Early seral pathways of vegetation change following repeated, short interval high-severity wildfire in a low elevation mixed-conifer-hardwood forest landscape of the Klamath Mountains, California

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Title: Early seral pathways of vegetation change following repeated, short interval high-severity wildfire in a low elevation mixed-conifer-hardwood forest landscape of the Klamath Mountains, California

Running Title: Early seral pathways of vegetation change

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Abstract

We compare early seral development between stands subject to single and repeated high-severity wildfire in low elevation mixed conifer-hardwood forests in the Klamath Mountains, California, USA. We used a before-after-control-impact (BACI) approach to assess changes in the density of conifer regeneration and the cover of multiple components of vegetation structure (conifers, hardwoods, shrubs, forbs, and graminoids) to compare pathways of seral development between plots that burned once and twice. Fifty-three field plots were established six years following high-severity fire in 2004. Nineteen of these experienced a second high-severity wildfire 11 years later (2015), and all plots were remeasured in 2016/2017. Conifer regeneration following the first fire was abundant, but was greatly reduced by the second fire. Plots that did not reburn increased in conifer, hardwood, and shrub cover, while those that reburned increased in forb cover and decreased in cover of woody vegetation. Despite conifer loss, we found little evidence of shifts to non-forested states following repeated fire due to resilience of resprouting hardwoods. Our results indicate that repeated high-severity fire has the potential to protract early seral development and catalyze transitions from mixed-conifer-hardwood forest to hardwood-dominated early seral conditions.

Key Words: reburn, state-change, Douglas-fir, early seral vegetation, hardwood resilience, BACI, compound disturbance
Introduction

Larger and more frequent wildfires are altering landscapes throughout forested regions of western North America (Westerling et al. 2006, Miller et al. 2012, Dennison et al. 2014). Increased stand density and fuel loading from a century of fire exclusion, coupled with longer fire seasons, more extreme fire weather days, and drier fuels (Liu et al. 2012, Abatzoglou and Williams 2016, Davis et al. 2017) are expected to increase the potential for fire activity in the coming decades. Although studies from several forest types across western North America demonstrate rapid regeneration of conifers following a single stand-replacing fire (Donato et al. 2009a, Kemp et al. 2016, Shatford et al. 2007), there is concern about potential transitions to non-forested states following repeated stand-replacing fire at short intervals. Plant communities with species that are adapted to a particular fire regime may experience a shift in species composition with alterations to the frequency and severity of fire (Bond and Keeley 2005, Odion et al. 2010). Resilience (sensu Holling 1973) and recovery back to a pre-disturbance state, as opposed to shifting to an alternative state, following stand-replacing events will be important to maintain the critical structures and functions of forested ecosystems. However, there are relatively few field studies that document changes in the structure and composition of forests following short-interval, repeated high-severity wildfire (Donato et al. 2009b).

The potential conversion from forest to alternative non-forest states has received considerable attention and conceptual development in recent years (Odion et al. 2010, Enright et al. 2015, Miller et al. 2019). Obligate-seeding species may experience local extirpation, particularly slow-maturing species, as the time between disturbances decreases and the in-situ seedbank is depleted (Enright et al. 2015). Short intervals between high-severity fires may shift from dominance of obligate-seeding species (e.g., conifers) to alternative ecological states, such
as meadows, shrublands, or hardwood forests if regeneration of obligate-seeding species is killed
before reaching reproductive maturity (Fig. 1). These states may be self-perpetuating provided
that fires continue to occur at a frequency high enough to prevent the recruitment of
reproductively mature trees, or those large enough to develop traits associated with fire
resistance. Dispersal and recruitment limitation may leave a previously forested area in a state of
prolonged arrested succession (Acacio et al. 2007, Tepley et al. 2017, Shrive et al. 2018), and
persistent large openings in forested landscapes resulting from short-interval repeated, high
severity fires have been observed in several forest types around the world (Bowman et al. 2016,

