

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

3 **Walker, X.J.**¹ Rogers, B.M.² Veraverbeke, S.³ Johnstone, J.F.^{4,5} Baltzer, J.L.⁶ Barrett, K.⁷ Bourgeau-
4 Chavez, L.⁸ Day, N. J.^{6,9} de Groot. W.J.¹⁰ Dieleman, C.M.¹¹ Goetz, S.¹² Hoy, E.¹³ Jenkins, L.K.^{8,14} Kane,
5 E.S.¹⁵ Parisien, M.-A.¹⁶ Potter, S.² Schuur, E.A.G.¹ Turetsky, M.^{11,17} Whitman, E.¹⁶ Mack, M.C.¹.

6 ¹ Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona, USA

7 ² Woods Hole Research Center, Falmouth, Massachusetts, USA

8 ³ Faculty of Science, Earth and Climate, Vrije Universiteit Amsterdam, Amsterdam, Netherlands

9 ⁴ Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

10 ⁵ Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska, USA

11 ⁶ Biology Department, Wilfrid Laurier University, Waterloo, Ontario, Canada

12 ⁷ School of Geography, Geology and Environment, University of Leicester, Leicester, United Kingdom

13 ⁸ Michigan Tech Research Institute, Michigan Technological University, Ann Arbor, Michigan, USA

14 ⁹ School of Science, Auckland University of Technology, Auckland, New Zealand

15 ¹⁰ Great Lakes Forestry Center, Canadian Forest Service, Natural Resources Canada, Sault Ste. Marie,
16 Ontario, Canada

17 ¹¹ Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

18 ¹² School of Informatics, Computing and Cyber Systems (SICCS), Northern Arizona University,
19 Flagstaff, Arizona, USA

20 ¹³ NASA Goddard Space Flight Center/Global Science & Technology, Inc., Greenbelt, Maryland, USA

21 ¹⁴ School for Environment and Sustainability, University of Michigan, Ann Arbor, Michigan, USA

22 ¹⁵ College of Forest Resources and Environmental Science, Michigan Technological University,
23 Houghton, Michigan, USA

24 ¹⁶ Northern Forestry Centre, Canadian Forest Service, Natural Resources Canada, Edmonton Alberta,
25 Canada

26 ¹⁷ Institute of Arctic and Alpine Research, Department of Ecology and Evolutionary Biology, University
27 of Colorado Boulder, Boulder, Colorado, USA.

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40 **Summary**

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

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54 **Main Text**

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

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

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

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

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

109 FWIs is small relative to the temporal and coarse-scale spatial variation used in this study (see
110 ‘Sources of variation in FWIs’ section of Supplementary Information and Supplementary Table
111 4). Our use of coarse resolution climate data is consistent with prior work modeling fire activity
112 and C emissions throughout the boreal forest⁹⁻¹¹. Although there are uncertainties with our
113 measurements of pre-fire conditions, modeled estimates of C pools and C combustion, and
114 interpolated FWI System components, the methods used to obtain these variables were
115 comparable between ecoregions.

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

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

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

143 The SEM for all sites combined aligned with our original hypothesized model (Fischer's
144 $C_{18}=28.40$, $p=0.06$, Figure 3b) and explained 43% of the variation in C combustion (marginal
145 $R^2=0.43$, conditional $R^2=0.72$). Note that for the Fischer's C-statistic the subscript numbers
146 represent the degrees of freedom, and a $p\text{-value}>0.05$ indicates that the model represents the data
147 well and that there are no missing paths based on Shipley's test of d-separation (see Methods).
148 Correlations between exogenous variables were either weak or non-significant (Table 2). Model
149 fit and explained variance for sites in Alaska ($C_{22}=23.75$, $p=0.36$, Figure 3c), Taiga Plains
150 ($C_{16}=18.45$, $p=0.30$, Figure 3d), Taiga Shield ($C_{18}=18.41$, $p=0.43$, Figure 3e), and Saskatchewan
151 ($C_{24}=33.12$, $p=0.10$, Figure 3f) were generally better than the SEM fit on all sites and showed
152 some ecoregion specificity in important drivers and feedbacks.

