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# Strong Legacy Effects of Prior Burn Severity on Forest Resilience to a High-Severity Fire

Lucas B. Harris,[1]* Stacy A. Drury,[2] and Alan H. Taylor[3]

[1]Department of Geography, The Pennsylvania State University, 302 Walker Building, University Park, Pennsylvania 16802, USA; [2]USDA Forest Service, Pacific Southwest Research Station, Davis, California, USA; [3]Department of Geography, Earth and Environmental Systems Institute, The Pennsylvania State University, 302 Walker Building, University Park, Pennsylvania 16802, USA

## ABSTRACT

Legacy effects from one disturbance may influence successional pathways by amplifying or buffering forest regeneration after the next disturbance. We assessed vegetation and tree regeneration in non-serotinous Sierra lodgepole pine (*Pinus contorta* var. *murrayana*) stands after a 1984 wildfire which burned with variable severity and again after a high-severity subsequent fire in 2012. The legacy effects of the 1984 fire were amplified; seedlings and saplings were abundant in areas initially burned at low severity (1267 stems ha$^{-1}$) despite high reburn severity, but regeneration was low in areas twice burned at high severity (31 stems ha$^{-1}$). Our results suggest that the severity of the 1984 fire may have influenced post-2012 tree regeneration by creating variable fuel loading, which may have affected soils, litter cover and shade after the 2012 fire and therefore affected seedling establishment and survival. A canopy seed bank of unburnt cones from trees killed by the 2012 fire potentially contributed to a strong effect of prior burn severity on regeneration after the 2012 fire despite a lack of serotinous or resprouting tree species, although the influence of this canopy seedbank was likely limited to the year following the fire. Our results suggest that a low- to moderate-severity fire increases forest resilience relative to a high-severity fire even when the next fire burns at high severity.

**Key words:** Repeated fires; Tree regeneration; Legacy effects; Forest resilience; High-severity wildfire; *Pinus contorta*.

## HIGHLIGHTS

- Severity of a prior fire determined tree regeneration after a high-severity reburn

- Forests twice burned at high severity had sparse tree regeneration
- Low-severity fire increased forest resilience to a subsequent high-severity fire

## INTRODUCTION

Successive disturbances, especially when occurring at relatively short intervals, may lead to persistent and sometimes surprising changes in vegetation (Zedler and others 1983; Paine and others 1998; Buma 2015). Such changes arise in part due to legacy effects of past disturbances on vegetation structure and composition, which interact with

subsequent disturbance to influence vegetation recovery (Paine and others 1998; Franklin and others 2000). As climate change leads to increased fuel aridity and area burned in western US forests (Abatzoglou and Williams 2016), a key question is how legacy effects of past disturbances influence forest recovery after a high-severity fire. Throughout, we use the term ''burn severity'' and descriptors such as ''high severity'' to refer to ''vegetation burn severity'' meaning the effects of fire on vegetation measured one or more years after the fire (sensu. Morgan and others 2014).

Work in dry pine and mixed-conifer forests of the western USA suggest that repeated fires (also called reburns) reinforce vegetation changes triggered by past fires, especially when one high-severity fire leads to vegetation types and structures which are prone to burn at high severity in the next fire (Odion and others 2010; Coop and others 2016; Lauvaux and others 2016). Repeated fires have the potential to drive persistent vegetation change even in more mesic, higher-elevation mixed-conifer and subalpine forests by dealing a double blow: a further reduction in live trees to act as seed sources and mortality of much of the tree regeneration (that is, seedlings and saplings) that established after the previous fire (Gray and Franklin 1997; Busby 2019; Turner and others 2019).

The characteristics of repeated fires may affect tree regeneration and therefore future forest cover. Prior research suggests that repeated high-severity leads to lower tree seedling density compared with a low-severity fire followed by a high-severity fire, because a past high-severity fire may more completely eliminate the seedbank and seed sources (Stevens-Rumann and Morgan 2016). Such results suggest that legacy effects from a past fire can influence forest resilience to the next fire (Johnstone and others 2016). Here we define forest resilience as the degree of perturbation a forest can withstand before transitioning to a new state (Holling 1973; Gunderson 2000), and legacies as the organisms and biologically derived patterns left after a disturbance which influence future ecosystem dynamics (Franklin and others 2000).

A growing body of research has examined successional pathways over successive fires (Donato and others 2009; Coop and others 2016; Stevens-Rumann and Morgan 2016; Turner and others 2019). However, most studies on repeated fire effects on forest change rely on space-for-time substitution (Pickett 1989) where nearby sites with different fire histories are surveyed and results are assumed to represent a time series at one location.

Field-based studies using repeated measurements to quantify vegetation change over two successive wildfires (for example, Coop et al., 2016) are scarce but provide key insights on interactions between repeated fires, vegetation and potential forest recovery.

In this study, we measured post-fire tree regeneration in stands dominated by Sierra lodgepole pine (Pinus contorta var. murrayana) following repeated fires in the southern Cascade Range, California, USA. Sierra lodgepole pine is a widespread subspecies, ranging from Baja California, Mexico, to central Oregon, USA (Critchfield 1980). We conducted this work in low-lying basins representative of those occurring throughout the southern Cascade Range, in which cold air pooling and nutrient-poor pumice soils favor lodgepole pine dominance (Youngberg and Dyrness 1965; Cochran and Berntsen 1973; Volland 1985). Vegetation and post-fire tree regeneration were assessed in 2008 following a 1984 wildfire that burned at a range of fire severities, and then again in 2019 following a 2012 wildfire that burned mainly at high severity. Building on an earlier analysis of tree regeneration at this site by Pierce and Taylor (2011), we assessed the influences of burn severity, stand structure and microsite characteristics (for example, cover of shrubs, logs and rocks) on tree seedling and sapling density following the 2012 fire. Through these analyses, we evaluated the legacy effects of the 1984 fire on subsequent forest change and whether the second, higher-severity 2012 fire diminished, reinforced or amplified these effects. We hypothesized that tree seedling and sapling density would be strongly correlated with density of and distance to cone-bearing trees following the 2012 fire, because Sierra lodgepole pine is not serotinous and therefore has to seed in from nearby surviving trees following a fire (Dahms 1963; Pierce and Taylor 2011). Consequently, we expected the second, predominantly high-severity 2012 fire to diminish any legacy effect of the 1984 fire because of the large reduction in density of surviving seed trees.

