



ORIGINAL RESEARCH

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Microenvironment characteristics and early regeneration after the 2018 Spring Creek Wildfire and post-fire logging in Colorado, USA

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Abstract

Background: Wildfires are increasing in size and severity in forests of the western USA, driven by climate change and land management practices during the 20th century. Altered fire regimes have resulted in a greater need for knowledge on best practices for managing burned landscapes, especially in instances where a return to a previous forested ecosystem is desired. We examined a large wildfire from 2018 in southern Colorado to understand how fire severity and post-fire logging influenced stand structure, fuels, vegetation, and soil microsite conditions.

Results: Two years post-fire and 1 year post logging, there was no difference in understory vegetation response. Logged plots demonstrated lower daily average temperature and minimum soil moisture and higher fuel loading across most fuel size classes relative to unlogged plots, which also corresponded with a loss of dead standing wood and little to no canopy cover. Early post-fire conifer regeneration was low across all plots, but lower soil moisture and higher soil temperature negatively impacted the density of regeneration.

Conclusions: Successful tree regeneration is mediated by multiple factors from the microsite to landscape scale. Here, we demonstrate the importance of those microsite conditions such as soil moisture and temperature in predicting conifer tree establishment in the early post-fire period. Careful consideration of soil impacts and the associated changes to forest conditions should be taken when conducting post-fire logging to prevent detrimental effects on microsite conditions and forest recovery.

Keywords: Salvage logging, Post-fire logging, Post-wildfire recovery, Tree regeneration

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Resumen

Antecedentes: Los incendios forestales están incrementándose en tamaño y severidad en los bosques de oeste de los EEUU, causados fundamentalmente por el cambio climático y prácticas de manejo durante el siglo XX. La alteración de los regímenes de fuego ha resultado en una mayor necesidad de conocimiento sobre las mejores prácticas para el manejo de paisajes quemados, especialmente en aquellas instancias en las cuales es deseable el retorno a ecosistemas forestales previos al fuego. Examinamos un gran incendio de 2018 en el sur de Colorado para entender cómo la severidad del fuego y la tala posterior influenciaron la estructura del rodal, los combustibles, la vegetación y las condiciones de los micrositios del suelo.

Resultados: Dos años después del incendio, y un año después de la tala, no hubo diferencias en la respuesta de la vegetación del sotobosque. Las parcelas taladas mostraron temperaturas diarias más bajas, humedades de suelo mínimas, y mayores cargas de combustible en todas sus clases de tamaño en relación a las parcelas no taladas, que también se correspondieron con una pérdida del material muerto en pie y muy poca o nada de cobertura del dosel. La regeneración temprana de coníferas en el post fuego fue baja en todas las parcelas, aunque la baja humedad y mayores temperaturas del suelo impactaron negativamente la densidad de la regeneración.

Conclusiones: La regeneración exitosa de árboles es mediada por múltiples factores desde los micrositios hasta escalas de paisaje. Aquí demostramos la importancia de las condiciones del micrositio tales como la humedad y la temperatura del suelo en la predicción del establecimiento de coníferas en períodos tempranos posteriores al evento de fuego. Una consideración especial sobre los impactos en el suelo y de los cambios asociados en las condiciones de los rodales cuando se conducen talas post incendio, deben tenerse en cuenta para prevenir efectos detrimentales en las condiciones de los micrositios y en la recuperación del bosque.

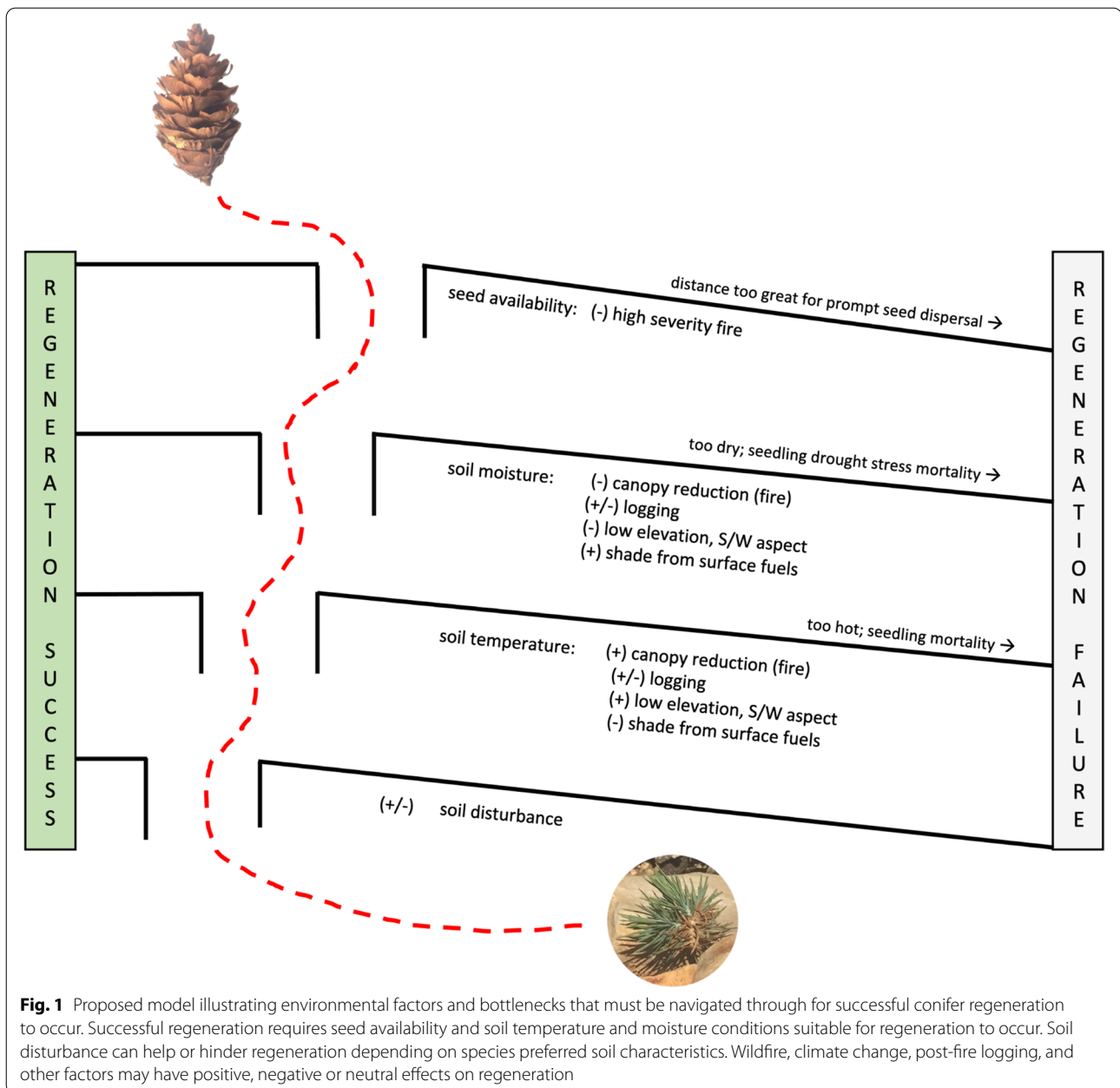
Background

Forests worldwide are facing unprecedented threats from changing disturbance regimes. Throughout the 20th century, western US forests were impacted by logging, grazing, and fire suppression (Kaufmann et al. 2000; Veblen et al. 2000), but the paramount threat affecting these forests today is how anthropogenic climate change has altered disturbance regimes and post-disturbance recovery (Abatzoglou and Williams 2016). Climate change is changing both how fire are burning with increases in both severity and extent of wildfires in western USA (Abatzoglou and Williams 2016; Parks et al. 2016; Parks and Abatzoglou 2020) and impacting post-fire recovery trajectories, through limiting tree regeneration (Davis et al. 2019a; Coop et al. 2020). Where temperature and precipitation have shifted beyond seedling tolerances of previously dominant tree species, ecosystem conversions may already be occurring (Stevens-Rumann et al. 2018; Davis et al. 2019a; Coop et al. 2020). Species located at trailing edges of their climate envelope are particularly vulnerable to conversion to non-forested states or may be displaced by other tree species better suited to conditions of the changing environment (Parks et al. 2019).

Successful post-fire tree regeneration is controlled by a number of factors, from broad-scale climate suitability to microsite characteristics. We propose a conceptual model for site-specific tree regeneration (Fig. 1). Seed availability is the first essential requirement for successful tree recruitment to occur. Distance to a living seed tree has been shown to be a primary driver of post-fire tree

regeneration (Chambers et al. 2016; Kemp et al. 2016; Welch et al. 2016; Stevens-Rumann and Morgan 2019). Given seed trees within dispersal distance, viable cone and seed production is necessary and can be episodic (Rother and Veblen 2017). Second, where seed trees are close enough to provide seed, microsite climate—specifically soil moisture and soil temperature—are key factors driving successful establishment. Many western conifers are more sensitive to drought and temperature extremes in the germinant stage, with seedling survival largely dependent on soil moisture and/or near-surface temperature falling within a narrow favorable range (Kueppers et al. 2017; Petrie et al. 2016; Hankin et al. 2019). Soil moisture and temperature are influenced by many factors and microsite conditions can vary even within a small area. Finally, soil disturbance resulting from logging or other human disturbances can result in compaction, runoff, erosion, and/or topsoil displacement, which may further alter conditions at the microsite level (Malvar et al. 2017). We test aspects of this model by examining site-level characteristics across a range of forest types, burn severities, and post-fire treatments.

