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Regeneration of montane forests 24 years after the 1988 Yellowstone fires: a fire-catalyzed shift in lower treelines?

Running head: Wildfire and lower-montane treeline dynamics

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22 **Abstract**

23 Forests near the lower limit of montane tree cover are expected to be particularly vulnerable to
24 warming climate, potentially converting to non-forest for prolonged periods if affected by
25 canopy-removing disturbances. Such disturbance-catalyzed shifts are by nature stochastic,
26 offering few opportunities to test these predictions. We capitalized on a landmark event
27 exemplary of recent large disturbances – the 1988 wildfires in Yellowstone National Park (USA)
28 – to investigate long-term (24-year) regeneration dynamics in Douglas-fir (*Pseudotsuga*
29 *menziesii* v. *glauca*) forests, which compose the lower treeline yet have received little study. We
30 tested the hypothesis that, under current conditions (warmest decades in last 6000 years), dry
31 lower-margin stands are less apt to attain self-replacement than adjacent, but more mesic, stands
32 farther from the ecotone. Mesic sites characterized by dense forests pre-fire regenerated robustly
33 regardless of burn severity, even in large high-severity patches, whereas dry sites did so only if
34 nearby seed sources survived (i.e., small patch size or moderate burn severity). Regeneration
35 continued over two decades, peaking between ~5-15 years, with mesic stands continuing
36 regenerating beyond 15 years to a greater degree than dry stands. Self-replacement of stands by
37 24 years post-fire was nearly universal in mesic stands, variable but common in dry stands not
38 adjacent to the lower ecotone, and uncommon in dry stands near the ecotone – particularly if
39 burned at high severity. Whether the lack of regeneration in ecotonal stands is categorically
40 directional with warming climate or part of a long-term cycle is unresolved, but we estimate that
41 the 1988 fires converted >4000 ha of lower-montane forest to grass/sage steppe for at least
42 several decades, possibly indefinitely given current trends in climate. These data support the
43 notion that climate-driven shifts in vegetation cover are likely to occur in punctuated fashion

44 with disturbances, with relatively abrupt implications for montane forest cover, biogeography,
45 and ecosystem function.

46

47 **Keywords:** climate change, Douglas-fir, ecotone, Greater Yellowstone Ecosystem, lower
48 montane forest, *Pseudotsuga menziesii*, Rocky Mountains, tree line, wildfire

49 **Introduction**

50 One of the most uncertain aspects of climate change is how it may shift the upper and
51 lower elevational limits of mountain forests. Most models suggest upward migrations of treelines
52 under a warming climate (Parmesan & Yohe 2003), but the potential mechanisms and rates of
53 such changes are unclear, confounding predictive capabilities (Soja et al. 2006). Studies of
54 treeline shifts and their consequences have so far focused primarily on forest expansion at the
55 upper, alpine ecotone (e.g., Harsch et al. 2009; Dirnböck et al. 2011). However, forests near the
56 low-elevation ecotone, where moisture regimes are just sufficient to support tree cover, are
57 among the most vulnerable to warming and drying (e.g., Breshears et al. 2005). Predictions for
58 the 21st century suggest replacement of many dry coniferous forests with steppe vegetation over
59 significant portions of western North America (Jiang et al. 2013). Such shifts in lower treelines
60 can strongly influence the extent and biogeography of montane forest landscapes, as well as
61 ecosystem functions including terrestrial carbon storage (Breshears & Allen 2002; Jiang et al.
62 2013; Millar and Stephenson 2015).

63 Climate-driven changes in vegetation distribution are most likely to occur as a series of
64 abrupt events rather than gradual migrations. Major change is catalyzed by disturbances such as
65 large wildfires, severe droughts, or insect outbreaks that break the inertia of a system dominated
66 by long-lived organisms (e.g., conifers) and allow the establishment of a different assemblage
67 (Cwyner 1987; Frelich & Reich 2010; Johnstone et al. 2010). For example, rates of treeline shift
68 associated with projected changes in temperature and precipitation alone are likely on the order
69 of <100 m per century (Loehle 2000), whereas losses exceeding 10,000 square kilometers of
70 forest have occurred after single events in the western USA (Breshears et al. 2005). Major
71 disturbances such as very large fires are expected to increase substantially in most North

72 American forests during the 21st century (Barbero et al. 2015). It is therefore essential to track
73 the fate of forests that define the lower limits of montane tree cover when they experience major
74 disturbances.

75 A landmark event that ushered in the current era of large disturbances under a warmer
76 climate was the 1988 fires in and around Yellowstone National Park, USA (Romme et al. 2011).
77 Driven by extreme winds and drought, the fires burned in a mosaic pattern over 600,000
78 hectares, ranking among the largest temperate-zone wildfires in recorded history. The resulting
79 landscape lent a wealth of novel insights into robust forest regeneration and ecosystem responses
80 following large wildfires (Turner et al. 1997, 1999, 2003, 2004, 2016; Romme et al. 2011), with
81 broad implications for other temperate forests (e.g., Lloret et al. 2002; Donato et al. 2009;
82 Christensen 2014). These insights came largely from subalpine lodgepole pine (*Pinus contorta* v.
83 *latifolia*) forests of the Yellowstone plateau. Little appreciated is that the 1988 fires also burned
84 significant areas of lower-montane forest dominated by interior Douglas-fir (*Pseudotsuga*
85 *menziesii* v. *glauca*). Although only 6% of the fires' area was in lower-montane forests, this
86 equated to ~35,000 hectares, which alone ranks among the top 5-10% of fires in the United
87 States (Barbero et al. 2015). The period since the fires has been characterized as exceptionally
88 warm regionally, with annual temperatures since the 1980s at their highest in the last 6000 years
89 (Shuman 2012).

90 Douglas-fir-dominated forests in the Greater Yellowstone Ecosystem (GYE) inhabit the
91 elevation zone below subalpine forests and above grass/sage steppe, thus forming the low-
92 elevation forest ecotone. Stands near the former are cool, mesic, dense forests, while stands near
93 the latter are warm, dry, open parklands (Arno & Gruell 1986; Bradley et al. 1992; Baker 2009;
94 Donato et al. 2013). The fire ecology and regeneration dynamics of interior Douglas-fir forests

95 are poorly understood (Baker 2009; Donato et al. 2013). Available data suggest a mixed-severity
96 fire regime with less frequent but more severe fires on mesic sites than on dry sites (Bradley et
97 al. 1992; Baker 2009), and that protracted post-disturbance regeneration over multiple decades is
98 common (Baker 2009; Donato et al. 2013), as in other Douglas-fir forests (Tepley et al. 2013;
99 Freund et al. 2014). Mesic stands are expected to regenerate faster and more abundantly than dry
100 stands (Baker 2009; Kemp et al. 2015), and may be less vulnerable to post-fire regeneration
101 failure under a warming climate than dry stands near the ecotone (Romme & Turner 1991).
102 Pollen records from the GYE indicate wide temporal variation in Douglas-fir's abundance over
103 the Holocene era, and concurrent variations in steppe vegetation suggest oscillations in lower
104 treelines through time (Whitlock 1993; Huerta et al. 2009). Upward shifts occurred during
105 warmer periods with high fire activity, while forest expansion occurred during cooler, wetter
106 periods (Huerta et al. 2009). The 21st century is projected to experience unprecedented rates of
107 climatic warming and large-fire activity (Westerling et al. 2011), which may re-organize
108 landscape vegetation patterns in Greater Yellowstone in uncertain ways. Twenty-first century
109 contraction of lower treelines was hypothesized previously (Romme & Turner 1991); however
110 the realization of such shifts, as well as basic tenets of post-fire regeneration dynamics, are vastly
111 understudied in Rocky Mountain Douglas-fir forests.

