Effects of postfire climate and seed availability on postfire conifer regeneration

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Abstract. Large, severe fires are becoming more frequent in many forest types across the western United States and have resulted in tree mortality across tens of thousands of hectares. Conifer regeneration in these areas is limited because seeds must travel long distances to reach the interior of large burned patches and establishment is jeopardized by increasingly hot and dry conditions. To better inform postfire management in low elevation forests of California, USA, we collected 5-yr postfire recovery data from 1,234 study plots in 19 wildfires that burned from 2004–2012 and 18 yrs of seed production data from 216 seed fall traps (1999–2017). We used these data in conjunction with spatially extensive climate, topography, forest composition, and burn severity surfaces to construct taxon-specific, spatially explicit models of conifer regeneration that incorporate climate conditions and seed availability during postfire recovery windows. We found that after accounting for other predictors both postfire and historical precipitation were strong predictors of regeneration, suggesting that both direct effects of postfire moisture conditions and biological inertia from historical climate may play a role in regeneration. Alternatively, postfire regeneration may simply be driven by postfire climate and apparent relationships with historical climate could be spurious. The estimated sensitivity of regeneration to postfire seed availability was strongest in firs and all conifers combined and weaker in pines. Seed production exhibited high temporal variability with seed production varying by over two orders of magnitude among years. Our models indicate that during droughts postfire conifer regeneration declines most substantially in low-to-moderate elevation forests. These findings enhance our mechanistic understanding of forecasted and historically documented shifts in the distribution of trees.

Key words: drought stress; ecosystem management; fire effects; postfire conifer regeneration; resilience; tree reproduction.

Introduction

Recovery of coniferous forests in the western United States following high-severity fire largely depends on the arrival of seeds into environments that allow for germination and seedling development. Unlike many hardwoods, the vast majority of conifers in this region lack the capacity to resprout after fire (Pausas and Keeley 2017) and thus are dependent on seedling recruitment for persistence after fires (obligate seeders). Other adaptations to recovery following fire (e.g., serotiny and soil seed banks) are uncommon in western U.S. conifers. As a result, seeds must often travel long distances to recolonize large, high-severity, fire patches (Haire and McGarigal 2010, Chambers et al. 2016, Stevens et al. 2017). However, typical dispersal distances of conifers are relatively short, with most conifer seedling recruitment occurring within 60 m of surviving trees (Rother and Veblen 2016, Welch et al. 2016), although long-distance (e.g., >200 m) dispersal is possible (Kemp et al. 2016). Following dispersal seeds must then germinate, and seedlings must become established and grow for forest recovery to take place. Seedlings lack extensive reserves, so seedling growth and survivorship is expected

to be sensitive to postfire environmental conditions. As a result, recruitment of conifers in postfire areas can be limited by local site conditions, such as soil conditions, topography, and moisture (Gray et al. 2005, Dobrowski 2011, Puhlick et al. 2012, Dobrowski et al. 2015).

Fire size, frequency, overall area burned, and severity have increased over the past several decades across many vegetation types in the western United States (Franco et al. 2006, Miller et al. 2009b, Mallek et al. 2013, Williams et al. 2013, Dennison et al. 2014, O'Connor et al. 2014, Kitzberger et al. 2017). The underlying factors that have led to increasing fire impacts in historically high-frequency/low-severity coniferous forests in the western United States include increased fuel loading from accumulation of surface and ladder fuels that have accelerated fire spread and intensity, largely from the past legacy of land use involving timber harvest, excessive grazing and, importantly, fire exclusion (Allen et al. 2002, Attiwill and Binkley 2013, Keeley and Safford 2016). These impacts have been exacerbated by changing climates that promote fire spread (Abatzoglou and Williams 2016). Climatic shifts can also interact with local site conditions as well as fire severity to further reduce seedling establishment (Tepley et al. 2017, Davis et al. 2019), resulting in landscape scale limitation to postfire recovery in conifer forests in the western United States (Savage et al. 2013).

Multiple studies have documented conifer recruitment failure following large, severe fire in western coniferous forests (e.g., Goforth and Minnich 2008, Falk 2013, Coop et al. 2016). In contrast, hardwood species in these forests (primarily *Quercus* spp.) have the ability to resprout following top-kill by fire, potentially leading to the conversion of conifer forests to other vegetation types, including broadleaf vegetation or grasslands (a process variously called "ecosystem transformation," "vegetation type conversion," as well as other terms; Keeley and Brennan 2012, Millar and Stephenson 2015). Such postfire vegetative restructuring drives changes in important ecosystem services (e.g., wildlife habitat, soil stability, carbon sequestration; Hurteau et al. 2014, Coop et al. 2016, Seidl et al. 2016). However, such shifts in species composition may also represent transition to an ecosystem state that may be ultimately more resilient to warmer, drier environments and greater disturbance frequencies (McWethy et al. 2019).

The increased incidence of high-severity fires followed by limited conifer recruitment poses serious challenges to forest managers. In this era of "megadisturbances" managers need to develop new insights, strategies, and tools to allow forests to adjust to these changing conditions (Millar and Stephenson 2015). These approaches are often centered on increasing disturbance *resistance* (remaining unchanged in the face of disturbance) and *resilience* (forest recovery to pre-disturbance composition or structure). Forest managers may be able to better plan for and promote resilience with the aid of spatially explicit forecasts of recruitment following high severity fire

(e.g., identifying sites and conditions that are at high risk for conifer recruitment failure that may be targeted for postfire management, seeding or planting).

In the low-elevation mixed conifer forests of California, broad patterns of postfire regeneration appear to be related to fire severity, land-use history, precipitation, distance to seed source, and other site-specific conditions (e.g., slope, vegetation type; Welch et al. 2016). Recently, Shive et al. (2018) developed a spatially explicit forecast model of natural postfire regeneration for mixed conifer forests of California and found regeneration probabilities to depend primarily on historical climate averages and estimated seed availability. This model did not incorporate potential effects of fluctuations in postfire climate and seed availability during the initial postfire regeneration window. However, conifer seed production is characterized by large fluctuations in annual seed output (Kelly and Sork 2002), which has the potential to influence postfire regeneration (Peters et al. 2005, Wright et al. 2014). Further, work by Young et al. (2019), using much of the same forest regeneration data as Shive et al. (2018), showed that at least under some circumstances recruitment was dependent on short-term (3 yr) postfire patterns of precipitation. These results suggest that the model presented by Shive et al. (2018) might be improved by incorporating postfire conditions.