## METHODS

### Study Area

This study was conducted within Lassen Volcanic National Park (LVNP), California. As reviewed by Parker (1993), Sierra lodgepole pine is common at 1800–2200 m elevation in LVNP and occurs in three primary settings: recently disturbed areas,

mixed with other tree species in uplands and as the dominant tree in lowlands. Sierra lodgepole pine is highly tolerant of wet and cold conditions and therefore often dominates low-lying areas experiencing cold air drainage and wet soils within LVNP (Taylor 1990; Parker 1993).

In 1984 the Badger Fire burned 563 ha of LVNP and the adjacent Lassen National Forest. This area burned again in the 2012 Reading Fire (10,876 ha). In 2008 Pierce and Taylor (2011) assessed vegetation change caused by the Badger Fire within three lodgepole pine-dominated study sites (40.552° N, 121.404° W) selected to be homogenous with respect to terrain and soils so that the influence of burn severity on tree regeneration could be isolated. These sites were in flat, low-lying basins in which cold air pooling and potentially coarse or low-nutrient substrate often exclude trees species other than lodgepole pine (Cochran and others 1967; Cochran and Berntsen 1973; Parker 1993). Plot elevation ranged from 1925 to 1950 m. The study area is underlain by andesite and basalt, but the surface is a mix of glacially deposited material and scoria often with high cover of gravel-sized pumice (Pierce and Taylor 2011). Pierce and Taylor (2011) described vegetation within the study area as lodgepole pine-dominated forests. Other tree species were present including white fir (*Abies concolor*), red fir (*A. magnifica* var. *magnifica*) and Jeffrey pine (*Pinus jeffreyi*). Rabbitbrush (*Ericameria nauseosa*) and *Ribes spp.* were the most common shrubs. Tobaccobrush (*Ceanothus velutinus*) and manzanita (*Arctostaphylos patula* and *A. nevadensis*) were more common on toeslope sites where Jeffrey pine or firs were more abundant.

Historical fire regimes in Sierra lodgepole pine stands are not well known, and many stands likely experienced periodic mixed-severity fires (that is, fires which contained patches of low, moderate and high severity as well as unburned patches). Fire scar and tree age structure analyses from southern Cascades lodgepole pine stands suggest that fire-return intervals are moderately long (point median intervals of 50–77 years) and that forests include areas that burned at high severity (Taylor and Solem 2001; Bekker and Taylor 2010). In lodgepole pine-dominated forests in central Oregon, fire-return intervals were 26–82 years with areas of low, moderate and high severity (Heyerdahl and others 2014), similar to mean site-level fire intervals (31–74 years) in southern Sierra Nevada lodgepole stands (Caprio 2008), and pulses of tree regeneration followed these fires (Keifer 1991). Lodgepole pine-dominated pumice basins, such as those in the present study, may have longer fire-return inter-

vals than surrounding mixed-conifer forest because they are less productive and slower to recover from disturbance and therefore tend to be more fuel-limited (Merschel and others 2018). These fire history data indicate the 28-year interval between fires in the present study is relatively short but within the historical range of variability for this forest type.

## Field Data

Patches that burned at low, moderate and high severity in the 1984 Badger Fire had been selected for study using 2005 aerial photographs as part of an earlier analysis by Pierce and Taylor (2011), and burn severity in these burn patches was verified in the field. Low-, moderate- and high-severity fire was defined as areas with less than 25% tree canopy cover loss, 25–75% loss and 75% or more loss, respectively. Pierce and Taylor (2011) selected one patch each of low-, moderate- and high-severity fire for analysis, and 10 circular plots of 250 $m^2$ were randomly located within each patch. Sites were located more than 400 m from roads, and Pierce and Taylor (2011) verified in the field in 2008 that the plot locations were relatively homogenous with respect to terrain, soils, forest type and pre-1984 forest structure although some plots were located near the edge of the respective burn severity patches. We subsequently refer to these patches as the low-severity, moderate-severity and high-severity sites in reference to the burn severity class of each site in the 1984 fire.

In summer 2008 Pierce and Taylor (2011) recorded the species and diameter (dbh) of all live trees, snags and logs at least 5 cm dbh in each plot. In addition, they assessed the presence of cones on live trees, and dead trees which likely survived the 1984 fire were identified based on the presence of needles or if they had intact bark. Pierce and Taylor (2011) assessed influences on seedling and sapling presence at the microsite scale by quantifying ground cover in four subplots (10 $m^2$) located equidistant from the center and edge of the plot in the four cardinal directions. Cover of logs (> 4 cm diameter), shrubs, forbs, grasses, large rocks (> 10 cm) and rock fragments (1–10 cm) were visually estimated in the subplots in the following cover classes: not present, less than 1%, 1–5%, 5–25%, 26–50%, 51–75%, 76–100%. Seedlings and saplings were tallied by species within the subplots. Additional details on field methods are provided in Pierce and Taylor (2011).

In 2019 we re-measured 9 out of 10 plots within each 1984 site ($n = 27$ total, Figure 1). We relo-
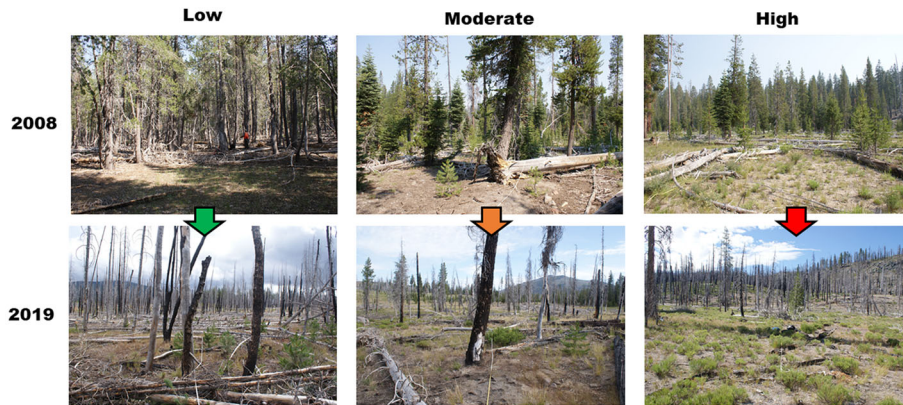
**Figire 1.** Paired photographs taken in 2008 and 2019 from three plots representative of low, moderate and high burn severity in the 1984 Badger Fire.