112 Here, we report on regeneration dynamics in lower-montane forests burned by the 1988
113 Yellowstone fires. We sought to test a central hypothesis that, under current climate conditions,
114 dry lower-margin forests would be less apt to attain self-replacement following fire than
115 adjacent, similarly composed forests farther from the lower ecotone. The nearly two-and-a-half
116 decades elapsed since the fires (at time of sampling) presented an excellent opportunity to
117 interpret patterns of forest establishment. We directly tested the concept of 'engineering

118 resilience' (rate of recovery), and evaluated the degree to which regeneration trends are
119 indicative of low 'ecological resilience' of ecotonal stands (potential for state change) (see
120 Peterson et al. 1998). Data supporting our central hypothesis would be consistent with the
121 expectation of disturbance-catalyzed treeline shifts in a warmer climate. We addressed the
122 following questions: (1) After 24 years, how does post-fire tree density vary between mesic and
123 dry stands, as influenced by burn severity? (2) To what degree does the major community
124 associate in these forests, lodgepole pine (high cone serotiny locally), increase in relative
125 abundance in large stand-replacement patches? (3) What are the temporal patterns of tree
126 establishment? (4) To what degree, and with what timing, are lower-montane forests self-
127 replacing following the 1988 fires, and how does this vary between mesic versus dry stands
128 (particularly those closest to the low-elevation treeline)?

129

130 **Methods**

131 *Study area*

132 The study area spans east-to-west across the Greater Yellowstone Ecosystem (GYE) (Fig.
133 1). The GYE is centered in northwest Wyoming, USA, and contains coniferous forests
134 representative of the Middle Rocky Mountains ecoregion (Omernik 1987). The northern GYE,
135 where study watersheds were concentrated, is characterized by mean July high temperatures of
136 25 °C, mean January lows of -15 °C, and mean annual precipitation of ~34 cm, mostly falling as
137 winter snow and spring rain (www.prism.oregonstate.edu). Lower-montane forests occupy
138 sloping terrain with well-drained, non-rhyolitic soils on the shoulders of the Yellowstone
139 Plateau. Sampled stands had average slopes of $29 \pm 4^\circ$ (S.D.), elevations of 2155 ± 83 m (S.D.),
140 and comprised a full range of aspects.

141 Lower-montane, Douglas-fir-dominated forests occur in scattered parcels across the GYE
142 (Fig. 1). Stands nearest the grass/sage ecotone are xeric in character, typically with low tree
143 densities, open/grassy understories, and presence of limber pine (*Pinus flexilis*) and Rocky
144 Mountain juniper (*Juniperus scopulorum*) (Bradley et al. 1992; Baker 2009). Farther from the
145 ecotone (higher local elevation and/or wetter), Douglas-fir grows in dense, multi-storied stands
146 mixed to varying degrees with lodgepole pine, Engelmann spruce (*Picea engelmannii*), and
147 subalpine fir (*Abies lasiocarpa*) (Bradley et al. 1992; Baker 2009). The shade-intolerant,
148 serotinous-coned lodgepole pine is perhaps the most important associate of Douglas-fir in the
149 GYE, often proliferating after severe fires (Bradley et al. 1992). The fire ecology of Rocky
150 Mountain Douglas-fir forests is poorly understood; studies indicate a mixed-severity fire regime
151 with low- to moderate-severity fires occurring at ~20-80 year intervals prior to effective fire
152 exclusion and large or high-severity fire events occurring at longer intervals of ~100-200 years
153 (Houston 1973, Loope & Gruell 1973, Barrett 1994, Littell 2002, Korb 2005, Baker 2009, Huerta
154 et al. 2009). The relative ratio of high- versus low-severity patches is thought to be greater in
155 mesic than in dry/ecotonal types (Bradley et al. 1992; Baker 2009).

156 The 1988 fires influenced lower-montane forests as a spatially disparate, mixed-severity
157 event (Fig. 1). Based on locally field-validated thresholds (Harvey 2015) in the relative
158 differenced normalized burn ratio (RdNBR; Miller & Thode 2007), lower-montane forests
159 experienced proportionally less high-severity fire (47% of area) than did adjacent subalpine
160 forests (61%). Mean patch size of high-severity burn (>90% canopy mortality) in lower-montane
161 forests was 160 ha, two orders of magnitude lower than that in subalpine forests (14,520 ha), and
162 the mean perimeter-to-area index was ~twice as high (unitless values of 191 and 91 in lower-
163 montane and subalpine forests, respectively). The above analysis was based on area-weighted

164 values, retaining burn patch integrity where patches crossed forest types, using Monitoring
165 Trends in Burn Severity data [www.mtbs.gov] and standard outputs from FRAGSTATS ver. 4
166 (McGarigal et al. 2012).

167

168 *Data collection*

169 Our sampling universe comprised lower-montane forests that were dominated by mature
170 Douglas-fir at the time of the 1988 fires (minimum basal area $10 \text{ m}^2 \text{ ha}^{-1}$, minimum tree density
171 80 ha^{-1} , $>50\%$ stems *P. menziesii*; see Table 1). Given our research focus on secondary
172 succession in response to canopy-opening disturbance, we sampled only areas that experienced
173 moderate- to severe fire effects ($>30\%$ overstory mortality); purely surface fires were not
174 studied. We sampled regeneration dynamics in eight watersheds (~second- to third-order),
175 identified *a priori* based on spatial data showing overlap between 1988 fire perimeters and
176 lower-montane forest. Sample watersheds were selected by going down the *a priori* list until
177 field time ran out. In each watershed, we measured vegetation in 6-8 stands, beginning from a
178 random start and spaced at 200-m intervals (to minimize the potential for spatial autocorrelation;
179 similar to Larson et al. 2013; Kemp et al. 2015) at a pre-determined azimuth to cross one or more
180 burn patches. Each watershed generally captured similar ranges in key abiotic and biotic
181 characteristics and, importantly, included both moderate- and high-severity burn, broad ranges of
182 distance to seed source, and both mesic and dry stands where both were present (Appendix B).

183 Sampling occurred during summer 2012. Within each stand, we collected data in a 30-m-
184 diameter (0.07 ha) circular plot: post-fire tree and other plant regeneration, pre-fire stand
185 structure, and abiotic characteristics. For post-fire regeneration, we recorded every tree stem in
186 variable-sized subplots according to the density of post-fire trees (*sensu* Kemp et al. 2015;

187 Harvey et al. 2016). Default subplot size was four 2 x 15 m rectangular quadrats (120 m² total
188 area) situated along cardinal directions from plot center. Subplot size was objectively decreased
189 to four 0.5 x 15 m quadrats (30 m² total area) or increased to the entire plot (707 m² total area) if
190 >200 or <10 trees were to be captured in the default subplot size, respectively. For each stem, we
191 recorded species, height (cm), age by bud-scar count (yr), and evidence of leader damage.
192 Postfire cover for each of shrubs, forbs, and graminoids was recorded to the nearest 5% in four
193 0.25-m² circular subplots, one in each plot quadrant. Ground cover of wood, litter, bryophyte,
194 soil, and rock was recorded in the same subplots. To enumerate pre-fire stand structure, we
195 recorded the number of standing and down (but standing pre-fire) trees (> 15 cm dbh) that were
196 rooted in the plot, noting species and current live/dead status. Distance to the nearest surviving
197 mature pre-fire tree – and to a contiguous (>1 ha) patch of such trees – was measured from plot
198 center with a TruPulse laser rangefinder. A similar distance measurement was made to the lower
199 ecotone, by direct field measurement or from aerial photos combined with spatial vegetation
200 data. Finally, we recorded the slope (deg), aspect (deg), and elevation (m) of each stand.

201

202 *Data analysis*

203 We categorized each stand as mesic or dry subtype based on a set of key abiotic and
204 biotic variables (Table 1). These variables were identified through multivariate ordination
205 (Appendix 1) of an independent set of unburned lower-montane Douglas-fir stands in the GYE,
206 from a separate study (Donato et al. 2013). Twenty-three of our 1988-Fire stands were classified
207 as mesic, and 32 as dry. In brief, mesic stands were farther from the lower treeline; were on
208 cooler aspects; and had higher pre-fire basal area, stem density, down wood abundance, and
209 canopy closure. Dry stands were closer to the lower treeline; were on warmer aspects; had

210 greater grass abundance; and had lower pre-fire basal area, stem density, down wood abundance,
211 and canopy closure. Mesic stands correspond generally to Fire Group Three (moist Douglas-fir
212 habitats) as described by Bradley et al. (1992), while dry stands correspond to Fire Groups One
213 and Two (dry Douglas-fir and limber pine habitats).

