

FINAL REPORT

Post-fire forest regeneration in a changing climate

JFSP PROJECT ID: 15-2-01-34

September 2017

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List of Abbreviations/Acronyms

CCA: constrained correspondence analysis
GIS: geographic information system
SD: standard deviation
USFS: United States Forest Service

Keywords

Forest, fire, tree, shrub, regeneration, seedling, climate change, drought, community, distribution

Acknowledgments

We thank the many dedicated field technicians who have helped to collect the data presented in this report and the numerous U.S. Forest Service staff who generously facilitated field logistics. We gratefully acknowledge funding from the Joint Fire Science Program, the UC Davis Department of Plant Sciences, Hatch Project CA-D-PLS-2017-H, and the U.S. Forest Service.

Abstract

Severe disturbance such as wildfire may create important opportunities for plant communities to reorganize in response to environmental change, including climate change. Disturbance may be particularly important in forests where the foundational plant species (trees) are long-lived and usually establish soon after disturbance. The response of post-fire tree establishment to post-fire weather conditions could therefore provide useful information about how forest communities will respond to climate change. We examined the effect of post-fire weather conditions on regenerating vegetation in fire-adapted forests in northern California, USA by surveying plots 4-5 years after 14 different wildfires that burned between 2004 and 2012. This time period (2004-2016) encompassed a wide range of annual weather conditions, including a period of extreme drought as well as relatively wet years. We related post-fire establishment patterns of trees, shrubs, and graminoids at 535 severely burned plots to the average climate at each plot and to departures from the average during the first 3 years after fire. For the most common tree species, we observed either (a) decreased establishment under unusually dry post-fire conditions or (b) low sensitivity of regeneration to post-fire weather. However, in general, post-fire regeneration patterns were explained more strongly by long-term climate and topography variables and local adult tree species abundance than by post-fire weather conditions. This observation suggests that surviving adult trees may contribute to a “biological inertia” that restricts the extent to which tree community composition will track changes in climate through post-disturbance regeneration. In contrast to our observations in trees, we observed substantial *increases* in shrub and graminoid cover under post-fire drought, suggesting that fire-driven forest-to-chaparral type conversion may become more common with increasing aridity resulting from climate change. Taken together, our conclusions imply that managers may need to allocate more resources to post-fire management (e.g., tree planting and shrub control) if they wish to (a) facilitate forest tree community in tracking shifts in climate and/or (b) maintain historical tree growth and survival rates given the potential for increasing shrub competition.

Objectives

Our overarching objective was to gain insight into how post-fire forest regeneration patterns in the yellow pine—mixed conifer forests of California may be influenced by future changes in climate. We proposed to address this question by evaluating how weather patterns in the years immediately following wildfire influence post-fire regeneration trajectories, accounting for the influence of site factors including pre-fire forest conditions, distance to seed source, and topography. The key to our approach was the idea that post-fire regeneration patterns under anomalous conditions (e.g., post-fire drought) could reflect expectations of regeneration patterns in a future in which conditions that are currently rare or anomalous become more frequent or commonplace.

We also proposed to examine whether evaluating regeneration patterns soon after wildfire was sufficient to understand likely longer-term recovery outcomes. Our approach involved taking advantage of an extensive existing dataset of post-fire forest regeneration data that our research group has collected to date and extending it with additional regeneration data collected from (a) fires that were immediately followed by the historic California drought of

2012-2015 and (b) revisits of the original plots 5-10 years following initial survey date (see Methods, below). Our research questions were as follows:

- 1) To what extent does post-wildfire weather affect regeneration trajectories?
 - a) How important are pre-disturbance conditions relative to post-fire weather? That is, what is the extent of biological inertia in the system?
 - b) How do the effects of post-fire weather on tree seedling establishment success differ by species?
 - c) How might the effects of weather on regeneration patterns depend on site factors such as long-term average climate and distance from seed source?
- 2) Are regeneration trajectories dependent primarily on the vegetation that establishes in the five years immediately following wildfire? That is, are the patterns observed within five years of fire representative of longer-term recovery trajectories, or do trajectories often diverge after this period?
- 3) How are regeneration patterns likely to change in the face of increasing drought stress?

Our questions and objectives related to the JFSP GRIN task statement in that they involved augmenting the graduate student investigator's ongoing dissertation research, furthering opportunity for the student to interact with forest managers, and contributing to enhanced understanding of issues relevant to forest and fire management. In particular, the proposal addressed the JFSP-identified priority area of interactions between climate change and fire effects—in this case, specifically as related to post-fire recovery trajectories. We met all study objectives. We augmented our existing post-fire regeneration dataset by surveying 332 previously unsurveyed plots from 6 different fires and revisiting 53 previously surveyed burned plots on 4 different fires. We revisited fewer plots than we intended because relocating plots was more difficult than we had anticipated, but the sample we obtained was sufficient for addressing our study questions. Our procedures for collecting and analyzing data and the resulting insights and management implications are outlined in the remainder of this report.

Background

Climate change is expected to substantially alter the distribution of sites that are environmentally suitable for specific plant species. However, in forests, where the foundational plant species (trees) are long-lived and often dispersal-limited, it is unclear whether species and communities will have sufficient capacity to disperse and reorganize in order to track changes in climate (McLachlan et al. 2005, Aitken et al. 2008). In fire-prone forest ecosystems where many tree species primarily recruit soon after disturbance (Shatford et al. 2007, Donato et al. 2009, Tepley et al. 2017), wildfire may present an important opportunity for forest trees to adapt and reorganize in response to climate change (Campbell and Shinneman 2017). However, recent efforts to identify such responses have been inconclusive, suggesting that when combined with wildfire, increasing aridity may either (a) lead to tree establishment declines and/or range contraction (Harvey et al. 2016, Tepley et al. 2017, Campbell and Shinneman 2017), or (b) have weak and/or highly species-specific effects (Savage and Mast 2005, Harvey et al. 2016, Liu 2016, Urza and Sibold 2017, Campbell and Shinneman 2017).

In forests, factors that influence establishment soon after disturbance can have a profound impact on long-term community trajectories. Areas where initial post-fire tree regeneration is poor can quickly become dominated by non-tree species (i.e., shrubs and herbaceous vegetation)

and remain so for decades (Russell et al. 1998, Savage and Mast 2005, Young and Peffer 2010, Lauvaux et al. 2016), and differences in establishment success among tree species can also have long-term effects on community composition (Barbour et al. 1990). A clear understanding of the sensitivity of post-fire vegetation establishment to variation in weather and climate is therefore essential for (a) predicting the extent to which forest composition and function will keep pace with climate change and (b) implementing post-fire forest management such as tree planting in situations where natural regeneration is not expected to meet management goals. The dependence of post-fire regeneration outcomes on site factors such as fire severity, pre-fire community composition, distance to seed source, and soil texture have been well documented (e.g., Turner et al. 1997, Greene et al. 2004, Larson and Franklin 2005, Donato et al. 2009, Crotteau et al. 2013, Cai et al. 2013, Welch et al. 2016). However, comparatively few studies have evaluated the effects of climate and weather on post-fire tree establishment dynamics, despite their potential importance for understanding how forests may respond to climate change.

