UC Berkeley
UC Berkeley Electronic Theses and Dissertations

Title

Altered fire regimes, severe fire and forest recovery in mixed conifer forests

Permalink

https://escholarship.org/uc/item/57r20411

Author

Shive, Kristen

Publication Date

2017

Peer reviewed|Thesis/dissertation

Altered fire regimes, severe fire and forest recovery in mixed conifer forests

by

Kristen L. Shive

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Scott L. Stephens, Co-Chair
Professor Kevin O'Hara, Co-Chair
Professor David Ackerly

Fall 2017

ABSTRACT

Altered fire regimes, severe fire and forest recovery in mixed conifer forests

by

Kristen L. Shive

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Scott Stephens, Co-Chair

Professor Kevin O'Hara, Co-Chair

Understanding how altered fire regimes are shifting vegetation communities across the landscape will be critical for managing forested landscapes during a time of global change. Moreover, altered fire regimes can inform ecological theories on alternative stable states and ecosystem resilience. I investigated how increases in high severity fire are affecting ecosystem properties both directly and indirectly, in ways that can support both land management decision-making as well as broader inquiries into state transitions. In terms of the indirect effects of severe fire, I examine how the application of rice mulch for erosion control in severely burned mixed conifer forests affects native plant communities. I found that rice mulch is linked with higher nonnative richness, including numerous species that have total fidelity to mulched areas, suggesting the mulch may have introduced these species. I also observed that the mulch is homogenizing the plant communities; both of these findings could have persistent effects on ecosystem properties. I also studied the direct effects of fire severity on forest regeneration patterns in mixed conifer forests across California, building a spatially-explicit predictive model of postfire conifer regeneration from 24 wildfires. To build this model I used a novel approach to characterize seed availability from maps of estimated basal area. I calculated estimated annual seed production from basal area by species at each pixel using established equations and then smoothed these maps of seed production to simulate a neighborhood effect at a variety of scales. The most important predictors in this model were 30-year mean annual precipitation (mm) and seed availability, highlighting both the initial biological filter (seed availability) and site suitability (annual precipitation). Finally, I used a combination of remotely-sensed data and field data to empirically evaluate the potential for shifts to alternative stable states after severe fire in Sierran mixed conifer. Because positive feedbacks are often responsible for maintaining a given vegetation state, I evaluated the evidence for the initiation of a positive feedback in severely burned vegetation communities at two sites in Yosemite National Park. Areas that burned severely in the 1990s that were regenerating as montane chaparral tended to reburn severe in more recent (2009, 2013) fires. When comparing areas that have burned once versus twice at

high severity, I found that areas twice-burned at high severity had a greater response of sprouting species, and of sprouting versus seeded individuals for the facultative seeder shrub species; twice-burned at high severity areas also had significantly higher cover of nonnative annual grasses. I also found that areas twice-burned at high severity had significantly fewer obligate seeder conifer seedlings. The once- and twice-burned areas also had distinct plant communities, though this difference was not driven by differences in homogeneity within the two communities. These data suggest that positive feedbacks are likely beginning to operate after the second severe fire event, and that this event causes a shift in the communities that may be indicative of alternative state. Collectively, these diverse projects contribute to our understanding of shifting vegetation communities under a time of global change.

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION

A century of fire suppression in the mixed conifer forests of California has led to significant changes in ecosystem structure and function (Parsons and DeBenedetti 1979, Collins et al. 2011). By elevating surface fuels and increasing tree densities, it has also resulted in the increased incidence and extent of severe, stand-replacing wildfire (Miller et al. 2009, Miller and Safford 2012, Mallek et al. 2013). In the short-term, the complete loss of surface litter and live vegetation after stand-replacing fire can dramatically increase erosion potential, necessitating mitigation treatments that can have indirect effects on the plant community (Robichaud et al. 2009). In the longer-term, extensive contiguous patches of severe fire can have profound implications on forest regeneration (Savage and Mast 2005).

I investigated how these relatively novel events affect native plant communities in three distinct projects. Chapter 2 (*Rice straw mulch for post-fire erosion control: assessing non-target effects on vegetation communities*) examines how postfire application of rice mulch for erosion control in severely burned areas affects native plant communities. Rice mulch has been promoted as an alternative to the more traditionally-used wheat straw, under the assumption that nonnative species that are able to grow in a rice field are unlikely to establish in dry forested habitats (Robichaud et al. 2000, Beyers 2004, USDA Forest Service 2015). I sampled and compared plant community response in areas that had been treated with rice mulch as well as control areas in the 2013 Rim Fire. I installed 134 plots that were measured in 2014, of which a subsample were re-measured in 2015. There was significantly higher nonnative forb cover, nonnative graminoid cover and nonnative species richness in rice mulched areas. In addition, 25 nonnative species occurred exclusively in mulched areas; collectively, these responses contributed to more homogenous plant communities in mulched areas versus unmulched areas in 2015. In contrast, mulch had no effect on total plant cover and conifer regeneration densities were generally unaffected. Although some individual species that are better-adapted to wetter environments (like that of a rice field) may be ephemeral with time, since the overall trends persisted in the second year postfire, nonnative species introductions and community evenness impacts attributed to rice mulch may have lasting effects on the plant community.

Chapters 3 and 4 consider the longer-term vegetation responses to severe fire. Because the increase in high severity patch size also increases the distance to live conifer seed sources, there is growing concern that many areas will not regenerate as forests for decades or more (Collins and Roller 2013, Welch et al. 2016). In addition to seed source limitations, conifer regeneration patterns are also driven by site conditions, including topography and climate. Land managers who want to actively reforest these areas need tools to guide their management decisions, and to help prioritize areas for treatment with scare resources. Even where active reforestation is not the goal, an improved understanding of postfire regeneration patterns can assist with long-term planning for habitat management.

For Chapter 3 (*From the stand-scale to the landscape-scale: predicting the spatial patterns of forest regeneration after disturbance*), I used data from 24 wildfires in yellow pine and mixed conifer forests from across California to create a spatially-explicit predictive model of conifer regeneration after fire. The model was created using a combination of variables that indicate site suitability (topographic variables, 30-year climate averages) as well as seed availability, the critical initial biological filter for regeneration. I used a novel approach to

estimate annual seed production from existing basal area maps at the 30m-pixel scale, and then created a smoothed surface of seed availability across each fire. I found that the probability of observing any conifer was highly dependent on 30-year average annual precipitation and seed availability. I also used the final model to predict the probability of conifer regeneration across an entire fire, creating a predictive map of a "new" fire (the 2014 King Fire). Using the model to create predictive maps on new fire events is an important support tool for postfire management planning.

Chapter 3 highlighted the importance of seed availability, and many other researchers have identified seed limitation as a potential cause of persistent vegetation type shifts to montane chaparral (Collins and Roller 2013, Welch et al. 2016). Another mechanism by which these type shifts could potentially occur is through repeated severe fire. In the Sierra Nevada, severely burned areas tend to regenerate as montane chaparral, which has fuel structures that tend to re-burn severely, particularly where the initial fire burned through forested areas and resulted in heavy surface fuel accumulation (Coppoletta et al. 2016). In turn, the regenerating chaparral vegetation responds positively to severe fire, given that most of the dominant species can sprout and/or have fire-cued germination and long-lived seed banks. This creates a positive feedback between severe fire and chaparral vegetation, which is likely to increase the probability that such sites will remain in an alternative, unforested state (Holling 1973).

For Chapter 4 (*Alternative stable states after disturbance in ecosystems with long recovery times: identifying positive feedbacks and community characteristics*), I examined the potential for a shift to an alternative stable state in severely burned areas, where montane chaparral is being maintained by the positive feedback of severe fire. I sampled plant community composition and abundance, conifer regeneration and fuels in once- and twice-severely burned areas to assess how these areas differ. I observed significantly lower conifer regeneration, lower surface fuels, lower species richness and a higher proportion of south-temperate (versus north-temperate) species in areas twice-burned severely. In addition, plant composition and abundance in each treatment was unique, driven in part by shifts in dominance by regeneration strategy, where annuals and fire-cued, sprouting species increased in dominance over obligate seeders in areas twice-burned at high severity. These results suggest that there is a shift in the montane chaparral communities after the second severe fire. Moreover, the shift in regeneration strategies and lack of the obligate seeding conifers suggests that severe fire can act as a positive feedback that can reinforce the chaparral state.

Collectively, these chapters are intended to help inform and improve science-based decision making in fire, fuels and forest management. These projects elucidate the significant changes to ecosystems that have occurred as a result of fire suppression and altered fire regimes, and their implications for recovering vegetation communities. Indirectly, this research offers support for forest management practices that restore forest health and forest structure, in turn reducing the incidence of severe fire. Healthy forests that are resilient to wildfire, pests and drought can alleviate many of the concerns about loss of forests, as well as the unintended consequences of mitigations that occur after severe fire (Stephens et al. 2014). I hope that my contributions to the literature will support improved forest management decision-making in the future.

Works cited

Beyers, J. L. 2004. Postfire Seeding for Erosion Control: Effectiveness and Impacts on Native Plant Communities. *Conservation Biology.* 18:947–956.

Collins, B. M., R. G. Everett, and S. L. Stephens. 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere.* 2:51.

Collins, B. M., and G. B. Roller. 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. *Landscape Ecology.* 28:1801–1813.

Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics.* 4:1–23.

Mallek, C., H. D. Safford, J. Viers, and J. Miller. 2013. Modern departures in fire severity and area by forest type, Sierra Nevada and southern Cascades, California, USA. *Ecosphere.* 4:1–28.

Miller, J. D., and H. Safford. 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and Southern Cascades, California, USA. *Fire Ecology.* 8:41–57.

Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009. Quantitative Evidence for Increasing Forest Fire Severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. *Ecosystems.* 12:16–32.

Parsons, D. J., and S. H. DeBenedetti. 1979. Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management.* 2:21–33.

Robichaud, P. R., J. L. Beyers, and D. G. ; Neary. 2000. Evaluating the effectiveness of postfire rehabilitation treatments.

Robichaud, P. R., S. A. Lewis, R. E. Brown, and L. E. Ashmun. 2009. Emergency post-fire rehabilitation treatment effects on burned area ecology and long-term restoration. Fire Ecology Special Issue 5:115–128.

Savage, M., and J. N. Mast. 2005. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research.* 35:967–977.

Stephens, S. L., N. Burrows, A. Buyantuyev, R. W. Gray, R. E. Keane, R. Kubian, S. Liu, F. Seijo, L. Shu, K. G. Tolhurst, and J. W. van Wagtendonk. 2014. Temperate and boreal forest mega-fires: characteristics and challenges. *Frontiers in Ecology and the Environment.* 12:115–122.

USDA Forest Service. 2015. Post-fire Treatment Effectiveness for Hillslope Stabilization. USDA Forest Service, Rocky Mountain Research Station, Moscow Fire Science Lab. http://forest.moscowfsl.wsu.edu/BAERTOOLS/HillslopeTrt/?page=Mulch.

Welch, K. R., H. D. Safford, and T. P. Young. 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. *Ecosphere.* 7:e01609.

CHAPTER 2: RICE STRAW MULCH FOR POST-FIRE EROSION CONTROL: ASSESSING NON-TARGET EFFECTS ON VEGETATION COMMUNITIES

Abstract

Straw mulch is commonly used for post-fire erosion control in severely burned areas, but this practice can introduce nonnative species, even when using certified weed-free straw. Rice straw has recently been promoted as an alternative to wheat, under the hypothesis that nonnative species that are able to grow in a rice field are unlikely to establish in dry forested habitats. We investigated this hypothesis in the severely burned areas of the 2013 Rim Fire in the Sierra Nevada that were treated with rice straw post-fire. In 2014, we installed 134 plots in mulched and control areas with >95% tree mortality and re-measured a subsample in 2015. Mulched areas had significantly higher nonnative forb cover, nonnative graminoid cover and nonnative species richness. In addition, 25 nonnative species occurred exclusively in mulched areas; collectively, these responses contributed to more homogenous plant communities in mulched areas versus unmulched areas in 2015. In contrast, mulch had no effect on total plant cover and conifer regeneration densities were generally unaffected, with the exception of a slight positive effect on Douglas-fir. We recommend more stringent testing for weed-free certification and that funding for nonnative species eradication be included with post-fire rehabilitation plans.

Introduction

With the increase in the occurrence, severity and extent of wildfires in the western US over the last several decades (Westerling *et al.* 2006; Miller *et al.* 2009), there has been a parallel increase in the application of post-fire emergency stabilization treatments (Robichaud *et al.* 2014). These treatments are applied in severely burned areas where the loss of vegetation and ground cover significantly elevates the risk of post-fire soil erosion, which can result in increased flooding, water supply contamination, loss of soil, soil nutrients and seedbanks, and the destruction of infrastructure such as roads, culverts and bridges (Robichaud *et al.* 2010a). Many treatments have been used to mitigate this risk, including seeding native grasses and forbs, seeding nonnatives (sometimes sterile), contour log felling and mulch application (agricultural wheat or rice straw, wood strands).

Straw mulch application has performed far better than other common erosion control treatments in terms of reducing soil erosion, runoff and sediment yield in surrounding streams (Groen and Woods 2008; Robichaud, Lewis, *et al.* 2013; Robichaud, Wagenbrenner, *et al.* 2013). This success is primarily because the mulch acts as the ground cover that the fire removed, which can help to physically hold soil in place and reduce the force of raindrop impact. This performance advantage has led to an increase in mulch application in recent years (Robichaud *et al.* 2014). Of the commonly applied treatments, seeding and straw mulch have the greatest potential to affect native plant communities. To date, seeding has received a great deal of research attention (see review by Peppin *et al.* 2010), but the effects of straw mulch on plant communities are less well-studied (but see Kruse *et al.* 2004; Dodson *et al.* 2010; Dodson and Peterson 2010; Morgan *et al.* 2014). The potential effects on native plant communities include changes in plant cover, shifts in response by life-form or life cycle and the introduction of nonnative species.

Mulch can potentially promote growth by stabilizing the soil and increasing soil moisture, but it can also suppress growth by creating a physical barrier to seedling germination and establishment (Robichaud *et al.* 2010a; Dodson and Peterson 2010). In the northern Cascades, Dodson and Peterson (2010) found that mulch cover was positively associated with higher plant cover, richness and conifer densities, except when mulch cover exceeded 70%. They also observed strong declines in plant responses when mulch depth exceeded 5 cm (Dodson and Peterson 2010). In contrast, Kruse et al. (2004) observed no facilitative effect on plant cover and negative effects on conifer regeneration. Morgan et al. (2014) also detected higher plant species richness with no clear trend in plant cover. These studies suggest that the effects of mulch on native plant communities are likely to be somewhat dependent on site and mulch characteristics.

The potential for nonnative species introductions via mulch application is particularly problematic because severely burned landscapes are already at a higher risk of nonnative species invasions. The disturbance alters dispersal dynamics and nutrient availability, reduces competition, and increases light levels, which can favor nonnative species that are well adapted to quickly colonize disturbed areas (Sutherland 2004; Martin *et al.* 2009). Altered disturbance regimes, such as the fire regimes in the Sierra Nevada (Parsons and DeBenedetti 1979), can further increase invasion risk (Moles *et al.* 2012). The nonnative plant response to wildfire is highly variable and dependent on a complex interaction of propagule availability, propagule pressure and local site conditions (Lockwood *et al.* 2005), and the long-term effects on ecosystems are equally variable (Rew and Johnson 2010). In some large, severe fires, post-fire abundance of nonnative species has been low or ephemeral (Kuenzi *et al.* 2008; Wright and Tinker 2012), whereas in other cases, post-fire invasions have substantially altered post-fire landscapes and their subsequent disturbance regimes (D'Antonio and Vitousek 1992). Because of the potential for post-fire invasions to have such significant impacts, post-fire management treatments that may further increase invasion risk are of concern.

In terms of invasion risk, the use of rice straw for erosion control has been promoted as a safe alternative to the more traditionally applied wheat straw, under the hypothesis that seeds from nonnative species that are established in wet rice fields will not be able to establish in drier, forested habitats (Robichaud *et al.* 2000; Beyers 2004; USDA Forest Service 2015). To date, four studies have examined the effects of straw mulch on plant communities in the western US, and all detected associations between mulch treatments and nonnative species (Kruse *et al.* 2004; Dodson *et al.* 2010; Dodson and Peterson 2010; Morgan *et al.* 2014). Three of these studies investigated the effects of wheat straw but only one study, located in northern California specifically investigated the effects of rice straw (Kruse *et al.* 2004). This study by Kruse et al. (2004) linked greater nonnative species density with the rice mulch, but this was limited to one species that is commonly found in disturbed environments (*Cirsium vulgare* (Savi) Ten. Show (bull thistle)), which they also found in unmulched areas. We contribute to this literature by investigating prevailing hypotheses about rice mulch and nonnative species, as well as the overall effects of mulch on native plant communities following the 2013 Rim Fire in the central Sierra Nevada, California. Post-fire, the Burned Area Emergency Response (BAER) team prescribed rice straw mulch application on 1,627 ha of severely burned forests, where tree mortality was >95%. To examine the effects of mulch on vegetation characteristics, we monitored field plots in rice-mulched and unmulched high severity areas for the first two years post-fire, asking:

1. Did rice mulch affect nonnative species richness and/or cover, overall plant cover, cover by life-form (graminoid, forb, shrub or tree) or conifer regeneration density? Did this effect differ between the first and second year post-fire?
2. Where the rice mulch did have an effect, was the magnitude of the effect dependent on the amount of mulch cover or mulch depth that was applied in 2014?
3. What effect did rice mulch have on plant community species composition and abundance, and did this effect differ by year?

Methods

Study site

The 2013 Rim Fire burned 104,131 ha, making it the largest recorded wildfire in the Sierra Nevada, California. The fire burned through chaparral, oak woodlands, ponderosa pine, red fir and mixed conifer forests. Our sampling area was restricted to the Stanislaus National Forest portion of the fire, where rice mulch was applied immediately post-fire in the fall of 2013, using helicopters to drop bales on 1,627 ha across 23 areas (Figure 1). The rice mulch was applied at a rate of 3.4 Mg ha^{-1} (1 ton ac), except two units where the application rate was 2.2 and 1.1 Mg ha^{-1} as part of a separate study on soil erosion. Treatment areas were selected by land managers based on considerations of slope steepness, downstream values at risk and soil burn severity. Soil burn severity determinations are based on a combination of remotely-sensed Burned Area Reflectance Classification (BARC) maps and ground-truthing. BARC maps are created by using the Normalized Burn Ratio, a ratio of the reflectance from Bands 4 and 7 in the Landsat satellite (Parson *et al.* 2010). Our study sites ranged in elevation from 930 m to 1930 m and included only areas that were mixed conifer forest pre-fire. These forests 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.).
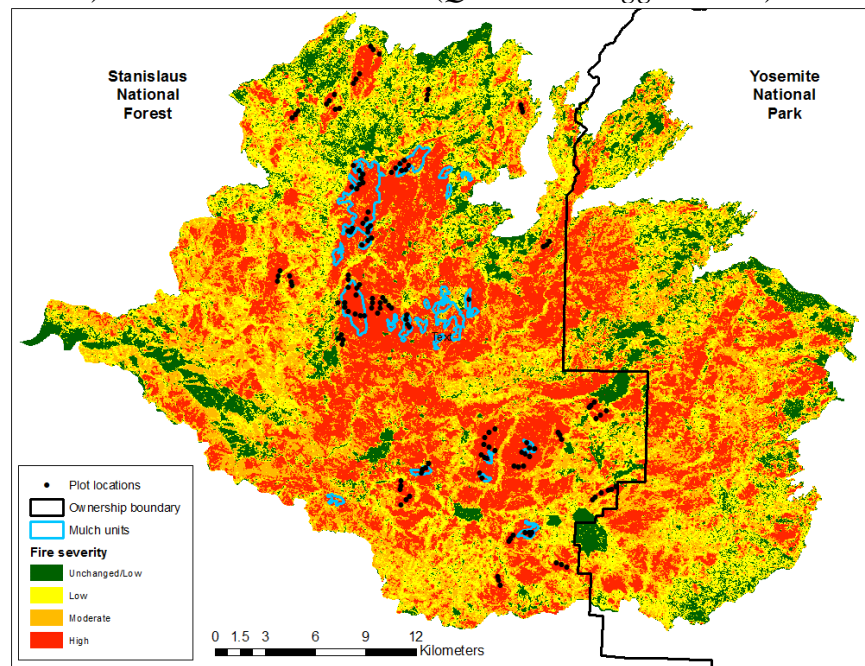

Figure 1. Vegetation fire severity map of the Rim Fire generated with severity class thresholds described in Miller and Thode (2007). Map includes plot locations and mulch treatment polygons.

In 2014, we selected 46 sites of 0.2 km^2 and within each of them 3-4 plots were randomly installed, totaling 134 vegetation plots: 52 in mulched and 82 in unmulched control areas (Figure 1). Thirty-five of these sites were co-located with a study focused on wildlife response to wildfire, which were selected based on known owl nest locations and limited to within 1km of existing road for access efficiency. We ensured that these wildlife-specific sites were also representative of our target population, which we defined as herbaceous plant communities that occur after severe, stand-replacing fire (>95% mortality) in mixed conifer forests. We confirmed that the sites co-located with owl nest locations were representative of the target population (mixed conifer that experienced >95% mortality from the fire) by assessing vegetation and burn severity variables in a GIS framework. Vegetation data was acquired from the USDA Forest Service (USDA Forest Service 2014) and burn severity was classified with the Relativized differenced Normalized Burn Ratio according to established thresholds (Miller and Thode 2007). The sites were then confirmed as representative in the field. An additional 11 sites (7 mulched and 4 unmulched) were randomly selected to increase sample size, using the same criteria for our target population and access via road. In 2015 we revisited 48 mulched plots (12 of these had been salvage logged after the 2014 measurements) and 49 unmulched plots (13 of these had been salvage logged after the 2014 measurements). All analyses were done on plots without salvage logging ($n_{mulched} = 36$, $n_{unmulched} = 36$), but we discuss some observed patterns based on all plots where appropriate.

