FINAL REPORT

Does repeated high severity fire in dry mixed conifer forests homogenize vegetation characteristics across scales?

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Abstract

Novel disturbance regimes have the potential to alter community trajectories and result in shifts to alternative stable states. In disturbance-adapted ecosystems with long recovery times, it may be difficult to assess when a community has transitioned to an alternate state versus being in an early seral state. This distinction is important for anticipating long-term changes in ecosystem services and habitat availability. In the mixed conifer forests of the Sierra Nevada, over a century of excluding fire from forests adapted to frequent, low to moderate severity fire has reduced ecosystem resilience to disturbance. It has dramatically increased fuel loads, which in combination with the changing climate, is increasing the occurrence and extent of high severity, stand-replacing fire. Large patches of high severity increase the distance to live conifers that can provide seed sources, which is raising concerns about persistent transitions from forest to montane chaparral. Despite this seed limitation, we propose that these areas are still in an early seral state because reforestation could still occur as seedlings progressively seed in from patch edges, given enough time. However, the occurrence of a second severe fire may trigger a state shift by initiating a positive feedback between chaparral vegetation and fire. We examined the potential for positive feedbacks and shifts to alternate states in two recent wildfires (2013 Rim Fire, 2009 Big Meadow Fire) which each burned over fire perimeters from the 1990s that had large patches of high severity. We used remotely-sensed data to examine the drivers of burn severity of the latter fires and found that areas previously burned at high severity tended to reburn severely. We also compared areas once- and twice-burned at high severity and found that the communities were more dominated by sprouting shrubs and nonnative annual grasses in areas twice-burned at high severity. In contrast, there were much fewer obligate seeding conifers regenerating in the twice-burned areas compared to once-burned areas. The areas also had distinct plant communities in multivariate space. Collectively, this empirical evidence offers some support that the second severe fire may initiate a positive feedback and shift the community into a new state.

Objectives

The project objective was to understand 1) how repeated severe fire affects regenerating forests and the potential for alternative stable states. The field project funded by the Joint Fire Science Program enabled use of empirical, stand-level data in concert with planned landscape-scale analyses.

Background

Altered disturbance regimes can result in major changes to ecosystem structure and function, raising concerns about habitat loss and shifts to alternative vegetation states (Boisramé et al., 2017a; Collins et al., 2011a; Franklin et al., 2005; Santi and Morandi, 2013; Schwilk et al., 2009; Stephens et al., 2015; Stevens et al., 2015, 2017; Tepley et al., 2017; Turner et al., 2013).

However, in disturbance-adapted ecosystems with slow recovery times, such as conifer forests, it may be difficult to detect when novel disturbance patterns are shifting ecosystems to an alternative stable state versus an early stage of recovery to the initial state (i.e. early seral).

A prime example of this is the mixed conifer forests of the Sierra Nevada, California, where the historically frequent, predominantly low to moderate severity fire regime has been altered by over a century of fire exclusion (Collins et al., 2011a; Parsons and DeBenedetti, 1979). This exclusion dramatically increased fuel loads, and when combined with the changing climate, has been implicated in increases in the incidence and patch size of severe, stand-replacing fire (Mallek et al., 2013; Miller and Safford, 2012; Miller et al., 2009; Westerling et al., 2006). The increase in high severity patch size has subsequently increased the distance to conifer tree seed sources, rendering large areas out of the zone of likely seed dispersal in the near future (Stevens et al., 2017). In addition, severely burned areas regenerate as montane chaparral in the early years postfire, where dominant shrubs are strong competitors with conifer seedlings. Thus, the concern about shifts to alternative states has primarily rested on the low rates of conifer regeneration in these areas (Collins and Roller, 2013; Kemp et al., 2016; Welch et al., 2016).

However, most of these observations have occurred within the first few years postfire, whereas forest regeneration occurs on decadal scales (Nagel and Taylor, 2005; Russell et al., 1998). In addition, most of the studies that documented low rates of regeneration did observe some regeneration nearer to patch edges, and through time this may enable reforestation across these patches as seedlings near patch edges mature and spread seed continuously in a wave-like front (Haire and McGarigal, 2010). For this reason, the low rates of conifer regeneration alone are unlikely to drive a persistent state change.

Under alternative stable state theory, several alternative community states have the potential to occupy a given site, and these states are maintained by positive feedbacks between biotic and abiotic factors (Scheffer, 2009). The alternative stable state concept is commonly represented with a "ball and cup" figure, which shows each state as a deep valley called the "basin of attraction" and the ecological community represented by the ball (Figure 1a). These distinct states can vary in terms of both ecosystem resilience and stability, but the resilience of the system is critical for determining the potential for a state change. Here we follow Holling's definition of resilience as a "measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist", and stability as "the ability of a system to return to an equilibrium state after a temporary disturbance" (Holling, 1973). The stronger the positive feedback, the greater resilience and stability in the community. Local stability is characterized by the width of the basin, whereas resilience and landscape-level stability is characterized by its depth. In a resilient ecosystem with a deep basin, a perturbation of sufficient energy to move the cup out of the basin is needed to transition the community between alternate states (Holling, 1973; Scheffer et al., 2001). This could include an individual disturbance event, or a slow transition of background state variables that slowly weaken ecosystem resilience (effectively flattening the basin) or that eventually cross a threshold that pushes the community to a new state.

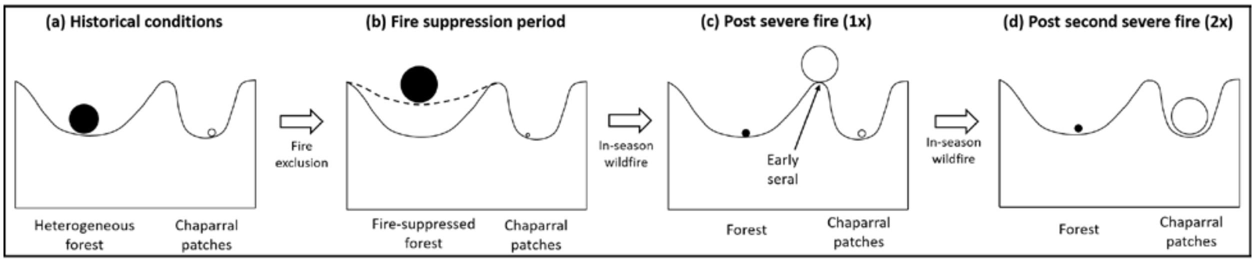


Figure 1. Ball-and-cup model of alternative stable states proposed for areas that were historically Sierran mixed conifer. In each diagram the ball represents vegetation communities and its size represents the relative differences in contiguous patch sizes between the following time steps: (a) Historic conditions, (b) fire suppression period, (c) after one severe fire and (d) after a second severe fire.

Despite the relative theoretical simplicity of this framework for understanding potential state changes, it can be challenging to apply in real-world ecosystems, particularly those that are long-lived and disturbance adapted (Schröder et al., 2005). Manipulative experiments that can more directly inform these questions are simply less feasible on these temporal and spatial scales (but see Blackhall et al., 2017). Even where these are possible, the time frame for answers may be too slow for land managers concerned with protecting specific species or habitats. We propose that identifying the key components of this framework (positive feedbacks, ecosystem resilience and stability, state characteristics) in these systems can inform the potential for state shifts ("type conversions") in shorter time frames.

Contextualizing ecosystems with altered disturbance regimes in terms of both current and historic dynamics is an important part of understanding shifts in resilience. Historically, mixed conifer forests in the Sierra Nevada were highly resilient to wildfire and stable at landscape scales, but had relatively low local stability. Historic reconstructions and areas with relatively restored fire regimes suggest that frequent, low to moderate-severity fire maintained a shifting mosaic of forest structure (Boisramé et al., 2017b; Collins et al., 2011b, 2015; Parsons and DeBenedetti, 1979). Within a given landscape, individual fires likely moved the ecosystem around the basin of attraction regularly, changing some of the species composition and structure at individual sites (low local stability). However, because the ecosystem is fire-adapted, the basin was deep (high resilience, high landscape stability). In our schematic, we consider the left basin ("heterogeneous forest") to include areas that were sometimes devoid of trees, but part of a shifting mosaic over time (Figure 1a). The frequent fires that occurred in these ecosystems maintained lower fuel loads, which in turn constrained fire severity, enabling a positive feedback between fire and forest structure.