214 For evaluation of our research questions, we adopted a parsimonious approach (Murtaugh
215 2007) of confidence interval inference (Brandstätter 1999; Donato et al. 2013b). Confidence
216 intervals (CIs) carry similar inferential power as parametric and likelihood tests but can more
217 readily convey information on effect sizes and variability (Brandstätter 1999; Altman et al.
218 2000). Data distributions in this study were non-normal and heavily zero-inflated, both for
219 responses and key predictor variables, making a regression framework less useful. Also, many
220 commonly analyzed predictors such as aspect, prefire tree density, and distance to lower treeline
221 were rolled into our integrative classification of stands as mesic and dry (see Table 1 and
222 Appendix 1). We constructed nonparametric bootstrapped 95% CIs that are free of distributional
223 assumptions, robust to abundant zeros, and allow for asymmetrical intervals about the median
224 (e.g., Altman et al. 2000). Bootstrapped intervals were constructed by resampling the data (with
225 replacement) to obtain an identical-sized dataset 1000 times, computing the median for each
226 resample, and obtaining a 95% CI from bias-corrected percentiles of the 1000 median values
227 (DiCiccio & Efron 1996; Davison and Hinkley 1997). Confidence intervals for each sample
228 group are graphed for visual interpretation; statistical inference is based on the 95% CI for the
229 difference in medians between groups (Altman et al. 2000).

230 For question 1 (regeneration density by stand type and burn severity), we computed
231 bootstrapped 95% CIs for total tree density for each of mesic and dry types as a function of stand
232 burn severity at the hectare scale (moderate vs. high; distinguished as < or > 90% overstory

233 mortality, respectively) and distance to live-tree edge (a measure of the fires' effect on seed
234 source proximity via burn patch size). For question 2 (lodgepole pine response), we computed
235 bootstrapped 95% CIs for lodgepole pine density as a function of distance from live-tree edge
236 and the relative abundance of lodgepole pine pre-fire, two key factors known *a priori* to drive
237 lodgepole pine abundance where cone serotiny is important, as in low elevations of the GYE
238 (Tinker et al., 1994; Schoennagel et al., 2003; Harvey et al. 2016). For question 3 (temporal
239 patterns), we parsed the bud-scar (age-proxy) data into 5-year bins, corresponding to the
240 approximate resolution of bud-scar counts on older seedlings/saplings (Urza & Sibold 2013),
241 then computed bootstrapped 95% CIs of tree densities for each age-class bin. We also compared
242 the temporal distribution of regeneration between mesic and dry forests via chi-square tests on
243 the 5-year binned age data. For question 4, we enumerated the post-fire year at which each stand
244 had attained self-replacement status, by comparing net cumulative establishment density to site-
245 specific pre-fire overstory density. While not without limitations, we adopted this flexible metric
246 as an informative threshold rather than a blanket or arbitrarily defined stocking standard, as it
247 accounts for site-to-site variation in productivity or carrying capacity (both between and within
248 dry and mesic types). Finally, we assessed the proportion of stands not effectively regenerating
249 (<10% of pre-fire density, including non-stocked plots) along the hypothesized gradient in
250 vulnerability to regeneration failure, from mesic stands (least vulnerable), dry stands not
251 immediately adjacent (>150 m) to the ecotone (moderately vulnerable), to dry stands near (< 150
252 m) the ecotone (most vulnerable).

253

254 **Results**

255 *Post-fire tree density in mesic and dry stands*

256 Across the study, 87% of plots (stands) were occupied by conifers (primarily Douglas-fir)
257 at 24 years post-fire, with densities ranging from (including non-stocked plots) 0 – 19,667 trees
258 ha⁻¹ and a median of 1250 trees ha⁻¹. Pre-fire densities (of trees >15 cm diameter at breast height
259 [dbh]) ranged from 85 – 622 trees ha⁻¹, with a median of 315 trees ha⁻¹. A mean of 75% of
260 quadrants within each plot were occupied post-fire (95% CI: 65-84% occupied), indicating well-
261 distributed trees within stands.

262 Regeneration between mesic and dry stands differed in both overall abundance and
263 response to burn severity (Fig. 2). Mesic stands had a median regeneration density of 3294 trees
264 ha⁻¹, more than an order of magnitude higher than dry stands, which had a median density of 195
265 trees ha⁻¹ (95% CI for difference in medians 1979-5572 trees ha⁻¹). Dry stands regenerated
266 primarily after moderate-severity fire (median 1425 trees ha⁻¹) and had significantly less
267 regeneration following high-severity fire (median 74 trees ha⁻¹) (95% CI for difference in
268 medians 354-5388 trees ha⁻¹); whereas mesic stands did not show this effect (Fig. 2).

269 Regeneration abundance showed a strong negative association with distance to live-tree edge
270 (Fig. 3). Median densities were highest within 100 m of edges (4598 and 781 trees ha⁻¹ in mesic
271 and dry stands, respectively), tapering to near zero beyond 100 m in dry stands but remaining
272 above 1500 trees ha⁻¹ well beyond 200 m in mesic stands (Fig. 3).

273

274 *Lodgepole pine response and seral community*

275 Lodgepole pine outnumbered all other secondary conifers combined, having increased in
276 presence and relative abundance from pre-fire stands. Greater pre-fire abundance of *P. contorta*
277 and greater distance to live-tree edge were associated with increases in *P. contorta* post-fire
278 relative abundance (Fig. 4). Stands with no pre-fire presence of *P. contorta* had a median of zero

279 % of *P. contorta* stems post-fire, while those with even a minimal pre-fire presence of *P.*
280 *contorta* (<5% of pre-fire stems) had a median of 16% post-fire (95%CI for difference 5-38%).
281 There was suggestive evidence of a further increase in post-fire importance of *P. contorta* with
282 greater pre-fire abundance (another 33% increase when pre-fire abundance exceeded 5%), but
283 variability was high (95% CI for difference -3-69%) (Fig. 4a). Post-fire relative abundance of
284 lodgepole pine was low at short and intermediate distances from live-tree edges (medians both
285 <4%), and greatest at distances >200 m (median 32%; 95% CI for increase 5-78%) (Fig. 4b).

286 Douglas-fir remained present in 80% of plots and constituted 69% of post-fire trees on
287 average, followed by lodgepole pine, which was present in 45% of plots and averaged 14% of
288 post-fire trees (Fig. 5a). Other species in descending order of representation were Engelmann
289 spruce, quaking aspen (*Populus tremuloides*), subalpine fir, Rocky Mountain juniper, and limber
290 pine (Fig. 5a). Composition of post-fire trees varied relatively little between mesic and dry
291 stands, particularly for Douglas-fir (65% in mesic stands, 72% in dry) and lodgepole pine (14%
292 and 15%, respectively). Mesic stands averaged greater abundance of subalpine fir (4.2% versus
293 1.8% in dry stands) and Engelmann spruce (10% versus 2%), but less quaking aspen (2% versus
294 8%). Mesic and dry stands did not differ in terms of other vegetation abundance: shrub cover
295 averaged 16% ±5% in mesic stands and 20% ±7% in dry stands, and graminoid cover averaged
296 23% ±8% and 21% ±6%, respectively (Table 1). Douglas-fir, the primary determinant of
297 average stand height, had a mean height of 1.5 m at 24 years post-fire (Fig. 5b). Combining with
298 the binned age data (see below), growth rates for Douglas-fir were estimated to average 10 cm
299 yr⁻¹. Lodgepole pine was the tallest component of the post-fire community (mean 2.6 m; Fig. 5b),
300 and grew at an estimated mean rate of 17 cm yr⁻¹. Browse damage on leaders was overall minor,
301 with a mean of 8% of stems.