cated the plots of Pierce and Taylor (2011) by first using the GPS location and subsequently determining the location of the plot center by trilateration using the distance between the plot center and each tree in the plot, which Pierce and Taylor (2011) recorded in 2008. By using multiple tree-plot center measurements per plot we were able to relocate plot centers with a high degree of spatial accuracy, although a limited degree of measurement error from both 2008 to 2019 likely exists. We were unable to relocate 3 plots in 2019, which could result from spatial uncertainty in the 2008 GPS locations combined with the altered visual appearance of the plots due to the Reading Fire effects (for example, tree mortality and consumption of snags and logs). We quantified tree regeneration and ground cover in each plot using the same methodology as in 2008. Additionally, we determined the status (live, snag or log) of each tree measured in 2008 and then measured the dbh of all trees that were alive in 2019.

## Burn Severity

Although fire-driven canopy cover change as assessed from aerial photography was used by Pierce and Taylor (2011) to select study sites prior to conducting fieldwork in 2008, we utilized the 2008 and 2019 field data to more accurately characterize burn severity at the plot level. The proportion of tree basal area killed (hereafter ''BA mortality'') from the 1984 and 2012 fires was used as a field-based measure of burn severity for both fires. In 2008 trees that had likely survived the 1984 fire were identified by Pierce and Taylor (2011) based on having either most of their bark intact or needles. We calculated BA mortality for 1984 using the ratio of non-surviving tree BA to BA of all trees in each plot. To calculate BA mortality in 2012 we used 2008 tree

dbh to better estimate dbh at the time of the fire and compared total BA by plot for trees that were alive in 2008 and dead in 2012 versus all trees alive in 2008. Note that our methods underestimate BA mortality in 1984 because live trees increased in BA and dead trees decayed between 1984 and the first field survey by Pierce and Taylor (2011) in 2008. To estimate this effect of 1984–2008 tree growth on our analyses, we used the growth rate of surviving trees from 2008 to 2019 to adjust 1984 BA mortality and repeated our analyses using these adjusted values (see Supporting Information). We concluded that our key results and conclusions are robust to the effect of 1984–2008 tree growth. We note that burn severity may be assessed using a broad range of indices measuring fire effects on overstory vegetation, understory vegetation and soils (Morgan and others 2014). We chose tree BA mortality as our field-based metric of burn severity because it could be calculated for both fires based on the available 2008 data, and because we were primarily interested in trees and tree regeneration. However, as a complementary measure of burn severity we used a remote sensing index of burn severity, the relativized differenced normalized burn ratio (RdNBR) (Miller and Thode 2007) from the Monitoring Trends in Burn Severity program (Eidenshink and others 2007). RdNBR indicates changes across vegetation strata, as evidenced by its strong relationship with the Composite Burn Index for fires in California forests (Miller and others 2009), and therefore is a complementary metric to tree BA mortality which just considers changes to the canopy.

## Tree Regeneration

Following the 2008 protocols, seedlings and saplings were counted in each 250 m$^2$ plot in 2019. Stems were tallied as small (< 0.5 m tall but ≥ 2

branch whorls), or large seedlings (0.5–1.4 m) and saplings (> 1.4 m but < 5 cm dbh). The minimum branch whorl criterium had been used by Pierce and Taylor (2011) to exclude current-year seedlings which are commonly considered to be ephemeral, and we followed the same protocols. To estimate age, branch whorls were counted on each stem. The Supporting Information provides a discussion of whorl counts in relation to seedling ages determined using tree ring counts for seedlings in the study site. Because the 2019 field measurements occurred seven years post-fire, whereas the 2008 measurements occurred 24 years post-fire, we also used a branch whorl-tree ring count regression developed by Pierce and Taylor (2011) to quantify the density of seedlings and saplings established prior to 1990 (hereafter ''1991 seedling density,'' see Supporting Information). This metric is an estimate of seedling and sapling density had the 2008 sites been surveyed seven years post-fire as was the case in 2019. The 1991 seedling density is likely conservative because it does not account for seedlings which died between 1991 and 2008.

To assess plot-level influences on tree seedling and sapling densities, we began by calculating Spearman rank correlation coefficients ($r_s$) between tree seedling and sapling density in 2019 and BA mortality, tree basal area and density, and ground cover from both the 2008 and 2019 field surveys. For the purposes of the plot-level analysis, ground cover estimates were aggregated to the plot level using the mean midpoint class value of the four subplots. Note that we also performed an analysis at the subplot level, which is described later in this subsection. We assessed significance of the correlations using a Holm–Bonferroni correction. Seedlings and saplings of all species were combined for our tree regeneration analysis because total and lodgepole pine seedling and sapling density were highly correlated ($r_s = 0.98$) and results with only lodgepole pine were highly similar (Table A1).

To build on the exploratory correlation analysis, we created a generalized linear model (GLM) of plot-level tree seedling and sapling abundance (counts) in 2019. Tree seedling and sapling counts were best modeled with a negative binomial distribution, using the glm.nb function in the MASS package in R (Venables and Ripley 2002). We used counts instead of tree seedling and sapling density for the GLM because negative binomial models are designed to handle count data. To address multicollinearity, we identified variables with $r_s$ greater than 0.7 and in each case retained the variable more strongly correlated with tree seedling and sapling counts. We then built a parsimonious

model using stepwise variable selection based on the Akaike information criterion (AIC, Akaike, 1974). We did not include interactions among predictor variables in the GLM. We retained two variables in the GLM which were non-significant ($P > 0.05$) because including these variables reduced the AIC and because we had ecological justifications for retaining both: Pierce and Taylor (2011) found seed source distance to be influential at our sites, and post-fire log cover may influence tree establishment by providing shade. Note that methods for variable selection and retention are widely debated, and that our goal was to explore potential influences on seedling and sapling counts rather than to create a predictive model (Murtaugh 2009; Shmueli 2010; Heinze and others 2018). To visualize the modeled effect of the most influential variable, BA mortality from the 1984 fire, on predicted tree seedling and sapling counts, we used the cplot function in the margins package in R (Leeper 2018).

