

1 **Landscape variation in tree regeneration and snag fall drive fuel loads in 25-yr old post-fire**  
2 **lodgepole pine forests**

3 **Running head: Drivers of post-fire fuel loads**

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15  
16 ECOLOGICAL APPLICATIONS (In press)

17

18 **ABSTRACT**

19 Escalating wildfire in subalpine forests with stand-replacing fire regimes is increasing the extent  
20 of early-seral forests throughout the western US. Post-fire succession generates the fuel for  
21 future fires, but little is known about fuel loads and their variability in young post-fire stands. We  
22 sampled fuel profiles in 24-year-old post-fire lodgepole pine (*Pinus contorta* var. *latifolia*) stands  
23 ( $n=82$ ) that regenerated from the 1988 Yellowstone Fires to answer three questions. (1) How do  
24 canopy and surface fuel loads vary within and among young lodgepole pine stands? (2) How do  
25 canopy and surface fuels vary with pre- and post-fire lodgepole pine stand structure and  
26 environmental conditions? (3) How have surface fuels changed between 8 and 24 years post-  
27 fire? Fuel complexes varied tremendously across the landscape despite having regenerated from  
28 the same fires. Available canopy fuel loads and canopy bulk density averaged  $8.5 \text{ Mg ha}^{-1}$  [range  
29  $0.0\text{-}46.6$ ] and  $0.24 \text{ kg m}^3$  [range:  $0.0\text{-}2.3$ ], respectively, meeting or exceeding levels in mature  
30 lodgepole pine forests. Total surface-fuel loads averaged  $123 \text{ Mg ha}^{-1}$  [range:  $43 - 207$ ], and 88%  
31 was in the 1000-hr fuel class. Litter, 1-hr, and 10-hr surface fuel loads were lower than reported  
32 for mature lodgepole pine forests, and 1000-hr fuel loads were similar or greater. Among-plot  
33 variation was greater in canopy fuels than surface fuels, and within-plot variation was greater  
34 than among-plot variation for nearly all fuels. Post-fire lodgepole pine density was the strongest  
35 positive predictor of canopy and fine surface fuel loads. Pre-fire successional stage was the best  
36 predictor of 100-hr and 1000-hr fuel loads in the post-fire stands and strongly influenced the size  
37 and proportion of sound logs (greater when late successional stands had burned) and rotten logs  
38 (greater when early successional stands had burned). Our data suggest that 76% of the young  
39 post-fire lodgepole pine forests have 1000-hr fuel loads that exceed levels associated with high-  
40 severity surface fire potential, and 63% exceed levels associated with active crown fire potential.

41 Fire rotations in Yellowstone National Park are predicted to shorten to a few decades and this  
42 prediction cannot be ruled out by a lack of fuels to carry repeated fires.

43

44 Keywords: succession, lodgepole pine, young forests, fire regimes, fuel dynamics, fuels, reburn,  
45 self-regulation

46

## 47 **INTRODUCTION**

48 Observed and projected increases in wildland fire extent and frequency have raised  
49 concern among scientists and forest managers regarding the consequences of escalating wildland  
50 fire activity (Flannigan et al. 2000, Scholze et al. 2006, Westerling et al. 2006, 2011, Krawchuk  
51 et al. 2009, Moritz et al. 2012, Stephens et al. 2013, Parks et al. 2015). Extreme fire seasons have  
52 become more common over the last three decades and have had major social and ecological  
53 consequences including loss of human life and infrastructure, escalating costs of fire prevention  
54 and suppression, changes in ecosystem services (e.g., water, timber, carbon storage, and  
55 recreation resources), and increasing extents of young forests (Schoennagel et al. 2006, Stephens  
56 et al. 2013). In subalpine forests across western North America, large fires historically burned  
57 during rare periods of extreme weather (Romme 1982, Lotan et al. 1985, Bessie and Johnson  
58 1995, Schoennagel et al. 2004). Projections of more frequent severe fire weather over a longer  
59 fire seasons suggest that a new wildland fire issue may emerge—the potential for extensive  
60 reburning of young forests (Schoennagel et al. 2006, Parks et al. 2015, 2016, Harvey et al. 2016).  
61 If realized, forest managers and scientists will be challenged to anticipate successional dynamics  
62 that ultimately generate the fuels for future fires. In this study, we evaluated patterns of fuel  
63 accumulation and abundance in young, post-fire lodgepole pine (*Pinus contorta* var. *latifolia*)

64 stands originating from the 1988 Yellowstone Fires to understand variation in fuel loads in  
65 young, post-fire forests.

66 Observations of natural fires in Yellowstone during the 1970s and 1980s suggested that  
67 young ( $\leq 40$  yrs) post-fire lodgepole pine were unlikely to burn because combustion from the  
68 first fire had reduced fuel loadings (Renkin and Despain 1992). The spread of fires that burned  
69 early during the 1988 fire season fit that expectation, slowing when patches of young forest were  
70 encountered (M. G. Turner and W. H. Romme, personal observations). However, fires that  
71 burned later in the 1988 fire season under extreme weather conditions burned readily through  
72 young lodgepole pine forests at seven (1981 Pelican Creek Fire) and 13 (1975 Arrow Fire) years  
73 post-fire. Recent fires in the Greater Yellowstone Ecosystem have reburned lodgepole pine  
74 stands at 12 (2000 Boundary fire), 24 (2012 Cygnet Fire) and 28 (2009 Bearpaw Fire) years  
75 post-fire. Parks et al. (2015) rigorously tested the ability of young forests to act as fire breaks and  
76 found that the likelihood of re-burning was reduced for 14 to 18 years in four northern Rocky  
77 Mountain forest landscapes. Harvey et al. (2016) also conducted rigorous sampling and analysis  
78 in northern Rocky Mountain forest landscapes, and found that burn severity was reduced for 10  
79 to 12 years in subalpine forests, but a second fire after that time was likely to be high severity.  
80 Both studies found that extreme burning conditions could negate any reduced likelihood of fire  
81 or burn severity in young forests.

82 Fuel dynamics following fire thus govern the likelihood that young stands will again burn  
83 (Parks et al. 2015, Harvey et al. 2016), but comprehensive measurements of post-fire fuel loads  
84 and variability in young stands are lacking. Previous fuel succession studies indicate that post-  
85 fire fuel loads capable of supporting fire vary by forest type. Western hemlock/Douglas-fir  
86 forests in Washington, USA (*Tsuga heterophylla/Pseudotsuga menziesii*; Agee and Huff 1987)

87 and subalpine fir forests in Montana, USA (*Abies lasiocarpa*; Fahnestock 1976) show high, post-  
88 fire fuel loads and potential for short-interval fire; however, lodgepole pine forests in Wyoming,  
89 USA (Romme 1982, Tinker and Knight 2000) and Scots pine/Norway spruce/Birch forests in  
90 northern Sweden (*Pinus sylvestris/Picea abies/Betula spp.*; Schimmel and Granström 1997)  
91 appeared to require extended periods of biomass accumulation to support subsequent fire. The  
92 objective of this study was to quantify fuel loads and variability at the landscape scale following  
93 a large, severe wildfire. The 1988 Fires in Yellowstone National Park provide an ideal  
94 opportunity for such a study because the post-fire forest landscape has received minimal human  
95 intervention and the consequences of the fires have been studied extensively (e.g., Turner et al.  
96 2003, Turner 2010, Romme et al. 2011).

97         After nearly 25 years of succession following high-severity fire, young lodgepole pine  
98 stands in Yellowstone National Park vary widely in structure and function (Turner et al. 2016),  
99 and have developed complex and varied fuel profiles. We sampled fuels across the forests  
100 regenerating from the 1988 fires to answer three questions: (1) How do canopy and surface fuel  
101 loads vary within and among young lodgepole pine stands across the burned landscape? (2) How  
102 do canopy and surface fuels vary with pre- and post-fire lodgepole pine stand structure and  
103 environmental conditions? (3) How have surface fuels changed between 8 and 24 years after the  
104 1988 Yellowstone Fires?

## 105 **STUDY AREA**

106         The subalpine plateau of Yellowstone National Park is a mostly roadless landscape  
107 dominated by lodgepole pine but also contains Engelmann spruce (*Picea engelmannii*), subalpine  
108 fir, and whitebark pine (*Pinus albicalus*) in lower numbers. Most of the park ranges between  
109 2100 and 2700 m in elevation. Soils include dry, infertile, rhyolitic substrates as well as more

110 mesic and slightly less infertile andesitic and former lake-bottom substrates (Turner et al. 2004).  
111 The hydrologic regime is dominated by winter snowfall which generally persists from late-  
112 October to late-May at 2100 m elevation (Despain 1990). Between 1981 and 2010 at Old  
113 Faithful, mean annual temperature was 1.2°C ranging from an average low of -17.6°C in January  
114 to an average high of 23.8°C in July (<http://www.wrcc.dri.edu/>). Mean annual precipitation  
115 ranges from 366 to 642 mm depending on geographic location and elevation  
116 (<http://www.wrcc.dri.edu/>).

