# Post-fire forest regeneration shows limited climate tracking and potential for drought-induced type conversion

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*Abstract.* Disturbance such as wildfire may create opportunities for plant communities to reorganize in response to climate change. The interaction between climate change and disturbance may be particularly important in forests, where many of the foundational plant species (trees) are long-lived and where poor initial tree establishment can result in conversion to shrub- or graminoid-dominated systems. The response of post-disturbance vegetation establishment to post-disturbance weather conditions, particularly to extreme weather, could therefore provide useful information about how forest communities will respond to climate change. We examined the effect of post-fire weather conditions on post-fire tree, shrub, and graminoid recruitment in fire-adapted forests in northern California, USA, by surveying regenerating vegetation in severely burned areas 4–5 yr after 14 different wildfires that burned between 2004 and 2012. This time period (2004–2016) encompassed a wide range of post-fire weather conditions, including a period of extreme drought. For the most common tree species, we observed little evidence of disturbance-mediated community reorganization or range shifts but instead either (1) low sensitivity of recruitment to post-fire weather or (2) weak but widespread decreases in recruitment under unusually dry post-fire conditions, depending on the species. The occurrence of a single strong drought year following fire was more important than a series of moderately dry years in explaining tree recruitment declines. Overall, however, post-fire tree recruitment patterns were explained more strongly by long-term climate and topography and local adult tree species abundance than by post-fire weather conditions. This observation suggests that surviving adult trees can contribute to a "biological inertia" that restricts the extent to which tree community composition will track changes in climate through post-disturbance recruitment. In contrast to our observations in trees, we observed substantial increases in shrub and graminoid establishment under post-fire drought, suggesting that shifts in dominance between functional groups may become more likely in a future with more frequent and intense drought.

*Key words: chaparral; climate change; fire; forest; recruitment; regeneration; shrub; tree; type conversion.*

## Introduction

Climate change is expected to substantially alter the distribution of sites that are environmentally suitable for specific plant species (Thomas et al. 2004, Loarie et al. 2008). 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 (Aitken et al. 2008, Campbell and Shinneman 2017). In fire-prone forest ecosystems where many tree species primarily recruit soon after disturbance, wildfire may present an important opportunity for forest communities to reorganize in response to climate change (Campbell and Shinneman 2017). A clear understanding of the sensitivity of post-fire vegetation establishment to variation in weather and climate is essential for (1) predicting the extent to which forest composition and function will keep pace with climate change and for (2) targeting post-fire forest management such as tree planting to areas where natural recruitment is not expected to meet management goals.

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 recruitment 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,

Donato et al. 2016, Lauvaux et al. 2016). Even in the absence of type conversion, climate change could result in substantial shifts in forest tree species composition, as differences in initial establishment success among tree species can correspond to variation in adult community composition (Barbour et al. 1990). While 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, Larson and Franklin 2005, Donato et al. 2009, Crotteau et al. 2013, Welch et al. 2016, Shive et al. 2018), comparatively few studies have evaluated the effects of climate and weather on post-fire tree recruitment dynamics. The limited work to date suggests that for some species in some sites, dry post-fire conditions are associated with reduced recruitment, but in other cases, post-fire weather does not significantly explain recruitment patterns (Savage and Mast 2005, Harvey et al. 2016, Urza and Sibold 2017, Stevens-Rumann et al. 2018). Simulation models (Campbell and Shinneman 2017, Liang et al. 2017) and projections based on contemporary climate associations (Tepley et al. 2017) also generally predict declines in conifer recruitment with increasing aridity at hot, dry range limits but not necessarily expansion at cool, wet range limits, where colonization of new sites may be poor due to dispersal limitation and/or limited availability of suitable sites.

Although work to date has identified and predicted specific cases of recruitment declines resulting from increasing aridity, little empirical research has directly addressed the potential for wildfire to facilitate or constrain species range shifts or type conversion given variation in weather and climate. Given a fixed range of climatic conditions under which establishment can occur, range shifts that would constitute climate tracking (sensu Bell et al. 2014, Zhu et al. 2014) under warming and/or drying conditions can be conceptualized as an increase in recruitment in historically cooler, wetter sites (as they become warmer and/or more mesic and thus more climatically suitable) and a decrease in recruitment in hotter, drier sites (as they become more xeric and thus less climatically suitable). Detecting this pattern through empirical observations requires examining recruitment patterns simultaneously under both (1) a range of post-fire weather conditions (to identify the sensitivity of recruitment to changing temperature or water availability, all else being equal) and (2) a range of long-term average climate (to identify whether sensitivity to changing conditions depends on the position within a species' range). To our knowledge, only one study to date (Stevens-Rumann et al. 2018) has examined the interactive influence of these two factors; the work found that during the recent unusually dry period from 2000 to 2015, tree recruitment in the U.S. Rocky Mountains was disproportionately reduced in hot, dry sites. However, no work has explored these interactions in individual tree species or in trees vs.

other vegetation types, aspects that are essential for understanding the potential for range shifts, community reorganization, and type conversion.

In this study, we examine vegetation establishment following 14 fires that burned in different years and thus were followed by contrasting weather conditions. We examine patterns along large gradients in long-term average climate and post-fire weather conditions, including a historic drought, to gain insight into the potential for disturbance to facilitate compositional and distributional shifts in a changing climate. Although post-fire conifer recruitment may decline overall into the future as fires burn larger contiguous areas containing few seed sources (i.e., surviving trees; Stevens et al. 2017, Shive et al. 2018, Steel et al. 2018), we focus on severely burned areas near conifer seed sources in order to center the analysis on the direct effect of weather and climate on recruitment patterns. In addition to evaluating the responses of individual tree species, we evaluate recruitment of multiple vegetation types (conifers, broadleaf trees, shrubs, and graminoids) to identify the potential for shifts in dominance among species and vegetation types, including type conversion from forest to chaparral, as climate changes.