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

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

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

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

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

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

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

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

237 Fire regimes are largely controlled by a combination of fuel availability, climate, and
238 ignition sources over broad temporal and spatial gradients. However, boreal wildfire occurrence,
239 spread, and C combustion are often modeled based on fire weather conditions^{6,9,26}. Similar to
240 studies conducted in different forest types in the western United States²⁹⁻³¹, we found that C
241 combustion per unit area was strongly influenced by topography and fuel availability. Models of
242 C combustion from boreal wildfires that rely on top-down controls without considering the
243 importance of bottom-up drivers will likely inaccurately estimate combustion and fail to capture
244 important complexities associated with the spatial and temporal variation of emissions. In
245 predicting future fire occurrence and C combustion, it is therefore important to consider how
246 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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271 **Author Contributions:**

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

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278 **Author Information:**

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280 Correspondence and requests for materials should be addressed to xanthe.walker@gmail.com

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282 **Competing interests:**

283 The authors declare no competing interests.

284 **References (Main Text)**

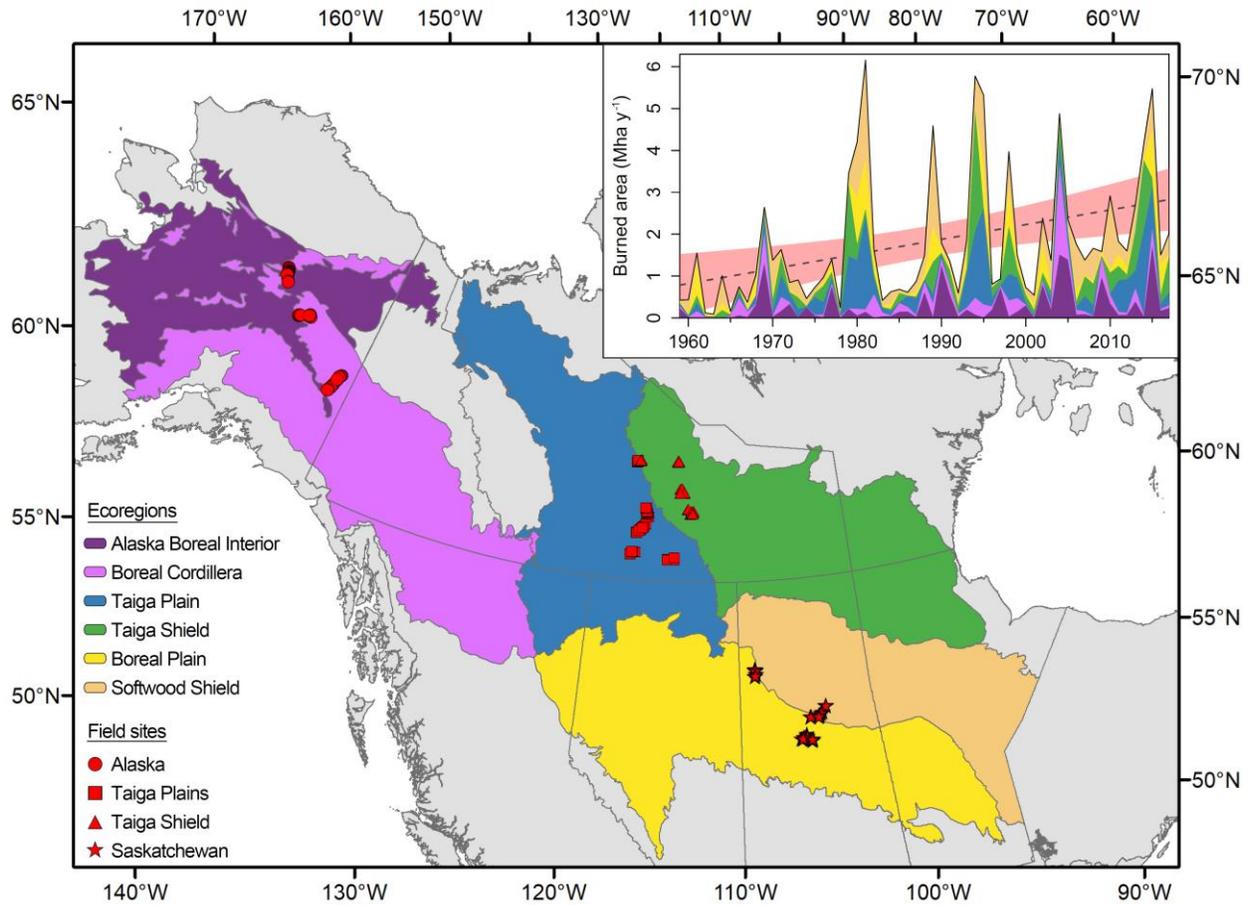
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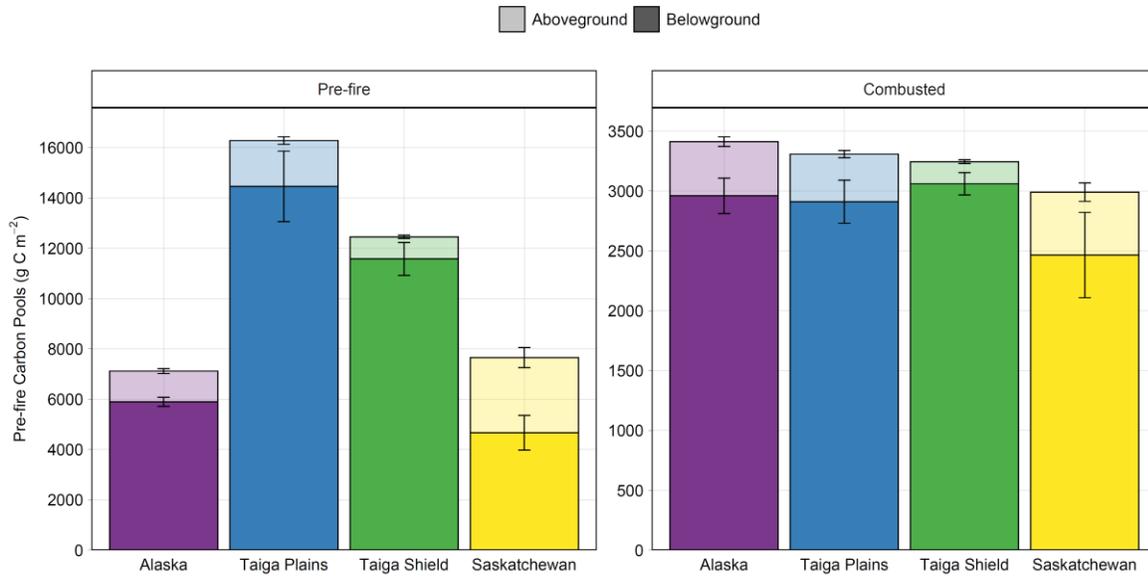
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361 **Figure 1. Map of studied ecoregions and field sites with inset showing total area burned**
 362 **(millions of hectares; Mha) for each ecoregion over time.** Grey dotted line in the inset
 363 represents the simple linear regression, with red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