One approach for gaining insight into potential impacts of climate change on post-fire regeneration trajectories is to examine the establishment that occurs under different post-fire weather scenarios. Regeneration patterns observed under anomalously dry post-fire conditions, for example, may reflect the patterns that could be expected in an overall hotter, drier climate. Applications of this approach (Savage and Mast 2005, Harvey et al. 2016, Urza and Sibold 2017) have revealed that for some species in some sites, dry post-fire conditions are associated with reduced regeneration, but in other cases, post-fire weather does not significantly or consistently explain regeneration patterns. An alternative approach for inferring climate change impacts on post-fire establishment involves examining regeneration patterns along spatial gradients in long-term average climate (Tepley et al. 2017); this approach has revealed that post-fire conifer establishment declines as long-term average aridity increases across space and, by extension, potentially through time. Similarly, simulation modeling has suggested that when combined with warming and drying, wildfire may accelerate range contraction of conifers at hot, dry range limits (by eliminating established adults from sites that are no longer suitable for establishment) but that colonization of new sites may be poor due to dispersal limitation and/or limited availability of climatically suitable sites (Campbell and Shinneman 2017).

Post-fire forest regeneration may depend on (a) spatial gradients in long-term average environmental (e.g., climatic) conditions and/or (b) shorter-term post-fire (e.g., weather) conditions, but work to date has only explored variation along one of these two axes of variation at a time. In this study, we examine post-fire regeneration patterns along multiple gradients in long-term average climate and post-fire weather conditions in an effort to reconcile conflicting prior results and evaluate the potential for disturbance to facilitate forests in responding to climate change.

We expected our exploration of regeneration patterns to reveal shifts in community composition and species distributions consistent with climate sensitivity; specifically, we hypothesized that in dry sites, anomalously dry post-fire conditions would suppress conifer regeneration and promote shrub establishment, while at the cooler, wetter extreme, anomalously dry conditions would lead to stronger conifer regeneration, at least up to a point (Fig. 1). Our prediction for cooler, wetter locations originates from the frequent observation that performance of conifer species near their cooler, wetter distributional limits is suppressed by factors that reduce growing season length (Barbour et al. 1991, Lo et al. 2010, Ettinger and HilleRisLambers 2013, Dolanc et al. 2013), including cooler temperatures and greater winter precipitation. Both of these factors contribute to a larger and/or longer-lasting snowpack, which prevents plants from

taking advantage of the otherwise cool, moist, high-productivity conditions in spring (Tague et al. 2009). Additionally, due to the common observation of conifer establishment pulses that coincide with extreme historical weather patterns (Brown et al. 1995, North et al. 2005), we expected that post-fire weather extremes (i.e., the presence or absence a single very dry year) would explain more variation in regeneration patterns than longer-term post-fire weather conditions.

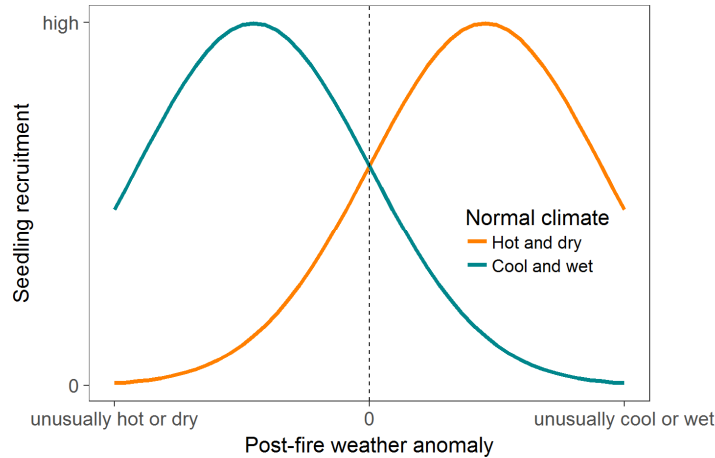


Fig. 1

Hypothesized regeneration patterns along a gradient of post-fire weather anomaly assuming effective tracking of climate change. In normally hot and dry sites (orange line), we hypothesize that abnormally dry post-fire conditions would reduce regeneration, while abnormally wet conditions would increase regeneration, at least to a point, after which conditions may become too wet for optimal establishment. We expect the opposite pattern in sites that are normally cool and wet (blue line).

Materials and Methods

Study System

We studied forest regeneration patterns following 14 wildfires that burned between 2004 and 2012 in yellow pine—mixed conifer forests (Safford and Stevens 2017) in the northern Sierra Nevada and southern Cascades mountains in California, USA (Fig. 2; Table 1). Our study sites experience a Mediterranean climate with wet winters and an annual summer dry period lasting from 4 to 6 months each year. Because most of our study fires are large and encompass broad topographic gradients, our study captures substantial environmental variation both within and among fires (Fig. 2). We surveyed fires that occurred over many years in order to sample variation in post-fire weather conditions. By design, therefore, our study includes fires that were followed by wet periods and others that were followed by dry periods (see Weather, climate, and solar exposure data; Fig. 2), including two fires that burned in 2012 and were followed by the extreme 2012-2015 California drought (Robeson 2015).

Forests in our study region are generally dominated by yellow pine (*Pinus ponderosa* Laws. and/or *Pinus jeffreyi* Balf.) and/or white fir (*Abies concolor* (Gordon & Glend.)), with other conifer and broadleaf tree species present in varying abundances depending on the site

(Table 1). Yellow pine is strongly shade-intolerant and establishes primarily in open and/or disturbed areas, while white fir is relatively shade-tolerant and can establish in closed-canopy forest as well as in disturbed areas (Burns and Honkala 1990, Zald et al. 2008). Within the southern Cascades and western Sierra Nevada, yellow pine and white fir primarily occur in areas with a mean annual precipitation of roughly 350-1750 mm y^{-1} and 1000 to 1500 mm y^{-1} , respectively (Burns and Honkala 1990).

Yellow pine—mixed conifer forests historically experienced frequent low-to-moderate severity fires (Miller and Safford 2017). As a consequence of a century of fire suppression, fires in this system are now generally much less frequent, larger, and higher severity (Mallek et al. 2013) and can create extensive areas with no seed sources for conifer re-establishment (Stevens et al. *in press*). Shrubs, which can resprout from the base and/or germinate from an often extensive bank of seeds that are scarified by fire (Kauffman and Martin 1990, Knapp et al. 2012), tend to rapidly dominate severely burned areas (Collins and Roller 2013, Welch et al. 2016) and, when initial conifer regeneration is poor, can remain dominant for many decades (Nagel and Taylor 2005, Lauvaux et al. 2016). In the absence of disturbance, many shrubs in the system are associated with more xeric conditions (Fites-Kaufman et al. 2007). Broadleaf (angiosperm) trees in the system can also readily resprout from the base or germinate from seeds that are generally large and animal-dispersed (McDonald and Tappeiner 1996). In contrast to shrubs and hardwoods, the primary conifers in the system do not resprout, germinate from seeds that have a maximum viability of one year, and are not serotinous.

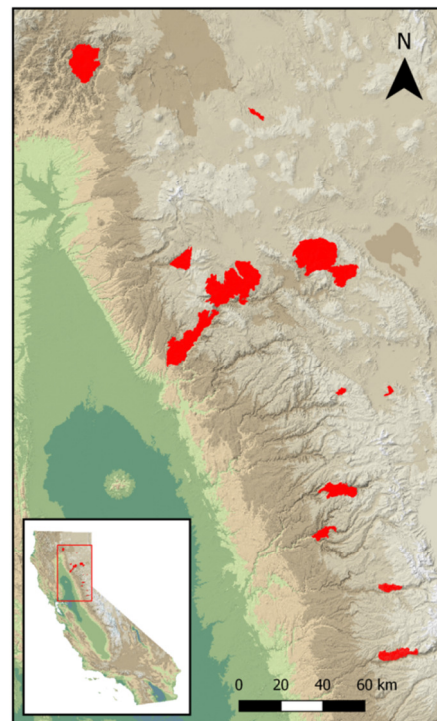


Fig. 2

Map of study fires (red polygons). The 14 study fires are represented as 12 distinct polygons because two pairs of fires partially overlapped. The inset image shows the state of California, USA, with a red box indicating the extent of the main map. Background color shading reflects elevation from green (low) to white (high).