Measurement
We measured understory characteristics using two perpendicular, 32.1 m transects to create an 809 m^2 (1/5th ac) plot. Along each transect, we estimated plant canopy cover using cover classes that were adapted from Daubenmire (1959) (<1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–95%, 96–100%) in ten 20x50 cm quadrats, for a total of 20 quadrats per plot (Daubenmire 1959). We recorded cover data by life-form, species and native status, including trees shorter than 1.37 m. Where appropriate, we also estimated mulch cover and measured mulch depth at each quadrat to the nearest millimeter. To characterize total species richness, we recorded all species occurring across the entire plot, identifying every plant to species according to the Jepson Manual of California (Baldwin *et al.* 2012). Where we did not have adequate plant parts to identify a plant to species, we identified it to the lowest possible taxonomic level, usually genus. Finally, we subsampled tree regeneration densities in a 60 m^2 circle using the Forest Service Region 5 post-fire regeneration protocol (Welch *et al.* 2016). We recorded distance to the nearest live tree of any species within 300m of the plot. Where none were visible, we recorded 300m as the minimum distance.

Statistical analyses
We used generalized linear mixed models (GLMMs) to assess the effects of rice mulch on univariate vegetation characteristics with the following distributions: total plant cover and cover by life-form (beta), richness (Poisson), exotic richness (negative binomial) and tree regeneration density by species (negative binomial). For all univariate variables, we created a base model that included known drivers of vegetation response: elevation, aspect and the year plots were measured (2014 or 2015). Because proximity to live trees is a known driver of conifer regeneration (Collins and Roller 2013; Welch *et al.* 2016), models for conifer seedlings additionally included distance from plot center to the nearest live tree. Site was also included as a random effect and because some plots were measured twice, plot was also included as a random

effect to account for repeated measures. We conducted initial tests with mulch as a categorical variable, year and their interaction; where there was an interaction, we subsequently tested all treatment contrasts. In addition, for variables where mulch had a significant effect, we then used conditional models on mulched plots only to test for linear and non-linear relationships with mulch cover, depth and their interaction as continuous variables. Non-linear relationships were modeled via inclusion of a squared term. We selected the best conditional model based on the delta Akaike Information Criterion (dAIC), which sets the model with the minimum AIC to zero and the remaining models are ranked by their difference in AIC. Because models with a dAIC < 2 are considered only weakly distinguishable, we examined all models with a dAIC < 2 for significant mulch cover or depth terms. dAIC and relevant p-values for all conditional models evaluated are available in the online supplementary material (Table S1). All univariate statistical analyses were performed using the glmmADMB package (Fournier *et al.* 2012; Skaug *et al.* 2013) in R.

To test for overall plant community composition and abundance differences by treatment we conducted perMANOVAs, a non-parametric permutation procedure, for both years in PC-ORD (McCune and Mefford 2011). Because this analysis requires equal sample sizes, we selected a subsample of the unmulched plots that best directly matched the mulched plots in terms of environmental setting characteristics (elevation and aspect) for both years. We used the Bray-Curtis dissimilarity measure with 9999 permutations, with $\alpha = 0.05$ (Anderson 2001). We then graphically examined community data in ordination space, using non-metric multidimensional scaling (NMDS). We conducted 500 runs with real data and 500 runs on randomizations from a random starting point, with an instability criterion of 0.00001. We allowed PC-ORD to choose the final number of axes based on relative stress levels and p-values < 0.05 (McCune and Grace 2002). The perMANOVAs and ordinations were based on a subset of species that occurred in at least 5% of the plots to reduce the influence of very uncommon species (McCune and Grace 2002). We also used PC-ORD to identify indicator species by treatment, using the same subset of matched plots that were used for perMANOVA tests. Species with an indicator value >25 and a p-value (based on a Monte Carlo test) of <0.05 were considered indicator species for that treatment (Dufrene and Legendre 1997). Finally, we calculated the Simpson Diversity Index for each plot in PC-ORD and then tested for differences by treatment and year using the GLMMs in R as described above. The Simpson Index represents the probability that two individuals drawn at random from a community are the same species, i.e. higher values of the index represent lower diversity (greater dominance by fewer species) (McCune and Grace 2002).

Results

In the summer of 2014, mulch cover on plots in mulched units averaged 53.9% (+/- 4.6%) but was highly variable across plots. Average mulch depth on plot ranged from 0.1 to 4.6 cm in 2014, averaging 1.1 cm across all plots (0.2 cm s.e.). Both remained highly variable but decreased substantially in 2015 (Figure 2).
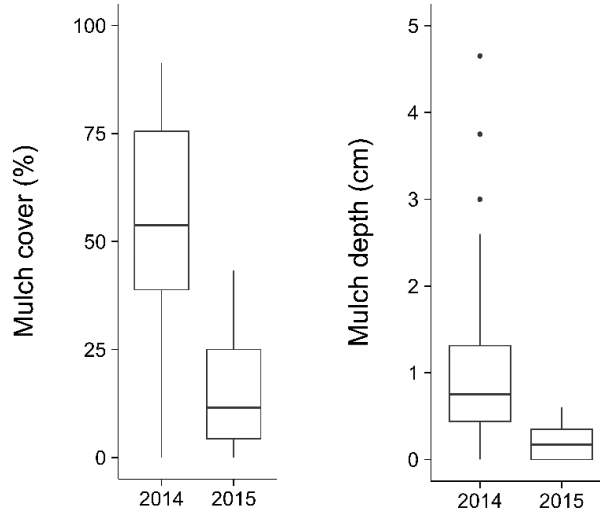
Figure 2. Mulch cover and mulch depth on mulched plots in both 2014 and 2015. The boxes define the 1st quartile (25th percentile) and 3rd quartile (75th percentile), and the line within the box defines the median. The whiskers extend to the highest value that is within 1.5 times the inter-quartile range and the dots are outliers that exceed this distance from the quartiles.

Plant cover

Mulch had no effect on total plant cover. There was significantly greater plant cover in the second growing season post-fire (p < 0.001; Figure 3), and these results held when partitioned by life-form. There was a significant interaction for nonnative forb cover (p = 0.018), and the treatment contrasts indicated a significant effect for mulch in both years (2014: p = 0.029; 2015 p = 0.008; Figure 3) where the magnitude of the effect was greater in 2015. Nonnative forb cover was higher in 2015 for both treatments (unmulched areas: p < 0.001; mulched areas: p = 0.034). Nonnative graminoid cover was variable but generally low (≤1%), due in part to graminoid stature, across both treatments in both years.
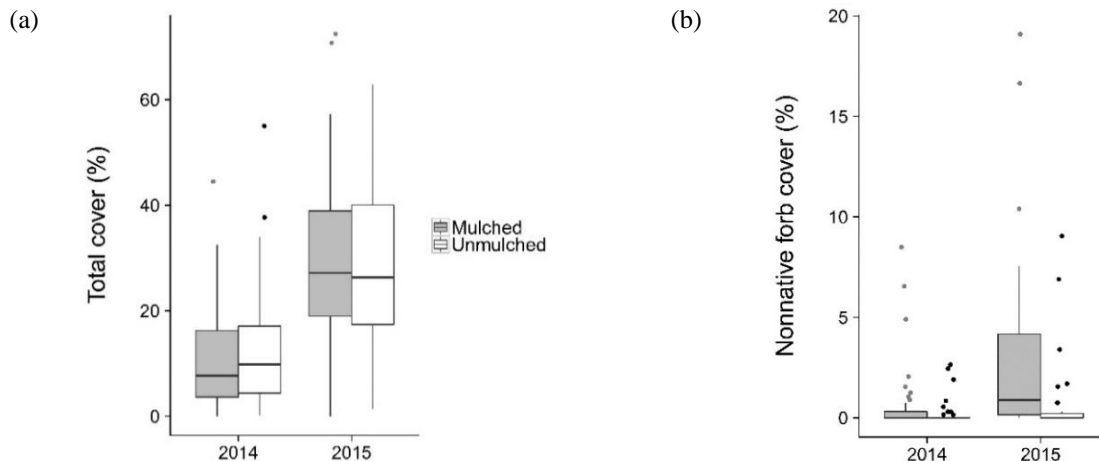
Figure 3. (a) Total plant cover and (b) nonnative forb cover by treatment and year (note differences in the y axes). The boxes define the 1st quartile (25th percentile) and 3rd quartile (75th percentile), and the line within the box defines the median. The whiskers extend to the highest value that is within 1.5 times the inter-quartile range and the dots are outliers that exceed this distance from the quartiles. For graph (b), the unmulched responses in particular are heavily zero-skewed, where only outliers are visible in 2014; note differences in the median and upper quartiles. Also note differences in y-axes.

9

Nonnative graminoid cover was not affected by treatment (p = 0.372) but was significantly higher in 2015 (p = 0.054). At least 70% of plots detected zero cover at the quadrat-level where the ocular estimates were made, but many had nonnative graminoid species observed at the plot-level census (presence/absence). Given this discrepancy and the low-cover stature of many nonnative graminoids, we also investigated the frequency nonnative graminoids observed. In 2014, at least one nonnative graminoid was observed on 77% of mulched plots (n=40) but only 40% (n=33) of unmulched plots. In 2015, nonnative graminoid frequency across plots was nearly equal (88.9% for mulched and 91.6% for unmulched plots).

Plant community composition

We observed a total of 331 species over the course of two post-fire growing seasons, of which 64 were nonnative (Table 1). Thirty-five of the nonnative species occurred across both treatments and four species occurred exclusively on unmulched plots (each occurring on ≤ 2 plots). The remaining 25 nonnative species occurred exclusively on mulched plots at a wide range of frequencies (Table 1). Of the nonnative species occurring on ≥ 10% of the mulched plots in 2014, *Brassica nigra* (L.) W.D.J. Koch (black mustard) increased in frequency by ~8% in 2015, *Persicaria maculosa* Gray (spotted ladysthumb)*, Erodium cicutarium* (L.) Aiton (redstem filaree), *Festuca perennis* (L.) Columbus & J.P. Sm. (Italian rye grass) and *Sorghum halapense* (L.) Pers. (Johnsongrass) increased by ≤ 5%; *Echinochloa crus-galli* (L.) P. Beauv. (barnyard grass) decreased by 11.1% (Table 1). When considering all plots measured, which includes those that were salvage logged between measurements, *E. crus-galli* had a lower decline (3.2%) and *P. maculosa*, *S. halepense* increased by <5%(data not shown). Two additional species with fidelity to mulched areas are not locally native, but native to California's Central Valley, where the rice mulch was grown: the grass *Leptochhloa fusca* (L.) Kunth var. *fascicularis* (Lam.) N. Snow (bearded sprangletop) and the forb *Symphiotrichium subulatum* (Michx.) G.L. Nesom var. *parviflorum* (Shinn.) S.D. Sundb (Eastern annual saltmarsh aster). *L. fusca* decreased in frequency in 2015 whereas *S. subulatum* increased ~5%. Despite being introduced from outside of our study area, these species were treated as natives in all subsequent analyses, as we used the native status established for the entire California Floristic Province in the Jepson Manual (Baldwin *et al.* 2012).

| | | Frequency | | | |
| | | Mulched | | Unmulched | |
Species by life-form and life cycle	*Cal-IPC Rating*	*2014*	*2015*	*2014*	*2015*
Forbs					
Annuals					
***Anthemis cotula* L.**		0.019	-	-	-
***Brassica nigra* (L.) W.D.J. Koch**	Moderate	0.134	0.222	-	-
Capsella bursa-pastoris (L.) Medik.		0.058	0.027	-	0.278
Cardamine hirsuta L.		0.019	-	0.03	-
Cerastium glomeratum Thuill.		0.038	0.083	-	0.111
Chenopodium album L.		-	0.056	0.01	0.056
***Dysphania botrys* (L.) Mosyakin & Clemants**		0.027		-	
Dysphania pumilio (R. Br.) Mosyakin & Clemants		-	-	-	0.028
***Erodium cicutarium* (L.) Aiton**	Low	0.135	0.167	-	-
Galium parisiense L.		-	0.194	-	0.056
Herniaria hirsuta L.		-	-	0.01	-

Lactuca salinga L.		0.135	0.278	0.03	0.139
Lactuca serriola L.		0.692	1.000	0.32	0.917
Logfia gallica (L.) Coss. & Germ.		-	0.028	-	0.111
Persicaria maculosa Gray		0.173	0.194	-	-
Polygonum aviculare L.		0.288	0.472	0.01	0.194
Pseudognaphalium luteoalbum (L.) Hillard & B.L. Burtt		0.135	0.222	0.038	0.250
Scleranthus annuus L. ssp. *annuus*		0.096	0.134	-	-
Senecio vulgaris L.		0.019	0.167		0.361
Sonchus asper (L.) Hill ssp. *asper*		0.519	0.889	0.03	0.528
Solanum nigrum L.		0.323	0.639	**-**	0.028
Spergularia bocconi (Scheele) Graebn.		0.038	0.027	0.03	-
Spergularia rubra (L.) J.S. Presl & C. Presl		0.017	0.139	-	-
Torilis arvensis (Huds.) Link	Moderate	0.077	0.361	0.05	0.028
Trifolium dubium Sibth.		0.019	0.278	-	0.361
Annuals or biennials					
Silene gallica L.		0.019	0.056	-	-
Sisymbrium altissimum L.		-	0.111	-	0.028
Tragopogon dubius Scop.		*0.077*	0.278	-	0.361
Biennials					
*Cirsium vulgare (Savi.) Ten.	Moderate	0.404	0.778	0.28	0.444
Verbascum blattaria L.		-	0.028	-	-
Verbascum thapsus L.	Low	0.019	0.167	-	0.028
Perennials					
*Convolvulus arvensis L.		0.481	0.472	0.63	0.417
Plantago lanceolata L.		0.115	0.139	0.01	0.278
Rumex acetosella L.	Moderate	0.115	0.167	0.07	0.028
Rumex crispus L.	Low	-	0.083	0.01	-
Silene latifolia Poir.		0.038	-	-	-
Taraxacum officinale F.H. Wigg.		0.019	0.028	-	0.028
Trifolium pratense L.		-	0.083	-	-
Grasses					
Annuals					
Aira caryophyllea L.		0.154	0.361	0.11	0.472
Avena barbata Pott ex Link	Moderate	0.019	0.056	-	-
Brachypodium distachyon (L.) P. Beauv.	Moderate	0.135	0.278	0.03	0.222
Briza minor L.		0.038	-	-	-
Bromus diandrus Roth	Moderate	0.077	0.083	-	-
Bromus hordeaceus L.	Low	0.115	-	0.03	0.056
Bromus madritensis ssp. *rubens* (L.) Husn.	High	0.038	-	-	-
Bromus sterilis L.		0.058	0.083	0.03	0.083
Bromus tectorum L.	High	0.038	0.444	0.15	0.472
Cynosurus echinatus L.	Moderate	0.019	0.25	0.03	0.222
Digitaria sanguinalis (L.) Scop.		0.077	0.028	-	-
Echinochloa crus-galli (L.) P. Beauv.		0.365	0.25	-	-
Festuca myuros L.	Moderate	0.154	0.583	0.34	0.556
Festuca perennis (L.) Columbus & J.P. Sm.	Moderate	0.115	0.167	-	-
Hordeum marinum ssp. gussoneanum (Parl.)	Moderate	0.096	0.139	-	0.028
Hordeum murinum L.	Moderate	0.096	0.028	-	0.028

Poa annua **L.**	0.038	-	-	-
Secale cereale **L.**	-	0.028	-	-
Triticum aestivum **L.**	0.038	-	-	-
Perennials				
Brachypodium pinnatum **(L.) P. Beauv.**	0.019	-	-	-
Phleum pretense L.	-	-	-	0.028
Polypogon australis Brongn.	-	0.056	-	0.028
Poa bulbosa L.	0.135	0.139	-	0.056
Poa compressa L.	0.366	0.389	0.25	0.194
***Sorghum halepense* (L.) Pers.**	0.135	0.167	-	-

Table 1. Frequency (number of plot occurrences) for all nonnative species. Ratings indicate potential impact severity to wildlands from the California Invasive Plant Council (Cal-IPC) (California Invasive Plant Council 2016), and species with asterisks (*) are rated noxious by the State of California. Species in bold occur only in mulched areas.

In 2014, three species with complete fidelity to mulched areas were indicator species for mulched areas, one of which is not native to the US (*E. crus-galli*) and two that are native to California's Central Valley (*S. subulatum* and *L. fusca*). The six other nonnative species that were indicator species for mulched areas were also present in unmulched areas, where they occurred at lower frequencies and abundance. Native indicator species for mulched areas included two shrubs, one tree and four forbs (Table 2). Only the native forb *Dichelostemma multiflorum* A. Heller (many flowered brodeia) was an indicator for unmulched areas. In 2015, nonnative indicators of mulched areas included *Lactuca serriola* L. (prickly lettuce) and *Sonchus asper* (L.) Hill (spiny sowthistle), species that were also observed at lower abundances in unmulched areas. *L. serriola* was observed on every mulched plot in 2015.

Mulched areas	2014	2015	Life-form
Nonnative			
Cirsium vulgare (Savi) Ten.	X		forb
*Echinochloa crus-galli (L.) P. Beauv.	X		graminoid
Lactuca serriola L.	X	X	forb
Polygonum aviculare L.	X		forb
Poa compressa L.	X		graminoid
Sonchus asper (L.) Hill	X	X	forb
Solanum nigrum L.	X		forb
Native			
Abies concolor (Gord. & Glend.) Lindl. ex Hildebr.	X		tree
Acmispon americanus (Nutt.) Rydb. var. *americanus*			
Ceanothus integerrimus Hook. & Arn.	X	X	shrub
Epilobium brachycarpum C. Presl.		X	forb
Erigeron canadensis L.	X		forb
*Leptochloa fusca var. *fascicularis* (Lam.) N. Snow	X		graminoid
Pseudognaphalium beneolens (Davidson) Anderb.	X		forb
Ribes roezlii Regel	X	X	shrub
*Symphyotrichum subulatum (Michx.) G. L. Nesom var. *parviflorum*	X		Forb
Viola lobata Benth.	X		forb

Native			
Carex species		X	forb
Chamaebatia foliolosa Benth.		X	forb
Dichelostemma multiflorum A. Heller	X		forb

Table 2. Indicator species for mulched and unmulched areas in 2014 and 2015. Asterisks indicate species exclusively observed in mulched areas.

Species richness had a significant interaction between year and mulch treatment (p = 0.0004). Subsequent contrast tests showed that mulch had a significant, positive effect (p = 0.0018) in 2014 but not in 2015 (p = 0.1187); richness was significantly higher overall in 2015 in both mulched and unmulched (p < 0.0001) areas (Fig. 4). The higher richness in mulched areas was driven primarily by nonnative species richness, which similarly had a significant interaction term (p <0.0001). Treatment contrasts indicated significantly higher nonnative species richness in mulched areas in both years (p < 0.0001) and higher nonnative richness in 2015 across mulched and unmulched areas (p < 0.0001) (Fig. 4). The best conditional model for nonnative richness was a non-linear relationship with mulch cover (p = 0.0201; Fig. 4). The addition of mulch depth and interactions between mulch depth and cover in the conditional candidate models did not improve model performance for nonnative richness. There was no difference in perennial richness between mulched and unmulched areas (p = 0.1859), but further investigation of the interaction for annual richness (p < 0.0001) indicated that mulched areas had significantly higher annual richness in 2014 (p < 0.0001) but not in 2015 (p = 0.1062); similar to overall richness, annual richness was higher in 2015 in both treatments (P < 0.0001 for both).
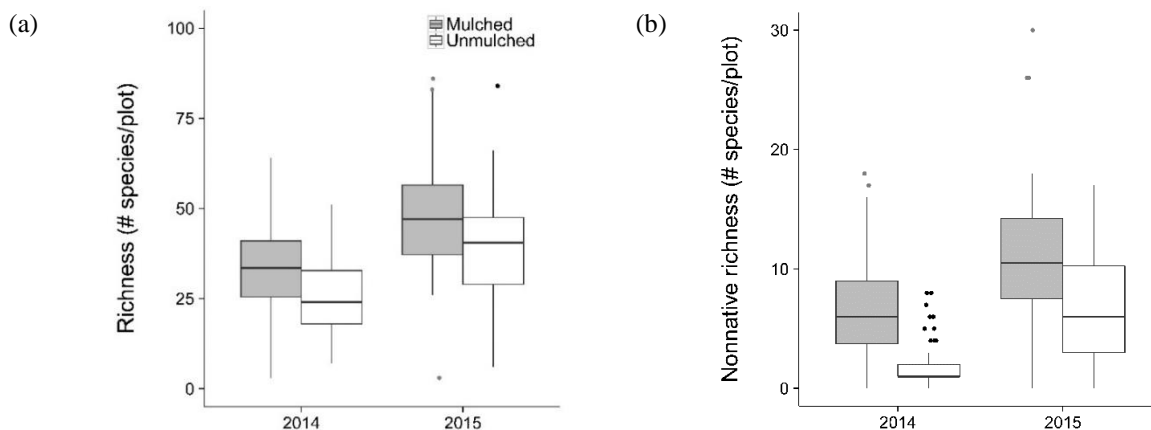
Figure 4. (a) Overall species richness, (b) nonnative richness by treatment and year. The boxes define the 1st quartile (25th percentile) and 3rd quartile (75th percentile), and the line within the box defines the median. The whiskers extend to the highest value that is within 1.5 times the inter-quartile range and the dots are outliers that exceed this distance from the quartiles. Note differences in y-axis.

Significant differences in plant communities were detected between mulched and unmulched areas in terms of species abundance in both 2014 and 2015 with perMANOVA tests (p = 0.0168, p = 0.0084, respectively). In contrast, the NMDS ordinations on abundance data did not show any clear separation (data not shown). There was a significant interaction between treatment and year for the Simpson's diversity index (p = 0.0292), for which subsequent treatment contrasts indicated significantly higher indices in mulched areas in 2015 (p = 0.0027)

versus no change through time for unmulched areas. In 2015, mulched areas had significantly higher indices over unmulched areas (p = 0.0004), but in 2014 there was no difference (p = 0.3090) (Fig. 5).
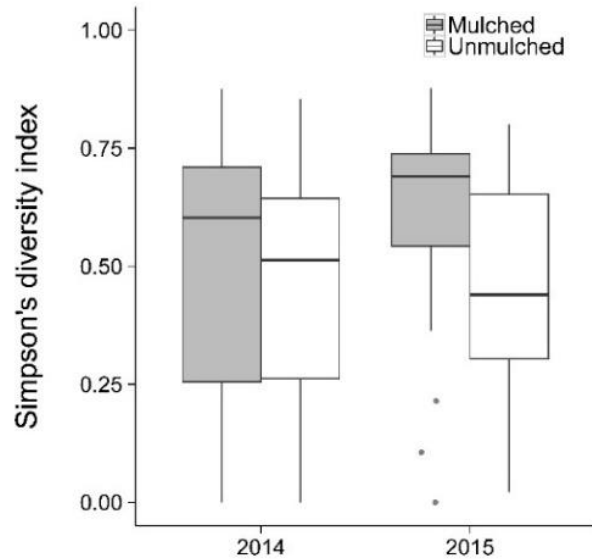
Figure 5. Simpson's Diversity Index by treatment and year. The boxes define the 1st quartile (25th percentile) and 3rd quartile (75th percentile), and the line within the box defines the median. The whiskers extend to the highest value that is within 1.5 times the inter-quartile range and the dots are outliers that exceed this distance from the quartiles.