We outline four factors that have been shown in the literature to specifically influence stand-level temperature and moisture: canopy cover, topographic factors (elevation, aspect), surface fuel cover/loading, and logging. First, wildfires often reduce canopy cover, which increases light availability at the surface, and can contribute to increased soil warming and drying (Davis et al. 2019b; Marcolin et al. 2019). While canopy cover can



help buffer climate changes for the understory (Davis et al. 2019b), canopy loss such as that caused by wildfire can reduce recruitment (Dobrowski et al. 2015). Canopy removal, such as with post-fire logging, can increase solar exposure leading to microsite soil temperature and soil moisture conditions outside of the window necessary for successful germination or seedling survival.

Second, topographic factors can have an outsized role in tree seedling recruitment and soil temperature and moisture, especially on the trailing edge of forests or on the edge of climatic tolerance for a specific species

(Kemp et al. 2016, Parks et al. 2019). Aspect and elevation have both been shown to be a driving force for tree recruitment (Chambers et al. 2016; Lopez Ortiz et al. 2019), but also may influence the soil temperature and moisture. Third, initial post-disturbance soil moisture and temperature may be ameliorated by conditions created by the surface fuel accumulation resulting from tree fall and decay (e.g., nurse logs; Castro et al. 2011, Ouzts et al. 2015), though excessive fuel loading may also inhibit plant growth. Accumulated litter, duff, and understory vegetation become ash, altering nutrient inputs, while

fire can expose mineral soil and alter edaphic characteristics such as soil structure, water infiltration, and available water capacity and increase hydrophobicity and erodibility of soils (Neary et al. 2005). Similarly, shrubs and early successional species may also play a facilitating role in later tree recruitment in areas lacking forest canopy by providing cover and altering microsite climate (Gómez-Aparicio et al. 2004; Ettinger and HilleRisLambers 2017).

Finally, post-fire logging can influence tree establishment success by altering numerous factors described above including canopy cover, vegetation cover, soil disturbance, and woody fuel accumulation potentially impacting long-term recovery (Donato et al. 2006; Keyser et al. 2009; Castro et al. 2011; Blair et al. 2016). The process of removing trees from a burned area can also contribute to soil disturbance, which may further alter conditions at the microsite level (Malvar et al. 2017). However, the impact of post-fire logging on ecosystems varies with many factors, including forest type, seasonal timing, and method of tree harvest, and elapsed time since fire (Beschta et al. 2004; Keyser et al. 2009; Leverkus et al. 2020). Little is known about post-fire logging across a range of forest types within the same fire footprint, and how logging affects microsite conditions necessary for forest recovery.

To test this conceptual model on early post-fire regeneration, and understand the impacts of post-fire logging on fuels, microsite conditions, and regeneration across an elevational gradient, we focused our study on a 2018 fire in southern Colorado. Study sites were established in low to moderate severity burned areas, high severity burned areas, and high severity, post-fire logged sites to answer the questions: (1) How does forest structure, surface fuels, and canopy characteristics differ amongst areas burned at low and high burn severity and those areas that experienced post-fire logging? (2) How does soil temperature and soil moisture differ among burn severities and areas that received post-fire logging and what drives these differences? and (3) How does short-term post-fire vegetation recovery and tree regeneration differ among severities with and without logging, and what drives these differences?

Methods

Study area

The Spring Creek Fire burned 43,000 ha in 2018 in the Sangre de Cristo range and Spanish Peaks Wilderness of the Southern Rocky Mountains of Colorado, USA (Fig. 2) and was the third largest fire in Colorado history at the time, and still ranks among the largest in the state. The fire burned across an elevational gradient from lower elevation shrub and grasslands up to high-elevation subalpine forests, impacting private, state, and

federal land. Environmental Site Potential (www.landfire.gov last accessed November 7, 2020) across our study area included: Southern Rocky Mountain Mesic (and Dry-Mesic) Montane Conifer Forest and Woodland, Inter-Mountain Basin Aspen-Mixed Conifer Forest and Woodland, *Quercus gambelii* Shrubland Alliance, and Southern Rocky Mountain Ponderosa Pine Woodland. Overall, the study areas were mixed-conifer forest with dominance of ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and white fir (*Abies concolor* Lindl. ex Hildebr.) at lower elevations. Higher elevation forests fell within two dominant forest types, the first being mixed conifer with predominantly limber pine (*Pinus flexilis* E. James) mixed with white fir, and to a lesser extent, Douglas-fir, ponderosa pine, and quaking aspen (*Populus tremuloides* Michx.). The second group of higher elevation forest was dominated by lodgepole pine (*Pinus contorta* Loudon) and quaking aspen, with occasional white fir. Plots ranged in elevation from roughly 2600 to 3000 m and this variability in forest type across a relatively small (approximately 400 m) elevational gradient demonstrates the forest species diversity found in this region (Allen and Pete 1990).

Plot selection

Across the study area, thirty-one plots were stratified into these three disturbance types: with a low to moderate severity fire (<50% tree mortality) without post-fire treatments (LS, $n=9$), high severity burned areas (90–100% tree mortality) without post-fire treatments (HS, $n=11$), and high severity burned sites that were subsequently logged (HL, $n=11$). Plots were established in a block design, in close geographic proximity and part of the same contiguous pre-fire stand, with similar forest type and topographical characteristics for all plots in a given block, including elevation, slope, and aspect (Table 1). Blocks were randomly selected within the suitable sites via ArcGIS and individual plot locations were randomly assigned in the field at a suitable block location. For all plots within a given block, the range of elevation amongst plots averaged less than 50 m, slope was within 5%, and aspect was within 45°, though it should be noted that the greatest variation in aspect occurred on plots with slopes < 5%. Severity was assessed visually according to tree mortality within the boundaries of the site, which consisted of a 0.08-ha circular plot. For plots in aspen/lodgepole forest, no LS burned areas were present, and thus two blocks contained only HS and HL. A total of 9 plots (3 blocks) were established in 2019, including 4 plots that were measured before logging operations began in 2019 and measured again in 2020. In 2020, an additional 22 plots were established across the three disturbance types. Plots were selected to avoid areas

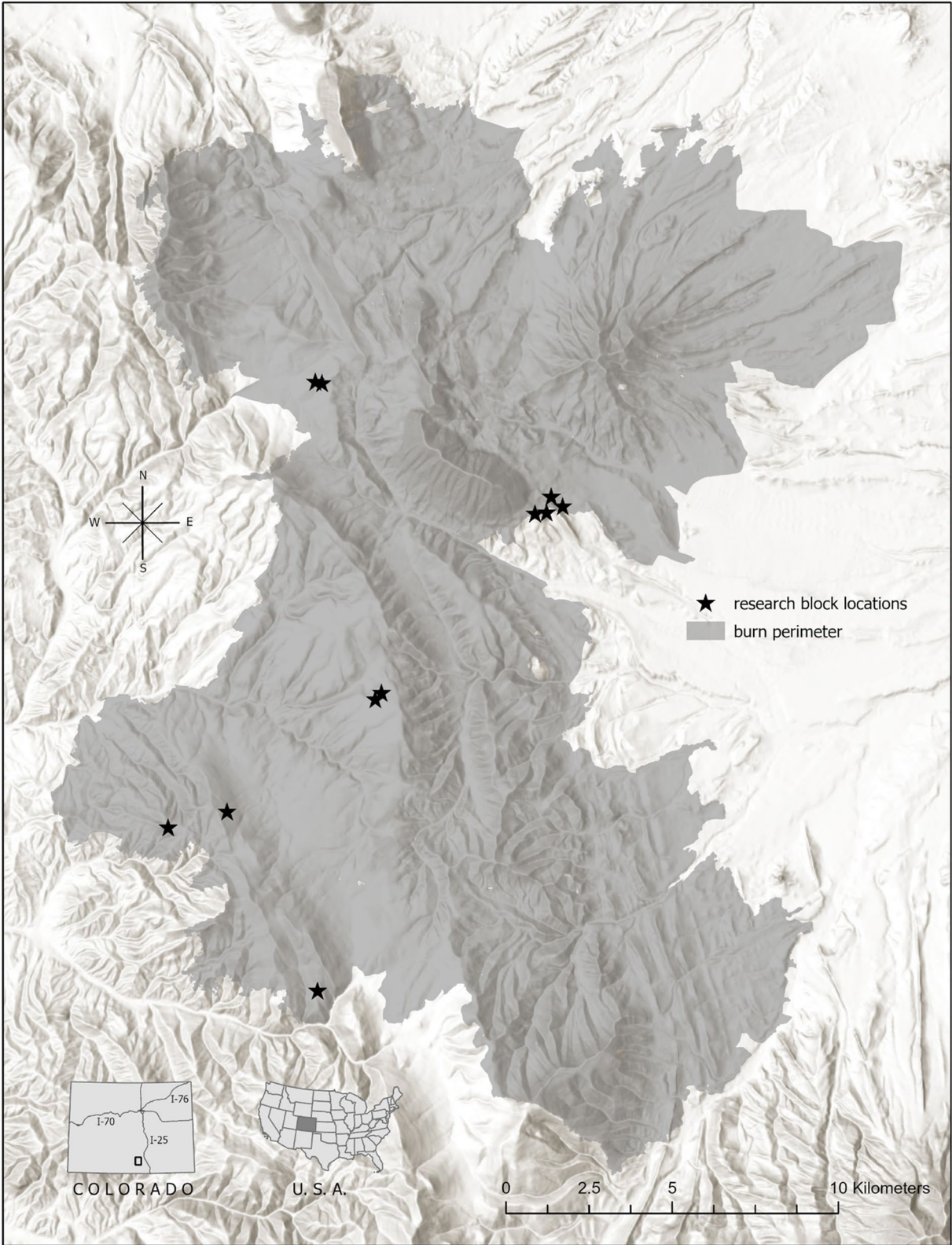


Fig. 2 Map of the Spring Creek Fire of 2018. Stars represent approximate locations of research blocks. Burn boundary derived from BAER soil burn severity map