Finally, we assessed the influence of microsite characteristics on tree regeneration by comparing the presence or absence of tree seedlings and saplings within each subplot in 2019 with the corresponding ground cover estimates using a Chi-squared test. A Holm–Bonferroni correction was again applied to assess significance at the subplot level, and only significant relationships ($P < 0.05$) are reported.

# RESULTS

## Burn Severity and Effects on Vegetation

Percent BA mortality differed among the low-, moderate- and high-severity sites in the 1984 fire, following the study design (Table 1). BA mortality was greater in the 2012 fire than in the 1984 fire in 25 of 27 plots, including 17 plots that had total tree mortality and only three plots that had less than 70% BA mortality.

The 2012 Reading Fire led to an order of magnitude decrease in average live tree density (Table 1) and an 87% decrease in average live tree BA. Between 2008 and 2019, there was a twofold increase in cover of shrubs and grasses, and cover of rock fragments also increased (Table 1). In 2019, shrub cover and rock fragment cover were highest at the high-severity site and grass cover was highest at the low-severity site (Table 1). Log cover was lowest at the low-severity site in 2008 but lowest at the high-severity site in 2019 (Table 1).

**Table 1.** Tree Regeneration, Burn Severity, Stand Structure and Ground Cover Characteristics in 2008 and 2019 by Site ($n = 9$ plots per site, mean $\pm$ SD), and Spearman Rank Correlation Coefficients ($r_s$) with 2019 Tree Regeneration Density (bold)

| Variable | Low-severity site | Moderate-severity site | High-severity site | $r_s$ with 2019 regeneration |
|---|---|---|---|---|
| Tree seedling and sapling density 2008 (stems ha$^{-1}$) | 4031 $\pm$ 3178 | 4556 $\pm$ 2716 | 1591 $\pm$ 1821 | 0.39 |
| Tree seedling and sapling density 1991 (stems ha$^{-1}$) | 1178 $\pm$ 974 | 1013 $\pm$ 780 | 440 $\pm$ 718 | 0.46 |
| **Tree seedling and sapling density 2019 (stems ha$^{-1}$)** | **1267 $\pm$ 1095** | **329 $\pm$ 303** | **31 $\pm$ 56** | |
| Tree basal area mortality 1984 (%) | 14.4 $\pm$ 9.9 | 41.6 $\pm$ 15.8 | 92.5 $\pm$ 14.0 | $-$ 0.88*** |
| Tree basal area mortality 2012 (%) | 89.2 $\pm$ 12.5 | 84.1 $\pm$ 30.8 | 93.8 $\pm$ 17 | $-$ 0.22 |
| RdNBR 1984 | 94 55 | 416 106 | 535 145 | $-$ 0.61* |
| RdNBR 2012 | 560 288 | 299 277 | 639 331 | $-$ 0.30 |
| Live tree basal area 2008 (m$^2$ ha$^{-1}$) | 46.8 $\pm$ 10.8 | 24.0 $\pm$ 7.3 | 4.6 $\pm$ 5.4 | 0.84*** |
| Live tree basal area 2019 (m$^2$ ha$^{-1}$) | 5.2 $\pm$ 5.8 | 3.7 $\pm$ 6.7 | 1.0 $\pm$ 3.0 | 0.32 |
| Cone-bearing lodgepole pine density 2008 (trees ha$^{-1}$) | 884 $\pm$ 329 | 476 $\pm$ 197 | 80 $\pm$ 100 | 0.80*** |
| Cone-bearing lodgepole pine density 2019 (trees ha$^{-1}$) | 93 $\pm$ 104 | 58 $\pm$ 96 | 13 $\pm$ 40 | 0.32 |
| Live tree density 2008 (trees ha$^{-1}$) | 1009 $\pm$ 317 | 627 $\pm$ 209 | 244 $\pm$ 179 | 0.73*** |
| Live tree density 2019 (trees ha$^{-1}$) | 98 $\pm$ 113 | 62 $\pm$ 106 | 22 $\pm$ 53 | 0.30 |
| Distance to seed source 2008 (m) | 2.3 $\pm$ 0.8 | 2.0 $\pm$ 0.7 | 13.1 $\pm$ 7.4 | $-$ 0.58* |
| Distance to seed source 2019 (m) | 18.8 $\pm$ 19.3 | 13.9 $\pm$ 14.0 | 28.1 $\pm$ 20.5 | $-$ 0.36 |
| Shrub cover 2008 (%) | 0.6 $\pm$ 1.0 | 4.4 $\pm$ 8.5 | 5.8 $\pm$ 3.4 | $-$ 0.60* |
| Shrub cover 2019 (%) | 3.6 $\pm$ 5.2 | 9.1 $\pm$ 5.3 | 12.4 $\pm$ 6.6 | $-$ 0.44 |
| Grass cover 2008 (%) | 7.2 $\pm$ 7.6 | 5.6 $\pm$ 5.3 | 8.3 $\pm$ 5.7 | $-$ 0.35 |
| Grass cover 2019 (%) | 23.0 $\pm$ 9.6 | 16.2 $\pm$ 7.9 | 12.2 $\pm$ 5.0 | 0.34 |
| Forb cover 2008 (%) | 1.4 $\pm$ 2.7 | 4.8 $\pm$ 5.8 | 3.1 $\pm$ 2.6 | $-$ 0.46 |
| Forb cover 2019 (%) | 6.4 $\pm$ 5.3 | 3.7 $\pm$ 5.6 | 3.6 $\pm$ 3.5 | 0.02 |
| Rock fragment cover 2008 (%) | 1.2 $\pm$ 1.2 | 5.7 $\pm$ 8.4 | 19.4 $\pm$ 16.6 | $-$ 0.71*** |
| Rock fragment cover 2019 (%) | 6.8 $\pm$ 3.9 | 14.7 $\pm$ 7.3 | 23.2 $\pm$ 8.7 | $-$ 0.74*** |
| Rock cover 2008 (%) | 0.2 $\pm$ 0.3 | 0.1 $\pm$ 0.3 | 0.7 $\pm$ 1.5 | $-$ 0.08 |
| Rock cover 2019 (%) | 1.3 $\pm$ 2.6 | 0.3 $\pm$ 0.7 | 1.1 $\pm$ 2.1 | $-$ 0.07 |
| Log cover 2008 (%) | 7.9 $\pm$ 5.2 | 15.6 $\pm$ 11.3 | 18.2 $\pm$ 10.2 | $-$ 0.52 |
| Log cover 2019 (%) | 15.6 $\pm$ 7.5 | 15.5 $\pm$ 6.7 | 11.7 $\pm$ 4.6 | 0.18 |
| Percentage lodgepole pine 2008 | 99.3 $\pm$ 0.8 | 91.0 $\pm$ 21.0 | 78.3 $\pm$ 34.4 | |
| Percentage lodgepole pine 2019 | 98.7 $\pm$ 2.9 | 94.4 $\pm$ 9.7 | 87.9 $\pm$ 17.1 | |