## METHODS

### Study system

We quantified forest regeneration patterns 4–5 yr 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. 1, 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. Our study fires ranged in size from 477 to 30,525 ha and encompassed broad topographic gradients in climate variables including temperature and precipitation (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 species are strongly shade intolerant, establish primarily in open and/or disturbed areas, and are relatively fire and drought tolerant as adults (Burns and Honkala 1990, Zald et al. 2008, Safford and Stevens 2017). In contrast, white fir is shade tolerant
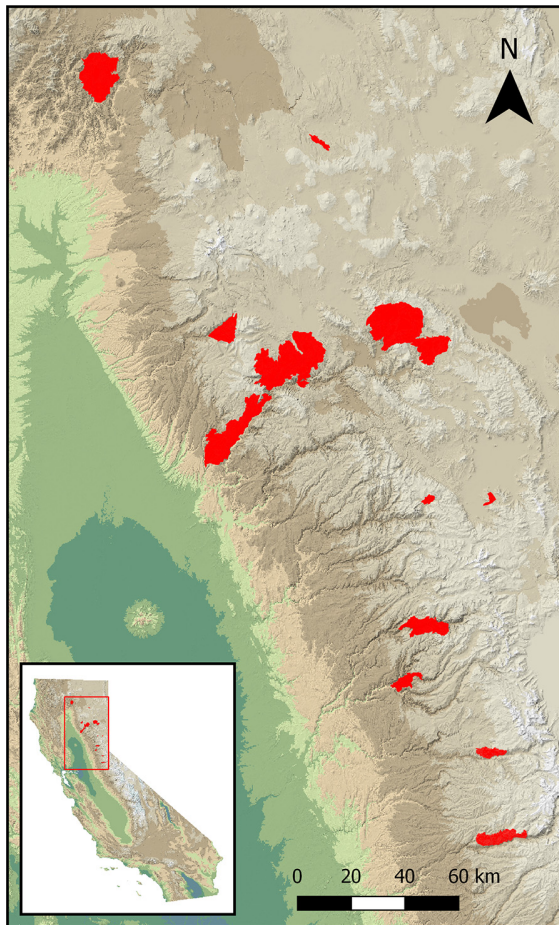
FIG. 1. Map of study fires (red polygons). The 14 study fires are represented as 12 distinct polygons because two pairs of fires partially overlapped. The inset image shows the state of California, USA, with a red box indicating the extent of the main map. Background color shading reflects elevation from green (low) to white (high).

and can establish in closed-canopy forest as well as in disturbed areas (Zald et al. 2008, Safford and Stevens 2017). It is relatively fire and drought intolerant and is often an indicator of more mesic site conditions (Burns and Honkala 1990, Safford and Stevens 2017). Solar exposure can have a strong effect on vegetation within our study region with, for example, pines and shrubs more abundant on south-facing slopes and shade-tolerant conifers more abundant on north-facing slopes, for a given elevation (Safford and Stevens 2017).

When initial post-fire conifer regeneration is poor, shrubs can rapidly dominate severely burned areas (Collins and Roller 2013, Welch et al. 2016) and can remain dominant for decades (Nagel and Taylor 2005, Lauvaux et al. 2016). Trees (especially shade-intolerant pines) that recruit after shrubs have come to dominate a site may remain suppressed under the shrub canopy for many years, but they often begin to grow rapidly once they eventually overtop the shrubs (Lauvaux et al. 2016).

## Plot selection

We drew from and added to an existing data set of post-fire vegetation plots described by Welch et al. (2016). Our data set included a total of 513 severely burned plots across 14 fires (Table 1). Plots were selected systematically, were located at least 200 m apart, and all experienced >75% mortality (by basal area) of pre-fire trees (see Appendix S1 for full plot selection details). We only included plots that had a potential tree seed source (i.e., one or more live mature trees of any conifer species) within 75 m, as previous work has documented poor conifer regeneration in this system when seed sources are further away (Welch et al. 2016). 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 (see Appendix S1).

We conducted plot surveys 4–5 yr following each wildfire (Table 1). We selected this timeframe because, in this and similar systems, the large majority of post-fire tree establishment usually occurs within 5 yr following fire (Harvey et al. 2016, Tepley et al. 2017, Urza and Sibold 2017), suggesting that this is the window in which potential recruitment-driven community compositional shifts would become apparent if they were going to occur.

At each sampling point, we established a 60-$m^2$ (4.37 m radius) circular plot. Within each plot, we located all tree seedlings, aged them by counting terminal bud scars, and tallied and identified to species all seedlings. 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 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 recruitment). To quantify potential sources of competition and/or facilitation for recruiting trees, we visually estimated the percent coverage of each plot by shrubs and graminoids and measured the modal height of the (co-)dominant shrub species.

