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Original Article

Landscape Heterogeneity Following High-Severity Fire in California's Forests

CHAD T. HANSON,[1] *Earth Island Institute, 2150 Allston Way, Suite #460, Berkeley, CA 94704, USA*

ABSTRACT Many at-risk wildlife species depend upon high-severity fire patches to create "complex early seral forest" (CESF) land cover, characterized by an abundance of snags, downed logs, shrub patches, and regeneration of trees. However, concern has been expressed about whether high-severity fire might result in persistent type conversion to nonforest, or from pine (*Pinus* spp.) dominance to forest predominantly consisting of white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and incense-cedar (*Calocedrus decurrens*), as opposed to heterogeneous natural succession and ephemeral occurrence of CESF. If type conversion is common, it could in time harm other at-risk species that depend on dense, late-successional forest for some of their habitat needs. I investigated postfire patterns in high-severity fire patches within yellow pine (*Pinus ponderosa* and *Pinus jeffreyi*) and mixed-conifer forests in California, USA, using field plots evenly spaced along random transects into the interior of patches within fires that occurred from 1999 to 2013. I found natural conifer regeneration in ≥80% of plots, even >300 m into patches. Conifer regeneration was greater closer to low–moderate-severity areas. Areas with lower conifer regeneration, where CESF would have the greatest longevity—comprised only 4.6% of these fire areas. Pine species dominated regeneration deeper into the interior of large high-severity patches, and fir–cedar-dominated at patch edges. Shrubs did not impede conifer regeneration, but greater densities of conifer saplings reduced shrubs, and sapling growth increased with time-since-fire. My findings suggest heterogeneous land-cover patterns are resulting from natural succession in high-severity fire patches.

KEY WORDS complex early seral forest, conifer regeneration, fire severity, postfire succession, wildlife.

High-severity fire was a natural part of historical fire regimes in yellow pine (ponderosa pine [*Pinus ponderosa*] and Jeffrey pine [*P. jeffreyi*] forests) and mixed-conifer forests (YPMC forests) of California, USA, often comprising 15–40% of the area burned (Baker 2014; Hanson et al. 2015; Hanson and Odion 2016*a, b*; Baker and Hanson 2017). Historical high-severity fire occurrence included both small and large patches, with some reaching hundreds, or occasionally even thousands, of hectares in size (Leiberg 1902; Baker 2014; DellaSala and Hanson 2015; Hanson and Odion 2016*a, b*). Largely as a result of fire suppression policies, there generally is now less wildland fire, and often less high-severity fire, annually in these forests in California and in many western regions of the United States than there was historically (Odion et al. 2014, 2016; Hanson et al. 2015; Doerr and Santín 2016). Postfire logging is common, leading to conservation concerns about native wildlife species associated with postfire conditions (Hanson 2014).

In a long evolutionary history with mixed-severity fire, numerous wildlife species, including birds, bats, and other mammals, have adapted to the "complex early seral forest" (CESF) habitat conditions (Fig. 1) created by such fire effects (Burnett et al. 2010, Buchalski et al. 2013, DellaSala et al. 2014, Hanson 2015, Hutto and Patterson 2016). Some snag-dependent birds, such as the black-backed woodpecker (*Picoides arcticus*), depend on larger patches of high snag density for nests and food (Hanson and North 2008). Other uncommon species, such as the Williamson's sapsucker (*Sphyrapicus thyroideus*), are associated with mature yellow pine forests in particular, especially after a decade or longer postfire (Hutto and Patterson 2016). Greater than 20 shrub–ground-nesting birds are associated with CESF in the Sierra Nevada Mountains (Siegel et al. 2012). Many of these species are experiencing persistent population declines in the Sierra Nevada mountains, and California overall, or have now become too rare for population trends to be determined. Several are also experiencing long-term declines across their entire ranges in the United States (Hanson 2014). Recent studies have also determined that high-severity fire creates foraging habitat for imperiled old-forest species such as the California spotted owl (*Strix occidentalis occidentalis*) and Pacific fisher (*Pekania pennant*; Bond et al. 2009, 2013; Hanson 2013, 2015).