Plot Selection

Within each of the 14 study fires, we selected study plot locations by overlaying a grid of points with 200 m x 200 m spacing, and we minimized other sources of environmental variation by including only points that had < 30% slope, were located on U.S. Forest Service (USFS) land, had not burned since the study fire, had not received management (e.g., tree planting) following the fire, and were classified using remotely-sensed imagery as having burned at moderate to high severity. For these purposes we used geospatial polygons of perimeters and severity classifications (using RdNBR; Miller and Thode 2007) of historical fires and (USDA Forest Service 2015), geospatial polygons of USFS post-fire management activities (USDA Forest Service 2016), and a 30 m-resolution digital elevation model (USGS 2016).

Within each fire, we selected survey plots from the grid of candidate points with the dual criteria of accessibility and of sampling across the available range of topographic conditions (elevation, slope, and aspect). For analysis, we only included plots that experienced > 75% basal area mortality (as assessed during the field survey; see “Field data collection,” below). Additionally, because previous work has documented poor conifer regeneration in this system when seed sources are > 60-200 m away (Welch et al. 2016), we only included plots that had a field-identified potential seed source (i.e., one or more live mature trees) < 75 m away. This resulted in a total of 535 surveyed high-severity plots (Table 1). We used these plots for all analyses except a community-level analysis, for which we incorporated additional unburned and lightly-burned reference plots on each fire. This analyses presented here used plots that had been surveyed by our research group prior to initiation of this JFSP-funded project (see Welch et al. 2016) as well as plots that we surveyed specifically for this project.

In addition to initial 4-5 year post-fire plot surveys, we revisited 53 previously surveyed severely-burned (i.e., >75% basal area mortality) plots (Table 1). These plots were located on fires that burned between 2004 and 2008 and were initially surveyed 5 years following fire, so our revisits occurred 3 to 7 years following the initial survey. The revisit data were not used for the analysis of the sensitivity of post-fire regeneration to weather variation; they were used only for the analysis of the consistency of post-fire recovery trajectories over time (see “Plot revisit analysis,” below).

Field Data Collection

We conducted all initial plot surveys 4-5 years following each wildfire (Table 1). We selected this timeframe because in this and similar systems, the large majority of post-fire tree establishment often occurs within 5 years following fire (Harvey et al. 2016, Tepley et al. 2017, Urza and Sibold 2017). At each sampling point, we established a 60 m² (4.37 m radius) circular plot. We visually estimated fire severity in and immediately surrounding each plot based on categories of basal area mortality of trees: unburned, low severity (0-25% mortality), moderate severity (25-75% mortality), and high severity (75-100% mortality). For all analyses presented here except the community-level analysis, we retained only the high-severity burned plots.

Table 1

Summary of fires included in the study.

Fire name	Fire year	Number of years following fire plots surveyed: initial (revisit)	Number of high-severity plots: initial (revisit)	Percentage of plots with regeneration (initial survey)			Percent cover of plots by vegetation lifeform (initial survey): mean (minimum, maximum)		Dominant tree species
				Yellow pine	White fir	Broadleaf trees	Shrubs	Graminoids	
American River	2008	5	19	21	53	11	25 (0, 80)	0 (0, 20)	WF, DF, YP, SP
Antelope	2007	5	38	21	0	0	26 (0, 100)	33 (0, 89)	DF, YP, WF
Bagley	2012	4	30	20	7	70	65 (2, 100)	2 (0, 30)	DF, YP, WF
Bassetts	2006	5	44	14	23	5	45 (0, 95)	0 (0, 30)	RF, WF
BTU Lightning	2008	5 (8)	43 (12)	26	28	40	16 (0, 95)	0 (0, 60)	WF, YP, SP
Chips	2012	4, 5	22	36	50	23	34 (2, 93)	0 (0, 90)	WF, SP
Cub	2008	5 (8)	61 (17)	13	46	10	32 (0, 90)	0 (0, 20)	WF, SP
Freds	2004	5 (12)	55 (2)	13	0	64	30 (0, 95)	5 (0, 47)	CO, WF, YP
Harding	2005	5	33	18	3	0	6 (0, 59)	30 (4, 80)	YP, IC
Moonlight	2007	5	62	5	8	3	40 (0, 98)	1 (0, 100)	YP, WF
Power	2004	5 (8)	73 (16)	22	0	63	25 (0, 95)	5 (0, 78)	YP, IC
Ralston	2006	5	18	50	0	83	42 (1, 85)	6 (0, 85)	BO, YP, DF
Rich	2008	4	5	100	60	60	40 (0, 90)	1 (0, 10)	WF, DF, IC, YP
Straylor	2004	5 (12)	32 (6)	3	0	3	6 (0, 80)	18 (2, 80)	YP, WJ

Note: Dominant tree species codes are as follows: WF, white fir; DF, Douglas-fir; YP, yellow pine; SP, sugar pine; RF, red fir (*Abies magnifica*); CO, canyon live oak (*Quercus chrysolepis*); IC, incense cedar; BO, black oak (*Quercus kelloggii*); WJ, western juniper (*Juniperus occidentalis*)

At each plot, we located all tree seedlings, aged them by counting terminal bud scars, and tallied and identified to species all seedlings ≥ 2 years old. As the only exception, seedlings of yellow pine (*Pinus ponderosa* and *P. jeffreyi*), which often intergrade and are difficult to distinguish from each other as young seedlings, were identified as “yellow pine”. We additionally tallied all resprouting broadleaved trees and identified them to species. We measured the height of the tallest seedling and resprout of each regenerating tree species in each plot. We additionally measured the distance from the plot center to the nearest reproductively mature tree (i.e., potential seed source for natural regeneration), though we retained only those plots < 75 m from the nearest seed source (see “Plot selection,” above). To quantify potential

sources of competition and/or facilitation for regenerating trees, we visually estimated the areal percent coverage of each plot by shrubs and graminoids and measured the modal height of the (co-) dominant shrub species. We followed the same field survey protocol for the revisits of the previously-surveyed plots.

Weather, Climate, and Solar Exposure Data

We sought to explain regeneration patterns using post-fire weather patterns as well as long-term average climate conditions (in addition to other environmental variables; see “Data preparation,” below) at each plot. We quantified long-term average (i.e., “normal”) climate conditions as the average annual water-year precipitation over the 30-year period from 1986 to 2015. We quantified post-fire weather in two ways: (1) average annual precipitation over the three water years (Oct-Sept) following each fire (hereafter referred to as “post-fire average precipitation”), and (2) the annual precipitation during the driest of the three water years following each fire (hereafter referred to as the “post-fire minimum precipitation”). The latter variable explained more variation in all regeneration response variables, so here we report the results of analyses using the “post-fire minimum precipitation” variable.

We computed post-fire weather variables as “anomalies” representing the degree of departure from long-term average precipitation. We quantified the anomalies as z-scores, or the number of standard deviations the post-fire values fall from each plot’s normal annual precipitation value, given the interannual precipitation variance over the 1986-2015 normal period. We obtained precipitation data from the monthly 4 km resolution PRISM dataset (PRISM Climate Group, Oregon State University 2016). For the community-level analysis (see “Statistical analysis,” below), we also used normal (1986-2015) temperature, which we obtained from the monthly 800 m resolution TopoWx dataset (Oyler et al. 2014). The TopoWx product builds on similar publicly-available datasets by incorporating remotely-sensed land surface temperature in addition to weather station data and by accounting for discontinuities in weather station readings related to station maintenance (Oyler et al. 2014, 2015). We extracted temperature and precipitation values each plot location using bilinear interpolation. In addition to climate and weather variables, we computed the solar exposure of each plot as the solar energy density received on March 15, based on a USGS DEM (USGS 2016) and computed in GRASS GIS (Neteler et al. 2012) using the `r.sun` function (Hofierka et al. 2002), which incorporates slope, aspect, and topographic shading (but not cloud attenuation).