117 Wildland fires within Yellowstone National Park generally ignite from lightning  
118 associated with convective summer storms and the 1988 Fires did so during the warmest, driest  
119 summer on record (Renkin and Despain 1992). These fires produced an extremely heterogeneous  
120 mosaic of burn severities across ~600,000 ha within the Greater Yellowstone Ecosystem  
121 (Christensen et al. 1989). Of the ~321,000 ha that burned inside the park, ~56% burned as stand-  
122 replacing fire, with 25% classified as severe-surface burn and 31% as high-severity crown fire  
123 (Turner et al. 1994). Post-fire lodgepole pine regeneration was rapid, abundant, and remarkably  
124 variable across the burned landscape, with post-fire tree densities ranging from zero to > 500,000  
125 stems ha<sup>-1</sup> (Turner et al. 1997, 1999, 2004; Turner 2010). Large stand-replacing fires historically  
126 occurred at a 100 to 300 year interval (Romme 1982, Millspaugh and Whitlock 1995), but  
127 scientists and managers alike found the 1988 fires to be surprising and noteworthy in fire extent,  
128 severity, and rate of forest recovery (Romme et al. 2011). Extreme fire weather in the study area  
129 is projected to become more frequent and longer in duration over the next century leading to a  
130 reduction in fire rotation from > 100 to < 30 years (Westerling et al. 2011).

## 131 **METHODS**

132           During the summer of 2012, we measured canopy, surface, and herbaceous fuels in 24-  
133 year-old post-fire forests across Yellowstone National Park. Ten plots were originally established  
134 in 1996 (Tinker and Knight 2000) and 72 plots were established in 1999/2000 (Turner et al.  
135 2004). Plots encompassed a wide range of post-fire stem density, two 1988 stand-replacing fire-  
136 severity categories (i.e., crown and high-severity surface fire), and four substrate categories:  
137 rhyolite – till, rhyolite – glacial, rhyolite – low base saturation, and andesite includes lake bottom  
138 sediments. Surface fuels had previously been measured in 1996 in 10 plots (Tinker and Knight  
139 2000) but no fuel measurements were collected in the Turner et al. (2004) plots in 1999/2000.  
140 All 82 plots were used to evaluate our first two questions, and the 10 plots sampled in 1996 were  
141 re-measured to address our third question. Sampling locations were separated by at least 1 km  
142 and spatial independence was confirmed using the Moran’s I test ( $P=0.192$ ). To our knowledge,  
143 this study includes one of only a few expansive fuels dataset collected within a single wildfire  
144 footprint.

### 145 ***Field measurements***

#### 146 *2012 Canopy, surface, and understory vegetation fuels*

147           We measured canopy, surface, and understory vegetation fuels at all 82 sites using a 0.25  
148 ha (50 x 50 m) fixed-area plot. Plots were oriented northward with a southerly baseline that ran  
149 east-west (see Turner et al. 2004). Twelve 20 m planar intercept fuels transects were oriented  
150 within each plot (Brown 1974, Brown et al. 1982). One-hr (<0.64 cm diameter) and 10-hr fuels  
151 (0.64–2.54 cm diameter) were tallied along the first 3 m of each transect, 100-hr fuels (2.54–7.62  
152 cm diameter) were tallied along the first 10 m, and 1000-hr fuels (>7.62 cm diameter) were  
153 measured along the full 20 m. Litter depth (cm) was measured at 3 locations spaced at 2- m

154 intervals at the beginning of each transect. Litter is defined as lightly decomposed recognizable  
155 organic matter and duff is defined as decomposed, unrecognizable organic matter. Duff was  
156 absent in all plots, which contrasts with boreal forests but is typical in young lodgepole pine  
157 forests.

158         We assessed canopy fuel profiles from estimates of stem density and size in each plot  
159 (Turner et al. 2016). Briefly, all trees were tallied by species inside three 2 m x 50 m belt  
160 transects that ran through the center and along the east and west boundaries of the plot. On a  
161 sample of lodgepole pine trees (n=25) in each plot, we measured basal diameter (0.1-cm  
162 resolution), diameter at breast height (dbh=1.37 m, 0.1 cm), tree height (0.1 m), crown base  
163 height (0.1 m), and crown width (0.1 m). Understory vegetation cover was estimated visually by  
164 species within twenty-five 0.25 m<sup>2</sup> quadrats and converted to biomass using allometric equations  
165 developed in Yellowstone for these species (Turner et al. 2004, 2016, Simard et al. 2011).

166         We also measured litter bulk density (kg m<sup>-3</sup>) in 14 plots that spanned a representative  
167 range of post-fire seedling densities. Twelve subsamples of litter were collected using a 0.30 x  
168 0.30 m quadrat and litter depth was recorded at the center of the quadrat. Litter was dried at 60°C  
169 for 24 hrs or until a constant mass was reached and weighed on an analytical balance to a  
170 hundredth of a gram. Care was taken to remove woody particles and mineral soil from each  
171 sample.

### 172 *1996 surface fuels*

173         In 1996, surface fuels were measured in 10 post-fire plots (Tinker and Knight 2000). At  
174 each plot, twenty-five 15.2 m transects were oriented at random azimuths on the east and west  
175 plot boundaries. Surface fuel loads were assessed along each transect using the planar intercept  
176 method (Brown 1974, Brown et al. 1982). One-hr (<0.64 cm diameter) and 10-hr fuels (0.64–

177 2.54 cm diameter) were tallied along the first 1.83 m of each transect, 100-hr fuels (2.54–7.62  
178 cm diameter) were tallied along the first 3.66 m, and 1000-hr fuels (>7.62 cm diameter) were  
179 measured along the full 15.2 m. Litter depth (cm) was measured along each transect at three  
180 locations (0.67 m apart). Duff was absent in all plots.

### 181 *Data processing*

182         Surface fuel loads were computed for each plot by summing intercept counts and transect  
183 lengths by size class, applying standard planar-intercept methods (Brown 1974, Brown et al.  
184 1982, Harmon et al. 1986), then scaling to the hectare. 1000-hr fuel loads were summarized and  
185 grouped into two classes—sound and rotten—depending on their decay status (Maser et al.  
186 1979). Sound logs include those with a sound bole regardless of branch, bark, and twig condition  
187 (i.e., decay classes 1 & 2). Rotten logs include those with a bole that breaks apart (i.e., decay  
188 classes 3, 4, & 5). Percent cover by species was converted to understory vegetation biomass  
189 using published relationships between percent cover and dry biomass (Turner et al. 2004, Simard  
190 et al. 2011). Mean litter bulk density ( $\text{kg m}^3$ ) was computed using a subsample of plots ( $n=14$ )  
191 and litter loads were computed for each plot by multiplying litter depth (m) by litter bulk density.  
192 Canopy fuel loads were calculated by applying custom lodgepole pine allometric equations  
193 (Copenhaver and Tinker 2014) to the randomly subsampled trees, taking their plot-wise mean,  
194 then scaling to the hectare with tree density. Foliage, 1-hr branch wood, and available canopy  
195 fuel loads are reported. Available canopy fuel load is defined as the proportion of canopy fuels  
196 available for pyrolysis and is computed as 100% of foliage plus 50% of 1-hr branch wood  
197 (Reinhardt et al. 2006). We define “crown” as pertaining to an individual tree and “canopy” as  
198 the sum of all individual trees within a stand (Cruz et al. 2003). Crown bulk density was  
199 computed using equation [1].

$$\text{Available crown bulk density (kg m}^{-3}\text{)} = \frac{\text{foliage(kg)} + 0.5(1 \text{ hr branchwood(kg)})}{\pi \left( \frac{\text{crown width(m)}}{2} \right)^2 * (\text{tree height(m)} - \text{crown base height(m)})} \quad [1]$$

200 Canopy bulk density was computed using the *biomass-percentile method* (Reinhardt et al. 2006).  
 201 Canopy length was determined by summing biomass through the canopy and reporting the  
 202 distance between the 10<sup>th</sup> and 90<sup>th</sup> percentile of biomass. Vertical fuel profiles were created for  
 203 each plot by splitting available canopy fuel load into 0.1 m vertical layers then dividing by the  
 204 volume of each layer (plot area x layer depth) (Sando and Wick 1972, Reinhardt et al. 2006). For  
 205 plotting purposes, a 1 m running mean was used to smooth the fuel profile and reduce extreme  
 206 values. Within-plot coefficient of variation (CV) was computed for each plot by computing fuel  
 207 loads for each measurement unit (i.e., transects (n=12 plot<sup>-1</sup>) and trees (n=25 plot<sup>-1</sup>)) and  
 208 aggregating these estimates into plot-level means, standard deviations, and CVs. Among-plot  
 209 (i.e., landscape-wide) CVs were also computed for each fuel category using among-plot means  
 210 and standard deviations (n=82).

### 211 ***Statistical analyses***

212 To examine fuel loads and their variability, we report means and standard errors of plot-  
 213 level fuel loads (Table 1), and within-plot and among-plot coefficient of variation (Table 2) for  
 214 three tree density classes and the total population. Differences among density classes were  
 215 determined using one-way ANOVA and Tukey's HSD at  $\alpha=0.05$ . Landscape-wide CVs pertain  
 216 to the whole study area and lack error estimates. We also calculated the proportion of the 82  
 217 plots that met or exceeded fuel loads associated with the potential for high-severity surface fire  
 218 (1000-hr fuel loads greater than 60 Mg ha<sup>-1</sup>; Sikkink and Keane 2012) and active or independent  
 219 crown-fire spread (crown bulk density greater than 0.12 kg m<sup>-3</sup>; Reinhardt et al. 2006).

220 To assess how fuel loads varied with pre- and post-fire stand structure and topo-climatic  
221 factors, we fit linear multiple regression models to predict fuel loads. Candidate predictor  
222 variables were selected based on the hypothesized ecological relationships and paired to each  
223 response variable (Table S1). Models were selected using the “best subsets” model selection  
224 routine to optimize the coefficient of determination ( $R^2$ ) while maintaining  $\alpha=0.05$  (Lumley and  
225 Miller 2009). Model residuals, fits, and transformation criteria were checked using methods  
226 recommended by Venables and Ripley (2002) and the presence of multicollinearity was  
227 evaluated using variance inflation factors. After model construction, the importance of individual  
228 predictor variables was evaluated by computing the proportion of  $R^2$  that each predictor variable  
229 contributes using the *lmg* metric in the relaimpo R package (Grömping 2006). *lmg* "quantifies the  
230 relative contributions of the regressors to the model's total explanatory value...by averaging  
231 sequential sums of squares over orderings of regressors" (Grömping 2006, 2007). Significant  
232 differences in *lmg* between predictor variables were tested by generating bootstrapped  
233 confidence intervals (999 iterations).