In addition to the shifting mosaic, some areas were likely persistently maintained as montane chaparral historically, due primarily to physiographic controls (Figure 1a). Positive feedbacks in Sierra montane chaparral also occur, where chaparral fuel structure and continuity generally support severe fire, and the dominant species (e.g. *Ceanothus integerrimus* Hook. & Arn., *Ceanothus cordulatus* Kellogg, *Arctostaphylos patula* E. Greene) can either sprout after fire, have fire-cued germination, or both. This feedback resulted in both high stability and resilience. Because both of these historic communities had high resilience, a particularly strong perturbation would have been required to push either community into another state, given the energy required to move the ball up and out of the deep basins (Figure 1a).

In contrast, over a century of fire exclusion has dramatically reduced forest resilience to wildfire, because high fuel loads greatly increase the probability that a wildfire will burn severely at scales that are outside of the historic range of variability (Fulé et al., 2012; Safford et al., 2009; Stevens-Rumann et al., 2013). Fire exclusion therefore effectively flattened the basin of attraction, making it easier for an individual perturbation to move the community to the alternative state (Figure 1b). It also shifts some of the areas that were persistent, physiographically-maintained chaparral to forest. This suggests that when fires burn severely in fire-suppressed forests, some areas are likely being restored to montane chaparral that were lost due to tree encroachment as a result of fire suppression (Nagel and Taylor, 2005). However, because the current extent of severe fire is beyond the historic range of variability (Safford and Stevens, 2017; Stephens et al., 2015), modern stand replacing fires and their subsequent regenerating chaparral vegetation are likely occurring in areas that were not physiographically maintained as such for long periods in the past.

We propose that even in the larger patches of high severity, the regenerating vegetation after a single severe fire event is likely to be an early seral stage rather than a state shift (Figure 1c). Reforestation could still occur given enough time for seedlings to seed in from patch edges, mature and continue to move across the landscape, a pattern that has been documented on older fires (Haire and McGarigal, 2010; Nagel and Taylor, 2005; Russell et al., 1998). We acknowledge that this pattern may be unlikely, given predictions for increasing fire frequency and severity (Westerling et al., 2011), but we propose that the "state" of the community after a single severe fire event is in an early seral condition, not yet a true shift to an alternative state.

In the ball-and-cup diagram, this early seral community would be poised on the ridge between the two states, to what may be considered a tipping point (Figure 1c) (Scheffer, 2009). In the absence of another fire, these areas would eventually become forest and roll back into the left basin. However, we hypothesize that a second severe fire would be the initiation of a positive feedback between fire and chaparral, which would push the community into the alternative, chaparral state (Figure 1d). We hypothesize that the second severe fire is the initiation of the positive feedback, and that areas once- versus twice-burned at high severity should therefore show some signals of being in distinct states. Figure 1 outlines differences in resilience and stability of the alternative states, in which the positive feedbacks are implicit. Figure 2 more clearly shows how positive feedbacks between vegetation structure and fire severity operate under both historic and current conditions, including our hypothesis that the first severe fire is a tipping point and the second fire initiates the positive feedback.

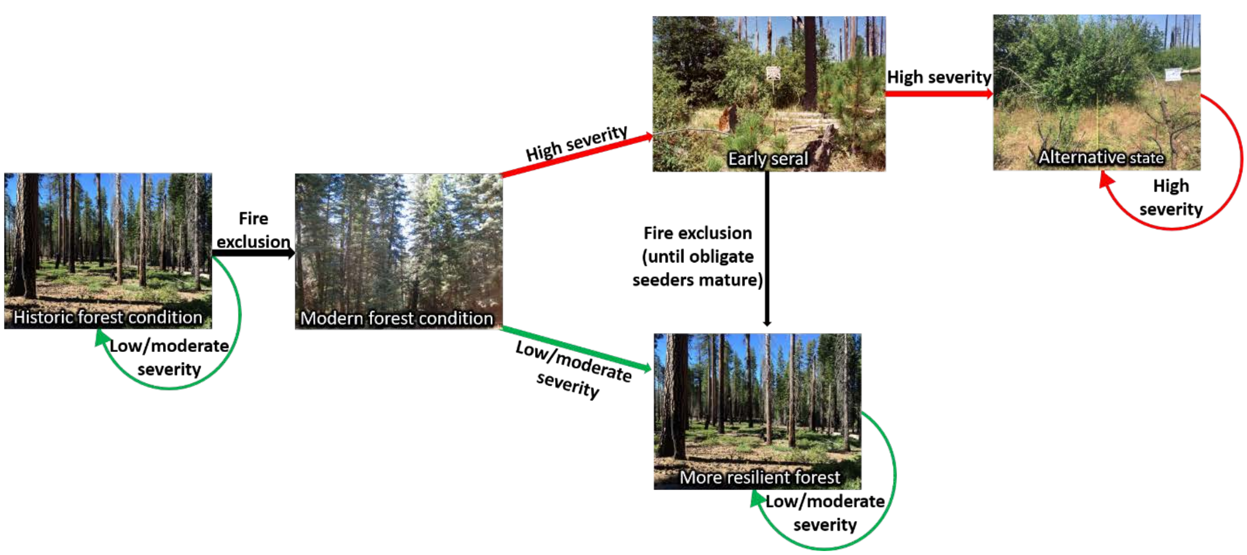


Figure 2. Positive feedbacks associated with both historic and current alternative states. Feedbacks are represented by looped arrows and transitions are represented by straight arrows. The fire severity that maintains a given state is shown within the loop. Note regenerating conifers in early seral stage that are absent in the alternate state. Photos from these stages are repeat photographs from a YNP monitoring plot before and after the second severe fire.

We investigated this proposed framework using a combination of remotely-sensed data and field data from two wildfires in Yosemite National Park (2009 Big Meadow Fire, 2013 Rim Fire) which each burned over fire perimeters from the 1990s that had large patches of high severity. These more recent, "reburn" fires also included areas that burned at high severity outside of the 1990 fire's footprints, enabling us to collect field data in once- and twice-severely burned areas with the same time-since-fire. In the absence of established plots that burned twice at high severity with measurements in between fires, we cautiously use this "space for time" substitution as a means to understand processes that operate over long periods of time (Pickett, 1989).

To empirically investigate the potential for initiation of a positive feedback, we first used landscape-level analyses to examine the importance of initial burn severity in predicting reburn severity on our sites, relative to other drivers. The tendency for sites previously burned at high severity in Sierran mixed conifer and recovering as montane chaparral to reburn severely has received some research attention, but these studies have focused on slightly higher elevations (Collins et al., 2009) or areas with a substantial history of active forests management (Coppoletta et al., 2016). To better identify it as a feedback that maintains the alternative state in this system, we also assessed how the vegetation may be promoted and stabilized by severe fire. We predicted that there would be shifts in dominance by regeneration mode and life history strategies that are more resilient to severe fire (sprouting, seedbanking and fire-cued germination, versus obligate seeders). We then also considered surface fuel loads for future reburn potential.

To further investigate the potential for distinct states between areas once- and twice-burned at high severity, which offer support for our hypothesis that the second severe fire may shift the community into an alternate state, we also examined several other vegetation community characteristics. We predicted that areas with repeated high severity fire may differ in vegetation community composition and abundance due to the increasingly restrictive environmental filter. Specifically, we predict that areas twice-burned at high severity will have lower overall richness and lower beta diversity. We also predict that trends observed in other work on the thermophilzation of plant communities in severely burned areas, quantified by shifts in richness by biogeographic affinity, may apply here (Stevens et al., 2015). Stevens et al. (2015) found that the increasing disturbance gradient similarly increased the proportion of south-temperate species, which is likely related to the increased openness and change in the microclimates experienced by seedlings in severely burned areas (Feddema et al., 2013).

Using a framework that focuses on positive feedbacks, rather than solely on seed limitation, will likely give us a more holistic view the potential for type conversion in these systems with altered disturbance regimes.

Materials and Methods

Study area

We focused on two large wildfires in Yosemite National Park (YNP) that reburned prior wildfires with large patches of high severity (>300 ha) (hereafter, 1990s fires). This included the 2009 Big Meadow Fire that re-burned the 1990 A-Rock Fire and the 2013 Rim Fire that re-burned the 1996 Ackerson Fire (Figure 3). Both the Ackerson and Rim Fires burned on both the Stanislaus National Forest and YNP, but here we focus on YNP lands only to control for management history. Both of the 1990s fires burned primarily through mixed conifer forests, which were dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), sugar pine (*Pinus lambertiana* Douglas), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), white fir (*Abies concolor* [Gordon & Glend.] Hildebr.), incense-cedar (*Calocedrus decurrens* [Torr.] Florin), coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) and California black oak (*Quercus kelloggii* Newb.). The reburn fires also burned in mixed conifer forests as well as more substantial components of montane chaparral, meadows, riparian areas and oak woodlands; smaller components of red fir (*Abies magnifica* Andr. Murray), lodgepole pine (*Pinus contorta* Loudon) and western white pine (*Pinus monticola* Douglas) forests occurred at higher elevations. The sites have a Mediterranean-type climate with cool, wet winters and hot, dry summers. Summary information for these fires is found in Table 1.

