

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

DANIEL C. DONATO,^{1,2,†} BRIAN J. HARVEY,³ AND MONICA G. TURNER⁴

¹Washington State Department of Natural Resources, Box 47014, Olympia, Washington 98504 USA

²School of Environmental and Forest Sciences, University of Washington, Seattle, Washington 98195 USA

³Department of Geography, University of Colorado, Boulder, Colorado 80309 USA

⁴Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA

Citation: Donato, D. C., B. J. Harvey, and M. G. Turner. 2016. Regeneration of montane forests 24 years after the 1988 Yellowstone fires: A fire-catalyzed shift in lower treelines? *Ecosphere* 7(8):e01410. 10.1002/ecs2.1410

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

Key words: climate change; Douglas-fir; ecotone; Greater Yellowstone Ecosystem; lower-montane forest; *Pseudotsuga menziesii*; Rocky Mountains; treeline; wildfire.

Received 29 March 2016; accepted 7 April 2016. Corresponding Editor: D. P. C. Peters.

Copyright: © 2016 Donato et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** daniel.donato@dnr.wa.gov

INTRODUCTION

One of the most uncertain aspects of climate change is how it may shift the upper and lower elevational limits of mountain forests. Most models suggest upward migrations of treelines under a warming climate (Parmesan and Yohe 2003), but the potential mechanisms and rates of such changes

are unclear, confounding predictive capabilities (Soja et al. 2006). Studies of treeline shifts and their consequences have so far focused primarily on forest expansion at the upper, alpine ecotone (e.g., Harsch et al. 2009, Dirnböck et al. 2011). However, forests near the low-elevation ecotone, where moisture regimes are just sufficient to support tree cover, are among the most vulnerable to warming

and drying (e.g., Breshears et al. 2005). Predictions for the 21st century suggest replacement of many dry coniferous forests with steppe vegetation over significant portions of western North America (Jiang et al. 2013). Such shifts in lower treelines can strongly influence the extent and biogeography of montane forest landscapes, as well as ecosystem functions including terrestrial carbon storage (Breshears and Allen 2002, Jiang et al. 2013, Millar and Stephenson 2015).

Climate-driven changes in vegetation distribution are most likely to occur as a series of abrupt events rather than gradual migrations. Major change is catalyzed by disturbances such as large wildfires, severe droughts, or insect outbreaks that break the inertia of a system dominated by long-lived organisms (e.g., conifers) and allow the establishment of a different assemblage (Cwynar 1987, Frelich and Reich 2010, Johnstone et al. 2010). For example, rates of treeline shift associated with projected changes in temperature and precipitation alone are likely on the order of < 100 m per century (Loehle 2000), whereas losses exceeding 10,000 km² of forest have occurred after single events in the western United States (Breshears et al. 2005). Major disturbances such as very large fires are expected to increase substantially in most North American forests during the 21st century (Barbero et al. 2015). It is therefore essential to track the fate of forests that define the lower limits of montane tree cover when they experience major disturbances.

A landmark event that ushered in the current era of large disturbances under a warmer climate was the 1988 fires in and around Yellowstone National Park, United States (Romme et al. 2011). Driven by extreme winds and drought, the fires burned in a mosaic pattern over 600,000 ha, ranking among the largest temperate-zone wildfires in recorded history. The resulting landscape lent a wealth of novel insights into robust forest regeneration and ecosystem responses following large wildfires (Turner et al. 1997, 2003, 2004, 2016, Romme et al. 2011), with broad implications for other temperate forests (e.g., Lloret et al. 2002, Donato et al. 2009, Christensen 2014). These insights came largely from subalpine lodgepole pine (*Pinus contorta* var. *latifolia*) forests of the Yellowstone plateau. Little appreciated is that the 1988 fires also burned significant areas of lower-montane forest dominated by interior Douglas-fir

(*Pseudotsuga menziesii* var. *glauca*). Although only 6% of the fires' area was in lower-montane forests, this equated to ~35,000 ha, which alone ranks among the top 5–10% of fires in the United States (Barbero et al. 2015). The period since the fires has been characterized as exceptionally warm regionally, with annual temperatures since the 1980s at their highest in the last 6000 yr (Shuman 2012).

Douglas-fir-dominated forests in the Greater Yellowstone Ecosystem (GYE) inhabit the elevation zone below subalpine forests and above grass/sage steppe, thus forming the low-elevation forest ecotone. Stands near the former are cool, mesic, dense forests, while stands near the latter are warm, dry, open parklands (Arno and Gruell 1986, Bradley et al. 1992, Baker 2009, Donato et al. 2013a, b). The fire ecology and regeneration dynamics of interior Douglas-fir forests are poorly understood (Baker 2009, Donato et al. 2013a). Available data suggest a mixed-severity fire regime with less frequent but more severe fires on mesic sites than on dry sites (Bradley et al. 1992, Baker 2009) and that protracted post-disturbance regeneration over multiple decades is common (Baker 2009, Donato et al. 2013a), as in other Douglas-fir forests (Tepley et al. 2013, Freund et al. 2014). Mesic stands are expected to regenerate faster and more abundantly than dry stands (Baker 2009, Kemp et al. 2015) and may be less vulnerable to postfire regeneration failure under a warming climate than dry stands near the ecotone (Romme and Turner 1991). Pollen records from the GYE indicate wide temporal variation in Douglas-fir's abundance over the Holocene era, and concurrent variations in steppe vegetation suggest oscillations in lower treelines through time (Whitlock 1993, Huerta et al. 2009). Upward shifts occurred during warmer periods with high fire activity, while forest expansion occurred during cooler, wetter periods (Huerta et al. 2009). The 21st century is projected to experience unprecedented rates of climatic warming and large-fire activity (Westerling et al. 2011), which may reorganize landscape vegetation patterns in Greater Yellowstone in uncertain ways. Twenty-first-century contraction of lower treelines was hypothesized previously (Romme and Turner 1991); however, the realization of such shifts, as well as basic tenets of postfire regeneration dynamics, is vastly understudied in Rocky Mountain Douglas-fir forests.