234 Empirical response variables and transformations include: litter ( $\log_{10}$ ), 1-hr ( $\log_{10}$ ), 10-  
235 hr, 100-hr ( $\log_{10}$ ), 1000-hr rotten ( $\log_{10}$ ), 1000-hr sound ( $\log_{10}$ ), total surface fuel, live herbaceous  
236 biomass, live shrub biomass ( $\log_{10}$ ), available canopy fuel load ( $\log_{10}$ ), mean crown base height  
237 ( $\log_{10}$ ), and canopy bulk density ( $\log_{10}$ ). Empirical predictor variables and transformations  
238 include: live stem density ( $\log_{10}$ ), live foliage, herbaceous, shrub biomass, live tree density, live  
239 basal area, canopy base height, and 1000-hr fuel load. Geospatial predictor variables were  
240 extracted from the following datasets using plot coordinates: pre-fire successional stage (Despain  
241 1990, NPS-YELL 1990), substrate (NPS-YELL 1997), mean annual precipitation and  
242 temperature (PRISM Climate Group 2012), and burn severity (dNBR; USDA Forest Service-

243 RSAC 2012). The following geomorphometric predictor variables were computed using a digital  
244 elevation model (Gesch 2007) and extracted using plot coordinates: derived slope and aspect  
245 (Gesch 2007), compound topographic index (i.e., wetness) (Evans et al. 2014), and potential  
246 solar radiation (Pierce et al. 2005). Aspect was transformed to a continuous distribution using  
247 Beers et al. (1966). Categorical dummy variables—pre-fire successional stage and substrate—  
248 were defined in our models using deviance (effects) contrasts to compare individual levels with  
249 the mean of all levels. Pre-fire successional stage reflects lodgepole pine successional stages  
250 identified by Despain (1990). LP0 represents post-fire stands where lodgepole pine has  
251 recolonized the site but has not yet produced a closed canopy. LP1 consists of a single cohort of  
252 dense, young lodgepole pine without tree seedlings in the understory. LP2 stands have closed  
253 canopies dominated by lodgepole pine with tree seedlings in the understory. LP3 and LP4 are  
254 multi-cohort stands with ragged canopy characteristics dominated by lodgepole pine. LP3  
255 contains Engelmann spruce and subalpine fir in the sub-canopy whereas LP4 stands occur on dry  
256 sites that do not support Engelmann spruce and subalpine fir.

257 Total crown area was modeled using linear regression between summed tree crown area  
258 and stand density. Changes in fuel loads and their variability between 1996 and 2012 were  
259 compared using paired t-tests and the ratio of change was calculated using the ratio of means for  
260 each surface fuel type plus standard error (Scheaffer et al. 2011).

## 261 **RESULTS**

### 262 *Fuel characteristics and variability*

263 Total surface fuel loads varied tremendously across the post-1988 Yellowstone fire  
264 landscape, ranging from 43.3 to 206.7 Mg ha<sup>-1</sup> (Figure 1; Table 1). Thousand-hr fuels averaged  
265 110.0±4.6 Mg ha<sup>-1</sup> and composed 88% of the total fuel—by far the greatest proportion. Sound

266 logs accounted for nearly 70% while rotten logs accounted for 30% of 1000-hr biomass but the  
267 distribution of biomass also varied with log size (Figure 2). 75.9% of stands had 1000-hr fuel  
268 loads greater than 65 Mg ha<sup>-1</sup>—a threshold specified by Sikkink and Keane (2012) for high-  
269 severity surface fire. Litter accounted for the greatest share of fine surface fuels—more than 1-hr  
270 surface fuels, herbaceous fuels, shrub fuels, and 10-hr fuels combined. Mean litter bulk density  
271 was 50.2±6.1 kg m<sup>-3</sup>, mean litter depth was 1.1±0.1 cm, and mean litter biomass was 5.61±0.46  
272 Mg ha<sup>-1</sup>. Fuel loads increased with density class for litter, 1-hr, and 100-hr fuel types but  
273 decreased for herbaceous biomass, rotten 1000-hr and total surface fuel loads (Table 1). Litter  
274 and rotten 1000-hr fuel within-plot variation decreased by density class but other fuel classes did  
275 not. Across all density classes, mean within-plot CVs were higher than landscape-wide CVs for  
276 the same fuel type (Table 2). In general, at the within- and among-plot scales, surface fuel  
277 variability was less than canopy fuel variability.

278 Live lodgepole pine densities in 2012 averaged 19,500 stems ha<sup>-1</sup> and ranged from 0 to  
279 344,000 trees ha<sup>-1</sup> (Turner et al. 2016). Available canopy fuels averaged 8.5 Mg ha<sup>-1</sup> and varied  
280 from 0.0 to 48.6 Mg ha<sup>-1</sup> over this wide range of stem density (Figure 1; Table 1). All canopy  
281 fuel characteristics (i.e., foliar biomass, 1-hr biomass, crown base height) increased with stem  
282 density. Within-plot CV for canopy fuels did not differ among density classes but was greater  
283 than the among-plot CV for canopy fuels (Table 2). Canopy bulk density ranged from 0.00 to  
284 2.28, and 63.9% of stands in this study are greater than the 0.12 kg m<sup>-3</sup> threshold for active and  
285 independent crown fire spread (Reinhardt et al. 2006).

### 286 *Effects of pre- and post-fire stand conditions and topo-climatic factors on fuels*

287 Models predicting dead and downed surface fuel loads fell into two general groups: fine  
288 fuels (e.g., litter, 1-hr, and 10-hr fuels) were best predicted by post-fire stand structure and coarse

289 fuels (e.g., 100-hr, 1000-hr) were best predicted by pre-fire forest structure variables (Table 3).  
290 Needle litter fuel load was positively associated with 1000-hr fuel load (both sound and rotten)  
291 and live stand density, but was negatively associated with mean annual precipitation ( $R^2=0.43$ ).  
292 Live stem density showed the greatest importance in predicting litter fuel loads (Table 5). One-hr  
293 fuel load was positively related to crown base height, mean annual precipitation, topographic  
294 wetness index, and slope ( $R^2=0.49$ ) with crown base height having greater importance than the  
295 other variables in our model (Table 5). Variation in lodgepole pine density and annual  
296 temperature were related to 10-hr fuels, but explained little variance ( $R^2=0.08$ ). One hundred-hr  
297 fuels were best predicted by pre-fire successional stage and annual precipitation ( $R^2=0.22$ ).  
298 Sound 1000-hr fuels were positively related to pre-fire successional stage ( $R^2=0.24$ ), whereas  
299 rotten 1000-hr fuels were negatively related to pre-fire successional stage ( $R^2=0.30$ ; Table 3;  
300 Figure 2). Total surface fuel loads were best predicted by pre-fire successional stage, mean  
301 annual temperature, mean annual precipitation, and aspect ( $R^2=0.31$ ). Herbaceous fuel load was  
302 best predicted by soil class and live tree basal area ( $R^2=0.25$ ). Shrub fuels were miniscule but  
303 were positively related to live stand density, elevation, and slope ( $R^2=0.25$ ). Importance values  
304 for predictors were not different from one another in 10-hr, 100-hr, 1000-hr, total fuel load,  
305 herbaceous, and shrub models (Table 5).

306 Live stem density was a strong, positive predictor of available canopy fuel ( $R^2=0.78$ ),  
307 canopy bulk density ( $R^2=0.87$ ), and crown base height ( $R^2=0.66$ ; Table 4), and had the greatest  
308 importance in predicting canopy fuel loads (Table 5). Vertical profiles of canopy bulk density  
309 display a shift in the distribution of canopy fuels with stem density (Figure 3). Low-density  
310 stands have lower canopy bulk density and a uniform vertical distribution whereas high-density

311 stands had high canopy bulk density concentrated at lower heights. Crown area increased with  
312 stand density ( $R^2=0.80$ ) and equaled ground area at  $\sim 12,000$  trees  $\text{ha}^{-1}$  (Figure 4).

### 313 *Change in surface fuel loads with time since fire*

314 Surface down and dead fuel loads in post-1988 wildfire forests generally increased with  
315 time since fire; however, 1-hr fuels did not change between 1996 and 2012 (Table 6). Rotten  
316 1000-hr fuels increased by a factor of four; other fuel classes increased by approximately half  
317 that rate (Table 6). Increasing fuel loads coincided with a sharp decrease in within-plot  
318 variability (Figure 5). 1000-hr fuel loads greater than the  $65 \text{ Mg ha}^{-1}$  threshold for severe surface  
319 fire (Sikkink and Keane 2012) were present in 10% of stands in 1996 and 90% of stands in 2012.

## 320 **DISCUSSION**

321 A quarter-century after the 1988 fires in Yellowstone National Park, substantial fuel  
322 loads cover much of the young forest landscape indicating that extensive and severe reburning  
323 may be possible, especially under severe fire weather conditions. Post-fire stand structure,  
324 especially live lodgepole pine stem density, was the single greatest predictor of canopy and fine  
325 fuel loads, but pre-fire successional stage was the most important predictor of large woody  
326 surface fuels. Stands in this study have passed the 10-to-18 year period where severe reburning  
327 potential is reduced (Parks et al. 2014, 2015, Harvey et al. 2016); however, some stands with low  
328 post-fire regeneration have low fuel loads and may provide some resistance to subsequent fire.