Data Preparation

At each plot, we determined the presence or absence by species of regenerating trees. For the presence/absence and height dominance models (see “Statistical analysis,” below), we considered white fir and yellow pine individually, as these were the two most abundant lowest-level taxa in our dataset and have contrasting life-history strategies (see “Study system,” above). We additionally considered “broadleaf trees,” which included all angiosperm trees. We considered only conifer seedlings that recruited during the first two years following the fire (i.e., that were aged ≥ 2 or ≥ 3 , depending on the age of the fire). We selected this age threshold in order to focus on individuals that (a) experienced the majority of the 3-year window of post-fire weather conditions that we quantified, (b) were old enough to reliably locate and identify to species, and (c) had survived their period of potentially greatest environmental sensitivity (Jackson et al. 2009) and thus had greatest potential to survive into the future. Because aging using bud scars is not reliable for broadleaf trees and because nearly all regenerating broadleaf

trees were resprouts, we considered all broadleaf trees to be the same age as the fire. At all plots where tree regeneration was present, we determined the height of the tallest recruiting individual of each species and determined whether it was taller than the modal height of the dominant shrub species (as an indicator of its potential dominance over the shrubs).

Plot Revisit Analysis

At each of the 53 previously-surveyed plots that we revisited, we compared the tree regeneration that we observed during the initial survey to the regeneration that we observed during the revisit. We did this by dividing plots into two categories based on initial tree regeneration (present or absent) and then summarizing the revisit tree regeneration for each of the two categories. We performed this analysis separately for yellow pine, white fir, and broadleaf trees.

Statistical Analysis

All analyses were performed using R (R Core Team 2015). We statistically evaluated the relationship between post-fire weather and tree regeneration by species (presence-absence at the plot level) using generalized linear regression models with a Bernoulli distribution. We used clustered cross-validation (*sensu* Roberts et al. 2017) to identify the set of predictor variables that best predicted regeneration in withheld subsets of the data in the absence of post-fire weather anomaly variables. We considered all possible combinations of the following predictor variables: normal precipitation (untransformed and quadratic forms), solar radiation, and seed tree distance. We refer to this model as the “baseline model.”

We then used the same cross-validation procedure to identify the extent to which the predictive error of the baseline model was reduced (or increased) by adding predictors representing the post-fire precipitation anomaly. We considered all possible combinations of the following variables: precipitation anomaly, its interaction with normal precipitation, a quadratic transformation of the precipitation anomaly, and an interaction between the quadratic transformation of normal precipitation and the precipitation anomaly. We performed this procedure for both post-fire anomaly characterizations (post-fire average precipitation and post-fire minimum precipitation; see above for definitions). If the predictive error of the model (as evaluated through cross-validation) was decreased by adding post-fire anomaly terms, we considered post-fire precipitation anomaly to be informative of regeneration patterns. We refer to the models including post-fire anomaly terms as “anomaly models.”

We used the same two-step modeling procedure to evaluate the influence of post-fire precipitation on the areal percent cover by shrubs and by graminoids—potential competitors of tree seedlings and resprouts—as well as on the dominance (by height) of seedlings over shrubs. We fit cover models using a beta distribution, which accommodates values between 0 and 1 (R package *betareg*; Cribari-Neto and Zeileis 2010). We fit dominance models (presence/absence of at least one seedling taller than shrub modal height) using a Bernoulli distribution, considering only those plots where tree regeneration was present in the first place. We centered and standardized all predictor variables prior to fitting models.

To characterize the relationship between post-fire precipitation anomaly and regeneration variables, we used all plots to fit the anomaly model with the best set of predictor variables for each response variable. We plotted hypothetical model predictions across a range of anomaly values bounded at ± 2 standard deviations from the mean anomaly value across all plots. We held all other predictor variables in the model at their means, with the exception of normal

precipitation, which we held at both a low value (20th percentile of normal precipitation across all plots; i.e., 686 mm) and a high value (80th percentile; i.e., 1811 mm) and plotted predictions for each.

Our analyses of presence/absence, percent cover, and height dominance describe the response of a single species or species group at a time. We additionally explored how post-fire precipitation is associated with community composition (species-specific relative abundance) of recruiting tree seedlings using constrained correspondence analysis (CCA). For this analysis, we aggregated plot data into multiple “topoclimate clusters” based on climate and topography. We incorporated data on species-specific local abundance of adult trees from additional unburned and lightly burned reference plots within each cluster. We defined seedling community composition based on abundances of the four most common regenerating tree species across all plots: yellow pine, white fir, sugar pine (*Pinus lambertiana*), and Douglas-fir (*Pseudotsuga menziesii*). We quantified abundance as the proportion of plots within a given topoclimate cluster that contained seedlings of the given species. As explanatory variables, we considered normal precipitation, minimum post-fire precipitation anomaly, normal temperature, solar exposure, and reference basal area of adults for each of the four focal species. To quantify the amount of variation in the regenerating tree community explained by different environmental variables, we performed one CCA using all explanatory variables, eight other CCAs that each involved dropping a single predictor, and one CCA that involved dropping all adult tree abundance data. We performed CCA in R using the *vegan* package (Oksanen et al. 2017).

Results

Our plots captured a wide range of variation in long-term average annual precipitation (441 to 2563 mm) and post-fire mean precipitation anomaly (-0.85 to 0.58 SD from long-term mean) (Fig. 3). The majority of the variation in climate and post-fire weather comes from differences among fires (which burned in different years), but some variation also exists among plots within each fire. Across all 14 fires, we observed substantial variation in the percentage of plots with regeneration of yellow pine, white fir, and broadleaf trees (3–100%, 0–60%, and 0–83%, respectively) and the average cover of shrubs and graminoids (6–65% and 0–33%, respectively; Table 1).

The best-fit models for explaining post-fire regeneration patterns differed substantially among plant species and vegetation types. Normal (i.e., long-term average) precipitation was an important predictor of regeneration for some species, with greater establishment of white fir in normally wetter sites and more extensive graminoid cover in normally drier sites (Fig. 4). In contrast, normal precipitation was not an important predictor of yellow pine regeneration or of shrub cover.

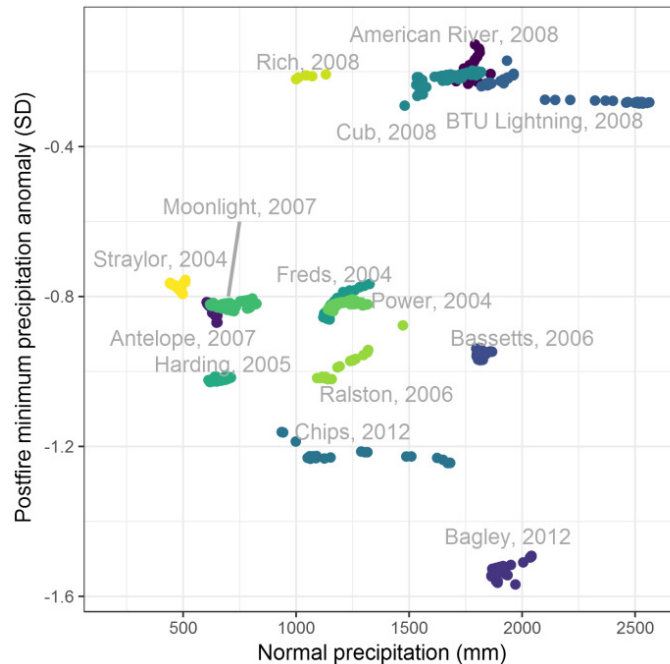


Fig. 3

Distribution of high-severity study plots with respect to normal precipitation and post-fire minimum precipitation anomaly. Clusters of plots reflect separate study fires and are labeled with the fire name and year. Mean precipitation anomaly reflects the extent to which the mean annual precipitation over the first three water years (Oct-Sept) following each fire departs from the long-term average (see Methods for details on quantifying anomaly terms).