The Klamath Mountains of northern California are renowned for their ecological
diversity (Whittaker 1960) and serve as a model system for conceptual development of
ecological state changes following repeated high-severity fire (Odion et al. 2010, Miller et al.
2019). This region is historically associated with a mixed-severity fire regime characterized by a
complex mosaic of patches at all levels of severity (Halofsky et al. 2009). Patches of stand-
replacing fire initially convert the mixed-conifer-hardwood forests of the Klamath Mountains
into early seral vegetation mostly consisting of basally-resprouting hardwoods and shrubs that
regenerate via resprouting or a persistent seed bank (Shatford et al. 2007). Conifers often have
strong post-fire recruitment that will eventually overtop other vegetation after a single stand-
replacing fire (Donato et al. 2009a, Halofsky et al. 2011). Drought has increased in recent years
(Diffenbaugh et al. 2015) and models of future climate and vegetation change project major
changes in the 21st century (Barbero et al. 2015, Serra-Diaz et al. 2018), but studies
documenting early seral pathways following fire are needed to assess the potential for vegetation
change and transitions to non-forest states with repeated wildfire in this region (Prichard et al.
Despite this, there are few studies documenting vegetation change following repeated, short-interval wildfire as studies with pre- and post-reburn data for such events are rare.

We assessed the empirical support for a conceptual model depicting different pathways of early seral development following single and repeated wildfires (Fig. 1). We leveraged a unique data set with observations before and after a high-severity wildfire that occurred eleven years following a previous fire in low elevation mixed conifer-hardwood forests of the Klamath Mountains. Our study objectives were to examine how conifer regeneration was affected by repeated high-severity fire in our study area and to assess whether there is evidence to support an ecological type change from a conifer-dominated forest to a non-forest or hardwood-dominated forest. We compared (1) changes in the density of conifer regeneration; (2) changes in multiple components of vegetation structure including the cover of conifers, hardwoods, shrubs, forbs, and graminoids; and (3) multivariate trajectories of vegetation change. The results of this study will provide important knowledge regarding the potential for transitions to non-forested states following short-interval high-severity fire and the ecological implications of these compound disturbances.

Methods

Study Site

The Klamath Mountains of northern California and southern Oregon are a hotspot of biological diversity characterized by tremendous environmental and topographic complexity. The region has a Mediterranean climate, with warm, dry summers and cool, wet winters. Fire has long been a driving force in shaping vegetation patterns of the Klamath Mountains (Whitlock et al. 2004, 2008), and has shaped the evolutionary pathways of individual species as well as landscape-level patterns of low density, multi-aged stands (Shatford et al. 2007, Whitlock et al. 2008).
Summer thunderstorms are a common source of ignition (Odion et al. 2010, Skinner et al. 2006) and Native Americans historically managed fire in the area (Whitlock et al. 2015). This region is primarily associated with a mixed-severity fire regime (Halofsky et al. 2009). During the pre-settlement period prior to fire exclusion, the fire return interval for our study vegetation type, Douglas-fir/hardwood ranged from 12-19 years (Taylor and Skinner 1998, Taylor and Skinner 2003), though a millennium-scale lake-sediment charcoal chronology nearby showed periods of less frequent fires and fire-free intervals of up to 180 years over the last 2,000 years (Colombaroli and Gavin 2010). Since 1987, wildfires burned approximately 30% of the area in northern California occupied by Douglas-fir or mixed conifer forest types, with ~10% of that area having burned at high severity (regionally calibrated threshold RdNBR >574; Miller et al. 2009, Miller et al. 2012).

Our study site was located in the southcentral portion of the Klamath Mountains, northwest of Hyampom, California (Fig. 2). The area is comprised of low elevation (500-1000 m) mixed-conifer and hardwood forests. Douglas-fir (Pseudotsuga menziesii) is the most common and dominant conifer, but other conifer species including ponderosa pine (Pinus ponderosa), Jeffrey pine (P. jeffreyi), sugar pine (P. lambertiana), and incense-cedar (Calocedrus decurrens) also occur. All of these conifer species are obligate seeders and rely on seed from surviving trees for regeneration. The hardwood component has a relatively high diversity of broadleaf trees and shrubs compared to other conifer-dominated regions. Evergreen and deciduous hardwoods are common in our study forest, especially tanoak (Notholithocarpus densiflorus), Pacific madrone (Arbutus menziesii), canyon live oak (Q. chrysolepis), California black oak (Quercus kelloggii), and Oregon white oak (Q. garryana). All hardwood species...
resprout vigorously after fire. Common shrub species include California lilac (*Ceanothus* spp.), manzanita (*Arctostaphylos* spp.), and poison oak (*Toxicodendron diversilobum*).