329 A surprising finding was the high variability in fuel conditions across the post-fire  
330 landscape suggesting substantial spatial variability in potential fire behavior and severity. Fine  
331 surface fuel loads in these 24-year old forests were generally less than those reported in mature  
332 lodgepole pine forests, but most stands contained sufficient litter and 1-hr fuels to support rapid  
333 surface fire spread. Coarse fuel loads were similar or higher than values observed in mature

334 lodgepole pine forests after other disturbance types (e.g., bark beetles and blowdown; Veblen  
335 2000, Woodall and Nagel 2007, Kulakowski and Veblen 2007), and stands with abundant coarse  
336 fuels are especially susceptible to prolonged smoldering with high biomass consumption and  
337 heat release (Byram 1959, Rothermel 1972, Scott and Reinhardt 2001, Sikkink and Keane 2012).  
338 Canopy fuel loads, and particularly canopy bulk density, attained or exceeded values reported in  
339 mature lodgepole pine forests, and ubiquitous low canopy base heights indicate that young stands  
340 may be susceptible to crown fire initiation and many stands can support active and independent  
341 crown fire spread. Fuel conditions in most stands suggest that fire may be difficult to control,  
342 particularly in places where fires must be suppressed (e.g., near infrastructure).

343         Surface fuel loads in developing lodgepole pine forests differed from those found in other  
344 young and mature forest types. Litter and 1-hr fuels were about *half* that found in 1, 3, and 19  
345 year old western hemlock/Douglas-fir stands in Washington, USA (Agee and Huff 1987) and 2,  
346 27, and 30 year old subalpine fir stands in Montana, USA (Fahnestock 1976), similar to Swedish  
347 Scots pine/Norway spruce/Birch boreal forests <20 year old (Schimmel and Granström 1997)  
348 and mixed-conifer stands in the Cascade range, USA measured one year after high-severity fire  
349 (Hudec and Peterson 2012), but *greater* than a 48 year old Jack pine (*Pinus banksiana*) stand that  
350 originated from fire in Ontario, Canada (Stocks 1987). The complete absence of duff in our study  
351 also differs from these studies but reflects results from other studies that documented little duff  
352 accumulation in lodgepole pine stands across Yellowstone National Park (Romme 1982, Litton  
353 et al. 2004, Kashian et al. 2013). Previous studies in mature, Rocky Mountain lodgepole pine  
354 forests report similar litter, 2-4 times *higher* 1-hr fuel loads, similar 10-hr fuel loads, and 10-20  
355 times *lower* 100-hr and 1000-hr fuel loads than were found in this study (Lawson 1973,  
356 Alexander 1979, Lotan et al. 1985, Battaglia et al. 2010). Studies in mature, Rocky Mountain

357 ponderosa pine (*Pinus ponderosa*) forests documented similar litter loads, 2 times *higher* 1-hr  
358 fuel loads, 2-10 times *higher* 10-hr fuel loads, and similar but low 100-hr and 1000-hr fuel loads  
359 than were observed in these post-1988 lodgepole pine forests (Mason et al. 2007, Klutsch et al.  
360 2009, Battaglia et al. 2010). Studies in mixed conifer forests (i.e., *Pinus spp.* /*Abies*  
361 *spp.*/*Calocedrus spp.*/*Quercus spp.*) in the Sierra and Cascade Mtn ranges observed 1-10 times  
362 *greater* litter and 1-hr fuel loads, 1-5 time *higher* 10-hr fuel loads, and 100-hr and 1000-hr fuel  
363 loads similar to loads observed this study (Schmidt et al. 2008, Van de Water and North 2011,  
364 Pierce et al. 2012, Hudec and Peterson 2012, Banwell and Varner 2014, Lydersen et al. 2015).

365         Our hypothesis that the legacy of pre-fire forest structure would greatly influence 100-hr  
366 and 1000-hr fuel loads and the proportion of rotten and sound logs was supported by the  
367 distribution of log sizes stratified by successional stage (Figure 2) but only weakly supported by  
368 our regression models (Table 3). Pre-1988 successional stages, as implemented in this study,  
369 were derived from a geospatial cover type map produced via aerial photo classification and field  
370 verification (Despain 1990, NPS-YELL 1990). We expect that regression results involving pre-  
371 fire successional stage could be improved if more detailed pre-fire stand structure measurements  
372 had been available. Still, our findings highlight the influence of pre-fire successional stage on  
373 coarse fuel loads and indicate that all old coniferous forests, or forests that otherwise had large  
374 trees at the time of the fire, will likely have more coarse wood after fire, as has been  
375 demonstrated after short-interval fire in the Pacific Northwest (Donato et al. 2016). Subsequent  
376 fires that burn in stands that had large tress prior to the first fire will likely have greater biomass  
377 consumption, flame residence time, heat release, and smolder for longer than will forests of  
378 small trees or sparse trees prior to the initial fire.

379 Lodgepole pine forests are unique in being able to develop an enormous canopy seedbank  
380 that facilitates abundant seedling establishment after fire (Clements 1910, Lotan et al. 1985).  
381 Twenty-four years' post-fire, canopy fuel loads attained or exceeded values reported in other  
382 young and mature forest types. On average, canopy fuel loads in these stands were ~5 times  
383 *higher* than values observed in 19 year old western hemlock/Douglas-fir forests in Washington,  
384 USA (Agee and Huff 1987) but similar to subalpine fir stands 27 and 30 years post-fire in  
385 Montana, USA (Fahnestock 1976). Approximately 45% of stands in this study have available  
386 canopy fuel loads *greater* than 10 Mg ha<sup>-1</sup> and the highest available canopy fuel load (48 Mg ha<sup>-1</sup>)  
387 <sup>1</sup>) in our study is *greater* than the maximum value found in mature lodgepole pine forests (Cruz  
388 et al. 2003, Reinhardt et al. 2006, Simard et al. 2011). Canopy bulk density was ~2-5 times  
389 *greater* than values found in mature lodgepole pine, ponderosa pine, and mixed conifer stands in  
390 Colorado, Idaho, and Montana, USA (Cruz et al. 2003, Fulé et al. 2004, Reinhardt et al. 2006,  
391 Simard et al. 2011, Roccaforte et al. 2015) but similar to untreated ponderosa pine and mixed  
392 conifer stands affected by fire suppression in Arizona, USA (Cruz et al. 2003, Hall and Burke  
393 2006, Reinhardt et al. 2006, Mason et al. 2007). Results from this study highlight the link  
394 between post-fire tree regeneration and the development of canopy and fine surface fuels  
395 suggesting that stands with the highest rates of light capture and biomass production also have  
396 the highest canopy and fine surface fuel loads. In forest types lacking such a seedbank, we would  
397 expect slower canopy fuel development and reduced crown fire potential after a quarter century  
398 of post-fire recovery.

399 Just how much of the landscape is now vulnerable to high-severity re-burning and/or  
400 active crown fire spread? If we assume that sampled stands represent the proportion of a given  
401 fuel characteristic across the burned landscape, then approximately 76% of the post-1988 fire

402 landscape is susceptible to high-severity surface fire and 63% is capable of active or independent  
403 crown fire spread. In a simulation study investigating surface-fire severity using the First Order  
404 Fire Effects Model (FOFEM), Sikkink and Keane (2012) found that dry coarse fuel loads above  
405 the 60 Mg ha<sup>-1</sup> threshold resulted in a mean fire line intensity greater than 120 Kw m<sup>-2</sup>, a mean  
406 fire residence time greater than 2 hours, and soil temperatures greater than 60° C to a > 6 cm  
407 depth. Using the mean intensity reported by Sikkink and Keane (2012), canopy fuels would be  
408 capable of igniting at 0.8 m canopy base height and 100% live foliar moisture content using van  
409 Wagner's (1977) crown fire initiation equation—encompassing approximately 90% of the stands  
410 sampled in this study.

411         Changes in surface fuels between 1996 and 2012 showed that fuel deposition from  
412 growing young trees and falling fire-killed trees were the dominant factors shaping surface  
413 woody fuels during the first 24 years of forest development (Table 6). Though our sample size is  
414 limited, these plots bridged the 10-18 year post-fire period beyond which fire potential and  
415 severity are not reduced by previous fire (Parks et al. 2014, 2015, Collins et al. 2015, Harvey et  
416 al. 2016). In our study, fuel loads increased by 175-430% during this window of time (1-hr fuels  
417 excepted; Table 6) and within-plot variability declined, indicating a transition from patchy to  
418 more spatially continuous fuel beds (Figure 5). Severe surface fire potential increased  
419 dramatically during this period due to snag fall from 10% of stands in 1996 to 90% of stands in  
420 2012. Overall, the rapid increase in surface fuel loads is consistent with Kashian et al.'s (2013)  
421 finding that ~50% of maximum needle and woody litter is recovered in the first 25 years after  
422 fire. Delayed post-fire snag fall likely accounts for increases in 100-hr and 1000-hr fuel loads  
423 since large fuel classes are subject to slow biomass turnover rates and can take ~125 years to

424 decompose completely (Kashian et al. 2013). The lack of change in 1-hr fuels was not surprising  
425 given the high biomass turnover rate for small diameter wood observed by Simard et al (2012).