302

303 *Temporal patterns of tree establishment*

304 Tree establishment continued for most of the 24 years since the fires, particularly in
305 mesic stands (Fig. 6). The peak period of ~5-15 years was similar between mesic and dry stands,
306 but the absolute magnitudes in each year were much lower in dry stands (Fig. 6). The temporal
307 pattern also differed, in that mesic stands continued regenerating in later years (>15 years) more
308 than did dry stands (Chi-square $\chi_4^2 = 22.3$, $P < 0.001$).

309

310 *Self-replacement*

311 In mesic stands, 90% of plots had reached site-specific self-replacement density by 11
312 years post-fire, topping at 96% by 14 years (Fig. 7a). In contrast, only 44% of dry stands had
313 reached self-replacement by 24 years post-fire, and the remaining plots were not on an upward
314 trend (Figs. 6b, 7a).

315 Stands that had not recovered toward forest by 24 years (non-stocked with trees or <10%
316 of pre-fire density) were found exclusively in dry stands (Fig. 7b). These stands were all within
317 150 m of the grassland ecotone and all contained <30 trees ha⁻¹ (half of these contained no trees
318 at all). Near the ecotone, 33% of stands that burned at moderate severity, and 63% of stands that
319 burned at high severity, were non- or minimally stocked (Fig. 7b).

320

321 **Discussion**

322 Twenty-four years after the 1988 Yellowstone fires, regeneration trends in lower-
323 montane forests indicated clearly distinct dynamics in dry stands near the lower treeline versus
324 mesic stands and those farther from the treeline. Regeneration of Douglas-fir and other species

325 was abundant in mesic stands, even in large high-severity patches, while regeneration was sparse
326 to absent (and apparently ceased) in dry stands near the lower ecotone. In the following sections,
327 we first discuss key patterns in regeneration as related to environmental setting, burn severity,
328 and time, then examine the degree to which these patterns provide support for hypothesized
329 shifts in lower treelines following major disturbances in a warming climate.

330

331 *Post-fire tree density in mesic and dry stands*

332 As hypothesized, regeneration density differed substantially between mesic and dry
333 Douglas-fir stands. Mesic stands characterized by cool (northeasterly) aspects, higher pre-fire
334 tree densities, and greater presence of mesic tree associates had ~17 times the median
335 regeneration density of dry stands characterized by warmer (southwesterly) aspects, lower pre-
336 fire densities, and dry tree associates. This finding is consistent with the relatively scant literature
337 on Rocky Mountain Douglas-fir forests, which suggests young forests on mesic sites often
338 exceed 1000 trees ha⁻¹ (Baker 2009) and reach full stocking within a few decades (Lyon 1971),
339 versus dry sites which commonly contain much lower densities (<150 trees ha⁻¹) in young stands
340 (Peirce 1915; Heyerdahl et al. 2006; Baker 2009).

341 Interestingly, mesic stands also differed from dry stands in that regeneration did not
342 decline with higher burn severity, even in large patches, suggesting that seedbeds and seed
343 sources were not limiting after full canopy-opening disturbance in mesic stands. In dry stands,
344 however, regeneration density declined with increasing burn severity, suggesting that either
345 seedbeds or seed sources (or both) became more limiting in high-severity areas. In this respect,
346 we surmise that our dry stands are most similar to the northern Rockies dry mixed-conifer forests
347 studied by Harvey et al. (2013) and Kemp et al. (2015), who also reported the highest

348 regeneration abundance after low-moderate severity fire. That dry stands only regenerated well if
349 live trees remained nearby (either via moderate severity fire or close proximity to live-tree edge)
350 suggests that the legacy of seed source distribution is the key driver of regeneration dynamics in
351 dry forests (Harvey et al. 2013; Kemp et al. 2015). Overall, dry Douglas-fir forests appear less
352 resilient to high-severity fire than are mesic Douglas-fir forests, in which severe burn patches are
353 thought to have been more common historically (Baker 2009).

354 The role of seed source distance was similar for mesic and dry stands (Fig. 3), but the
355 former generally had higher densities across all distances – perhaps most importantly at the
356 longest distances. The relationship for dry stands was consistent with conventional seed dispersal
357 curves for interior conifers (McCaughey et al. 1986) and empirical observations in other dry
358 forests (Kemp et al. 2015), with regeneration declining to low or zero values beyond ~100-200
359 m. For mesic stands, however, regeneration densities were still relatively high well beyond 200
360 m, similar to findings from relatively mesic coastal Douglas-fir forests west of the Cascade
361 Range crest (Shatford et al. 2007; Donato et al. 2009). This pattern is likely the cumulative result
362 of infrequent long-distance dispersal events (wind updrafts, over-snow transport, etc.) occurring
363 over the 24 years since the fires, with mesic locales being the most receptive to continued
364 establishment (see below). The spatial complexity of mixed-severity fires in lower-montane
365 forests rarely produces seed-source distances exceeding the range at which mesic stands
366 regenerated (Donato et al. 2009; Kemp et al. 2015), suggesting that mesic stands are quite
367 resilient to even very large events such as the 1988 Yellowstone fires.

368

369 *The seral community: role of lodgepole pine and successional implications*

370 Perhaps the most important compositional response was the increased frequency and
371 density of lodgepole pine (Fig. 5), which became dominant or co-dominant with Douglas-fir in
372 15% of plots following fire. Shade-intolerant lodgepole pine is well-known for robust
373 regeneration after severe fires (e.g., Turner et al. 1997), in part due to serotinous cones which
374 open when heated by fire. Indeed, the highest levels of cone serotiny in *P. contorta* occur at
375 lower elevations in the GYE, in proximity to our study areas (Tinker et al., 1994; Schoennagel et
376 al., 2003). The places where lodgepole pine tended to increase in relative abundance (Fig. 4) are
377 consistent with the role of serotiny: the areas where it was present before the fire and areas most
378 distant from live-tree edges, as regeneration from serotinous cones is not necessarily tied to
379 surviving trees (Kemp et al. 2015; Harvey et al. 2016). The increase in *P. contorta* relative
380 abundance resulted from the species' insensitivity to distance-to-live-edge whereas other species'
381 abundances declined with distance from edge. Where present, the greater initial height growth of
382 lodgepole pine (Fig. 5) suggests it will potentially dominate the canopy profile of early- to mid-
383 seral stands.

384 Post-fire tree species composition was largely similar to that of the pre-fire community,
385 but a few shifts will likely have implications for long-term succession. Although Douglas-fir
386 remained the dominant species in 80% of the plots that had tree regeneration, minor increases in
387 several other species translated to a drop in the relative dominance of Douglas-fir, from 95% of
388 stems pre-fire to 69% post-fire (Table 1, Fig. 5). The small relative increases of Engelmann
389 spruce and subalpine fir in mesic stands, and quaking aspen in dry stands (likely a mix of both
390 seedlings and sprouts), reflect a regeneration window afforded by the fires, and suggest an initial
391 floristics pattern wherein the species that will appear over the next sere (including shade-
392 tolerant/late-successional species) establish concurrently after disturbance (see Turner et al.

393 1999; Donato et al. 2012; McKenzie & Tinker 2012). Mature Douglas-fir forests in the GYE
394 tend to be dominated in the over- and understory by their namesake species, in part due to its
395 high tolerance of drought and its own shade (Minore 1979). Our data indicate that the 1988 fires
396 created a window for other species to establish and increased stand-level diversity for at least the
397 next several decades.