Here, we report on regeneration dynamics in lower-montane forests burned by the 1988 Yellowstone fires. We sought to test a central hypothesis that, under current climate conditions, dry lower-margin forests would be less apt to attain self-replacement following fire than adjacent, similarly composed forests farther from

the lower ecotone. The nearly two-and-a-half decades elapsed since the fires (at time of sampling) presented an excellent opportunity to interpret patterns of forest establishment. We directly tested the concept of “engineering resilience” (rate of recovery) and evaluated the degree to which regeneration trends are indicative of

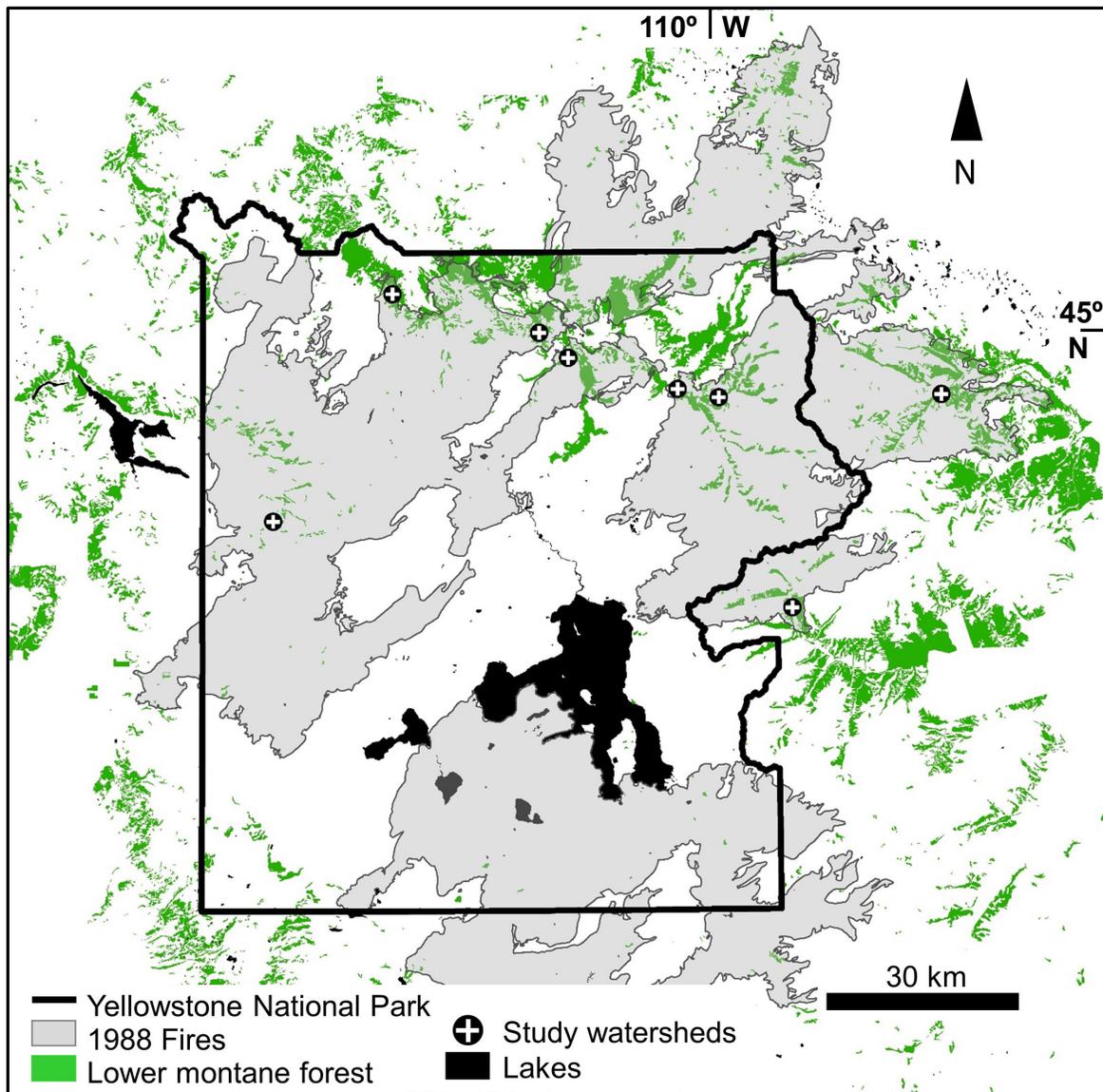


Fig. 1. Study area in the Greater Yellowstone Ecosystem (GYE). Lower-montane forests dominated by Douglas-fir occur in scattered parcels on the shoulders of the Yellowstone Plateau and were affected by the 1988 fires as a spatially disparate mixed-severity event. Each of the eight study watersheds contained six to eight sample stands spaced at 200-m intervals. Sources for spatial data courtesy of the National Park Service and US Forest Service.

low “ecological resilience” of ecotonal stands (potential for state change) (see Peterson et al. 1998). Data supporting our central hypothesis would be consistent with the expectation of disturbance-catalyzed treeline shifts in a warmer climate. We addressed the following questions: (1) After 24 yr, how does postfire tree density vary between mesic and dry stands, as influenced by burn severity? (2) To what degree does the major community associate in these forests, lodgepole pine (high cone serotiny locally), increase in relative abundance in large stand-replacement patches? (3) What are the temporal patterns of tree establishment? (4) To what degree, and with what timing, are lower-montane forests self-replacing following the 1988 fires, and how does this vary between mesic vs. dry stands (particularly those closest to the low-elevation treeline)?

METHODS

Study area

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

Lower-montane, Douglas-fir-dominated forests occur in scattered parcels across the GYE (Fig. 1). Stands nearest the grass/sage ecotone are xeric in character, typically with low tree densities, open/grassy understories, and presence of limber pine (*Pinus flexilis*) and Rocky Mountain juniper (*Juniperus scopulorum*) (Bradley et al. 1992, Baker 2009). Farther from the ecotone (higher local elevation and/or wetter), Douglas-fir grows in dense, multistoried stands mixed to varying degrees with lodgepole pine, Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) (Bradley et al. 1992, Baker 2009). The shade-intolerant,

serotinous-coned lodgepole pine is perhaps the most important associate of Douglas-fir in the GYE, often proliferating after severe fires (Bradley et al. 1992). The fire ecology of Rocky Mountain Douglas-fir forests is poorly understood; studies indicate a mixed-severity fire regime with low/moderate-severity fires occurring at approximately 20- to 80-yr intervals prior to effective fire exclusion and large or high-severity fire events occurring at longer intervals of approximately 100–200 yr (Houston 1973, Loope and Gruell 1973, Barrett 1994, Littell 2002, Korb 2005, Baker 2009, Huerta et al. 2009). The relative ratio of high- vs. low-severity patches is thought to be greater in mesic than in dry/ecotonal types (Bradley et al. 1992, Baker 2009).

The 1988 fires influenced lower-montane forests as a spatially disparate, mixed-severity event (Fig. 1). Based on locally field-validated thresholds (Harvey 2015) in the relative differenced normalized burn ratio (RdNBR; Miller and Thode 2007), lower-montane forests experienced proportionally less high-severity fire (47% of area) than did adjacent subalpine forests (61%). Mean patch size of high-severity burn (>90% canopy mortality) in lower-montane forests was 160 ha, two orders of magnitude lower than that in subalpine forests (14,520 ha), and the mean perimeter-to-area index was approximately twice as high (unitless values of 191 and 91 in lower-montane and subalpine forests, respectively). The above analysis was based on area-weighted values, retaining burn patch integrity where patches crossed forest types, using Monitoring Trends in Burn Severity data [www.mtbs.gov] and standard outputs from FRAGSTATS version 4 (McGarigal et al. 2012).