*Stars indicate significance based on a Holm–Bonferroni correction: \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001. ''Percentage lodgepole'' is the percentage of live tree basal area which was comprised of lodgepole pine at the site level, and we did not calculate $r_s$ for this variable due to the lack of live trees at some individual plots. The ground cover variables are given in percentage aerial cover as visually estimated in the field in 2019 and by Pierce and Taylor (2011) in 2008.*

## Tree Regeneration

In 2019, tree seedling and sapling density was 69% lower at the low-severity site than in 2008, 93% lower at the moderate-severity site and 98% lower at the high-severity site (Table 1). Compared with estimated tree seedling and sapling density relative to 1991 (also seven years post-fire), tree seedling and sapling density in 2019 was similar within the low-severity site, 68% lower at the moderate-severity site and 93% lower at the high-severity site. The proportional differences in seedling and sapling density among sites were greater in 2019 than in 2008 or relative to 1991, demonstrating relatively sparser tree regeneration at the moderate- and high-severity sites in 2019.

The species composition of tree regeneration also changed from 2008 to 2019. Most (87%) seedlings and saplings were lodgepole pine in 2019, with the remainder being Jeffrey pine (8%) and white fir (5%). In 2008, only 58% of seedlings and saplings were lodgepole pine and white fir (36%) was proportionally more abundant. Relative to 1991, only 43% of seedlings and saplings were lodgepole pine

and 44% were white fir, and therefore the compositional differences in 2019 are not just due to a shorter post-fire time interval. Although 102 red fir seedlings and saplings were present in 2008 (4% of total), there was no red fir regeneration in 2019. Jeffrey pine was also proportionally less abundant in 2008 (2%) but more abundant in an absolute sense than in 2019.

Based on branch whorl counts, 67% of small seedlings established in 2016–2017 and 96% established after 2012 (Figure A1). Among larger seedlings, 88% had established after 2012 according to branch whorl counts. All the saplings surveyed in 2019 had established before the 2012 fire.

## Influences on tree Regeneration

Tree seedling and sapling density in 2019 was strongly correlated with BA mortality from the 1984 fire (Table 1), and two related variables, live tree basal area and density of live cone-bearing trees in 2008. Surprisingly, tree seedling and sapling density in 2019 was not significantly correlated with BA mortality from the 2012 fire, and neither were associated variables such as live tree density or basal area in 2019. Tree seedling and sapling density in 2019 was negatively related to cover of rock fragments in both 2008 and 2019, as well as 2008 shrub cover.

The GLM of tree seedling and sapling counts in 2019 contained 8 variables including 6 that were significant ($P < 0.05$) (Table 2). Tree regeneration was negatively related to BA mortality from 1984, which was the strongest influence in the GLM (Figure 2). Negative relationships were also observed with 2008 grass cover, 2008 log cover, 2019 shrub cover and 2019 forb cover. Tree seedling and sapling counts were positively related to forb cover

in 2008, 2008 seed source distance and 2019 log cover. We note that in the process of addressing multicollinearity, we removed some variables that were moderately to strongly correlated with seedling and sapling counts including live tree density and BA, cover of rock fragments, BA mortality from 2012 and density of cone-bearing trees in 2008.

At the subplot level, the presence of tree seedlings or saplings varied significantly with cover of rock fragments ($P < 0.001$). Tree seedlings or saplings were most likely to be found in subplots with less than 1% cover of rock fragments (Figure 3). In addition, the presence of tree seedlings or saplings in 2019 was significantly related to log cover in 2008 ($P < 0.05$) at the subplot level. Seedlings and saplings were absent in all subplots
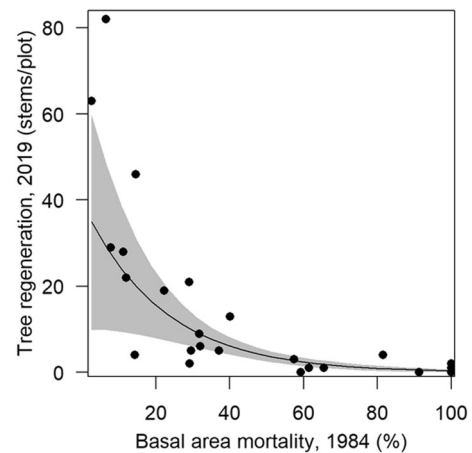


**Figure 2.** Observed tree seedling and sapling counts by plot in 2019 (points, $n = 27$) and the effect of 1984 tree mortality (percentage of basal area killed) on modeled tree regeneration (line) with bounds representing a 95% confidence level (shaded area).