## 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 at each plot. We quantified long-term average (i.e., "normal") climate conditions as the average annual water-year precipitation over the 30-yr period from 1986 to 2015. We quantified post-fire weather in two ways: (1) average annual precipitation over the three water years (October–September) 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). We computed post-fire weather variables as anomalies

TABLE 1. Summary of the fires included in the study.

| Fire name | Fire year | No. years following fire plots surveyed | No. high-severity plots | Plots with regeneration (%) | | | Cover of plots by vegetation lifeform (%)† | | Elevation range of plots (m) | Dominant tree species |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Yellow pine | White fir | Broadleaf trees | Shrubs | Graminoids | | |
| American River | 2008 | 5 | 18 | 17 | 50 | 11 | 26 (0, 80) | 7 (0, 30) | 1,438–1,968 | WF, DF, YP, SP |
| Antelope | 2007 | 5 | 37 | 22 | 0 | 0 | 27 (0, 100) | 2 (0, 70) | 1,471–1,830 | DF, YP, WF |
| Bagley | 2012 | 4 | 30 | 20 | 7 | 70 | 65 (2, 100) | 5 (0, 95) | 816–1,292 | DF, YP, WF |
| Bassetts | 2006 | 5 | 38 | 8 | 24 | 5 | 45 (0, 95) | 3 (0, 70) | 1,715–2,151 | RF, WF |
| BTU Lightning | 2008 | 5 | 43 | 26 | 28 | 40 | 16 (0, 95) | 5 (0, 96) | 992–1,882 | WF, YP, SP |
| Chips | 2012 | 4, 5 | 22 | 36 | 50 | 23 | 34 (2, 93) | 2 (0, 65) | 1,381–1,912 | WF, SP |
| Cub | 2008 | 5 | 61 | 13 | 46 | 10 | 32 (0, 90) | 2 (0, 70) | 1,280–2,025 | WF, SP |
| Freds | 2004 | 5 | 54 | 11 | 0 | 65 | 30 (0, 95) | 6 (0, 67) | 1,267–1,872 | CO, WF, YP |
| Harding | 2005 | 5 | 32 | 19 | 3 | 0 | 6 (0, 59) | 5 (0, 35) | 1,604–2,061 | YP, IC |
| Moonlight | 2007 | 5 | 57 | 4 | 9 | 4 | 41 (0, 98) | 4 (0, 50) | 1,584–2,047 | YP, WF |
| Power | 2004 | 5 | 72 | 22 | 0 | 64 | 28 (0, 95) | 5 (0, 50) | 1,096–1,851 | YP, IC |
| Ralston | 2006 | 5 | 14 | 50 | 0 | 79 | 40 (1, 85) | 6 (0, 85) | 692–1,276 | BO, YP, DF |
| Rich | 2008 | 4 | 4 | 100 | 50 | 50 | 25 (0, 90) | 10 (3, 18) | 1,029–1,820 | WF, DF, IC, YP |
| Straylor | 2004 | 5 | 31 | 0 | 0 | 3 | 5 (0, 80) | 10 (0, 30) | 1,501–1,742 | YP, WJ |

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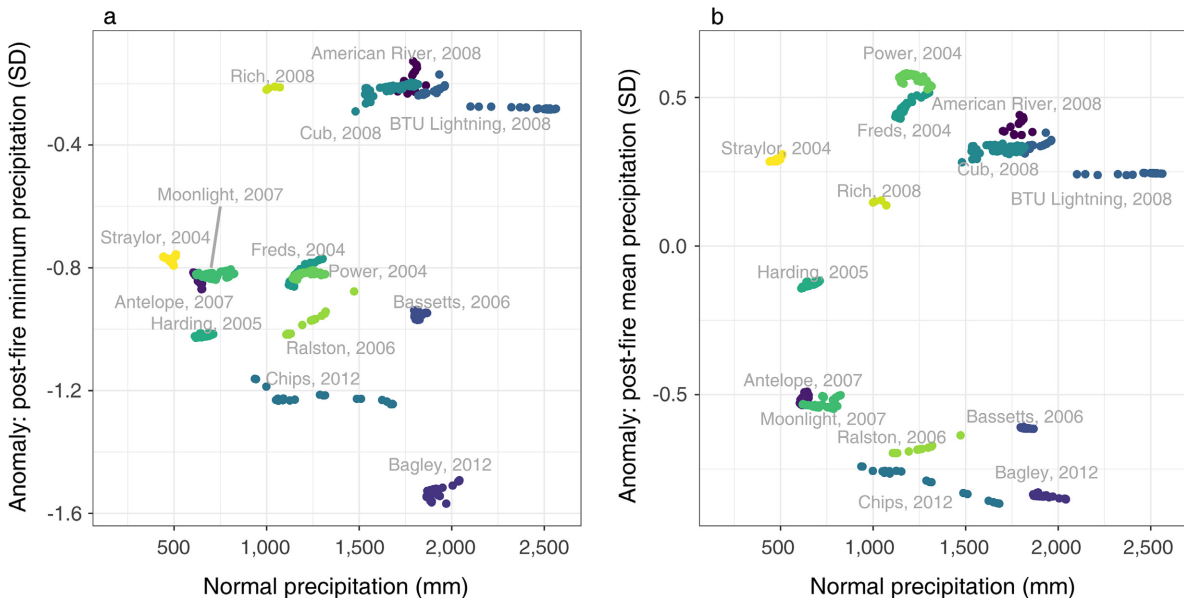†Values are means with minimum and maximum in parentheses.



FIG. 2. Distribution of high-severity study plots (points) with respect to normal precipitation and to (a) the anomaly term reflecting minimum post-fire precipitation and (b) the anomaly term reflecting mean post-fire precipitation. Clusters of plots reflect separate study fires and are labeled with the fire name and year. The anomaly reflecting minimum post-fire precipitation represents the extent to which the annual precipitation during the driest of the three waters years (Oct–Sept) following each fire departs from the long-term average precipitation at any given plot. The anomaly based on mean post-fire precipitation reflects the extent to which the mean annual precipitation over the first three waters years following each fire departs from the long-term average (see *Methods* for details on quantifying anomaly terms). SD, standard deviation.

(quantified as $z$ scores) representing the degree of departure from long-term average precipitation (see Appendix S1). Scale-free point estimates of climate variables at each plot location were obtained from the 4-km resolution PRISM precipitation data set (PRISM Climate Group 2018) and the 800-m resolution TopoWx temperature data set (Oyler et al. 2014) using bilinear interpolation.