Table 1 Topographical and forest type data for all blocks across study area, with mean and standard deviation of elevation, slope, aspect, and maximum distance between sites within a block. Blocks 8 and 9 contained no LS treatment due to high severity fire in lodgepole/aspen forest type. All other blocks contain one each LS, HS, and HL site. “Mixed-PIPO” indicates a mixed conifer forest dominated by ponderosa pine pre-fire, “mixed-PICO” indicates a mixed conifer forest dominated by lodgepole pine, “mixed-PIFL” is a mixed conifer forest dominated by limber pine, “PICO/POTR” was a mixed lodgepole pine and aspen-dominated forest

| Block | Forest type | Elevation (m) | | | Slope (°) | | | Aspect (°) | | | Max distance between sites (m) |
|-------|--------------|---------------|------|------|-----------|----|----|------------|-----|-----|--------------------------------|
| | | LS | HS | HL | LS | HS | HL | LS | HS | HL | |
| 1 | Mixed - PIPO | 2624 | 2702 | 2670 | 4 | 5 | 6 | 40 | 110 | 52 | 654 |
| 2 | Mixed - PIPO | 2634 | 2710 | 2652 | 5 | 10 | 6 | 130 | 112 | 101 | 513 |
| 3 | Mixed - PIPO | 2733 | 2743 | 2685 | 7 | 2 | 8 | 233 | 94 | 13 | 252 |
| 4 | Mixed - PIPO | 2661 | 2746 | 2674 | 15 | 8 | 7 | 80 | 255 | 65 | 264 |
| 5 | Mixed - PICO | 2900 | 2877 | 2894 | 5 | 6 | 5 | 280 | 220 | 200 | 213 |
| 6 | Mixed - PICO | 2873 | 2878 | 2888 | 8 | 6 | 5 | 290 | 220 | 260 | 295 |
| 7 | Mixed - PIFL | 2994 | 2956 | 2993 | 16 | 17 | 14 | 50 | 70 | 50 | 172 |
| 8 | PICO/POTR | na | 2995 | 2989 | na | 3 | 3 | na | 270 | 270 | 208 |
| 9 | PICO/POTR | na | 3007 | 2998 | na | 4 | 5 | na | 200 | 290 | 89 |
| 10 | Mixed - PIFL | 3019 | 3027 | 3017 | 7 | 10 | 7 | 200 | 230 | 240 | 253 |
| 11 | Mixed - PIFL | 3027 | 3031 | 3029 | 5 | 3 | 2 | 15 | 290 | 360 | 168 |

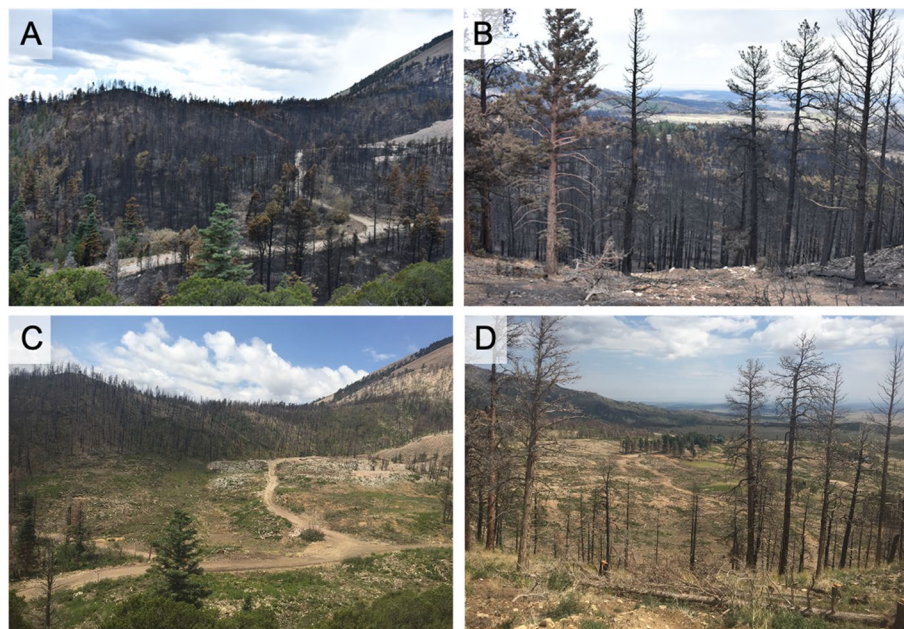


Fig. 3 Photos before (A, B) and after (C, D) clear cutting logging operations in the Spring Creek Fire. Pre-logging photos taken by Steve Keppers in July 2018. Post logging photos taken by the Jesse Wooten in August 2020

with significant pre-fire management treatments, such as thinning or prescribed fire. We confirmed visually in the field and through post hoc analyses that plots within a block were similar to one another in terms of pre-fire density and species composition. Total basal area was not significantly different among LS and HS plots ($33.6 \text{ m}^2 \text{ ha}^{-1}$ and $26.5 \text{ m}^2 \text{ ha}^{-1}$, respectively, $P > 0.54$), but given the

extensive logging activity, we were not able to determine pre-logging basal area, except for those plots that were measured in 2019 prior to logging.

Logging, which was predominantly clear cutting with no residual basal area remaining, was commissioned shortly after the fire and completed by October 2019 (Fig. 3). Burn severity was assessed as a percent of trees dead by 1–2

years post-fire on a plot. Logging methods varied slightly but were predominantly hand-felling and the use of feller-bunchers. The goal of all logging operations was to remove all standing dead material for commercial use, with remaining fuels largely removed and not left on study sites.

Sampling design

Each plot was designed as a 0.08-ha circular plot (adapted from Schapira et al. 2021) with four, 16.1 m long transects oriented in the cardinal directions from the plot center. Each plot center was staked, adult trees were tagged, and plot measurements such as slope, aspect, elevation, and coordinates were recorded. Distance to live seed source by species was also recorded up to 150 m from the plot center using a Nikon Forestry Pro range finder. Adult tree species and relative decay classes, when applicable, were noted for all trees within the circular plot. Tree seedling regeneration by species was quantified within the entire 0.08 ha plot. We broke the plot into four sections along central transects and walked outward from the plot center, tallying seedlings and using pin flags to avoid double counting.

At each plot, fine woody fuels were measured using modified Brown (1974) transects. One-hour fuels (0–0.64 cm diameter) were measured along 7 m of each transect, while 10- and 100-h fuels (corresponding to size classes, 0.65–2.54, 2.55–7.62 cm diameters) were measured along 16 m or the full length of each transect. Substrate and vegetation ground cover measurements were collected at 68 locations along transects, noting substrate (litter, bareground, rock) and, if present, plant functional group (graminoid, forb, shrub, tree). Litter and duff depth measurements were taken three times along each of the four transects for a total of 12 measurements and averaged per plot. Coarse woody fuels (1000-h fuels; >7.62 cm) were measured within a 6.9-m radius subplot, where any log with a diameter exceeding 7.62 cm was recorded as well as the diameter at both ends (Sikkink and Keane 2008).

Aerial canopy cover, including both live and dead standing material, was estimated with a densitometer at 60 points along transects and summed per plot. Distance to live seed source was measured for the three closest living individuals averaged by species up to 150 m. At plots lacking a visible seed source tree or where distances exceeded 150 m for relevant species, 500 m was recorded as the distance for analysis purposes.

Soil temperature, moisture, and disturbance

Two to three temperature sensors were installed in each of our 31 plots. The sensors used were a combination of “HOBO Pendant Temperature Data Loggers” and “8-bit Temperature Smart Sensors,” both from Onset

Computer Corporation (ONSET, Product ID: #UA-002-08, #S-TMA-M006). Sensor selection and placement was consistent within blocks, e.g., Pendant Sensors were placed at one set of LS, HS, and HL plots, and 8-bit Temperature Smart Sensors at another set, however both types of temperature sensors were installed at 7 plots in order to verify the consistency of collected measurements. All temperature sensors were installed at depths of 2.5 cm below soil surface.

Two “Soil Moisture Smart Sensors” were installed at depths of 4 cm below soil surface at 4 blocks, or a total of 12 plots, with measurements for these sensors recorded using “HOBO Weather Stations” and “HOBO Micro Stations” (ONSET, Product ID’s #SMA-M003, #H21-001, #H21-002, #H21-USB). All temperature and soil moisture sensors were programmed to record measurements at intervals of 30 minutes, beginning with their installation in the field during the early growing season (May 2020) and continuing until their removal at the end of August and early September. This created a time series of soil temperature and soil moisture measurements across disturbance treatments for the duration of the field season and also allowed for an examination of specific daily measurements (e.g., max daily temperature, minimum daily moisture) for all plots. Data collected by HOBO Weather and Micro Stations experienced periodic gaps in the time series collection, ranging from 5 days to a month, as a result of equipment failure due to weather and wildlife interference. As such, a continuum of soil moisture and soil temperature data is present for all dates throughout the field season, but not all plots are necessarily represented on every given date. As sensor deployment and removal occurred over a span of several days, the dataset was trimmed to remove the initial few days while sensors were adjusting to plot specific soil conditions, and the final stretch of days spanning sensor removal at all plots, for a total record of 95 days extending from May 24th to August 27th, 2020.

Statistical analysis

All statistical analysis was performed in R version 4.0.3 (2020-10-10) (RStudio Team 2019) with an $\alpha=0.05$ as the threshold for statistical significance. Surface fuel loadings were stratified by fuel size class (1, 10, 100, and 1000-h fuels) prior to analysis. Surface fuels, surface substrate, vegetation cover, and canopy cover were analyzed using a two-way analysis of variance (ANOVA) using block and disturbance treatment (LS, HS, HL) as predictor variables, followed by Tukey’s HSD test when significance was determined. We visually tested assumptions of normality and equal variance on residuals.