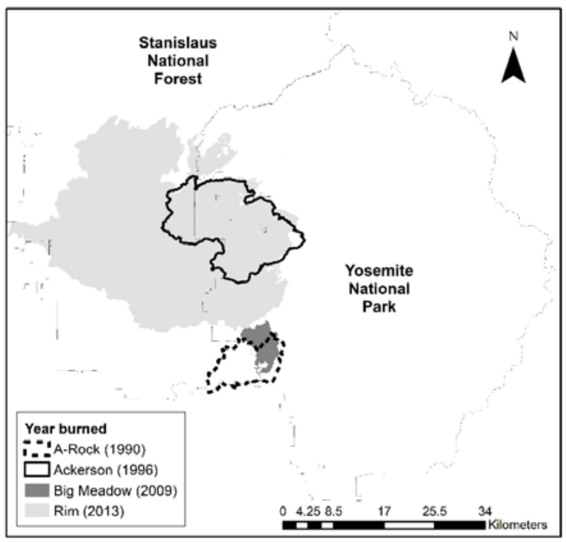


Figure 3. Map of study area. Reburn analyses were conducted for entire footprint of Big Meadow Fire and for the Rim Fire within YNP. Field data was collected on twice-severely burned areas in the overlapping fires, and once-severely burned areas of the Rim and Big Meadow that did not burn in the 1990s fires.

1990s Fire	Year Burned	Hectares	Reburn fire	Year reburned	Postfire year sampled
A-Rock	1990	7,191	Big Meadow	2009	7
Ackerson	1996	23,956	Rim (in YNP)	2013	3

Table 1. Summary information for the wildfires sampled in this study.

Re-burn severity

We examined the drivers of burn severity for the fires we call reburns (Big Meadow and Rim) that occurred within YNP. Though we call these fires reburns, our analyses also include portions of the reburn fires that are outside of the footprint of the 1990s fires to better understand the legacy of burn history relative to other drivers of fire severity.

Data Sources

We used the YNP Geospatial Fire History Database to identify all fires within the footprints of the reburns. We excluded all wildfires prior to 1984, because this was the earliest time at which severity data was available, and because areas burned prior to this date likely had enough fuel accumulation to resemble pre-fire conditions. We also excluded smaller fires (<4 ha) because spatial information on these fires was generally not reliable; this exclusion should not have much effect on our results, because fires of this size comprised <0.1% of the areas analyzed. Some of the prior wildfires and prescribed fires were only partially in the footprint of the reburn fires, and some overlapped each other. In the Big Meadow Fire, 46 ha burned in six prescribed fires between 1989 and 2008, and 1,875 ha burned in three wildfires between 1988 and 2008. In the Rim Fire footprint within YNP, 7,080 ha burned in 29 prescribed fires between 1989 and 2012, and 23,537 ha burned in 37 wildfires between 1985 and 2011. Wildfires included fires that were managed for suppression objectives as well as resource objectives (fires formerly known as "Wildland Fire Use"). We used these data to extract the number of years since the last fire, where areas without any prior fire history were assigned 100 years; we also calculated the number of times each pixel burned from 1984 to 2013.

Continuous burn severity imagery was obtained from the Monitoring Trends in Burn Severity website (www.MTBS.gov) for 2011-2013, and for 1984-2010 we used the Lutz et al. (2011) burn severity atlas for YNP for all fires ≥ 40 ha (Lutz et al., 2011). Burn severity maps were generated from 30m pixel Landsat imagery, using the Relativized differenced Normalized Burn Ratio (RdNBR) (Miller and Thode, 2007). RdNBR is derived by calculating the Normalized Burn Ratio (NBR) ratio that is sensitive to chlorophyll and moisture (using the near- and mid-infrared, Landsat bands 4 and 7) for both pre- and postfire imagery, which are then differenced (dNBR) and relativized (RdNBR) to account for variation in pre-fire cover. We predicted the continuous RdNBR burn severity for the reburns using the Initial Assessment (IA) which is created immediately postfire.

We chose the IA over the Extended Assessment (EA) because it may help distinguish between first- and second order fire effects. In shrub-dominated vegetation that has a heavy sprouting response, the EA may detect two areas at moderate severity, but these may differ in how they burned and how much woody fuel was consumed. Assuming similar pre-fire vegetation, one site could be moderate severity because only a portion of the live vegetation burned, whereas the other could be moderate severity because all of the live vegetation burned but has sprouted back by one year postfire. This difference in on-site fire intensity could in turn affect the amount of surface fuel consumed and impacts to soils and seedbanks. For all previous fires, we used classified EA maps for the predictor values, since in this case the longer-term vegetation response is more likely to influence future fire behavior. We classified burn severity using the thresholds outlined in Miller and Thode (2007) to define undetected change, low (<25% mortality), moderate (25-90% mortality) and high (>90% mortality) severity. Undetected change within a fire perimeter is either unburned or of low severity with little change to the canopy, which limits change detection. We converted these images to 30m point grids for all of the reburns and extracted both the RdNBR value for the reburn and past-fire classified burn severity.

We extracted prior burn severity class to each pixel, for all prior wildfires and prescribed fires where severity maps were available. For areas that had experienced multiple fires, we extracted the maximum severity class, since the vegetation and fuels structure in those areas is likely shaped most strongly by the prior high severity fire event. For areas that were prescribed burned but where burn severity maps were unavailable, we set the severity class to low, since the vast majority of area prescribed burned in YNP burns at low severity (Kelly Singer, Prescribed Fire Specialist, personal communication).

There were also roadside mechanical thinning treatments on the in both the Rim (105 ha) and Big Meadow (18 ha), and an additional 63 ha was masticated in the Big Meadow footprint. We assigned these treatments separately from fire treatments to the appropriate pixels. There was more extensive salvage logging and planting on the Stanislaus National Forest, prompting us to exclude the Rim Fire on those lands. The effects of logging and planting treatments on burn severity were beyond the scope of this study, and has been more extensively investigated elsewhere (Lydersen et al., 2017; McGinnis et al., 2010; Thompson et al., 2007a).

We used Digital Elevation Models (DEMs) acquired from the USGS to extract elevation data (U.S. Geological Survey, 2014), and generated slope and aspect from the DEM using ESRI ArcMap 10.4. We also generated Topographic Position Index using the Jenness Tool, which creates a classified raster of canyons, gentle slopes, steep slopes and ridgetops (Jenness et al., 2013). We set the thresholds for canyons and ridges at -2 and 2 respectively, and used 16.7° slope as the cut-off for gentle versus steep slopes. This value was selected because it corresponds to the 30% slope that is the standard threshold for differences in fine dead fuel moisture and probability of ignition in on-site fire behavior calculations (Deeming et al., 1974).

We downloaded 30-year climate averages (1981 – 2010) for climatic water deficit (mm) (CWD), annual precipitation (mm) (PPT), actual evapotranspiration (mm) (AET), April 1 snow water equivalent (mm) (Snowpack) and minimum monthly temperature (degrees Celsius) (TMIN) from the California Climate Commons (http://climate.calcommons.org/). These climate averages were modelled using the Basin Characterization Model (Flint et al., 2013). We extracted the climate and topographic data to each point.

We used daily Crane Flat weather station data for daily weather variables during each fire (http://www.wrcc.dri.edu/), including relative humidity, minimum and maximum relative humidity, minimum and maximum temperature and wind speed. We used Fire Family Plus version 4.1 (Bradshaw and McCormick, 2009) to calculate commonly used fire weather/danger indices for each day, the Burning Index (BI) and Energy Release Component (ERC). ERCs are a measure of potential energy release at a flaming front and is more closely linked with fuel type and fuel moisture, particularly in larger fuels size classes. The BI is related to potential flame length over a fire danger rating area; it is calculated with both ERC and a spread component model, and is generally considered more sensitive to fine fuels and wind. We then cross-walked the point grid with daily fire progression maps and assigned the fire weather variables to each point.

Statistical models

We used spatial auto-regression (SAR) analysis to examine the drivers of re-burn severity (Wimberly et al., 2009). SAR analyses include a spatial error term which indirectly models unmeasured, but spatially structured, variables. This term also accounts for spatial autocorrelation, enabling us to include every Landsat burn severity pixel rather than a subsample. We used a nearest neighborhood distance of 30m, following methods used in Pritchard and

Kennedy (2014) and Stevens-Rumann et al. (2016). For each model, we confirmed that our residuals were not autocorrelated at this distance using Moran's I. We predicted continuous RdNBR (IA) values for each reburn event in separate models, and in both cases predicted the burn severity of the entire "reburn" fire, including areas outside of the initial fire footprint, in order to better consider the role of prior burn severity relative to other drivers. For both models, we evaluated a suite of weather, past fire severity and history, topography and vegetation predictor variables (Table 2).