Conifer regeneration
In general, conifer regeneration was highly variable, where most plots had no regeneration across either treatment in either year (Figure 6). For all conifer species together, regeneration was significantly less abundant in 2015 than in 2014 due to mortality of 2014 seedlings (p < 0.001; Figure 7). When considering only plots that were measured in both years, mean mortality rates for 2014 germinants were higher in mulched areas versus unmulched areas for the more shade-tolerant Douglas-fir and white fir, but were lower in mulched areas for the remaining species, particularly for ponderosa and sugar pine. However, the only significant difference in mortality rates was higher white fir percent mortality in mulched areas versus unmulched areas (p = 0.034, Figure 6). Combining surviving seedlings and new germinants for 2015, densities did not exceed 2014 values on mulched plots, and Douglas-fir and ponderosa pine only slightly exceeded 2014 densities on unmulched plots. For individual species, there was no effect of mulch or difference by year for the abundance of ponderosa pine, sugar pine, or incense-cedar (p-values are 0.937, 0.540, 0.756 respectively; Table S2). For Douglas-fir, there was a marginally significant interaction (p = 0.069); treatment contrasts indicated a marginally significant, positive effect in 2014 (p = 0.072) but no effect in 2015 (p = 0.280). The best conditional model for 2014 with dAIC included mulch depth, but this term was not significant (p = 0.404). In terms of differences by year, Douglas-fir regeneration was significantly higher in 2015 in unmulched plots (p = 0.005) but there was no difference for mulched plots (p = 0.225), suggesting there was no linear or non-linear relationship between Douglas-fir density and the amount of mulch cover or depth. There was a significant interaction between mulch treatments and year for white fir (p = 0.007),

14

but the only significant difference within treatment contrasts was the lower white fir abundance in 2015 for mulched plots ($p < 0.001$; Table S2). Summary data for regeneration density by species, treatment and year can be found in the online supplementary material (Table S2).

(a) 2014 (b) 2015
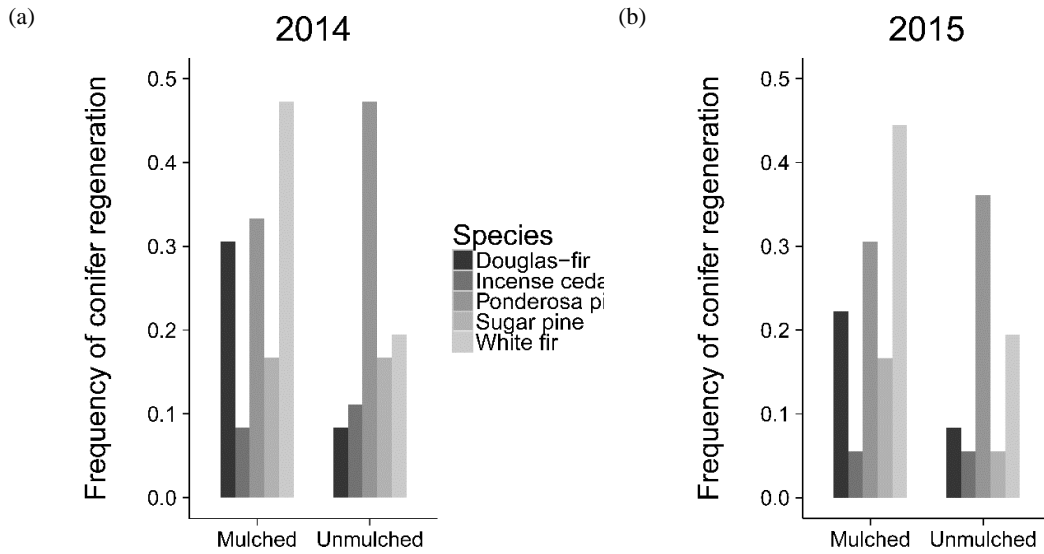
Figure 6. Frequency of conifer regeneration across plots by treatment and species for (a) 2014 and (b) 2015.
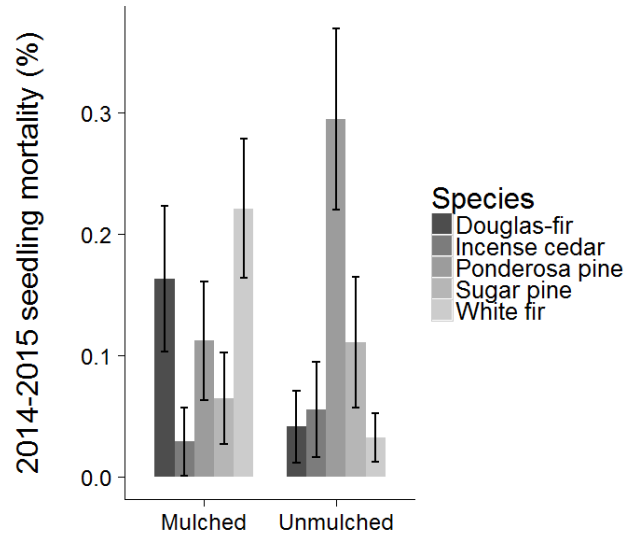
Figure 7. Mean seedling mortality rates with standard error by treatment and species. Percent mortality was calculated only for plots that were measured in both years ($n_{mulched} = 36$, $n_{unmulched} = 36$).

Discussion

Our results suggest that the increasing use of mulch for erosion control (Robichaud *et al.* 2014) may also increase the risk of unintended nonnative species introductions after wildfire. We detected significantly greater nonnative species richness and cover in mulched areas over unmulched areas, similar to other studies throughout the western US (Dodson and Peterson 2010;

Dodson and Root 2013; Morgan *et al.* 2014), including one specifically examining rice straw mulch (Kruse *et al.* 2004). These studies documented greater occurrence of nonnatives in mulched areas, but also detected the same nonnative species in unmulched areas. We similarly found greater frequency and cover of many nonnative species (e.g. *C vulgare*, *S. asper*, *L. serriola*) in mulched areas that also occurred in unmulched areas. However, this study is the first to document nonnative species that were completely exclusive to mulched areas, providing robust evidence for nonnative introductions via rice mulch. Of the 25 species found only in mulched areas, we acknowledge that many of the species with low frequency (1-2 plots) could have already been present and the fidelity to mulched areas could have occurred by chance. However, we find it highly unlikely that the 8 species that occurred on ≥10% of mulched plots occurred by chance, particularly since three are known associates in rice fields (*L. fusca, E. crus-galli, P. maculosa*) and two species are native to wet, marshy areas of California's Central Valley (*L. fusca* and *S. subulatum*), where the rice was grown. In addition to our study, certified weed-free rice mulch from a different supplier in a different county introduced many of the same species on the 2014 King Fire in northern California (Blake Engelhardt, Eldorado National Forest botanist, personal communication, 2015).

This is raising concern over the process for weed-free certification requirements, which do not actually guarantee that the straw bales are free of any nonnative species seed; rather, the standards only require that no federal or state-listed noxious species are observed in the supplier's agricultural fields by state inspectors (California Department of Food and Agriculture 2013). Our detection of *S. halapense*, which is listed as noxious by the State of California (California Department of Food and Agriculture 2016), in mulched areas suggests that the current certification process is not adequate. Moreover, this certification approach is inherently limited because state and federal noxious species lists tend to focus on species that are considered noxious in an agricultural setting, with less consideration for potential impacts to wildlands. In addition to *S. halapense*, we observed two species in mulched areas that are ranked as having high potential for impacts to wildlands by the California Invasive Plant Council (Cal-IPC), and 12 that were ranked as moderate (Table 1, California Invasive Plant Council 2016). Because they are not designated as noxious, these species could be present during certification inspections but the supplier would still be certified "weed-free."

More broadly, the introduction of these nonnative rice field associates in our sites violates the assumption that these species cannot establish in drier forested habitat, at least in the short-term. However, we acknowledge that our monitoring is limited to just two years post-fire, and further monitoring will be required to see if these species will persist in the long-term. These species may be ephemeral in upslope mixed conifer forest habitat, since many are adapted to wetter habitats (*E. crus-galli, P. maculosa, L. fusca*); however, they maybe more likely to persist in riparian areas. In addition to increases in *S. halapense* frequency for plots that were mulched and later salvaged, field crews observed generally higher densities of *S. halepense* in salvaged areas, particularly in skid trails. Further research is needed to verify this observation, but it would not be surprising that an additional disturbance could facilitate further proliferations of these introduced species, particularly species such as *S. halepense* that thrive in a variety of disturbed environments and can spread by both seed and rhizome fragments (Howard 2004). The introduction of this species should be of some concern because of its noxious status in agricultural settings (California Department of Food and Agriculture 2016), which may suggest the potential for problems in wildland settings. In addition, several species that were detected

only in mulched areas in 2014 were also detected on at least one unmulched plot in 2015 (Table 1), suggesting the potential for spread outside of treatment areas.

One of the greatest concerns with nonnative species introductions is the potential for a species to promote positive feedbacks that favor itself over other native species, eventually leading to state changes and/or disturbance regime changes (D'Antonio and Vitousek 1992; Suding *et al.* 2004). Of the species observed, *Bromus tectorum* and *Bromus madritensis* ssp. *rubens* have been linked to altered fire regimes (D'Antonio and Vitousek 1992) and both are ranked as potentially having high impacts to wildlands by Cal-IPC (California Invasive Plant Council 2016). *B. madritensis* occurred on only 1 mulched plot and *B. tectorum* occurred relatively equally across treatments, with dramatic increases in *B. tectorum* frequency across both treatments in 2015 (Table 1). Of the remaining species, our understanding of the potential impacts at their current levels of invasion is somewhat hindered by a relative lack of research on invasions in mountainous regions (Pauchard *et al.* 2009). If the remaining species do not cause state changes, some of the nonnative response could be ephemeral and decline with increasing canopy closure by shrubs or trees in the future, since most are shade-intolerant (Martin *et al.* 2009; Bohlman *et al.* 2016). Even in this case, there could be longer-term impacts if these species are prevalent enough to alter seedbank dynamics, allowing for propagule pressure build-up that could result in a stronger response after another disturbance (Lockwood *et al.* 2005). Furthermore, temporary displacement of native species could have cascading effects on other trophic levels.

We were encouraged that there were no detectable differences in overall plant cover by treatment. Our results are in contrast to Dodson and Root (2010), who detected a positive relationship between mulch cover and total plant cover; however, we did not test continuous mulch cover because mulch as a categorical variable was not significant in the full model. The differences between these results may be partly due to our inclusion of plots explicitly chosen to be in control areas rather than relying on variation in mulch cover within mulched areas to serve as a baseline (Dodson and Peterson 2010). We were further encouraged that conifers were generally unaffected by mulch, with the exception of a marginally significant, positive mulch effect on Douglas-fir densities. We hypothesize this effect is driven in part by increased soil moisture retention, yet we would have expected this same effect on at least some of the other species as well. Investigation of mulch effects on these species on other fires is warranted. More broadly, our finding of no effect to a marginal, but positive, effect on conifer seedlings is similar to Dodson and Peterson (2010), who reported a positive effect of mulch cover <25% on lodgepole pine, with no effect at levels >25% in north-central Washington, USA. However, this finding is in contrast to Kruse *et al.* (2004) who found a negative effect on conifer regeneration in forests that were more similar to ours, dominated by Douglas-fir, red and white fir pre-fire. This difference in response may be because Kruse *et al.* (2004) examined the relationship between mulch and conifers at the quadrat-scale, whereas we examined conifer occurrence at the plot scale. It is possible that where we had deep mulch, we did not have conifers either, but that there is enough variability in mulch depth at our plot scale for some regeneration to occur.

More generally, where mulch application did have an effect in at least one year (nonnative forb cover, richness, nonnative richness, annual richness, Douglas-fir density), we did not detect any relationship with mulch depth in conditional tests, and relationships with mulch cover were generally weak. Despite the weak signal, the nonlinear relationships between mulch cover and richness/nonnative richness are interesting, because Dodson and Peterson (2010) also observed weak nonlinear relationships, with a similar peak in response around 60% cover.

Despite the weak signal, the nonlinear response may reflect a meaningful trend given the similarity between studies. In our study, the lack of effect for mulch depth and relatively weak effects for mulch cover on nonnative richness indicates that the presence of any mulch may ultimately be more important than the amount of mulch applied.

We found our results for plant community composition and abundance by species somewhat more difficult to interpret. Because of significant differences between treatments with the perMANOVA test and Simpson's Diversity Index, the lack of any visual separation observed with NMDS ordinations was surprising. We interpret this to mean that differences may be significant but not very large. Higher Simpson's Indices in mulched areas indicate a less even community that is dominated by a few species, which is likely driven by the greater nonnative response on mulched sites. Similar to the concerns raised above about nonnative species, even if this homogenization is ephemeral with canopy closure, it could have cascading effects on other trophic levels and alter seedbank dynamics.

Because mulch is currently considered the most efficacious treatment for post-fire erosion control (Robichaud *et al.* 2010b; Robichaud, Lewis, *et al.* 2013; Robichaud, Wagenbrenner, *et al.* 2013; Robichaud, Jordan, *et al.* 2013), the potential introduction of nonnative species and homogenization of plant communities presents a trade-off for managers. We believe that stricter certification requirements or sterilization of the straw via radiation or heat treatments could alleviate this problem. Until this happens, Burned Area Emergency Rehabilitation (BAER) prescriptions for post-fire rice mulch treatments should also consider including plans and funding for nonnative plant monitoring and eradication. This may be difficult to implement, considering that the treatment is already more costly than others (Robichaud *et al.* 2014); however, given the potential for unintended consequences, such mitigations will be important for future post-fire rehabilitation efforts.

Considered more broadly, another way to reduce the potentially adverse effects of straw mulch or other rehabilitation treatments (Beschta *et al.* 2004) would be to reduce the need to apply them to begin with. Much of the forest that burned in the Rim Fire had dramatically changed in the last century as a result of fire exclusion and harvesting (Collins *et al.* 2011, 2015), making them much more vulnerable to high severity fire (Lydersen *et al.* 2014). Fire hazard reduction and forest restoration treatments that reduce tree densities and surface fuels are very effective at reducing the intensity of wildfires (Fulé *et al.* 2012), suggesting that by mitigating fire severity, forest restoration treatments could reduce the need for rehabilitation. To that end, management strategies that enhance forest resilience and decrease the size of high severity forest patches should remain an overarching management goal (Stephens *et al.* 2012, 2016).

Works Cited

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral ecology* 26, 32–46. doi:10.1111/j.1442-9993.2001.01070.pp.x.

Baldwin BG, Goldman DH, Keil DJ, Patterson R, Rosatti TJ, Wilken DH (Eds) (2012) 'The Jepson Manual Vascular Plants of California, Second Edition.' (University of California Press.: Berkeley, CA.)

Beschta R, Rhodes J, Kauffman J, Griesswell R, Minshall G, Karr J, Perry D, Hauer E, Frissell C (2004) Postfire management on forested public lands of the western United States. *Conservation Biology* 18, 957–967. doi:10.1111/j.1523-1739.2004.00495.x.

Beyers JL (2004) Postfire Seeding for Erosion Control: Effectiveness and Impacts on Native Plant Communities. *Conservation Biology* 18, 947–956. doi:10.1111/j.1523-1739.2004.00523.x.

Bohlman GN, North M, Safford HD (2016) Shrub removal in reforested post-fire areas increases native plant species richness. *Forest Ecology and Management* 374, 195–210. doi:10.1016/j.foreco.2016.05.008.

California Department of Food and Agriculture (2013) California voluntary weed-free forage inspection protocol. http://phpps.cdfa.ca.gov/PE/interiorexclusion/CPTM/pdf/CAProceduresforWFF.pdf.

California Department of Food and Agriculture (2016) California Noxious Weeds. https://www.cdfa.ca.gov/plant/ipc/encycloweedia/weedinfo/winfo_table-sciname.html.

California Invasive Plant Council (2016) California Invasive Plant Inventory Database. http://www.cal-ipc.org. Accessed: 10/1/2016.

Collins BM, Everett RG, Stephens SL (2011) Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere* 2, 51. doi:10.1890/ES11-00026.1.

Collins BM, Lydersen JM, Everett RG, Fry DL, Stephens SL (2015) Novel characterization of landscape-level variability in historical vegetation structure. *Ecological Applications* 25, 1167–1174. doi:10.1890/14-1797.1.

Collins BM, Roller GB (2013) Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. *Landscape Ecology* 28, 1801-1813 doi:10.1007/s10980-013-9923-8.

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual review of ecology and systematics* 63–87. doi:10.1146/annurev.es.23.110192.000431.

Daubenmire RF (1959) Canopy coverage method of vegetation analysis. *Northwest Science* 33, 43–64.

Dodson EK, Peterson DW (2010) Mulching effects on vegetation recovery following high severity wildfire in north-central Washington State, USA. *Forest Ecology and Management* 260, 1816–1823. doi:10.1016/j.foreco.2010.08.026.

Dodson EK, Peterson DW, Harrod RJ (2010) Impacts of erosion control treatments on native vegetation recovery after severe wildfire in the Eastern Cascades, USA. *International Journal of Wildland Fire* 19, 490–499. doi:10.1016/j.foreco.2010.08.026.

Dufrene M, Legendre P (1997) Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345–366. doi:10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.

Fournier D, Skaug H, Ancheta J, Ianelli J, Magnusson A, Maunder M, Nielsen A, Sibert J (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27, 233–249. doi:10.1080/10556788.2011.597854.

Fulé PZ, Crouse JE, Roccaforte JP, Kalies EL (2012) Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management* 269, 68–81. doi:10.1016/j.foreco.2011.12.025.

Groen AH, Woods SW (2008) Effectiveness of aerial seeding and straw mulch for reducing post-wildfire erosion, north-western Montana, USA. *International Journal of Wildland Fire* 17, 559–571. doi:10.1071/WF07062.

Howard JL (2004) Sorghum halepense. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, http://www.fs.fed.us/database/feis/.

Kruse R, Bend E, Bierzychudek P (2004) Native plant regeneration and introduction of non-natives following post-fire rehabilitation with straw mulch and barley seeding. *Forest Ecology and Management* 196, 299–310. doi:10.1016/j.foreco.2004.03.022.

Kuenzi AM, Fulé PZ, Sieg CH (2008) Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. *Forest Ecology and Management* 255, 855–865. doi:10.1016/j.foreco.2007.10.001.

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution* 20, 223–228. doi:10.1016/j.tree.2005.02.004.

Lydersen JM, North MP, Collins BM (2014) Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. *Forest Ecology and Management* 328, 326–334. doi:10.1016/j.foreco.2014.06.005.

Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and the Environment* 7, 142–149. doi:10.1890/070096.

McCune B, Grace JB (2002) 'Analysis of ecological communities.' (MjMSoftware Design: Gleneden Beach, OR, US.)

McCune B, Mefford MJ (2011) 'PC-ORD. Multivariate Analysis of Ecological Data.' (MjM Software: Gleneden Beach, OR, U.S.A.)

Miller JD, Safford HD, Crimmins M, Thode AE (2009) Quantitative Evidence for Increasing Forest Fire Severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12, 16–32. doi:10.1007/s10021-008-9201-9.

Miller JD, Thode AE (2007) Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sensing of the Environment* 109, 66–80. doi:10.1016/j.rse.2006.12.006.

Moles AT, Flores-Moreno H, Bonser SP, Warton DI, Helm A, Warman L, Eldridge DJ, Jurado E, Hemmings FA, Reich PB, Cavender-Bares J, Seabloom EW, Mayfield MM, Sheil D, Djietror JC, Peri PL, Enrico L, Cabido MR, Setterfield SA, Lehmann CER, Thomson FJ (2012) Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology* 100, 116–127. doi:10.1111/j.1365-2745.2011.01915.x.

Morgan P, Moy M, Droske CA, Lentile LB, Lewis SA, Robichaud PR, Hudak AT (2014) Vegetation Response after Post-Fire Mulching and Native Grass Seeding. *Fire Ecology* 10, 49–62. doi:10.4996/fireecology.1003049.

Parson A, Robichaud PR, Lewis SA, Napper C, Clark JT (2010) Field guide for mapping post-fire soil burn severity. http://www.treesearch.fs.fed.us/pubs/36236.

Parsons DJ, DeBenedetti SH (1979) Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management* 2, 21–33. doi:10.1016/0378-1127(79)90034-3.

Pauchard A, Kueffer C, Dietz H, Daehler CC, Alexander J, Edwards PJ, Arévalo JR, Cavieres LA, Guisan A, Haider S, Jakobs G, McDougall K, Millar CI, Naylor BJ, Parks CG, Rew LJ, Seipel T (2009) Ain't no mountain high enough: plant invasions reaching new elevations. *Frontiers in Ecology and the Environment* 7, 479–486. doi:10.1890/080072.

Peppin D, Fulé PZ, Sieg CH, Beyers JL, Hunter ME (2010) Post-wildfire seeding in forests of the western United States: An evidence-based review. *Forest Ecology and Management* 260, 573–586. doi:10.1016/j.foreco.2010.06.004.

Rew LJ, Johnson MP (2010) Reviewing the Role of Wildfire on the Occurrence and Spread of Invasive Plant Species in Wild land Areas of the Intermountain Western United States. *Invasive Plant Science and Management* 3, 347–364. doi:10.1614/IPSM-08-107.1.

Robichaud PR, Ashmun LE, Sims BD; (2010a) 'Post-fire treatment effectiveness for hillslope stabilization.' (U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO) http://www.treesearch.fs.fed.us/pubs/35691.

Robichaud PR, Ashmun LE, Sims BD; (2010b) 'Post-fire treatment effectiveness for hillslope stabilization.' http://www.treesearch.fs.fed.us/pubs/35691.

Robichaud PR, Beyers JL, Neary DG; (2000) 'Evaluating the effectiveness of postfire rehabilitation treatments.' http://www.treesearch.fs.fed.us/pubs/4571.