The Sims Fire was ignited by a fallen power line in July 2004 and burned approximately 1,630 ha during moderate drought conditions according to the Palmer Drought Severity Index (PDSI) (Appendix Fig. 1). This landscape was largely departed from presettlement fire regimes documented in the fire scar and tree ring records with no evidence of fire in at least the last 100 years. The fire included an approximately 700 ha patch of high- and very high-severity fire (RdNBR >750) (Fig. 2). The first few years following the Sims Fire were characterized by warmer than normal temperatures. Although the first year post-fire had unusually high precipitation, the third and fourth years post-fire were characterized by moderate drought. The Saddle Fire was ignited by lightning in June 2015 and burned 624 ha. Most of the Saddle Fire burned within the footprint of the previous Sims Fire, and a large portion of the reburned occurred in an approximately 300 ha patch of high- and very high-burn severity (Fig. 2). The fire occurred following three years of moderate drought. Climatic conditions in the two years following the Saddle Fire were warmer and drier than normal and characterized by moderate drought (Appendix Fig. 1).

**Field methods**

In 2010, six years after the 2004 Sims Fire, a series of one hundred 60 m² (0.006 ha) circular plots were established on a 200 m grid system to monitor regeneration of the area burned in the Sims Fire. Some plots were not measured or relocated slightly due to inaccessibility. Since we were interested in the effects of repeated, high-severity fire, we limited our analysis to the fifty-three plots that experienced complete mortality of all trees and RdNBR values ≥574 (Fig. 2) in the 2004 Sims Fire. A total of thirty-four plots within the once-burned Sims Fire were
resampled in the summer of 2016. The nineteen plots burned again in the Saddle Fire were
resampled again in the summer of 2017 (see Appendix 1 for a timeline of fire occurrence and
sampling dates).

All plots were sampled according to an established regeneration plot protocol from the
US Forest Service Common Stand Exam (USDA Forest Service 2007). Field measurements at
both the first (2010) and second (2016/2017) samplings included ocular estimates of the percent
cover of multiple components of vegetation structure including conifers, hardwoods, shrubs,
forbs, and graminoids. As we only sampled areas with complete overstory mortality, all conifers
on our plots established after the Sims Fire. The age for each individual was determined by
counting bud scars or branch whorls and recorded. The technique of aging by bud scars or
branch nodes is not entirely accurate and tends to underestimate age (Hankin et al. 2018, Urza
and Sibold 2013). However, Hankin et al. (2018) found that the most accurate estimates of tree
age by this method were in California Douglas-fir, our primary study tree. In Urza and Sibold
(2013), the most accurate aging for Douglas-fir was between 8-11 years of age (approaching
100% accuracy at 10 years), roughly the age of most of our conifer recruits.

Data analysis

We used a before-after-control-impact (BACI) study design to investigate the impacts of
repeated high-severity wildfire. This approach focuses on comparing the change in a response
variable over time. In our case, we compare the change in cover between those samples
experiencing the impact of a second, short interval burn with those that experienced an initial
burn but not a second burn. Comparing change standardizes response variables, incorporates the
multi-temporal aspect of the data, and facilitates interpretation (van Mantgem et al. 2001). By
focusing our statistical analysis on the change in individual components of vegetation structure
rather than on the cover before and after the second fire we were better able to characterize the impact of the second fire and quantify the dynamic nature of early seral vegetation structure.

We first checked for spatial autocorrelation in the cover of each component of vegetation structure and the density of conifer and hardwood regeneration. Spatial autocorrelation may result in violation of the assumption of independence among observations, which can increase the rate of Type I errors, or the false rejection of a null hypothesis of no effect (Dormann et al. 2007). We used the correlog function in the ncf package in R (R Core Team 2018) to calculate Moran’s I to assess the correlation between observations at spatial lags from 200 to 1000 m in each group of plots and for each time period. The value of Moran’s I approaches 1 when observations close to each other are more similar and exhibit positive spatial autocorrelation, while values approaching -1 are indicative of negative autocorrelation. Values close to zero are spatially independent.

We used t-tests to compare changes in the abundance of individual components of vegetation structure (van Mantgem et al. 2001) and test the null hypothesis of no difference between means. These included percent cover of conifers, hardwoods, shrubs, graminoids, and forbs. We also compared the density of conifer seedlings and hardwood resprouts. In cases where the assumption of equal variances between each of the two samples was violated, we used Welch’s unequal variances t-test. Welch’s t-test is considered more reliable when samples have unequal variances and sample sizes (Derrick et al. 2016).