We first tested all candidate variables individually and considered all significant variables as candidates for inclusion in the final model. For highly correlated variables (>0.85, Nash and Bradford, 2001), we selected only the variable for which the single variable model had the lowest AIC to avoid multicollinearity. We generated the final model for each reburn by examining all possible combinations of the final candidate variables. Since models with <2 delta AIC (dAIC, the difference in AIC between each model and the model with the lowest AIC) are considered indistinguishable, for models with dAIC <2 we chose the model with the fewest explanatory variables as the most parsimonious. More extensive explanation of these methods can be found in Wemberly et al. (2009) and Prichard and Kennedy (2014). All SAR analyses were conducted using the *spdep* package in R (R Core Team, 2017).

Variable Group	**Individual variables**
Topographic	Slope (percent) Aspect (degrees) Elevation (m) Topographic position index
Weather	Maximum temperature (C) Minimum temperature (C) Maximum relative humidity (%) Minimum relative humidity (%) Wind speed (mph)
Indices/derived variables	Burning Index (BI) Energy Release Component (ERC)
30-year climate averages	Annual precipitation (mm) Snowpack (mm) Climatic water deficit (mm) Actual evapotranspiration (mm) Minimum annual temperature (C) Maximum annual temperature (C)
Vegetation	Vegetation type
Fire history	Number of times burned Number of years since last fire Maximum past fire severity (categorical)

Table 2. Candidate variables for SAR models on reburn severity.

Vegetation response

To understand how repeated high severity fire is affecting vegetation regeneration, we installed 111 plots in the footprints of the Big Meadow and Rim fires. We installed 53 plots in the repeated high severity areas (hereafter HH for high-high) and 58 plots in areas once-burned at high severity (hereafter UH for unburned-high). Plots were installed on 200 m grids in the center of patches.

Field data collection
Two 22.7 m long, perpendicular transects defined each 0.04 ha circular field plot. We sampled plant cover by species using point-intercept on both transects for a total of 140 points per plot. We also recorded shrub height and crown diameter for every individual by species and regeneration strategy (sprouted, seeded) that intercepted one transect and calculated estimated biomass using established allometric equations (McGinnis et al., 2010). Species richness was estimated by recording a census across the entire plot. When we could not identify a plant to the species level, we identified it to the lowest taxa possible, usually to the genus level. Conifer seedlings were tallied by species in an 8 m radius sub-circle (0.02 ha). We sampled surface fuels on three 15.24 m transects using standard planar-intercept techniques (Brown, 1974).

Statistical analyses
To test for differences in univariate variables by burn status, we used a combination of linear mixed models (LMMs) and generalized linear mixed models (GLMMs) with the reburn fire as a random effect. We modelled conifer regeneration density and all richness variables in a GLMM with either a Poisson or negative binomial distribution. To assess richness by biogeographical affinity, we used a database from by Stevens et al. (2015) to assign species as north- and south-temperate in affinity, which was derived from Raven and Axelrod (1978). Of the 295 unique plants observed in this study, we identified 227 to the species level, of which we were able to assign 188 a biogeographic affinity. The remaining 39 identified species not assigned an affinity included 11 nonnatives and 28 that did not have a biogeographic affinity assigned (Raven and Axelrod, 1978). Fuels and relative vegetation cover data were analyzed with a LMM. We transformed both fine and coarse woody debris by taking the log and square root, respectively, to meet normality assumptions for the residuals. We calculated additive cover including multiple "hits" per point, allowing for >100% cover. Because relative cover of live vegetation is proportion data, we normalized the data and used a logit transformation, adjusting 0's and 1's by 0.025 (Warton and Hui, 2011).

All models also included slope, aspect and elevation and number of years since last fire, since these variables can independently influence vegetation characteristics. Models for conifer seedling regeneration additionally included distance to lesser-burned (moderate, low or unburned) edge as a proxy for distance to seed source, which we calculated using the Near Tool in ArcMap 10.4.1. All univariate analyses were performed with the *lme4* package in R (R Core Team, 2017).

Multivariate analyses of the plant community included a permutational Multivariate Analysis of Variance (perMANOVA) test for community differences (Anderson, 2001) by fire history and a multivariate analysis of group dispersion procedure (PERMDISP2) (Anderson, 2006) to examine dispersion within treatment. The PERMDISP2 procedure is the multivariate analogue to the Levene's test for normality, which can also be used as a measure of beta diversity (Anderson et al., 2006). We created a visual exploration of community differences using a Non-metric Multidimensional Scaling (NMDS) ordination and evaluated community evenness by treatment by calculating Shannon's Index. To assess species fidelity and abundance to each treatment, we used an Indicator Species Analysis (ISA) and considered species with p-values < 0.05 and Indicator Values >25 as treatment indicators (Dufrene and Legendre, 1997). Multivariate analyses were performed in R using the *vegan* package, except for the ISA, which was performed with the *indicspecies* package (R Core Team, 2017).

Results and Discussion

Results

1. Evidence for positive feedbacks

1.1 Reburn severity

The best models for predicting the RdNBR (IA) of each reburn event shared three common predictors (Table 3), which varied somewhat in their relationship to reburn severity. In the Rim Fire, RdNBR (IA) was lower in areas with prior burn severity classes of undetected change and low severity, relative to areas that had no fire history. However, areas that had burned with a maximum severity of moderate or high prior to the Rim Fire had mean RdNBR (IA) in the high severity class. In contrast, increasing burn severity from undetected change/unburned to high severity was associated with increasing Big Meadow RdNBR (IA), where the mean for prior moderate and high were in the high severity class, but with prior high severity resulting in much higher RdNBR (IA) values (Figure 4a). For vegetation type, montane chaparral generally reburned much more severely than other vegetation types, where both the mean and median response for these classes was in the high severity category and mean RdNBR (IA) exceeded all other vegetation types (Figure 4b). The models differed in that Oak Woodlands were also associated with increased severity on the Big Meadow Fire, whereas on the Rim Fire, the Meadow type also reburned severely. Meadow areas included both wet meadows and dry postfire grass dominated areas which likely contributed to the mixed response. Finally, increasing ERC was associated with increasing burn severity on the Rim Fire but had a negative effect on Big Meadow fire severity (Table 3).

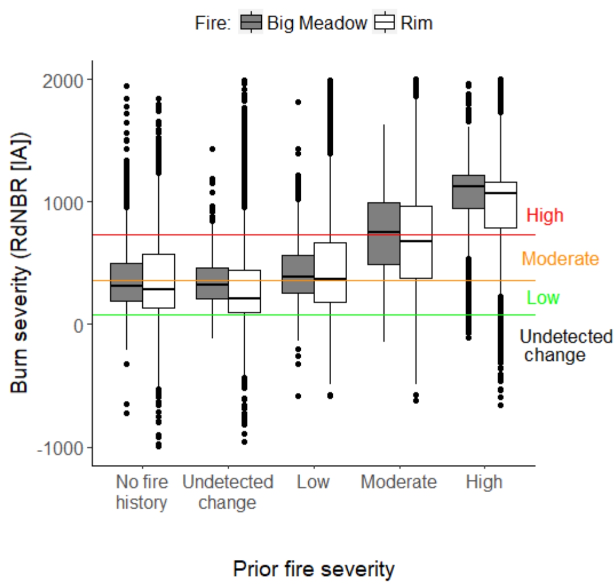
Several variables were only important in the individual models. In the Rim Fire, increasing BI, number of times burned, time-since-fire and AET all had a positive relationship with Rim RdNBR (IA). In the Big Meadow Fire, increasing annual precipitation (mm), minimum daily RH and daily maximum temperature all decreased predicted burn severity. The Big Meadow Fire model additionally included non-fire treatments, where thinning decreased RdNBR (IA) and mastication increased it.