Robichaud PR, Jordan P, Lewis SA, Ashmun LE, Covert SA, Brown RE (2013) Evaluating the effectiveness of wood shred and agricultural straw mulches as a treatment to reduce post-wildfire hillslope erosion in southern British Columbia, Canada. *Geomorphology* 197, 21–33. doi:10.1016/j.geomorph.2013.04.024.

Robichaud PR, Lewis SA, Wagenbrenner JW, Ashmun LE, Brown RE; (2013) Post-fire mulching for runoff and erosion mitigation; Part I: Effectiveness at reducing hillslope erosion rates. *Catena* 105, 75–92. doi:10.1016/j.*Catena*.2012.11.015.

Robichaud PR, Rhee H, Lewis SA (2014) A synthesis of post-fire Burned Area Reports from 1972 to 2009 for western US Forest Service lands: trends in wildfire characteristics and post-fire stabilisation treatments and expenditures. *International Journal of Wildland Fire* 23, 929–944. doi:10.1071/WF13192.

Robichaud PR, Wagenbrenner JW, Lewis SA, Ashmun LE, Brown RE, Wohlgemuth PM; (2013) Post-fire mulching for runoff and erosion mitigation; Part II: Effectiveness in reducing runoff and sediment yields from small catchments. *Catena* 105, 93–111. doi:10.1016/j.catena2012.11.016.

Skaug H, Fournier D, Nielsen A, Magnusson, A, Bolker B (2013) 'Generalized Linear Mixed Models using AD Model Builder.' (R package version 0.7.5)

Stephens SL, Collins BM, Biber E, Fulé PZ (2016) U.S. federal fire and forest policy: emphasizing resilience in dry forests. *Ecosphere* 7, e01584. doi:10.1002/ecs2.1584.

Stephens SL, McIver JD, Boerner REJ, Fettig CJ, Fontaine JB, Hartsough BR, Kennedy PL, Schwilk DW (2012) The Effects of Forest Fuel-Reduction Treatments in the United States. *BioScience* 62, 549–560. doi:10.1525/bio.2012.62.6.6.

Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* 19, 46–53. doi:10.1016/j.tree.2003.10.005.

Sutherland S (2004) What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologia* 141, 24–39. doi:10.1007/s00442-004-1628-x.

USDA Forest Service (2014) Classification and Assessment with LANDSAT of Visible Ecological Groupings (CALVEG). http://www.fs.usda.gov/detail/r5/landmanagement/resourcemanagement/?cid=stelprdb5347192. Accessed: 3/1/2014.

USDA Forest Service (2015) Post-fire Treatment Effectiveness for Hillslope Stabilization. http://forest.moscowfsl.wsu.edu/BAERTOOLS/HillslopeTrt/?page=Mulch. Accessed: 10/1/2014.

Welch KR, Safford HD, Young TP (2016) Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. *Ecosphere* 7, e01609. doi:10.1002/ecs2.1609.

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940–943. doi:10.1126/science.1128834.

Wright BR, Tinker DB (2012) Canada thistle (Cirsium arvense (L.) Scop.) dynamics in young, postfire forests in Yellowstone National Park, Northwestern Wyoming. Plant Ecology 213, 613–624. doi:10.1007/s11258-012-0026-4.

CHAPTER 3: FROM THE STAND-SCALE TO THE LANDSCAPE-SCALE: PREDICTING THE SPATIAL PATTERNS OF FOREST REGENERATION AFTER DISTURBANCE

Abstract

Shifting disturbance regimes can have cascading effects on many ecosystems processes. This is particularly true when the scale of the disturbance no longer matches the regeneration strategy of the dominant species. In the yellow pine and mixed conifer forests of California, over a century of fire exclusion and the warming climate are increasing the incidence and contiguous area of stand-replacing wildfire, which is altering regeneration dynamics by dramatically increasing the distance from live tree seed sources. This has raised concerns about limitations in natural reforestation and the potential for conversion to shrub-dominated ecosystems, which in turn has implications for shifts in wildlife habitat, carbon storage and timber management. We used a California region-wide dataset with 1,848 plots across 24 wildfires in yellow pine and mixed conifer forests to build a spatially-explicit habitat suitability model for forecasting postfire forest regeneration. To model the effect of seed availability, the critical initial biological filter for regeneration, we used a novel approach to predicting spatial patterns of seed availability by estimating annual seed production from existing basal area maps. The probability of observing any conifer was highly dependent on 30-year average annual precipitation and seed availability. We then used this model to predict regeneration probabilities across the entire extent of a "new" fire (the 2014 King Fire), which highlights the spatial variability inherent in postfire regeneration patterns. Forecasting postfire regeneration patterns spatially can help anticipate shifts in ecosystem properties, supporting researchers interested in investigating questions surrounding alternative stable states, and the interaction of altered disturbance regimes and the changing climate. This work can also support land managers by providing a tool that can help inform postfire management planning.

Introduction

The spatial pattern of an ecological disturbance can have significant consequences for many ecological processes, including vegetation regeneration, wildlife habitat, nutrient cycling and susceptibility to future disturbance (Turner 1989). In forested ecosystems that are shaped by wildfire, the spatial pattern of fire severity, or the amount of tree mortality in a given area, can shape postfire vegetation regeneration patterns. In turn, these patterns shape longer-term demographic processes and community trajectories (Turner et al. 1997). Spatial patterns of severity are particularly important in forests where the foundation species lack serotiny, long-lived soil seed banks, or sprouting ability, because regeneration patterns will be dependent on the spatial configuration of live, remnant individuals to provide a seed source. (Haire and McGarigal 2010, Crotteau et al. 2013, Collins and Roller 2013, Dodson and Root 2013, Harvey et al. 2016, Donato et al. 2016, Welch et al. 2016).

Understanding the relationship between the spatial patterns of fire severity and postfire regeneration processes across the landscape is critical in the face of changing fire regimes. Shifts in the spatial patterns of severity could have significant effects on postfire forest regeneration if the scale and severity of the disturbance no longer matches the regeneration traits of the dominant species (Stevens et al. 2017, Collins et al. 2017). A prominent example of this potential

disconnect is in many of the semi-arid conifer forests of the western US, where the historic fire regime created a heterogeneous landscape that was characterized by frequent, low to moderate severity fires with smaller patches of high severity (where all or nearly all trees are killed) (Parsons and DeBenedetti 1979, Stephens and Collins 2004, Collins et al. 2009, Collins and Stephens 2010, Perry et al. 2011). This heterogeneity provided a diversity of habitats across space and also likely enabled the persistence of the foundation conifer species through time by generally limiting the distance between live tree seed sources after disturbance. Over the last century, fire frequency has been greatly reduced in western semi-arid conifer forests as a result of fire exclusion policies (Stephens and Ruth 2005, Sugihara et al. 2006). The lack of fire, together with high-grade logging of large trees in many areas, has led to increases in fuels, forest density, and the component of fire-intolerant species (Safford and Stevens 2017). As a result, modern fires tend to burn through a more homogeneous forest with a more continuous fuel bed than under pre-settlement conditions. In concert with ongoing climate warming and increasing growing-season water deficits, these conditions have led to more severe fires with increased high severity patch sizes in some forested areas (Miller et al. 2012, Miller and Safford 2012); today, high severity patches of thousands of hectares are not uncommon. By increasing the distance to live trees, this increase in high severity patch size may result in limited reforestation and potential shifts to montane chaparral, which can be maintained by positive feedbacks with fire (Coppoletta et al. 2016, Tepley et al. 2017). A better understanding of the relationship between severity patterns and regeneration processes in these ecosystems can help anticipate potential shifts in vegetation type and structure, and how such shifts may affect ecosystem services such as carbon storage, wildlife habitat, and water yield (Turner et al. 2013).

In addition to seed source proximity, postfire conifer establishment is also modified by other biotic and abiotic drivers that vary spatially across the landscape. Other biotic drivers of conifer tree regeneration patterns include competition (Dodson and Root 2013), facilitation (Keyes et al. 2009), herbivory (Vander Wall 2008) and local stand structure and species traits (Dobrowski et al. 2015). Broader-scale abiotic drivers include topography and climate, where climate parameters for the regeneration niche are distinct from those occupied by mature trees (Dobrowski et al. 2015); finer-scale variations in abiotic conditions, including microclimates, are also critical for conifer establishment (Gray et al. 2005, Puhlick et al. 2012, Dobrowski et al. 2015). Understanding the relative importance of remnant seed tree spatial patterns to these other drivers can bolster our understanding of community assembly after landscape-scale disturbance. Moreover, it can improve spatially-explicit predictions of postfire conifer regeneration that can be used to support land management planning.

To better understand the relationship between spatial patterns of burn severity and regeneration processes in non-serotinous conifer forests, we used data from 1,848 plots in 24 wildfires that burned in mixed conifer and yellow pine forests throughout California to build a habitat suitability model for postfire conifer regeneration. Recent work using data from 14 of these fires detected proximity to seed sources as a primary driver (Welch et al. 2016); here we build on that work by more closely examining the importance of spatial patterns relative to other drivers of postfire conifer regeneration, with the goal of scaling these findings from the plot scale to the landscape scale so that they can be used in a forecasting framework. This approach produces prediction maps that can be generated immediately postfire to help land managers prioritize areas for planting or other postfire treatments, depending on management goals. These maps can also inform questions about ecological change after disturbance under altered fire regimes.

Our ability to effectively scale plot data to an entire fire event or across a landscape is necessarily limited to the data that are available at those scales. Data on broad-scale abiotic drivers, such as topography and climate, are widely available; however, finer-scale biotic drivers such as competing vegetation, herbivory, microclimates and distance to individual seed trees generally are not. Several authors have used Euclidean distance to nearest, "lesser burned" edge to represent distance to seed sources in high severity areas (where lesser burned edge refers to the distance to patches of lower burn severity where at least some seed trees survived) (Bonnet et al. 2005, Harvey et al. 2016, Kemp et al. 2016). However, this approach does not fully incorporate the importance of spatial pattern, because it ignores high severity patch size and configuration. It is possible to have two sampling locations with equal Euclidean distance to lesser burned edge, but that are situated in otherwise very different patch sizes, patch shapes, and topographic position relative to the prevailing wind, which in turn would influence the total seed availability at each plot. Our goal was to improve on this approach using techniques to better model this important, initial biological filter by estimating neighborhood effects.

To examine the relative importance of spatial pattern and to predict the spatial pattern of postfire conifer regeneration after future fires, we asked:

1) What environmental variables are most important for forecasting postfire conifer regeneration?
2) How can we best scale plot-level relationships to the scale of the landscape with seed availability proxies?
3) How do forecast models with seed availability proxies compare with field-based models that include variables for competition and individual seed sources?

Methods

Study sites

We used a region-wide monitoring dataset collected by the US Forest Service (USFS) Region 5 Ecology Program and partners at the University of California-Davis (Welch et al. 2016) and Humboldt State University (DeSiervo et al. 2015). A total of 1,848 plots were installed in 24 wildfires throughout California (Figure 1) that burned between 1999 and 2013. Plots were measured between one and twelve years postfire, with most measured five years after fire (Table 1). Plots were installed between 1,000m and 2,500m in elevation, across a range of forest types that were conifer-dominated pre-fire, with an emphasis on forest types that included a substantial component of the following species' of interest: 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) and coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*). Less than 10% percent of plots were located in areas with notable components of red fir (*Abies magnifica* A. Murray bis), lodgepole pine (*Pinus contorta* Louden ssp. *murrayana* [Grev. & Balf.] Critchf.), western white pine (*Pinus monticola* Douglas) or knobcone pine (*Pinus attenuata* Lemm.). The forests we studied fall primarily into the general "yellow pine-mixed conifer" category described by Safford and Stevens (2017). For each fire, plots were located at the vertices of a 200 m grid overlaid across the severity map of the fire in ArcMap. Plots were primarily located in high (40% of plots) and moderate severity (29% of plots) areas, with the remaining plots distributed in low severity (20%) and unburned (10%) areas (severity classes were defined using established thresholds in Miller and Thode (2007), described below). One

exception to this design was the 2013 Rim Fire, where the same field data collection protocol was used, but the methods for randomizing the plot locations differed. There plots were co-located with a wildlife study and study on mulch effects on vegetation (Shive et al. 2017); only unmulched control plots were included in this analysis. For all fires, areas with intensive postfire management, such as salvage logging and planting, were excluded from analysis. We did not attempt to control for pre-fire treatments.
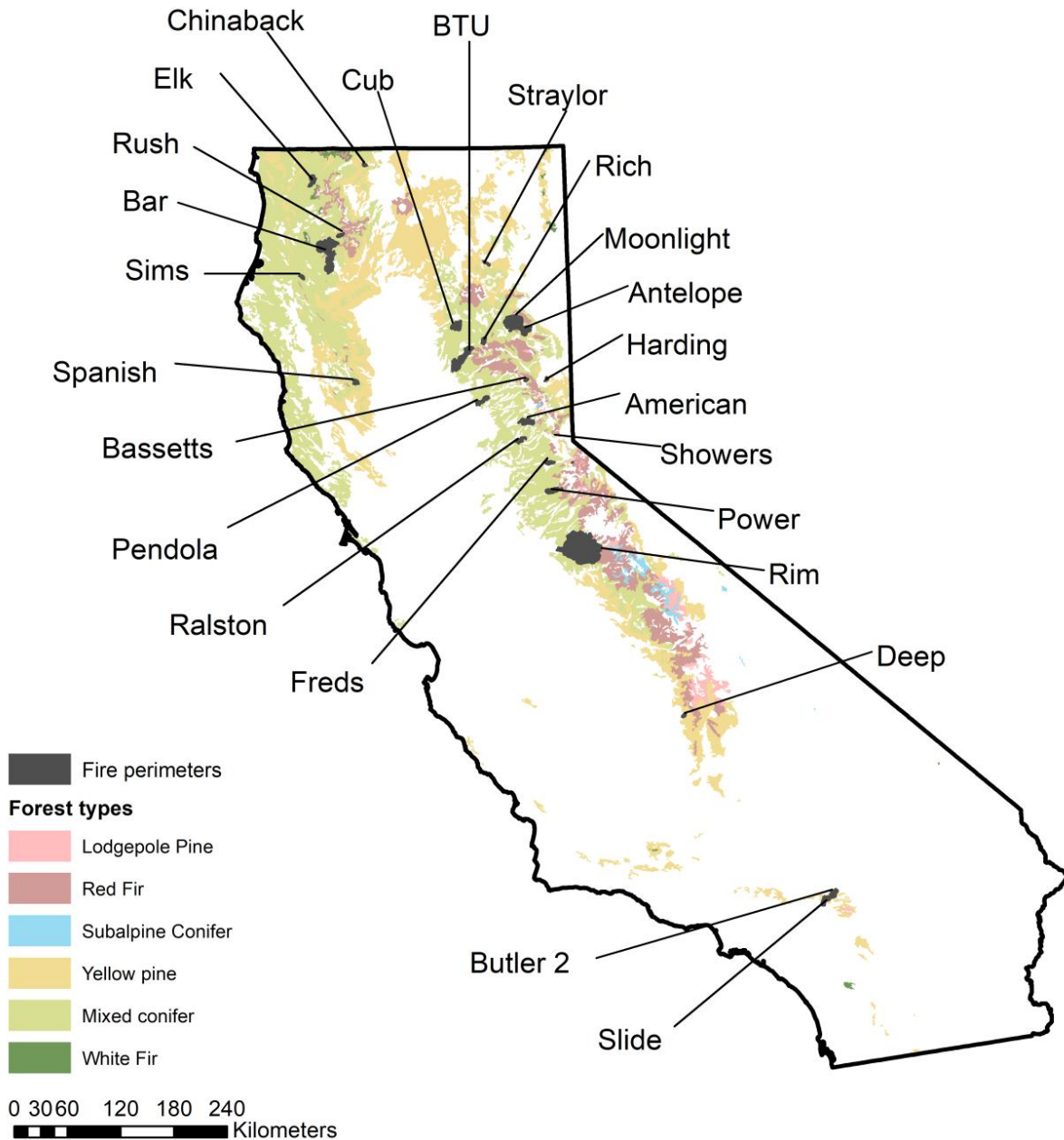

Figure 1. Locations of all fires where plots were measured across the state of California. Forest types were derived from California Wildlife Habitat Relationship (WHR) Types, acquired from the USFS Pacific Southwest Region Geospatial Data website (https://www.fs.usda.gov/main/r5/landmanagement/gis). Fire perimeters were buffered by 2km to increase visibility in the figure.

Fire name	Fire Year	# Years Postfire	National Forest	Size (ha)	# plots
American River	2008	5	Tahoe	8,480	78
Antelope	2007	5	Plumas	9,351	91
Bar	2006	5	Shasta-Trinity, Klamath	40,858	84
Bassets	2006	5	Tahoe	939	79
BTU Lightening	2008	5	Plumas	21,340	95
Butler 2	2007	5	San Bernardino	5,980	56
Chinaback Complex	2007	5	Klamath	1,280	72
Cub Complex	2008	5	Lassen	8,406	118
Deep	2004	5	Sequoia	1,364	23
Elk Complex	2007	5	Klamath	5,747	49
Freds	2004	5,7,8	Eldorado	3,298	44,6,6
Harding	2005	5	Tahoe	954	73
Moonlight	2007	5	Plumas	26,595	118
Pendola	1999	11,12	Tahoe	4,752	33,47
Power	2004	5	Eldorado	6,987	106
Ralston	2006	5	Eldorado, Tahoe	3,227	74
Rich	2008	3,4	Plumas	2,703	74,37
Rim	2013	1,2	Stanislaus	104,131	53,41
Rush	2006	5	Klamath	2,021	55
Showers	2002	7	Lake Tahoe Basin Management	129	10
Sims	2004	6,9	Shasta-Trinity, Six Rivers	1,541	68,10
Slide	2007	5	San Bernadino	5,208	52
Spanish	2003	7	Mendocino	2,584	158
Straylor	2004	5	Lassen	1,413	40

Table 1. List of wildfires used in analysis. For fires measured over multiple years, plot counts per year are listed in the same sequence as the number of years postfire measured.

Field data collection
Regeneration data were recorded in 60 m² plots. Regeneration of conifer seedlings <1.37m tall were tallied by species and age; age was determined by counting branch whorls. Crews made ocular estimates of cover by lifeform (tree, shrub, forb and graminoid) and ground cover (litter, rock, wood and bare soil). Stand tree density was estimated in an 8m radius plot, and stand basal area and density of live and dead overstory trees were collected by species using variable radius plots, delineated by basal area gauges with basal area factors that ranged from 5-40, depending on site characteristics (Avery and Burkhard 2015). Finally, distance to potential seed source was recorded for all focal conifer species that were visible from the plot using a laser range finder. Potential seed sources were live trees that were bearing cones or had borne cones in the previous year.

Remote sensing products
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 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 temperature (degrees Celsius) (TMIN) from the California Climate Commons (http://climate.calcommons.org/). These climate averages were modelled using long-term weather stations as inputs to the Basin Characterization Model (Flint et al. 2013).

Continuous burn severity imagery was obtained from USFS Region 5 (http://www.fs.usda.gov/main/r5/landmanagement/gis). 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 assigned the raw RdNBR values for both the Initial Assessments (IA), which were created immediately postfire, and the Extended Assessments (EA), which were created approximately one year postfire, to each regeneration plot. Because IAs were not available for four wildfires (Freds, Pendola, Power, Spanish), we created a model to predict IA values from EAs, using the remaining 18 fires in a simple linear regression model that included both EA and its squared term to estimate a nonlinear relationship (Adj. $r2 = 0.728$). The IA performed much better than the EA in terms of AIC when tested against regeneration probability independently (AIC: 1926.68 and 1973.27, respectively) and so was used in all models. We then also assigned values for all potential climate variables (Table 2) to each sample plot in ArcMap.

We obtained estimates of basal area by species from Gradient Nearest Neighbor Structure (Species-Size) Maps produced by the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA) lab, a collaborative research group at the USFS Pacific Northwest Research Station and Oregon State University (Ohlmann and Gregory 2002). These maps estimate basal area by species at the 30m pixel scale that are based on nearest-neighbor relationships between remotely sensed Landsat data and USFS Forest Inventory and Analysis (FIA) plots. Kappa coefficients, which measure intra-group agreement for categorical calculations, for our species of interest were as follows: Douglas-fir (0.5644), incense-cedar (0.5093), Jeffrey pine (0.4362), ponderosa pine (0.5018), sugar pine (0.4176), white fir (0.5465) (Ohmann et al. 2012). Because the LEMMA product was generated in 2012, it reflected postfire forest structure on all fires except for the Rim Fire; we reduced the basal area estimates in the Rim Fire using burn severity maps. This involved classifying the burn severity maps into seven classes of percent basal area mortality (0%, 1-10%, 10- 25%, 25-50%, 50-75%, 75-90%, 90-100%) as modelled by Miller et al. (2009), and multiplying the LEMMA basal area estimate by the midpoint for each class. For the highest severity class (90-100% basal area mortality), we used 100% rather than the midpoint (95%) because it was more representative of that class in those fires. Data from the Rim Fire documented 99.5% basal area loss in the highest severity category (unpublished data, K. Shive). In addition, other work in the Rim Fire showed that basal area loss in the highest severity class was >95% for most plots (Lydersen et al. 2016).

Creating seed availability proxies (SAPs)
Euclidean distance. We measured the shortest distance from each sampling point to the nearest, lesser-burned edge (pixels categorized as unburned, low or moderate severity in the classified burn severity map). For plots located in non-high severity pixels, distance was set to zero. We used the Near tool in ArcMap to measure distances.
LEMMA-based. To estimate relative seed availability across the landscape, we calculated annual seed production from basal area as modelled by LEMMA (Ohmann et al. 2012). We calculated species-specific annual seed production for each 30m pixel (number of seeds per 900m2) using established equations based on seed mass by species and basal area (Greene and Johnson 1994). These equations reflect established relationships that generally describe increases in the number of seeds produced with increasing tree crown size within a given species, but overall lower numbers of seeds produced for heavier seeded species relative to

lighter seeded species (Venable 1992). To calculate seed production, we converted basal area to leaf mass (Equation 2, Greene and Johnson 1994) and then estimated seed production based on leaf mass and individual seed mass (Equation 5, Green and Johnson 1994). We calculated seed mass by species from the average number of seeds per pound (USFS 1974, USFS 1990). The equations provided in Greene and Johnson (1994) were intended for use with basal area of individual trees, but because we lack detailed stand structure data, we used total basal area by species for each pixel as an estimate of the relative magnitude of seed production across the landscape. We then summed the number of seeds produced by each species for each pixel.