We additionally computed actual evapotranspiration (AET) and climatic water deficit (CWD), based on the temperature and precipitation data, to evaluate as alternative climate and weather predictors. Precipitation models performed approximately as well as or better than the AET and CWD models, potentially because our data set contained relatively little variation in post-fire temperature anomaly, so that AET and CWD anomaly had little explanatory power beyond precipitation. Additionally, the fact that water balance is represented by multiple variables (AET and CWD) complicates interpretation of model fits. Thus, for simplicity, we focus on results from the precipitation models in the main text and water balance models in Appendix S1.

Finally, we also wished to account for the effect of solar radiation on vegetation patterns, as radiation contributes to energy availability and temperature and water stress that often vary at a fine scale due to topography (Bennie et al. 2008). In yellow pine and dry mixed-conifer forests, south-facing slopes, which are exposed to greater radiation, are often considered harsher and often have lower tree densities, a greater proportion of pines, and higher shrub cover (Fites-Kaufman et al. 2007, Safford and Stevens 2017). We attempt to account for some of this variability in order to more effectively isolate the influence of post-fire weather variation on recruitment patterns. We computed the solar exposure (incoming solar radiation energy) at each plot given its slope, aspect, and the shading effect of surrounding topography (see Appendix S1). While it is possible to incorporate solar radiation directly into calculations of AET and CWD (e.g., Dobrowski et al. 2013, Flint et al. 2013), we chose to use it as a separate predictor because (1) AET and CWD values from water balance models that incorporate solar radiation have not been validated at scales smaller than watersheds and (2) this allowed us to maintain a consistent model structure across precipitation- and water balance-based models.

### Data preparation

The tree species and species groups we evaluated were white fir, yellow pine, and "broadleaf trees," which included all angiosperm trees. We evaluated for each species or species group at each plot (1) presence or absence of trees that established within 2 yr of the fire (based on estimated tree age) and (2) whether any individuals were taller than the modal height of the dominant shrub species (as an indicator of their potential dominance over the shrubs). We focused on tree seedlings that recruited within 2 yr of the fire in order to base the analysis on individuals that (1) experienced the majority of the 3-yr window of post-fire weather conditions that we quantified, (2) were old enough to reliably locate and identify to species, and (3) 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. We chose to model the presence/absence (as opposed to abundance) of trees because (1) relatively few plots had trees (Table 1), making it difficult to develop robust abundance models, and (2) presence/absence may respond more predictably than abundance near species range limits (Pironon et al. 2017).

### Regression analysis

We performed analyses using R 3.4.1 (R Core Team 2018). We statistically evaluated the relationship between post-fire weather and tree recruitment by species (presence/absence at the plot level) using generalized linear regression models with a Bernoulli distribution. Our data set contains multiple plots per fire, but variation in post-fire weather exists primarily at the fire level. To account for this clustered data structure and to protect against developing overfitted models, we performed model selection using clustered cross-validation (see Appendix S1). We first used the cross-validation approach to identify the set of predictor variables that resulted in the most accurate predictions of regeneration presence/absence in withheld subsets of the data in the absence of post-fire weather anomaly variables. The predictors that we evaluated were normal climate (precipitation, AET, or CWD, each separately), seed tree distance, and solar exposure. We refer to the resulting model (a separate model for each tree species group) 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 (see Appendix S1). We refer to the model including post-fire anomaly term(s) as the "anomaly model."

We used a similar two-step modeling procedure to evaluate the influence of post-fire precipitation on the percent cover of shrubs and of graminoids, potential competitors of tree seedlings and resprouts, as well as on the dominance (by height) of seedlings over shrubs (for full modeling details, see Appendix S1). 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. We centered and standardized all predictor variables prior to fitting models. We characterized and plotted the relationship between post-fire precipitation anomaly and regeneration variables through scenario analysis (see Appendix S1).

In addition to performing the presence/absence, percent cover, and height dominance analyses for precipitation anomalies (average post-fire precipitation and minimum post-fire precipitation), we repeated the

analyses for modeled climatic water deficit (CWD; average post-fire and maximum post-fire) and actual evapotranspiration (AET; average post-fire and minimum post-fire) following the procedure described above. Because the anomaly term reflecting minimum post-fire precipitation improved upon baseline models more consistently than did other anomaly terms (Appendix S1: Table S1), we primarily focus here on models using the minimum precipitation anomaly term. Using the other anomaly terms (Appendix S1: Fig. S1) led to the same general qualitative conclusions; we describe specific differences in the supplemental results (Appendix S1: *Results*).

### Community analysis

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, in order to compare the post-fire species composition of establishing tree seedlings with the species composition of nearby surviving adult trees, we aggregated plot data into multiple "topoclimate categories" based on climate and topography (see Appendix S1). We incorporated data on species-specific local abundance of adult trees from additional comparable unburned and lightly burned reference plots within each topoclimate category (see Appendix S1). 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 based on the mean number of seedlings, by species, across all of the high-severity plots within each topoclimate category considering only seedlings that, based on estimated ages, had recruited in the first 3 yr following the fire.

As explanatory variables for the CCA, we considered normal precipitation, the anomaly term reflecting minimum post-fire precipitation, normal temperature, solar exposure, and basal area of adults (from the nearby climatically similar unburned and lightly burned reference plots) for each of the four focal conifer 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 (441–2,563 mm;

Fig. 2), the anomaly reflecting minimum post-fire precipitation (−1.57 to −0.13 SD from long-term mean; Fig. 2a), and the anomaly reflecting mean post-fire precipitation (−0.87 to 0.58 SD from long-term mean; Fig. 2b). 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 (Fig. 2). Across all 14 fires, we observed substantial variation in the percentage of plots with regeneration of yellow pine, white fir, and broadleaf trees (0–100%, 0–50%, and 0–79%, respectively) and the average cover of shrubs and graminoids (5–65% and 2–10%, respectively; Table 1).