Seedling density plus 1 was log transformed and multiple plot-specific factors were examined as predictor

variables (maximum daily soil temperature, minimum daily soil temperature, mean daily soil temperature, minimum soil moisture, mean daily soil moisture, log transformed deciduous density, distance to living tree, bare ground, canopy cover, aspect, elevation, CWD, and disturbance treatments) in univariate linear models. A multivariate regression model was not performed given the limited degrees of freedom, especially for soil moisture variables, as well as the lack of significance in most variables and the high correlation among variables. We considered the nesting of factors, such as bare soils and canopy cover, within treatment type; however, disturbance treatments occupy different ranges of canopy cover and bare soil and cannot be extrapolated beyond these ranges. Slope was excluded as slope was generally low across all plots (<20%). Aspect was transformed using a Beer's transformation for analysis (Beers et al. 1966). We tested assumptions of normality using a Shapiro-Wilk's test and equal variances using a Levene's test prior to performing all linear regressions.

Soil temperature and soil moisture data was collected between late May through late August. Temperature sensors produced a time series of maximum daily soil temperature data from all $N=31$ plots, and soil moisture data from $N=12$ plots. Within blocks, we subtracted the daily maximum temperature of HL from LS and also of HS from LS, creating two sets of data showing the maximum daily temperature difference between logged and low severity plots, and the difference between high and low severity plots. Maximum daily temperature differences (from LS), average daily soil moisture, and minimum daily soil moisture were also analyzed using a repeated measures two-way analysis of variance (ANOVA) using block, time, and disturbance treatment (LS, HS, HL) as predictor variables, followed by Tukey's HSD test when significant.

Results

Forest structure, living trees, and surface fuels

Post-fire tree mortality by density averaged 57.5% in LS plots, 99.8% in HS plots, and 100% in HL plots. Mean canopy cover was highest in LS, which was significantly greater than in HS ($P=0.005$), which in turn was greater than cover at HL ($P<0.001$) where canopy cover was close to zero (Table 2). Mean total stand density (both

live and dead trees), was significantly higher in LS and HS compared to HL where the majority of stand dead material was removed ($p<0.0001$). There was a significant difference in live stand density between LS and HS plots ($p<0.0001$). HL plots had standing trees remaining on only 1 of 11 plots. Live trees were significantly closer to plot centers on LS plots ($F=47.7$, $p<0.0001$), and there was no significant difference in distance to live trees between HL and HS plots.

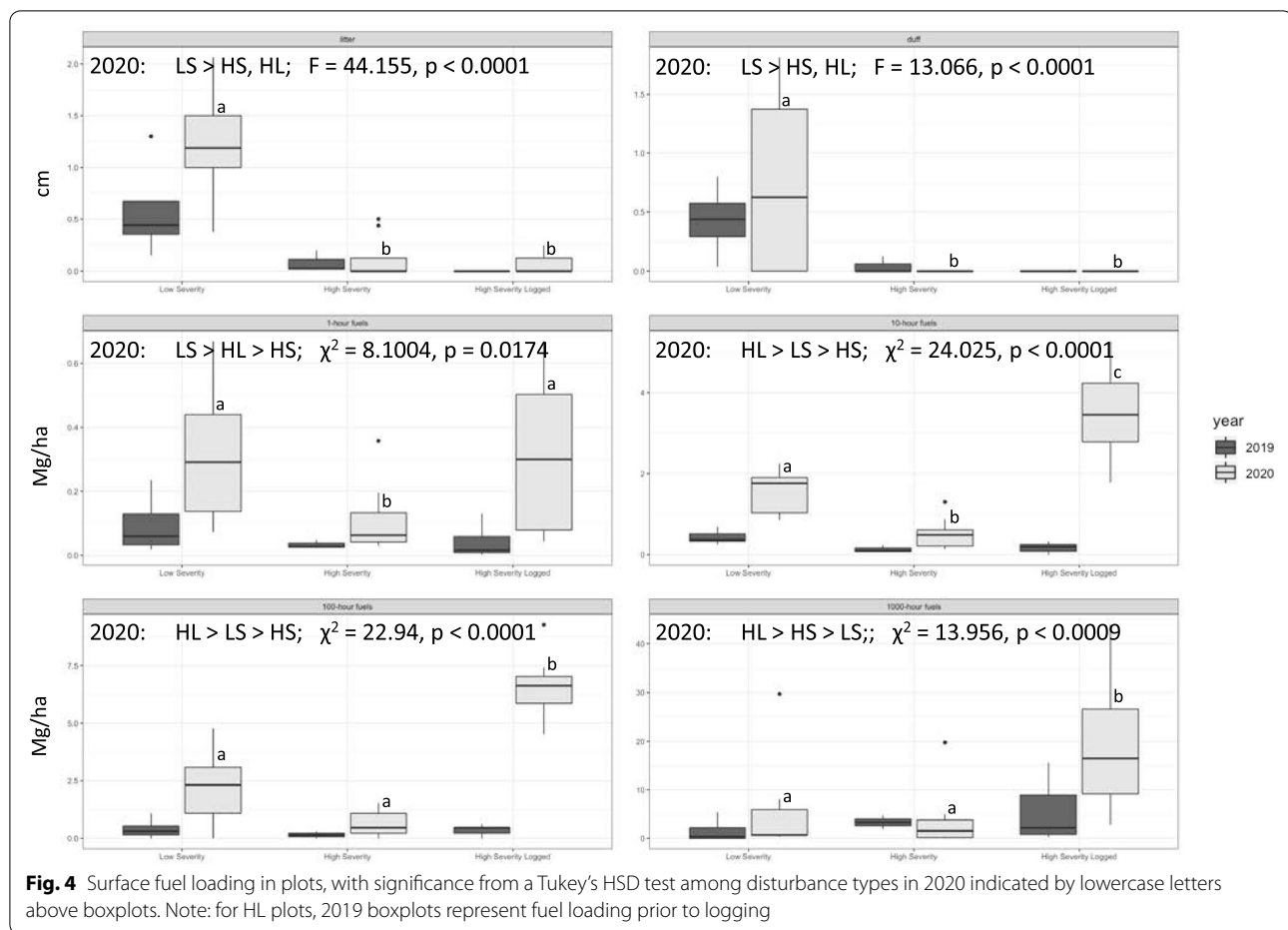
Among areas that burned at high severity, logged plots (HL) contained statistically higher surface fuel loading than their unlogged counterparts (both LS and HS) across all fine woody debris classes ($F=102.4$, $P<0.0001$; Fig. 4), with the exception of the 1-h fuel class, where there was no significant difference in fuel loads between HL and LS plots. Similarly, for 1000-hour fuels, logged plots had significantly higher fuel loading than unlogged high severity or low severity plots ($F=8.991$, $P=0.001$). Surface substrate was grouped into two categories: (1) bare ground combined with exposed rock or (2) litter combined with woody debris. Plots in LS had higher cover of combined litter and woody debris than HL, which in turn had greater cover than HS ($F=32.66$, $p<0.0008$). As follows, percent coverage of combined bare ground and rock was greatest in HS, followed by HL then LS. LS plots had greater depths of litter ($F=44.155$, $p<0.00001$) and duff ($F=13.066$, $p<0.00001$) than other plots. While HL plots had a greater area covered by litter than HS, there was no significant difference in depths of litter of duff and litter between plot categories ($F=0.413$, $P=0.5266$).

Soil temperature, moisture, and disturbance

During the late spring (05/26/20–06/18/20), maximum daily soil temperature was lowest in LS plots, and HL daily maximum temperatures were significantly higher than those in HS plots. During this period, peak daily temperature was, on average, 1°C hotter in HL than HS ($P=0.0299$; Fig. 5). During the hottest part of the summer (06/24/20–07/17/20), there was no statistical difference ($P=0.9505$) between max daily temperature at HL and HS nor when evaluating the season as a whole (05/24/20–08/27/20; $P=0.5834$). Soil temperatures

Table 2 Plot categories with canopy cover, stand density of live and dead trees (trees ha⁻¹), and mortality means, with standard deviations in parentheses

| Site code | Disturbance | Canopy cover (%) | Total density (trees ha ⁻¹) | Tree mortality (%) | # replicates |
|-----------|------------------------------|------------------|---|--------------------|--------------|
| LS | Low-moderate severity fire | 61.5% (15.0%) | 565 (220) | 57.5% (13.7%) | 9 |
| HS | High severity fire | 40.5% (17.6%) | 500 (241) | 99.8% (0.7%) | 11 |
| HL | High severity fire + logging | 0.3% (0.9%) | 9 (30) | 100% (0.0%) | 11 |



in HS exceeded HL during the later field season (07/23/20–8/27/20) and were 0.9°C hotter ($P = 0.0234$).