Data collection

Our sampling universe comprised lower-montane forests that were dominated by mature Douglas-fir at the time of the 1988 fires (minimum basal area 10 m²/ha, minimum tree density 80 trees/ha, > 50% stems *P. menziesii*; see Table 1). Given our research focus on secondary succession in response to canopy-opening disturbance, we sampled only areas that experienced moderate-to severe fire effects (>30% overstory mortality); purely surface fires were not studied. We sampled regeneration dynamics in eight watersheds (approximately second- to third-order), identified a priori based on spatial data showing overlap

Table 1. Prefire stand structure, abiotic character, and postfire vegetation cover in sampled mesic and dry Douglas-fir-dominated stands burned by the 1988 Yellowstone Fires.

Metric	Mesic stands (<i>n</i> = 23)	Dry stands (<i>n</i> = 32)
Prefire basal area (m ² /ha)	40 (35–45)	30 (25–36)
Prefire stem density of trees >15 cm dbh (trees/ha)	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)	2,133 (2,097–2,169)	2,169 (2,142–2,196)
Aspect (cosine-transformed, 0 = NE, 2 = SW)	0.33 (0.19–0.47)	1.33 (1.07–1.59)
Slope (°)	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 (143–1,568)	194 (29–2,262)
Postfire shrub cover at 24 yr (%)	16 (11–21)	20 (13–27)
Postfire graminoid cover at 24 yr (%)	23 (15–31)	21 (15–27)

Notes: Data are means and 95% CIs, except distances to seed wall and grassland ecotone (highly non-normal) which are medians and 5th–95th percentiles. See Appendix S2 for further details of classification of mesic and dry stands.

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

between 1988 fire perimeters and lower-montane forest. Sample watersheds were selected by going down the a priori list until field time ran out. In each watershed, we measured vegetation in six to eight stands, beginning from a random start and spaced at 200-m intervals (to minimize the potential for spatial autocorrelation; similar to Larson et al. 2013, Kemp et al. 2015) at a predetermined azimuth to cross one or more burn patches. Each watershed generally captured similar ranges in key abiotic and biotic characteristics and, importantly, included both moderate- and high-severity burn, broad ranges of distance to seed source, and both mesic and dry stands where both were present (Appendix S1).

Sampling occurred during summer 2012. Within each stand, we collected data in a 30 m diameter (0.07 ha) circular plot: postfire tree and other plant regeneration, prefire stand structure, and abiotic characteristics. For postfire regeneration, we recorded every tree stem in variable-sized subplots according to the density of postfire trees (sensu Kemp et al. 2015, Harvey et al. 2016). Default subplot size was four 2 × 15 m rectangular quadrats (120-m² total area) situated along cardinal directions from plot center. Subplot size was objectively decreased to four 0.5 × 15 m quadrats (30-m² total area) or increased to the entire plot (707-m² total area) if >200 or <10 trees were to be captured in the default subplot size, respectively. For each stem, we recorded species, height (cm), age by bud-scar count (yr), and evidence of leader

damage. Postfire cover for each of shrubs, forbs, and graminoids was recorded to the nearest 5% in four 0.25-m² circular subplots, one in each plot quadrant. Ground cover of wood, litter, bryophyte, soil, and rock was recorded in the same subplots. To enumerate prefire stand structure, we recorded the number of standing and down (but standing prefire) trees (>15 cm diameter at breast height [dbh]) that were rooted in the plot, noting species and current live/dead status. Distance to the nearest surviving mature prefire tree—and to a contiguous (>1 ha) patch of such trees—was measured from plot center with a TruPulse laser rangefinder. A similar distance measurement was made to the lower ecotone, by direct field measurement or from aerial photos combined with spatial vegetation data. Finally, we recorded the slope (°), aspect (°), and elevation (m) of each stand.

Data analysis

We categorized each stand as mesic or dry subtype based on a set of key abiotic and biotic variables (Table 1). These variables were identified through multivariate ordination (Appendix S2) of an independent set of unburned lower-montane Douglas-fir stands in the GYE, from a separate study (Donato et al. 2013a, b). Twenty-three of our 1988 fire stands were classified as mesic and 32 as dry. In brief, mesic stands were farther from the lower treeline; were on cooler aspects; and had higher prefire basal area, stem density, down wood abundance, and

canopy closure. Dry stands were closer to the lower treeline; were on warmer aspects; had greater grass abundance; and had lower prefire basal area, stem density, down wood abundance, and canopy closure. Mesic stands correspond generally to Fire Group 3 (moist Douglas-fir habitats) as described by Bradley et al. (1992), while dry stands correspond to Fire Group 1 and Fire Group 2 (dry Douglas-fir and limber pine habitats).

For evaluation of our research questions, we adopted a parsimonious approach (Murtaugh 2007) of confidence interval (CI) inference (Brandstätter 1999, Donato et al. 2013b). CIs carry similar inferential power as parametric and likelihood tests but can more readily convey information on effect sizes and variability (Brandstätter 1999, Altman et al. 2000). Data distributions in this study were non-normal and heavily zero-inflated, both for responses and for key predictor variables, making a regression framework less useful. Also, many commonly analyzed predictors such as aspect, prefire tree density, and distance to lower treeline were rolled into our integrative classification of stands as mesic and dry (see Table 1; Appendix S2). We constructed nonparametric bootstrapped 95% CIs that are free of distributional assumptions, robust to abundant zeros, and allow for asymmetrical intervals about the median (e.g., Altman et al. 2000). Bootstrapped intervals were constructed by resampling the data (with replacement) to obtain an identical-sized data set 1000 times, computing the median for each resample, and obtaining a 95% CI from bias-corrected percentiles of the 1000 median values (DiCiccio and Efron 1996, Davison and Hinkley 1997). CIs for each sample group are graphed for visual interpretation; statistical inference is based on the 95% CI for the difference in medians between groups (Altman et al. 2000).