The best-fit models for explaining regeneration patterns 4–5 yr following fire differed substantially among plant species and vegetation types (Appendix S1: Tables S3–S5). Normal (i.e., long-term average) precipitation was an important predictor of recruitment for some species, with greater recruitment of white fir in normally wetter sites, greater establishment of broadleaf trees in sites with intermediate normal precipitation, and more extensive graminoid cover in normally drier sites (Fig. 3 and Appendix S1: Fig. S1 and Tables S3 and S4). In contrast, normal precipitation was not an important predictor of yellow pine recruitment or of shrub cover. Higher solar exposure was strongly associated with reduced probability of regeneration of white fir and increased cover of graminoids (Appendix S1: Tables S3 and S4).

We quantified the post-fire precipitation anomaly based on both the minimum precipitation in the 3 yr following fire and the mean precipitation over the same window (see *Methods*). Using post-fire minimum precipitation improved predictions of post-fire regeneration more consistently than did post-fire mean precipitation (Appendix S1: Table S1). For white fir, models predicted reduced recruitment probability under stronger post-fire drought (i.e., more negative minimum precipitation anomaly). In a hypothetical site that is on average relatively wet (i.e., ~1,800 mm normal annual precipitation), the median predicted probability of recruitment of white fir seedlings (i.e., predicted proportion of plots with at least one seedling) decreases from approximately 33% under weak post-fire drought (anomaly = −0.25 SD) to approximately 17% under strong post-fire drought (anomaly = −1.25 SD; Fig. 3a). Despite the large magnitude of these differences in predicted mean recruitment (nearly 50% reduction between wet and dry periods), improvement in model predictive accuracy was relatively small (Appendix S1: Table S1).

The best precipitation anomaly model for white fir recruitment does not include an interaction between normal precipitation and precipitation anomaly (Appendix S1: Table S3), indicating a similar relative reduction in predicted recruitment under post-fire drought regardless of the long-term climate at a given site. Although predicted white fir presence appears more sensitive to post-fire precipitation in wet than in dry sites (Fig. 3a), the *relative* change is the same under both
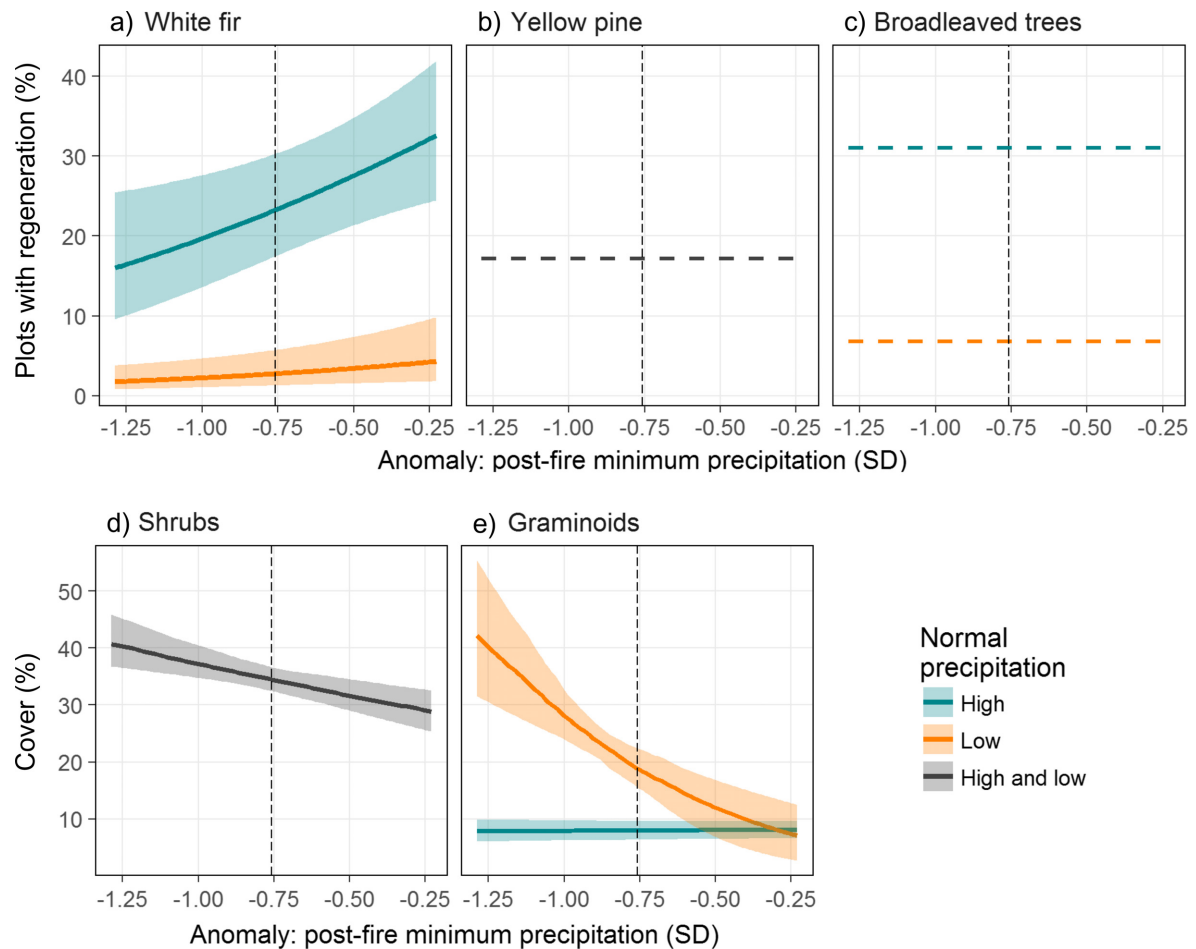
Fig. 3. Predicted regeneration patterns along variation in the anomaly term reflecting minimum post-fire precipitation. The fits depicted are those of the best-performing post-fire anomaly model for each of the five response variables shown (panels a–e). The range of precipitation anomaly values depicted reflects ± 2 SD 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 (1,811 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 yellow pine and shrubs), we depict regeneration independent of normal precipitation (gray line). Shaded bands reflect 95% confidence around the mean value. When the best model for a response variable did not include precipitation anomaly (yellow pine and broadleaved trees), we show the mean response value as a horizontal dashed line. SD, standard deviation.