We converted each burn severity pixel to a 30m point grid across each fire perimeter with a 500m buffer. Total estimated annual seed production was assigned to each point, which was used to create smoothed surfaces of seed availability using Gaussian density kernels centered at each point. Seed dispersal curves are generally modelled with fat-tailed exponential or lognormal curves (Clark et al. 1999, Greene and Johnson 2000), but these were not available for landscape-level modelling in ArcMap 10.4. We created these smoothed surfaces using a range of bandwidths (or radii) from 50m to 500m at 50m intervals (Figures 2c, d, e). Since the bandwidths are greater than the distance between points, this creates a contiguous surface of overlapping kernels with variable density values, in this case seed production (Figure 2e). We created the smoothed surfaces using the Kernel Interpolation Tool with Barriers in ArcMap 10.4.
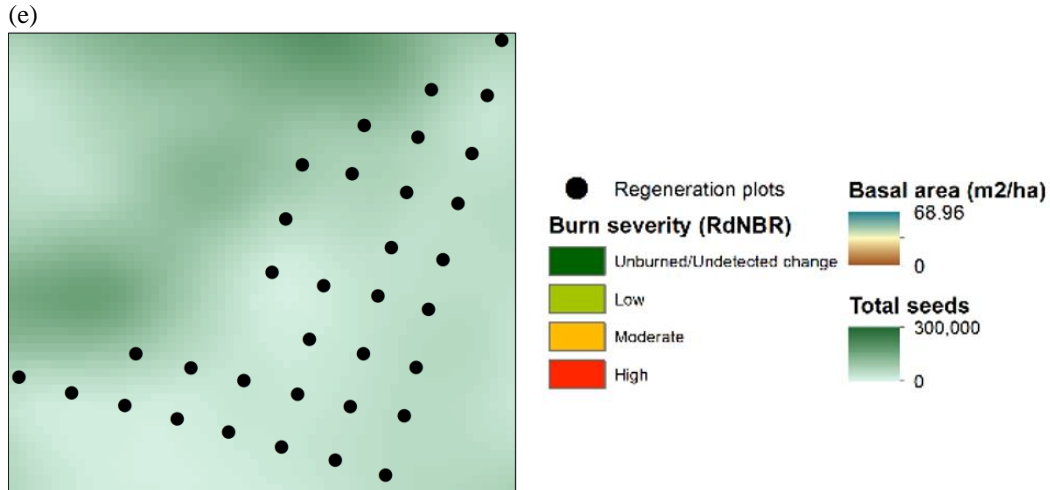
(e)
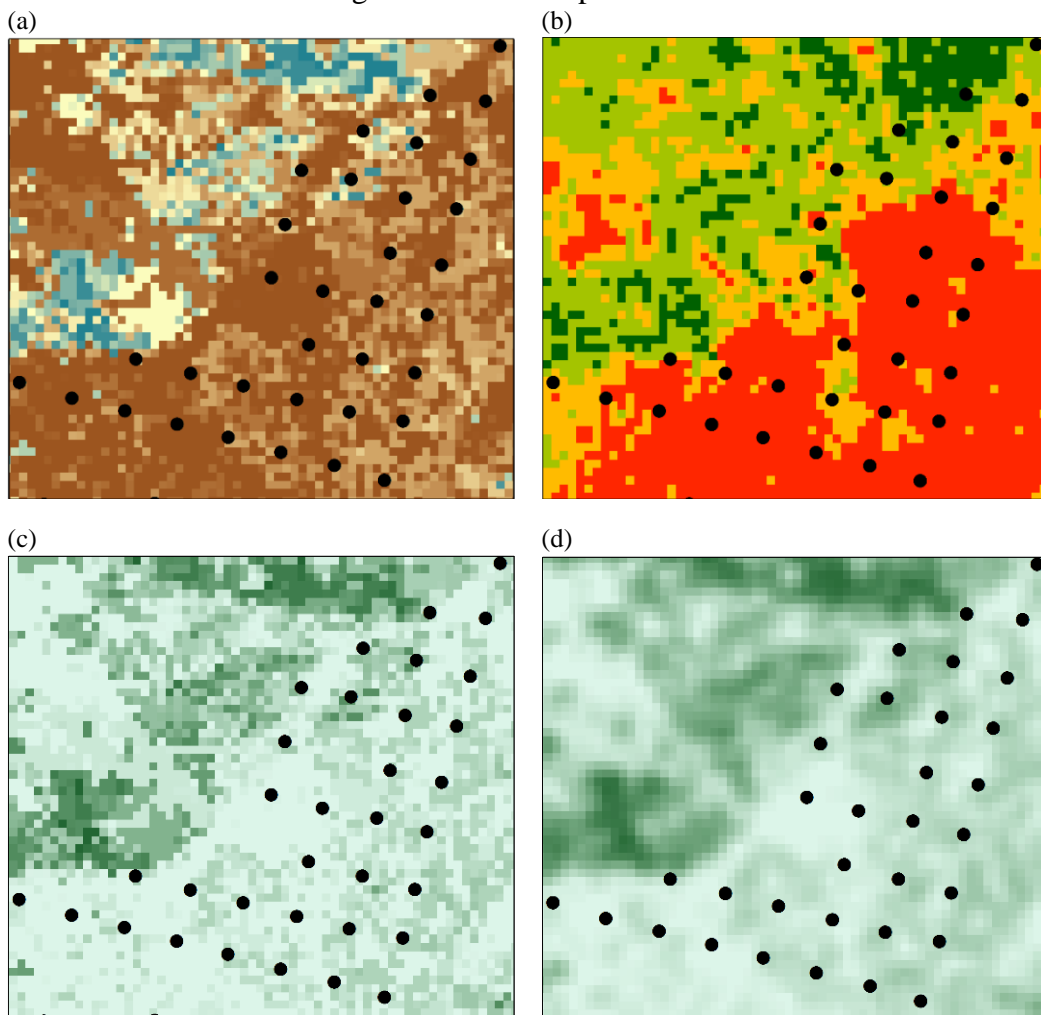
Figure 2. Work flow for creating kernel surface as a proxy of relative seed availability. This involved confirming that the LEMMA basal area estimates (a) generally matched the burn severity imagery (b), to ensure the LEMMA reflected postfire patterns. Basal area was converted to annual seed production (c) and smoothed using a kernel surface; surfaces generated from a 50m (d) and 250m (e) bandwidth shown here.

Statistical models

We used generalized additive models (GAMs, (Hastie et al. 2001) to build binomial models for predicting the probability of conifer regeneration, lumping our six species of interest (Douglas-fir, incense-cedar, Jeffrey pine, ponderosa pine, sugar pine, white fir) into a single presence/absence variable. Because we were building these models to forecast regeneration across an entire fire, including on future wildfires, we examined only variables that could be predicted after a fire and therefore available for use in a forecasting framework; hereafter we refer to these models as "forecast" models. We examined a suite of potential climatic, topographic, burn severity and SAP variables (Table 2) to build two forecast models, which predicted the probability of observing: (1) at least one regenerating conifer, and (2) two or more regenerating conifers of any species. We also included time-since-fire as the number of years after the fire that the measurements were taken.

Variable Group	Variable (units)
Climatic	Actual evapotranspiration (mm) Annual precipitation (mm) Climatic water deficit (mm) Minimum temperature (°C) Snow water equivalent, April 1 (mm)
Topographic	Elevation (m) Aspect (degrees) Slope (percent)
Seed availability proxies (SAPs)	Kernel surface of seed production at 10 bandwidths (50-500m) Euclidean distance to unburned, low or moderate severity edge

Burn severity	Initial Assessment (RdNBR)
	Extended Assessment (RdNBR)
Field-derived	Shrub cover (percent)
	Litter cover (percent)
	Live tree basal area (m^2 ha^{-1})
	Distance to live tree seed source (m)

Table 2. Candidate variables for the forecast model and field-derived variables used in the full model.

      To find the best forecast models, we compared candidate models including all variables other than a SAP term, and dropped non-significant terms one at a time; however, since several of the climate variables were correlated, we also checked for changes in AIC with and without these terms. Further model examinations included visual inspections of partial residual plots as well as p-values for relevant variables. The partial residual plots show the magnitude of change in the odds of regeneration, relative to the odds at the variable's mean, which is set to one. The partial residuals plot for each variable represents the expected change in the odds of the response while controlling for all other variables in the model. We also included the individual fire as a random effect to account for differences between fires that we were unable to measure in the field. Once we determined the best topographic and climatic predictors, we then used this as a base model and compared models with SAPs at different scales (50-500m) to determine the most important neighborhood of seed availability for predicting regeneration with AIC. All analyses were performed using the *mgcv* package in R (Wood 2006).

      To better understand how well the kernel-based SAPs helped predict regeneration relative to other methods, we then compared the best forecast model with models where we substituted the SAP with: 1) no spatial term, 2) Euclidean distance to nearest, lesser-burned edge, and 3) field-derived distance to seed tree. This comparison held the rest of the model the same, enabling the evaluation of the SAP itself. Next, we also wanted to better understand how much information is lost when using the limited number of variables available for prediction (Table 2) at the landscape-scale after a new wildfire. In the forecasting framework, spatially and temporally variable responses such as regenerating shrub cover cannot be readily predicted across the landscape, yet we know these are important drivers of postfire conifer regeneration (Collins and Roller 2013, Welch et al. 2016). To evaluate how our forecast model performed in comparison to models with these important, local-scale drivers, we compared it to a "full" model with field-derived variables that were determined to be significant on a subset of our fires by Welch et al. (2016); specifically, this included variables that represented competition (shrub cover), microsites (litter cover) and seed sources (distance to individual live trees).

Model validation and predictive map

To account for variability between fires, and to mimic forecasting a future fire based on past fires, we used the leave-one-out method of model validation, leaving each fire out of the model and predicting it with a model from the remaining 23 fires. Using the predictions from the cross-validation procedure, we created a reliability diagram by binning these predictions into the following seedling-presence probability classes: 0-0.2, 0.2-0.4, 0.4-0.6, 0.6-0.8 and 0.8-1.0. Within each category, we calculated the frequency of observed positive cases (conifers present) in the total number of observations in that category for each fire, excluding instances where the

number of observations for an individual fire within a class was <5. We then created box plots with the probability classes on the x-axis and observed frequency of positive cases per fire per class on the y-axis, as a means to show the expected variability in prediction values.

To create an example of a regeneration probability predictive map, we first converted the burn severity raster to a point grid on a "new" fire (the 2014 King Fire) and created the relevant SAP using the 2012 LEMMA basal area estimates, adjusted by the basal area mortality classes from RdNBR (described above for the Rim Fire). We then overlaid all relevant climatic and topographic variables and assigned values to each point in the point grid. Using the forecast model with all fires included, we then predicted the probability of conifer regeneration at each point. To show the inherent variability in the model, we binned the point predictions into the same classes used for the reliability diagram and converted them to a raster which was color coded to match box plots from the reliability diagram.

Results

Annual precipitation and continuous burn severity (IA) had the largest effect on the odds of regeneration, demonstrated by their percent of chi-squared (22.0% and 21.8% respectively) (Figure 3). The odds of regeneration were roughly 7 times greater at precipitation levels greater than 2,000 mm than at locations with average precipitation (~1200 mm). Burn severity (IA) had the highest estimated odds of regeneration at low (RdNBR = 69-315) to moderate (315-640) burn severity values, with a declining effect on odds of regeneration in the high severity class (>640). The odds of regeneration were ~60% less at sites with very high burn severity (>1000) relative to sites with more moderate severity (<500). Increasing estimated annual seed input generated from the 150m neighborhood kernel surface strongly increased the odds of regeneration, but the percentage of total chi squared was low (6.5%). However, an exploratory model without the correlated burn severity (IA) variable increased the percent chi squared to 39%, much higher than any other variable; this suggests that these two variables together are the most important drivers of regeneration.
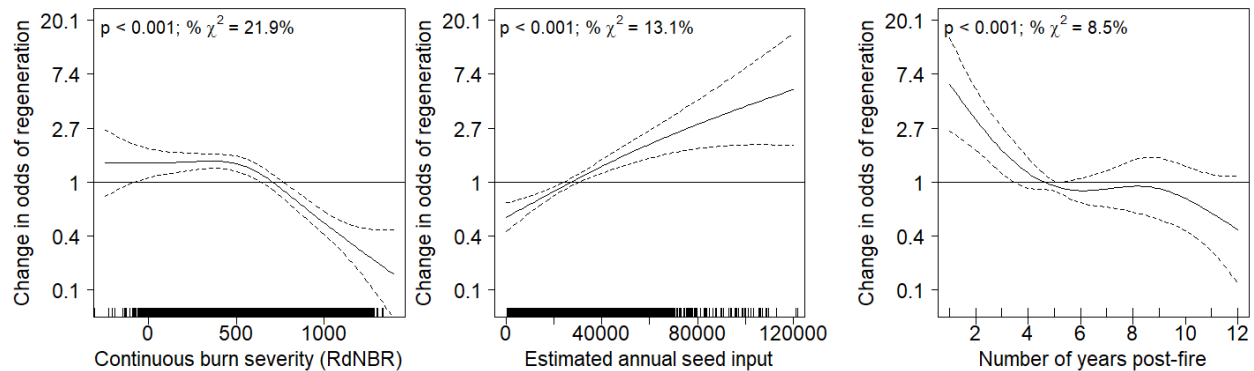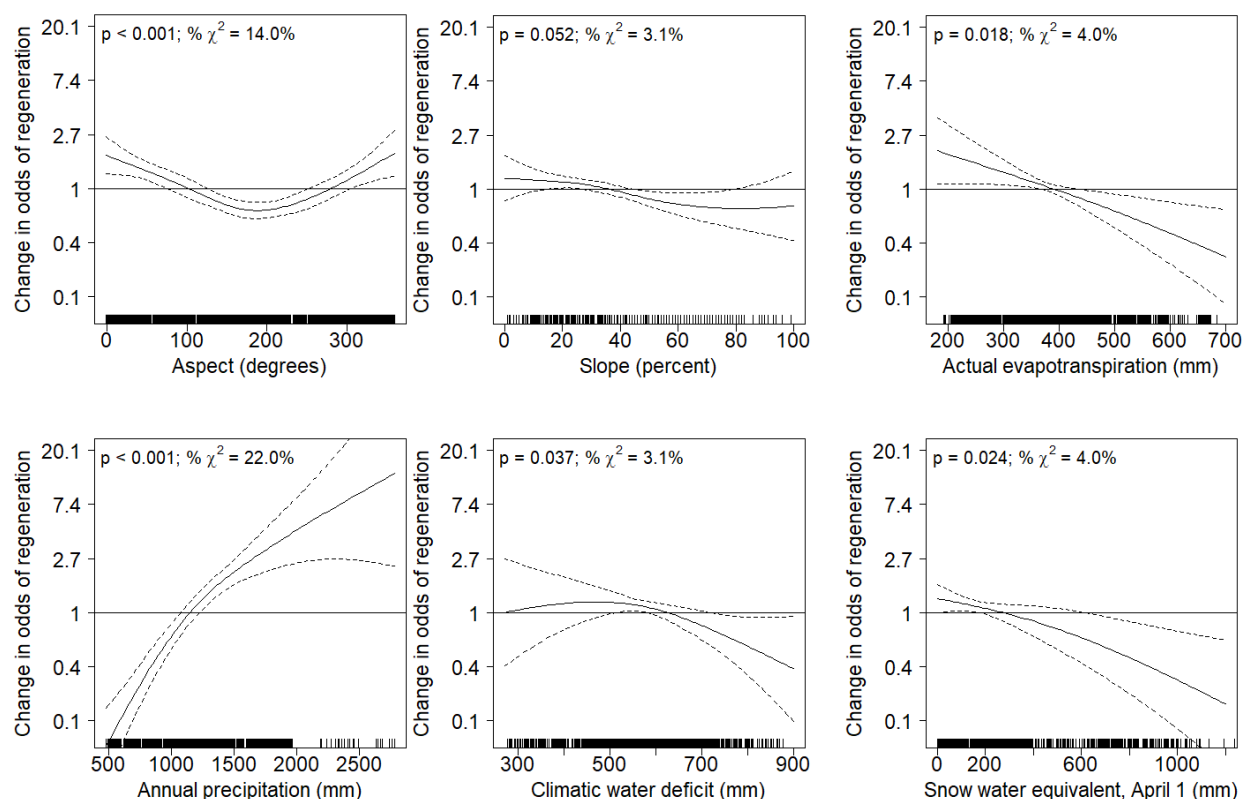
Figure 3. Partial residual plots for model predicting seedling presence/absence of any of the six conifer species of interest. Residual plots show how each variable (x-axis) influences the probability of conifer regeneration (y-axis), given all other variables are in the model. The response at the variable's mean is set to one on the y-axis; deviations from one are the magnitude of change in the log-odds of observing regeneration. P-values and the percentage of chi-squared attributed to each of these predictors are in the upper left corner.

Aspect explained 14% of the variation, where north- and east-facing aspects had a positive effect on the odds of regeneration. The estimated odds of regeneration declined through time, with the highest probabilities predicted for fires measured in the first few years postfire. The remaining explanatory variables included in the model improved model fit as assessed by AIC and the reliability diagrams, but had percent chi squared values <5%. Increasing slope, AET, CWD and snowpack values all had a generally weak, negative effect on the odds of regeneration (Figure 3). Minimum temperature and elevation were not significant, and models with and without out either variable did not differ in terms of AIC and so both were eliminated from the final model. All reports of variable relationships with estimated odds of regeneration are made given all other variables are in the model.

The forecast model with Euclidean distance (p = 0.583; AIC: 2050.10) was no better than a model with no SAP term (AIC: 2049.62). The best neighborhood size for the kernel-based SAP was 150m (p < 0.001; AIC: 2024.85). However, SAP neighborhoods of 200m and 250m all had dAIC < 2, suggesting no real difference between these neighborhood sizes. Not surprisingly, field-measured locations of nearest potential seed tree performed the best (p < 0.001; AIC: 1983.51). The full model that included field-derived data on shrub cover (p < 0.001), litter cover (p = 0.017), live tree basal area (p = 0.110) and distance to individual seed tree (p < 0.001)

performed substantially better (AIC: 1956.80) than any forecast model. Differences between these models in terms of predicted versus actual observations are shown in Figure 4.
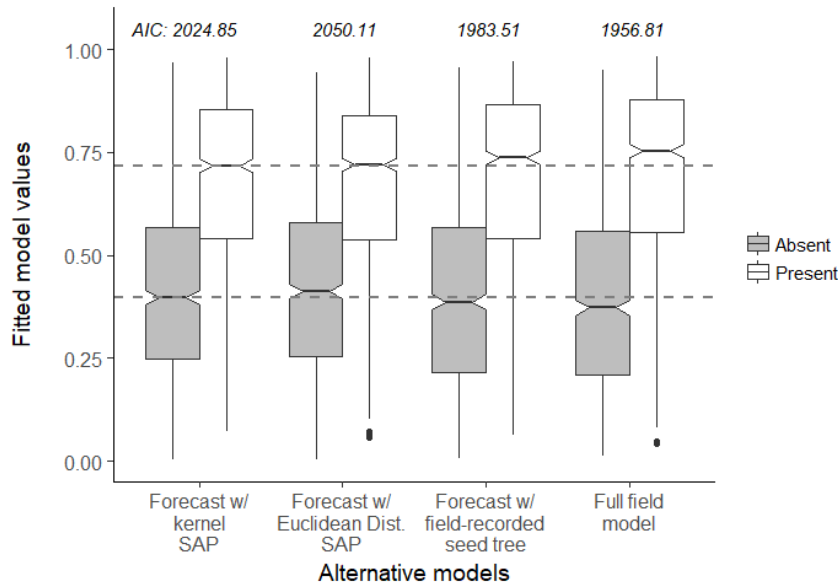

Figure 4. Boxplots showing model predicted probability of conifer regeneration by actual observed presence/absence for competing models. The forecast models differ by variable representing seed availability: the kernel based SAP, Euclidean distance and field-derived distance to seed tree. The full model includes field-derived distance to seed tree as well as shrub cover, litter cover and live tree basal area. Dashed lines show the median fitted values for the forecast model for comparison with all other models. The boxes define the 1st quartile (25th percentile) and 3rd quartile (75th percentile), and the line within the box defines the median. The whiskers extend to the highest value that is within 1.5 times the inter-quartile range and the dots are outliers that exceed this distance from the quartiles. AICs for each model appear at the top of the graph.

Finally, the conditional model for observing more than one conifer (AIC: 932.49) had few terms: burn severity-IA ($p < 0.001$), years-post-fire ($p = 0.003$), AET ($p = 0.013$) and the kernel-based SAP at 250m ($p = 0.002$), rather than 150m that was selected for the presence/absence model.

Model validation and forecasting
The leave-one-out validation procedure showed good agreement between the predicted classes and empirical distributions of regeneration frequencies across fires, as shown in the reliability diagram (Figure 5). Most fires were variously slightly over- or under-predicted across classes, and none were consistently over- or under-predicted across all categories or by more than one class. The distributions of observed frequencies per predictive category per fire (Figure 5a) demonstrate the amount of variability to expect in the probability of regeneration in a future fire. For example, at locations with a predicted probability of regeneration in the lowest category one should expect regeneration levels between 1-28% most of the time although there is still a small chance that the probability could be as low as 0% and as high as 38%. Figure 5b and Table 3 show the range of observed densities across all fires by the predicted probability class. For the same locations in the lowest category, one can expect a range of densities from 0 – 14,666 seedlings ha^{-1}, with a median value of 66.

Figure 5. Predictive map showing the probability of observing at least one regenerating conifer at the 60m^2 (field plot) scale for the 2014 King Fire. The reliability diagram (a) is created from the leave-one-out model validation procedure. Predictions are binned into five classes (x-axis) and the actual frequency of conifer regeneration per fire within each class is plotted on the y-axis. (b) Range of observed densities per fire across these same classes, excluding outliers >15,000 seedlings ha^{-1}. Boxes define the 1st quartile (25th percentile) and 3rd quartile (75th percentile) with the line inside the box as the median. The whiskers extend to the highest value that is within 1.5 times the inter-quartile range, and the dots are outliers that exceed this distance from the quartiles.