We quantified the post-fire precipitation anomaly as the degree to which the precipitation in the driest of the three years following the fire deviated from the long-term average at each plot (see *Methods*). For white fir, models predicted reduced regeneration probability under stronger post-fire drought (i.e., more negative post-fire minimum precipitation anomaly). In a hypothetical site that is on average relatively wet (i.e., ~1800 mm normal annual precipitation), the median predicted probability of establishment of white fir seedlings (i.e., predicted proportion of plots with at least one seedling) decreases from approximately 33% under weak post-fire drought (minimum precipitation anomaly = -0.25 SD) to approximately 18% under strong post-fire drought (anomaly = -1.25 SD) (Fig. 4). Despite the large magnitude of these differences in predicted mean establishment, improvement in model predictive accuracy was relatively small (Fig. 5; see below).

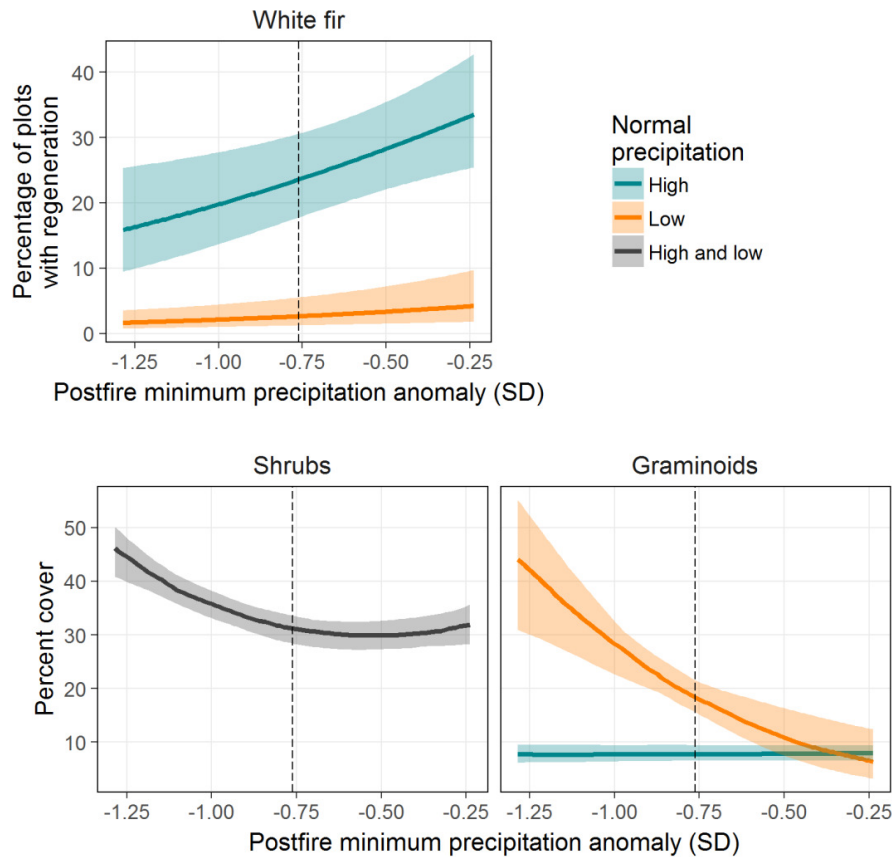


Fig. 4

Predicted regeneration patterns along a gradient of post-fire minimum precipitation anomaly. The fits depicted are those of the best-performing post-fire anomaly model for each of the three response variables shown (shade-tolerant conifers, shrubs, and graminoids). The range of post-fire minimum precipitation anomaly values depicted reflects ± 2 standard deviations from the mean anomaly value observed across all surveyed plots. The mean anomaly value (-0.76 SD) is shown as a vertical dashed line. When the best model included a term for normal precipitation (this was the case for shade-tolerant conifers and graminoids), we depict model predictions at both low (orange lines) and high (blue lines) levels of normal precipitation, reflecting the 20th percentile (686 mm) and 80th percentile (1811 mm) of values, respectively, across all plots surveyed. When the best model did not include a term for normal precipitation (this was the case for shrubs), we depict regeneration independent of normal precipitation (gray line). Shaded bands reflect 95% confidence around the mean value.

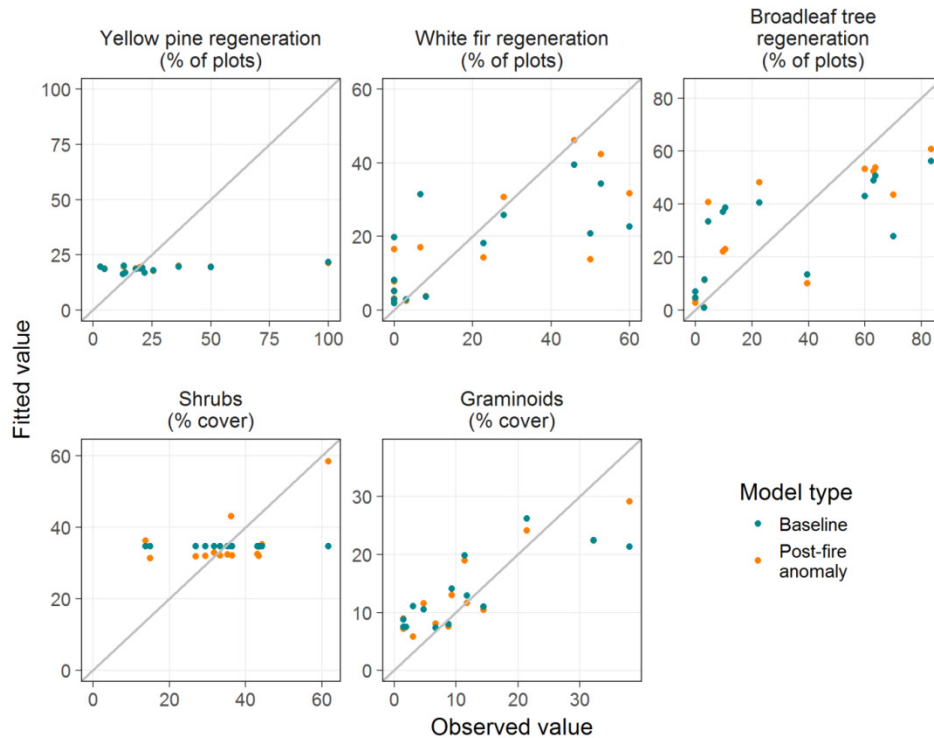


Fig. 5

Model-fitted vs. observed regeneration values for all high-severity burned plots, summarized by fire, for the best precipitation baseline model (blue points) and the best post-fire minimum precipitation anomaly model (orange points), for five different regeneration responses (panels). Each point depicts a different fire. For tree regeneration (top row of panels), point positions reflect the percentage of plots within each fire that contained at least one seedling ≥ 2 y old of the given species or species group. For percent cover variables (bottom row of panels), values reflect the mean percent cover of the given vegetation type (shrubs or graminoids) across all plots within each fire.