scenarios; that is, on the scale of the linear response variable (logit-transformed percent), the absolute change in probability of presence does not differ significantly based on normal precipitation. Nonetheless, this does indicate that in environments where white fir presence is greater (i.e., wet sites), a given increase post-fire precipitation leads to a greater *absolute* increase (in percentage points) in predicted probability of presence. In contrast to the models for white fir, the models predicting recruitment of yellow pine were not improved (i.e., cross-validation error rates were not reduced) by inclusion of an anomaly term reflecting minimum post-fire precipitation (Fig. 3b and Appendix S1: Table S1 and Fig. S5).

In the case of broadleaf trees, only the anomaly term representing mean (and not minimum) post-fire

precipitation improved model fits (Appendix S1: Fig. S1). The anomaly model for broadleaf trees included an interaction between normal climate and post-fire precipitation anomaly, whereby in dry sites, unusually dry post-fire conditions were associated with declines in broadleaf tree recruitment, whereas in wet sites, unusually dry post-fire conditions were associated with modest increases in broadleaf tree recruitment (Appendix S1: Fig. S1). However, the post-fire anomaly term contributed only very minimally to reducing predictive error (i.e., from 23.3% to 23.1%; Appendix S1: Table S1).

Models predicting cover of shrubs and graminoids were improved by including an anomaly term reflecting post-fire minimum precipitation; both vegetation types are

predicted to have substantially greater cover given a more negative anomaly term (Fig. 3d, e). For example, mean model-predicted shrub cover increases from approximately 29% under weak post-fire drought (anomaly = −0.25 SD) to approximately 40% under strong post-fire drought (anomaly = −1.25 SD; Appendix S1: Fig. S1). 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 (Appendix S1: Fig. S1). In the case of yellow pine, height dominance over shrubs was dependent on normal climate (i.e., there was an interaction between normal climate and post-fire anomaly), whereby maximum height dominance in dry sites occurred in unusually dry post-fire conditions, and maximum height dominance in wet sites occurred in unusually wet post-fire conditions. However, uncertainty surrounding the influence of precipitation anomaly was high (Appendix S1: Fig. S1, Table S5). Finally, models predicting height dominance of broadleaved trees over shrubs were not improved by inclusion of a post-fire precipitation anomaly term; broadleaved trees were dominant in height in most plots (80%) where they were present.

For white fir recruitment and height dominance, yellow pine height dominance, and graminoid cover, using the anomaly term based on minimum post-fire precipitation to explain patterns resulted in greater predictive accuracy than using the term based on mean precipitation anomaly (Appendix S1: Table S1); the opposite was true for broadleaf tree recruitment and shrub cover. The best-performing anomaly representation (mean or minimum post-fire precipitation) generally yielded a modest improvement, if any, in predictive performance (Appendix S1: Table S1 and Fig. S4). For example, for the regeneration response for which predictions were most improved by incorporating a precipitation anomaly (i.e., white fir presence/absence), mean predictive error decreased by 1.5 percentage points (from 13.4% to 11.9%; Appendix S1: Table S1). The modest absolute reduction, however, corresponds to a roughly 11% relative reduction in model error.

Quantifying post-fire anomaly as post-fire AET improved predictive accuracy to a similar extent as, though in some cases more than and in others less than, precipitation anomaly (Appendix S1: Table S1 and Fig. S5). CWD anomaly terms improved models less substantially. When anomaly terms did improve models, the predictions of regeneration response given variation in the anomaly were, with some exceptions, qualitatively similar regardless of the anomaly term used (Appendix S1: Fig. S1 and Appendix S1: *Supplemental Results*).

We used constrained correspondence analysis (CCA) to explore community-level shifts in post-fire regeneration patterns. CCA revealed that 78% of the multivariate 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 (of nearby surviving adult trees) by species (Appendix S1: Table S6). Dominance of particular species among the recruiting seedlings was associated with different normal climate signatures (Fig. 4). 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 recruiting 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 in the regenerating community (12–21% per variable; Appendix S1: Table S6). Individual adult species abundances explained the least variation (1–3% per species), with the anomaly term reflecting minimum post-fire precipitation also explaining relatively little variation (7%).

## DISCUSSION

### *Tree recruitment*

Our study revealed species-specific sensitivity of post-fire tree recruitment to post-fire weather. The tree species
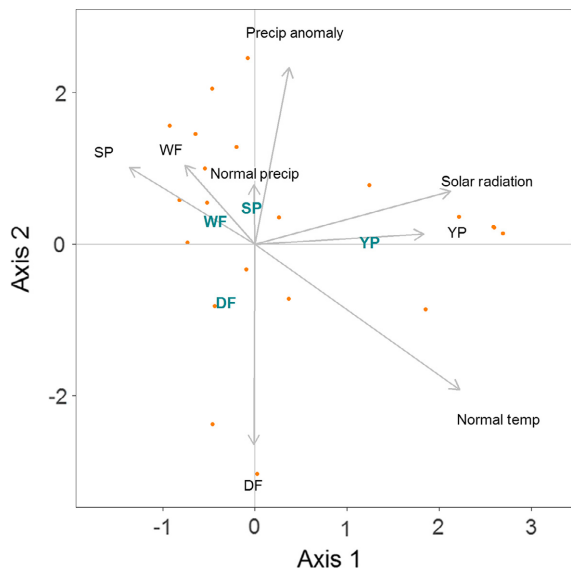