Model	Predicted probability class	Observed densities (seedlings ha^{-1})			
		Minimum	Maximum	Median	Mean (s.e.)
At least one conifer	0.0 – 0.2	0	14,666	0	144 (86)
	0.2 – 0.4	0	15,333	0	317 (55)
	0.4 – 0.6	0	17,166	166	672 (101)
	0.6 – 0.8	0	380,166	333	3,665 (985)
	0.8 – 1.0	0	201,666	1,333	6,301 (755)
Two or more conifers	0.0 – 0.2	166	14,666	333	975 (232)
	0.2 – 0.4	166	17,166	500	1,419 (190)
	0.4 – 0.6	166	84,000	833	2,640 (4100
	0.6 – 0.8	166	380,167	1,666	7,724 (1,447)
	0.8 – 1.0	166	201,667	2,833	9,661 (1,899)

Table 3. Minimum, maximum, median, mean and standard error (s.e.) of observed conifer seedlings ha^{-1} for all 24 wildfires included in the forecast model by predicted probability class. Seedlings rounded down to whole number.

Translating this to a map predicting the probability of regeneration at five years postfire on the King Fire (Figure 5) shows that 33% of the fire area, or 12,975 hectares, has less than a 40% probability (the two lowest prediction classes) of having at least a single regenerating conifer. For the probability of finding more than one conifer in a 60 m2 plot area (Figure 6), 38% of the fire area is in the two lowest prediction classes.
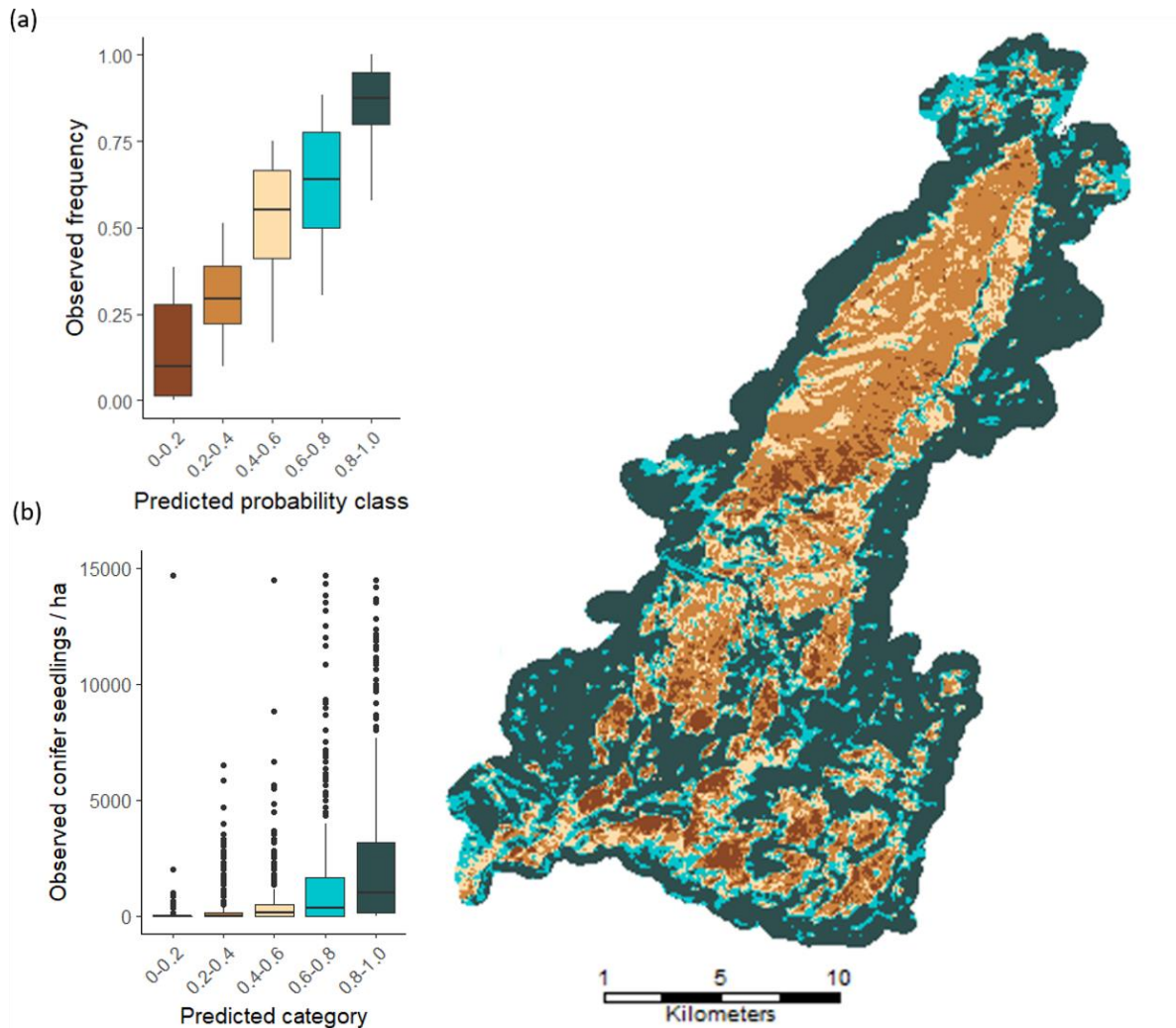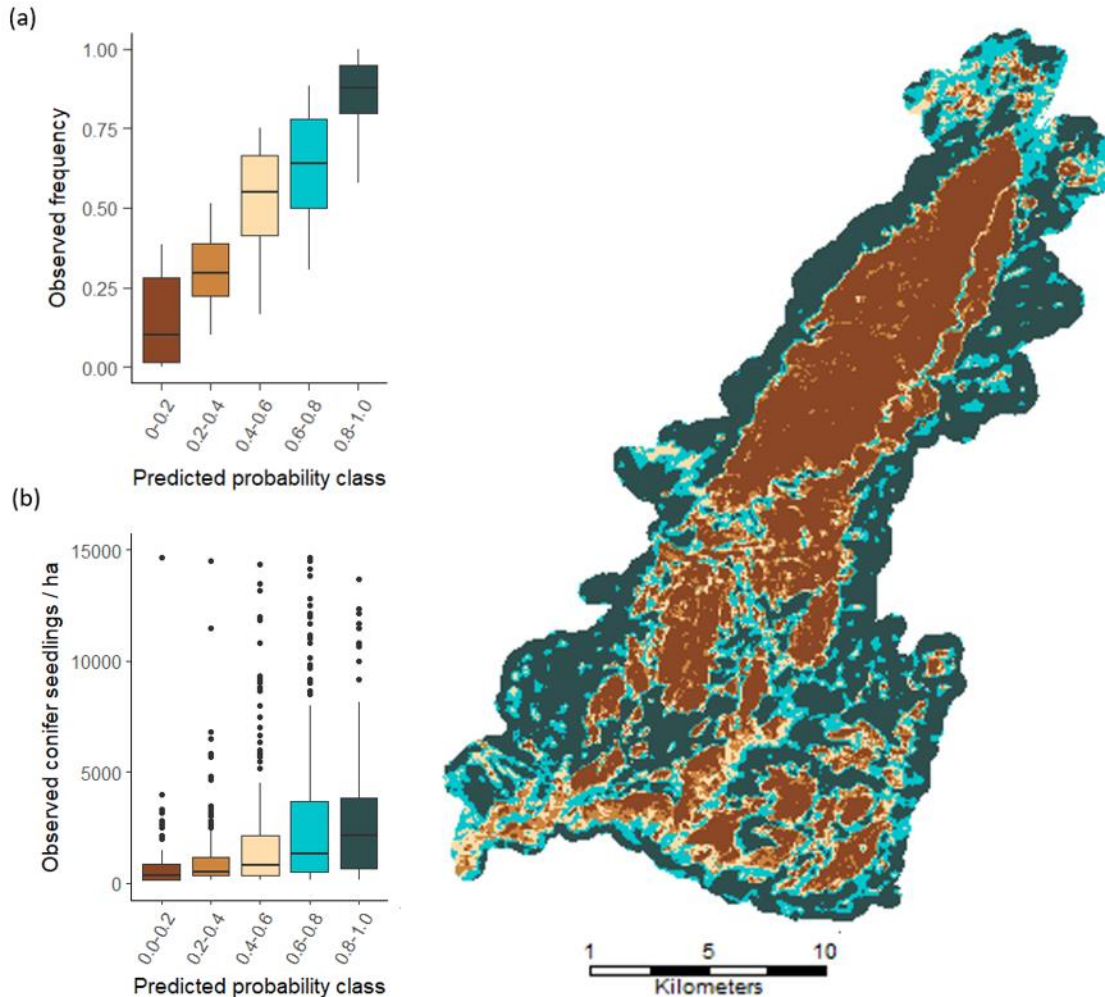

Figure 6. Predictive map showing the probability of observing more than one regenerating conifer at the 60m^2 (field plot) scale for the 2014 King Fire. The reliability diagram (a) is created from the leave-one-out model validation procedure. Predictions are binned into five classes (x-axis) and the actual frequency of conifer regeneration per fire within each class is plotted on the y-axis. (b) Range of observed densities per fire across these same classes, excluding outliers >15,000 seedlings ha^{-1}. Boxes define the 1st quartile (25th percentile) and 3rd quartile (75th percentile) with the line inside the box as the median. The whiskers extend to the highest value that is within 1.5 times the inter-quartile range, and the dots are outliers that exceed this distance from the quartiles.

Discussion

Continuous burn severity, the kernel-based SAP and annual precipitation were the primary drivers of postfire conifer regeneration. It was not surprising that precipitation is a major driver of regeneration patterns, since conifer seedlings are very sensitive to soil moisture (USDA Forest Service 1990), particularly in a Mediterranean climate. Snowpack can benefit Mediterranean climate ecosystems by providing a slow release of moisture in the spring and summer drought

36

period. The weak negative trend in our model is likely related to a correlation with elevation, since our species of interest are generally found at lower elevations, and may also be due to decreasing growing season length and reduced productivity at higher elevations. The negative effect of AET was initially surprising; since AET is usually considered a surrogate for productivity, we expected to see a positive relationship with regeneration probability. With more investigation, we found that the effect of AET varies somewhat with time since fire. On older fires (measured ≥ five years postfire), regeneration probabilities declined with higher AET values (>450mm), and this trend was strongest on the oldest fires and as PPT increased. In contrast, on fires measured < five years postfire, there was a positive effect on regeneration probabilities at both moderate (300-450mm) and high AET values. We hypothesize that the increased productivity associated with increasing AET is having a disproportionate, positive effect on competing vegetation (shrub, grass, hardwood). The longer the time-since-fire, the more time for other vegetation to grow and become more competitive with conifer seedlings. Exploratory models of the relationship of shrub cover with AET were weak, but did support this hypothesis.

When scaling from the plot scale to the landscape scale in a forecasting framework, the intermediate performance of the kernel-based SAPs versus field-derived distance to seed tree and models with no spatial term suggests that the SAPs are a reasonable proxy for neighborhood seed availability. The 150m neighborhood (or bandwidth) SAP is somewhat larger than the "rule-of-thumb" for dispersal in these systems, which holds that most seeds generally disperse within 1-2 tree heights of the parent tree (McDonald 1980). The 150m neighborhood exceeds this rule of thumb since the tallest trees in these systems are generally up to 40-50 m. We speculate that the larger neighborhood is the result of lumping all species, including species such as white fir and incense-cedar that produce lighter seeds that may travel farther than the rule-of-thumb suggests. This rule of thumb also does not incorporate long-distance seed dispersal, which is less common but likely important for regeneration patterns, especially for the pine species which have significant animal dispersal (Clark et al. 1999, Vander Wall 2008). In addition, as a proxy based on remote sensing, it is likely that there are live trees in areas that were not detected by LEMMA, many of which may occur near the edge of a high severity patch, that are contributing to the seed rain.

Although we hypothesized the kernels would perform better than Euclidean distance to lesser-burned edges, we were initially surprised that Euclidean distance did no better than models without any seed proxy term, even when compared for high severity areas only. However, Euclidean distance was correlated with burn severity, which is not entirely surprising since burn severity is likely to decrease near patch edges. When burn severity was removed, Euclidean distance became significant. In our forecast model, we retained inclusion of both burn severity and a SAP term because severity of an individual pixel and potential for seed rain do represent different phenomena, despite their close relationship.

That distance to seed source is a major driver (and limitation) for postfire conifer regeneration patterns is echoed in other studies in similar systems (Greene and Johnson 2000, Bonnet et al. 2005, Franklin and Bergman 2011, Collins and Roller 2013, Dodson and Root 2013, Harvey et al. 2016, Kemp et al. 2016, Welch et al. 2016). Our documentation of these patterns is not new. However, our study is unique in its scope (based on 1,848 field plots across 24 wildfires throughout California) and in our explicit consideration of the neighborhood as a means to scale plot-level data to the landscape. Although one other study also used kernel-based methods to examine the importance of neighborhood characteristics (Haire and McGarigal

2010), our study presents a novel approach by creating a contiguous surface from these kernels and building a predictive framework.

The predicted spatial patterns of regeneration at five years postfire on the King Fire suggest that patch configuration and size are critical for postfire conifer regeneration probabilities. Approximately one third of the fire area (or, 12,975 ha) has <40% probability of having at least one regenerating conifer by five years postfire. Our model suggests that this is a product of high severity patch size, which in part determines the amount of land that receives adequate seed rain to ensure reforestation. Some research suggests that overstory recruitment occurs on decadal scales, so these patterns may yet change with time (Russell et al. 1998, Haire and McGarigal 2010). Haire and McGarigal (2010) have also shown that re-colonization of the foundation tree species generally occurs in a wave-like front, where seedlings establish somewhat near parent trees, grow and themselves disperse seeds further into patch interiors. Our spatially-explicit forecast model suggests the same trend, where probabilities were higher nearer to the lesser-burned edge. However, the applicability of these studies to modern fires is limited because of changes in fire severity and high severity patch size. Modern fires are much larger, with fires such as the 2014 King Fire and 2013 Rim Fire burning tens of thousands to over a hundred thousand hectares, with individual high severity patch sizes that are thousands of hectares in size. Maximum fire size in the study by Russell et al. (1998) was 100 ha, and the maximum individual high severity patch size examined by Haire and McGarigal (2010) was 947 ha. Larger high severity patches may enhance the probability of shifts to persistent montane chaparral, because of the increased time scales required for conifers to repopulate large patches. This is primarily because longer time frames increase the probability of a another fire event, which is likely to burn again at high severity due to the fuel type, resulting in a positive feedback between chaparral and fire (Collins and Stephens 2010, Coppoletta et al. 2016, Tepley et al. 2017). In addition, these long time scales may make seedling survival progressively less likely, as climate warming compresses the regeneration niche for the current conifer dominants (Feddema et al. 2013, Savage et al. 2013, Bell et al. 2014).

Because the low probabilities of regeneration are driven in part by proximity to seed sources, it suggests that forest restoration treatments designed to reduce fuels, and in turn fire severity and the size of individual high severity patches, could alter postfire trajectories for stand development (Stephens et al. 2016). In addition to minimizing distance to seed source, such treatments could also buffer against drastic changes to the regeneration niche by retaining some forest canopy cover, which has an important moderating influence on realized climate at the soil surface and can increase seedling survival (Dobrowski et al. 2015).

It is important to note that within some areas with low regeneration probabilities, there are potentially areas that were not forested historically, because they are less suitable sites that may be more physiographically prone to severe fire (windward, south- or west-facing upper slopes, for example). It is possible that these areas are only forested as a result of a century of fire exclusion, which enabled tree expansion into previously unsuitable habitats (Nagel and Taylor 2005). For example, one of the smaller high severity patches (~400 ha) at the southern end of the King Fire has very low probability of regeneration across the patch, because despite having relatively high seed input, the annual precipitation values at that location are very low. In general, such areas could be inferred by annual precipitation, topographic position and heat load to delineate areas where a lack of regeneration may not be of great concern.

Moreover, it is important to consider what probability of regeneration across these large patches is sufficient to meet historic forest densities that are likely more resilient to wildfire,

pests and the changing climate. For example, of the 18,272 ha that burned severely in the King Fire, 2,304 ha are in the 0-20% probability class and 9,199 ha are in the 20-40% probability class, most of which occurs in the large, interior high severity patch. Observed seedling densities in these classes had very wide ranges, but median densities were 0 seedlings ha^{-1} for both classes, where 71% of the plots in these classes had no regeneration. Moreover, whorl counts indicate that in high severity areas measured in this study, over 70% of the seedlings observed were ≤ 3 years old. This has important implications for the likelihood of reforestation. First-year seedling mortality is highly dependent on site conditions and species, where pines on favorable sites can have mortality rates as low as ~50%, but average mortality rates across species and sites can be as high as 80% (Fowells and Stark 1965). Mortality of first-year seedlings in high severity areas may be even higher, since the study by Fowells and Stark (1965) used exclosures on all sites and managed competing vegetation on a subset of them. Another study that tracked seedlings through time found that mortality rates by year three can range from 57–70% of the initial seedling population (Fowells and Schubert 1951).

Given the high percentage of young seedlings in the dataset, it is likely that some of the regeneration predicted at five years postfire will not survive into the future. In addition, the model also shows significant decreases in regeneration probabilities on older fires, likely reflecting declines with increased shrub dominance. There is therefore a good chance that current regeneration densities in these probability classes at five years postfire may not be adequate to create a forest that resembles historic forest densities (Collins et al. 2011) or meet desired management conditions. However, it is also important that managers using this tool for reforestation planning consider the inverse problem created in some of the highest probability classes when seedling densities are too high. In the King Fire, areas in the 80-100% category had an observed median density of 4,458 seedlings ha^{-1}, which is likely too high to create fire- or drought-resilient forests, even if there is notable seedling mortality over time (Lydersen et al. 2014, Young et al. 2017). Given that this class is located mostly in lower-severity areas that also have an intact overstory, seedling densities in these areas could result in overly dense forests that are highly susceptible to water stress, fire, and insect and disease outbreaks unless thinning disturbances are permitted to occur, such as regular fires or fire surrogates (mechanical or hand thinning, e.g.).

Model limitations
There are numerous assumptions in our model as well as sources of uncertainty. First, the kernel-based SAPs were based on LEMMA map products, which are themselves modelled using FIA plots found at low density across the landscape (Ohmann et al. 2012). In addition, although we calculated annual seed production, this approach does not explicitly model seed dispersal. Although there is some disagreement on the best shape of a dispersal kernel, none have suggested using a Gaussian distribution, which we used here. The lognormal and a "fat-tailed" kernel are considered more accurate representations of seed dispersal (Clark et al. 1999, Greene and Johnson 2000), but these shapes are not readily available for kernel interpolations across a landscape in ArcMap. Sensitivity analyses on surfaces produced with the other available kernel shapes (Exponential, Quartic, Constant, Polynomial, Epanechnikov) showed little change in the models; this is likely due to our use of the kernel at each 30m pixel, rather than centering the kernels on individual trees dispersing seeds. Stem mapping by species and size class would be required to truly map and predict seed dispersal, but this is likely too intensive to be practical at these scales since detailed stand structure data at the scale of an entire fire is generally lacking,

and distinguishing species with publicly available remote sensing techniques is not yet reliable enough.

Another limitation of our model is our inability to predict temporal variations in postfire weather patterns and masting. The timing and occurrence of favorable weather conditions and mast-year seed production could have a substantial impact on regeneration patterns (Brown 2006, Keyes and González 2015, Rother and Veblen 2017). Although we could include postfire weather patterns for the fires studied here, we could not translate them into a forecasting framework because annual weather patterns are difficult to predict into the future. In addition, masting patterns vary within species across their range, yet detailed data on mast years after the fires studied here are unavailable. Even if they were, it would also be difficult to predict into the future for a forecast model. Future work could create a suite of models that assumed favorable versus unfavorable conditions and variable masting patterns, to show a range of possible outcomes.

Finally, lumping together conifer species with different shade, drought and fire tolerances increased our sample size of actual observations, but also probably muted some responses. For example, the best SAP scale for predicting regeneration may vary by species due to differences in seed size and morphology. Future work will examine the dominant conifer species separately and compare differences in response to the individual variables between them. We also lumped all age classes of observed regeneration, however we know that mortality of first-year seedlings is particularly high, and that prediction of established seedlings (perhaps > three years old) would give a better indication of future reforestation patterns and densities. We explored models predicting established seedlings, but they performed very poorly. We hypothesize this is because survival and establishment are likely more tied to localized competition and microsite characteristics, features that we are unable to model at the landscape scale.

Management implications

This spatially-explicit predictive model can aid managers of non-serotinous, yellow pine and mixed conifer forests in California and neighboring parts of the North American Mediterranean climate zone to predict where postfire regeneration five years after fire is likely to meet, or not meet, management target densities. Prediction maps such as those in Figures 5 and 6 identify areas where regeneration probabilities are lowest, which can be used to prioritize limited resources for planting where a forested condition is desired. Because of the size of the sampling unit and presence/absence approach, the model predicts the probability of observing one conifer seedling, of any of the six focal species, in a 60m2 area. To translate that to something more meaningful for management decision making, managers can refer to Table 3 and Figure 5b, which shows the range of observed seedling densities across fires within each probability class. We suggest using the median value as the estimated density, since the mean is heavily skewed by outliers. At the scale of the landscape, this model can help managers better anticipate variability for long-term planning.

Because there is always variability on the ground, we recommend that managers use this model in concert with the field tool developed by Welch et al. (2016). Their tool outlines field-observed characteristics that can be used to locally fine-tune the predictions from the forecast map.

Conclusions

The spatially-explicit model developed in this study highlights the variability in regeneration potential across a burned landscape. The probability of successful germination and regeneration is modified by climatic and topographic characteristics, but the most limiting factor for regeneration is the critical, initial biological filter of seed availability. We found that remote-sensing based proxies for seed source (burn severity and the kernel-based SAP) were reasonable approximations for field-derived seed sources measurements for modelling at the landscape scale.

The results of this modelling emphasize the importance of forest restoration treatments that can help limit high severity patch size and increase forest resilience to wildfire (Fulé et al. 2012, Stephens et al. 2013). Predicted seedling densities from our modelling show that without management intervention, the largest high severity patch in the King Fire could remain shrub-dominated for an extended period, even if it doesn't burn again. Where forest persistence is desired, restoration treatments in live forests that are designed to reduce high severity patch sizes when fire does occur may be the most effective approach. In addition to maintaining forested conditions where desired, reducing individual patch sizes of high severity can promote habitat heterogeneity across the landscape, thereby benefitting a wider suite of species and ecosystem services (Turner 2010, North et al. 2012, Mallek et al. 2013, Turner et al. 2013).

Works Cited

Avery, T. E., and H. E. Burkhard. 2015. Avery, T.E., H.E. Burkhard. 2015. Forest Measurements, fifth edition. Waveland Press, Long Grove, IL, USA. 456 p. Fifth. Waveland Press, Long Grove, Illinois, USA.