For question 1 (regeneration density by stand type and burn severity), we computed bootstrapped 95% CIs for total tree density for each of mesic and dry types as a function of stand burn severity at the hectare scale (moderate vs. high, distinguished as < or > 90% overstory mortality, respectively) and distance to live-tree edge (a measure of the fires' effect on seed-source proximity via burn patch size). For question 2 (lodgepole pine response), we computed bootstrapped 95% CIs for lodgepole pine density as a function

of distance from live-tree edge and the relative abundance of lodgepole pine prefire, two key factors known a priori to drive lodgepole pine abundance where cone serotiny is important, as in low elevations of the GYE (Tinker et al. 1994, Schoenagel et al. 2003, Harvey et al. 2016). For question 3 (temporal patterns), we parsed the bud-scar (age-proxy) data into 5-yr bins, corresponding to the approximate resolution of bud-scar counts on older seedlings/saplings (Urza and Sibold 2013), then computed bootstrapped 95% CIs of tree densities for each age-class bin. We also compared the temporal distribution of regeneration between mesic and dry forests via chi-square tests on the 5-yr binned age data. For question 4, we enumerated the postfire year at which each stand had attained self-replacement status, by comparing net cumulative establishment density to site-specific prefire overstory density. While not without limitations, we adopted this flexible metric as an informative threshold rather than a blanket or arbitrarily defined stocking standard, as it accounts for site-to-site variation in productivity or carrying capacity (both between and within dry and mesic types). Finally, we assessed the proportion of stands not effectively regenerating (< 10% of prefire density, including non-stocked plots) along the hypothesized gradient in vulnerability to regeneration failure, from mesic

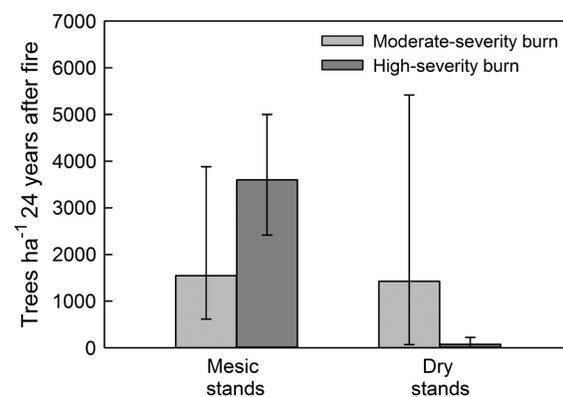


Fig. 2. Tree regeneration density in lower-montane Douglas-fir dominated forests 24 yr after the 1988 Yellowstone fires, by environmental setting and burn severity. Bar graphs are medians and bootstrapped 95% CIs. Mesic stands had higher regeneration overall and also did not show the negative response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

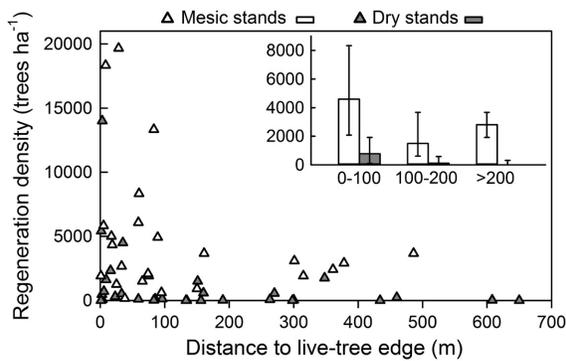


Fig. 3. Tree regeneration density in lower-montane forests burned by the 1988 Yellowstone fires, as a function of distance from live-tree edge (patch of surviving mature trees >1 ha). Inset shows medians and bootstrapped 95% CIs by distance class. Dry stands followed a typical curve expected for interior 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 beyond 200 m from live-tree edges.

stands (least vulnerable), dry stands not immediately adjacent (> 150 m) to the ecotone (moderately vulnerable), to dry stands near (< 150 m) the ecotone (most vulnerable).

RESULTS

Postfire tree density in mesic and dry stands

Across the study, 87% of plots (stands) were occupied by conifers (primarily Douglas-fir) at 24 yr postfire, with densities ranging from

(including non-stocked plots) 0 to 19,667 trees/ha and a median of 1250 trees/ha. Prefire densities (of trees >15 cm dbh) ranged from 85 to 622 trees/ha, with a median of 315 trees/ha. A mean of 75% of quadrants within each plot were occupied postfire (95% CI: 65–84% occupied), indicating well-distributed trees within stands.

Regeneration differed between mesic and dry stands in both overall abundance and response to burn severity (Fig. 2). Mesic stands had a median regeneration density of 3294 trees/ha, more than an order of magnitude higher than dry stands, which had a median density of 195 trees/ha (95% CI for difference in medians 1979–5572 trees/ha). Dry stands regenerated primarily after moderate-severity fire (median 1425 trees/ha) and had significantly less regeneration following high-severity fire (median 74 trees/ha) (95% CI for difference in medians 354–5388 trees/ha), whereas mesic stands did not show this effect (Fig. 2). Regeneration abundance showed a strong negative association with distance to live-tree edge (Fig. 3). Median densities were highest within 100 m of edges (4598 and 781 trees/ha in mesic and dry stands, respectively), tapering to near zero beyond 100 m in dry stands but remaining above 1500 trees/ha well beyond 200 m in mesic stands (Fig. 3).

Lodgepole pine response and seral community

Lodgepole pine outnumbered all other secondary conifers combined, having increased in presence and relative abundance from prefire stands. Greater prefire abundance of *P. contorta*

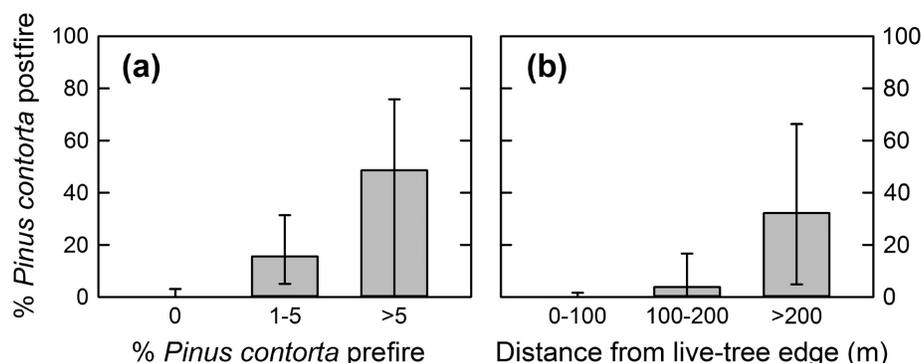


Fig. 4. Relative abundance of *Pinus contorta* in postfire stands as a function of (a) the prefire abundance of *P. contorta* (% of prefire stems) and (b) distance from live-tree edge. Data are medians and bootstrapped 95% CIs. *P. contorta* increased in relative abundance with prefire presence and at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

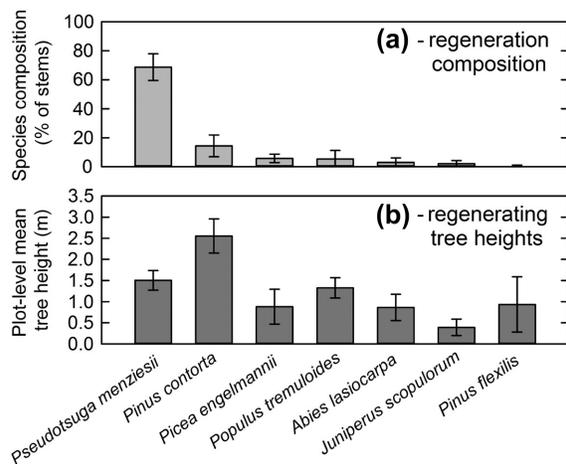


Fig. 5. Species composition (a) and height of regenerating trees (b) in lower-montane forests 24 yr after the 1988 Yellowstone fires. Data are means and 95% CIs. Douglas-fir maintained population dominance; lodgepole pine, where present, was significantly taller than other species.