FIG. 4. Plot of the constrained correspondence analysis (CCA). Positions of plot topoclimatic categories (orange points) reflect their distance with respect to their regenerating tree species composition, as constrained by environmental predictors (gray arrows with black text). Blue boldface text labels indicate average position of individual regenerating tree species across all plot categories. Environmental predictor variables include normal climate, solar exposure, the anomaly term reflecting post-fire minimum precipitation, 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; precip, precipitation; temp, temperature.

exhibiting the greatest sensitivity to post-fire weather conditions, white fir, showed a decrease in recruitment under post-fire drought, consistent with its classification as a drought-sensitive component of the yellow pine–mixed-conifer community (Safford and Stevens 2017). The sensitivity of recruitment to precipitation anomaly (i.e., proportional change in probability of presence) was not significantly dependent on normal climate (i.e., including an interaction between anomaly and normal precipitation did not improve model fit; Appendix S1: Table S2). However, its consistent *proportional* reduction in occurrence with increasing post-fire precipitation across normal precipitation levels translates to a greater *absolute* reduction in wetter sites (where it is generally more abundant; Fig. 3a).

Consistent recruitment declines throughout the range of a species (or more substantial declines at the wet vs. dry end of the species range) under warming and/or drying conditions suggest that its distribution will not closely track shifts in climate, as climate tracking implies disproportionate contraction and expansion dependent on normal climate (e.g., disproportionate contraction at the dry extreme of its distribution as conditions become drier). Our results add to accumulating evidence that when recruitment of a tree species is sensitive to post-fire weather, recruitment tends to decline given increasing aridity (Harvey et al. 2016, Campbell and Shinneman 2017, Tepley et al. 2017, Urza and Sibold 2017, Stevens-Rumann et al. 2018) and does not readily increase in areas where climatic suitability is apparently increasing (Zhu et al. 2011, Campbell and Shinneman 2017, Liang et al. 2017). As one exception, the response of broadleaved trees to the anomaly term reflecting mean (but not minimum) post-fire precipitation did show a weak signal of climate tracking: recruitment responded negatively to post-fire precipitation in dry sites and positively in wet sites (Appendix S1: Fig. S1). However, sensitivity in dry sites was much greater than sensitivity in wet sites, implying population contraction in dry sites given post-fire drought without commensurate expansion in wet sites. Additionally, the anomaly term reduced model predictive error minimally, indicating its effect is weak and the pattern may not be generalizable. Nonetheless, it aligns well with independent predictions of increased recruitment and dominance of broadleaved trees at mid-elevations of the Sierra Nevada under future climate scenarios (Lenihan et al. 2008, Liang et al. 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; Appendix S1: Table S1) was relatively small. Given that our data set spans a wide range of variation in numerous environmental conditions, all of which may be associated with variation in recruitment, it is not surprising that any one variable explains a small proportion of the variation. Small directional changes in community composition may accumulate to substantial shifts over many generations (Jackson and Sax 2010),

though the long generation time of white fir will likely constrain the rate of any shifts if driven by changes in recruitment alone.

Yellow pine did not exhibit any significant sensitivity to post-fire weather (i.e., model cross-validation error 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 classification 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 (particularly a single strong drought year) due to the ability of trees to resprout from an established root base (McDonald and Tappeiner 1996). Other empirical studies to date have identified low or statistically nonsignificant sensitivity of post-fire tree recruitment to post-fire weather variation in multiple species (e.g., Harvey et al. 2016, Urza and Sibold 2017) and at an ecosystem level (Cai et al. 2013).

For a young (i.e., 2–5 yr old) tree, experiencing an anomalously dry 3-yr period may be much the same as experiencing any three representative years during a consistently dry (e.g., future) period. To the extent that this is the case, the absence of substantial increases or decreases in tree recruitment (or decreases in dry areas without commensurate increases in wet areas) given drought in the 3 yr following fire suggests that disturbance may not facilitate climate tracking of species ranges, at least through changes in recruitment patterns, even when the disturbance removes the established trees from a site. A recent broad-scale analysis across California forest landscapes (including both burned and unburned areas) also suggested that regeneration has not been consistently tracking recent climate change; regeneration patterns appeared more strongly driven by local non-climatic factors (Serra-Diaz et al. 2016). Limited natural response of the tree community to weather and climate variation may make the forest more susceptible to type conversion under climate change.

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, Feeley et al. 2011). The difference may arise from our explicit focus on the recruitment stage: the rapid community shifts observed in other studies may occur primarily through differential growth and mortality as opposed to recruitment. Over longer time periods, however, continued migration, and particularly range expansion, will depend on recruitment in addition to mortality and growth (Clark et al. 1998). Recruitment in newly suitable areas 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 newly suitable sites appear to explain slow forest community expansion

observed elsewhere (Bertrand et al. 2011). In contrast, disturbance can trigger rapid range contraction and type conversion at dry range limits when increasing aridity precludes post-disturbance recruitment (Donato et al. 2016).