Finally, we compared multivariate trajectories of vegetation change using principal components analysis (PCA) to reduce the dimensionality of plant functional groups into gradients of early seral vegetation structure. PCA is based on linear relationships between variables (McCune et al. 2002) and is effective at characterizing the inherently multivariate
nature of vegetation structure (Reilly and Spies 2015). We performed the PCA in PC-ORD 7 (McCune and Mefford 2018) using the correlation coefficients between structural variables in cross-products matrix. We included observations from all years in a single ordination. Cover estimates were square root transformed to reduce the effect of dominant functional groups (McCune et al. 2002). We used a randomization test to determine the significance of each axis based on the number of randomizations with an eigenvalue for that axis that is equal to or larger than the observed eigenvalue. In order to compare trajectories of change, we then plotted multivariate vectors change between the first and second sampling for each plot with all observations at the first sampling translated to the origin.

Results

Temporal and Spatial Patterns of Regeneration

Conifer recruits mostly consisted of Douglas-fir (>95%) but there were small components of incense cedar, ponderosa pine, and Jeffrey pine. In 2010, six years after the Sims Fire, conifer regeneration was much greater in the area that would subsequently burn in the Saddle Fire (Fig. 3). In both areas, conifer regeneration generally increased continuously until four years following the Sims Fire, then decreased. The number of conifer recruits was much lower in 2016/17 in both areas, but the decrease was far greater in the plots that were burned by the Saddle Fire. There was some recruitment of conifers in the area that did not reburn between the first and second sampling, but the total number of seedlings was greatly reduced by the second sampling.

Although some regeneration that established after the Sims Fire survived the Saddle Fire, we observed very few seedlings in the plots that burned by the remeasurement two years after the Saddle Fire.
Across both fires and samplings, hardwoods and shrubs generally made up most of the vegetative cover (medians range from ~5 to 20% cover), followed by forbs graminoids, and conifers which were primarily below 10% cover (Fig. 4). However, cover varied between individual fires and sampling times. In plots affected by the Saddle Fire, conifer and hardwood cover were highest at the first sampling, and decreased by the second sampling. Conifer and hardwood cover were generally lower in plots only affected by the Sims Fire where they were higher at the second sampling. Shrub cover was similar in both areas at the first sampling (median ~10%), but was lower at the second sampling following the Saddle Fire and higher at the second sampling in plots that only experienced the Sims Fire. Forb cover was similar in both areas at the first sampling but was higher at the second sampling following the Saddle Fire and lower at the second sampling in plots that only experienced the Sims Fire. Graminoid cover was highest in the Sims Fire at the first sampling and lower in plots that did not experience another fire, but was similar at both sampling times in the Saddle Fire.

We found no evidence of spatial autocorrelation at lags between 200 and 1,000 m in either fire at either sampling period with the exception of conifer cover at the first sampling following the Sims Fire in plots that did not reburn. Conifer cover showed strong negative ($r = -0.7$) spatial autocorrelation at lags of 200 m in the Sims Fire at the first sampling.

Changes in vegetation structure

We found significant differences in the changes over time of most components of vegetation structure including conifer density and cover, and cover of hardwoods and forbs (Table 1, Fig. 5). Hardwood and shrub cover increased by slightly over 10% over time in plots that did not experience a second fire, while forbs decreased by ~3%. Following the Saddle Fire, the largest decrease occurred in conifer cover (~13%), though hardwood and shrub cover both
decreased as well. Forb cover increased by ~7% following the Saddle Fire. Graminoid cover decreased slightly over time in plots that experienced only the Sims fire as well as those burned in the Saddle Fire, but the change was not significantly different between the two.

Trajectories of Vegetation Change

The PCA identified two major gradients in early seral vegetation structure that were significant in the eigenvalue randomization tests (Table 2). The first significant component accounted for 39% of the variance and had strong ($r \geq 0.5$) negative correlations with cover of conifers and hardwoods, and a strong positive correlation with cover of graminoids and forbs. The second significant component accounted for another 23% of the variance had a strong negative correlation with cover of shrubs. A third non-significant axis accounted for an additional 16% of the variance and had a strong negative correlation with conifer cover.

Multivariate vectors of change differed between plots burned once in the Sims Fire and those that experienced a second burn by the Saddle Fire (Fig. 6). Direction and magnitude of change was variable within both groups of plots, but change that occurred in the absence of a second fire was primarily towards the negative end of Axis 1, which was strongly associated with greater cover of conifers and hardwoods (Table 2). Plots that burned a second time in the Saddle Fire primarily experienced shifts towards the positive end of Axis 1, which was positively associated with cover of graminoids and forbs. Most of the Saddle plots moved towards the positive end of Axis 2, which was strongly associated with decreased shrub cover and increased cover of forbs and graminoids.