The best precipitation anomaly model for white fir regeneration does not include an interaction between normal precipitation and precipitation anomaly, indicating similar relative reductions in predicted regeneration under post-fire drought regardless of the long-term climate at a given site. However, because regeneration is more prevalent in normally wetter sites, the same 50% relative reduction in establishment probability with stronger post-fire drought translates to a greater absolute reduction in regeneration in these sites (Fig. 4). As an example, although the regeneration probability of white fir in a wet site (i.e., ~1800 mm normal annual precipitation) is predicted to decrease from 33% to 18% (an absolute reduction of 15%) with a 1 SD decrease in post-fire minimum precipitation, in drier sites (i.e., ~685 mm normal annual precipitation), the probability decreases from approximately 8% to 3% (an absolute reduction of only 5%). In contrast to the models for white fir, the models predicting regeneration of yellow pine and broadleaf tree species were not improved (i.e., cross-validation error rates were not reduced) by inclusion of a post-fire minimum precipitation anomaly term.

Models predicting cover of shrubs and graminoids were improved by including post-fire minimum precipitation; both vegetation types were predicted to have greater cover given a more negative post-fire minimum precipitation anomaly. For example, model-predicted shrub cover increases from approximately 30% under weak post-fire drought (minimum precipitation anomaly = -0.25 SD) to approximately 44% under strong post-fire drought (minimum precipitation anomaly = -1.25 SD) (Fig. 4). Relatedly, models predict that white fir seedlings, given they are present, are less likely to be dominant in height over shrubs given dry post-fire conditions. Models predicting height dominance of yellow pine and hardwood trees over shrubs were not improved by inclusion of a post-fire precipitation anomaly term.

We used constrained correspondence analysis (CCA) to explore community-level shifts in post-fire regeneration patterns. CCA revealed that approximately 61% of the variation (i.e., “inertia”; Legendre and Legendre 2012) in tree seedling species composition among topoclimatic plot clusters could be explained by normal precipitation, precipitation anomaly, solar exposure, and reference basal area by species (Table 2). Dominance of particular species among the recruiting seedlings was associated with different normal climate signatures (Fig. 6). For example, dominance of Douglas-fir regeneration was associated with low solar exposure; dominance of yellow pine regeneration was associated with high solar exposure and high normal temperature, and dominance of white fir and sugar pine regeneration was associated with greater normal precipitation and lower normal temperature. Increasing (i.e., wetter) post-fire precipitation anomaly explained regenerating community composition in roughly the same direction as did increasing normal precipitation, with increased dominance of white fir and sugar pine under anomalously wet post-fire conditions. For any given regenerating tree species, increased dominance was clearly associated with increased dominance of adult conspecifics in nearby reference plots. Normal climate and solar exposure variables explained the greatest proportion of multivariate variation (i.e., inertia; Legendre and Legendre 2012) in the regenerating community (14-16% per variable for a total of 47%; Table 2). Individual adult species abundances explained the least variation (0-4% per species), but when adult abundances were considered jointly, they explained more variation (8%) than post-fire minimum precipitation anomaly (4%), leaving the precipitation anomaly term as the variable explaining the least amount of variation in the regenerating tree community.

Table 2

Proportion of the variation (i.e., “inertia”; Legendre and Legendre 2012) in the regenerating tree community composition that was explained by environmental explanatory variables in the constrained correspondence analysis (CCA). In addition to the full predictor set, we show variance explained by predictor sets that exclude specific variables individually (as well as jointly, in the case of reference tree species basal area).

Environmental explanatory variables used	Proportion of variation explained	Change in proportion variation explained relative to full predictor set
All	0.61	0
All except normal precipitation	0.47	-0.14
All except normal temperature	0.45	-0.16
All except solar exposure	0.46	-0.15
All except post-fire minimum precipitation anomaly	0.57	-0.04
All except white fir reference basal area	0.61	-0.00
All except Douglas-fir reference basal area	0.57	-0.04
All except sugar pine reference basal area	0.61	-0.00
All except yellow pine reference basal area	0.60	-0.01
All except all reference basal area	0.53	-0.08

Note: The full predictor set includes the following environmental variables: normal precipitation, normal temperature, solar exposure, minimum post-fire precipitation anomaly, and reference basal area of white fir, Douglas-fir, sugar pine, and yellow pine.

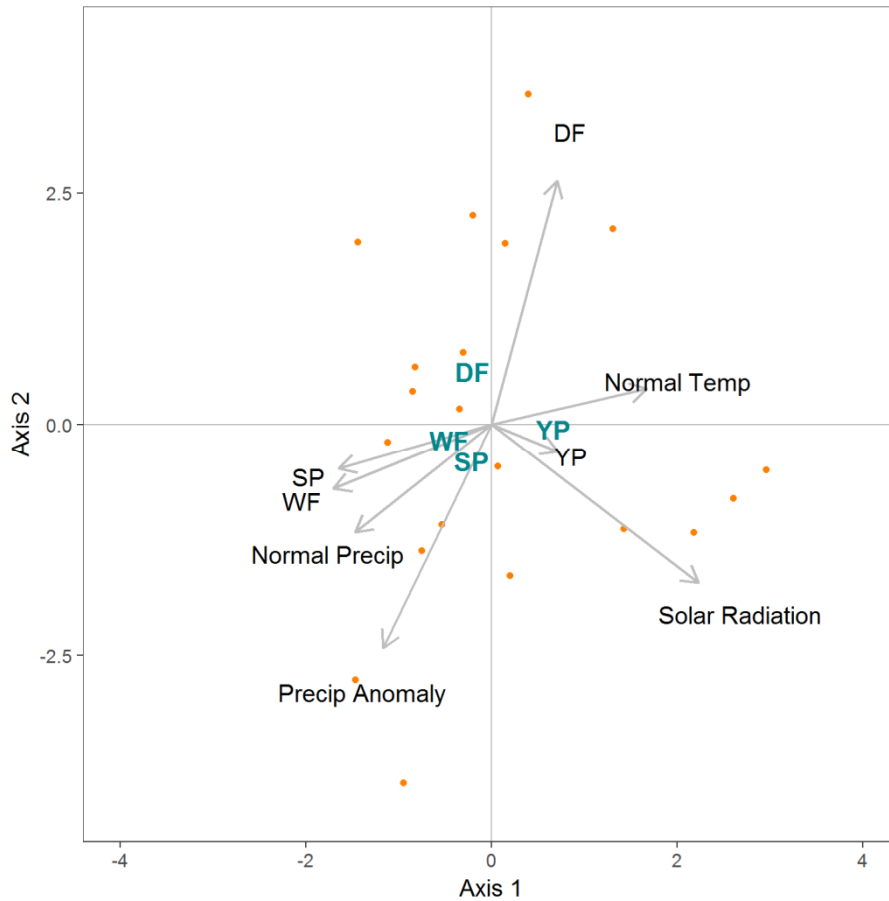


Fig. 6

Plot of the constrained correspondence analysis (CCA). Positions of plot categories (orange points) reflect their distance with respect to their regenerating tree species composition, as constrained by environmental predictors (gray arrows with black text). Blue boldface text labels indicate average position of individual regenerating tree species across all plot categories. Environmental predictor variables include normal climate, solar exposure, minimum post-fire precipitation anomaly, and basal area of adult trees of each of four species (two-letter codes). DF: Douglas-fir; YP: yellow pine; SP: sugar pine; WF: white fir.

Our analysis of plot revisits revealed a strong correspondence between presence or absence of regenerating trees at the initial survey and presence or absence upon revisit three to seven years later. For broadleaf trees and white fir, less than 10% of plots that had no seedlings at the initial survey had any seedlings upon revisit; similarly, 77-85% of the plots that did have seedlings during the initial survey had seedlings upon revisit (Fig. 7). Yellow pine regeneration was less consistent: 19% of plots with no regeneration upon initial survey had regeneration upon revisit, and 69% of plots that did have seedlings during the initial survey had seedlings upon revisit.