Ecological benefits of multiple successional pathways following high-severity fire, including the complex and biodiverse forests that can result from areas of slower, low-density conifer regeneration, have been increasingly recog-

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[1]*E-mail: cthanson1@gmail.com*

Figure 1. Complex early seral forest habitat created by high-severity fire in an area with no postfire logging or artificial tree planting in the Star Fire of 2001 at 12 years postfire, Eldorado National Forest, Sierra Nevada. Photo by Chad Hanson.

nized (Donato et al. 2012, Hanson 2014). Ecologists have also acknowledged the ecological importance for biodiversity of high-severity fire patches within the mosaic of mixed-severity effects (DellaSala et al. 2014, Tingley et al. 2016, White et al. 2016). However, concern has been expressed by land managers that current high-severity patches may in some cases burn too hot and get too large in YPMC forests. It has been hypothesized that these ecosystems may not be adapted to current fire regimes, potentially leading to type conversion to nonforest, or persistent conversion of yellow pine forests to fir–cedar forests primarily consisting of white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and incense-cedar (*Calocedrus decurrens*; USFS 2004, Collins and Roller 2013, Peterson et al. 2015, Hessburg et al. 2016, Welch et al. 2016). Some land-management agencies have promoted postfire logging and other postfire management based on the assumption that it will reduce fuels, influence future fire behavior, and facilitate forest regeneration in large high-severity fire patches that would not otherwise regenerate forests (Collins and Roller 2013, Peterson et al. 2015, Hessburg et al. 2016). Large postfire logging projects accompanied by herbicide spraying and tree planting are often proposed within high-severity areas of national forests in California to promote conifer regeneration and increase forest recovery for spotted owl nesting–roosting habitat (USFS 2016).

However, there is now a strong consensus among hundreds of scientists that such postfire management is ecologically damaging and inconsistent with maintaining ecological integrity (http://johnmuirproject.org/wp-content/uploads/2015/09/Final2015ScientistLetterOpposingLoggingBills.pdf). Indeed, the U.S. Forest Service has reported that postfire logging on national forest lands in the Rim Fire of 2013 in the Sierra Nevada killed 72% of the natural conifer regeneration, where such logging occurred (USFS 2016); this is similar to findings from Donato et al. (2006) in forests of northwestern California. However, it has also been hypothesized that, in the absence of shrub removal and artificial conifer planting, high or complete shrub cover will preclude natural postfire conifer regeneration—especially for pine species—because it creates a lack of sunlight and competition for nutrients and water (USFS 2004, 2016; Collins and Roller 2013).

Thus, the question of type conversion versus heterogeneous natural succession, following high-severity fire, is relevant to conservation of populations of native wildlife species. If type conversion is common in YPMC forests after high-severity fire, over time this could have adverse effects for spotted owl nesting–roosting habitat, Pacific fisher denning–resting habitat, and even habitat for black-backed woodpeckers, which require dense, mature forest affected by recent higher severity fire. Conversely, if natural succession is consistently rapid and abundant, consistent with the current "reforestation" goals of federal land-management agencies (Welch et al. 2016), this would provide a high abundance of dense, mature conifer stands, but would adversely affect declining shrub-nesting species and aerial insectivores by substantially limiting the spatiotemporal extent of CESF on the landscape (Donato et al. 2012, DellaSala et al. 2014). On the other hand, heterogeneous natural succession, occurring at different rates and densities and following varied trajectories, can provide habitat for a wide range of native wildlife species at multiple spatial and temporal scales.

I surveyed unmanaged (no prefire clearcutting, or postfire logging, shrub eradication, or artificial conifer planting) high-severity fire patches in YPMC forests in the Sierra Nevada and San Bernardino mountains of southern California. Broadly, my objective was to determine if postfire patterns were more consistent with type conversion or heterogeneous natural succession. In this context, I investigated natural succession in high-severity fire patches in YPMC forests in terms of natural conifer regeneration at increasing distances from low–moderate-severity areas, the influence of shrub cover on natural conifer regeneration, effect of conifer regeneration on shrub cover, and influence of time-since-fire on conifer regeneration.