## 426 **CONCLUSION**

427 For land management agencies to develop informed adaptation and mitigation strategies  
428 to attenuate adverse impacts of increased fire activity to human life, infrastructure, and  
429 ecological services, quantitative data on the variability and dynamics of fuel beds in young  
430 forests will become increasingly important. On lands implementing passive management  
431 strategies such as 'wildland fire use', management personnel should acknowledge that young  
432 forests may have heavy fuel loads—like those in many of the stands in this study—capable of  
433 sustaining stand-replacing fire. On lands under active management, post-fire salvage logging  
434 may be implemented to reduce long-term coarse fuel loads and lessen resistance to control.

435 In conclusion, the tremendous variation in fuel loads across the post-1988 fire landscape  
436 suggest that stand age alone is a poor surrogate for predicting fuel conditions in young lodgepole  
437 pine stands that regenerated naturally from stand-replacing fire. Surprisingly, these stands have  
438 already developed fuel conditions that are likely to sustain reburning. Most of the post-1988 fire  
439 lodgepole pine forests can likely sustain high-severity surface fire and active crown fire,  
440 although we anticipate that fire behavior and effects will vary spatially across the landscape. In  
441 the future, fire rotations in Yellowstone National Park are predicted to be shorter than were  
442 typical historically (Westerling et al. 2011), and this prediction cannot be ruled out by a lack of  
443 fuels to carry repeated fires at intervals of a few decades.

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- 657

660 Table 1: Fuel characteristics in low, moderate, and high density stands. Means are reported with one standard error. Letters indicate row-wise differences (Tukey's HSD,  $\alpha=0.05$ ).

	Density class			
	Low (<1000 stem ha <sup>-1</sup> )	Moderate (1000–50,000 stem ha <sup>-1</sup> )	High (>50,000 stem ha <sup>-1</sup> )	All
Sample size	n = 18	n = 56	n = 9	n = 82
Stand density (trees ha <sup>-1</sup> )	430 (67)	8,771 (1149)	124,474 (36482)	19508 (5645)
Crown				
Mean crown base height (m)	0.14 (0.02) <sup>a</sup>	0.47 (0.03) <sup>b</sup>	0.69 (0.07) <sup>c</sup>	0.42 (0.03)
Crown bulk density (kg m <sup>3</sup> )	0.60 (0.07) <sup>a</sup>	0.75 (0.04) <sup>a</sup>	1.51 (0.17) <sup>b</sup>	0.80 (0.04)
Canopy				
Foliage biomass (Mg ha <sup>-1</sup> )	0.84 (0.18) <sup>a</sup>	8.27 (0.73) <sup>b</sup>	15.12 (3.65) <sup>c</sup>	7.49 (0.76)
1-hr branch biomass (Mg ha <sup>-1</sup> )	0.26 (0.06) <sup>a</sup>	2.43 (0.21) <sup>b</sup>	3.81 (1.09) <sup>b</sup>	2.14 (0.22)
Available canopy fuel load <sup>†</sup> (Mg ha <sup>-1</sup> )	0.97 (0.20) <sup>a</sup>	9.50 (0.84) <sup>b</sup>	16.64 (4.25) <sup>c</sup>	8.53 (0.87)
Total canopy biomass (Mg ha <sup>-1</sup> )	3.52 (0.74) <sup>a</sup>	34.94 (3.11) <sup>b</sup>	63.73 (15.62) <sup>c</sup>	31.63 (3.25)
Canopy length (m)	3.48 (0.34) <sup>a</sup>	3.77 (0.12) <sup>a</sup>	1.77 (0.32) <sup>b</sup>	3.49 (0.13)
Canopy bulk density <sup>§</sup> (kg m <sup>3</sup> )	0.03 (0.00) <sup>a</sup>	0.24 (0.02) <sup>b</sup>	0.66 (0.12) <sup>c</sup>	0.24 (0.03)
Live surface fuels				
Herbaceous (Mg ha <sup>-1</sup> )	1.71 (0.10) <sup>a</sup>	0.98 (0.09) <sup>b</sup>	0.81 (0.15) <sup>b</sup>	1.11 (0.07)
Shrub (Mg ha <sup>-1</sup> )	0.10 (0.03) <sup>a</sup>	0.15 (0.02) <sup>a</sup>	0.13 (0.05) <sup>a</sup>	0.13 (0.02)
Dead surface fuels				
Litter depth (cm)	0.59 (0.16) <sup>a</sup>	1.19 (0.10) <sup>b</sup>	1.73 (0.36) <sup>b</sup>	1.10 (0.09)

Litter (Mg ha <sup>-1</sup> )	2.98 (0.78) <sup>a</sup>	5.96 (0.51) <sup>b</sup>	8.70 (1.80) <sup>b</sup>	5.61 (0.46)
1-hr (Mg ha <sup>-1</sup> )	0.10 (0.01) <sup>a</sup>	0.18 (0.02) <sup>b</sup>	0.29 (0.04) <sup>c</sup>	0.17 (0.01)
10-hr (Mg ha <sup>-1</sup> )	2.02 (0.19) <sup>a</sup>	2.35 (0.11) <sup>a</sup>	2.35 (0.33) <sup>a</sup>	2.28 (0.09)
100-hr (Mg ha <sup>-1</sup> )	4.45 (0.32) <sup>a</sup>	4.95 (0.23) <sup>a</sup>	7.18 (1.13) <sup>b</sup>	5.08 (0.22)
Sound 1000-hr (Mg ha <sup>-1</sup> )	78.48(7.54) <sup>a</sup>	82.52 (5.64) <sup>a</sup>	53.96 (7.83) <sup>a</sup>	78.55 (4.31)
Rotten 1000-hr (Mg ha <sup>-1</sup> )	39.24(4.84) <sup>a</sup>	31.13 (2.68) <sup>a,b</sup>	17.64 (5.33) <sup>b</sup>	31.42 (2.23)
Total surface fuel load (Mg ha <sup>-1</sup> )	127.27 (10.62) <sup>a</sup>	127.09 (5.62) <sup>a</sup>	90.12 (10.33) <sup>b</sup>	123.12(4.70)

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<sup>†</sup> Available canopy fuel load = foliage + 0.5\*(1-hr branch wood)

<sup>§</sup> Computed using the biomass-percentile method (Reinhardt et al. 2006)

665 Table 2: Within- and among-plot variability of fuel loads and fire behavior parameters in low, moderate, and high density stands. Within-plot variability estimates are mean coefficient of variation (CV, in percent) with one standard error. Letters indicate row-wise differences (Tukey's HSD,  $\alpha=0.05$ ). Among-plot coefficient of variation was computed using the population standard deviation and mean and do not include error rates.

Within-plot variation (CV)					
by stem-density class					
	Low (<1000 stems ha <sup>-1</sup> )	Moderate (1000– 50,000 stems ha <sup>-1</sup> )	High (>50,000 stems ha <sup>-1</sup> )	Within all plots	Among- plot variation
Sample size	n = 18	n = 56	n = 9	n = 82	n=82
Crown					
Mean crown base height	113.1 (26.7) <sup>a</sup>	70.8 (3.9) <sup>b</sup>	45.3 (4.8) <sup>b</sup>	76.7 (3.4)	65.5
Available crown bulk density	116.8 (26.9) <sup>a</sup>	103.2 (5.4) <sup>a</sup>	93.9 (7.9) <sup>a</sup>	105.0 (6.6)	112.4
Canopy					
Foliage biomass	123.4 (25.3) <sup>a</sup>	113.8 (3.8) <sup>a</sup>	97.4 (11.6) <sup>a</sup>	114.0 (5.9)	96.3
1-hr branch biomass	128.8 (25.2) <sup>a</sup>	120.6 (4.0) <sup>a</sup>	105.2 (12.6) <sup>a</sup>	120.6 (5.9)	96.1
Available canopy fuel load	124.1 (25.3) <sup>a</sup>	114.7 (3.9) <sup>a</sup>	98.5 (11.8) <sup>a</sup>	114.9 (5.9)	96.2
Total canopy biomass	123.1 (25.3) <sup>a</sup>	113.4 (3.8) <sup>a</sup>	97.0 (11.5) <sup>a</sup>	113.6 (5.9)	96.1
Dead surface fuels					
Litter	131.7 (17.5) <sup>a</sup>	97.2 (5.7) <sup>b</sup>	75.8 (4.8) <sup>b</sup>	101.9 (5.6)	74.4
1-hr	89.5 (7.0) <sup>a</sup>	85.7 (4.3) <sup>a</sup>	65.7 (6.2) <sup>a</sup>	84.3 (3.4)	70.4
10-hr	84.0 (7.4) <sup>a</sup>	74.2 (3.1) <sup>a</sup>	80.2 (10.6) <sup>a</sup>	76.9 (2.9)	36.5

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100-hr	59.1 (3.3) <sup>a</sup>	60.3 (3.5) <sup>a</sup>	68.3 (5.0) <sup>a</sup>	60.9 (2.6)	39.8
Sound 1000-hr	51.0 (3.8) <sup>a</sup>	47.8 (6.0) <sup>a</sup>	52.8 (4.0) <sup>a</sup>	49.0 (1.9)	49.9
Rotten 1000-hr	68.9 (4.1) <sup>a</sup>	67.5 (4.0) <sup>a</sup>	53.0 (8.8) <sup>a</sup>	66.2 (3.1)	64.9
Total surface fuel load	39.5 (2.6) <sup>a</sup>	35.5 (1.5) <sup>a</sup>	34.5 (2.3) <sup>a</sup>	36.2 (1.2)	34.9

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Table 3: Predictive linear models illustrating the effects of post-fire stand structure, topo-

670 climatic factors, and pre-fire successional stage on dead surface fuel loads in 24-year-old

lodgepole pine stands.