Bell, D. M., J. B. Bradford, and W. K. Lauenroth. 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography* 23:168–180.

Bonnet, V. H., A. W. Schoettle, and W. D. Shepperd. 2005. Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. *Canadian Journal of Forest Research* 35:37–47.

Brown, P. M. 2006. Climate effects on fire regimes and tree recruitment in Black Hills ponderosa pine forests. *Ecology* 87:2500–2510.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80:1475–1494.

Collins, B. M., R. G. Everett, and S. L. Stephens. 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere* 2:art51.

Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. van Wagtendonk, and S. L. Stephens. 2009. Interactions Among Wildland Fires in a Long-Established Sierra Nevada Natural Fire Area. *Ecosystems* 12:114–128.

Collins, B. M., and G. B. Roller. 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. *Landscape Ecology* 28:1801–1813.

Collins, B. M., and S. L. Stephens. 2010. Stand-replacing patches within a "mixed severity" fire regime: quantitative characterization using recent fires in a long-established natural fire area. *Landscape Ecology* 25:927–939.

Collins, B. M., J. T. Stevens, J. D. Miller, S. L. Stephens, P. M. Brown, and M. P. North. 2017. Alternative characterization of forest fire regimes: incorporating spatial patterns. *Landscape Ecology* 32:1543–1552.

Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. *Ecological Applications* 26:686–699.

Crotteau, J. S., J. Morgan Varner III, and M. W. Ritchie. 2013. Post-fire regeneration across a fire severity gradient in the southern Cascades. *Forest Ecology and Management* 287:103–112.

DeSiervo, M. H., E. S. Jules, and H. D. Safford. 2015. Disturbance response across a productivity gradient: postfire vegetation in serpentine and nonserpentine forests. *Ecosphere* 6:1–19.

Dobrowski, S. Z., A. K. Swanson, J. T. Abatzoglou, Z. A. Holden, H. D. Safford, M. K. Schwartz, and D. G. Gavin. 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species: Tree recruitment patterns in the western US. *Global Ecology and Biogeography* 24:917–927.

Dodson, E. K., and H. T. Root. 2013. Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in a ponderosa pine forest, Oregon, USA. *Forest Ecology and Management* 302:163–170.

Donato, D. C., B. J. Harvey, and M. G. Turner. 2016. Regeneration of montane forests 24 years after the 1988 Yellowstone fires: A fire-catalyzed shift in lower treelines? *Ecosphere* 7:e01410.

Feddema, J. J., J. N. Mast, and M. Savage. 2013. Modeling high-severity fire, drought and climate change impacts on ponderosa pine regeneration. *Ecological Modelling* 253:56–69.

Flint, L., A. Flint, J. H. Thorne, and R. Boynton. 2013. Fine-scale hydrologic modeling for regional landscape applications: the California Basin Characterization Model development and performance. *Ecological Processes* 2.

Fowells, H. A., and G. H. Schubert. 1951. Natural reproduction in certain cutover pine-fir stands in California. *Journal of Forestry* 49:192–196.

Fowells, H. A., and N. B. Stark. 1965. Natural regeneration in relation to environment in the mixed conifer forest type of California. USDA Pacific Southwest Research Station. *Research Paper PSW- 24*.

Franklin, J., and E. Bergman. 2011. Patterns of pine regeneration following a large, severe wildfire in the mountains of southern California. *Canadian Journal of Forest Research* 41:810–821.

Fulé, P. Z., J. E. Crouse, J. P. Roccaforte, and E. L. Kalies. 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management* 269:68–81.

Gray, A. N., H. S. J. Zald, R. A. Kern, and M. North. 2005. Stand Conditions Associated with Tree Regeneration in Sierran Mixed-Conifer Forests. *Forest Science* 51:198–210.

Greene, D. F., and E. A. Johnson. 1994. Estimating the Mean Annual Seed Production of Trees. *Ecology* 75:642–647.

Greene, D. F., and E. A. Johnson. 2000. Tree recruitment from burn edges. *Canadian Journal of Forest Research* 30:1264–1274.

Haire, S. L., and K. McGarigal. 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. *Landscape Ecology* 25:1055–1069.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches: Drought and post-fire tree seedlings. *Global Ecology and Biogeography* 25:6.

Hastie, T., R. Tibshirani, and J. Friedman. 2001. The Elements of Statistical Learning. Data Mining, Inference, and Prediction. Springer-Verlag, NY.

Kemp, K. B., P. E. Higuera, and P. Morgan. 2016. Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. *Landscape Ecology* 31:619–636.

Keyes, C. R., and R. M. González. 2015. Climate-influenced ponderosa pine (*Pinus ponderosa*) seed masting trends in western Montana, USA. *Forest Systems* 24:021.

Keyes, C. R., D. A. Maguire, and J. C. Tappeiner. 2009. Recruitment of ponderosa pine seedlings in the Cascade Range. *Forest Ecology and Management* 257:495–501.

Lydersen, J. M., B. M. Collins, J. D. Miller, D. L. Fry, and S. L. Stephens. 2016. Relating Fire-Caused Change in Forest Structure to Remotely Sensed Estimates of Fire Severity. *Fire Ecology* 12:99–116.

Lydersen, J. M., M. P. North, and B. M. Collins. 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. *Forest Ecology and Management* 328:326–334.

Mallek, C., H. D. Safford, J. Viers, and J. Miller. 2013. Modern departures in fire severity and area by forest type, Sierra Nevada and southern Cascades, California, USA. *Ecosphere* 4:1–28.

McDonald, P. M. 1980. Seed dissemination in small clearcuttings in north-central California. US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station.

Miller, J. D., and H. Safford. 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and Southern Cascades, California, USA. *Fire Ecology* 8:41–57.

Miller, J. D., C. N. Skinner, H. D. Safford, E. E. Knapp, and C. M. Ramirez. 2012. Trends and causes of severity, size, and number of fires in northwestern California, USA. *Ecological Applications* 22:184–203.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sensing of the Environment* 109:66–80.

Nagel, T. A., and A. H. Taylor. 2005. Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California, USA1. *The Journal of the Torrey Botanical Society* 132:442–457.

North, M., P. Stine, K. O'Hara, W. Zielinski, and S. Stephens. 2012. An ecosystem management strategy for Sierran mixed-conifer forests. 2nd printing with addendum. General Technical Report, USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Ohlmann, J. L., and M. J. ; Gregory. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest neighbor imputation in coastal Oregon, U.S.A. *Canadian Journal of Forest Research* 32:725–741.

Ohmann, J., M. Gregory, and H. Roberts. 2012. GNN Accuracy Assessment Report California Sierra Nevada (Modeling Region 232). Model Type: Basal-Area by Species-Size Combinations. Page 26. Oregon State University and USFS Pacific Northwest Research Station.

Parsons, D. J., and S. H. DeBenedetti. 1979. Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management* 2:21–33.

Perry, D. A., P. F. Hessburg, C. N. Skinner, T. A. Spies, S. L. Stephens, A. H. Taylor, J. F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. *Forest Ecology and Management* 262:703–717.

Puhlick, J. J., D. C. Laughlin, and M. M. Moore. 2012. Factors influencing ponderosa pine regeneration in the southwestern USA. *Forest Ecology and Management* 264:10–19.

Rother, M. T., and T. T. Veblen. 2017. Climate Drives Episodic Conifer Establishment after Fire in Dry Ponderosa Pine Forests of the Colorado Front Range, USA. *Forests* 8:159.

Russell, W. H., J. McBride, and R. Rowntree. 1998. Revegetation after four stand-replacing fires in the Lake Tahoe Basin. *Madroño* 45:40–46.

Safford, H. D., and J. T. Stevens. 2017. Natural Range of Variation (NRV) for yellow pine and mixed conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. General Technical Report, USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Savage, M., J. N. Mast, and J. J. Feddema. 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. *Canadian Journal of Forest Research* 43:570–583.

Shive, K. L., B. L. Estes, A. M. White, H. D. Safford, K. L. O'Hara, and S. L. Stephens. 2017. Rice straw mulch for post-fire erosion control: assessing non-target effects on vegetation communities. *International Journal of Wildland Fire* 26:538–549.

Stephens, S. L., J. K. Agee, P. Z. Fule, M. P. North, W. H. Romme, T. W. Swetnam, and M. G. Turner. 2013. Managing Forests and Fire in Changing Climates. *Science* 342:41–42.

Stephens, S. L., and B. M. Collins. 2004. Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. *Northwest Science* 78:12–23.

Stephens, S. L., B. M. Collins, E. Biber, and P. Z. Fulé. 2016. U.S. federal fire and forest policy: emphasizing resilience in dry forests. *Ecosphere* 7:e01584.

Stephens, S. L., and L. W. Ruth. 2005. Federal forest policy in the United States. *Ecological Applications* 15:532–542.

Stevens, J. T., B. M. Collins, J. D. Miller, M. P. North, and S. L. Stephens. 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. *Forest Ecology and Management* 406:28–36.

Sugihara, N. G., J. van Wagtendonk, J. Fites-Kaufman, A. E. Thode, and J. K. Agee, editors. 2006. Fire in California's Ecosystems. University of California Press.

Tepley, A., J. Thompson, H. Epstein, and K. Anderson-Teixeira. 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. *Global Change Biology* 23.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual review of ecology and systematics* 20:171–197.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849.

Turner, M. G., D. C. Donato, and W. H. Romme. 2013. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. *Landscape Ecology* 28:1081–1097.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67:411–433.

U.S. Geological Survey. 2014. U.S. Geological Survey, The National Map. t http://nationalmap.gov/3dep_prodserv.html.

USDA Forest Service. 1990. Silvics of North America Volume 1: Conifers. United States Department of Agriculture (USDA), Forest Service.

Vander Wall, S. B. 2008. On the relative contributions of wind vs. animals to seed dispersal of four Sierra Nevada pines. *Ecology* 89:1837–1849.

Venable, D. L. 1992. Size-Number Trade-Offs and the Variation of Seed Size with Plant Resource Status. *The American Naturalist* 140:287–304.

Welch, K. R., H. D. Safford, and T. P. Young. 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. *Ecosphere* 7:e01609.

Wood, S. N. 2006. Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC Press.

Young, D. J. N., J. T. Stevens, J. M. Earles, J. Moore, A. Ellis, A. L. Jirka, and A. M. Latimer. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecology Letters* 20:78–86.

CHAPTER 4: ALTERNATIVE STABLE STATES AFTER DISTURBANCE IN ECOSYSTEMS WITH LONG RECOVERY TIMES: IDENTIFYING POSITIVE FEEDBACKS AND COMMUNITY CHARACTERISTICS

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.

Introduction

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.
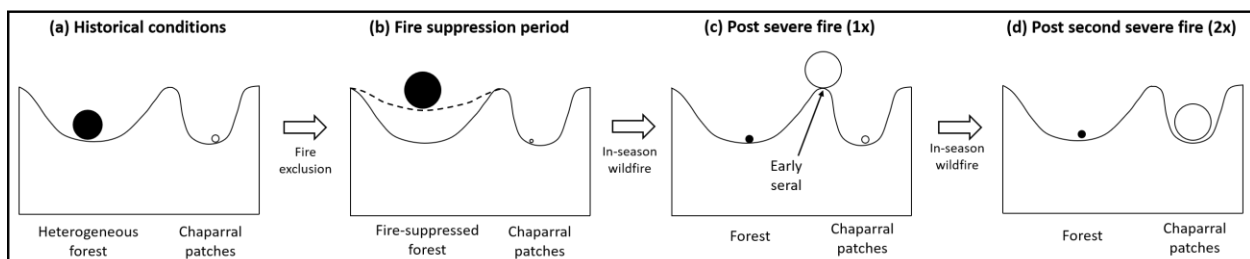
Figure 1. Ball-and-cup model of alternative stable states proposed for areas that were historically Sierran mixed conifer. In each diagram the ball represents vegetation communities and its size represents the relative differences in contiguous patch sizes between the following time steps: (a) Historic 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.
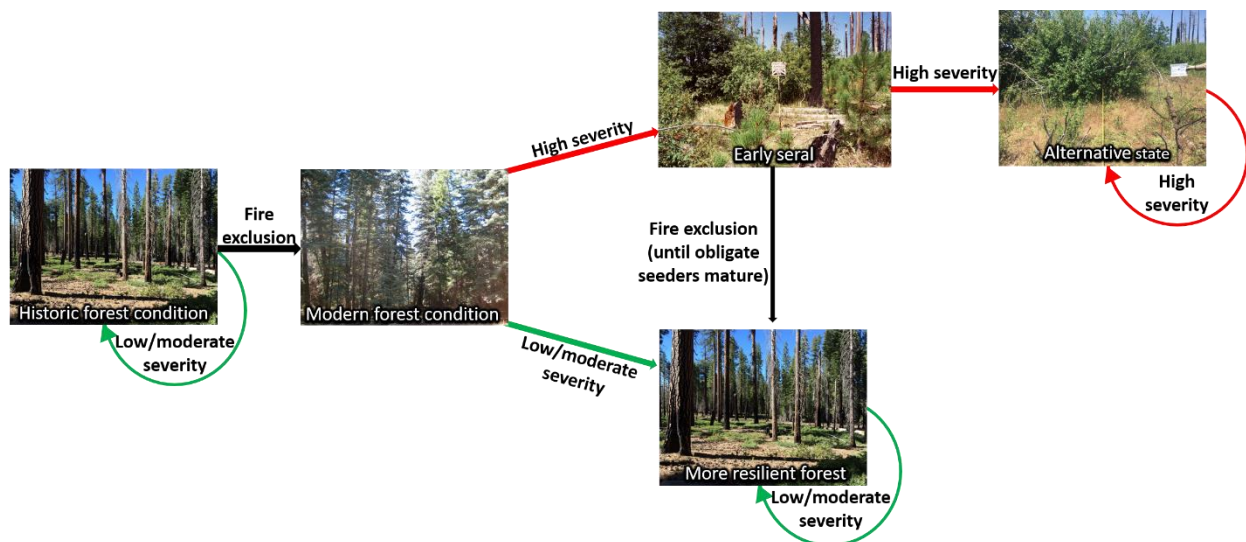

Figure 2. Positive feedbacks associated with both historic and current alternative states. Feedbacks are represented by looped arrows and transitions are represented by straight arrows. The fire severity that maintains a given state is shown within the loop. Note regenerating conifers in early seral 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.

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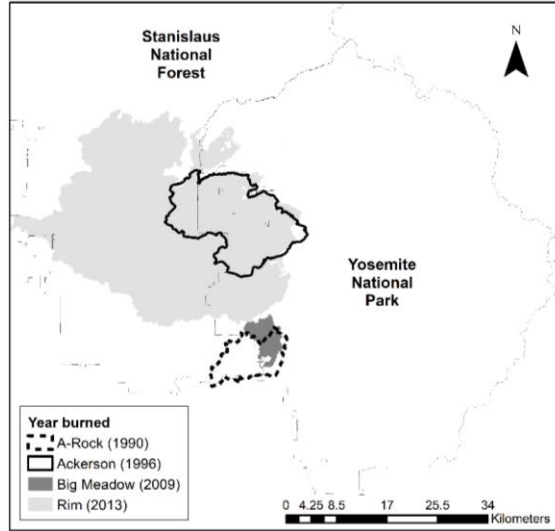
Figure 3. Map of study area. Reburn analyses were conducted for entire footprint of Big Meadow Fire and for the Rim Fire within YNP. Field data was collected on twice-severely burned areas in the overlapping fires, and once-severely burned areas of the Rim and Big Meadow that did not burn in the 1990s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

51

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
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).
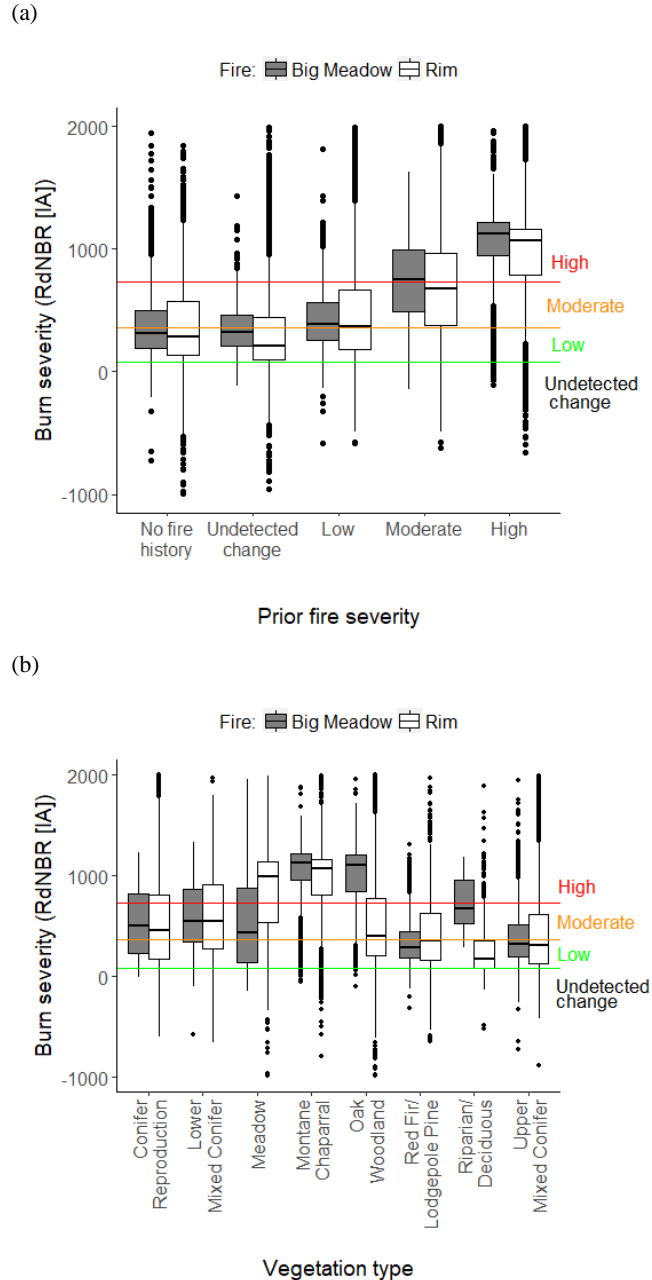
(a)

(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).
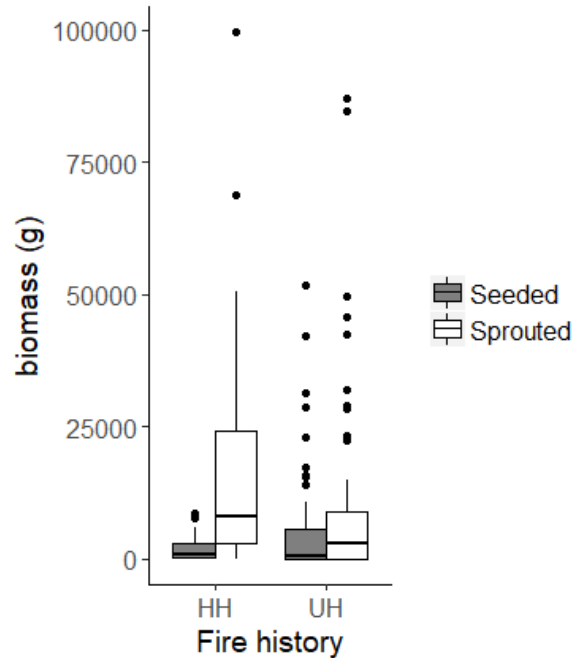

Figure 5. Estimated total shrub biomass by regeneration strategy.

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 ($\pm$ 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 ($\pm$ 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 >100 m from a lesser burned edge ($N_{high-high}$ = 48, $N_{unburned-high}$ = 30), there was still a highly significant difference between treatments (p < 0.001), with mean seedling densities in UH areas of 909 ($\pm$ 391) seedlings ha^{-1} versus 34 ($\pm$ 19) seedlings ha^{-1} in HH areas.
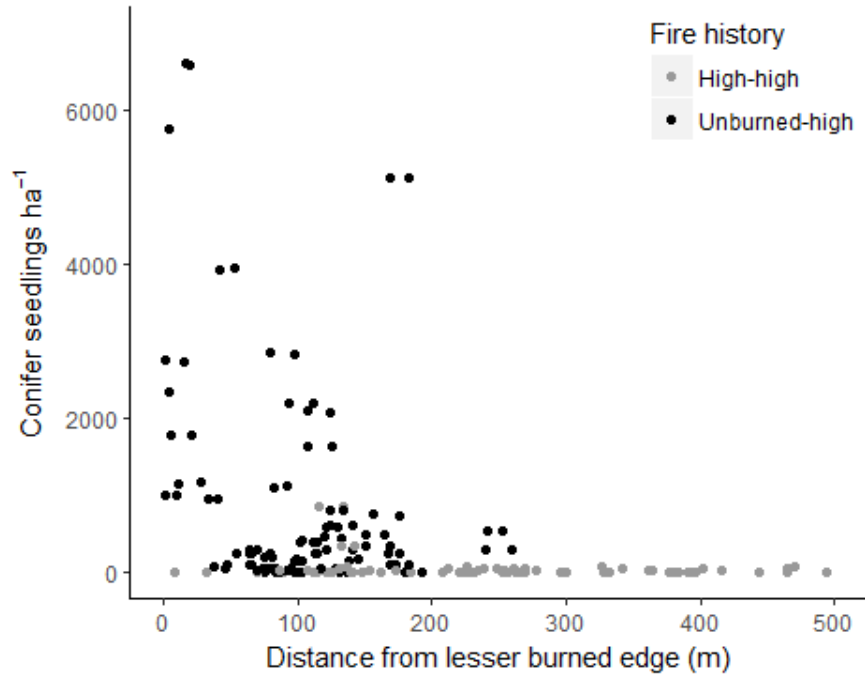
Figure 6. Conifer seedling densities by fire history at a range of distance to lesser-burned edge. Three unburned-high plots with densities $> 7,000$ seedlings ha^{-1} were excluded for plot readability.