STUDY AREA

My study areas included the McNally Fire (Jul–Aug 2002) in the Sequoia National Forest, the Star Fire (Aug–Sep 2001) in the Eldorado and Tahoe National Forests, the American River Complex Fire (Jun–Jul 2008) in the Tahoe National Forest, the Butler2 Fire (Oct 2007) in the San Bernardino National Forest, the Rim Fire (Aug–Oct 2013) in the Stanislaus National Forest, and 2 of the fire areas surveyed by Collins and Roller (2013) in the northern Sierra Nevada—the Pigeon Fire (Aug 1999) and Rich Fire (Jul–Aug 2008; Fig. 2). Forests surveyed within these fire areas were, prior to these fires, primarily consisting of ponderosa pine, Jeffrey pine, sugar pine (*Pinus lambertiana*), white fir, incense-cedar, Douglas-fir, and California black oak (*Quercus kelloggii*), with shrubs mainly consisting of mountain whitethorn (*Ceanothus cordulatus*), deer brush (*C. integerrimus*), and greenleaf manzanita (*Arctostaphylos patula*). Landscape and climate characteristics of each fire area, in terms of temperature, precipitation, elevation, and land use, are shown in Table 1.

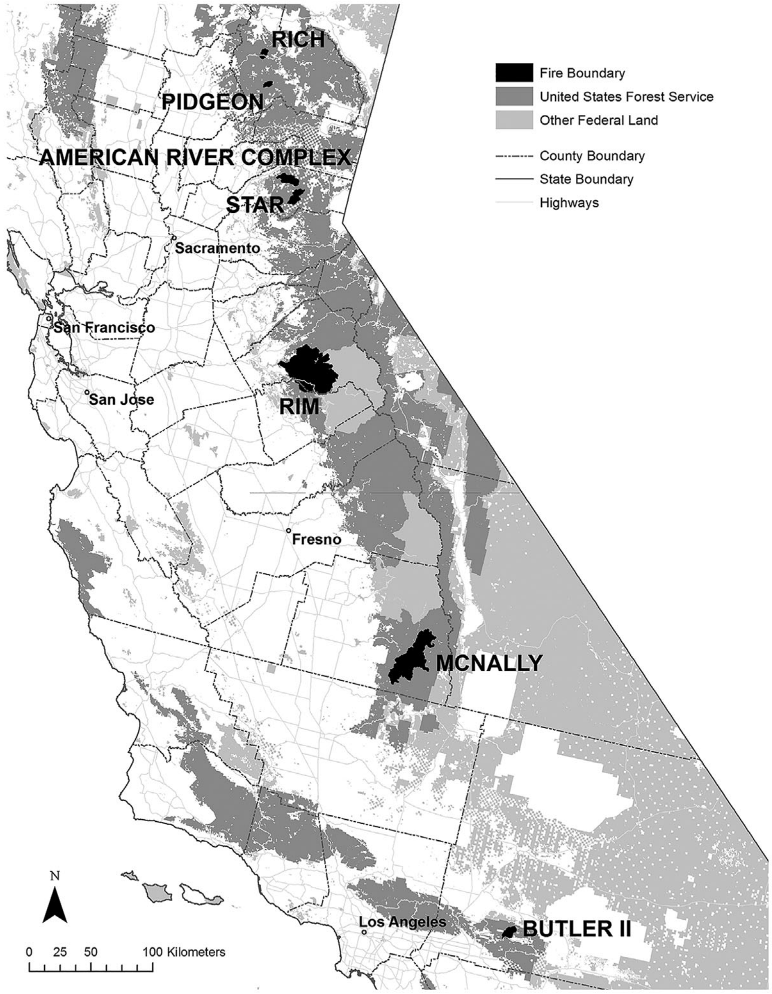

Figure 2. Locations of the Pigeon Fire of 1999, Star Fire of 2001, McNally Fire of 2002, Butler2 Fire of 2007, American River Complex Fire of 2008, Rich Fire of 2008, and Rim Fire of 2013 in yellow pine and mixed-conifer forests of the Sierra Nevada and San Bernardino Mountains, California, USA.

METHODS

I used U.S. government satellite imagery to locate high-severity fire patches (www.mtbs.gov), using a Relative delta Normalized Burn Ratio standard threshold of 641 to define high-severity fire areas, based on the difference between prefire reflectance of green foliage and 1-year postfire reflectance (Miller and Thode 2007). To ensure the absence of prefire clearcutting, postfire logging, shrub eradication, and artificial conifer planting, I used satellite imagery (http://www.google.com/earth/explore/products/) to assess prefire conditions, the FACTS database (http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327833), and field inspections of potential study sites, to ensure that areas with postfire management were excluded.