and greater distance to live-tree edge were associated with increases in *P. contorta* postfire relative abundance (Fig. 4). Stands with no prefire presence of *P. contorta* had a median of 0% of *P. contorta* stems postfire, while those with even a minimal prefire (<5% of prefire stems) had a median of 16% postfire (95% CI

for difference 5–38%). There was suggestive evidence of a further increase in postfire importance of *P. contorta* with greater prefire abundance (another 33% increase when prefire abundance exceeded 5%), but variability was high (95% CI for difference –3–69%) (Fig. 4a). Postfire relative abundance of lodgepole pine was low at short and intermediate distances from live-tree edges (medians both <4%), and greatest at distances >200 m (median 32%; 95% CI for increase 5–78%) (Fig. 4b).

Douglas-fir remained present in 80% of plots and constituted 69% of postfire trees on average, followed by lodgepole pine, which was present in 45% of plots and averaged 14% of postfire trees (Fig. 5a). Other species in descending order of representation were Engelmann spruce, quaking aspen (*Populus tremuloides*), subalpine fir, Rocky Mountain juniper, and limber pine (Fig. 5a). Composition of postfire trees varied relatively little between mesic and dry stands, particularly for Douglas-fir (65% in mesic stands, 72% in dry) and lodgepole pine (14% and 15%, respectively). Mesic stands averaged greater abundance of subalpine fir (4.2% vs. 1.8% in dry stands) and Engelmann spruce (10% vs. 2%), but less quaking aspen (2% vs. 8%). Mesic and dry stands did not differ in terms of other vegetation abundance: shrub cover averaged 16% \pm 5% in mesic stands and 20% \pm 7% in dry stands, and graminoid cover

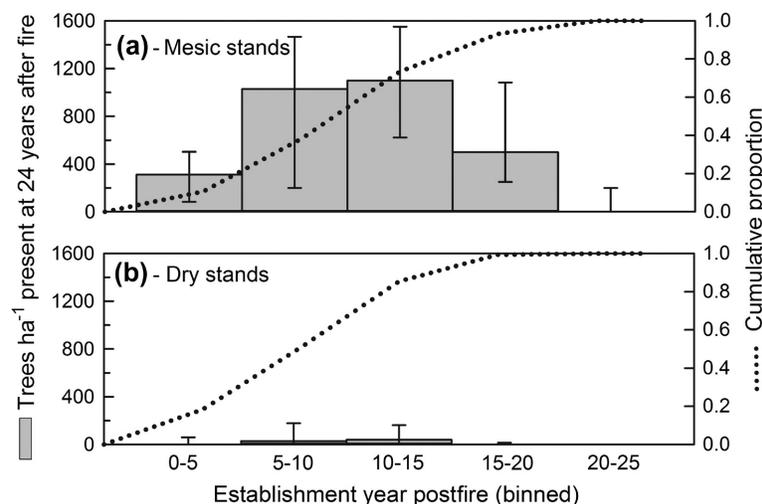


Fig. 6. Temporal establishment pattern for trees present 24 yr after the 1988 Yellowstone fires. Data are medians and bootstrapped 95% CIs. In addition to higher establishment rates, mesic stands continued regenerating in later years (>15 yr) more than did dry stands ($\chi_4^2 = 22.3$, $P < 0.001$).

averaged $23\% \pm 8\%$ and $21\% \pm 6\%$, respectively (Table 1). Douglas-fir, the primary determinant of average stand height, had a mean height of 1.5 m at 24 yr postfire (Fig. 5b). Combining with the binned age data (see below), growth rates for Douglas-fir were estimated to average 10 cm/yr. Lodgepole pine was the tallest component of the postfire community (mean 2.6 m; Fig. 5b), and grew at an estimated mean rate of 17 cm/yr. Browse damage on leaders was overall minor, with a mean of 8% of stems.

Temporal patterns of tree establishment

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

Self-replacement

In mesic stands, 90% of plots had reached site-specific self-replacement density by 11 yr postfire, topping at 96% by 14 yr (Fig. 7a). In

contrast, only 44% of dry stands had reached self-replacement by 24 yr postfire, and the remaining plots were not on an upward trend (Figs. 6b and 7a).

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

DISCUSSION

Twenty-four years after the 1988 Yellowstone fires, regeneration trends in lower-montane forests indicated clearly distinct dynamics in dry stands near the lower treeline vs. mesic stands and those farther from the treeline. Regeneration of Douglas-fir and other species was abundant in mesic stands, even in large high-severity patches, while regeneration was sparse to absent (and apparently ceased) in dry stands near the lower ecotone. In the following sections, we first discuss key patterns in regeneration as

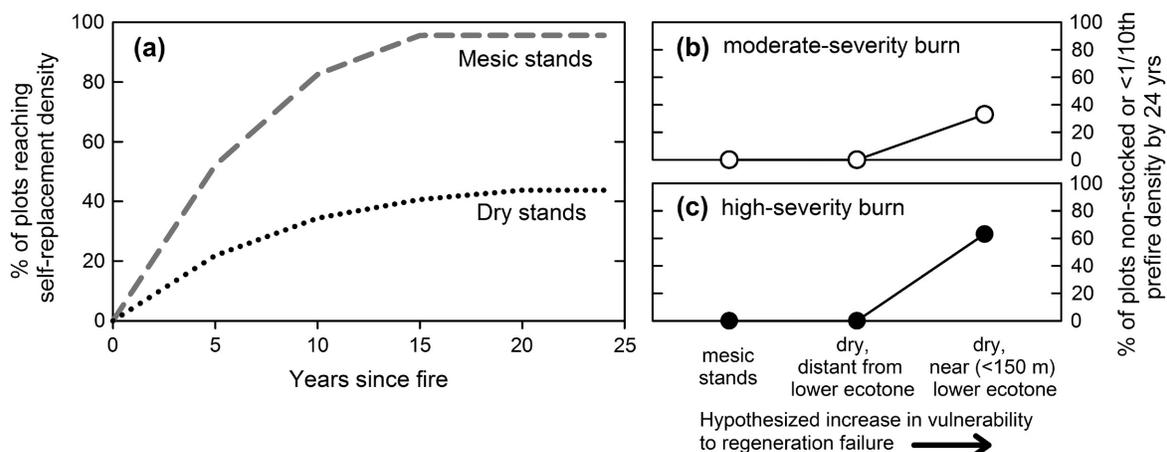


Fig. 7. Self-replacement trends for lower-montane forests burned by the 1988 Yellowstone fires. The proportion reaching stand replacement (panel a) was near 100% for mesic stands by 15 yr, but below 50% for dry stands by 24 yr postfire, and not increasing. The proportion of plots effectively not regenerating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

related to environmental setting, burn severity, and time and then examine the degree to which these patterns provide support for hypothesized shifts in lower treelines following major disturbances in a warming climate.