**Table 2.** Results of the Generalized Linear Model of Pot-level Tree Seedling and Sapling Counts

| Variable | Estimate | SE | z | P |
|---|---|---|---|---|
| Intercept | 4.711 | 0.427 | 11.04 | < 0.001 |
| **Basal area mortality, 1984** | − 0.046 | 0.008 | − 5.90 | < 0.001 |
| **Forb cover, 2008** | 0.150 | 0.040 | 3.78 | < 0.001 |
| **Grass cover, 2008** | − 0.067 | 0.022 | − 3.06 | 0.002 |
| **Log cover, 2008** | − 0.059 | 0.022 | − 2.71 | 0.007 |
| **Shrub cover, 2019** | − 0.076 | 0.029 | − 2.57 | 0.010 |
| **Forb cover, 2019** | − 0.076 | 0.031 | − 2.40 | 0.016 |
| Seed source distance, 2008 | 0.071 | 0.045 | 1.58 | 0.114 |
| Log cover, 2019 | 0.026 | 0.016 | 1.58 | 0.115 |

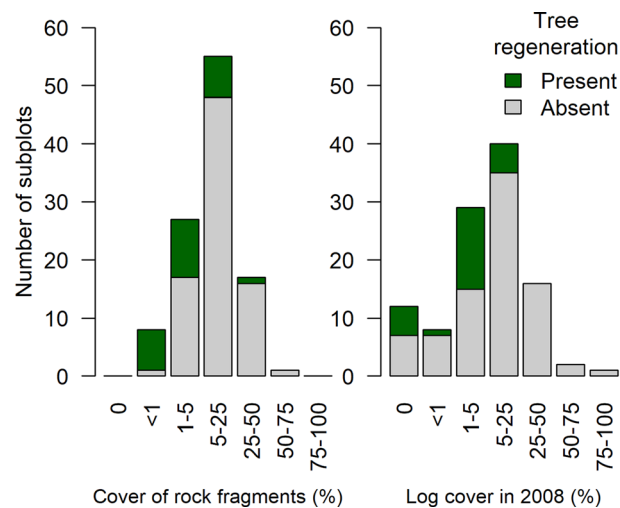*Significant (P < 0.05) variables are in bold.*

**Figure 3.** Presence of tree regeneration within subplots ($n = 108$) by coverage of rock fragments in 2019 and log cover in 2008.

that had greater than 25% log cover in 2008 (Figure 3).

## DISCUSSION

### Vegetation Change

The higher-severity 2012 fire led to widespread vegetation change including complete tree mortality in 63% of plots, an order of magnitude decrease in live tree density and more shrubs, grasses and exposed rock fragments compared to the effects of the 1984 fire. The greater tree mortality from the 2012 fire was consistent with extreme weather during the 2012 fire compared with moderate weather during the 1984 fire, although the possibility that the 1984 fire led to increased BA mortality in 2012 by damaging trees or increasing surface fuels loads cannot be excluded (see Supporting Information for a full discussion of burn severity).

After the 1984 fire, the density of tree seedlings and saplings was consistent with forest recovery across all sites. However, tree regeneration after the 2012 fire differed markedly by site, demonstrating strong legacy effects from the 1984 fire and amplification of those effects by the 2012 fire. The low-severity site had on average 1267 stems/ha of tree seedlings and saplings after the 2012 fire, indicating likely forest recovery. However, lower seedling and sapling density at the moderate-severity site and very low density at the high-severity site suggests slow recovery to forests (Figure 1). Lack of nearby seed sources tends to result in sparse post-fire tree regeneration among obligate seeders, delaying forest recovery (Stevens-Rumann

and Morgan 2019). Additionally, Sierra lodgepole pine stands are particularly slow to recover from stand-replacing disturbances because they tend to occupy sites with harsh microclimates and poor soils, as evidenced by decades-old burns and clearcuts with sparse or absent tree regeneration (Cochran 1973; Merschel and others 2018). Our results show that one fire can shape successional pathways following the next fire even if the next fire is mainly stand replacing (that is, complete tree mortality).

The species composition of tree regeneration also shifted strongly away from white fir (85% decrease in proportion of stems from 2008 to 2019) and toward increased lodgepole pine dominance following the 2012 fire. This shift is consistent with Sierra lodgepole pine's role as a shade-intolerant species which can colonize harsh environments, compared with white fir's higher shade tolerance (Parker 1993; Chappell and Agee 1996). In harsh environments such as the frost-prone basins in this study or on poor soils, lodgepole pine stands are commonly self-replacing and therefore disturbance is not necessary to maintain lodgepole pine dominance (Despain 1983; Lotan and others 1985; Parker 1986, 1993; Taylor and Solem 2001). However, some of our plots were located in toeslope environments where establishment of other tree species is not necessarily limited by extreme temperatures or poor soils (Cochran and Berntsen 1973). In these areas, stand-replacing disturbances favor lodgepole pine, whereas dominance of shade-tolerant species such as white fir increases with time since disturbance (Franklin and Dyrness 1988; Taylor 2000; Taylor and Solem 2001). At such sites where

lodgepole pine is seral to other tree species, stand-replacing fire should favor early dominance by lodgepole pine as we observed after the 2012 fire.

## Influences on Plot-Level Tree Regeneration

Our results demonstrate that tree mortality from the 1984 fire, and the resulting patterns of live tree BA, cone-bearing tree density and live tree density in 2008, shaped tree regeneration patterns following the 2012 fire. These relationships follow similar trends to serotinous stands of Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*), where post-fire seedling density tends to be closely associated with the prefire density of serotinous trees (Tinker and others 1994; Turner and others 1997; Harvey and others 2014). We did not expect a similar relationship between prefire density of seed trees and post-fire tree seedling and sapling density in Sierra lodgepole pine, whose non-serotinous character (Mowat 1960) and paucity of seed dispersal beyond 20–60 m from live trees (Dahms 1963; Dahms and Barrett 1975) imply that nearby live trees are the main seed source for post-fire regeneration (Pierce and Taylor 2011).

Because tree seedling and sapling density in 2019 was not closely related to live tree density or distance to seed source in 2019, we sought other explanations for the patterns of tree regeneration in 2019. From a demographic perspective, post-fire tree regeneration may be limited by propagule availability or by limitations on tree establishment and survival (Davis and others 2018). Accordingly, we offer two explanations for the close relationship between patterns of tree mortality from the 1984 fire and tree seedling and sapling density following the 2012 fire: (1) that many cones with viable seed survived the 2012 fire and acted as a post-fire canopy seed bank, and therefore that propagule availability did limit tree regeneration but in an unexpected way; and (2) that higher tree mortality in 1984 led to harsher conditions for tree establishment and survival, due to greater fire effects on soils and understory vegetation as well as lack of shade in 2019.