The McNally, Star, American River Complex, Butler2, and Rim fires met the needs of the study design because of large areas of mixed-severity fire in ponderosa–Jeffrey pine and

Table 1. Elevation, climate[a] (temp and precipitation), and land-use characteristics of the 7 fire areas within yellow pine and mixed-conifer forests occurring from 1999 to 2013 in California, USA. ARC, American River Complex.

Land-use characteristic	Pigeon	Star	McNally	Butler2	ARC	Rich	Rim
Elevation of transects (m)	1,650–1,621	1,558–1,883	2,215–2,483	2,243–2,376	1,352–1,795	1,426–1,577	1,364–1,672
Mean annual temp (°C)	10.2	9.0	6.4	8.8	10.8	11.0	11.3
Mean annual precipitation (cm)	178	169	61	82	175	105	102
Land use[b]	G	R–G	R	G	R	G	G

[a] Climate data are from PRISM (http://www.prism.oregonstate.edu/normals/).
[b] "G" refers to National Forest lands managed under a "General" multiple-use designation; though all forests sampled in this study were mature when fire occurred and no tree plantations were sampled, some selective logging occurred in past years or decades in some of these areas. "R" refers to designated Roadless Areas on national forests, where logging and road building is generally prohibited, and where there is little or no history of logging or road-building.

mixed-conifer forest with no prefire or postfire logging, and no shrub eradication or artificial conifer planting. However, most of the area and plot locations in the fires studied in Collins and Roller (2013) had been clearcut prior to the fires, subjected to postfire logging and plantation establishment following fires or, in some cases, were nearly pure black oak forest both before and after fire. I excluded these areas and the Storrie Fire because most of that fire area reburned in the 2012 Chips Fire, and this study was focused on mature forests that burned at high severity. What remained for study purposes, from the fires surveyed by Collins and Roller (2013) were minor portions of the Pigeon Fire of 1999, and Rich Fire of 2008, both of which I surveyed (Table 2).

From 2013 through 2015, in YPMC forests, I surveyed high-severity fire patches in 0.02-ha square plots (with the corners pointing in the 4 cardinal directions) along random transects from the edge of patches into the middle, with the center point of the first plot located 25 m into the high-severity fire patch, and each subsequent plot along the linear transects spaced by 200 m. I defined high-severity fire patches such that any high-severity fire pixels with sides touching were considered to be part of the same patch. In practical terms, this protocol meant that high-severity fire patches were $\geq$3 pixels (each pixel was 30 m $\times$ 30 m) in size, to have $\geq$1 plot in a given transect, though I collected nearly all data in much larger patches, with $\geq$2 plots (Tables 2 and S1 [available online]). In some cases, postfire logging or tree-planting in a portion of the high-severity fire patch, or topography, required that I begin a given transect well inside the patch (e.g., from the edge of a postfire logging unit), rather than at the edge of the high-severity fire patch.

For each plot, I recorded the density of conifer regeneration by species group (pine and fir–cedar), the species and height of the 5 tallest regenerating conifers $\geq$0.5-m tall, and percent shrub cover (to the nearest 5%). Using Geographic Information System (GreenInfo Network), I also determined the distance from each plot's center point to the nearest edge of the high-severity fire patch, and nearest low–moderate-severity inclusion within the interior of large high-severity fire patches ($>$150 m inside high-severity fire patches).

I analyzed the effect of distance into high-severity fire patches on natural conifer regeneration using a Kruskal–Wallis test to assess whether categories of increasing distance ($\leq$50 m, 51–150 m, 151–300 m, and $>$300 m into high-severity fire patches) affected levels of conifer regeneration, and proportion of pine versus fir–cedar (for plots with $\geq$2 regenerating conifer seedlings–saplings; Rosner 2000, NCSS 2017). I also used Kruskal–Wallis tests to test if distance ($\leq$50 m and $>$50 m) from low–moderate-severity inclusions in the interior of large high-severity fire patches ($>$150 m into such patches) affected levels of conifer regeneration and proportion of pine versus fir–cedar. I limited these analyses to plots for which the high-severity fire patch edge was $\geq$50% farther away than the closest low–moderate-severity inclusion to minimize the influence of patch edges relative to the low–moderate-severity inclusions.