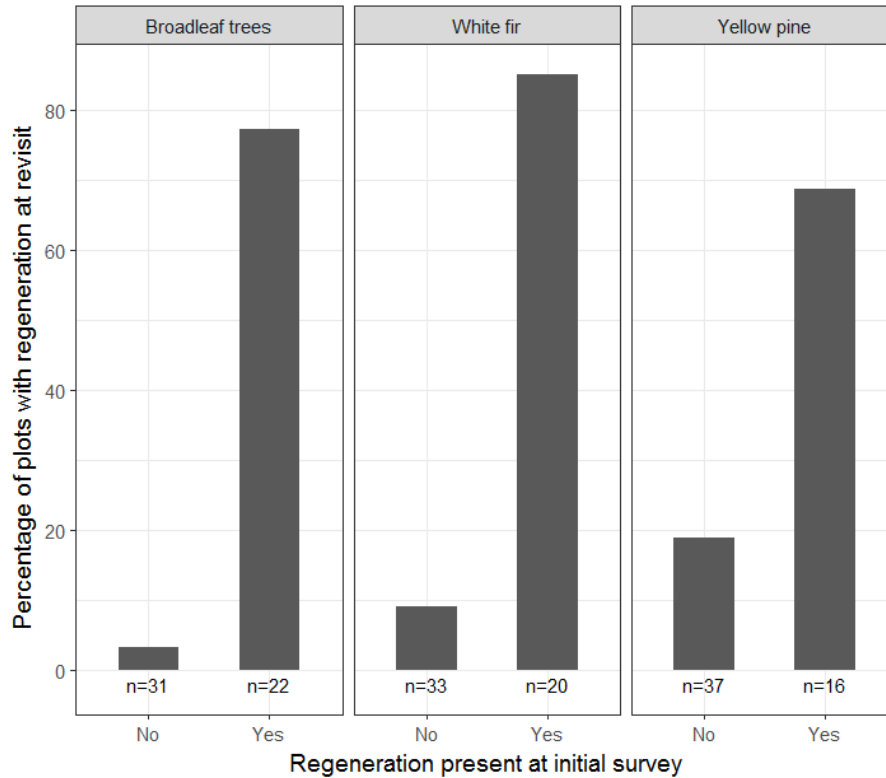


Fig. 7

The proportion of resurveyed plots with regenerating tree seedlings 3 to 7 years following the initial survey, categorized based on the presence or absence of tree seedlings during the initial survey (5 years following fire). Numbers below each bar represent the number of resurveyed plots that did and did not have tree seedlings during the initial survey.

Discussion

Tree Regeneration

We observed limited sensitivity of post-fire vegetation regeneration to post-fire weather. The tree species exhibiting greatest sensitivity to post-fire weather conditions, white fir, showed a decrease in regeneration under post-fire drought, regardless of normal climate. Regeneration declines throughout the range of a species under warming and/or drying suggest that its distribution will not closely track shifts in climate, as climate tracking would imply expansion into previously climatically marginal sites (e.g., the wet extreme of its distribution as conditions become drier; Fig. 1). Our results add to accumulating evidence that that when regeneration of a tree species is sensitive to post-fire weather and/or climate, it tends to decline given increasing aridity (Harvey et al. 2016, Tepley et al. 2017, Urza and Sibold 2017, Campbell and Shinneman 2017) and does not readily increase in areas where climatic suitability is increasing (Zhu et al. 2011, Campbell and Shinneman 2017).

Although white fir showed sensitivity to post-fire precipitation anomaly, the amount of variation that was explained by post-fire weather (i.e., the reduction in predictive error) was low (Fig. 5). This implies that regardless of changes in post-fire weather and climate, post-fire regeneration patterns will remain largely unchanged, all else equal. This conclusion is further

supported by the fact that yellow pine and broadleaf trees did not exhibit any significant sensitivity to post-fire weather (i.e., model predictions did not improve when a post-fire anomaly term was added). Yellow pine seedlings may be less sensitive to drought than white fir seedlings, particularly in exposed, severely-burned areas, given their strategy as shade-intolerant species and tendency to quickly grow a long taproot (Larson 1963). Similarly, broadleaf tree regeneration is likely relatively insensitive to short-term fluctuations in aridity due to the ability of trees to resprout from an established root base (McDonald and Tappeiner 1996). The lack of any substantial increases or decreases in yellow pine and broadleaf tree regeneration given post-fire weather variation suggests that climate change may not initially lead to range contraction—at least through changes in establishment patterns—even when severe wildfire removes the established trees from a site. We note that our results only apply to severely burned areas where a seed source is present; overall, high-severity fires, which often produce large areas with no seed source and therefore poor tree regeneration (Welch et al. 2016), may very well contribute to range contraction.

Our results contrast with reports of substantial and rapid distributional shifts of plant species and communities associated with recent climate change (Beckage et al. 2008, Kelly and Goulden 2008, Lenoir et al. 2010, Feeley et al. 2011). The difference may arise from our explicit focus on tree establishment: the rapid community shifts observed in these other studies may occur primarily through differential growth and mortality as opposed to establishment. Over longer time periods, however, continued migration—and particularly range expansion—will depend on establishment in addition to mortality and growth (Clark et al. 1998). Establishment may respond more slowly to climate change given it requires both effective seed dispersal from reproductive adults and availability of sites not already occupied by established individuals (Urban et al. 2012). Persistence of established individuals and limited potential for dispersal into suitable sites appear to at explain slow forest community shifts observed elsewhere (Bertrand et al. 2011). However, our study, which focuses on disturbed areas near exiting seed sources, demonstrates that even when seeds and sites are available, tree establishment may not rapidly respond to climate change.

The Role of Biological Inertia

A potential explanation for the limited sensitivity of regeneration to post-fire weather is that the species composition of the nearby surviving adult trees imposes a “biological inertia” on the system by influencing the species composition of the available seed. This interpretation is supported by our observation of a strong correspondence between the dominance of a given species in the regenerating tree community and dominance of adult trees of the same species in nearby unburned stands (Fig. 6), a pattern that is often observed following fire (e.g., Agee and Smith 1984, Zald et al. 2008, Donato et al. 2009) and in tree infilling in the absence of substantial disturbance (Dolanc et al. 2012). It is additionally supported by the strong relationship between normal climate and regeneration in most of our regeneration models and in the community composition analysis (Fig. 6, Table 2), particularly when compared with the relatively weak influence of the post-fire weather anomaly in these analyses. Young seedlings have not experienced “normal climate,” but normal climate does explain the distribution of adult trees (Lutz et al. 2010), which in turn can influence the regenerating tree community through seed availability.

Our observation of a strong correspondence in community composition between regenerating trees and residual adults suggests that forest compositional shifts under climate change may be slow as long as adult trees persist locally, and that climate change may influence

forest compositional shifts more strongly through its impacts on adult trees. It also implies that it may be necessary to rethink the notion that the establishment stage is the most environmentally-sensitive life stage of trees (Grubb 1977). Indeed, the extreme California drought of 2012-2015 triggered dramatic increases in mortality of established trees (Young et al. 2017), whereas the current study—which includes fires that were followed by the same drought—finds that seedling establishment was not strongly affected. Juvenile tree growth may also be generally less sensitive than adult growth to interannual weather variation (Ettinger and HilleRisLambers 2013). Limited sensitivity of young trees to climate variability implies a high degree of resistance—a trait often associated with low vulnerability to stressors (Harrison 1979)—but it may create underlying instability by delaying range shifts and accompanying community compositional change, while transferring vulnerability to the adult stage. Rather than continuously responding to gradual changes in climate, adult mortality tends to occur episodically due to extreme events such as drought, which are expected to increase in frequency and intensity with climate change (Allen et al. 2015).