<i>Dead surface fuels</i>	df	R <sup>2</sup>	Parameter	β	se	t-value	p-value
Log <sub>10</sub> (Litter fuels) (Mg ha <sup>-1</sup> )	78	0.43	Intercept	0.41	0.57	0.72	0.474
			1000-hr fuel biomass	0.003	0.000	3.11	0.003
			Log <sub>10</sub> (lodgepole pine density)	0.31	0.05	6.31	<0.001
			Mean annual precipitation	-0.002	0.001	-2.70	0.009
Log <sub>10</sub> (1-hr fuels) (Mg ha <sup>-1</sup> )	77	0.49	Intercept	-2.19	0.31	-7.11	<0.001
			Mean crown base height	0.71	0.09	7.75	<0.001
			Mean annual precipitation	0.001	0.000	2.83	0.006
			Topographic wetness index	0.02	0.009	2.15	0.034
			Slope	0.02	0.007	2.08	0.041
10-hr fuels (Mg ha <sup>-1</sup> )	79	0.08	Intercept	0.89	0.55	1.63	0.106
			Log <sub>10</sub> (lodgepole pine density)	0.36	0.14	2.55	0.013
			Mean annual temperature	-0.03	0.01	-1.96	0.053
Log <sub>10</sub> (100-hr fuels) (Mg ha <sup>-1</sup> )	78	0.22	Intercept	0.67	0.02	28.91	<0.001
			Early pre-fire successional stage (LP1)	-0.15	0.06	-2.63	0.012
			Middle pre-fire successional stage (LP2)	0.17	0.04	4.66	<0.001
			Late pre-fire successional stage (LP3/4)	-0.01	0.03	-0.49	0.62
Log <sub>10</sub> (Sound-1000-hr fuels) (Mg ha <sup>-1</sup> )	77	0.24	Intercept	0.65	0.52	1.25	0.216
			Early pre-fire successional stage (LP1)	-0.32	0.09	-3.72	<0.001
			Middle pre-fire successional stage (LP2)	0.07	0.06	1.10	0.275
			Late pre-fire successional stage (LP3/4)	0.17	0.05	3.66	<0.001
			Elevation	0.001	0.000	2.08	0.040
Log <sub>10</sub> (Rotten-1000-hr fuels) (Mg ha <sup>-1</sup> )	77	0.30	Intercept	2.62	0.44	5.91	<0.001
			Early pre-fire successional stage (LP1)	0.22	0.12	1.82	0.073
			Middle pre-fire successional stage (LP2)	-0.38	0.08	-4.71	<0.001
			Late pre-fire successional stage (LP3/4)	0.004	0.07	0.07	0.95
			Mean annual precipitation	-0.002	0.000	-2.79	0.007
Total surface fuels (Mg ha <sup>-1</sup> )	75	0.31	Intercept	379.68	59.70	6.36	<0.001
			Early pre-fire successional stage (LP1)	-24.23	14.40	-1.68	0.10
			Middle pre-fire successional stage (LP2)	-6.89	10.81	-0.64	0.53
			Late pre-fire successional stage	18.99	8.01	2.37	0.02

(LP3/4)				
Mean annual precipitation	-0.042	0.10	-4.03	<0.001
Mean annual temperature	-2.42	0.72	-3.34	0.001
Aspect	-15.94	6.28	-2.54	0.013

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675 Table 4: Predictive linear models illustrating the effects of post-fire stand structure, topo-  
climatic factors, and pre-fire successional stage on live surface and canopy fuel loads in 24-year-  
old lodgepole pine stands.

<i>Live surface fuels</i>	df	R <sup>2</sup>	Parameter	β	se	t- value	p- value
Live herbaceous fuels (Mg ha <sup>-1</sup> )	77	0.25	Intercept	2.09	0.34	6.25	<0.001
			Log <sub>10</sub> (lodgepole pine density)	-0.24	0.09	-2.78	0.007
			Rhyolite–till	-0.14	0.19	-0.73	0.470
			Rhyolite–glacial	-0.12	0.16	-0.70	0.484
			Rhyolite–low base saturation	-0.23	0.11	-2.12	0.037
Log <sub>10</sub> (Live shrub fuels) (Mg ha <sup>-1</sup> )	78	0.25	Intercept	-8.75	1.63	-5.36	<0.001
			Log <sub>10</sub> (lodgepole pine density)	0.35	0.10	3.60	<0.001
			Elevation	0.002	0.01	4.27	<0.001
			Fire severity (dNBR)	0.001	0.01	2.70	0.009
<i>Live canopy fuels</i>							
Log <sub>10</sub> (Available canopy fuels) (Mg ha <sup>-1</sup> )	81	0.78	Intercept	-1.27	0.12	-10.70	<0.001
			Log <sub>10</sub> (lodgepole pine density)	0.54	0.03	16.95	<0.001
Log <sub>10</sub> (Mean crown base HT) (Mg ha <sup>-1</sup> )	79	0.66	Intercept	-1.16	0.08	-15.12	<0.001
			Log <sub>10</sub> (lodgepole pine density)	0.24	0.02	12.01	<0.001
			Slope	-0.01	0.004	-2.24	0.028
Log <sub>10</sub> (Canopy bulk density) (kg m <sup>-3</sup> )	81	0.91	Intercept	-3.39	0.09	-39.62	<0.001
			Log <sub>10</sub> (lodgepole pine density)	0.70	0.02	29.98	<0.001

Table 5: The relative contribution of predictor variables to the models explanatory power with significant differences evaluated using bootstrapped confidence intervals. Each predictor's effect on the response is denoted using positive (+) and negative signs (-).

Fuel class response variables	Stand structure and environmental predictor variables											Interpretation	
	Live stand density	Crown base height	1000-hr fuel load	Pre-fire successional stage	Substrate	Mean annual precipitation	Mean Annual Temperature	Compound topographic index	Elevation	Slope	1988 dNBR		Aspect
<i>Dead surface fuels</i>													
Litter	0.66 <sup>a</sup> (+)	-	0.13 <sup>b</sup> (+)	-	-	0.21 <sup>a,b</sup> (-)	-	-	-	-	-	-	<ul style="list-style-type: none"> <li>Litter biomass varied positively with post-fire stand attributes linked to litter deposition (i.e., stand density) and 1000-hr fuel loads, which promote drier soil conditions found on site with high numbers of logs (Remsburg and Turner 2006). Annual precipitation was negatively related to litter biomass possibly due to suppressed decomposition rates.</li> </ul>
1-hr	-	0.78 <sup>a</sup> (+)	-	-	-	0.09 <sup>b</sup> (+)	-	0.02 <sup>b</sup> (+)	-	0.01 <sup>b</sup> (+)	-	-	<ul style="list-style-type: none"> <li>1-hr fuels increased with post-fire stand attributes (i.e. canopy base height and stand density) related to lower branch pruning and with moisture availability.</li> </ul>
10-hr	0.70 <sup>a</sup> (+)	-	-	-	-	-	0.30 <sup>a</sup> (-)	-	-	-	-	-	<ul style="list-style-type: none"> <li>10-hr fuels were weakly predicted by post-fire stand attributes linked to litter deposition (i.e., stand density) and mean annual temperature.</li> </ul>
100-hr	-	-	-	1.0 (+,-)	-	-	-	-	-	-	-	-	<ul style="list-style-type: none"> <li>100-hr fuels varied negatively with early and late pre-fire successional stages and positively with middle pre-fire successional stages. These relationships are believed to stem from the sizes of pre-fire trees and logs.</li> </ul>

1000-hr— sound	-	-	-	0.99 <sup>a</sup> (+,-)	-	-	-	-	0.01 <sup>b</sup> (+)	-	-	-	<ul style="list-style-type: none"> <li>• Sound 1000-hr fuels varied negatively with early and middle pre-fire successional stages and positively with late pre-fire successional stages. The greatest sound 1000-hr fuel loads occurred on sites with large size classes of pre-fire trees and logs.</li> </ul>
1000-hr— rotten	-	-	-	0.99 <sup>a</sup> (-)	-	-	-	-	0.01 <sup>b</sup> (-)	-	-	-	<ul style="list-style-type: none"> <li>• Rotten 1000-hr fuels varied positively with early pre-fire successional stage and negatively with middle and late pre-fire successional stages. Rotten 1000-hr fuels are highest on sites with small size classes of pre-fire trees and logs.</li> </ul>
Total surface	-	-	-	0.28 <sup>a</sup> (+)	-	0.34 <sup>a</sup> (-)	0.27 <sup>a</sup> (-)	-	-	-	-	0.12 <sup>a</sup> (-)	<ul style="list-style-type: none"> <li>• Total surface fuel load varied positively with pre-fire successional stage and negatively with mean annual temperature, mean annual precipitation, and aspect.</li> </ul>
<i>Live surface fuels</i>													
Live herbaceous	0.38 <sup>a</sup> (-)	-	-	-	0.61 <sup>a</sup> (-)	-	-	-	-	-	-	-	<ul style="list-style-type: none"> <li>• Herbaceous biomass declined with post-fire stand basal area (i.e., restricted light and soil resources) and increased with substrate quality.</li> </ul>
Live shrub	0.25 <sup>a</sup> (+)	-	-	-	-	-	-	-	-	0.50 <sup>a</sup> (+)	0.25 <sup>a</sup> (+)	-	<ul style="list-style-type: none"> <li>• Shrub biomass varied positively with post-fire stand density (i.e., restricted light and soil resources) and elevation.</li> </ul>
<i>Live Canopy fuels</i>													
Available canopy fuel	1.0 (+)	-	-	-	-	-	-	-	-	-	-	-	<ul style="list-style-type: none"> <li>• Available canopy fuel load varied positively with post-fire stand density.</li> </ul>
Crown base height	0.96 <sup>a</sup> (+)	-	-	-	-	-	-	-	-	0.04 <sup>b</sup> (-)	-	-	<ul style="list-style-type: none"> <li>• Canopy bulk density increased with post-fire stand density. High density stands were found to have the greatest foliar biomass and the lowest canopy length.</li> </ul>
Canopy bulk density	1.0 (+)	-	-	-	-	-	-	-	-	-	-	-	<ul style="list-style-type: none"> <li>• Canopy base height increased with post-fire stand density as a result of density-dependent lower branch pruning.</li> </ul>

Table 6: Changes in surface fuel loads between 1996 and 2012 in 10 remeasured plots.