Here, we ask how postfire fluctuations in climate and seed production affect regeneration for a suite of conifer species, and discuss the management implications. We analyze these dynamics by extending the model presented in Shive et al. (2018) to account for these fluctuations and by tailoring the model to provide taxon-specific predictions for firs and pines. We hypothesized that (1) more xeric postfire conditions are associated with lower probability of conifer regeneration and (2) including metrics of postfire climate will improve model performance relative to models premised on historical climate (i.e., Shive et al. 2018). Additionally, we quantify temporal variation in conifer seed production and its potential impact on postfire regeneration. While we cannot predict the postfire environment with certainty, producing a set of prediction maps that span a range of plausible postfire conditions could significantly improve management planning. For example, managers may wish to plan for a range of postfire conditions or emphasize scenarios where drought is more intense and frequent. These scenarios provide a glimpse of a process by which forests may change in response to future conditions (Thorne et al. 2018) when recent droughts could be similar to the expected average climate.

METHODS

Study system

We modeled postfire regeneration in yellow pine and mixed-conifer forests in California, USA. The climate of the region is Mediterranean with mean annual

precipitation ranging from 536 to 2,144 mm (Appendix S1: Table S1). Forests in this region are primarily composed of ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*P. lambertiana*), and black oak (*Quercus kelloggii*). Prior to European colonization, these forests typically burned at intervals of 11–16 yr, but many sites have experienced fire exclusion over the last century (Safford and Stevens 2017). We incorporated data from 19 separate fires occurring between 2004 and 2012 in these forests, with fire elevations ranging from 245 to 2,600 m and fire areas from 940 to 40,860 ha (Fig. 1, Appendix S1: Tables S1, S2).

Seed production measurements

We used annual seed production data from seed fall traps located in long-term forest demography plots (Das et al. 2016) in Yosemite and Sequoia National Parks to assess natural variability in seed production. Plots were generally 1 ha in area. The plots were further divided into 25-m^2 subplots, with nine 0.25-m^2 seed traps placed in two or more interior subplots. Seeds produced from 1999 to 2017 were collected, taxonomically sorted, and counted after spring snowmelt in the following year. We selected 12 demography plots (216 seed fall traps) that most closely matched the species composition and elevational range of the fires in our postfire regeneration database and that had minimal missing data. The plots were comprised primarily of white fir, ponderosa pine, incense cedar, sugar pine, and Jeffrey pine (Appendix S1: Table S3).
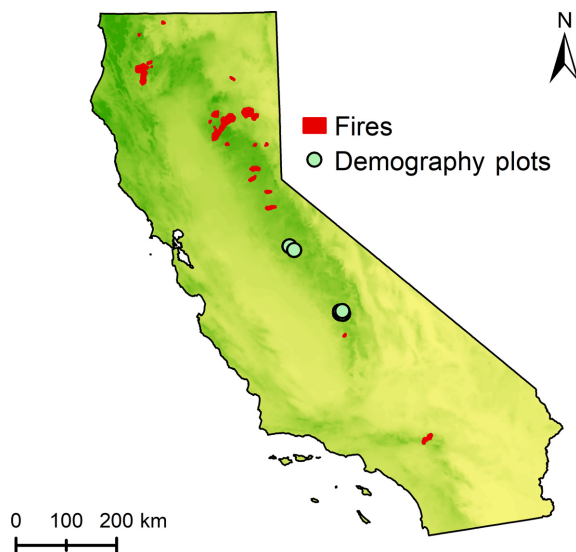

FIG. 1. Locations of 19 fires and 12 long-term forest demography plots used in this study. Background color indicates mean annual precipitation.

Postfire regeneration measurements

We aggregated postfire regeneration data collected by Welch et al. (2016) and Young et al. (2019). Vegetation measurements were taken in 60-m^2 (4.4 m radius) plots stratified across postfire landscapes. The plot size was designed by Welch et al. (2016) to assess whether natural regeneration achieved a target of approximately 175 seedlings/ha. Plot centers were located at the nodes of a 200-m grid, such that the closest possible distance between plots was 200 m. To reduce model complexity and standardize models, we used only data that were collected during the fifth year after a fire burned ($N = 1,234$), thereby eliminating the need to include number of years postfire as a predictor variable. Previous studies indicate that in this and similar systems the large majority of postfire tree establishment usually occurs within 5 yr following fire (Harvey et al. 2016, Tepley et al. 2017, Urza and Sibold et al. 2017). We excluded plots with evidence of management interventions, including areas where cut stumps or regularly spaced seedlings were seen during field sampling and areas mapped as treated by the USFS Forest Activity Tracking System database (USDA Forest Service 2016). For each plot we determined if there was postfire recruitment in three taxonomic categories: conifers, firs (*Abies*), and pines (*Pinus*). Douglas-fir was not modeled as its own category of recruitment because it was not well represented in seed production data from forest demography plots. Following methods from Shive et al. (2018) plots were considered to have postfire recruitment if they contained at least one seedling (<1.37 m tall). Additionally, because trees sometimes grow taller than 1.37 m within 5 yr of germination (Oliver and Dolph 1992), plots with at least one sapling that germinated after the fire (i.e., age determined by bud scars) were considered to have postfire conifer recruitment. Mean burn severity (RdNBR) across all study plots was 534, which corresponds to 57% loss of basal area (Appendix S1: Fig. S1) and falls in the moderate severity class of Miller and Thode (2007). Plots ranged in elevation from 480 to 2,522 m (Appendix S1: Tables S1).

Candidate predictor variables

To create models that can be applied across broad spatial scales we selected candidate predictor variables that may be derived from GIS and remote sensing products as opposed to measurements that must be collected in the field. Candidate predictor variables included indices of long-term historical climate, short-term postfire climate, topography, burn severity, and seed availability. Values for predictors were extracted from raster surfaces using bilinear interpolation. We included a subset of predictors selected by Shive et al. (2018). Burn severity was measured using the satellite-derived relative differenced Normalized Burn Ratio (RdNBR; 30-m resolution; Miller et al. 2009*a*, USDA Forest Service 2018). Slope

and aspect were derived from 30-m resolution elevation rasters (U.S. Geological Survey 2018). Long-term average (1981–2010) precipitation (PPT) and climate water deficit (CWD) were extracted from 270-m resolution Basin Characterization Model (BCM) rasters (Flint et al. 2013, Thorne et al. 2015).