Discussion

This study provides a unique opportunity to observe the effects of repeated, short interval wildfire on the trajectories of early seral development. We found a major reduction in the conifer
component with repeated wildfire, which highlights the vulnerability of young, regenerating post-fire conifer stands to fire. Our results indicate that resprouting hardwoods are a key component of forest resilience to repeated high-severity fire in the Klamath Mountains. Although we found no evidence of a shift towards non-forested states, our findings document a transition away from mixed-conifer-hardwood forests to an alternative early seral trajectory towards hardwood dominated forest. Collectively, our results indicate that repeated high-severity fire prolongs early seral conditions and has the potential to be an important mechanism for future conversion of conifer to hardwood-dominated forests in the Klamath Mountains.

Patterns of Conifer Regeneration

Our findings are consistent with several other studies documenting resilience of Douglas-fir to a single high-severity fire in the Klamath Mountains (Shatford et al. 2007, Donato et al. 2009a, Tepley et al. 2017, Lopez Ortiz 2019), as well as other conifer species in different regions of the western North America (Kemp et al. 2016). Resilience of Douglas-fir forests to stand-replacing fire is likely related to the ability of this species to disperse relatively long distance. Although some studies suggest that conifer dispersal decreases rapidly at 100 m from a seed source (Kemp et al. 2016, Hermann and Lavender 1990, Rother and Veblen 2016), robust regeneration of Douglas-fir has also been observed over 400 m away from a seed source (Donato et al. 2009a, Donato et al. 2009b).

The large decrease in regeneration following the second fire is consistent with the findings of other studies documenting the vulnerability of young stands to fire (Stevens-Rumann and Morgan 2016). Previous studies found that high-severity burn patches tend to reburn at high-severity when subsequent fires occurred (Odion et al. 2010), a pattern related to a combination of low resistance of young conifers with thin bark to fire and higher snag density, woody debris,
and pyrogenic shrub and hardwood cover following the first fire (Alexander et al. 2006, Thompson et al. 2007, Thompson and Spies 2010, Coppoletta et al. 2016). Collectively, our results and those of others support conceptual models depicting delayed recovery of obligate seeding species (i.e. conifers) in the absence of a long enough period without fire to allow for trees to establish and reach maturity (Odion et al 2010, Enright et al. 2015, Miller et al. 2019).

At two years postfire, the reburned areas had much lower regeneration than was present two years after the first fire. Lack of regeneration following the second fire is likely due to a combination of factors including dispersal and recruitment limitation associated with drought conditions in the years following the second fire. Donato et al. (2009b) found ample Douglas-fir regeneration two years following short interval reburn (15 years), but the patches of high-severity fire were smaller (<100 ha) than in our study (~300 ha). Dispersal limitation may be more of a factor following repeated fire than following a single fire as any in-situ seeds that survived the first fire would no longer be present. In addition, low water availability may also limit conifer regeneration (Hogg and Schwarz 1997, Dunne and Parker 1999, Johnstone et al. 2010, Dodson and Root 2013, Rother et al. 2015, Harvey et al. 2016, Tepley et al. 2017, Shive et al. 2018). The second fire in 2015 occurred in the midst of a multiyear drought characterized by lower precipitation and warmer temperatures than normal (Appendix Fig. 1). Although the drought officially ended in 2015, it was still warmer and drier than the first year following the Sims Fire (2005). Given that post-fire recruitment in Douglas-fir forests may continue for a period of up to a decade, it is still too early to conclude after only two years that conifers will never establish. However, it seems unlikely that they will regain dominance immediately given the rapid recovery of hardwoods after repeated fire and slower height growth associated with regeneration established at longer time lags following fire (Tepley et al. 2017).
Alternative trajectories of early seral development

Our field-based study provides empirical evidence to test conceptual models of early seral development following repeated wildfire in Douglas-fir forests of the Klamath Mountains (Fig. 2). Conifer forests dominated by Douglas-fir appear to be resilient to a single high-severity fire, but are subject to transitions from the conifer to hardwood dominated forests following short interval repeated fire. Even after experiencing two very high-severity events, hardwoods persisted and attained levels of cover that were almost equal to the levels observed before the second fire. Resprouting hardwoods are an important mechanism of forest resilience in other forests of northern California (Cocking et al. 2014) and other mixed conifer-hardwood forests of North America (Coop et al. 2016, Hagan et al. 2016). Although hardwoods maintain high levels of cover following repeated fires, cover alone may not reflect the potential for loss of vigor and death of some resprouting clumps observed in other resprouting species after multiple short interval fires (Fairman et al. 2016, Fairman et al. 2017).