I used a Spearman's rank correlation test to assess whether increasing percent shrub cover affected density of natural conifer regeneration (Rosner 2000, Glantz 2005). I chose Spearman's test for this analysis because it is meant to be used for nonparametric data and has good statistical power for such data (Yue et al. 2002). I used plots $>$100 m from any low–moderate-severity edge or inclusion for this analysis to limit the potential influence of proximity to mature trees in terms of conifer seed sources (Haire and McGarigal 2010). I only included fire areas $\geq$3 years old, consistent with other research investigating the relationship between shrub cover and conifer regeneration only after at least a few years postfire, when shrubs reached maturity (Collins and Roller 2013). I also used a Spearman's rank correlation to test whether categories of increasing density of naturally regenerated conifer saplings, defined as regenerating conifers equal to or taller than "breast height" ($\geq$1.37 m tall), affected levels of shrub cover based on the tallest 5 saplings/plot (or 1–4 if fewer than 5 saplings $\geq$1.37 m tall existed in the plot). For this analysis, I determined ranking by adding the heights, in meters, of the tallest saplings together; the analysis was limited to plots with $\geq$1 conifer sapling $>$1.37 m tall.

Finally, I used a Kruskal–Wallis test to determine whether conifer regeneration progresses in height with increasing time-since-fire, consistent with natural succession, versus

Table 2. Survey information by fire and spatial characteristics of high-severity (HS) fire, including percentages of the total area of high-severity fire that are $\leq$50 m, 51–150 m, 151–300 m, and $>$300 m from low–moderate-severity (LM) fire edges or inclusions in each fire area, and percentages of the total fire areas consisting of high-severity fire $>$300 m from LM edges or inclusions within yellow pine and mixed-conifer forests of the Sierra Nevada and San Bernardino Mountains, California, USA. All area figures are in hectares, and figures for HS patches pertain to those $\geq$3 pixels in size. ARC, American River Complex.

Fire or spatial characteristic	Pigeon	Star	McNally	Butler2	ARC	Rich	Rim
Fire year	1999	2001	2002	2007	2008	2008	2013
Survey year(s)	2013	2013	2013–2014	2013–2014	2013	2013	2014–2015
Fire size	1,946	6,817	59,303	5,980	8,381	778	104,038
% HS	11.9	48.5	36.1	54.1	27.6	28.8	30.9
No. HS patches	75	180	2,548	178	307	95	3,261
Mean HS patch size	2.9	18.1	8.1	17.9	7.3	7.9	9.6
Max. HS patch size	33.8	2,093	3,150	1,845	1,517	413	4,734
% of HS $\leq$50 m	85.7	49.9	63.0	50.2	56.3	63.2	64.2
% of HS 51–150 m	14.3	32.2	27.2	28.9	29.7	27.2	29.4
% of HS 151–300 m	0.0	14.2	8.5	14.7	12.9	8.9	5.8
% of HS $>$300 m	0.0	3.7	1.3	6.2	1.2	0.8	0.6
% of fire area $>$300 m	0.0	1.8	0.5	3.3	0.3	0.2	0.2

being halted by maturation of shrub cover after several years postfire, as some have hypothesized (Collins and Roller 2013, Welch et al. 2016). I organized the fires in this study into 3 time-since-fire groups (pertaining to the no. of years postfire at the time of sampling in each fire area): 1–2 years; 5–7 years; and 11–14 years. The dependent variable was the mean height of the 5 tallest regenerating conifers in each plot, or the mean height of the 1–4 tallest, if fewer than 5 conifer seedlings–saplings occurred in a given plot. Seedlings <0.50-m tall were recorded as 0.25 m in height—the midpoint between 0.0 m and 0.50 m—and regenerating conifers ≥0.50 m in height were rounded to the nearest meter. Using the same time-since-fire categories mentioned above, I also used a Kruskal–Wallis test to determine whether the maximum difference in height, between the shortest and tallest individual regenerating conifers in a given plot (within plots with ≥2 regenerating conifers), increased over time, consistent with natural succession and continual recruitment, or remained static, indicating one-time recruitment or stalled–impeded regeneration. In all analyses, I assessed significance at $\alpha = 0.05$.