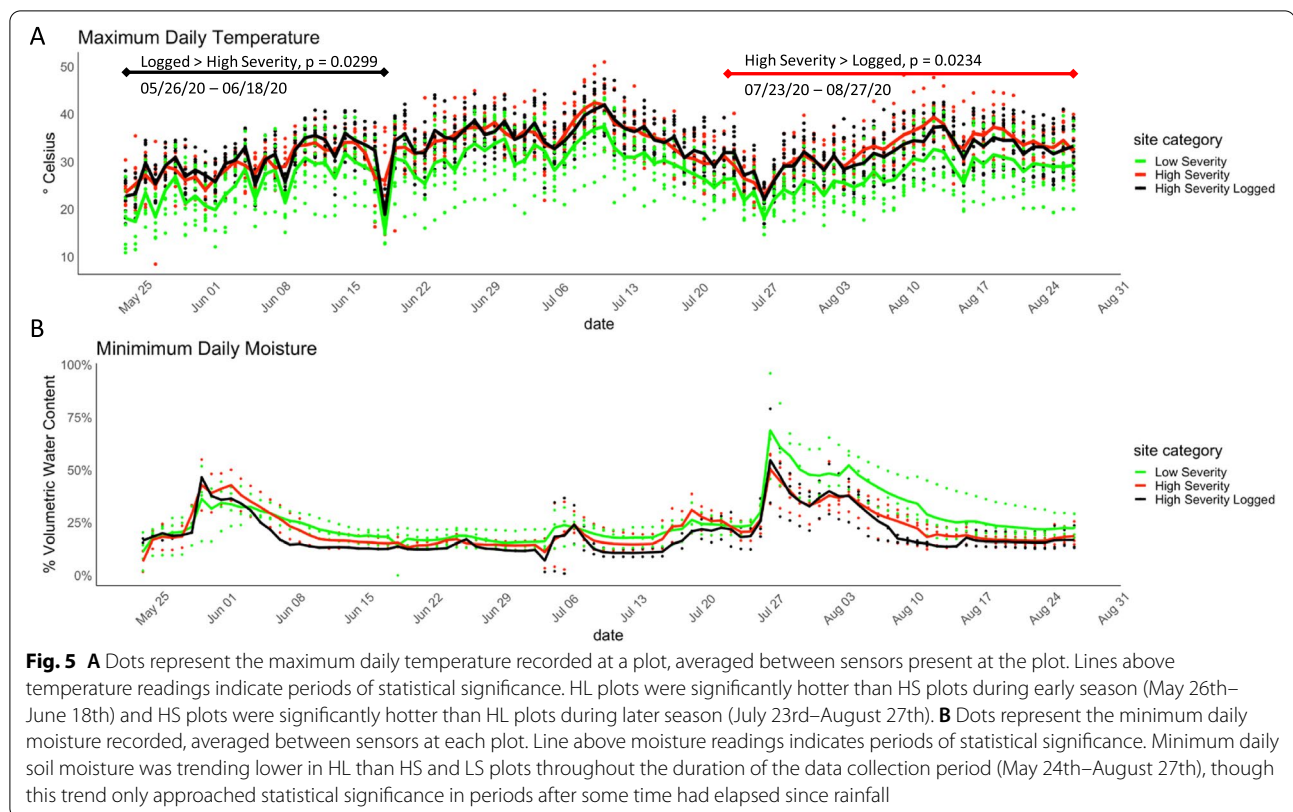
LS plots had the highest daily average and daily minimum soil moisture levels throughout the entire field season, ($P = 0.0044$, $P < 0.00001$, respectively). Our data was limited by equipment malfunction, but the trends we saw indicated that daily average and daily minimum soil moisture levels in HL rose during rainfall events above levels in HSs. However, between rain events, HL plots exhibited lower soil moisture than HS plots (Fig. 5).

Maximum, minimum, and mean daily soil temperature was higher in places of little canopy cover ($R^2 > 0.2$, $P < 0.01$, max temp: Fig. 6). Minimum daily soil temperature also had a positive relationship with increases in bare ground cover ($R^2 = 0.27$, $P = 0.004$). However, mean daily soil temperature and maximum daily soil temperature did not have a significant relationship with bare ground cover ($R < 0.09$, $P > 0.1$). Soil moisture variability was not explained by canopy cover or the percentage of bare ground ($R < 0.05$, $P > 0.3$). Neither soil moisture nor

temperature was significantly correlated with surface fuel loads ($R < 0.01$, $P > 0.4$).

Vegetation responses and tree regeneration

Graminoids had significantly higher cover at LS plots than either HL or HS ($F = 8.25$, $P = 0.0016$), but no other differences were observed in the cover of functional groups (forbs, shrubs or resprouting trees, or all vegetation cover combined $F < 1.00$, $P > 0.20$) among treatments. Both Gambel oak (*Quercus gambelii* Nutt. var. *gambelii*) and quaking aspen demonstrated comparable regeneration across all disturbance treatments, with seedlings or re-sprouts present in 100% of plots that previously contained the species. While we did not distinguish between resprouts and new germinants, many appeared to be resprouting out of top-killed individuals. Mean densities of *Quercus gambelii* at LS, HS, and HL plots were 14,500, 6250, and 10,000 stems ha^{-1} , respectively. Mean densities of *Populus tremuloides* at LS, HS and HL plots were 3500, 7500, and 3250 stems ha^{-1} , respectively. Between LS, HS and HL, there was no significant difference in the density of resprouting Gambel oak ($F = 2.2169$, $P = 0.1714$) or



quaking aspen ($F = 1.1839$, $P = 0.3331$) nor when totals for both species were combined ($F = 0.3999$, $P = 0.6743$). Gambel oak was only found on lower elevation plots with no Gambel oak above 2743m, meanwhile aspen is found across the range of our plots with increasing density at higher elevation ($R^2 = 0.15$, $P = 0.03$).

Conifer seedlings were present on 19 of the 31 plots two years post-fire (Table 3). Mean conifer seedling density across all sites was 1980 trees ha^{-1} , however excluding the 12 plots without any regeneration mean density almost doubles to 3230 trees ha^{-1} for the remaining 19 plots. Lodgepole pine seedlings dominated, occurring on 90% of the plots that had lodgepole as a part of the pre-fire overstory, and densities on these plots ranged from 487 to 21,375 trees ha^{-1} . Of the 12 plots with non-lodgepole seedlings, 6 were LS plots, 4 were HS plots, and 2 were HL plots. Douglas-fir seedlings occurred on 43% of sites with Douglas-fir pre-fire and were found on sites of all disturbance types. Four LS sites had a mean Douglas-fir seedling density of 72 trees ha^{-1} , while the three HS sites had a mean density of 25 trees ha^{-1} , and the two HL sites with Douglas-fir seedling had a mean density of 18 trees ha^{-1} . White-fir was present on 15% of sites, one of these four plots was a HL disturbance history, while the rest of the white-fir was only present on LS plots ($n=3$). Only one limber pine seedling was observed across all

plots. Though mature pre-fire ponderosa pine was present at 22 plots, no seedlings were observed.

Total transformed conifer tree regeneration was negatively correlated with maximum, minimum, and mean daily summer soil temperatures ($R^2 > 0.14$, $P < 0.03$, Fig. 6). Minimum daily soil moisture was positively correlated with conifer tree regeneration ($R^2 = 0.41$, $P = 0.03$), though not the mean daily soil moisture ($R^2 = 0.20$, $P = 0.16$). Distance to seed source trended toward significance with a slight negative relationship ($P = 0.087$). Bare ground cover, aspect, elevation, log deciduous seedling/resprout density, CWD, and mean daily soil moisture did not differ among plot types ($R^2 < 0.01$, $P > 0.2$). Log transformed conifer seedling density did not significantly vary between HL, LS, and HS ($F = 0.21$, $P = 0.81$).

Discussion

We were able to examine the majority of the factors described in our model (Fig. 1) to describe the mechanisms by which fire severity and post-fire logging affect tree seedling germination. Distance to seed source appears to be an important limit on tree regeneration, consistent with many other studies (e.g., Kemp et al. 2016, Chambers et al. 2016). Distance to live seed source presents a significant obstacle to recruitment for obligate seeding conifers in burned areas (Kemp et al. 2016), particularly species with heavier