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370 **Figure 2. Average above- and belowground pre-fire and combusted carbon (C) pools for each**
 371 **ecoregion group.** Pre-fire C pools in the left panel and C combusted in the right panel are divided
 372 into aboveground (top bars in lighter colors) and belowground (bottom bars in darker colors)
 373 components for each ecoregion group. Note differences in the y-axis scale between panels. Error bars
 374 represent standard error of the mean, but do not account for random effects. See Supplementary Table
 375 7 for model fits. There were no significant differences between ecoregion groups in above- or
 376 belowground C pools in the pre-fire stand or combusted based on linear mixed effects models with
 377 random effects of projects and individual fires nested within projects (Supplementary Table 6).

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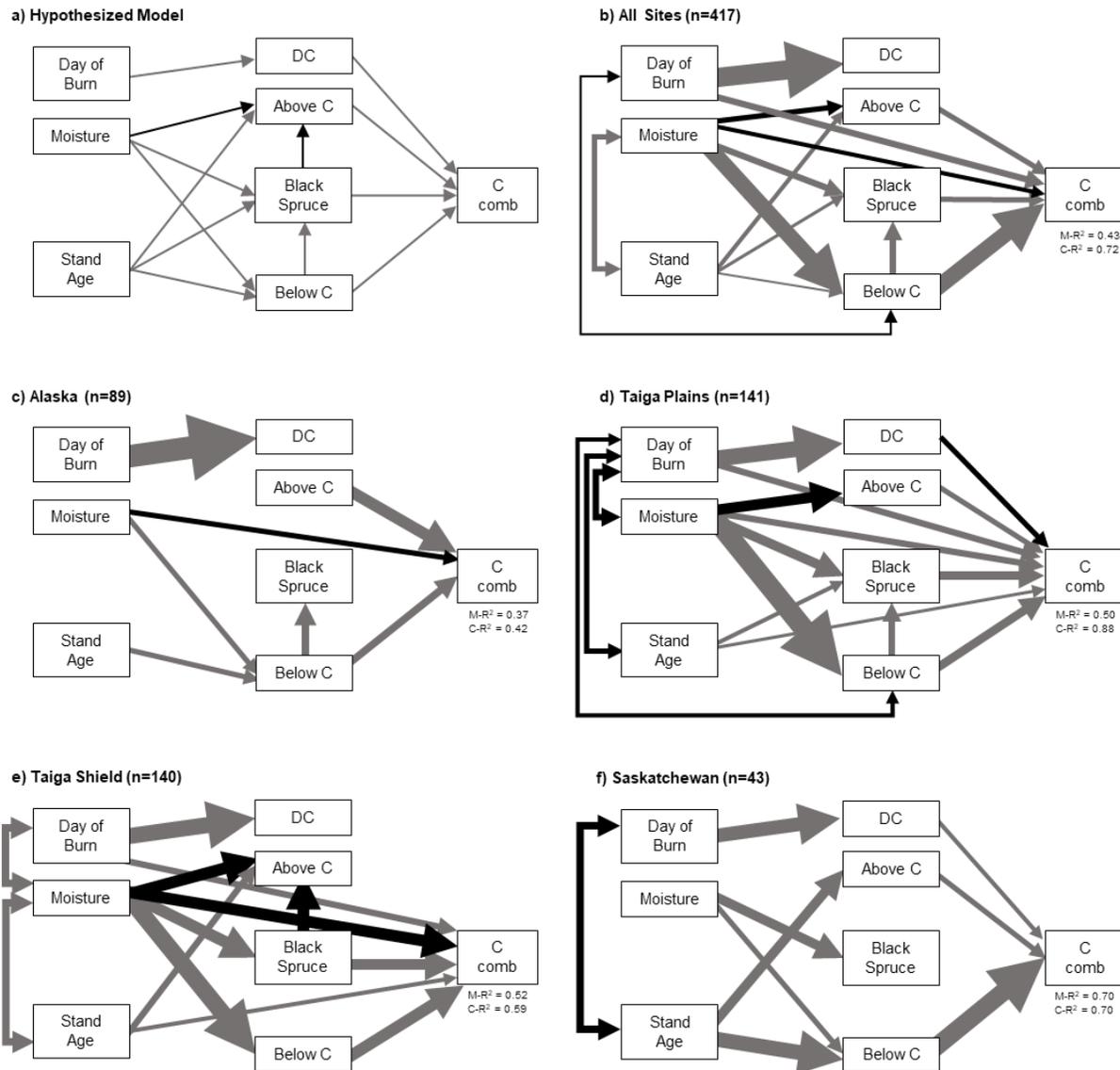
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390 **Table 1. Results of variance partitioning for total C combustion (g C m⁻²) in relation to top-**
 391 **down and bottom-up variables for all sites combined, Alaska, Taiga Plains, Taiga Shield, and**
 392 **Saskatchewan.** Values represent adjusted R² values for the unique variation explained by top-down
 393 and bottom-up variables and the shared variance between these groups. Note that the significance of
 394 shared variation cannot be tested and that a negative shared variation occurs when there is no
 395 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

396 * p-value <0.05



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398 **Figure 3. Structural equation modeling results testing a hypothesized network of top-down and**
 399 **bottom-up controls on C combustion.** Structural equation models hypothesized (a) and fitted for all
 400 sites combined (b), Alaska (c), Taiga Plains (d), Taiga Shield (e), and Saskatchewan (f). Grey lines
 401 represent positive effects and black lines represent negative effects. Single-headed arrows represent
 402 direction of causal relationships. Double-headed arrows represent non-causal relationships or
 403 correlations between exogenous variables. Only significant ($p < 0.05$) lines are shown and they are
 404 scaled to the effect size. See Table 2 for effect sizes. Marginal R^2 (M-R²) represents the variation
 405 explained by the fixed effects only and conditional R^2 (C-R²) is a measure of the variation explained
 406 by both the fixed and random effects. Day of Burn = calendar day of burn; Moisture = moisture class
 407 on a six-point scale ranging from xeric (1) to subhygric (6); Stand Age = age of stand at time of fire
 408 (years); DC = Drought Code; Above C = aboveground C combusted (g C m^{-2}); Black Spruce =
 409 proportion of black spruce in a stand based on density (0-1); Below C = belowground C combusted (g
 410 C m^{-2}); C comb = C combusted (g C m^{-2}).

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

	All sites	Alaska	Taiga Plains	Taiga Shield	Sask- atchewan
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

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422 **Methods**

423 *Study areas and data acquisition*

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

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

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

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

476 *Statistical analyses*

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

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

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

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

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

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

528 *Data availability*

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

531 *Code availability*

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

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