398

399 *Temporal patterns of tree establishment*

400 Tree establishment in lower-montane forests following the 1988 fires has been a multi-
401 decade process, with a relatively slow start (Fig. 6). This finding differs from adjacent subalpine
402 forests of the GYE, which often fill in with lodgepole pine within a few years of fire (Turner et
403 al. 1997, 2003, 2016). In more mesic coastal Douglas-fir forests, regeneration windows
404 commonly last several decades (Tappeiner et al. 1997; Poage et al. 2009; Tepley et al. 2013;
405 Freund et al. 2014); thus, our study stands may have experienced only a portion of their eventual
406 establishment. However, the clear tapering pattern by the third decade (Fig. 6) suggests
407 establishment has largely ceased for at least the time being. With a median density of 3294 trees
408 ha⁻¹, most mesic stands are already at or approaching full occupancy (and on a trajectory toward
409 density-dependent mortality), making additional establishment unlikely until something
410 stimulates a change (e.g., additional disturbance). In dry stands, establishment had diminished to
411 near zero by 15 years post-fire and thereafter was significantly less than in mesic stands (Fig. 6);
412 this was despite being well below full occupancy in many cases (relative to pre-fire densities),
413 suggesting some other limitation on new establishment. As such, any further regeneration would
414 occur as a semi-distinct age class rather than an extension of the current one, as observed for
415 some coastal Douglas-fir forests (Poage et al. 2009; Tepley et al. 2013). Importantly, the window

416 for tree establishment is not limited to the first several years or even the first decade after fire,
417 likely providing a buffer against periods of unfavorable conditions (e.g., drought) should they
418 occur during the initial post-fire years (Harvey et al. 2016).

419

420 *Self-replacement trends and potential lower treeline shifts – directional or cyclical?*

421 A key objective of this study was to evaluate the potential for shifts in lower-montane
422 treelines, given the extent of the 1988 Yellowstone fires (Turner et al. 2003; Romme et al. 2011)
423 and the exceptionally warm climatic conditions since (Shuman 2012). Although an even longer
424 time since fire would be ideal for assessing such state shifts, the quarter-century elapsed since the
425 1988 fires can provide useful insight. In dry forests nearest the ecotone – presumably the most
426 vulnerable to type conversion (Rehfeldt et al. 2006; Jiang et al. 2013) – nearly two-thirds of
427 stands that burned with complete overstory mortality have experienced an effective lack of
428 regeneration even 24 years after fire, and the remaining stands are not progressing toward self-
429 replacement (Fig. 7). This cessation or lack of post-fire tree establishment near the lower treeline
430 is consistent with hypotheses of upward treeline shifts (Romme & Turner 1991), but a key
431 question is for how long: Are these truly directional shifts under a warmer climate, or cyclical
432 dynamics of marginal forests? In other words, is this an indication of low ‘ecological resilience’
433 (state change) or merely low ‘engineering resilience’ (rate of recovery) (Peterson et al. 1998)?

434 A cyclical-dynamics interpretation (i.e., slow engineering resilience but not indicative of
435 state change) would be best supported if ecotonal forests have historically developed along a
436 very slow pathway, such that the current lack of regeneration is within normal system behavior.
437 The literature on Rocky Mountain Douglas-fir forests is unfortunately too scant to draw such
438 comparisons. Anecdotal observations from the early 20th century suggest that failure or

439 prolonged delay of regeneration following severe fires has occurred in dry Douglas-fir forests in
440 the past (e.g., Peirce 1915; Baker 2009) (however one study reported evidence of regeneration
441 within a few decades of past stand-replacing fires in GYE Douglas-fir forests, some of which
442 were apparently the dry type (Littell 2002)). Likewise, periodic encroachment of Douglas-fir into
443 low-elevation grasslands, the inverse of the above dynamic, is known to occur during favorable
444 periods with little or no disturbance (Arno & Gruell 1986; Heyerdahl et al. 2006). Taken
445 together, these observations suggest a plausible dynamic in which Douglas-fir forests establish
446 on the most marginal (otherwise grassland) sites only during intermittent periods of favorable
447 climate (wet, cool, low moisture deficits) and low disturbance activity, then periodic severe
448 disturbances and warmer conditions convert sites back to grassland for an extended period, with
449 forests eventually ‘encroaching’ again (i.e., re-establishing) during favorable periods and
450 beginning the cycle anew (see Whitlock 1993; Powell & Hanson 2006; Huerta et al. 2009). Thus,
451 it is plausible that our data may be depicting a portion of this very long-term cycle.

452 Support for a directional-shift interpretation (i.e., erosion or loss of ecological resilience)
453 includes the uniquely absent regeneration processes occurring near the lower treeline relative to
454 other locales, and current and projected future trends in climate (regeneration conditions). A
455 widespread lack of regeneration was distinct to ecotonal stands; mesic stands as well as dry
456 stands not immediately adjacent to the ecotone did not exhibit this response. Stands without
457 significant tree regeneration are currently dominated by grasses, herbs, and shrubs, with no sign
458 of new or continuing tree establishment (Figs. 6,7), which is at least consistent with conversion
459 to non-forest. Although the use of self-replacement density as a best-approximation threshold for
460 regeneration success (given the lack of relevant literature on these forests) is likely imperfect, the
461 near-complete lack or stagnation of tree establishment in ecotonal stands is not dependent on any

462 threshold definition and, after a quarter-century of post-fire time, appears consistent with not just
463 a slow rate of recovery, but little to no recovery. Moreover, the potential for tree establishment to
464 resume in marginal low-elevation (warm, dry) areas stands appears low based on current trends
465 in climate (Jiang et al. 2013; Rehfeldt et al. 2006). Cool, moist weather-years are projected to be
466 increasingly rare by the mid-21st century, with years of high moisture deficits (dry) by current
467 standards becoming the norm (Westerling et al. 2011). Thus, the data and trends are at least
468 consistent with hypotheses that ongoing shifts in climate are sufficient to break ecotonal stands'
469 relatively low ecological resilience and effect a state shift.

470 A definitive distinction between these two interpretations may be beyond what can be
471 concluded with any current dataset, but there are some common implications for long-term forest
472 cover under either dynamic. For example, if our findings are half of a cyclical dynamic, we can
473 at least conclude that the cycle is a long one. Data from dry ecotonal Douglas-fir forests of the
474 GYE indicate that most stands are not recently encroached (for example, due to fire exclusion);
475 rather they are long-established stands with co-dominant trees commonly 150-250 years old
476 (Donato et al. 2013). Even if regeneration were to commence or resume in severely burned
477 ecotonal stands, the time required for tree establishment and growth on these marginal sites (>2-
478 3 decades to reach breast height based on our data) suggests the 1988 fires effectively eliminated
479 forest cover near much of the ecotone for at least a half-century, likely much longer. Spatial data
480 (National Park Service, US Forest Service) indicate that, of the ~35,000 ha of lower-montane
481 forest burned in the 1988 fires, ~6600 ha were within 150 m of the grassland ecotone and burned
482 with high severity. With 63% of such stands not returning toward forest cover (Fig. 7c), we
483 estimate that over 4000 ha have been effectively converted to non-forest for an extended period.
484 Whether this conversion is categorically directional or long-term cyclical, the change was

485 relatively abrupt and suggests that several key ecosystem functions – such as wildlife habitat,
486 hydrological processes, and carbon and energy balance – are likely to reflect those of sagebrush
487 grassland rather than forest for much of the coming century.

488

489 *Conclusions*

490 Our findings provide support for two widely posited, but difficult to test, predictions
491 regarding climate change and forests (e.g., Breshears et al. 2005; Rehfeldt et al. 2006; Jiang et al.
492 2013). First, we found empirical evidence consistent with a prolonged contraction of tree cover
493 near the lower (warm, dry) forest margin under a warming climate, a response distinct from
494 similarly-composed forests farther from the lower ecotone where post-fire resilience was high.
495 Whether these changes are part of a long-term cycle associated with fluctuating conditions for
496 tree establishment in marginal sites, versus categorically directional with ongoing climate
497 change, is unresolved, but both dynamics share some common implications for reduced montane
498 forest cover in the coming century. Second, this change occurred as an abrupt event catalyzed by
499 a large disturbance, suggesting that the direction of treeline shifts may be predictable, but that
500 their timing is punctuated and stochastic. Further understanding the nature of these changes
501 across a range of mountain regions and disturbance types, as well as their implications for
502 landscape ecology, ecosystem function, and the provision of ecosystem services (Millar &
503 Stephenson 2015) will be essential for informed ecosystem management in the coming decades.