Seed availability predictors were calculated using 30-m resolution interpolated maps of predicted basal area for each conifer species (Ohmann et al. 2011). In the Sierra Nevada, the coefficient of determination between predicted and observed conifer basal area was 0.5811 (genus-specific coefficients were not reported). To predict regeneration in fires that burned after the production of basal area maps we used a logistic model fit to data from Miller et al. (2009b) to adjust basal area according to burn severity (Appendix S1: Fig. S1). We modified seed production equations used by Shive et al. (2018) to account for nonlinear relationships between basal area and leaf mass and between leaf mass and seed production (Greene and Johnson 1994: Eqs. 2 and 5). Seed density estimates were derived from seed production using a half-Gaussian dispersal kernel and a range of dispersal parameter (σ) values ranging in 10-m intervals from 5 m to 195 m. Average predicted seed density was then scaled to average observed seed production from the seed trap data.

Short-term postfire climate candidate predictors consisted of a modified version of predictors used by Young et al. (2019). We calculated average annual (June–May) and summer (June–September) precipitation for postfire periods beginning immediately after the fire and ending 1, 2, 3, 4, or 5 yr following the fire. Mean postfire precipitation was strongly correlated with mean historical precipitation (Appendix S1: Table S4). Because the stress of a single particularly dry year may be predictive, we also examined minimum precipitation during the postfire period. In addition to raw precipitation values we considered precipitation anomalies or departures from long-term average precipitation at each site. We calculated anomalies as z-scores, or the number of standard deviations (with respect to historical interannual variation) that the observation fell from the historical mean at the site. Because stress resulting from the interaction of temperature, soil properties, and precipitation may affect recruitment, we also tested models premised on postfire climatic water deficit and summer vapor pressure deficit (VPD). As we did with precipitation, we examined average and maximum (most stressful year) values, raw values, and anomalies. Postfire precipitation and climatic water deficit were extracted from 270-m resolution BCM rasters (Flint et al. 2013) and VPD was extracted from 4-km resolution Parameter-elevation Regressions on Independent Slopes Model (PRISM) rasters (Daly et al. 1994).

Statistical models

We used generalized additive models (Wood 2017) to model the probability of postfire recruitment within postfire regeneration plots. We constructed separate models for three taxonomic categories: conifers, firs (*Abies*), and pines (*Pinus*). Generalized additive models provide estimates of effects of predictor variables and variable interactions on the probability of regeneration using smooth functions. To protect against developing overfitted models, model performance was evaluated using leave-one-fire-out cross-validation, wherein data from one fire were iteratively excluded from model training and used for model evaluation. The pooled evaluation data for all fires was then used to calculate the area under the receiver operating characteristic curve (AUC) and the classification error rate (CER). In addition to these metrics we also visually examined marginal response curves and reliability diagrams. To reduce potential overfitting and simplify model interpretation we constrained response functions for seed availability and climate variables to monotonic functions by using shape constrained splines or linear as opposed to smoothed response when necessary (Pya and Wood 2015). All analyses were conducted in R version 3.5.1 (R Core Team 2018). Generalized additive models and shape constrained additive models were fit using the mgcv version 1.8-28 and scam version 1.2-5 packages, respectively (Pya and Wood 2015, Wood 2017).

Beginning with a subset of predictors selected by Shive et al. (2018), we used a two-step model selection process. Predictors initially included in the model were mean historical precipitation, burn severity, seed availability, slope, and aspect. For each taxon we first selected the seed dispersal kernel that resulted in the highest out-of-sample AUC. We then compared the resulting models, which included mean historical precipitation and non-climate variables (i.e., the baseline models) against models that included postfire climate variables and models that included no historical or postfire climate. We tested a total of 65 variable combinations, including interactions between seed availability and precipitation as well as between pre- and postfire precipitation (Appendix S1: Table S5). Highly correlated ($|\rho| > 0.65$) predictor variables were never included in the same model. We examined semivariograms and calculated Moran's I statistics to detect potential spatial autocorrelation of model residuals between plots within each fire.

To examine the impact of variable precipitation and seed production on conifer regeneration we used the best-performing (highest AUC) all-conifer model to project probability of postfire recruitment to the full spatial extent of each of the 19 fires included in this study. We used historical mean and a range of projected future mean precipitation to represent high and low precipitation scenarios for the postfire period (270-m resolution BCM rasters). Dry conditions were represented by the MIROC-ESM RCP8.5 scenario (Watanabe et al. 2011), while relatively wet conditions were represented by the CNRM-CM5 RCP8.5 scenario (Voldoire et al. 2013). Seed production was scaled to periods of low, average, and high seed production using the 10th percentile, mean, and 90th percentile of the 5-yr moving mean of

seed production. We also examined the predicted probability of postfire conifer recruitment with respect to elevation and precipitation scenarios for a transect on the west slope of the Sierra Nevada (latitude 38° N, longitude 119.6°–121.1° W, elevation 25–2,543 m, distance 131.7 km). All non-climate variables on the transect were held at the mean values of the postfire regeneration data. We used California's 2014 King Fire to visualize spatial differences in projected recruitment under variable postfire climate and seed production scenarios and to make direct comparisons to the results presented in Shive et al. (2018).

RESULTS

Seed production

Production of conifer seeds varied markedly between years (Fig. 2). Median annual seed production in firs (*Abies*) and pines (*Pinus*) was correlated (Spearman rank correlation, $\rho = 0.55$, $P < 0.05$). Median conifer seed production during the five years with the highest production (2001, 2003, 2006, 2008, 2013; 377 seeds/m^2) exceeded median seed production during other years (38.3 seeds/m^2) by a factor of 9.85. Median seed production for the year with highest production (2001, 568 seeds/m^2) exceeded the year with the lowest production (2000, 3.56 seeds/m^2) by a factor of 160 (Appendix S1: Fig. S2). The mean, 10th percentile, and 90th percentile of the 5-yr moving mean of seed production were, respectively, 176, 130, and 251 seeds/m^2 (resulting scaling factors for low, mean, and high seed production periods were 0.740, 1.00, and 1.42).