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.
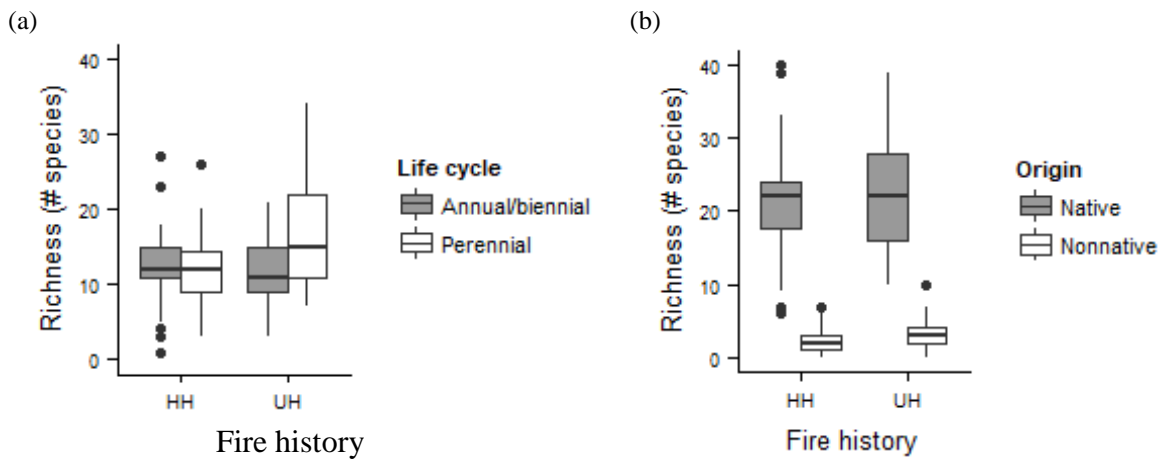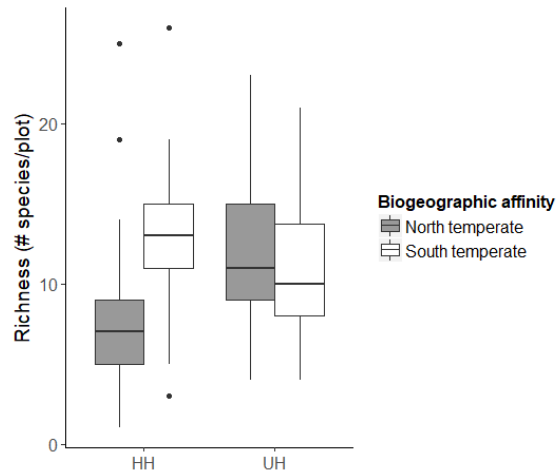
(c)

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 ($\pm$ 2.60) Mg ha^{-1} in UH areas and 11.89 ($\pm$ 1.80) Mg ha^{-1} in HH areas (p < 0.001). Coarse woody debris averaged 69.48 ($\pm$ 9.97) Mg ha^{-1} in UH areas and 35.02 ($\pm$ 5.29) Mg ha^{-1} in UH areas (p = 0.005). Mean litter depth was higher in UH (3.25 $\pm$ 0.19 cm) versus HH areas (2.35 $\pm$ 0.19 cm) (p = 0.003), as was duff depth (UH: 0.21 $\pm$ 0.04 cm, HH: 0.13 $\pm$ 0.03 cm, p = 0.005; Figure 8).
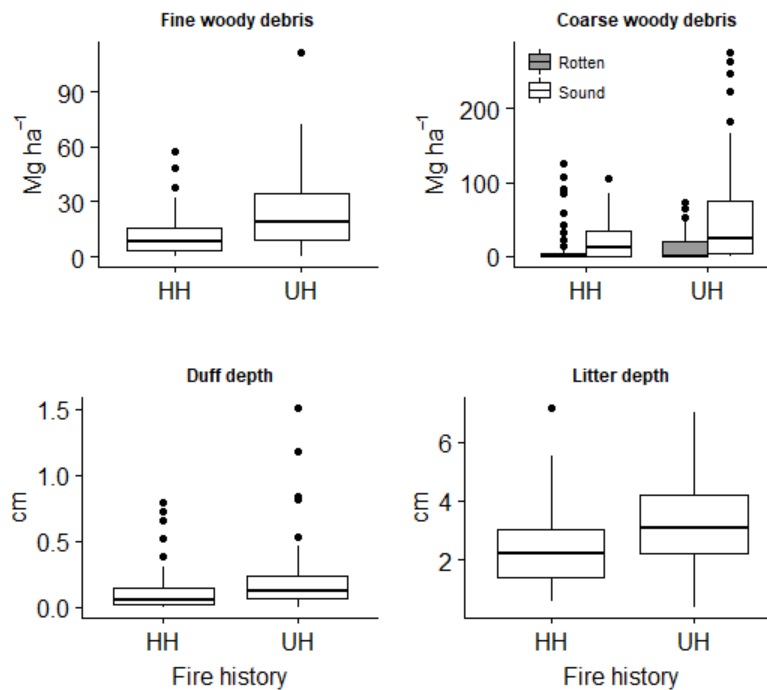

Figure 8. Total fine and coarse woody debris loads and average litter and duff depth. HH stands for repeated high severity areas and UH stands for once-burned at high severity.

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).
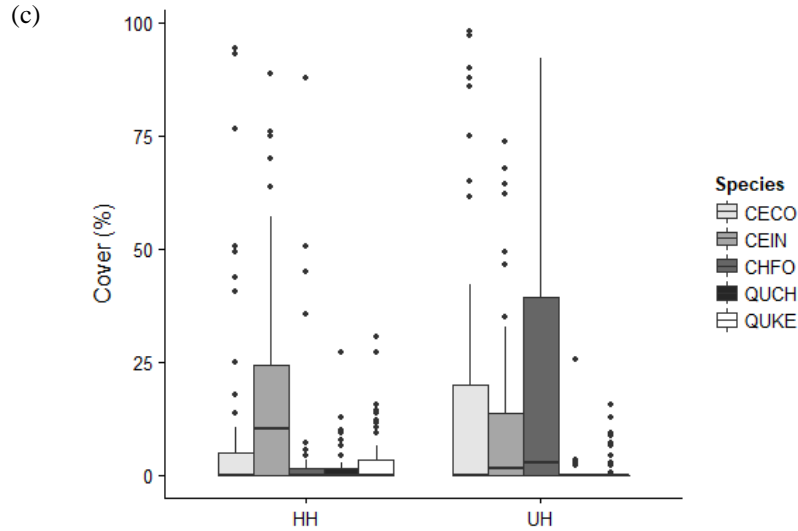
(a)

(b)

61

(c)
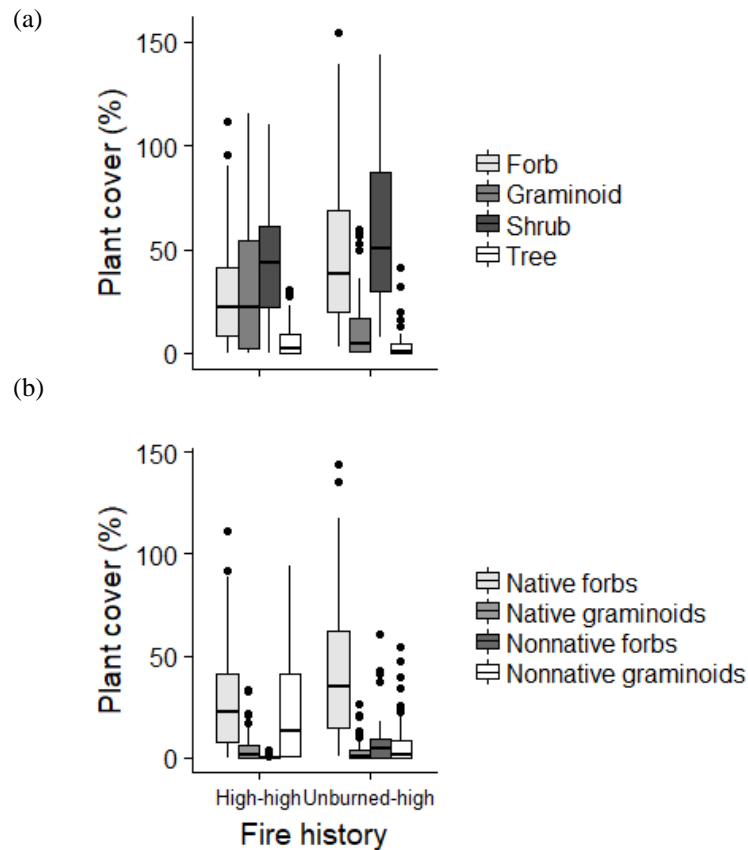
Figure 9. Relative plant cover (%) by lifeform (a), by plant origin for forbs and graminoids (b) and by dominant shrub and sprouting tree species (c), including: *C. cordulatus* (CECO), *C. integerrimus* (CEIN), *C. foliolosa* (CHFO), *Q. chrysolepis* (QUCH) and *Q. kelloggii* (QUKE). Percent cover may 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 ($p = 0.513$).
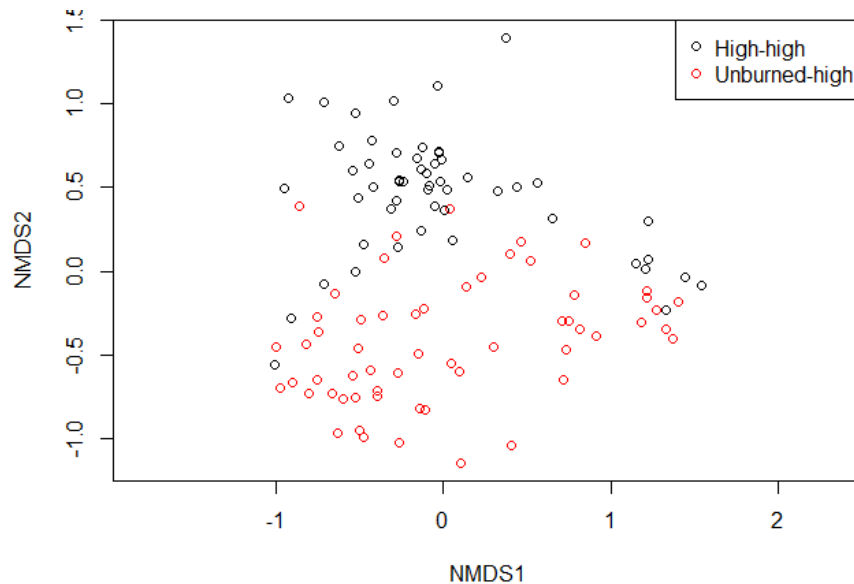

Figure 10. Non-metric multidimensional scaling (NMDS) ordination of plant communities by plot, colored by fire history.

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.

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.

Works cited

Anderson, M.J. (2006). Distance-Based Tests for Homogeneity of Multivariate Dispersions. Biometrics 62, 245–253.

Anderson, M.J., Ellingsen, K.E., and McArdle, B.H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.* 9, 683–693.

Blackhall, M., Raffaele, E., Paritsis, J., Tiribelli, F., Morales, J.M., Kitzberger, T., Gowda, J.H., and Veblen, T.T. (2017). Effects of biological legacies and herbivory on fuels and flammability traits: A long-term experimental study of alternative stable states. *J. Ecol.* 105, 1309–1322.

Boisramé, G., Thompson, S., Collins, B., and Stephens, S. (2017a). Managed Wildfire Effects on Forest Resilience and Water in the Sierra Nevada. *Ecosystems* 20, 717–732.

Boisramé, G.F.S., Thompson, S.E., Kelly, M., Cavalli, J., Wilkin, K.M., and Stephens, S.L. (2017b). Vegetation change during 40 years of repeated managed wildfires in the Sierra Nevada, California. *For. Ecol. Manag.* 402, 241–252.

Bradshaw, L., and McCormick, E. (2009). FireFamily Plus user's guide, version 4 (Ogden, Utah, USA: USDA Forest Service Rocky Mountain Research Station).

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., and Pyke, D. (2004). Effects of Invasive Alien Plants on Fire Regimes. *BioScience* 54, 677–688.

Brown, J.K. (1974). Handbook for inventorying downed woody material. (Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station).

Chambers, M.E., Fornwalt, P.J., Malone, S.L., and Battaglia, M. (2016). Patterns of conifer regeneration following high severity wildfire in ponderosa pine - dominated forests of the Colorado Front Range. *For. Ecol. Manag.* 378 57-67 378, 57–67.

Collins, B.M., and Roller, G.B. (2013). Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. *Landsc. Ecol.* 28, 1801–1813.

Collins, B.M., Miller, J.D., Thode, A.E., Kelly, M., van Wagtendonk, J.W., and Stephens, S.L. (2009). Interactions Among Wildland Fires in a Long-Established Sierra Nevada Natural Fire Area. *Ecosystems* 12, 114–128.

Collins, B.M., Everett, R.G., and Stephens, S.L. (2011a). Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere* 2, art51.

Collins, B.M., Everett, R.G., and Stephens, S.L. (2011b). Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. *Ecosphere* 2, art51.

Collins, B.M., Lydersen, J.M., Everett, R.G., Fry, D.L., and Stephens, S.L. (2015). Novel characterization of landscape-level variability in historical vegetation structure. *Ecol. Appl.* 25, 1167–1174.

Coppoletta, M., Merriam, K.E., and Collins, B.M. (2016). Post-fire vegetation and fuel development influences fire severity patterns in reburns. *Ecol. Appl.* 26, 686–699.

D'Antonio, C.M., and Vitousek, P.M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 63–87.

Deeming, J.E., Lancaster, J.W., Fosberg, M.A., and Schroeder, M.J. (1974). The National Fire-Danger Rating System. (Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture).

Dodson, E.K., and Root, H.T. (2013). Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in a ponderosa pine forest, Oregon, USA. *For. Ecol. Manag.* 302, 163–170.

Dufrene, M., and Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.

Feddema, J.J., Mast, J.N., and Savage, M. (2013). Modeling high-severity fire, drought and climate change impacts on ponderosa pine regeneration. *Ecol. Model.* 253, 56–69.

Franklin, J., Syphard, A.D., He, H.S., and Mladenoff, D.J. (2005). Altered Fire Regimes Affect Landscape Patterns of Plant Succession in the Foothills and Mountains of Southern California. *Ecosystems* 8, 885–898.

Fulé, P.Z., Crouse, J.E., Roccaforte, J.P., and Kalies, E.L. (2012). Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *For. Ecol. Manag.* 269, 68–81.

Haire, S.L., and McGarigal, K. (2010). Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (Pinus ponderosa) in New Mexico and Arizona, USA. *Landsc. Ecol.* 25, 1055–1069.

Holling, C.S. (1973). Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.

Jenness, J., Brost, B., and Beier, P. (2013). Land Facet Corridor Designer: Extension for ArcGIS (Jenness Enterprises).

Jiménez Esquilín, A.E., Stromberger, M.E., Massman, W.J., Frank, J.M., and Shepperd, W.D. (2007). Microbial community structure and activity in a Colorado Rocky Mountain forest soil scarred by slash pile burning. *Soil Biol. Biochem.* 39, 1111–1120.

Keeley, J.E. (1991). Seed germination and life history syndromes in the California chaparral. *Bot. Rev.* 57, 81–116.

Keeley, J.E. (2006). Fire Management Impacts on Invasive Plants in the Western United States. *Conserv. Biol.* 20, 375–384.

Kemp, K.B., Higuera, P.E., and Morgan, P. (2016). Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. *Landsc. Ecol.* 31, 619–636.

Knapp, E.E., Weatherspoon, C.P., and Skinner, C.N. (2012). Shrub Seed Banks in Mixed Conifer Forests of Northern California and the Role of Fire in Regulating Abundance. *Fire Ecol.* 8, 32–48.

Lutz, J.A., Key, C.H., Kolden, C.A., Kane, J.T., and van Wagtendonk, J.W. (2011). Fire Frequency, Area Burned, and Severity: A Quantitative Approach to Defining a Normal Fire Year. *Fire Ecol.* 7, 51–65.

Lydersen, J.M., Collins, B.M., Brooks, M.L., Matchett, J.R., Shive, K.L., Povak, N.A., Kane, V.R., and Smith, D.F. (2017). Evidence of fuels management and fire weather influencing fire severity in an extreme fire event. *Ecol. Appl.*

Mallek, C., Safford, H.D., Viers, J., and Miller, J. (2013). Modern departures in fire severity and area by forest type, Sierra Nevada and southern Cascades, California, USA. *Ecosphere* 4, 1–28.

McGinnis, T.W., Shook, C.D., and Keeley, J.E. (2010). Estimating aboveground biomass for broadleaf woody plants and young conifers in Sierra Nevada, California, forests. *West. J. Appl. For.* 25, 203–209.

Miller, J.D., and Safford, H. (2012). Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and Southern Cascades, California, USA. *Fire Ecol.* 8, 41–57.

Miller, J.D., and Thode, A.E. (2007). Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sens. Environ.* 109, 66–80.

Miller, J.D., Knapp, E.E., Key, C.H., Skinner, C.N., Isbell, C.J., Creasy, R.M., and Sherlock, J.W. (2009). Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. *Remote Sens. Environ.* 113, 645–656.

Monsanto, P.G., and Agee, J.K. (2008). Long-term post-wildfire dynamics of coarse woody debris after salvage logging and implications for soil heating in dry forests of the eastern Cascades, Washington. *For. Ecol. Manag.* 255, 3952–3961.

Nagel, T.A., and Taylor, A.H. (2005). Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California, USA1. *J. Torrey Bot. Soc.* 132, 442–457.

Nash, M.S., and Bradford, D.S. (2001). Parametirc and non parametric (MARS: Multivariate additive regression splines) Logistic regressions for prediction of a dichotomous response variable with an example for presence/absence of amphibians (Washington, DC: U.S. Environmental Protection Agency).

Parsons, D.J., and DeBenedetti, S.H. (1979). Impact of fire suppression on a mixed-conifer forest. *For. Ecol. Manag.* 2, 21–33.

Pickett, S.T.A. (1989). Space-for-Time Substitution as an Alternative to Long-Term Studies. In Long-Term Studies in Ecology: Approaches and Alternatives, G.E. Likens, ed. (New York, NY: Springer New York), pp. 110–135.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing (Vienna, Austria).

Raven, P.H., and Axelrod, D.I. (1978). Origin and Relationships of the California Flora (Berkeley, California: University of California Press).

Rother, M.T., and Veblen, T.T. (2016). Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. *Ecosphere* 7, n/a-n/a.

Russell, W.H., McBride, J., and Rowntree, R. (1998). Revegetation after four stand-replacing fires in the Lake Tahoe Basin. *Madroño* 45, 40–46.

Safford, H.D., and Stevens, J.T. (2017). Natural Range of Variation (NRV) for yellow pine and mixed conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. (Albany, CA: USDA Forest Service, Pacific Southwest Research Station).

Safford, H.D., Schmidt, D.A., and Carlson, C.H. (2009). Effects of fuel treatments on fire severity in an area of wildland–urban interface, Angora Fire, Lake Tahoe Basin, California. *For. Ecol. Manag.* 258, 773–787.

Santi, P., and Morandi, L. (2013). Comparison of debris-flow volumes from burned and unburned areas. *Landslides* 10, 757–769.

Scheffer, M. (2009). Critical Transitions in Nature and Society (Princeton University Press).

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature* 413, 591–596.

Schröder, A., Persson, L., and De Roos, A.M. (2005). Direct experimental evidence for alternative stable states: a review. *Oikos* 110, 3–19.

Schwilk, D.W., and Westoby, A.E.M. (2003). Flammability Is a Niche Construction Trait: Canopy Architecture Affects Fire Intensity. *Am. Nat.* 162, 725–733.

Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J., Bailey, J.D., Fettig, C.J., Fiedler, C.E., Harrod, R.J., Moghaddas, J.J., and Outcalt, K.W. (2009). The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. *Ecol. Appl.* 19, 285–304.

Scott, J.H., and Burgan, R.E. (2005). Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. Bark Beetles Fuels Fire Bibliogr. 66.

Stephens, S.L., Lydersen, J.M., Collins, B.M., Fry, D.L., and Meyer, M.D. (2015). Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. *Ecosphere* 6, art79.

Stevens, J.T., Safford, H.D., Harrison, S., and Latimer, A.M. (2015). Forest disturbance accelerates thermophilization of understory plant communities. *J. Ecol.* 103, 1253–1263.

Stevens, J.T., Collins, B.M., Miller, J.D., North, M.P., and Stephens, S.L. (2017). Changing spatial patterns of stand-replacing fire in California conifer forests. *For. Ecol. Manag.* 406, 28–36.

Stevens-Rumann, C., and Morgan, P. (2016). Repeated wildfires alter forest recovery of mixed-conifer ecosystems. *Ecol. Appl.* 26, 1842–1853.

Stevens-Rumann, C., Shive, K., Fulé, P., and Sieg, C.H. (2013). Pre-wildfire fuel reduction treatments result in more resilient forest structure a decade after wildfire. *Int. J. Wildland Fire* 22, 1108.

Suding, K.N., Gross, K.L., and Houseman, G.R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19, 46–53.

Tepley, A., Thompson, J., Epstein, H., and Anderson-Teixeira, K. (2017). Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. *Glob. Change Biol.* 23.

Thompson, J.R., Spies, T.A., and Ganio, L.M. (2007a). Reburn severity in managed and unmanaged vegetation in a large wildfire. *Proc. Natl. Acad. Sci.* 104, 10743–10748.

Thompson, J.R., Spies, T.A., and Ganio, L.M. (2007b). Reburn severity in managed and unmanaged vegetation in a large wildfire. *Proc. Natl. Acad. Sci.* 104, 10743–10748.

Turner, M.G., Donato, D.C., and Romme, W.H. (2013). Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. *Landsc. Ecol.* 28, 1081–1097.

van Wagtendonk, K. (2012). Fires in Previously Burned Areas: Fire Severity and Vegetation Interactions in Yosemite National Park. Rethink. Prot. Areas Chang. World Proc. 2011 George Wright Soc. Bienn. Conf. Parks Prot. Areas Cult. Sites.

van Wagtendonk, J.W., van Wagtendonk, K.A., and Thode, A.E. (2012). Factors Associated with the Severity of Intersecting Fires in Yosemite National Park, California, USA. *Fire Ecol.* 7, 11–31.

Warton, D.I., and Hui, F.K.C. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92, 3–10.

Welch, K.R., Safford, H.D., and Young, T.P. (2016). Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. *Ecosphere* 7, e01609.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., and Swetnam, T.W. (2006). Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940–943.

Westerling, A.L., Bryant, B.P., Preisler, H.K., Holmes, T.P., Hidalgo, H.G., Das, T., and Shrestha, S.R. (2011). Climate change and growth scenarios for California wildfire. *Clim. Change* 109, 445–463.

Wimberly, M.C., Cochrane, M.A., Baer, A.D., and Pabst, K. (2009). Assessing fuel treatment effectiveness using satellite imagery and spatial statistics. *Ecol. Appl.* 19, 1377–1384.