The potential for post-fire canopy seed bank in non-serotinous trees was previously described by Larson and Franklin (2005) as an explanation for high seedling densities of *Pseudotsuga menziesii* observed 11 years after an October fire in the western Cascade Range. As they noted, this phenomenon is only possible if fire occurs after the seed crop has matured but before it has been released from cones, and if the fire kills trees without exposing cones to too much heat (Larson and Franklin 2005). Our study sites burned August 11–12 in 2012, and Sierra lodgepole pine cones generally open and disperse seed from late August–November (Dahms and Barrett 1975; Critchfield 1980). Therefore, seed in cones that were not killed by the 2012 fire could have dispersed post-fire increasing regeneration especially in areas that burned at low severity in the 1984 fire and high severity in the 2012 fire. Additionally, photographs taken within the 2012 fire (south of the study area) from a brief survey in September 2012 show unburned lodgepole pine cones and dispersed seed on mineral soil in areas of stand-replacing fire as well as cones still remaining on trees killed by the fire (Figure 4). Because density of cone-bearing trees was tenfold greater at the low-severity site than the high-severity site following the 1984 fire, many more surviving cones were potentially available in tree canopies within low-severity plots after the 2012 fire which could have generated the differences in tree regeneration among sites.

Cone serotiny is an evolutionary adaptation to recurring high-severity fire which enables rapid post-fire forest recovery (Perry and Lotan 1979; Lamont and others 1991; Schwilk and Ackerly
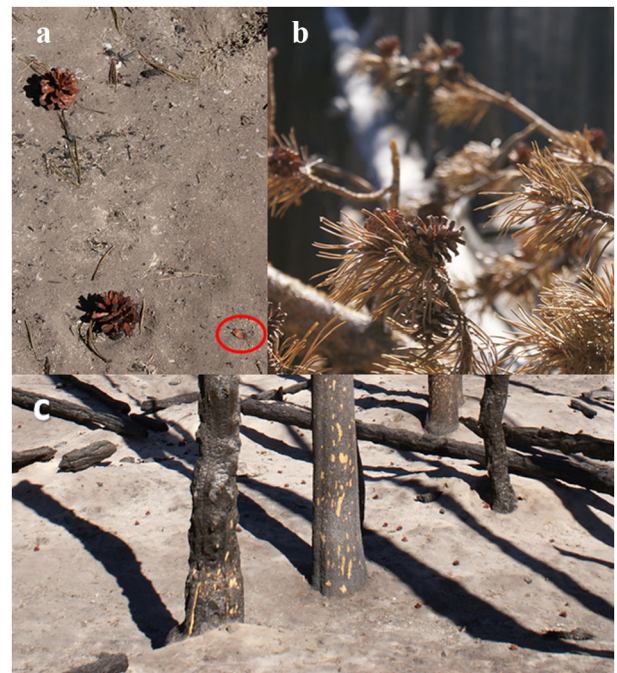


**Figure 4.** Photographs taken September 20, 2012, of lodgepole pine stands following the 2012 Reading burn: **A** lodgepole pine cones and seed (circled) on mineral soil; **B** cones on a downed tree killed by the fire; **C** unburned lodgepole pine cones on the forest floor in an area of complete tree mortality.

2001). However, our results suggest that late seedfall (that is, September onward) could also be an effective strategy for forest recovery from infrequent high-severity fire if cones and viable seed survive on trees. Late summer–fall seedfall is also a feature of other conifers in the Cascade and Sierra Nevada ranges, but lodgepole pine seed crops fluctuate less year-to-year (Bates 1930; Fowells and Schubert 1956; Dahms and Barrett 1975) and therefore lodgepole pine is more consistently poised to take advantage of fires which kill trees but do not consume cones. Although canopy seedbanks in non-serotinous trees may be uncommon following fire, they may be of immense local importance where present by providing a seed source even when surviving trees are far away (Gray and Franklin 1997; Larson and Franklin 2005).

A canopy seed bank could influence tree regeneration for more than one year via two mechanisms: (1) some seeds remain viable for more than one year after the cones open or (2) some cones remain closed for more than one year. Seeds may remain viable for decades in serotinous Rocky Mountain lodgepole pines, even when trees have died from beetle attack and therefore cones have not been exposed to heat (Aoki and others 2011). Viable seeds have even been documented in partially open serotinous cones nine years after a beetle outbreak, within both cones in the canopy and on the forest floor (Teste and others 2011). However, Mowat (1960) sampled cones from 13 Sierra lodgepole pine stands in Oregon and found no viable seed in open cones older than one year, suggesting that the first mechanism is unlikely. Perhaps caching of seed by birds or rodents could result in delayed seed germination (Tomback and others 2001), or perhaps viable seed could persist in the canopy of dead trees if the cones remained unopen (the second mechanism), but we lack evidence for these mechanisms. We also note that fire-damaged trees could have survived for several years after the 2012 fire and continued producing cones during that time, but could have died prior to the 2019 field survey. In summary, if unburnt cones provided a seed source only in the year following the 2012 fire, which seems likely based on prior knowledge, then a canopy seed bank cannot be the primary explanation for patterns of tree regeneration at our site because tree establishment continued through 2019.

Our second explanation for patterns of tree regeneration in 2019 is that higher tree mortality from the 1984 fire led to harsher conditions for tree establishment and survival after the 2012 fire. High-severity forest fires lead to high fuel loading of coarse woody debris (CWD, that is, > 7.6 cm diameter), which in turn increases the risk of fires with high burn severity in the years to decades following the fire (Coppoletta and others 2016; Nelson and others 2016; Stevens-Rumann and Morgan 2016; Stephens and others 2018). At harsh sites where surface fuels are sparse, CWD may act as the primary means of fire spread and therefore exert a particularly strong influence on fire behavior (Agee 1981). In turn, high-intensity surface fire may limit post-fire tree establishment by removing litter cover and consuming woody debris or shrubs which could otherwise provide shade. This statement may seem counterintuitive because Rocky Mountain lodgepole pine is commonly thought to depend on exposed mineral soil for successful seedling establishment and is also known to be shade-intolerant (Patten 1969; Lotan and others 1985). However, Sierra lodgepole pine establishment in sites with cold air drainage or limited soil moisture or nutrients may be aided by a layer of litter and duff which moderates soil temperature and moisture and provides nutrients (Stuart and others 1989; Karps 2006). Shading by woody debris and sometimes shrubs may also improve survival of both Sierra and Rocky Mountain lodgepole pine seedlings by ameliorating harsh microclimatic conditions (Cochran 1973; Cochran and Berntsen 1973; Lotan and Perry 1983; Stuart and others 1989; Karps 2006). We also note, however, that competing vegetation may also reduce tree seedling establishment and survival and that the negative relationship that we found between plot-level tree seedling and sapling counts and 2019 shrub and forb cover may indicate a negative effect of competition.