504

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512

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685 **Table 1.** Pre-fire stand structure, abiotic character, and post-fire vegetation cover in sampled
 686 mesic and dry Douglas-fir-dominated stands burned by the 1988 Yellowstone Fires.

Metric	Mesic stands (n=23)	Dry stands (n=32)
Prefire basal area (m ² ha ⁻¹)	40 (35-45)	30 (25-36)
Prefire stem density of trees >15 cm dbh (trees ha ⁻¹)	385 (338-432)	265 (234-302)
Prefire dominance by <i>Pseudotsuga</i> (% of stems)	93 (88-97)	97 (94-100)
Prefire mesic-associate† abundance (% of stems)	7 (3-12)	2 (0-5)
Prefire dry-associate† abundance (% of stems)	0 (0-0)	1 (0-2)
Elevation (m)	2133 (2097-2169)	2169 (2142-2196)
Aspect (cosine-transformed, 0=NE, 2=SW)	0.33 (0.19-0.47)	1.33 (1.07-1.59)
Slope (degrees)	30 (27-33)	28 (25-31)
Distance to live-tree edge after 1988 fires (m)	65 (5-376)	115 (2-608)
Distance to grassland ecotone (m)	555 (143-1568)	194 (29-2262)
Post-fire shrub cover at 24 years (%)	16 (11-21)	20 (13-27)
Post-fire graminoid cover at 24 years (%)	23 (15-31)	21 (15-27)

687 Data are means and 95% CIs, except distances to seed wall and grassland ecotone (highly non-
 688 normal) which are medians and 5th-95th percentiles.

689 See Appendix 1 for further details of classification of mesic and dry stands.

690 † Mesic associates include *Pinus contorta*, *Picea engelmannii*, and *Abies lasiocarpa*; dry
 691 associates include *Juniperus scopulorum* and *Pinus flexilis*.

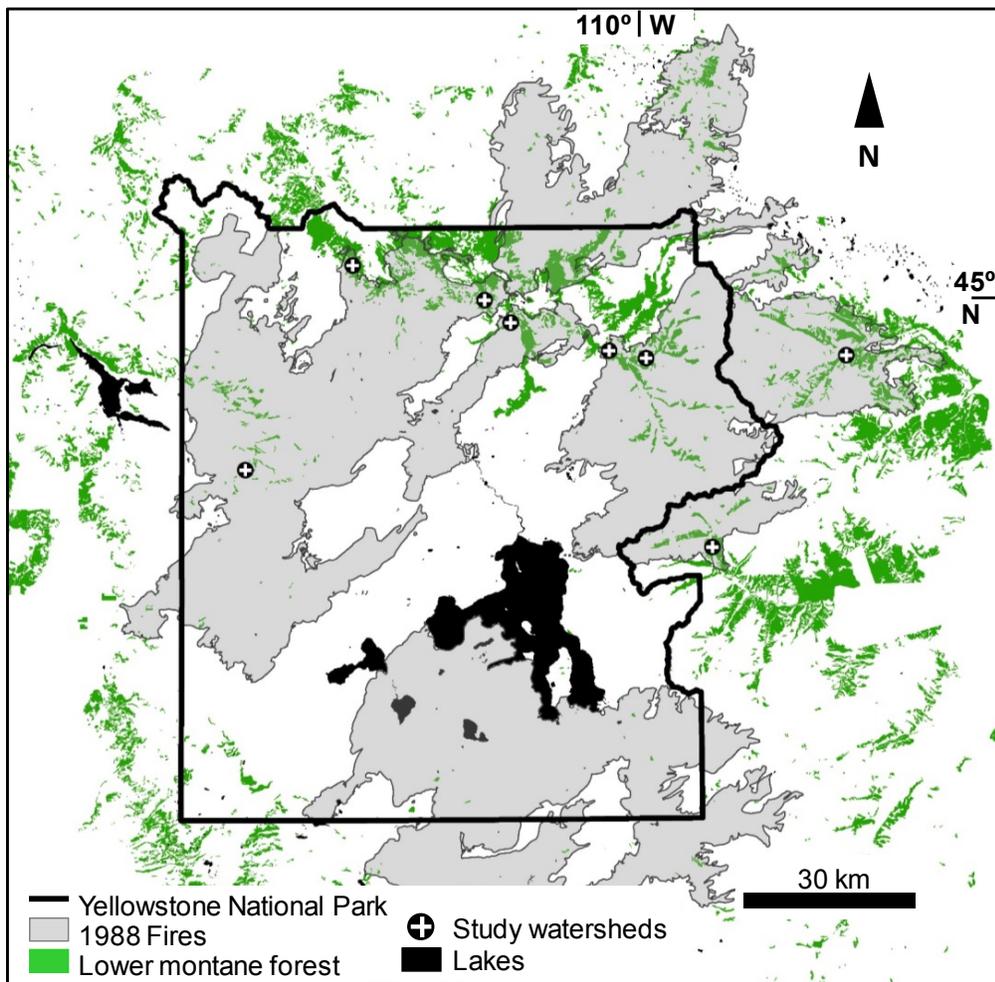
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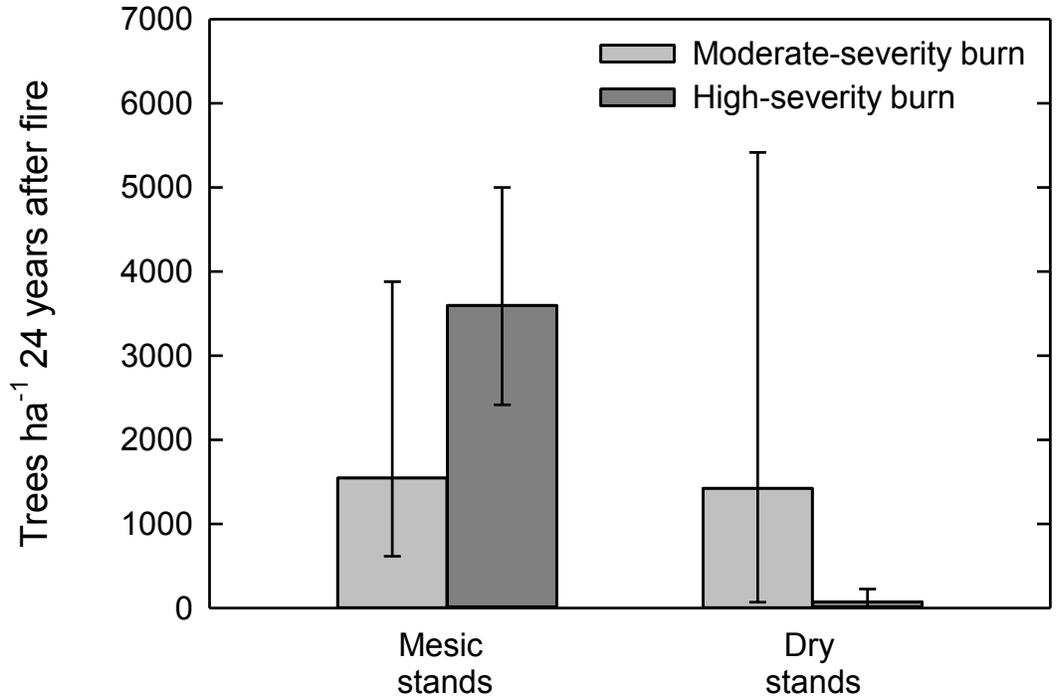