Fir seeds were most abundant, comprising 77.9% (133,666/171,629) of the total conifer seeds collected from seed-fall traps but 46.6% of the basal area of conifers in the surrounding plots. Among fir seeds, 50.1% were identified to the species level, with the remaining seeds identified to the genus level only. The five years with the highest seed production for firs were the same as for conifers as a whole and median fir seed production during these years (307 seeds/m^2) exceeded median seed production during other years (15.1 seeds/m^2) by a factor of 20.3. Median fir seed production for the year with highest production (2001, 467 seeds/m^2) exceeded the year with the lowest production (2000, 1.33 seeds/m^2) by a factor of 350. The mean, 10th percentile, and 90th percentile of the 5-yr moving mean of fir seed production were, respectively, 140, 102, and 216 seeds/m^2 (resulting scaling factors for low, mean, and high seed production periods were 0.730, 1.00, and 1.54).

Pine seeds comprised 7.37% of total conifer seeds (12,657/171,629) but 35.2% of conifer basal area in surrounding plots. Among pine seeds, 80% were identified to the species level, with the remaining seeds identified to the genus level only. Median pine seed production during the five years of highest production for pines (2001, 2005, 2013, 2014, 2017; 12.6 seeds/m^2) exceeded median seed production during other years (1.56 seeds/m^2) by a factor of 8.07. Median seed production during the year with the highest seed production (2001, 22.4 seeds/m^2) exceeded the year with the lowest production (1999, 0.556 seeds/m^2) by a factor of 40.4. The mean, 10th percentile, and 90th percentile of the 5-yr moving mean of pine seed production were, respectively, 11.9, 8.47, and 15.6 seeds/m^2 (resulting scaling factors
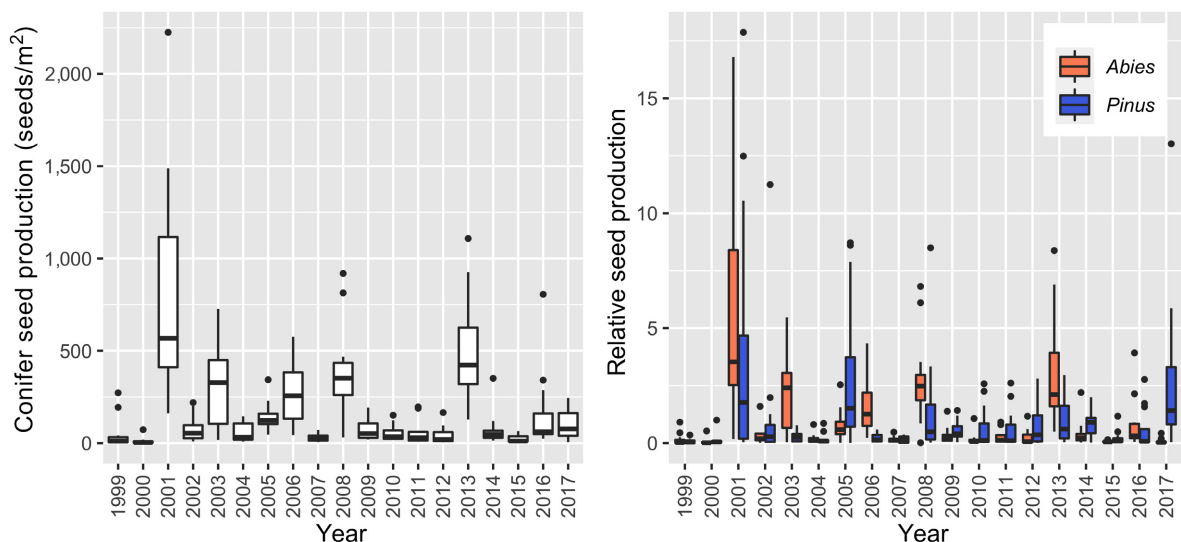

FIG. 2. Annual and taxonomic variation in conifer seed production in 12 study plots located in mixed-conifer forests of Yosemite and Sequoia National Parks. Seed production for each plot is the mean seed production across 18 seed traps stratified throughout the plot. Relative seed production (right) is scaled to mean seed production for the taxon. Box plots depict median, interquartile range, and Tukey-style whiskers (McGill et al. 1978).

for low, mean, and high seed production periods were 0.711, 1.00, and 1.31).

Postfire recruitment models

We found that some models that included postfire climate modestly outperformed models with historical precipitation as the only climate variable (i.e., our baseline models). However, performance differences were small and the baseline models tended to outperform models that included postfire climate as often as not. Postfire climate variables that improved model performance for one taxa sometimes resulted in decreased model performance in another taxa. Three classes of postfire climate variables contributed to models that outperformed historical-precipitation-only models and had response functions where wetter conditions led to higher probability of regeneration. These included: mean annual postfire precipitation, annual postfire precipitation anomaly, and minimum annual postfire precipitation anomaly (Table 1). We did not detect evidence of residual spatial autocorrelation within fires for any of the models included in Table 1. Models that included both historical precipitation and other postfire climate variables (i.e., maximum postfire climatic water deficit, mean postfire summer vapor pressure deficit) sometimes also achieved higher performance than historical-precipitation-only models, however these models produced the odd result of predicting higher regeneration when historical conditons were wetter but when postfire conditions were drier. We excluded these models from Table 1

because they lacked mechanistic explanation. Given the large number of postfire climate models tested (67) and the multiple predictors in our models, some instances of improved predictive performance over the historical-climate-only model may be due to chance or correlation with other variables.

The model of conifer recruitment with the highest AUC and lowest CER included mean postfire precipitation in the 3-yr window following fire. Among the predictor variables, 3-yr postfire precipitation had the greatest effect on recruitment, as measured by its proportion of total chi-squared values (0.64). Precipitation, burn severity, slope, and seed availability all had monotonic marginal response curves (Fig. 3 and Appendix S1: Fig. S3). Higher precipitation, lower burn severity, lower slope, and higher seed availability resulted in higher probabilities of recruitment (Appendix S1: Figs. S3–S6). More north-facing aspects resulted in higher probabilities of conifer recruitment. The best-performing seed availability proxy used a half-Gaussian dispersal kernel with $\sigma = 35$ m (mean dispersal distance of 28 m, 95% of seeds dispersing within 68.6 m of their sources).