RESULTS

There was an overall effect of distance into high-severity fire patches ($H_3 = 21.90$, $P < 0.001$), with mean natural conifer regeneration of 3,803 stems/ha (SD = 4,977), 1,850 stems/ha (SD = 4,507), 798 stems/ha (SD = 2,062), and 336 stems/ha (SD = 490) at distances of ≤50 m ($n = 20$ plots), 51–150 m ($n = 15$ plots), 151–300 m ($n = 22$ plots), and >300 m ($n = 25$ plots) into high-severity fire patches, respectively. Based on a Dunn nonparametric test for multiple comparisons (Zar 2010), there was a significant difference in the density of natural conifer regeneration between the ≤50-m category and all other distance categories, but there were no differences between the 51–150-m, 151–300-m, and >300-m distance categories.

Within the interior of large high-severity fire patches, there was an effect of distance to low–moderate-severity inclusions ($H_1 = 5.58$, $P = 0.02$), with mean natural conifer regeneration of 1,650 stems/ha (SD = 3,101) at ≤50 m from inclusions ($n = 9$ plots) and 237 stems/ha (SD = 342) at >50 m from inclusions ($n = 26$ plots). Overall, there was natural conifer regeneration in 85% of high-severity fire plots. For plots >300 m from high-severity fire-patch edges and >100 m from low–moderate-severity inclusions, 80% had natural conifer regeneration ($n = 15$). Mean regeneration of these was 417 stems/ha (SD = 591).

There was also an overall effect of distance into high-severity fire patches with regard to species composition of conifer regeneration ($H_3 = 10.60$, $P = 0.01$), with mean natural pine regeneration proportions of 0.19 (SD = 0.25), 0.49 (SD = 0.42), 0.56 (SD = 0.40), and 0.54 (SD = 0.40) at distances of ≤50 m ($n = 19$ plots), 51–150 m ($n = 10$ plots), 151–300 m ($n = 17$ plots), and >300 m ($n = 16$ plots) into high-severity fire patches, respectively. Based on a Dunn nonparametric test for multiple comparisons, there was a difference in the density of natural conifer regeneration between the ≤50-m category and the >151–300-m, and >300-m distance categories, but there were no other differences among groups.

There was no effect of distance to low–moderate-severity inclusions within large high-severity fire patches on species composition of conifer regeneration ($H_1 = 0.01$, $P = 0.93$). Plots ≤50 m ($n = 8$) and >50 m ($n = 16$) from low–moderate-severity inclusions, within the interior of large high-severity fire patches, had mean pine regeneration proportions of 0.66 (SD = 0.36) and 0.60 (SD = 0.40), respectively.

Percent shrub cover was not correlated with density of conifer regeneration in high-severity fire patches ($r_{21} = -1.63$, $P = 0.12$, $n = 23$). In plots with 95–100% cover of native shrubs ($n = 21$), mean conifer regeneration was 1,012 stems/ha (SD = 1,992). There was an inverse correlation between plots with the highest rankings in terms of conifer saplings ≥1.37 m in height and percent shrub cover ($r_{12} = -2.52$, $P = 0.03$, $n = 14$).

There was an overall effect of time-since-fire on natural succession processes, with regenerating conifers getting progressively taller from 1 to 2 years ($n = 26$), 5 to 7 years ($n = 23$), and 11 to 14 years ($n = 22$) postfire ($H_2 = 33.50$, $P < 0.001$). In addition, there were progressively wider gaps in height between the shortest and tallest conifer regeneration within the plots from 1 to 2 years ($n = 25$), 5 to 7 years ($n = 19$), and 11 to 14 years ($n = 18$) postfire ($H_2 = 44.77$, $P < 0.001$; Fig. 3). In both of these time-since-fire analyses, there were significant differences between the 1–2-years-postfire and 11–14-years-postfire categories, and between the 5–7-years-postfire and 11–14-years-postfire categories, based on a Dunn nonparametric test for multiple comparisons, but there were no differences between the 1–2-years-postfire and 5–7-years-postfire categories.