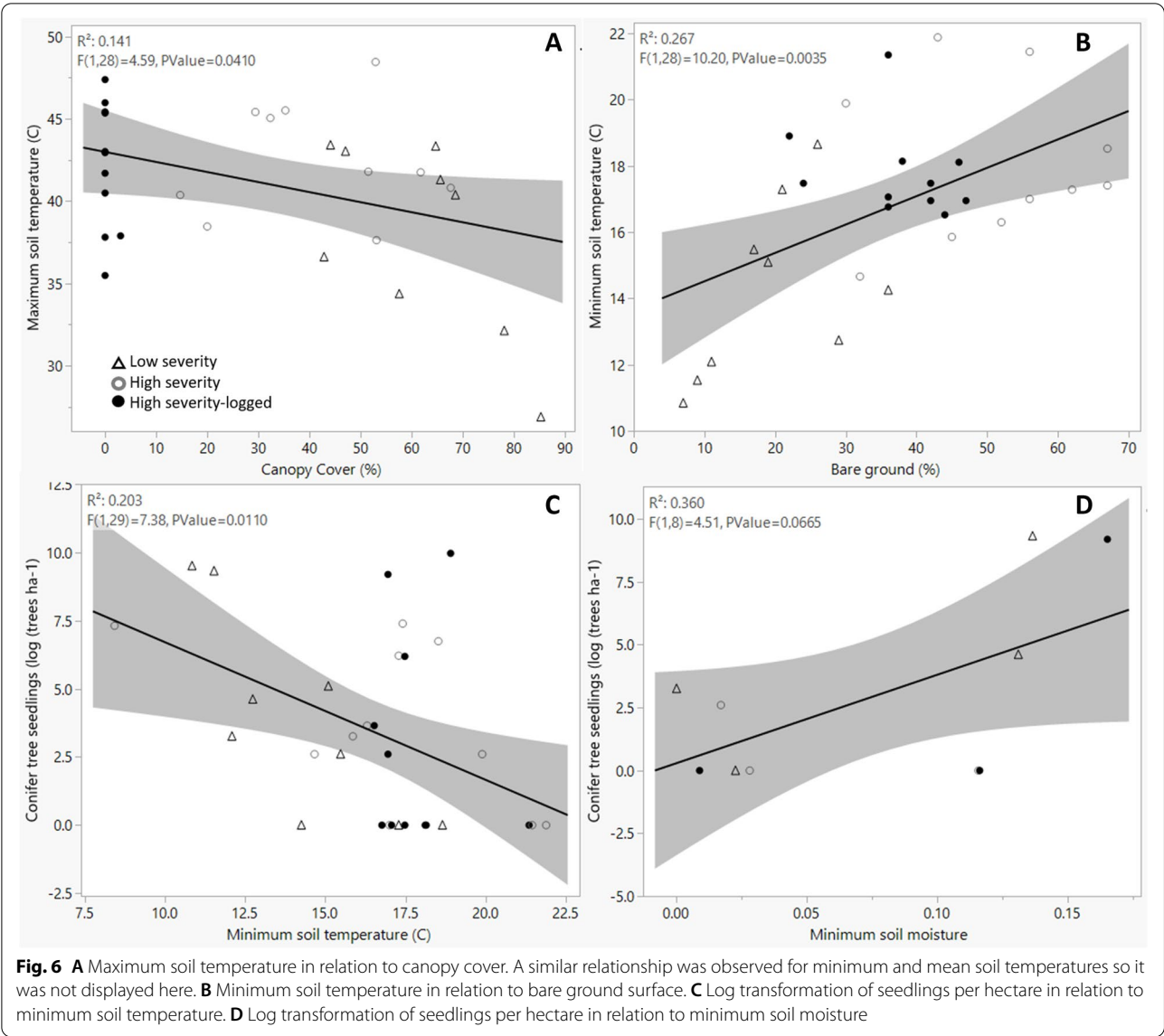


Table 3 Dominant pre-fire conifer species observed, number of plots these species were detected and the number of plots seedlings were observed. Percentage represents proportion of plots that had a species pre-fire where they were also observed post-fire, and the mean density of seedlings by species on those sites where at least one seedling as observed (sites with no regeneration of that species are excluded)

| Species | Observed overstory presence (# of plots) | Seedling presence (# of plots) | Percentage of plots with species pre-fire where seedlings were present post-fire | Mean density for sites with seedlings (trees ha ⁻¹) |
|----------------|--|--------------------------------|--|---|
| Lodgepole pine | 10 | 9 | 90% | 6718 |
| Douglas-fir | 21 | 9 | 43% | 44 |
| White fir | 27 | 4 | 15% | 122 |
| Limber pine | 9 | 1 | 11% | 12 |
| Ponderosa pine | 22 | 0 | 0% | 0 |
| All species | 31 | 19 | 61% | 3230 |

seeds (e.g., ponderosa pine, limber pine) that are less likely to benefit from long-distance wind-dispersal (Chambers et al. 2016). However, on our sites, there was only a weak relationship between early post-fire conifer tree establishment and distance to a living tree, likely driven by both the large lodgepole pine dominance in these early seedlings and our blocked study design that favored relatively close distances to a living tree in all plots, as well as the short post-fire window of observation.

Logging resulted in higher surface fuel loadings across nearly all fuel size classes and resulted in greater fuel continuity (Donato et al. 2013). Fuel loads increased from pre- to post-logging on the same plots, though this change in fuel loading did not exceed recommended loadings nor influence soil temperature or moisture. Soil temperature and moisture varied between LS, HS, and HL plots at different times throughout the growing season, and together served as another filter on tree regeneration. Soil temperature had a negative relationship with canopy cover and a positive relationship with bare ground cover. Across all plots, seedling density was highly variable in this early post-fire period, with several conifer species showing little to no early post-fire regeneration. The largest plant response observed was from resprouting deciduous species, indicating the potential for transition, at least in the near term, from conifer to deciduous dominance.

Influencing factors of soil moisture and soil temperature

Soil moisture and soil temperature varied between disturbance types at specific times throughout the growing season. Our research showed that HL plots demonstrated reduced daily minimum soil moisture and daily average soil moisture between May and August. Soil temperature varied between HS and HL plots during these months but did not vary significantly across the season as a whole, contrary to what has been shown in previous studies (Maher et al. 2005; Rother et al. 2015). Canopy cover and standing and downed fuels varied by disturbance type and influenced soil temperature, which may have long-term implications for plot suitability for tree regeneration (Donato et al. 2006; Keyser et al. 2009; Marcolin et al. 2019), but did not strongly drive early post-fire tree regeneration trends. Especially at higher percentages of canopy cover, canopy cover helped moderate soil temperature (Maher et al. 2005; Davis et al. 2019b), but not soil moisture at two cm depths. As the canopy becomes sparser, moderating effects decrease (von Arx et al. 2013), leading to greater solar exposure of the surface and leads to subsequent soil heating and drying (Marcolin et al. 2019). Thus in areas that experienced a clear cut these changes in site conditions may play a stronger driving

role in driving recovery compared to areas with some dead and living standing trees.

Some studies have shown the sheltering effects of coarse woody debris to be more important in promoting establishment than the amount of solar exposure from canopy gaps (Gray and Spies 1997; Hill and Ex 2020), with some studies indicating retained downed timber and slash resulting from logging can offset higher temperatures and moisture deficits in microsites (Castro et al. 2011; Marcolin et al. 2019). CWD did not influence soil temperature or soil moisture. We did not strategically place probes under fuel versus in open areas, nor did we analyze the proximity of seedlings to CWD. Surface fuels naturally accumulate as standing dead material begins to fall with longer time since fire, as others have found across the intermountain west (e.g., Roccaforte et al. 2012; Fornwalt et al. 2018; Stevens-Rumann et al. 2020), thus we may expect a stronger relationship between loading and soil temperature and moisture in the years to come.

The role of soil moisture, temperature, and competing vegetation on regeneration

The seedbed conditions at a microsite, including the specific soil moisture, temperature, and forest floor substrate (i.e., the microsite), at a given location and can influence the ability of germination of tree seedlings (Rother et al. 2015, Fig. 1). Our study confirms that seedlings were more prevalent under moderate soil temperatures and increased soil moisture (Petrie et al. 2016). Both higher maximum and mean daily soil temperatures resulted in lower establishment rates, as did lower minimum soil moistures. Low soil moisture during the summer months is also associated with recruitment failure (Davis et al. 2019a), but on our sites, the best moisture driver was single daily minimum soil moisture, rather than a seasonal minimum. There are likely other important drivers of soil moisture and temperature that we were unable to observe given a relatively small sample size, especially for soil moisture. Wildlife interference with soil moisture and temperature data logging equipment led to occasional equipment failure, reducing sample size during certain periods of data collection throughout the field season.

Lower soil moisture in HL plots may exacerbate the harsh post-fire climatic conditions that are particularly pronounced at low elevations that others have shown (Coop et al. 2020). Furthermore, the reduced soil moisture in HL plots may undermine planting efforts if moisture deficits and drought stress exceed the tolerance of planted seedlings. Early conifer tree regeneration demonstrates vulnerability to extremes, whether that is single day minimum soil moisture or maximum summer temperatures (Rother et al. 2015), thus reducing extreme

fluctuations through canopy presence, surface fuels loading, or reducing planting regeneration efforts to more moderate, mid-elevation plots may be critical for long term regeneration success.

Tree regeneration was highly variable, in part because we captured a wide range of forest types in this study. Lodgepole seedlings, Gambel oak, and quaking aspen resprouts were prevalent at most plots where they occurred pre-fire, which aligns with research examining other recent fires in the region (Rodman et al. 2020). Non-lodgepole conifer seedlings were observed in less than half of the plots. The absence of other conifer seedlings is not necessarily surprising, given that this study occurred two years post-fire, and others have found it may take 5–10 years for 50% or more of seedlings to establish (Stevens-Rumann et al. 2018).

As reinforced here, post-fire dominance of deciduous resprouting species has been observed in multiple studies (Roccaforte et al. 2012; Coop et al. 2016; Stoddard et al. 2020). Gambel oak and quaking aspen recruits or resprouts occurred both 1 and 2 years post-fire at 100% of plots where they had been present previously, with Gambel oak averaging 10,000 stems ha^{-1} , and aspen averaging over 5000 stems ha^{-1} . Research on the Leroux Fire in Arizona, which burned through similar forest types as the Spring Creek Fire, found vigorous aspen response in the first year after fire, but observed that densities declined to below pre-fire levels over the following decade in all burn severity classes (Stoddard et al. 2018). While long-term patterns on the Spring Creek Fire will require repeated observations in the years to come, short-term transitions to dominance of these deciduous species are likely to persist without the prevalence of conifer regeneration or heavy ungulate browsing.

While no relationship between shrub cover or resprouting species density and tree seedlings was observed, other research has found mixed relationships, with some studies indicating increased competition between seedlings and post-fire shrub response (Welch et al. 2016), and others showing positive associations with tree recruitment (Davis et al. 2019a). Of course, tree regeneration depends not only on seed availability and competition, but also climate conditions conducive to recruitment (Davis et al. 2019a). The effects of increased warming and reduced soil moisture are already being felt in some forest types or for some species, where burned forests reveal climate conditions no longer conducive to tree regeneration (Parks et al. 2019; Coop et al. 2020). Here, we see evidence that increasing soil temperatures and decreases in soil moisture is driving lower conifer tree regeneration establishment. Longer-term studies are needed to understand the long-term trajectory of these forests,

especially as cone and seed production can be episodic in this region (Rother and Veblen 2017).

Management implications

Increased fuel loading in high severity, logged plots are similar to findings in other studies (e.g., Donato et al. 2006; Peterson et al. 2015; Leverkus et al. 2020). Though CWD increased in logged plots, mean loading falls within the optimum range of CWD for balancing fire risk with ecological benefits of downed materials as identified by Brown et al. (2003). Logging should not be used for short-term surface fuel reduction, but is likely to reduce long-term fuel accumulation compared to burned-only sites. Logging treatments may still be useful for plot preparation for restoration actions and may be desired to recoup lost timber value, but careful attention should be paid to the effects of soil compaction and organic matter removal that accompanies these actions (Powers et al. 2005). If land managers seek to restore burned areas to a forested state and intend to implement a logging treatment, minimizing heavy equipment usage and altering implementation to include snag retention is important for maintaining canopy and improving soil conditions (DeLong and Kessler 2000; Lindenmayer and Noss 2006).