The model of fir recruitment with the highest AUC was premised on mean historical precipitation and did not include postfire climate. This model tied for the lowest CER with a model that included mean postfire precipitation in the four-year window following fire. Response curves for these and other variables were qualitatively similar to response curves for the conifer models described above (Appendix S1: Figs. S7–S10). Among

TABLE 1. Comparisons of models of postfire recruitment premised on alternate climate variables for conifers, pines, and firs.

Response and model	Climate variables in model	AUC	CER
Conifer recruitment			
C1	mean PPT 0–3 yr postfire	0.7747	0.2869
C2	PPT anomaly 0–5 yr postfire, mean PPT 1981–2010	0.7728	0.2958
C3	mean PPT 1981–2010	0.7726	0.2934
C4	minimum PPT anomaly 0–2 yr postfire, mean PPT 1981–2010	0.7709	0.2942
C5	no climate	0.6502	0.3906
Fir recruitment			
F1	mean PPT 1981–2010	0.8712	0.1750
F2	mean PPT 0–4 yr postfire	0.8702	0.1750
F3	PPT anomaly 0–5 yr postfire, mean PPT 1981–2010	0.8681	0.1767
F4	minimum PPT anomaly 0–5 yr postfire, mean PPT 1981–2010	0.8681	0.1831
F5	no climate	0.8099	0.2399
Pine recruitment			
P1	PPT anomaly 0–3 yr postfire, mean PPT 1981–2010	0.6432	0.3476
P2	minimum PPT anomaly 0–5 yr postfire, mean PPT 1981–2010	0.6408	0.3582
P3	mean PPT 1981–2010	0.6400	0.3476
P4	mean PPT 0–5 yr postfire	0.6356	0.3476
P5	no climate	0.5589	0.3655

Notes: Models are ordered by their out-of-sample (leave-one-fire-out) area under the receiver operating characteristic curve (AUC). Shown for each response variable are the best-performing (highest AUC) model that included the following climate variables: (1) mean annual postfire precipitation (C1, F2, P4), (2) mean annual postfire precipitation anomaly and mean historical precipitation (C2, F3, P1), (3) minimum annual postfire precipitation anomaly and mean historical precipitation (C4, F4, P2), (4) mean historical precipitation (C3, F1, P3), and (5) no climate variables (C5, F5, P5). CER refers to classification error rate. PPT refers to precipitation. Non-climate variables included in each model were seed availability, burn severity, slope, and aspect.
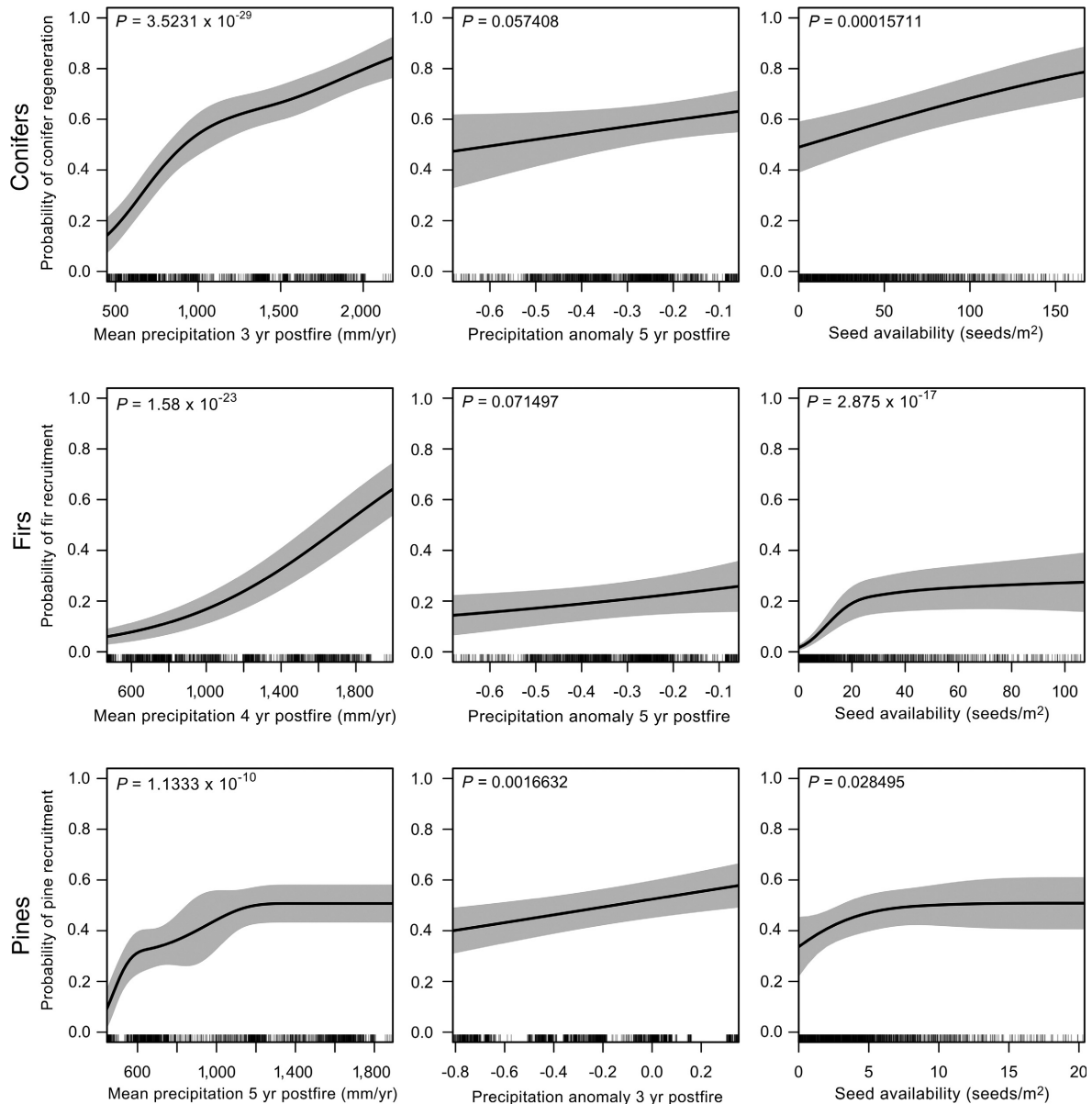
Fig. 3. Marginal response curves for average postfire precipitation, postfire precipitation anomaly, and seed availability in conifers, firs, and pines. Each curve depicts probability of regeneration as a function of one predictor when all other predictors are held at their mean value. Gray bands depict two standard errors from the mean. Ticks along the *x*-axis depict the distribution of the predictor variable among the 1,234 plots. Shown are response curves premised on the top-performing model for each predictor (Table 1). Marginal response curves for other models and variables may be found in supplementary materials (Appendix S1: Figs. S3–S14).