Variable	***Rim***			***Big Meadow***		
	Estimate	Standard error	p-value	Estimate	Standard error	p-value
Intercept	229.17	40.44	< 0.001	5082.15	313.43	< 0.001
Fire severity						
Undetected change	-5.70	2.48	0.021	126.01	11.74	< 0.001
Low	-2.72	2.48	0.273	140.05	10.27	< 0.001
Moderate	5.92	2.52	0.019	186.44	10.54	< 0.001
High	14.19	2.63	< 0.001	235.36	11.22	< 0.001
Slope	0.05	0.00	< 0.001	--	--	--
ERC	2.49	0.43	< 0.001	-13.73	4.16	0.001
BI	0.68	0.15	< 0.001	--	--	--
Time-since-fire	1.17	0.12	< 0.001	--	--	--
Times burned	10.42	1.55	< 0.001	--	--	--
AET	0.04	0.01	0.004	--	--	--
Minimum RH	--	--	--	-10.34	1.26	< 0.001
Maximum temperature	--	--	--	-16.14	2.14	< 0.001
Annual precipitation	--	--	--	-1.94	0.20	< 0.001

Mechanical treatments						
Mastication	--	--	--	28.78	13.85	0.038
Thinning	--	--	--	-35.78	15.00	0.017
Vegetation type						
Conifer reproduction	5.08	4.12	0.217	38.69	26.80	0.149
Lower Mixed Conifer	2.79	3.55	0.432	40.37	24.16	0.095
Meadow	8.28	3.69	0.025	53.53	23.86	0.025
Montane Chaparral	14.55	3.55	< 0.001	90.14	23.59	< 0.001
Oak Woodlands	4.55	3.61	0.208	85.90	24.24	< 0.001
Red fir/Lodgepole pine	1.50	3.52	0.669	10.81	24.31	0.657
Upper Mixed Conifer	-0.15	3.43	0.965	13.96	24.06	0.562

Table 3. Results from the reburn severity analyses. Abbreviations stand for: Energy Release Component (ERC), Burning Index (BI), actual evapotranspiration (AET) and relative humidity (RH).

(a)



(b)

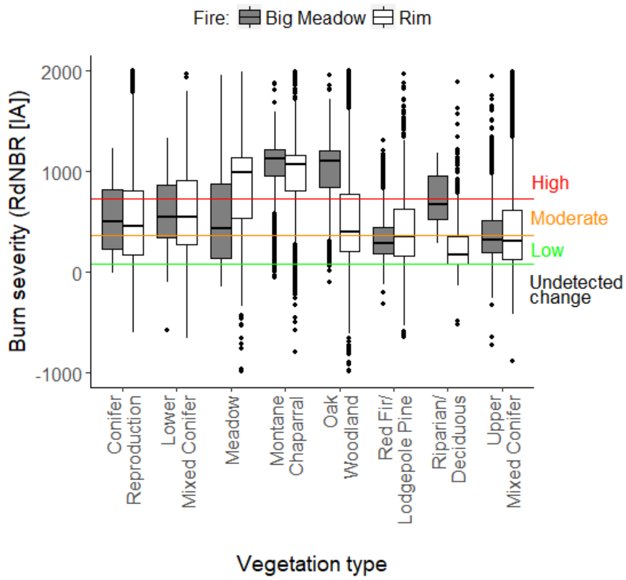


Figure 4. Burn severity (RdNBR [IA]) by (a) maximum prior burn severity class and (b) pre-fire vegetation type. Colored lines correspond to RdNBR (IA) thresholds for burn severity class. Roughly 0.2% of extreme RdNBR (IA) values were removed to improve plot readability.

1.2 Dominance by regeneration strategy

The only obligate seeding shrub detected with >1% mean cover was *Arctostaphylos viscida* C. Parry, which still occurred at very low cover across both HH and UH areas. There was no difference in *A. visicida* by cover or frequency. Since the dominant shrub species across both UH and HH areas are facultative seeders (*C. integerrimus*, *C. cordulatus*, *C. foliolosa*, *A. patula*), we focused on differences in sprouting versus seeded individuals. To better understand how these individuals are dominating the sites in terms of resource use, we examined estimated biomass rather than cover. There was higher estimated shrub biomass in HH areas, but the difference in median response was modest and this effect was not significant ($p = 0.065$). Differences in individual shrub biomass by regeneration strategy were highly significant, with higher biomass for seeded individuals in the UH areas ($p = 0.007$) but higher biomass in sprouting individuals in HH areas ($p < 0.001$; Figure 5).

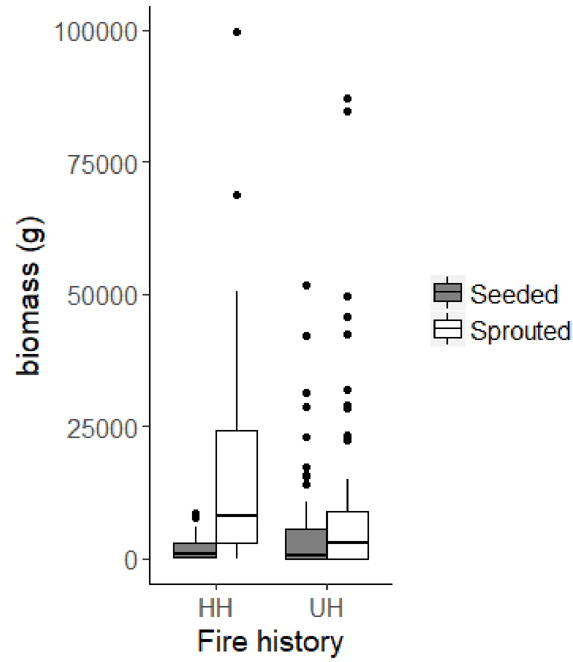


Figure 5. Estimated total shrub biomass by regeneration strategy.

HH areas generally had higher cover of sprouting tree species, but these differences were not significant (*Quercus chrysolepis* Liebm., $p = 0.173$; *Q. kelloggii*, $p = 0.075$). For the obligate seeding conifers, we attempted to compare cover between UH and HH areas and although there were conifer seedlings present in both areas, no conifer seedlings were detected on point intercept lines in HH areas. Obligate seeding conifer seedling densities were significantly lower in areas twice-burned at high severity (HH) ($p < 0.001$, Figure 6). UH areas had a mean of 1,355 (± 330) seedlings ha^{-1} and a median of 298 conifers ha^{-1} (range: 0 - 10,545 ha^{-1}). In contrast, HH areas had a mean of 31 (± 17) seedlings ha^{-1} and a median of 0 ha^{-1} (range: 0 - 846 ha-1). There was a significant and negative relationship with distance to seed source ($p = 0.010$). However, the distribution of plots across distance to seed source (defined using distance to lesser-burned edge as a proxy) was unequal across treatments, with the unburned-high severity plots (UH) generally occurring closer to potential conifer seed sources. In a test of the subset of the data that included only plots <300 m from a lesser burned ($N_{high\text{-}high} = 57$, $N_{unburned\text{-}high} = 33$), there was still a highly significant difference between treatments ($p < 0.001$), with mean seedling densities in UH areas of 1,355 (± 330) seedlings ha^{-1} and a median of 298 conifers ha^{-1} (range: 0 - 10545 ha^{-1}) versus a mean of 43 (± 28) seedlings ha^{-1} and median of 0 conifers ha^{-1} (range: 0 - 846 ha^{-1}) in HH areas.