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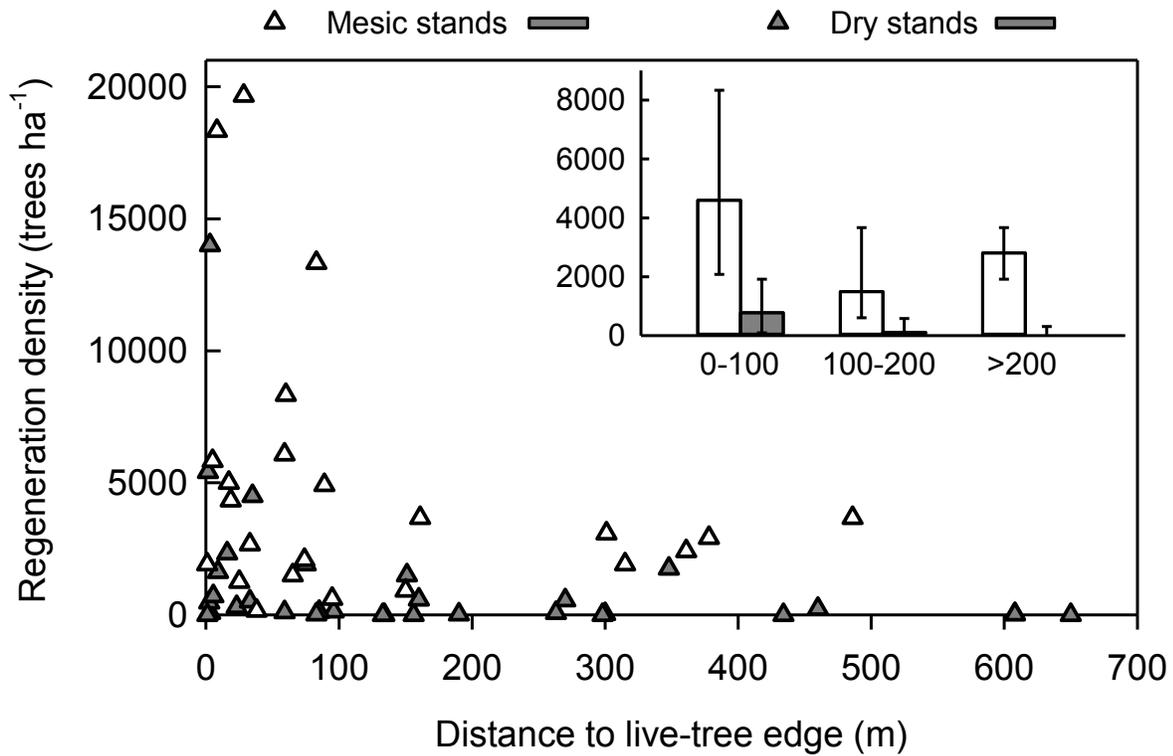
700 **Figure 1:** Study area in the Greater Yellowstone Ecosystem (GYE). Lower-montane forests
 701 dominated by Douglas-fir occur in scattered parcels on the shoulders of the Yellowstone Plateau,
 702 and were affected by the 1988 fires as a spatially disparate mixed-severity event. Each of the
 703 eight study watersheds (+ symbols) contained 6-8 sample stands spaced at 200-m intervals.
 704 Sources for spatial data courtesy of the National Park Service and U.S. Forest Service.

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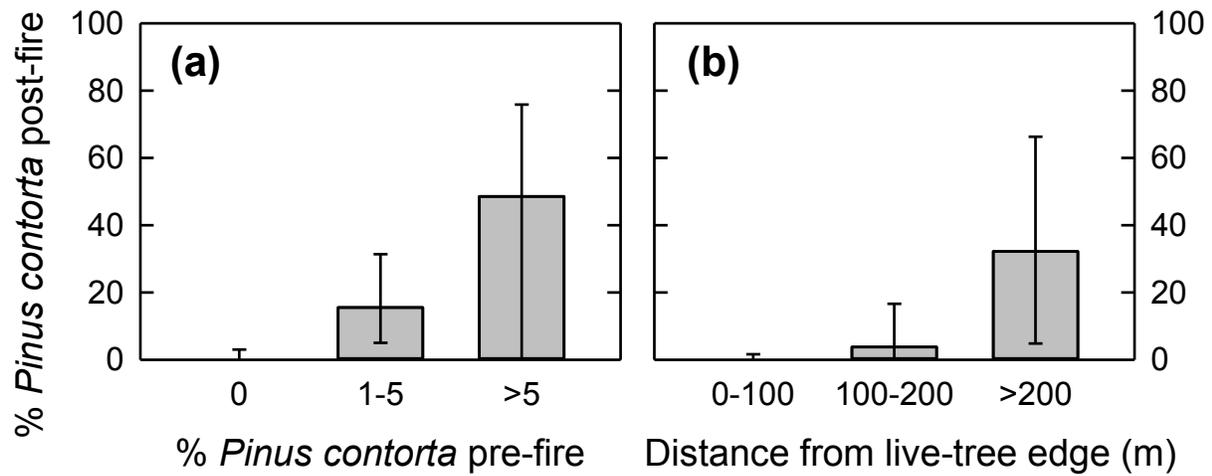
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Figure 2. Tree regeneration density in lower-montane Douglas-fir dominated forests 24 years after the 1988 Yellowstone fires, by environmental setting and burn severity. Bar graphs are medians and bootstrapped 95% CIs. Mesic stands had higher regeneration overall and also did not show the negative response to high-severity fire that did dry stands.



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Figure 3. Tree regeneration density in lower-montane forests burned by the 1988 Yellowstone fires, as a function of distance from live-tree edge (patch of surviving mature trees >1 ha). Inset shows medians and bootstrapped 95% CIs by distance class. Dry stands followed a typical curve expected for interior Douglas-fir forests (densities approach zero beyond 100-200 m), but mesic stands had higher densities at all distances and maintained median values >1500 ha⁻¹ beyond 200 meters from live-tree edges.



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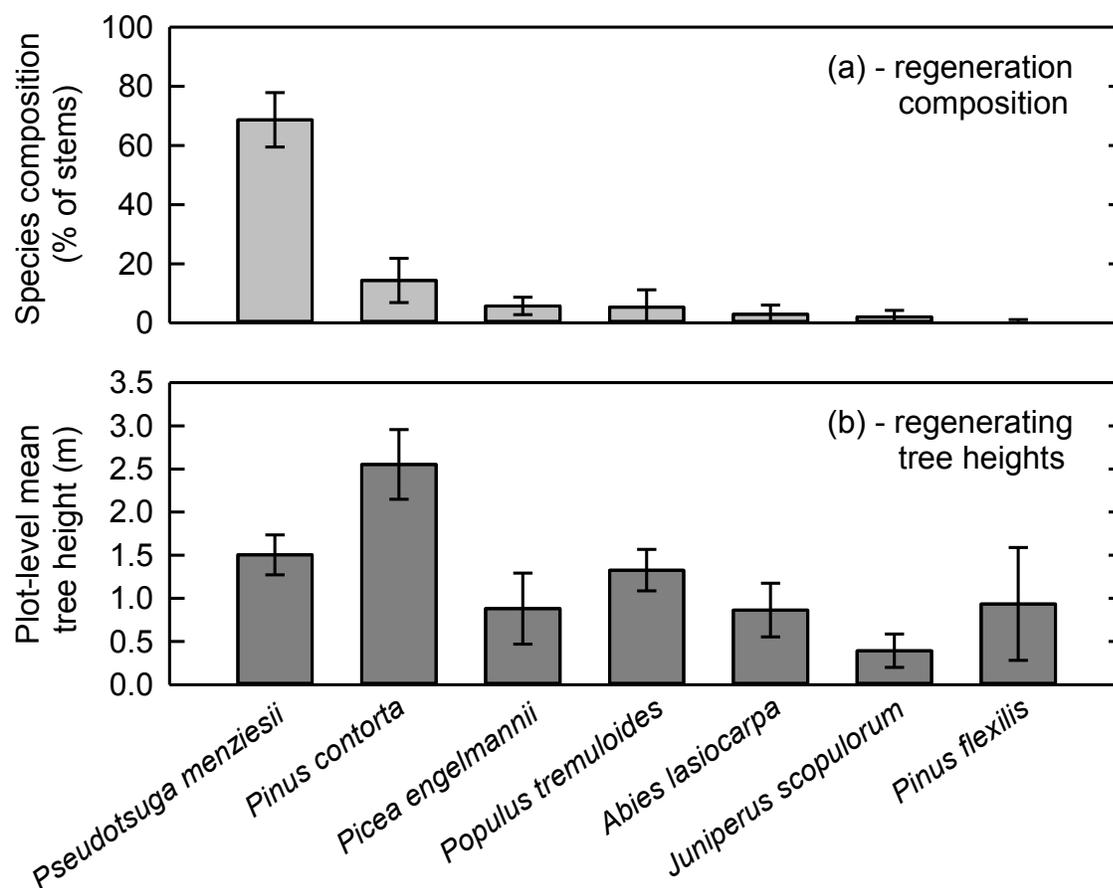
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Figure 4. Relative abundance of *Pinus contorta* in post-fire stands as a function of (a) the pre-fire abundance of *Pinus contorta* (% of pre-fire stems) and (b) distance from live-tree edge. Data are medians and bootstrapped 95% CIs. *Pinus contorta* increased in relative abundance with pre-fire presence and at the farthest distances from live-tree edge.