the predictor variables, mean postfire precipitation, mean historical precipitation, and seed availability had the greatest effect on recruitment, as measured by their proportion of total chi-squared. The best-performing seed availability proxy used a half-Gaussian dispersal kernel with $\sigma = 145$ m (mean dispersal distance of 116 m, 95% of seeds dispersing within 284 m of their sources).

The model of pine recruitment with the highest AUC included postfire precipitation anomaly in the three-year window following fire and mean historical precipitation. This model tied with two other models for the lowest CER. The other models that tied for lowest CER included either mean precipitation in the five-year window following fire or mean historical precipitation. Response curves for these and other variables were

qualitatively similar to those described above, except that burn severity had a hump-shaped marginal response curve, with low to moderate burn severities resulting in higher recruitment probability than high burn severity. Among the predictor variables, mean postfire precipitation, mean historical precipitation, and burn severity had the greatest effect on recruitment, as measured by their proportion of total chi-squared (Appendix S1: Figs. S11–S14). The best-performing seed availability proxy used a half-Gaussian dispersal kernel with $\sigma = 45$ m (mean dispersal distance of 36 m, 95% of seeds dispersing within 88.2 m of their sources). The influence of estimated seed availability on regeneration was strongest in firs and all conifer combined and weaker in pines (Fig. 3, Appendix S1: Figs. S3–S14).

The sensitivity of regeneration to postfire precipitation varied among models and taxa. In the all-conifer models, sensitivity of regeneration to postfire precipitation was substantially higher in the model premised on mean postfire precipitation compared to the model premised on mean postfire precipitation anomaly. In contrast, the pine model premised on postfire precipitation anomaly was substantially more sensitive to postfire precipitation than the model premised on mean postfire precipitation. In firs, sensitivity of regeneration to postfire precipitation was relatively consistent between the postfire mean precipitation model and the postfire precipitation anomaly model. Differences in the sensitivity

of regeneration to postfire precipitation between models (particularly among the all-conifer and pine models) represent unresolved uncertainty in how these systems respond to postfire climate.

Postfire regeneration scenarios

Predicted probability of conifer regeneration varied markedly under scenarios of variable postfire precipitation and seed production (Figs. 4 and 5, Appendix S1: Figs. S15–S20). Using our model (Table 1, model C1) to project conifer regeneration to the full spatial extent of the 19 fires included in our data set, and using postfire precipitation data for these fires, we project that 42.3% of burned area (78,511 ha/185,448 ha) had no conifer recruitment at a 60-m^2 spatial resolution 5 yr after fire. If mean precipitation following these fires had reflected mean precipitation for the 1951–1980 period, we expect that 35.6% of burned area would have had no conifer recruitment (32.7% and 37.6% under high and low seed production scenarios). Under a scenario of mean precipitation for the 1981–2010 period we expect that 36.1% of burned area would have no recruitment (33.1% and 38.1% under high and low seed production scenarios). Under average precipitation for the drier end-century (2070–2099) scenario (MIROC-ESM RCP8.5) we expect the percentage of burned area with no conifer recruitment could reach 49.4% (45.8% and 51.9% under high
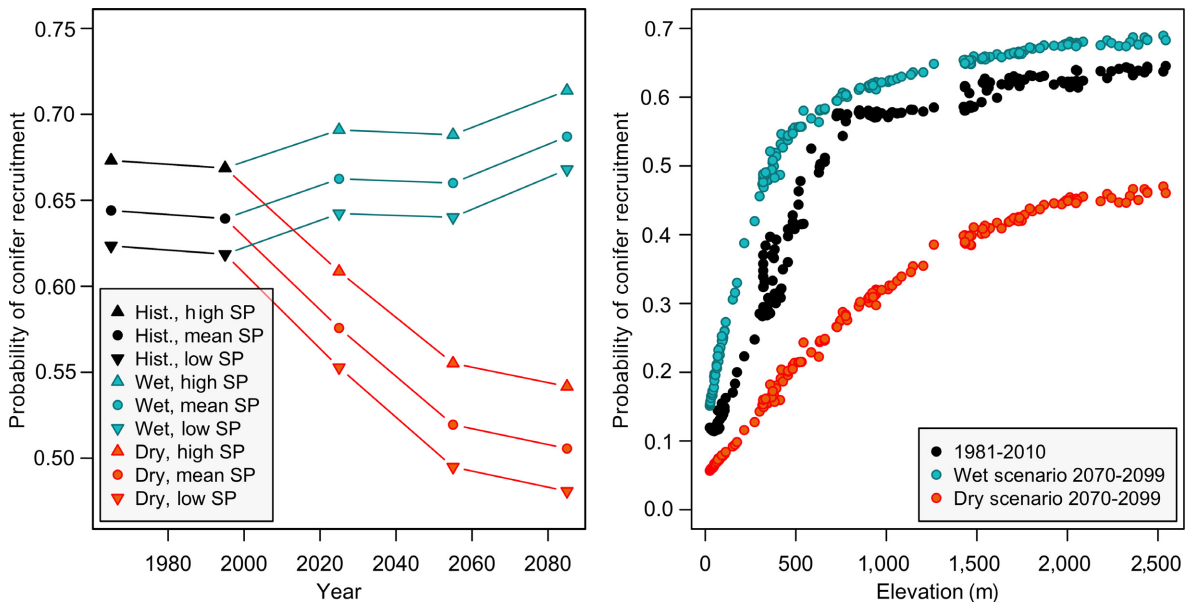