DISCUSSION

My findings were consistent with heterogeneous natural succession rather than type conversion to nonforest. In unmanaged high-severity fire patches, natural postfire conifer regeneration was often quite abundant in ponderosa–Jeffrey pine and mixed-conifer forests of California, including in many areas more than several hundred meters into high-severity patches and areas with complete shrub cover. Pine species are tending to dominate the new regenerating stands, even in areas consisting mostly of white fir, incense-cedar, and Douglas-fir prior to the fires, and especially in the interior areas of large, high-severity fire patches. Moreover, with increasing time-since-fire, conifer regeneration is getting taller, inconsistent with concerns about native shrubs stalling growth or killing off conifer seedlings. The height difference between shortest and tallest regenerating conifers is getting larger, suggesting continual recruitment of new conifer seedlings over time after fire, similar to findings by Shatford et al. (2007) in northwestern California. These results are also broadly consistent with the heterogeneity, and influence of patch-size, distance to live-tree edges, and time-since-fire, found in the large 1988 Yellowstone fires within different forest types (Donato et al. 2016, Turner et al. 2016).

Conifer regeneration was more common in plots within high-severity fire patches in my results than in Collins and Roller (2013) and Welch et al. (2016), which were also

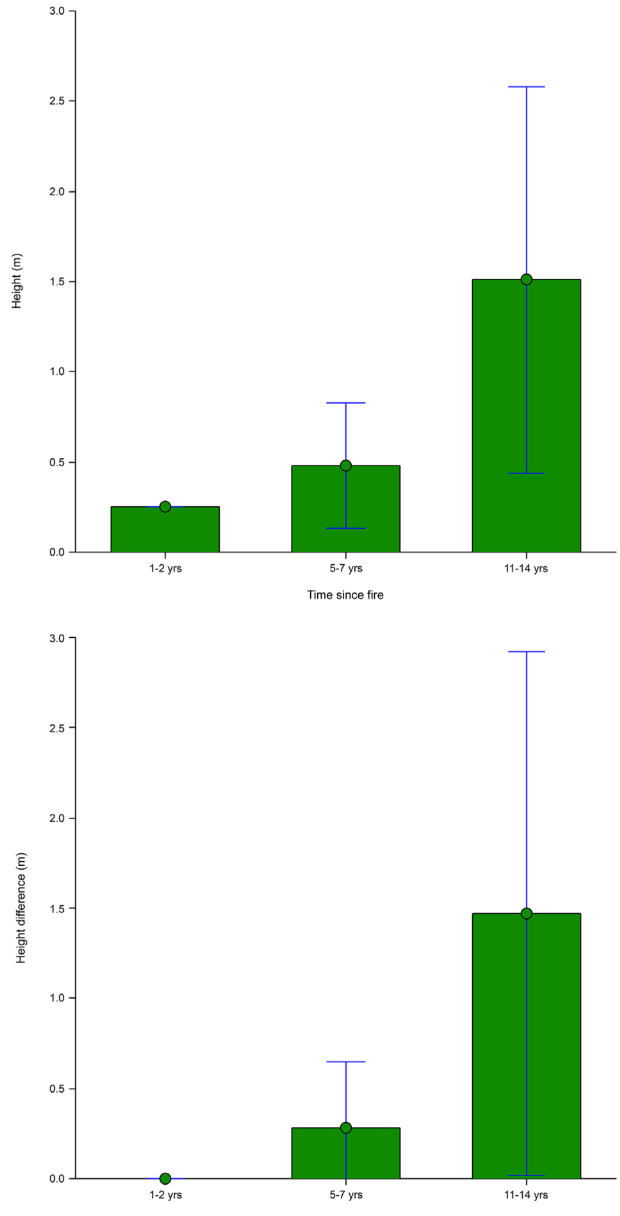

Figure 3. The tallest postfire regenerating conifers at 1–2 ($n = 26$ plots), 5–7 ($n = 23$ plots), and 11–14 ($n = 22$ plots) years postfire for fires occurring from 1999 to 2013 (top; means and SDs shown), and the height difference between the shortest and tallest conifer regeneration within plots at 1–2 ($n = 25$ plots), 5–7 ($n = 19$ plots), and 11–14 ($n = 18$ plots) years postfire (bottom; means and SDs shown) in 0.02-ha-square plots spaced by 200 m along transects through high-severity fire patches in yellow pine and mixed-conifer forests of the Sierra Nevada and San Bernardino Mountains, California, USA.

focused on the Sierra Nevada. However, my plots were 3.5 times larger than those in Welch et al. (2016), and >22 times larger than the plots that pertained to the great majority of data collected (plots pertaining to stems <1.37 m tall) in Collins and Roller (2013). Thus, my plots would likely have captured more of the variation of natural succession at small spatial scales.

