Nature does not permit the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Springer Nature journal content cannot be used for inter-library loans and librarians may not upload Springer Nature journal content on a large scale into their, or any other, institutional repository.

These terms of use are reviewed regularly and may be amended at any time. Springer Nature is not obligated to publish any information or content on this website and may remove it or features or functionality at our sole discretion, at any time with or without notice. Springer Nature may revoke this licence to you at any time and remove access to any copies of the Springer Nature journal content which have been saved.

To the fullest extent permitted by law, Springer Nature makes no warranties, representations or guarantees to Users, either express or implied with respect to the Springer nature journal content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.

Please note that these rights do not automatically extend to content, data or other material published by Springer Nature that may be licensed from third parties.

If you would like to use or distribute our Springer Nature journal content to a wider audience or on a regular basis or in any other manner not expressly permitted by these Terms, please contact Springer Nature at

onlineservice@springernature.com