Greater snag retention may not reduce long-term fuel loads, but the retained canopy cover, in the short term, can reduce soil moisture loss from solar exposure, increase favorable microsites for tree regeneration, and provide wildlife habitat. While the logging methods in this study were clear cuts with large-scale fuel removal during the summer and fall, some studies indicate reduced ecological impact when logging occurs during the winter (Wolf et al. 2008). Other methods of logging, including cable or helicopter-based tree harvesting methods, reduce fuel deposition and may also reduce soil disturbance, but are cost-prohibitive in areas with low timber value (Lindenmayer and Noss 2006; Leverkus et al. 2020).

Resprouting of deciduous species dominated this early post-fire period with variable conifer regeneration. Where conifer dominance is desired post-fire, planting may be warranted to assist in early recovery to conifer dominant forest. This may be especially helpful in areas subject to frequent drought or located at the lower elevational or latitudinal ranges of desired tree species, where increased soil temperatures and moisture deficits may not be favorable for unassisted regeneration. Future research is needed to explore if the canopy created by early seral plant species (particularly by resprouting quaking aspen and Gambel oak) may offset soil moisture deficits and stabilize temperature differences in logged plots, potentially creating more favorable conditions for conifer regeneration. Monitoring seedling densities at

5 and 10 years post-fire may offer valuable insights into recovering forest trajectories across plot categories, potentially indicating if conifer forest recovery is likely or if a strong initial response of resprouting species may foreshadow transition to deciduous-dominant states.

Conclusions

This study examined soil microclimate and tree regeneration in areas that burned at low severity, high severity, and areas burned at high severity that were subsequently logged. Soil temperature and moisture are driven, in part, by canopy cover and the proportion of bare ground cover, which in turn impact conifer tree regeneration. Early post-fire species establishment was dominated by resprouting species and serotinous conifers. Across all conifer species, temperature and moisture did impact early post-fire seedling establishment. Canopy cover, especially live canopy cover found on low severity burned plots, increased soil moisture and decreased soil temperature during the growing season. Changes in plot conditions that occur during post-fire logging may further affect plot microclimate and therefore regeneration success. As forests experience novel and perhaps harsher climatic conditions, post-fire logging requires increased planning and considerations to offset potential negative ecological impacts.

Abbreviations

LS: Low to moderate severity; HL: High severity fire and logged; HS: High severity; CWD: Coarse woody debris; ANOVA: Analysis of variance.

Acknowledgements

Thank you to the private landowners and forest managers, as well as the foresters with the Colorado State Forest Service who allowed this research on their property. Thank you to Vausha Snyder, Maya Velasco, Zane Dickson Hunt, Kelby Woodard, Rachael O'Niell, Sara Painter, and Rasmus Davis for field work assistance. Thank you Miranda Redmond for early, friendly reviews.

Authors' contributions

JW assisted in project design, conducted field work and wrote the manuscript. CSSR led project design and assisted in field work, analysis, and manuscript edits. ZS assisted in field work and analysis and provided manuscript edits. MR assisted in project design and manuscript edits. The author(s) read and approved the final manuscript.

Funding

The Colorado Mountain Club, Colorado State University, and Joint Fire Science Program 16-1-01-20.

Availability of data and materials

The datasets generated and analyzed during the current study are available in the FRAMES repository, <https://www.frames.gov/>.

Declarations

Ethics approval and consent to participate

This project did not involve human subjects and therefore no ethics approval was required.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 29 November 2021 Accepted: 10 May 2022

Published online: 13 June 2022

References

- Abatzoglou, J.T., and A.P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences* 113 (42): 11770. <https://doi.org/10.1073/pnas.1607171113>.
- Allen, R. B., & Peet, R. K. 1990. Gradient analysis of forests of the Sangre de Cristo Range, Colorado. *Canadian Journal of Botany* 68(1): 193–201. <https://doi.org/10.1139/b90-026>.
- Beers, T.W., P.E. Dress, and L.C. Wensel. 1966. Notes and Observations: Aspect Transformation in Site Productivity Research. *Journal of Forestry* 64 (10): 691–692. <https://doi.org/10.1093/jof/64.10.691>.
- Beschta, R.L., J.J. Rhodes, J.B. Kauffman, R.E. Gresswell, G.W. Minshall, J.R. Karr, D.A. Perry, F.R. Hauer, and C.A. Frissell. 2004. Postfire Management on Forested Public Lands of the Western United States. *Conservation Biology* 18 (4): 957–967. <https://doi.org/10.1111/j.1523-1739.2004.00495.x>.
- Blair, D.P., L.M. McBurney, W. Blanchard, S.C. Banks, and D.B. Lindenmayer. 2016. Disturbance gradient shows logging affects plant functional groups more than fire. *Ecological Applications* 26 (7): 2280–2301. <https://doi.org/10.1002/eap.1369>.
- Brown, J.K. 1974. *Handbook for inventorying downed woody material*. Gen. Tech. Rep. INT-16. Ogden: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.
- Brown, J.K., E.D. Reinhardt, and K.A. Kramer. 2003. *Coarse woody debris: Managing benefits and fire hazard in the recovering forest*. Gen. Tech. Rep. RMRS-GTR-105. Ogden: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Castro, J., C.D. Allen, M. Molina-Morales, S. Mara  n-Jim  nez,  . S  nchez-Miranda, and R. Zamora. 2011. Salvage Logging Versus the Use of Burnt Wood as a Nurse Object to Promote Post-Fire Tree Seedling Establishment. *Restoration Ecology* 19 (4): 537–544. <https://doi.org/10.1111/j.1526-100X.2009.00619.x>.
- Chambers, M.E., P.J. Fornwalt, S.L. Malone, and M.A. Battaglia. 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range. *Forest Ecology and Management* 378: 57–67. <https://doi.org/10.1016/j.foreco.2016.07.001>.
- Coop, J.D., S.A. Parks, S.R. McClerman, and L.M. Holsinger. 2016. Influences of prior wildfires on vegetation response to subsequent fire in a reburned Southwestern landscape. *Ecological Applications* 26 (2): 346–354. <https://doi.org/10.1890/15-0775>.
- Coop, J.D., S.A. Parks, C.S. Stevens-Rumann, S.D. Crausbay, P.E. Higuera, M.D. Hurteau, A. Tepley, E. Whitman, T. Assal, B.M. Collins, K.T. Davis, S. Dobrowski, D.A. Falk, P.J. Fornwalt, P.Z. Ful  , B.J. Harvey, V.R. Kane, C.E. Littlefield, E.Q. Margolis, et al. 2020. Wildfire-Driven Forest Conversion in Western North American Landscapes. *BioScience* 70 (8): 659–673. <https://doi.org/10.1093/biosci/biaa061>.
- Davis, K.T., S.Z. Dobrowski, P.E. Higuera, Z.A. Holden, T.T. Veblen, M.T. Rother, S.A. Parks, A. Sala, and M.P. Maneta. 2019a. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences* 116 (13): 6193. <https://doi.org/10.1073/pnas.1815107116>.
- Davis, K.T., S.Z. Dobrowski, Z.A. Holden, P.E. Higuera, and J.T. Abatzoglou. 2019b. Microclimatic buffering in forests of the future: The role of local water balance. *Ecography* 42 (1): 1–11. <https://doi.org/10.1111/ecog.03836>.