It is hypothetically possible that continued establishment in later post-fire years (i.e., years beyond the 5 y post-fire window) would result in detectable shifts in regeneration patterns. However, in this and similar systems, the large majority of post-fire tree establishment often occurs within 5 years following fire (Harvey et al. 2016, Tepley et al. 2017, Urza and Sibold 2017), suggesting that this is the window in which regeneration-driven shifts would become apparent if they were going to occur. Indeed, our plot revisits revealed that the large majority of plots that contained tree seedlings 5 years following fire still contained seedlings 3 to 7 years later (Fig. 7). Perhaps more notably, among plots that had no seedlings 5 years following fire, only a small percentage had seedlings 3 to 7 years later. This consistency in the regeneration trajectory implies that when regeneration patterns are poor 5 years following fire, they are likely to remain poor for at least as many years beyond that. This consistency was strongest for broadleaf trees and weakest for yellow pine, suggesting that yellow pine is more capable of establishing in later post-fire years than other tree species. This finding contrasts with results of other studies which suggest that in the longer term, delayed post-fire tree establishment is often dominated by shade-tolerant species that can grow beneath the existing vegetation, particularly shrubs (Lauvaux et al. 2016). It is possible that over a longer time period (i.e., with future revisits in later years) we would observe the same patterns.

Shrub and Graminoid Establishment

In contrast to the limited response of tree regeneration to post-fire weather variation, establishment of shrubs and graminoids showed strong sensitivity, with substantially higher cover under drier post-fire conditions. Expansion of these vegetation types under increasing aridity is consistent with their dominance on harsher, drier sites in the study region and suggests further increases in shrub and graminoid dominance with increasing aridity resulting from climate change. Although it is not possible to distinguish causation from correlation through our observational approach, the fact that shrub cover and white fir establishment respond in opposite directions to post-fire drought is suggestive of competitive dynamics (e.g., increased shrub dominance due to poor initial conifer regeneration or vice-versa), an interpretation that is supported by manipulative studies (e.g., Conard and Radosevich 1982).

Science Delivery

We presented the results of this project at two professional meetings: the Ecological Society of America Annual Meeting in Portland, Oregon (August 2017) and the Northwest Scientific Association Annual Meeting in Ashland, Oregon (March 2017). The presentation at the latter meeting was part of a special organized session on northern California fire ecology. Many of the presenters and attendees of the session were members or affiliates of the U.S. Forest Service Pacific Southwest Region Ecology Program, which has as primary objectives conducting and communicating to forest managers the scientific research that is relevant to California forest management.

We also interfaced substantially with the California Fire Science Consortium (a member of the JFSP Fire Science Exchange Network), primarily through presentation of a webinar describing the results of the project (August 2017). The presentation was well attended (>50 attendees) by California forest managers (both Federal- and state-level) and researchers. We also attended a multi-day fire science field trip (August 2017) that was co-sponsored by the California Fire Science Consortium, and we interacted extensively with the attendees—who included California fire science researchers (from both academia and agencies) and managers (both Federal- and state-level)—including communicating and discussing the results of this project.

Conclusions, Management Implications, and Future Research Directions

Our study provides empirical evidence that post-fire tree regeneration patterns may not shift rapidly as climate changes. The limited sensitivity of tree establishment in these Mediterranean-climate forests appears to be due largely to a strong “biological inertia” associated with local surviving adult trees, which influence post-fire recovery patterns through their influence on the availability and species composition of seeds for tree establishment. Resistance of tree establishment to climate variation, however, does not imply resistance of the overall forest community or even of the tree community specifically. If tree seedling regeneration does not respond to climate change, climate change vulnerability may be associated primarily with adult trees and potentially materialized as mortality events. Further, our results suggest that increasing aridity may lead to increasing post-fire dominance of shrubs and graminoids, signaling a stronger potential for forest-to-chaparral type conversion following fire as a consequence of climate change. Our work is focused on severely burned areas where a tree seed source is present; areas far from seed sources may experience even more pronounced shifts.

Because natural post-fire tree regeneration patterns may not shift substantially in response to climate change, direct management intervention to shift tree community composition (e.g., preferential planting and/or removal of particular tree species) may be necessary if naturally recruiting trees do not meet management criteria for a community well-adapted to present and/or expected future climate. Facilitating establishment of a well-adapted tree community may reduce the probability of future undesired impacts of climate change, such as large tree mortality events. Additionally, given the potential increases in post-fire shrub establishment under increasing aridity, managers may need to allocate more resources toward post-fire shrub control if they wish to maintain historical tree seedling survival and growth rates, at least in areas with strong shrub seed banks. Finally, the increased potential for high-severity fire to induce forest-to-chaparral type conversion in a warming, drying world further highlights the importance of management intended to counteract the effects of fire suppression and reduce

the proportion of wildfire that is burning at high severity. Such management includes thinning, prescribed burning, and managed wildfire (North et al. 2012).

There are several clear opportunities for future research to shed additional light on the interaction between wildfire and climate change in shaping forest communities. First, simply incorporating additional, more recent fires under the same study design could increase the potential for detecting sensitivity of post-fire regeneration to weather and climate variation—particularly by increasing the range of variation in post-fire weather conditions that are represented by the dataset. Additionally, performing further revisits of the study plots at regular intervals may enable more refined conclusions regarding the long-term recovery of burned areas. Such an analysis may reveal, for example, that recovery trajectories can diverge beyond the 12-year timeframe evaluated in this study and/or that divergence is more likely under certain conditions than others. Finally—and particularly relevant for management of post-fire forest recovery—it would be valuable to investigate the conditions that affect the outcomes of post-fire planting, shrub control, and other management, especially relative to natural regeneration. In a potential future scenario of declining natural tree regeneration and increasing shrub dominance following fire, it will be important to understand the extent to which different management actions can influence forest recovery trajectories.

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

The following products were produced during the course of the project:

- Manuscript for submission to peer-reviewed academic journal – completed
- Doctoral dissertation – in progress
 - Student: Derek Young, UC Davis Graduate Group in Ecology
- Conference abstract: Ecological Society of America Annual Meeting, August 2017
 - Title: Post-fire forest regeneration under climate change
- Conference abstract: Northwest Scientific Association Annual Meeting, March 2017
 - Title: Post-fire forest regeneration in a changing climate
- Webinar: California Fire Science Consortium Webinar, August 2017
 - Title: Post-fire forest regeneration and restoration und climate change: insight from natural and managed settings

Appendix C: Metadata

The data collected through this project reflect the biophysical characteristics of over 400 60-m² circular plots that were surveyed 4 to 12 years following wildfires that burned in yellow pine and mixed-conifer forests in northern California. One dataset (plot.csv) represents plot-level variables, including vegetation attributes (e.g., percent cover by shrubs and graminoids, height of shrubs, species of shrubs, fire severity, and distance to seed tree), as well as plot status/information (e.g., geospatial coordinates, fire name, fire year, survey year, identity as new survey or revisit of an existing plot, and identity as burned plot or unburned reference plot). A second dataset (tree_species.csv) represents tree data for each species of tree in each plot. It contains, for each plot and tree species, counts of tree seedlings by age, height of the tallest seedling, and the count and basal area of adult trees. Both datasets contain plot ID numbers in order to link the plot-level data with the tree species-level data. For each plot record, there may be zero, one, or multiple tree species records depending on the number of tree species present in each plot.

Each of the two datasets is accompanied by metadata following the “FGDC Biological Data Profile” standard of the Content Standard for Digital Geospatial Data (FGDC-STD-001.1-1999). The data and accompanying metadata will be archived in the JFSP-recommended repository, the Forest Service Research Data Archive, upon publication of a peer-reviewed paper presenting the data.