Postfire tree density in mesic and dry stands

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

Interestingly, mesic stands also differed from dry stands in that regeneration did not decline with higher burn severity, even in large patches, suggesting that seedbeds and seed sources were not limiting after full canopy-opening disturbance in mesic stands. In dry stands, however, regeneration density declined with increasing burn severity, suggesting that either seedbeds or seed sources (or both) became more limiting in high-severity areas. In this respect, we surmise that our dry stands are most similar to the northern Rockies dry mixed-conifer forests studied by Harvey et al. (2013) and Kemp et al. (2015), who also reported the highest regeneration abundance after low/moderate-severity fire. That dry stands only regenerated well if live trees remained nearby (either via moderate-severity fire or close proximity to live-tree edge) suggests that the legacy of seed-source distribution is the key driver of regeneration dynamics in dry forests (Harvey et al. 2013, Kemp et al. 2015). Overall, dry Douglas-fir forests appear less resilient to high-severity fire than are mesic Douglas-fir forests, in which severe burn patches are thought to have been more common historically (Baker 2009).

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

The seral community: role of lodgepole pine and successional implications

Perhaps the most important compositional response was the increased frequency and density of lodgepole pine (Fig. 5), which became dominant or codominant with Douglas-fir in 15% of plots following fire. Shade-intolerant lodgepole pine is well known for robust regeneration after severe fires (e.g., Turner et al. 1997), in part due to serotinous cones which open when heated by fire. Indeed, the highest levels of cone serotiny in *P. contorta* occur at lower elevations in the GYE, in proximity to our study areas (Tinker et al. 1994, Schoennagel et al. 2003). The places where lodgepole pine tended to increase in relative abundance (Fig. 4) are consistent with the role of serotiny: the areas where it was present before the fire and areas most distant from live-tree edges, as regeneration from serotinous cones is not necessarily tied to surviving trees (Kemp et al. 2015, Harvey et al. 2016). The increase in *P. contorta*

relative abundance resulted from the species' insensitivity to distance-to-live-edge, whereas other species' abundances declined with distance from edge. Where present, the greater initial height growth of lodgepole pine (Fig. 5) suggests it will potentially dominate the canopy profile of early- to mid-seral stands.

Postfire tree species composition was largely similar to that of the prefire community, but a few shifts will likely have implications for long-term succession. Although Douglas-fir remained the dominant species in 80% of the plots that had tree regeneration, minor increases in several other species translated to a drop in the relative dominance of Douglas-fir, from 95% of stems prefire to 69% postfire (Table 1, Fig. 5). The small relative increases of Engelmann spruce and subalpine fir in mesic stands, and quaking aspen in dry stands (likely a mix of both seedlings and sprouts), reflect a regeneration window afforded by the fires and suggest an initial floristics pattern wherein the species that will appear over the next sere (including shade-tolerant/late-successional species) establish concurrently after disturbance (see Turner et al. 1999, Donato et al. 2012, McKenzie and Tinker 2012). Mature Douglas-fir forests in the GYE tend to be dominated in the over- and understory by their namesake species, in part due to its high tolerance of drought and its own shade (Minore 1979). Our data indicate that the 1988 fires created a window for other species to establish and increased stand-level diversity for at least the next several decades.

Temporal patterns of tree establishment

Tree establishment in lower-montane forests following the 1988 fires has been a multidecade process, with a relatively slow start (Fig. 6). This finding differs from adjacent subalpine forests of the GYE, which often fill in with lodgepole pine within a few years of fire (Turner et al. 1997, 2003, 2016). In more mesic coastal Douglas-fir forests, regeneration windows commonly last several decades (Tappeiner et al. 1997, Poage et al. 2009, Tepley et al. 2013, Freund et al. 2014); thus, our study stands may have experienced only a portion of their eventual establishment. However, the clear tapering pattern by the third decade (Fig. 6) suggests establishment has largely ceased for at least

the time being. With a median density of 3294 trees/ha, most mesic stands are already at or approaching full occupancy (and on a trajectory toward density-dependent mortality), making additional establishment unlikely until something stimulates a change (e.g., additional disturbance). In dry stands, establishment had diminished to near zero by 15 yr postfire and thereafter was significantly less than in mesic stands (Fig. 6); this was despite being well below full occupancy in many cases (relative to prefire densities), suggesting some other limitation on new establishment. As such, any further regeneration would occur as a semidistinct age class rather than an extension of the current one, as observed for some coastal Douglas-fir forests (Poage et al. 2009, Tepley et al. 2013). Importantly, the window for tree establishment is not limited to the first several years or even the first decade after fire, likely providing a buffer against periods of unfavorable conditions (e.g., drought) should they occur during the initial postfire years (Harvey et al. 2016).

Self-replacement trends and potential lower treeline shifts: Directional or cyclical?

A key objective of this study was to evaluate the potential for shifts in lower-montane treelines, given the extent of the 1988 Yellowstone fires (Turner et al. 2003, Romme et al. 2011) and the exceptionally warm climatic conditions since (Shuman 2012). Although an even longer time since fire would be ideal for assessing such state shifts, the quarter-century elapsed since the 1988 fires can provide useful insight. In dry forests nearest the ecotone—presumably the most vulnerable to type conversion (Rehfeldt et al. 2006, Jiang et al. 2013)—nearly two-thirds of stands that burned with complete overstory mortality have experienced an effective lack of regeneration even 24 yr after fire, and the remaining stands are not progressing toward self-replacement (Fig. 7). This cessation or lack of postfire tree establishment near the lower treeline is consistent with hypotheses of upward treeline shifts (Romme and Turner 1991), but a key question is for how long: Are these truly directional shifts under a warmer climate, or cyclical dynamics of marginal forests? In

other words, is this an indication of low “ecological resilience” (state change) or merely low “engineering resilience” (rate of recovery) (Peterson et al. 1998)?