Although we found limited conifer recruitment after the second fire, it is possible that the area will eventually be able to return to a conifer-dominated forest in the absence of another wildfire in the next few decades. In the single burn, total regeneration declined but recruitment continued over 12 years at low rates of establishment. Kemp et al. (2016) found higher Douglas-fir abundance on sites with a longer time since fire in the northern Rockies, and Tepley et al. (2017) found that conifers made up a low but increasing percentage of the aboveground biomass 7-28 years post-fire in the Klamath Mountains. Thus, conifer recruitment may continue into the future, but if so, then likely at a much greatly reduced rate over a longer period of time. In fire-generated chaparral patches in the Sierra Nevada and southern Cascades, conifers eventually overtopped shrubs after 50-70 years across much of the area in the absence of fire (Russell et al.
Likewise, many hardwood forests in this region have been encroached by Douglas-fir during the 20th century due to fire exclusion (Long et al. 2018). Additionally, regional heavy seed crop years for Douglas-fir happen every 3-12 years (USFS 2012), and the years after the second fire could have been low seed-producing years. Although resprouting broadleaf species grow more quickly and may outcompete conifers for light and water in early seral conditions, studies have found that the mycorrhizal connections formed between hardwoods, *Arctostaphylos* spp., and conifer seedlings after disturbance facilitate seedling establishment (Borchers and Perry 1990, Horton et al. 1999, Simard 2009). *Ceanothus* spp. fix nitrogen, which could contribute the important macronutrient to the soil and help forest recovery after fire (Busse et al. 1996, Busse 2000). In conifer plantations where the hardwood component has been removed or killed in post-logging treatments, forest resilience may be low as hardwood species will have to reestablish from seed as opposed to resprouting.

**Conclusions**

The findings of this study are consistent with projections of future vegetation in the Klamath Mountains. Both Lenihan et al. (2008) and Sheehan et al. (2015) projected shifts towards hardwoods the Klamath Mountain in the coming decades using mechanistic ecosystem models (MC2). Repeated, short-interval fires are likely to be an important pathway to ecosystem type change under future disturbance and climate regimes. Climate change may compound these effects and hasten the loss of conifer-dominated forest ecosystems (Tepley et al. 2017, Serra-Diaz et al. 2018). However, projected losses of conifer forest will likely require drastic increases in fire activity as only 3.5% of the Klamath Mountains burned twice at any severity during 1985-2012 (Grabinski et al. 2017).
Assessing the trade-offs among the ecological implications of large patches of high-severity reburn is complex and requires consideration of a variety of ecological outcomes. There is little evidence that the large patches of high-severity fire in our study were part of the presettlement range of variability in this region (Spies et al. 2018) and high-severity wildfires have negative effects on species dependent on dense, multi-layered old growth forests [e.g., the Northern Spotted Owl (*Strix occidentalis caurina*)]. However, such disturbances are relatively rare and may also enhance some aspects of landscape diversity given current rates of reburn in this region. Twentieth century fire exclusion reduced the extent of biodiverse early seral and open vegetation types such as meadows and chaparral in the Klamath Mountains (Skinner 1995). Recent fires have reversed declining trends of early seral habitats (Phalan et al. 2019), enabled the expansion of some declining early seral species (Reilly et al. 2019), and may foster understory diversity. However, almost 20% of the understory cover in our study was composed of non-native annual grasses and forbs which may further threaten conifer regeneration (Reilly et al. In Review).

Despite a relatively small sample size and limitations due to differences in time since fire and climatic conditions following the fires, this study provides an empirical evaluation of conceptual models of repeated fire effects on transitions between alternative vegetation states using field observations from pre- and post-reburn. Repeated wildfire in this region has the potential to protract early seral development and catalyze a transition from mixed conifer-hardwood to a hardwood-dominated early seral conditions characterized by greater cover of forbs. Our results demonstrate the resilience of conifers (e.g. Douglas-fir) to a single high-severity wildfire, as well as with the vulnerability of conifer regeneration to short, interval reburn. As in other regions, hardwood species are extremely resilient to both single and repeated
wildfire and will likely be a key component to forest resilience in the next century as fire activity increases.