Means are reported with one standard error and the range of observations in each time period.

Statistics reflect paired t-tests.

Surface fuel type	1996 (Mg ha <sup>-1</sup> )	2012 (Mg ha <sup>-1</sup> )	t	p-value (two-tailed)	Ratio of change (2012/1996)
1-hr fuels	0.13±0.02 [0.07, 0.22]	0.14±0.02 [0.06, 0.26]	-0.34	0.744	1.07±0.22
10-hr fuels	0.98±0.15 [0.00, 1.92]	2.37±0.16 [1.52, 3.27]	-5.96	<0.001	2.41±0.43
100-hr fuels	2.92±0.39 [0.40, 4.42]	5.07±0.46 [1.97, 6.66]	-3.82	0.004	1.74±0.26
1000-hr fuels–Sound	26.85±4.14 [11.40, 50.16]	60.61±7.42 [25.54, 95.78]	-3.99	0.003	2.26±0.44
1000-hr fuels–Rotten	11.07±2.08 [1.72, 19.71]	47.66±6.79 [23.15, 79.20]	-6.18	<0.001	4.31±0.70
Total Fuel Load	41.95±5.16 [24.01, 74.92]	115.84±9.61 [60.17, 160.54]	-7.49	<0.001	2.76±0.37

## FIGURE CAPTIONS

Figure 1: The great range of variability in 24-year-old lodgepole pine forest structure and fuel characteristics developing after the 1988 Yellowstone fires. Photos taken in 2012 by K. N. Nelson and M. G. Turner.

Figure 2: Vertical variation in canopy bulk density by stand density. Canopy bulk density was estimated for 0.1 meter vertical strata by summing available canopy fuel load within each strata then dividing by the volume of each layer (plot area x strata depth) for each plot and smoothed for plotting using a 1 meter running mean.

Figure 3: The relationship between stem density and percent crown area. Crown area is defined as the percent of ground area covered by tree crowns assuming circular crowns and even tree spacing.

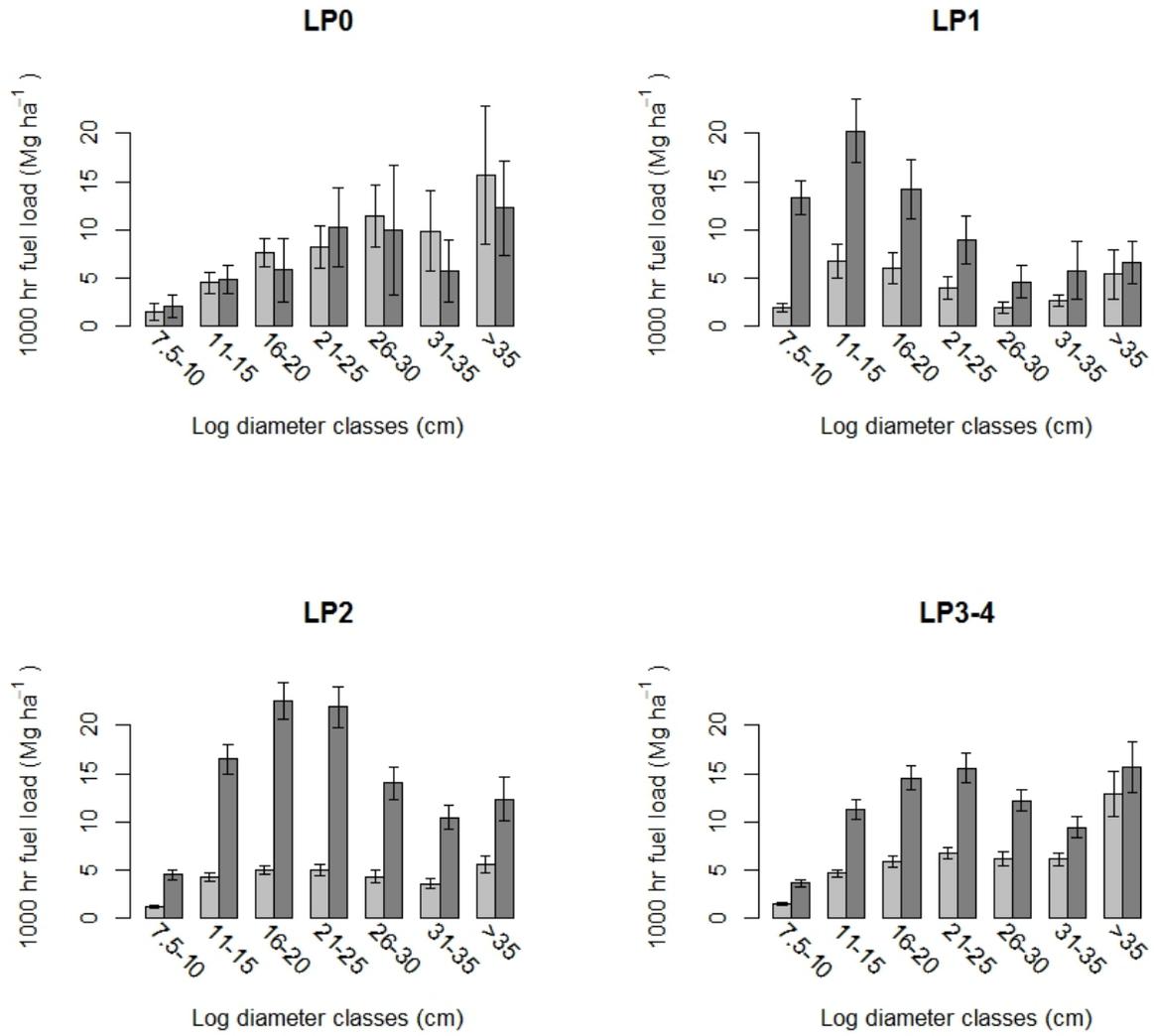
Figure 4: Coarse fuel loads by log size and decay status for each pre-fire successional stage. Rotten log fuel loads are depicted with light gray bars and sound log fuel loads are depicted with dark gray bars. Pre-fire vegetation successional stages (Despain 1990) include: LP0—post-fire stands where lodgepole pine has recolonized the site but has not yet produced a closed canopy, LP1—dense, young lodgepole pine in a single cohort without tree seedlings in the understory, LP2—closed canopy lodgepole pine with tree seedlings in the understory, LP3—multi-cohort stands with ragged canopy characteristics dominated by lodgepole pine but containing Engelmann spruce and subalpine fir in the sub-canopy, LP4—seral lodgepole pine stands on dry sites without Engelmann spruce and subalpine fir. LP3 and LP4 have similar above-ground biomass characteristics and were combined to enhance sample size.

Figure 5: Within-plot coefficient of variation for surface fuel loads in 1996 and 2012. Asterisks indicate significant differences between years using a two-sided, paired t-test ( $\alpha=0.05$ ).