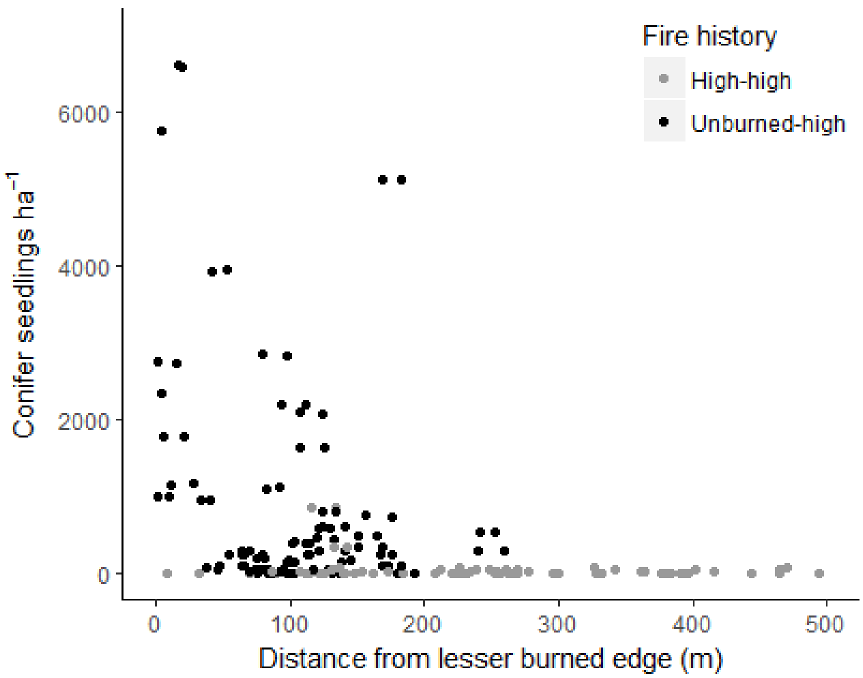
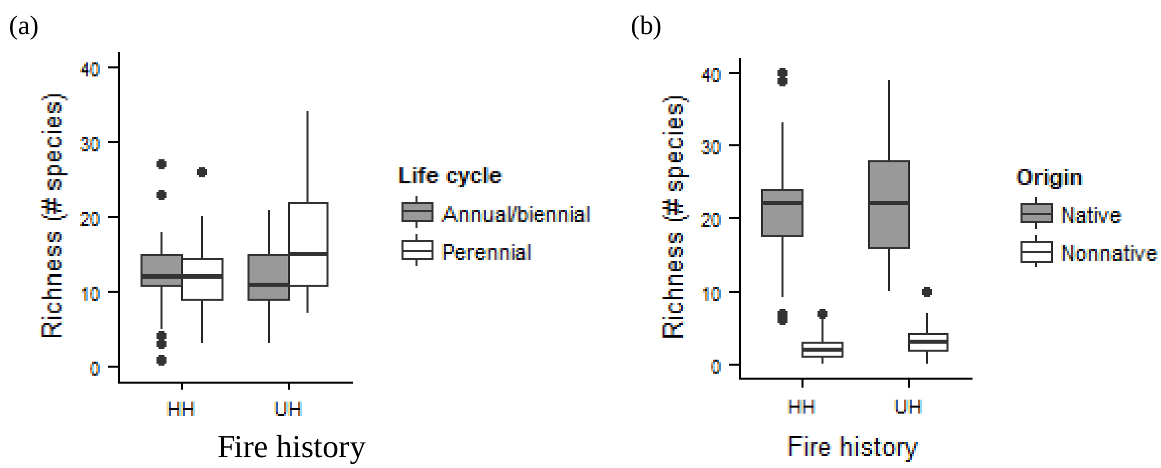


Figure 6. Conifer seedling densities by fire history at a range of distance to lesser-burned edge. Three unburned-high plots with densities > 7,000 seedlings ha^{-1} were excluded for plot readability.

Dominance by life history strategy differed somewhat between UH and HH areas, where there was no significant difference in annual richness ($p = 0.880$) but perennial richness was greater in UH areas ($p < 0.001$; Figure 7). Cover of annuals was significantly higher in the HH areas for both annual forb cover ($p = 0.003$) and annual graminoid cover ($p < 0.001$). There was no significant difference in perennial cover for either forbs or graminoids.



(c)

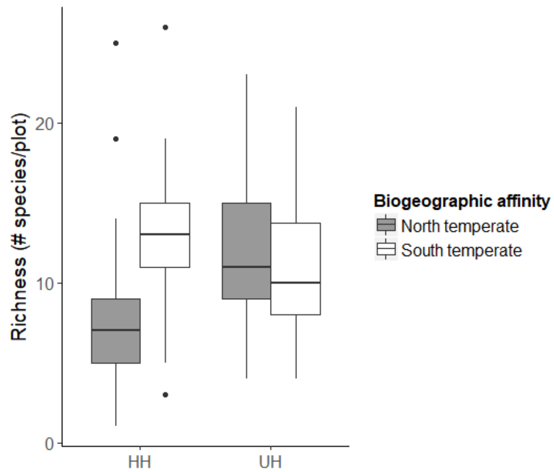


Figure 7. Species richness across treatments for (a) life cycle, (b) origin and (c) biogeographic affinity.

1.3 Fuels

We observed lower woody fuel loads in HH areas versus in the UH areas and differences were highly significant across all fuels classes. Fine woody debris averaged 24.17 (± 2.60) Mg ha^{-1} in UH areas and 11.89 (± 1.80) Mg ha^{-1} in HH areas ($p < 0.001$). Coarse woody debris averaged 69.48 (± 9.97) Mg ha^{-1} in UH areas and 35.02 (± 5.29) Mg ha^{-1} in UH areas ($p = 0.005$). Mean litter depth was higher in UH (3.25 ± 0.19 cm) versus HH areas (2.35 ± 0.19 cm) ($p = 0.003$), as was duff depth (UH: 0.21 ± 0.04 cm, HH: 0.13 ± 0.03 cm, $p = 0.005$; Figure 8).

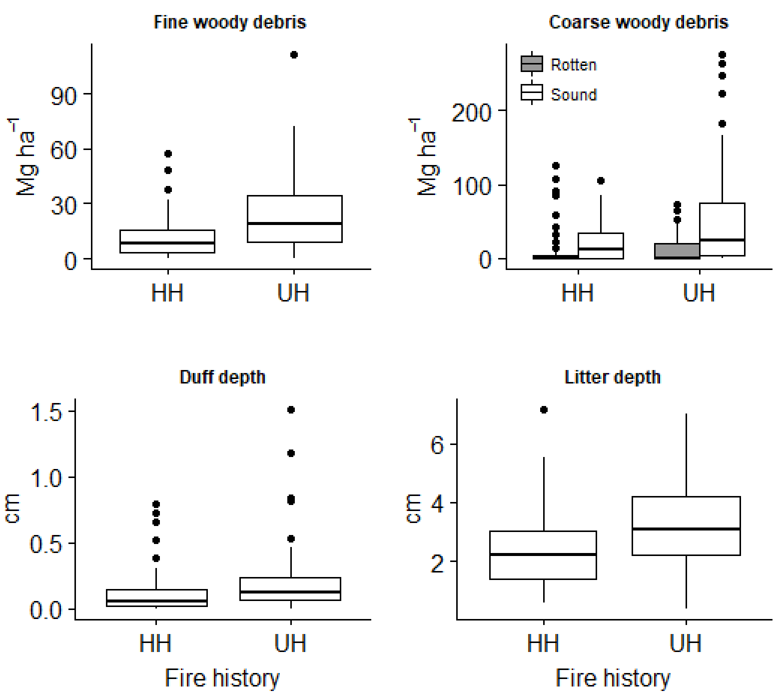


Figure 8. Total fine and coarse woody debris loads and average litter and duff depth. HH stands for repeated high severity areas and UH stands for once-burned at high severity.

2. Evidence for distinct states

Plant community composition and abundance

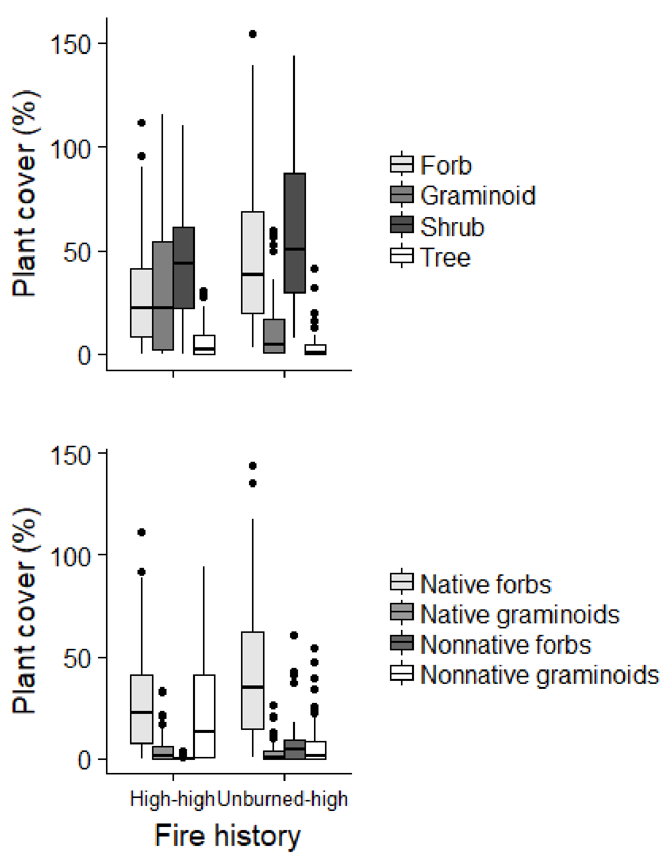
We observed 295 species across both treatments, 28 of which were nonnative. Of all species observed, 140 were observed in both treatments, with 97 exclusively found in UH areas and 56 exclusive to HH areas. The majority of species that were exclusively found on either treatment were observed at low frequency. For example, when excluding species that occurred on <5% of the plots, the treatments had 98 species in common, with only 7 unique to UH plots and 4 unique to HH plots.