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Table 1. Results from t-tests comparing the change in the density of conifer regeneration and cover of multiple components of early seral vegetation structure in fifty-three 60 m² plots subject to single (n=34) and repeated high-severity wildfire (n=19).

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<th>Sims and Saddle Fire (2x burned)</th>
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<td>-1.6%</td>
<td>-0.08</td>
<td>39.6</td>
<td>0.94</td>
</tr>
</tbody>
</table>

Table 2. Percent of variance explained by the first two dimensions of a principal component analysis along with correlation coefficients for cover of multiple components of early seral vegetation structure in plots subject to single and repeated high-severity wildfire. Axes with an * were significant (p=0.001) based on an eigenvector based randomization test.

<table>
<thead>
<tr>
<th>Component</th>
<th>Axis 1*</th>
<th>Axis 2*</th>
<th>Axis 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>% of variance explained</td>
<td>39%</td>
<td>23%</td>
<td>16%</td>
</tr>
<tr>
<td>Conifer cover</td>
<td>-0.469</td>
<td>0.444</td>
<td>-0.743</td>
</tr>
<tr>
<td>Hardwood cover</td>
<td>-0.822</td>
<td>0.160</td>
<td>0.152</td>
</tr>
<tr>
<td>Shrub cover</td>
<td>0.153</td>
<td>-0.811</td>
<td>-0.472</td>
</tr>
<tr>
<td>Forb cover</td>
<td>0.547</td>
<td>0.456</td>
<td>-0.108</td>
</tr>
<tr>
<td>Graminoid cover</td>
<td>0.843</td>
<td>0.253</td>
<td>-0.110</td>
</tr>
</tbody>
</table>
Figure 1. A conceptual model of possible vegetation state change after short-interval, high-severity fire in mixed conifer-hardwood forests of the Klamath Mountains in northern California.

Figure 2. Study location and patterns of burn severity (RdNBR) in the Sims (2004) and Saddle Fire (2015). Inset in the top left shows the location of the Klamath Mountains in northern California and southwestern Oregon, USA. The hatched area overlaying the Sims Fire perimeter is the perimeter of the Saddle Fire which is presented in the inset in the bottom right corner.

Figure 3. Timing of conifer establishment for: a) the Sims Fire in 2010, b) after the Sims Fire and prior to the Saddle Fire in 2010, and c) in 2016 following only the Sims Fire, and d) in 2017 following both the Sims Fire and the Saddle Fire.

Figure 4. Distribution of cover of conifers, hardwoods, shrubs, forbs, and graminoids in early seral plots that experienced a second high-severity fire in 2015 (Saddle 2x burned) and plots that only burned during the first fire in 2004 (Sims 1x burned). Fires and sampling times are abbreviated as follows: SM1=Sims Time 1 (2010), SM2=Sims Time 2 (2016), SD1=Saddle Time 1(2010), SD2=Saddle Time 2 (2017).

Figure 5. Comparison of changes in cover of conifers, hardwoods, shrubs, forbs, and graminoids between samplings in early seral plots that burned only in the first fire in 2004 (Sims 1x burned) and plots that experienced a second high-severity fire in 2015 (Saddle 2x burned).

Figure 6. Multivariate trajectories of early seral vegetation change based on a principal components analysis of cover of conifers, hardwoods, shrubs, forbs, and graminoids. Plots are translated to the origin, which represents the first sampling in 2010, six years following the Sims Fire. Vectors show contrasting directional change in vegetation structure between those that experienced a second high-severity fire in 2015 (Saddle Fire) and those that did not experience a second fire (Sims Fire).
Appendix 1 – Recent climate trends near the Sims and Saddle Fires study area outside of Hyampom, California.

Figure 1. Recent trends climate trends (1980-2019) for the Sims and Saddle Fires study area in Trinity County near Hyampom, California: a) the annual temperature (deg. F) departure from normal (2001-2010), b) the growing season (May, June, July, August) precipitation percent of normal (2001-2010), and c) the Palmer Drought Severity Index (PDSI). Data accessed from https://wrcc.dri.edu/wwdt/time/ on 1/22/2019.
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215x279mm (300 x 300 DPI)
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203x152mm (300 x 300 DPI)
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