- DeLong, S.C., and W.B. Kessler. 2000. Ecological characteristics of mature forest remnants left by wildfire. *Forest Ecology and Management* 131 (1): 93–106. [https://doi.org/10.1016/S0378-1127\(99\)00203-0](https://doi.org/10.1016/S0378-1127(99)00203-0).
- Dobrowski, S.Z., A.K. Swanson, J.T. Abatzoglou, Z.A. Holden, H.D. Safford, M.K. Schwartz, and D.G. Gavin. 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. *Global Ecology and Biogeography* 24 (8): 917–927. <https://doi.org/10.1111/geb.12302>.
- Donato, D.C., J.B. Fontaine, J.L. Campbell, W.D. Robinson, J.B. Kauffman, and B.E. Law. 2006. Post-Wildfire Logging Hinders Regeneration and Increases Fire Risk. *Science* 311 (5759): 352. <https://doi.org/10.1126/science.1122855>.
- Donato, Daniel C., J.B. Fontaine, J.B. Kauffman, W.D. Robinson, and B.E. Law. 2013. Fuel mass and forest structure following stand-replacement fire and post-fire logging in a mixed-evergreen forest. *International Journal of Wildland Fire* 22 (5): 652–666. <https://doi.org/10.1071/WF12109>.
- Ettinger, A., and J. HilleRisLambers. 2017. Competition and facilitation may lead to asymmetric range shift dynamics with climate change. *Global Change Biology* 23 (9): 3921–3933. <https://doi.org/10.1111/gcb.13649>.
- Fornwalt, P.J., C.S. Stevens-Rumann, and B.J. Collins. 2018. Overstory Structure and Surface Cover Dynamics in the Decade Following the Hayman Fire, Colorado. *Forests* 9 (3): 152. <https://doi.org/10.3390/f9030152>.
- Gómez-Aparicio, L., R. Zamora, J.M. Gómez, J.A. Hódar, J. Castro, and E. Baraza. 2004. Applying Plant Facilitation to Forest Restoration: A Meta-Analysis of the Use of Shrubs as Nurse Plants. *Ecological Applications* 14 (4): 1128–1138. <https://doi.org/10.1890/03-5084>.
- Gray, A.N., and T.A. Spies. 1997. Microsite Controls on Tree Seedling Establishment in Conifer Forest Canopy Gaps. *Ecology* 78 (8): 2458–2473. [https://doi.org/10.1890/0012-9658\(1997\)078\[2458:MCOTSE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[2458:MCOTSE]2.0.CO;2).
- Hankin, L.E., P.E. Higuera, K.T. Davis, and S.Z. Dobrowski. 2019. Impacts of growing-season climate on tree growth and post-fire regeneration in ponderosa pine and Douglas-fir forests. *Ecosphere* 10 (4): e02679. <https://doi.org/10.1002/ecs2.2679>.
- Hill, E.M., and S. Ex. 2020. Microsite conditions in a low-elevation Engelmann spruce forest favor ponderosa pine establishment during drought conditions. *Forest Ecology and Management* 463: 118037. <https://doi.org/10.1016/j.foreco.2020.118037>.
- Kaufmann, M.R., C.M. Regan, and P.M. Brown. 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: Age and size structure in unlogged and logged landscapes of central Colorado. *Canadian Journal of Forest Research* 30 (5): 698–711. <https://doi.org/10.1139/x99-255>.
- Kemp, K.B., Higuera, P.E. and Morgan, P. 2016. Fire legacies impact conifer regeneration across environmental gradients in the US northern Rockies. *Landscape Ecology* 31 (3): 619–636.
- Keyser, T.L., F.W. Smith, and W.D. Shepperd. 2009. Short-term impact of post-fire salvage logging on regeneration, hazardous fuel accumulation, and understory development in ponderosa pine forests of the Black Hills, SD, USA. *International Journal of Wildland Fire* 18 (4): 451–458. <https://doi.org/10.1071/WF08004>.
- Kueppers, L.M., E. Conlisk, C. Castanha, A.B. Moyes, M.J. Germino, P. de Valpine, M.S. Torn, and J.B. Mitton. 2017. Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. *Global Change Biology* 23 (6): 2383–2395. <https://doi.org/10.1111/gcb.13561>.
- Leverkus, A.B., L. Gustafsson, D.B. Lindenmayer, J. Castro, J.M. Rey Benayas, T. Ranius, and S. Thorn. 2020. Salvage logging effects on regulating ecosystem services and fuel loads. *Frontiers in Ecology and the Environment* 18 (7): 391–400. <https://doi.org/10.1002/fee.2219>.
- Lindenmayer, D.B. and Noss, R.F. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. *Conservation Biology* 20(4): 949–958.
- Lopez Ortiz, M.J., T. Marcey, M.S. Lucash, D. Hibbs, J.P.A. Shatford, and J.R. Thompson. 2019. Post-fire management affects species composition but not Douglas-fir regeneration in the Klamath Mountains. *Forest Ecology and Management* 432: 1030–1040. <https://doi.org/10.1016/j.foreco.2018.10.030>.
- Maher, E.L., M.J. Germino, and N.J. Hasselquist. 2005. Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine tree-line ecotone. *Canadian Journal of Forest Research* 35 (3): 567–574. <https://doi.org/10.1139/x04-201>.
- Malvar, M.C., F.C. Silva, S.A. Prats, D.C.S. Vieira, C.O.A. Coelho, and J.J. Keizer. 2017. Short-term effects of post-fire salvage logging on runoff and soil erosion. *Forest Ecology and Management* 400: 555–567. <https://doi.org/10.1016/j.foreco.2017.06.031>.
- Marcolin, E., R. Marzano, A. Vitali, M. Garbarino, and E. Lingua. 2019. Post-Fire Management Impact on Natural Forest Regeneration through Altered Microsite Conditions. *Forests* 10 (11). <https://doi.org/10.3390/f10111014>.
- Neary, D.G., K.C. Ryan, and L.F. DeBano. 2005. *Wildland fire in ecosystems: effects of fire on soils and water. Gen. Tech. Rep. RMRS-GTR-42-vol.4*. Ogden: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Ouzts, J., Kolb, T., Huffman, D. and Meador, A.S. 2015. Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. *Forest Ecology and Management* 354: 281–290.
- Parks, S.A., and J.T. Abatzoglou. 2020. Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests From 1985 to 2017. *Geophysical Research Letters* 47 (22): e2020GL089858. <https://doi.org/10.1029/2020GL089858>.
- Parks, S.A., S.Z. Dobrowski, J.D. Shaw, and C. Miller. 2019. Living on the edge: Trailing edge forests at risk of fire-facilitated conversion to non-forest. *Ecosphere* 10 (3): e02651. <https://doi.org/10.1002/ecs2.2651>.
- Parks, S.A., C. Miller, J.T. Abatzoglou, L.M. Holsinger, M.-A. Parisien, and S.Z. Dobrowski. 2016. How will climate change affect wildland fire severity in the western US? *Environmental Research Letters* 11 (3): 035002. <https://doi.org/10.1088/1748-9326/11/3/035002>.
- Peterson, D.W., E.K. Dodson, and R.J. Harrod. 2015. Post-fire logging reduces surface woody fuels up to four decades following wildfire. *Forest Ecology and Management* 338: 84–91. <https://doi.org/10.1016/j.foreco.2014.11.016>.
- Petrie, M.D., A.M. Wildeman, J.B. Bradford, R.M. Hubbard, and W.K. Lauenroth. 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. *Forest Ecology and Management* 361: 328–338. <https://doi.org/10.1016/j.foreco.2015.11.028>.
- Powers, R.F., D.A. Scott, F.G. Sanchez, R.A. Voldseth, D. Page-Dumroese, J.D. Elioff, and D.M. Stone. 2005. The North American long-term soil productivity experiment: findings from the first decade of research. *Forest Ecology and Management* 220: 31–50. <https://doi.org/10.1016/j.foreco.2005.08.003>.
- Rocafort, J.P., P.Z. Fulé, W.W. Chancellor, and D.C. Laughlin. 2012. Woody debris and tree regeneration dynamics following severe wildfires in Arizona ponderosa pine forests. *Canadian Journal of Forest Research* 42 (3): 593–604. <https://doi.org/10.1139/x2012-010>.
- Rodman, K.C., T.T. Veblen, T.B. Chapman, M.T. Rother, A.P. Wion, and M.D. Redmond. 2020. Limitations to recovery following wildfire in dry forests of southern Colorado and northern New Mexico, USA. *Ecological Applications* 30 (1): e02001. <https://doi.org/10.1002/eap.2001>.
- Rother, M.T. and Veblen, T.T. 2017. Climate drives episodic conifer establishment after fire in dry ponderosa pine forests of the Colorado Front Range, USA. *Forests* 8(5): 159.
- Rother, M.T., T.T. Veblen, and L.G. Furman. 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. *Canadian Journal of Forest Research* 45 (11): 1607–1616. <https://doi.org/10.1139/cjfr-2015-0033>.
- RStudio Team. 2019. RStudio: Integrated Development for R. <http://www.rstudio.com/>.
- Schapira, Z., C. Stevens-Rumann, D. Shorrock, C. Hoffman, and A. Chambers. 2021. Beetlemania: Is the bark worse than the bite? Rocky Mountain subalpine forests recover differently after spruce beetle outbreaks and wildfires. *Forest Ecology and Management* 482: 118879. <https://doi.org/10.1016/j.foreco.2020.118879>.
- Sikkink, P.G., and R.E. Keane. 2008. A comparison of five sampling techniques to estimate surface fuel loading in montane forests. *International Journal of Wildland Fire* 17: 363–379.
- Stevens-Rumann, C.S., A.T. Hudak, P. Morgan, A. Arnold, and E.K. Strand. 2020. Fuel Dynamics Following Wildfire in US Northern Rockies Forests. *Frontiers in Forests and Global Change* 3: 51. <https://doi.org/10.3389/ffgc.2020.00051>.
- Stevens-Rumann, C.S., K.B. Kemp, P.E. Higuera, B.J. Harvey, M.T. Rother, D.C. Donato, P. Morgan, and T.T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. *Ecology Letters* 21 (2): 243–252. <https://doi.org/10.1111/ele.12889>.

- Stevens-Rumann, C.S., and P. Morgan. 2019. Tree regeneration following wildfires in the western US: a review. *Fire Ecology* 15 (1): 15. <https://doi.org/10.1186/s42408-019-0032-1>.
- Stoddard, M., P. Fulé, D. Huffman, A. Sánchez Meador, and J. Roccaforte. 2020. Ecosystem management applications of resource objective wildfires in forests of the Grand Canyon National Park, USA. *International Journal of Wildland Fire* 29. <https://doi.org/10.1071/WF19067>.
- Stoddard, M.T., D.W. Huffman, P.Z. Fulé, J.E. Crouse, and A.J. Sánchez Meador. 2018. Forest structure and regeneration responses 15 years after wildfire in a ponderosa pine and mixed-conifer ecotone, Arizona, USA. *Fire Ecology* 14 (2): 12. <https://doi.org/10.1186/s42408-018-0011-y>.
- Veblen, T.T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* 10 (4): 1178–1195. [https://doi.org/10.1890/1051-0761\(2000\)010\[1178:CAHIOF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[1178:CAHIOF]2.0.CO;2).
- Von Arx, G., Graf Pannatier, E., Thimonier, A. and Rebetez, M. 2013. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. *Journal of ecology* 101(5): 1201–1213.
- Welch, K.R., H.D. Safford, and T.P. Young. 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. *Ecosphere* 7 (12): e01609. <https://doi.org/10.1002/ecs2.1609>.
- Wolf, A.T., Parker, L., Fewless, G., Corio, K., Sundance, J., Howe, R. and Gentry, H. 2008. Impacts of summer versus winter logging on understory vegetation in the Chequamegon-Nicolet National Forest. *Forest Ecology and Management* 254(1): 35–45.

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