UH areas had slightly higher total species richness ($p = 0.002$, Figure 7) than the HH areas, where both native and nonnative species followed the same trend (both $p < 0.001$). Tree ($p < 0.001$), forb ($p = 0.005$) and shrub ($p = 0.048$) richness were all significantly higher in UH areas, but there was no difference in richness for graminoids ($p = 0.376$). For richness by geographic affinity, there were significantly more north-temperate species observed in the UH areas than the HH areas ($p = 0.006$), but there was no difference in richness for south-temperate species ($p = 0.198$). South-temperate species made up a greater proportion of species observed in HH sites ($p < 0.001$, Figure 7).

Total relative plant cover was slightly higher in UH areas ($p = 0.048$) and shrub cover ($p = 0.019$) was much higher (Figure 9). For the dominant shrub species, UH areas had much greater cover of *C. cordulatus* ($p = 0.058$) and *Chamaebatia foliolosa* Benth. ($p < 0.001$), whereas HH areas had a much higher cover of *C. integerrimus* ($p = 0.014$; Figure 9). Forb cover was also higher in UH areas ($p = 0.004$). In contrast, graminoid cover was significantly higher in HH areas ($p < 0.001$, Figure 9).

(a)

(b)



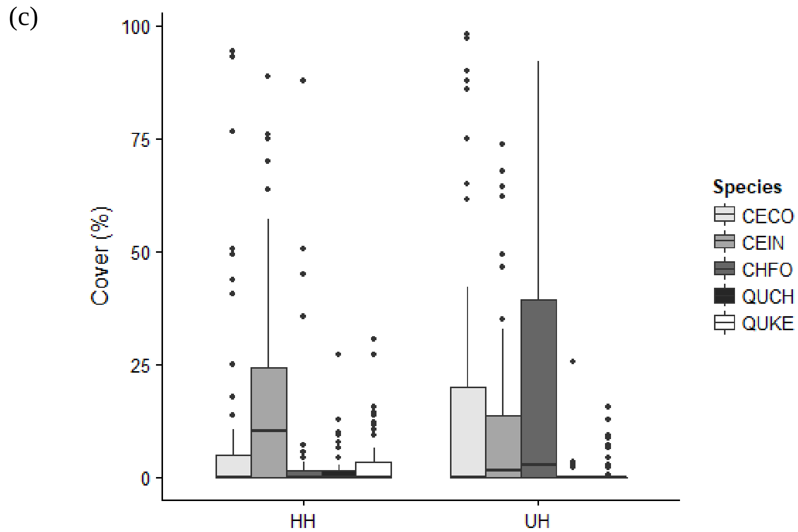


Figure 9. Relative plant cover (%) by lifeform (a), by plant origin for forbs and graminoids (b) and by dominant shrub and sprouting tree species (c), including: *C. cordulatus* (CECO), *C. integerrimus* (CEIN), *C. foliolosa* (CHFO), *Q. chrysolepis* (QUCH) and *Q. kelloggii* (QUKE). Percent cover may exceed 100% because it is additive for all overlapping species.

There was higher total native cover in UH areas ($p < 0.001$) but no difference in total nonnative cover by treatment ($p = 0.102$). Both native ($p = 0.033$) and nonnative ($p < 0.001$) forbs were higher in UH areas, but nonnative graminoid cover was much higher in HH areas ($p < 0.001$). There was no difference in native graminoid cover by treatment ($p = 0.155$; Figure 9). The nonnative graminoid cover was dominated by cheat grass (*Bromus tectorum* L.), which had a median of 0% on UH plots and 8% on HH plots, with cover on some HH plots as high as 85%. There was no significant difference in cheat grass frequency across plots ($p = 0.513$).

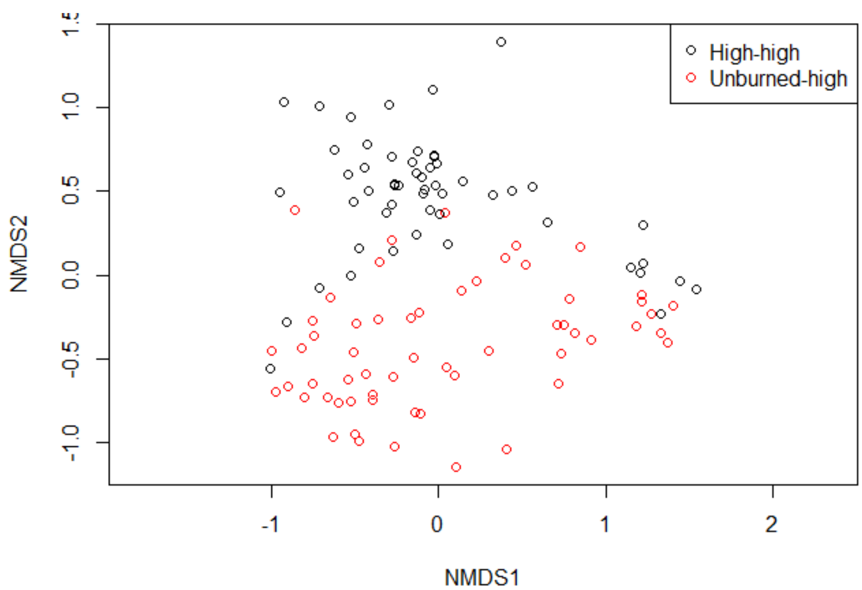


Figure 10. Non-metric multidimensional scaling (NMDS) ordination of plant communities by plot, colored by fire history.

Multivariate tests on the plant community (excluding species that occurred on <5% of the plots) indicated a significant difference between HH and UH areas (p = 0.001), which is reflected in the NMDS ordination (Figure 10). The PERMDISP2 procedure, which is also a method of assessing differences in beta diversity, did not indicate that this difference was due to within-group variation (p = 0.900). Shannon Evenness Indices similarly did not differ by treatment (UH or HH) (p = 0.309). Indicator species for HH included one shrub (*Eriodictyon californicum* (Hook. & Arn.) Torrey), and eight out of ten indicators were annuals, which included the nonnative *B. tectorum*. Indicator species for UH areas included seedlings of two of the obligate seeder, foundation conifer species (ponderosa pine, white fir), three shrubs and one nonnative forb species *(Lactuca serriola* L.) (Table 4). Only four of 11 indicators in UH areas were annuals.

High-high	**Tree**	**Shrub**	**Forb**	**Graminoid**
Acmispon nevadensis (S. Watson) Brouillet var. *nevadensis*			X	
***Bromus tectorum* L.**				X
Clarkia rhomboidea Douglas			X	
Eriodictyon californica (Hook. & Arn.) Torrey		X		
Gayophytum diffusum Torrey & A. Gray			X	
Gilia capitata Sims spp. *mediomontana* V. Grant			X	
Lupinus grayi S. Watson			X	
Phacelia heterophylla Pursh var. *virgata* (Greene) R.D. Dorn			X	
Quercus chrysolepis Liebm.	X			
Stephanomeria virgata Benth. ssp. *pleurocarpa* (Greene) Gottlieb			X	
Unburned-high				
Abies concolor (Gordon & Glend.) Hildebr.	X			
Carex sp.				X
Ceanothus parviflorus Eschsch.		X		
Cornus nutallii Audubon		X		
Epilobium brachycarpum C. Presl			X	
Erigeron canadensis L.			X	
***Lactuca serriola* L.**			X	
Pinus ponderosa Lawson & C. Lawson	X			
Pseudognaphalium beneolens (Davidson) Anderb.			X	
Ribes roezlii Regel	X			
Rosa bridgesii Crepin		X		

Table 4. Indicator species by fire history from ISA. Nonnnative species are highlighted in bold.

Discussion

Our data suggest that a positive feedback between severe fire and chaparral vegetation beginning to operate on our sites, which could maintain these communities in an alternative state. Our landscape-level analysis detected the highest reburn severity in areas that had burned severely in the past and were dominated by montane chaparral. This is not surprising given the structure of the regenerating vegetation, as well as the high surface fuel loads that can occur after the first severe fire with the biomass from extensive tree mortality accumulating through time (Coppoletta et al., 2016; Lydersen et al., 2017). When the second fire occurs, it is burning in a somewhat novel fuel type, with chaparral structure but extremely high fuel loads that approach fuel conditions that occur after extreme events such as logging or blowdown in many areas (Scott and Burgan, 2005). These trends also generally seem to hold outside of the Sierra Nevada where postfire vegetation is shrub dominated (Thompson et al., 2007b). In contrast, Stevens-Rumman et al. (2016) detected consistent reductions in burn severity across all prior burn severity classes. This is likely due to the shorter growing seasons and lower productivity in the Northern Rockies, leading to a slower postfire vegetation response with less biomass (Stevens-Rumann and Morgan, 2016).