FIG. 4. Projected changes to conifer recruitment under future climate and seed production scenarios (Table 1, model C1). Left panel: mean probability of postfire conifer recruitment across the full spatial extent of the 19 fires included in this study with respect to historical and projected future mean precipitation and variable seed production. High and low seed production scenarios scale seed production to the 0.9 and 0.1 quantiles of the 5-yr moving average of observed seed production. Other predictors were held at their historical values. Right panel: probability of postfire conifer recruitment with respect to elevation for a transect of the west slope of the Sierra Nevada (latitude = 38° N) under historical and projected future precipitation scenarios. Other predictors were held at mean values from postfire recruitment plots. Legend abbreviations: SP, seed production; Hist., historical precipitation; Dry, MIROC-ESM RCP8.5; Wet, CNRM-CM5 RCP 8.5.
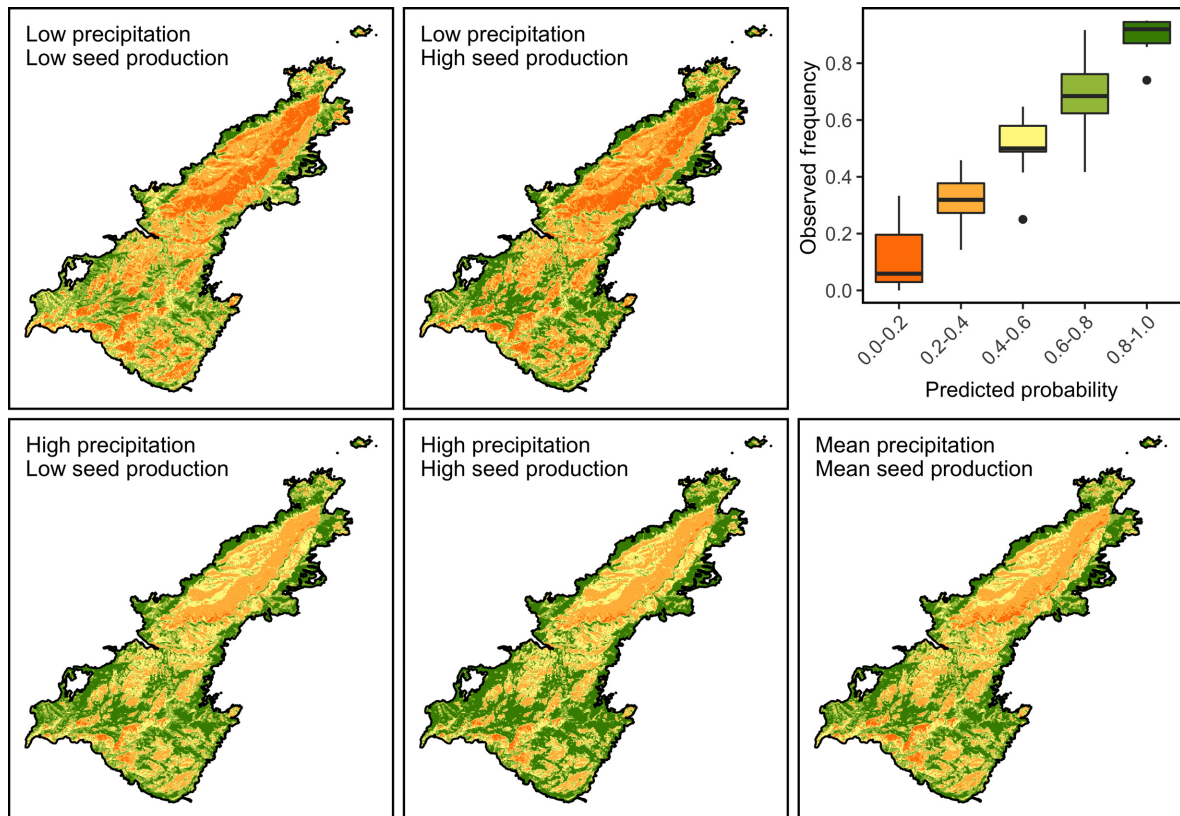
FIG. 5. Postfire conifer recruitment scenarios for the 2014 King Fire, under scenarios of variable postfire precipitation and seed production (Table 1, model C1). Reliability diagram in upper right is based on leave-one-fire-out cross-validation. High and low postfire precipitation conditions depicted here correspond to mean annual precipitation for mid-century (2040–2069) under the CNRM-CSM5 and MIROC-ESM scenarios, respectively. Mean precipitation was based on the period 1981–2010. Relative postfire seed production scenarios correspond to the 0.1 and 0.9 quantiles of the 5-yr moving average of seed production measured in seed traps (Fig. 2, Appendix S1: Fig. S2).

and low seed-production scenarios). Conversely, under average conditions for the wetter end-century scenario (CNRM-CM5 RCP8.5) we expect the percentage of burned area with no conifer recruitment could decrease to 31.3% (28.6% and 33.2% under high and low seed production scenarios). Projected declines in conifer regeneration under drought scenarios were especially pronounced in low-to-moderate-elevation coniferous forests (~500–1,300 m; Fig. 4).

DISCUSSION

This study advances previous research (Shive et al. 2018, Young et al. 2019) by incorporating postfire climate, postfire seed availability, and taxon-specific responses into spatially explicit models of postfire conifer regeneration. Overall, we found that models premised on postfire and historical precipitation performed similarly. Models premised on postfire climate achieved only modest improvements over models premised on historical climate only. Given that historical and postfire precipitation are highly correlated it may be difficult to

statistically distinguish which climate metrics are most predictive. Postfire climate has a clear mechanistic connection to regeneration because it reflects the actual abiotic conditions experienced by plants during the postfire period. Historical climate could be important insofar as it drives biological community composition and soil conditions. Models that incorporate both historical climate and postfire climate anomaly offer a middle ground where both the direct effects of postfire climate and the indirect effects of historical climate can be included. Results from these models (i.e., C2, F3, P1) suggest that both postfire and historical climate may contribute to regeneration success.