Figure 1



**Figure 2**



*Figure 3*

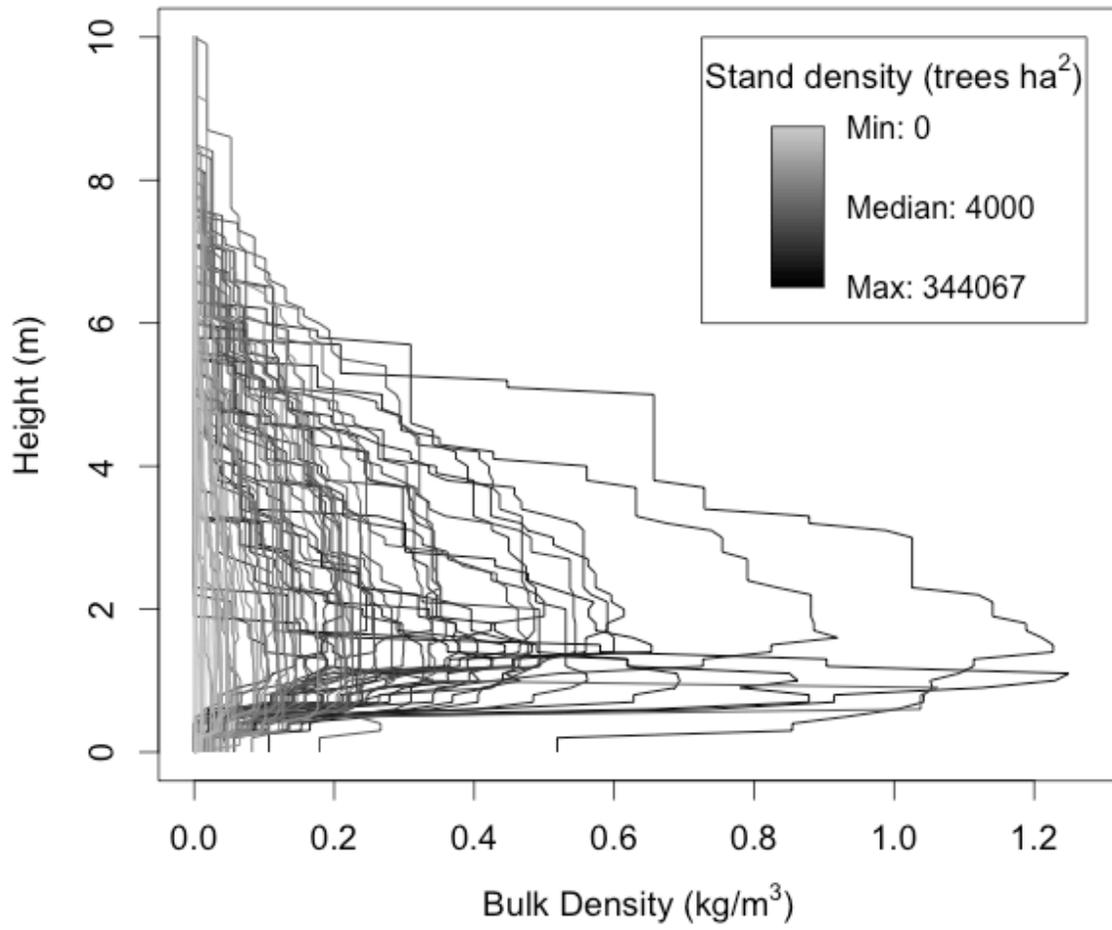


Figure 4

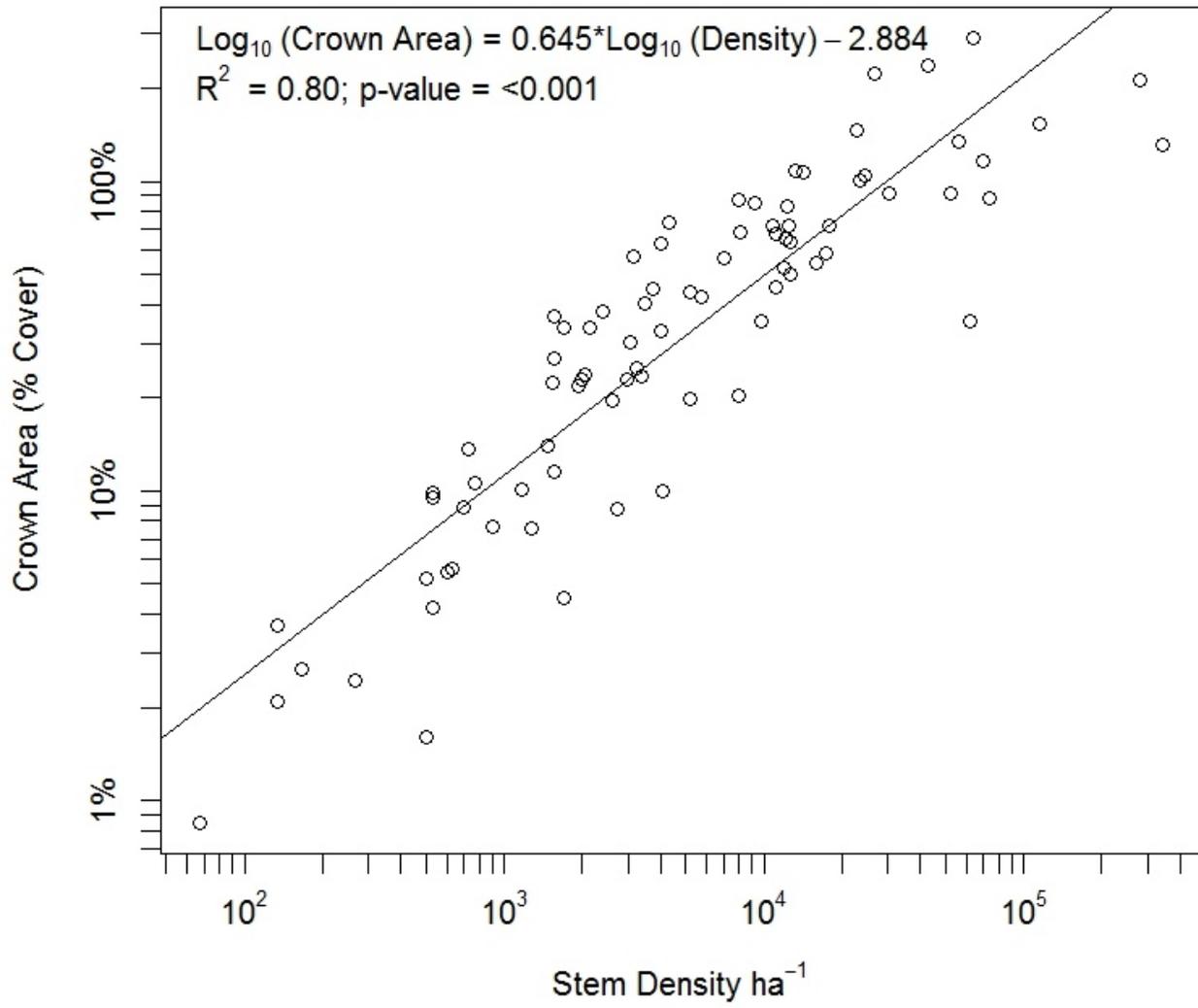
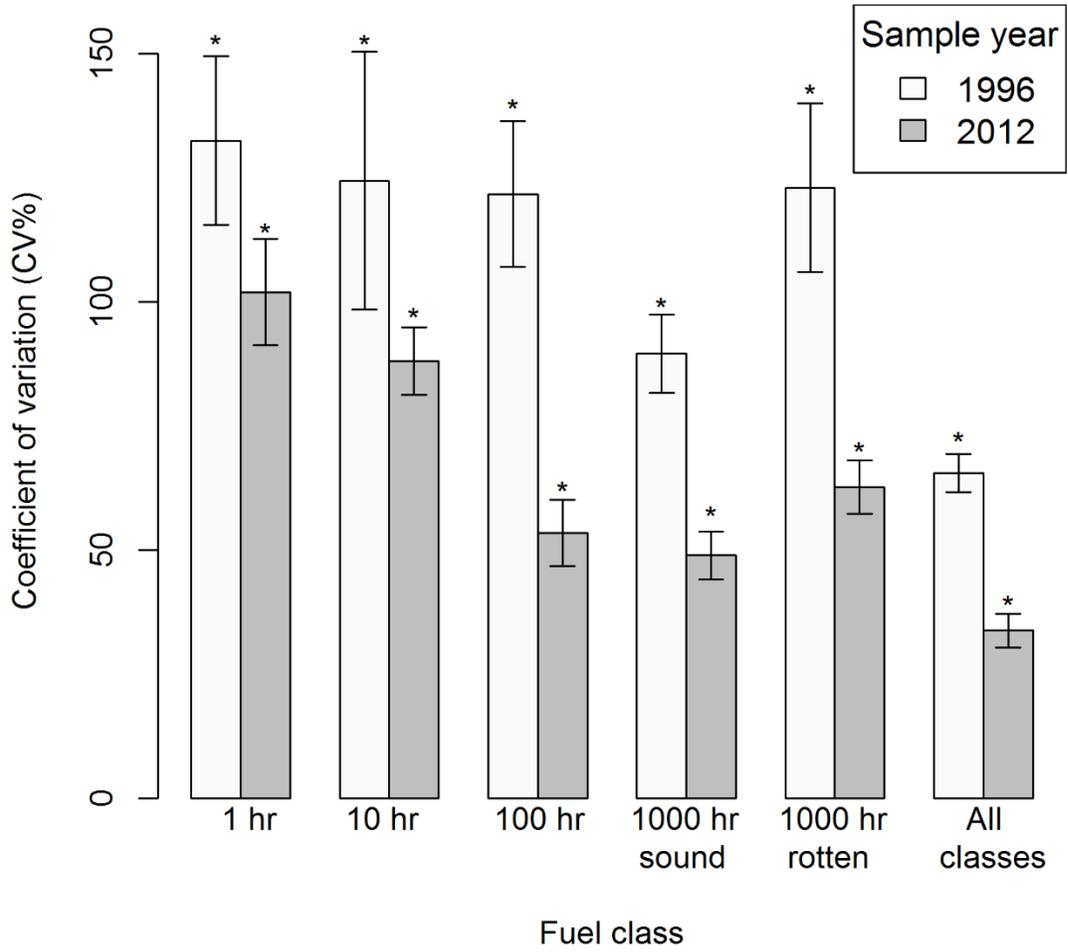


Figure 5



## SUPPORTING INFORMATION

Table S1: Candidate predictor variables, their sources, and the models that used them as candidates in model selection.

Predictor variable	Acquisition method	Candidate variables used in model selection by response variable type			
		Fine surface fuels	Coarse surface fuels	Live surface fuels	Canopy fuels
Live foliage, herb, shrub biomass	Empirical	X			
Live tree density	Empirical	X		X	X
Live basal area	Empirical			X	
Canopy base height	Empirical	X			
1000-hr fuel load	Empirical	X		X	
Pre-fire successional stage (Despain 1990, NPS-YELL 1990)	Downloaded		X	X	
Substrate (NPS-YELL 1997)	Downloaded			X	
Mean annual precipitation (PRISM Climate Group 2012)	Downloaded	X	X	X	X
Mean annual temperature (PRISM Climate Group 2012)	Downloaded	X	X	X	X
Compound topographic index (Evans et al. 2014)	Derived	X	X	X	X
Potential solar radiation (Pierce et al. 2005)	Derived	X	X	X	X
Elevation (Gesch 2007)	Downloaded	X	X	X	X
Slope (Gesch 2007)	Downloaded	X	X	X	X
Aspect (Gesch 2007)	Downloaded	X	X	X	X
dNBR fire severity (USDA Forest Service-RSAC 2012)	Derived		X	X	