Although our data set captures substantial environmental variation (Fig. 2), including a drought of historically unprecedented magnitude (Robeson 2015), ongoing climate change may present even more intense extremes (Overpeck and Udall 2010) that could have a stronger potential to influence recruitment patterns than the variation we captured in our data set. Additionally, it is possible that other important weather variables not captured by this study influence regeneration dynamics. We focused on precipitation because water availability should be at least colimiting to establishment, both in the driest sites (where low precipitation contributes to greater drought stress) and in the wettest sites (where precipitation influences germination timing and growing season length; Barbour et al. 1991, Dolanc et al. 2013, Ettinger and HilleRisLambers 2013), but temperature is likely also important (Urza and Sibold 2017). Our data set contains insufficient interannual variation in temperature anomaly to explore its influence independently, but the effects of both temperature and precipitation are incorporated into the actual evapotranspiration (AET) and climatic water deficit (CWD) variables that we use as alternatives to explain regeneration. Models that use these variables yield similar qualitative conclusions as the precipitation models that we present here (see Appendix S1).

Density of nearby seed sources is known to be an important driver of post-fire conifer regeneration in this and similar systems (Tepley et al. 2017, Shive et al. 2018). For our regression models, we quantified seed availability using a rough proxy: the distance to the nearest reproductive conifer. The choice not to quantify the density of surrounding seed sources (sensu Shive et al. 2018), combined with our constraint that study plots be within 75 m of reproductive trees, may explain why we observe a weak (if any) effect of seed tree distance on regeneration patterns. However, this sampling scheme also helps to avoid any systematic conflation of seed distance with the weather and climate variables, which are the primary predictors of interest. Additionally, our cross-validation approach helps to ensure that the inferred effects of climate and weather variables are generalizable and not the result of spurious correlations driven by variation in seed availability or other variables. Our community analysis, in contrast, does (indirectly) account for seed source density in that it explains regenerating tree community composition using species-specific basal area in the unburned forest near the burned plots.

### The role of biological inertia

An additional 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. 4), a pattern that is often observed following fire (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 solar exposure) and regeneration in most of our regeneration models (Appendix S1: Table S3) and in the community composition analysis (Fig. 4, Appendix S1: Table S6), particularly when compared with the relatively weak influence of the post-fire weather anomaly in these analyses (Appendix S1: Tables S1 and S6). Normal climate and solar exposure can influence the distribution of adult trees (Dobrowski 2010, Lutz et al. 2010), potentially more directly than they influence patterns of regeneration, as the post-fire weather that young seedlings experience is often not representative of the long-term average climate.

Our observation of a correspondence in community composition between recruiting 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. 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 recruitment was not strongly affected. 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). Until substantial shifts in adult species composition occur, limited community reorganization during regeneration could create opportunities for other vegetation types to become more dominant.

Our results apply specifically to severely burned areas where a seed source is present, as our study focused on these areas. Overall, high-severity fires, which often produce large contiguous severely burned patches with no seed source and therefore poor tree recruitment (Welch et al. 2016, Shive et al. 2018), may contribute substantially to tree species range contraction (Campbell and Shinneman 2017). Climate change and management legacies are expected to result in increases in the amount of contiguous severely burned areas with no seed sources (Stevens et al. 2017), suggesting that across landscapes, reductions in recruitment under post-fire drought may be more substantial than the shifts we observe specifically in sites near residual adults.

### Shrub and graminoid recruitment

In contrast to the limited response of tree establishment to post-fire weather variation, recruitment of shrubs and graminoids showed strong sensitivities, 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., decreased conifer recruitment due to strong initial shrub establishment or vice versa), an interpretation that is supported by manipulative work (Conard and Radosevich 1982). A previous observational study in our system, using much of the same plot data, documented a strong inverse relationship between shrub cover and recruitment (Welch et al. 2016). Given the long time period required for conifers to dominate in burned areas that initially become dominated by shrubs (Lauvaux et al. 2016), increases in shrub cover and height dominance relative to tree seedlings under post-fire drought could represent early signs of climate-driven forest type conversion to chaparral, particularly when coupled with increases in the frequency of fires that remove establishing trees.

### Importance of temporal variation in weather and extreme events

Most of the post-fire recruitment responses that were sensitive to post-fire precipitation (white fir recruitment and height dominance, yellow pine height dominance, and graminoid cover) were more sensitive to the anomaly term reflecting minimum post-fire precipitation (i.e. the driest of the 3 yr following the fire) than to the term reflecting mean post-fire precipitation (i.e., average drought intensity over the 3 yr following the fire). Although the difference in most cases is small, the pattern is suggestive of the importance of extreme weather events soon after fire in shaping regeneration patterns. If the mechanism of drought-induced mortality in small seedlings is hydraulic failure (McDowell et al. 2008), an extreme dry year (even if flanked by two wet years) could cross a threshold that may not be crossed by a series of several moderately dry years. Via this mechanism, drought may affect recruitment in multiple seedling cohorts. In contrast, if an unusually dry year reduces recruitment by preventing germination, an alternative mechanism that may explain our observations, it would impact only one cohort per dry year. The nearly twofold range of variation in white fir occurrence that we observe along variation in post-fire anomaly suggests that the mechanism(s) in operation affect multiple cohorts.

In contrast to conifer recruitment and graminoid cover, hardwood recruitment and shrub cover is better explained by the *mean* precipitation anomaly, likely reflecting the fact that much of the shrub and hardwood response we observed derived from stems resprouting from surviving underground structures, which can buffer the influence of any one year. In addition, once shrub recruitment occurs, growth accumulates (contributing to cover) over each post-fire year.

Differential responses of vegetation types to different forms of post-fire weather variation suggest that future post-fire recruitment patterns will depend on changes both in mean conditions and in the frequency and intensity of extreme events. Analyses of recruitment in response to temporal variation in weather can account for the influence of extreme events as well as the influence of biological inertia, factors that cannot be isolated when examining variation along spatial gradients alone. The work to date suggests that changes in mean and extreme conditions will substantially impact forest communities; additional research into the impacts of climate variability on tree recruitment will help in developing more refined predictions of future changes.

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