In addition, combustion of logs such as those left behind by the 1984 fire heats soils and therefore may alter the suitability for tree establishment by changing soil nutrients and killing fine roots and soil organisms (Smith and others 2016). In support of this effect, seedlings were completely absent in 2019 from subplots which contained greater than 25% log cover in 2008. In fact, within pile burns, which may be considered an extreme case of CWD combustion, tree density remained sparse for 50 years in Rocky Mountain lodgepole pine stands despite abundant nearby seed sources (Rhoades and Fornwalt 2015). Therefore, combustion of CWD may locally inhibit lodgepole pine establishment for decades. In summary, despite high and relatively uniform tree mortality across our plots in the 2012 fire, differences in fuel loading due to the 1984 fire caused variability in ground cover and shading after 2012 which likely affected the suit-

ability for tree establishment and survival. Prefire CWD might also influence post-fire conditions for seedling establishment and survival in other forest types, especially in harsh sites where litter cover and shade may be necessary to moderate temperature and soil moisture, but further research would be needed to establish these relationships.

## Limitations

Because we opportunistically re-measured plots from an earlier study, and also because post-wildfire studies are by necessity natural experiments, our study has some key limitations. This study was conducted within the perimeter of a single 1984 fire, meaning that we do not have replicates of fires and site conditions which limits the scope of the inferences. Furthermore, 2008 data were only available within one patch each of low-, moderate- and high-severity fire, and therefore we have no replicates of burn patches to evaluate uncertainty. Likewise, our sample size was low within each burn patch ($n = 9$ plots per patch). The patches were homogenous with respect to terrain and soils and are broadly representative of lodgepole-dominated basins which occur throughout the southern Cascade Range (Franklin and Dyrness 1988; Pierce and Taylor 2011; Merschel and others 2018). The flat terrain at the study sites was advantageous for removing confounding influences of terrain on fire behavior and tree regeneration among the study sites, but fire and vegetation dynamics may differ on steep slopes in complex terrain. In addition, our metrics of seed source do not fully capture propagule availability and therefore unmeasured differences in propagule availability may have generated differences in tree regeneration following the 1984 and 2012 fires. Due to lack of replicate fires and sites in our study in addition to our limited sample size, further research is necessary to evaluate the degree to which our results apply beyond our study sites.

Comparisons between seedling density in 2008 and 2019 may also be confounded by differences in time since fire and by differences in post-fire climate. Pierce and Taylor (2011) demonstrated that tree establishment was still ongoing more than 20 years after the 1984 fire, and therefore seedling and sapling densities are likely to continue increasing at this site. However, when we compared estimated seedling density as of 1991 to seedling density in 2019, tree regeneration was still greater after the 1984 fire than after the 2012 fire in the moderate- and high-severity sites. Therefore, the differences in seedling density that we observed among burn severity classes and time periods are not simply an artifact of different time intervals between fires and field surveys.

Interannual fluctuations in climate strongly influence tree establishment, and high drought intensity and low soil moisture have been shown to limit tree establishment in the western USA (Stephens and others 2018; Davis and others 2019). California experienced a severe drought from 2012 to 2015, including record-low snowpack in the Sierra Nevada and high multiyear drought stress on vegetation (Asner and others 2015; Belmecheri and others 2016). In general, sparse tree establishment would be expected under these conditions. However, Pierce and Taylor (2011) found that tree establishment was negatively correlated with three-year snowpack at our study site, which they attributed to late-lying snow limiting tree establishment by shortening the growing season. Moreover, pumice soils tend to retain moisture throughout the summer and tree establishment in pumice basins is more likely to be limited by soil nutrients than soil moisture (Youngberg and Dyrness 1964, 1965; Zeigler 1978). Therefore, the 2012–2015 drought may not have constrained tree establishment at our site and possibly even increased the climatic suitability for tree establishment via earlier snowmelt in the spring. We do not know the extent to which differences in post-fire climate following the 1984 and 2012 fires contributed to observed differences in seedling and sapling density between 2008 and 2019, and therefore the effect of post-fire climate is a key uncertainty in our analysis.

## CONCLUSION

We found that tree mortality from the 1984 fire was strongly related to patterns of tree seedling and sapling density in 2019 and that the legacy effects of the 1984 fire were amplified by the 2012 fire, despite high tree mortality across all sites in the 2012 fire. Our results suggest that variability in CWD produced by one fire may affect post-fire seedling establishment and survival through effects on soils, litter cover and shade, even when tree mortality from the next fire is uniformly high. This legacy effect of CWD may apply to other harsh environments in which litter, logs and woody plants facilitate tree regeneration by ameliorating environmental stress. In addition, the potential for cones from dead trees to act as a seed source in non-serotinous stands in the year following a disturbance has been sparsely investigated (Larson and Franklin 2005) and deserves further research.

Our results suggest that prescribed fires or fires managed for resource benefit, which are commonly lower severity than wildfires that escape suppression efforts, may reduce the long-term risk of forest loss even if the next fire causes high tree mortality. More broadly, our results suggest that strong and sometimes unexpected interactions between fire and vegetation, mediated by the stochastic effects of fire weather, influence vegetation change through repeated fires. Legacy effects of prior disturbances on forest resilience are particularly important given increasing concern that wildfires will generate lasting vegetation change across forests of western North America in the context of changing climate and disturbance regimes (Coop and others 2020), and this study highlights the need to better understand these legacies.

## ACKNOWLEDGMENTS

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