A cyclical-dynamic interpretation (i.e., slow engineering resilience but not indicative of state change) would be best supported if ecotonal forests have historically developed along a very slow pathway, such that the current lack of regeneration is within normal system behavior. The literature on Rocky Mountain Douglas-fir forests is unfortunately too scant to draw such comparisons. Anecdotal observations from the early 20th century suggest that failure or prolonged delay of regeneration following severe fires has occurred in dry Douglas-fir forests in the past (e.g., Peirce 1915, Baker 2009) (however, one study reported evidence of regeneration within a few decades of past stand-replacing fires in GYE Douglas-fir forests, some of which were apparently the dry type [Littell 2002]). Likewise, periodic encroachment of Douglas-fir into low-elevation grasslands, the inverse of the above dynamic, is known to occur during favorable periods with little or no disturbance (Arno and Gruell 1986, Heyerdahl et al. 2006). Taken together, these observations suggest a plausible dynamic in which Douglas-fir forests establish on the most marginal (otherwise grassland) sites only during intermittent periods of favorable climate (wet, cool, low moisture deficits) and low disturbance activity, then periodic severe disturbances and warmer conditions convert sites back to grassland for an extended period, with forests eventually “encroaching” again (i.e., re-establishing) during favorable periods and beginning the cycle anew (see Whitlock 1993, Powell and Hanson 2006, Huerta et al. 2009). Thus, it is plausible that our data may be depicting a portion of this very long-term cycle.

Support for a directional-shift interpretation (i.e., erosion or loss of ecological resilience) includes the uniquely absent regeneration processes occurring near the lower treeline relative to other locales, and current and projected future trends in climate (regeneration conditions). A widespread lack of regeneration was distinct to ecotonal stands; mesic stands as well as dry stands not immediately adjacent to the ecotone did not exhibit this response. Stands without significant tree regeneration are currently

dominated by grasses, herbs, and shrubs, with no sign of new or continuing tree establishment (Figs. 6 and 7), which is at least consistent with conversion to non-forest. Although the use of self-replacement density as a best-approximation threshold for regeneration success (given the lack of relevant literature on these forests) is likely imperfect, the near-complete lack or stagnation of tree establishment in ecotonal stands is not dependent on any threshold definition and, after a quarter-century of postfire time, appears consistent with not just a slow rate of recovery, but little to no recovery. Moreover, the potential for tree establishment to resume in marginal low-elevation (warm, dry) areas stands appears low based on current trends in climate (Rehfeldt et al. 2006, Jiang et al. 2013). Cool, moist weather-years are projected to be increasingly rare by the mid-21st century, with years of high moisture deficits (dry) by current standards becoming the norm (Westerling et al. 2011). Thus, the data and trends are at least consistent with hypotheses that ongoing shifts in climate are sufficient to break ecotonal stands’ relatively low ecological resilience and effect a state shift.

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

been effectively converted to non-forest for an extended period. Whether this conversion is categorically directional or long-term cyclical, the change was relatively abrupt and suggests that several key ecosystem functions—such as wildlife habitat, hydrological processes, and carbon and energy balance—are likely to reflect those of sagebrush grassland rather than forest for much of the coming century.

CONCLUSIONS

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

ACKNOWLEDGMENTS

We thank W. Hanson, D. Krusen, M. Stidham, and Z. Osterholz for help with field data collection and D. Abbruzzese, J. Irons, W. Romme, and A. Winegarden for helpful insights and assistance with spatial analyses. D. Abendroth, S. Gunther, and R. Renkin provided land-agency support for field work. The manuscript also benefited from constructive

comments from three anonymous reviewers. Funding was provided by the Joint Fire Science Program, grant numbers 09-1-06-3 and 11-1-1-7.

LITERATURE CITED

- Altman, D., D. Machin, T. Bryant, and M. Gardner, editors. 2000. *Statistics with confidence: confidence intervals and statistical guidelines*. Second edition. BMJ Books, London, UK.
- Arno, S. F., and G. E. Gruell. 1986. Douglas-fir encroachment into mountain grasslands in southwestern Montana. *Journal of Range Management* 39:272–276.
- Baker, W. L. 2009. *Fire ecology in Rocky Mountain landscapes*. Island Press, Washington, D.C., USA.
- Barbero, R., J. T. Abatzoglou, N. K. Larkin, C. A. Kolden, and B. Stocks. 2015. Climate change presents increased potential for very large fires in the contiguous United States. *International Journal of Wildland Fire* 24:892–899. <http://dx.doi.org/10.1071/WF15083>
- Barrett, S. W. 1994. Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* 4:65–76.
- Bradley, A. F., W. C. Fischer, and N. V. Noste. 1992. Fire ecology of the forest habitat types of eastern Idaho and western Wyoming (GTR-INT-290). USDA Forest Service Intermountain Research Station, Ogden, Utah, USA.
- Brandstätter, E. 1999. Confidence intervals as an alternative to significance testing. *Methods of Psychological Research* 4:33–46.
- Breshears, D. D., and C. D. Allen. 2002. The importance of rapid, disturbance-induced losses in carbon management and sequestration. *Global Ecology and Biogeography* 11:1–5.
- Breshears, D. D., et al. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences USA* 102:15144–15148.
- Christensen, N. L. 2014. An historical perspective on forest succession and its relevance to ecosystem restoration and conservation practice in North America. *Forest Ecology & Management* 33:312–322.
- Cwynar, L. C. 1987. Fire and the forest history of the North Cascade Range. *Ecology* 68:791–802.
- Davison, A. C., and D. V. Hinkley. 1997. *Bootstrap methods and their applications*. Cambridge University Press, New York, New York, USA.
- DiCiccio, T. J., and B. Efron. 1996. Bootstrap confidence intervals. *Statistical Science* 11:189–228.