Most studies, including ours, focus on just one reburn event, but continuous severe reburning is required to truly be a positive feedback. Other studies that have documented three or more reburn events that follow the same trend we observed, suggesting a longer-term feedback may be setting up on our sites (van Wagtendonk, 2012; van Wagtendonk et al., 2012). The fine fuel loads in our HH areas have woody debris within the ranges for shrub fuel models in the Big Meadow Fire only (Scott and Burgan, 2005). We assume that this is because the fire was sampled seven years postfire versus the three years postfire on the Rim Fire, where fine woody debris has not had enough time to accumulate. Despite these current fine fuel loads that are in range, the low accumulation of litter and duff may indicate a lack of continuity to carry much fire at present. In addition to surface fuels, for these areas to reburn severely yet again also depends on accumulation of dead branches within live individuals, which takes time to develop (Schwilk and Westoby, 2003). We did not assess the proportion of dead stems within living individuals, and so we lack a method for characterizing how receptive the shrubs would be to carrying fire on these sites. However, with relatively high total plant cover and current fine fuel loads, we suspect that the system will support severe fire in the future, particularly with the substantial cheat grass component.

A small wildfire did occur in 2017 in the Big Meadow HH area during very hot and dry conditions, but the fire behavior was not severe (Kelly Singer, Prescribed Fire Specialist, personal communication). We suspect that the mild fire behavior observed fire had more to do with time since fire than long-term potential for another severe fire event. Work at a slightly higher elevation in YNPs Illilouette Basin suggests that previously burned areas do not readily support fire for roughly nine years (Collins et al., 2009), and the fires we sampled were both “younger” (measured three and seven years postfire) and so these sites may need more time for contiguous fuels to develop. In addition, the nine-year threshold in Collins et al. (2009) was for all fuel types, and this timeline may be longer in shrub-dominated areas where fuel accumulation is slower than in forested areas.

The initiation of a positive feedback on our sites is further supported by the shift in regeneration strategies and life history traits in HH areas toward traits that are more resilient and adapted to severe fire. There was significantly higher biomass of sprouting individuals versus seeded individuals in HH areas. In addition to sprouting ability, most of the dominant shrub species (*Ceanothus*, *Arctostaphylos*) are prolific seeders that can form a long-lived soil seedbank (Knapp et al., 2012) and have refractory seeds that respond well to fire (Keeley, 1991). Between fire-cued germination and sprouting ability, these species are likely to continue to dominate the site after future fires. We also observed higher annual graminoid cover in HH areas, though annual forb cover was lower. Annuals are well-poised to respond well to fire given their short life cycle. In this case, most of the annual graminoid cover was dominated by cheat grass, which has been documented as a driver of fire-vegetation feedbacks across extensive areas of the Great Basin (Brooks et al., 2004; D'Antonio and Vitousek, 1992). Cheat grass invasions postfire in the Sierra Nevada are not unique to our site (Keeley, 2006), but it has not yet been implicated in shifting states as it has in the Great Basin.

HH areas also had much lower densities of the original community's foundation species, the obligate seeding conifers. This difference was reinforced by the ISA, where both ponderosa pine and white fir were indicators for UH areas but no conifers were identified for HH areas. Although our study design was slightly imbalanced in terms of distance to seed source between once- and twice-severely burned areas, examining a subset of data that was in a more similar range of distances yielded the same result. We suspect that the differential response at similar distances may be due in part to the ability of dense onsite shrubs to sprout immediately after the second fire, which compete with regenerating conifers for light and moisture (Collins and Roller, 2013). The high annual graminoid cover in HH areas could also be outcompeting conifer seedlings (Dodson and Root, 2013). Excessive soil heating is another possibility; given the high fuels loads onsite, soil heating may have caused changes to soil chemistry, productivity or mycorrhizal communities (Jiménez Esquilín et al., 2007; Monsanto and Agee, 2008). A more focused investigation of this trend and its underlying cause is warranted.

We also detected other significant differences in the HH and UH plant communities, suggesting the potential for distinct states. There is a clear distinction between the overall plant community composition and species abundance in both the NMDS and perMANOVA results. Much of this difference is likely driven by differences in shrub species dominance and the ubiquity of a nonnative annual grass in HH areas. HH areas also had fewer north-temperate species and higher south-temperate species (though the latter difference was not significant). This shift is interesting, as Stevens et al. (2015) detected a reduction in proportion of north-temperate species along an increasing disturbance gradient of both fire severity and pre-fire thinning and burning treatments. That we saw fewer north-temperate species between areas twice-burned at high severity suggests that the "thermophilization" of plant communities is exacerbated not only by changes in canopy cover as evidenced by the severity gradient in Stevens et al. (2015), but potentially also by a tolerance for repeated severe fire. It also suggests that repeated severe fire results in an increasingly restrictive environmental filter on plant community composition.

Conclusions (Key Findings) and Implications for Management/Policy and Future Research:

Collectively, these data suggest that where forests are desired, it may be necessary to exclude fire until the obligate seeders exceed the shrub canopy layer and are more likely to survive a fire. It is also possible that cooler season burns could result in lower severity fires, that in turn could reduce fuels and competing cover enough to give regenerating conifers a chance to establish. Of the studies that have documented the slow process of reforestation from fires that burned at least several decades ago (Haire and McGarigal, 2010; Russell et al., 1998), it is unclear how much fire occurred between the initial fire and their measurements. In the case of Nagel and Taylor (2005), they did document numerous fires, but the patch sizes they studied were much smaller than we are considering here. The interaction of the positive feedback with the seed limitations that are occurring across large patches of high severity (Chambers et al., 2016; Collins and

Roller, 2013; Rother and Veblen, 2016; Welch et al., 2016) could result in a sort of “double whammy” in these systems.

Our data suggests that a positive feedback between fire and vegetation is developing on our sites, and that the areas twice-burned at high severity may be shifting to an alternative state. We recognize that a series of stochastic events, such as a large seed crop and favorable weather immediately after a fire event, could alter this trajectory, though such events are likely to be relatively rare in comparison with the likelihood of continued repeated fire, particularly under the warming climate (Westerling et al., 2011). In addition, the large patch sizes will necessarily cover a range of topography, soil types, etc., which may result in a more heterogenous response through time.

Without the capacity to follow these sites for decades or more and through numerous fires, or conduct a large-scale and long-term experiment, it is not possible to conclusively say if and when a state shift has occurred (Schröder et al., 2005). However, our identification of key components of the alternative stable state framework, from historic to current conditions, may be a reasonable alternative to waiting decades for that certainty. Fundamental to this framework was our identification of how the loss of resilience via fire exclusion and novel burning patterns could set up the system for a state shift. We then used empirical evidence to examine the initiation of a positive feedback and community characteristics that may be early indicators of a state shift, which offers some support that a shift is underway.

Because a persistent shift in community states would have significant consequences for wildlife habitat and ecosystem services, anticipating its occurrence through these proxy measures is also critical for supporting management decisions. Implicit in our ball-and-cup diagram is that significant energy is required to move a system that is resilient (i.e., in a deep basin) and being maintained by a positive feedback (Figure 1c). If our HH sites do represent an alternative state, then significant management intervention would be required if a forested state is desired (Suding et al., 2004). By improving our understanding of where a community lies in state space, and how current and historic disturbance regimes shape ecosystem resilience and stability, our approach can help support both managers and scientists working to understand vegetation shifts during a time of global change.

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Appendix B: List of Completed/Planned Scientific/Technical Publications/Science Delivery Products

Doctoral Dissertation Chapter:

- Alternative stable states after disturbance in ecosystems with long recovery times: identifying positive feedbacks and community characteristics

Submitted manuscript:

- Shive, K.L., J.T. Stevens, H.D. Safford, S.L. Stephens, K.L. O'Hara. *In review.* Alternative stable states after disturbance in ecosystems with long recovery times: identifying positive feedbacks and community characteristics. *Submitted to Ecology.*

Presentations:

- Repeated severe fire and the potential for forest type conversion. 2018. State of California Drought Mortality Task Force. Invited talk for monthly task force meeting. Sacramento, CA.

- High severity "reburns" in Sierran mixed conifer: fuels, tree regeneration and plant communities. 2017. Association for Fire Ecology. Orlando, FL.

Webinar

- High Severity "Re-Burns" in Sierra Mixed Conifer. 2018. California Fire Science Consortium: http://www.cafiresci.org/events-webinars-source/snreburnshive?rq=Shive

Appendix C: Metadata

Data and metadata have been uploaded to JFSP and data will be made publicly available at the Forest Service Research Data Archive (www.fs.usda.gov/rds/archive) once manuscript is accepted for publication.