My finding, that increasing shrub cover is not correlated to decreased conifer regeneration, indicates that the postfire management practices of shrub eradication (through mastication or herbicides) and artificial conifer planting, which are currently common on national forests, are unwarranted (Hanson 2014). Notably, my results in this regard are consistent with observations about postfire natural succession published nearly a century ago. For example, Show and Kotok (1924:43) noted that "the amount of [conifer] reproduction present in the brush fields to-day is very much greater than would seem on superficial examination, for in many places the young trees are just beginning to break through the brush canopy and to become easily visible." It may be that native shrubs help protect growing conifer seedlings–saplings from herbivory, and may provide a beneficial mix of sunlight and partial shade, as well as soil nutrients such as nitrogen, given that many fire-following shrubs are nitrogen-fixers (DellaSala et al. 2014). Indeed, an historical U.S. Forest Service report regarding natural succession in a large high-severity fire patch in mixed-conifer forests of the southern Sierra Nevada made this observation: "The stand apparently grew up as [conifer] seedlings with the brush as nurse and protection" (Mattoon 1904:25).

Though conifer regeneration was lower several hundred meters into large high-severity fire patches than it was closer to patch edges, there was nevertheless considerable conifer seedling–sapling regeneration, consistent with recent research in the southwestern United States (Owen et al. 2017). These findings contradict hypotheses about permanent conversion to nonforest after large high-severity fire patches (USFS 2004, Collins and Roller 2013, Peterson et al. 2015, Hessburg et al. 2016). It may be that birds and mammals play a larger role in postfire seed dispersal than previously assumed. Further, seeds may often survive in cones and forest duff and litter, even hundreds of meters from the nearest live tree (Pounden et al. 2014).

These farthest interior areas of large high-severity fire patches, with potential for low–slower conifer regeneration in some such areas, spatially represent a small fraction of even the largest wildland fires in forests of California. In the 104,038-ha Rim Fire of 2013 in the Sierra Nevada, high-severity fire areas ≤50 m from low–moderate-severity edges and inclusions comprise nearly two-thirds of the total high-severity fire hectares, and high-severity fire areas >300 m from low–moderate-severity edges and inclusions comprise <1% of total high-severity fire hectares. This indicates considerable heterogeneity in the Rim Fire, not only between low–moderate-severity and high-severity fire areas, but also within large high-severity fire patches. This is broadly consistent with research in large fires in the northern Rocky Mountains (Harvey et al. 2016), and contrary to assumptions that the Rim Fire was a large, homogenizing, high-severity fire (Ponisio et al. 2015).

I found that, within large high-severity fire patches, CESF land cover is likely to decrease more rapidly after fire in locations that are closer to high-severity patch edges, as greater densities of conifers more quickly succeed montane chaparral. This is consistent with reports on natural succession from the early and mid-20th century (Boerker 1915, Show and Kotok 1924, Cronemiller 1959, Baker and

Hanson 2017), and with research in ponderosa pine forests in the southwestern United States (Haire and McGarigal 2010).

This heterogeneity within large high-severity fire patches helps explain how such patches, mapped by U.S. Geological Survey researchers in the late 1800s (Leiberg 1902, DellaSala and Hanson 2015), and by other early surveys and reconstruction studies (USFS 1911; Baker 2014; DellaSala and Hanson 2015; Hanson and Odion 2016*a*, *b*), did not lead to loss of forest cover across vast expanses. Notably, much of the natural conifer regeneration documented in this study occurred during severe drought conditions, including all of the regeneration in the 104,038-ha Rim Fire of 2013.

MANAGEMENT IMPLICATIONS

Though much remains to be learned about natural succession following high-severity fire, including large patches, in ponderosa–Jeffrey pine and mixed-conifer forests, my results indicate that allowing natural postfire succession, at varying rates, is consistent with conservation goals for maintaining natural heterogeneity and biodiversity (Thompson et al. 2009, Hutto and Patterson 2016). To incorporate this concept into desired conditions and goals for future forest conservation and management will, operationally, require land managers to recognize that complex early seral forest habitat is in fact "forest"—just as late-successional forest is an integral and essential part of the forest ecosystem.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1. Transect locations, and plots per transect, in each fire area within yellow pine and mixed-conifer forests that burned from 1999 to 2013 in California, USA, that I surveyed in this study.