- Dirnböck, T., F. Essl, and W. Rabitsch. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology* 17:990–996.
- Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath Mountains. *Canadian Journal of Forest Research* 39:823–838.
- Donato, D. C., J. L. Campbell, and J. F. Franklin. 2012. Multiple successional pathways and precocity in forest development: Can some forests be born complex? *Journal of Vegetation Science* 23:576–584.
- Donato, D. C., B. J. Harvey, W. H. Romme, M. Simard, and M. G. Turner. 2013a. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. *Ecological Applications* 23:3–20.
- Donato, D. C., M. Simard, W. H. Romme, B. J. Harvey, and M. G. Turner. 2013b. Evaluating post-outbreak management effects on future fuel profiles and stand structure in bark beetle-impacted forests of Greater Yellowstone. *Forest Ecology & Management* 303:160–174.
- Frelich, L. E., and P. B. Reich. 2010. Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? *Frontiers in Ecology and the Environment* 8:371–378.
- Freund, J. A., J. F. Franklin, A. J. Larson, and J. A. Lutz. 2014. Multi-decadal establishment for single-cohort Douglas-fir forests. *Canadian Journal of Forest Research* 44:1068–1078.
- Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* 12:1040–1049.
- Harvey, B. J. 2015. Causes and consequences of spatial patterns of fire severity in Northern Rocky Mountain Forests: the role of disturbance interactions and changing climate. Thesis. University of Wisconsin, Madison, Wisconsin, USA.
- Harvey, B. J., et al. 2013. Influence of recent bark beetle outbreak on fire severity and post-fire tree regeneration in montane Douglas-fir forests. *Ecology* 94:2475–2486.
- Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. High and dry: postfire drought and large stand-replacing burn patches reduce postfire tree regeneration in subalpine forests. *Global Ecology and Biogeography* 25:655–669.
- Heyerdahl, E. K., R. F. Miller, and R. A. Parsons. 2006. History of fire and Douglas-fir establishment in a savanna and sagebrush-grassland mosaic, southwestern Montana, USA. *Forest Ecology and Management* 230:107–118.
- Houston, D. B. 1973. Wildfires in northern Yellowstone National Park. *Ecology* 54:1111–1117.
- Huerta, M. A., C. Whitlock, and J. Yale. 2009. Holocene vegetation-fire-climate linkages in northern Yellowstone National Park, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 271:170–181.
- Jiang, X., S. A. Rauscher, T. D. Ringler, D. M. Lawrence, A. P. Williams, C. D. Allen, A. L. Steiner, D. M. Cai, and N. G. McDowell. 2013. Projected future changes in vegetation in western North America in the 21st century. *Journal of Climate* 2013:3671–3687.
- Johnstone, J. F., T. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* 16:1281–1295.
- Kemp, K. B., P. E. Higuera, and P. Morgan. 2015. Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. *Landscape Ecology* 31:619–636. <http://dx.doi.org/10.1007/s10980-015-0268-3>
- Korb, N. T. 2005. Historical fire regimes and structures of Douglas-fir forests in the Centennial Valley of southwest Montana. Thesis. Colorado State University, Fort Collins, Colorado, USA.
- Larson, A. J., R. T. Belote, C. A. Cansler, S. A. Parks, and M. S. Dietz. 2013. Latent resilience in ponderosa pine forest: effects of resumed frequent fire. *Ecological Applications* 23:1243–1249.
- Littell, J. S. 2002. Determinants of fire regime in lower elevation forests of the northern greater Yellowstone ecosystem. Thesis. Montana State University, Bozeman, Montana, USA.
- Lloret, F., et al. 2002. Wildfires and landscape patterns in the eastern Iberian Peninsula. *Landscape Ecology* 17:745–759.
- Loehle, C. 2000. Forest ecotone response to climate change: sensitivity to temperature response functional forms. *Canadian Journal of Forest Research* 30:1632–1645.
- Loope, L. L., and G. E. Gruell. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. *Quaternary Research* 3:425–443.
- Lyon, L. J. 1971. Vegetal development following prescribed burning of Douglas-fir in south-central Idaho (RP-INT-105). USDA Forest Service Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- McCaughey, W. W., W. C. Schmidt, and R. C. Shearer. 1986. Seed dispersal characteristics of conifers

- in the inland mountain West. Pages 50–62 in R. C. Shearer, editor. *Conifer tree seed in the inland mountain West*. General Technical Report INT-023. USDA Forest Service Intermountain Research Station, Ogden, Utah, USA.
- McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- McKenzie, D. A., and D. B. Tinker. 2012. Fire-induced shifts in overstory tree species composition and associated understory plant composition in Glacier National Park, Montana. *Plant Ecology* 213:207–224.
- Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349:823–826.
- Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR). *Remote Sensing of Environment* 109:66–80.
- Minore, D. 1979. Comparative autecological characteristics of northwestern tree species—a literature review. USDA Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.
- Murtaugh, P. A. 2007. Simplicity and complexity in ecological data analysis. *Ecology* 88:56–62.
- Omernik, J. M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* 77:118–125.
- Parnesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Peirce, E. S. 1915. The regeneration of denuded areas in the Bighorn Mountains by Douglas-fir. *Forestry Quarterly* 13:300–307.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18.
- Poage, N. J., P. J. Weisberg, P. C. Impara, J. C. Tappeiner, and T. S. Sensenig. 2009. Influences of climate, fire, and topography on contemporary age structure patterns of Douglas-fir at 205 old forest sites in western Oregon. *Canadian Journal of Forest Research* 39:1518–1530.
- Powell, S. L., and A. J. Hanson. 2006. Conifer cover increase in the Greater Yellowstone Ecosystem: frequency, rates, and spatial variation. *Ecosystems* 10:204–216.
- Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. *International Journal of Plant Science* 167:1123–1150.
- Romme, W. H., and M. G. Turner. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. *Conservation Biology* 5:373–386.
- Romme, W. H., et al. 2011. Twenty years after the 1988 Yellowstone fires: lessons about disturbance and ecosystems. *Ecosystems* 14:1196–1215.
- Schoennagel, T., M. G. Turner, and W. H. Romme. 2003. The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. *Ecology* 84:2967–2978.
- Shatford, J., D. E. Hibbs, and K. Puettman. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyou: How much, how soon? *Journal of Forestry* 105:139–146.
- Shuman, B. 2012. Recent Wyoming temperature trends, their drivers, and impacts in a 14,000-year context. *Climatic Change* 112:429–447.
- Soja, A. J., N. M. Tchepakova, N. H. F. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. I. Pargenova, F. S. Chapin, and P. W. Stackhouse. 2006. Climate-induced boreal forest change: predictions versus current observations. *Global and Planetary Change* 56:274–296.
- Tappeiner, J. C., D. Huffman, D. Marshall, T. A. Spies, and J. D. Bailey. 1997. Density, ages, growth rates in old-growth and young-growth forests in coastal Oregon. *Canadian Journal of Forest Research* 27:638–648.
- Tepley, A. J., F. J. Swanson, and T. A. Spies. 2013. Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA. *Ecology* 94:1729–1743.
- Tinker, D. B., W. H. Romme, W. W. Hargrove, R. H. Gardner, and M. G. Turner. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. *Canadian Journal of Forest Research* 24:897–903.
- Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67:411–433.
- Turner, M. G., W. H. Romme, and R. H. Gardner. 1999. Prefire heterogeneity, fire severity and plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* 9:21–36.
- Turner, M. G., W. H. Romme, and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment* 1:351–358.
- Turner, M. G., D. B. Tinker, W. H. Romme, D. M. Kashian, and C. M. Litton. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* 7:751–775.

- Turner, M. G., T. G. Whitby, D. B. Tinker, and W. H. Romme. 2016. Are postfire lodgepole pine stands converging in structure and function 24 years after the 1988 Yellowstone Fires? *Ecology*, *in press*. <http://dx.doi.org/10.1890/15-1585.1>
- Urza, A. K., and J. S. Sibold. 2013. Nondestructive aging of postfire seedlings for four conifer species in northwestern Montana. *Western Journal of Applied Forestry* 28:22–29.
- Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences USA* 108:13165–13170.
- Whitlock, C. 1993. Postglacial vegetation and climate of Grand Teton and southern Yellowstone National Parks. *Ecological Monographs* 63:173–198.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1410/supinfo>