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747 **Figure 5.** Species composition (a) and height of regenerating trees (b) in lower-montane forests

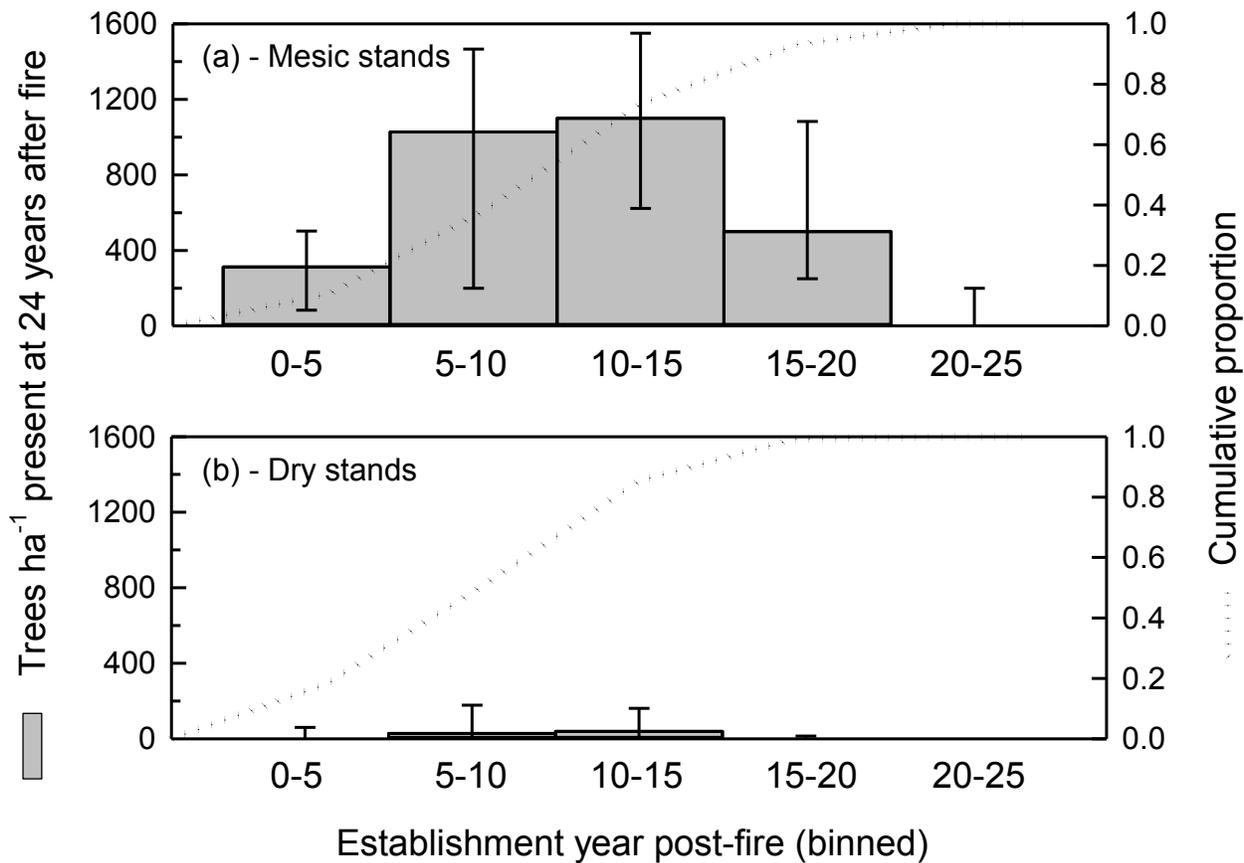
748 24 years after the 1988 Yellowstone fires. Data are means and 95% CIs. Douglas-fir maintained

749 population dominance; lodgepole pine, where present, was significantly taller than other species.

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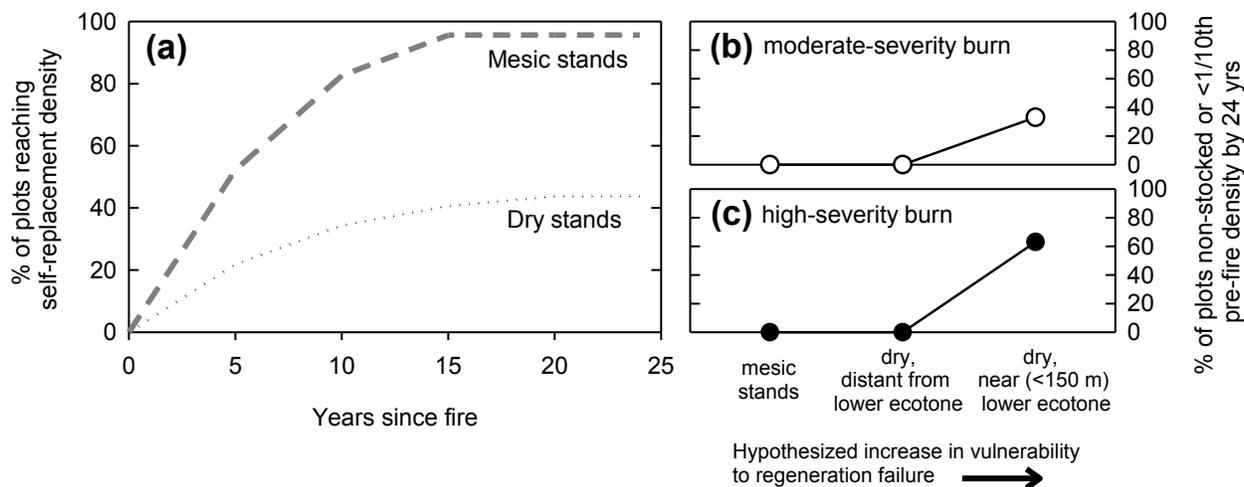
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Figure 6. Temporal establishment pattern for trees present 24 years after the 1988 Yellowstone fires. Data are medians and bootstrapped 95% CIs. In addition to higher establishment rates, mesic stands continued regenerating in later years (>15 years) more than did dry stands (Chi-square $\chi_4^2 = 22.3$, $P < 0.001$).

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775 **Figure 7.** Self-replacement trends for lower-montane forests burned by the 1988 Yellowstone
776 fires. The proportion reaching stand replacement (panel a) was near 100% for mesic stands by 15
777 years, but below 50% for dry stands by 24 years post-fire, and not increasing. The proportion of
778 plots effectively not regenerating (non-stocked or <1/10th pre-fire density; panels b and c) was by
779 far the highest in dry stands closest to the grassland ecotone that burned with high severity (n=23
780 mesic stands, 19 dry stands distant from ecotone, and 13 dry stands near ecotone). Stands
781 classified as not effectively regenerating had <30 seedlings and saplings ha⁻¹.

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