Several prior studies support the importance of postfire climate for tree regeneration, however there is no clear consensus on which climate variables most influence regeneration patterns. Young et al. (2019), using much of the same data as used in this paper, found that minimum precipitation anomaly (i.e., driest year) during the 3 yr following a fire was most predictive of regeneration of white fir. Urza and Sibold (2017) found that mean growing season precipitation during the 5 yr

following a fire was most predictive of regeneration in western larch (*Larix occidentalis*), Engelmann spruce (*Picea engelmannii*), and Douglas-fir, while winter precipitation during the 5 yr following a fire was most predictive in lodgepole pine (*Pinus contorta*). Davis et al. (2019) found that three drought stress metrics (summer VPD, soil moisture, and maximum surface temperature) during the year of germination were strong drivers of annual postfire recruitment in ponderosa pine and Douglas-fir. Growing-season moisture conditions may be especially important in preventing desiccation of first-year seedlings (Moyes et al. 2013). Two studies found that climatic water deficit anomaly during the 3 yr following a fire was negatively associated with regeneration in a variety of conifer species (Harvey et al. 2016, Stevens-Rumann et al. 2018), however these studies did not assess other climate predictors. In contrast to these studies, Rodman et al. (2019) found that 3-yr postfire climate (mean and anomaly of climatic water deficit and actual evapotranspiration) did not improve predictions of regeneration in ponderosa pine or Douglas-fir relative to models that included historical mean climate. In our own analyses we found modest support for only three metrics of postfire climate: mean annual (June–May) postfire precipitation, mean annual postfire precipitation anomaly, and minimum annual postfire precipitation anomaly. Consistent with previous studies, drier postfire conditions were associated with lower probability of recruitment. Our results support the importance of the 3–5 yr postfire climate period used by prior studies, with potential variability in the length of the window between taxonomic groups and ecological context.

Postfire recruitment models performed well for conifers and firs and less well for pines. The best pine recruitment models exhibited nearly twice the error rate (CER) of the best fir models (Table 1). The relatively poor performance of the pine models could be partially attributable to stronger intraspecific species interactions in pine recruitment. For instance, pines in our region are generally more shade intolerant than fir species (Safford and Stevens 2017) and are therefore more sensitive to competition. Higher rates of seed predation and seed dispersal from animals (zoochory) in pines may also contribute to the relatively poor performance of the pine models (Vander Wall 2002, Zwolak et al. 2010, Frock and Turner 2018). The influence of seed availability in the pine models was low relative to the all conifer and fir models (Fig. 3, Appendix S1: Figs. S3–S14). This low sensitivity to seed availability in pines may indicate there may be unaccounted for factors in our modeled estimates of pine seed availability. When making projections to new fires (e.g., the King Fire) our model assumed uniform mortality across taxonomic groups as a function of RdNBR. Research that assesses taxon-specific mortality to wildfire in the context of satellite-derived mortality estimates could improve model predictions.

Though our results differ somewhat from a previous analysis based on much of the same data as used in this study (Young et al. 2019) our main finding of modest support for the importance of postfire climate as a driver of conifer regeneration is consistent with the previous study. Noteworthy contrasts between our findings include: (1) the seed availability proxy we used (modified from Shive et al. 2018) improved performance of the regeneration models where the seed availability proxy used by Young et al. (2019) (distance to seed source) did not; (2) while Young et al. (2019) found that 3-yr postfire minimum precipitation anomaly (driest year) improved predictions of white fir regeneration we found that this variable worsened predictions of fir regeneration; (2) while Young et al. (2019) found that postfire climate variables worsened predictions of yellow pine regeneration we found that 3-yr mean postfire precipitation anomaly may improve (improved AUC, equal CER) predictions of pine regeneration relative to models premised on historical precipitation. Differences may be attributable to non-identical (but overlapping) datasets as well as differences in modeling approaches, response variables, and model evaluation criteria. Whereas Young et al. (2019) used linear models to analyze regeneration occurring within two years after a fire in high-burn-severity plots with nearby seed sources ($N = 513$), we used nonlinear models to analyze regeneration occurring within 5 yr after fire across the full range of seed availability and burn severity ($N = 1,234$). While we evaluated model performance using plot-specific performance metrics (leave-one-fire-out AUC and CER), Young et al. (2019) evaluated model performance using a fire-specific performance metric (mean leave-one-fire-out mean absolute value of the difference between the observed and predicted proportion of plots with regeneration in each fire). Our analyses also differed in terms of the explanatory variables used. Our models used a more mechanistic representation of seed availability (incorporating the density and size of nearby trees as opposed to simply the distance to the nearest reproductive tree), incorporated burn severity as a predictor, and used alternative topographic metrics (slope and aspect as opposed to modeled solar radiation). Our models likely detected an influence of seed availability where the models of Young et al. (2019) did not because of the more mechanistic representation of seed availability and larger range of values in our data.

In this study we built correlative models with additive effects to predict postfire regeneration. Integrating hierarchical processes into the models could result in improved model performance. For instance, recruitment is biologically dependent on presence of seeds, and a model that treats seed availability as necessary to recruitment as opposed to an additive factor that influences recruitment probability would more effectively capture this biological process. Attempts to capture this effect using interaction terms resulted in implausible and apparently overfit response curves. The current models result in unrealistic predictions of non-trivial recruitment probability when estimated seed availability is zero.

Perhaps due to rare long-distance dispersal events not captured by our Gaussian kernels, regeneration can occur at low levels far from seed sources, and climate and topography can thus affect regeneration outcomes even in the center of large, high-severity patches. Improvements in the accuracy of predictor variables could also lead to improved model performance. For instance, empirical maps of postfire live tree size and distribution, as opposed to interpolated estimates could improve the accuracy of the seed availability model. Such detailed maps could be efficiently produced with drone acquired imagery and automated image processing (Michez et al. 2016, Fernández-Guisuraga et al. 2018).

Considering future scenarios, our model estimates that over 42% of the area of the 19 fires included in this study (784 km^2) had no natural conifer regeneration, emphasizing the need for postfire forest management (e.g., seeding or planting) if the focus is to maintain coniferous forests following large, high-severity fires. The models are intended to aid management decisions for postfire recovery planning (e.g., identifying sites and conditions that are at high-risk for conifer recruitment failure that may be targeted for postfire management). By providing managers with a range of postfire regeneration scenarios the models may improve postfire management planning. To the degree that variability in near-term climate and seed production is known, managers can plan for anticipated conditions. Known patterns in El Niño and Pacific Decadal Oscillations can facilitate near-term (1–2-yr) climate predictions (Biondi et al. 2001, Chen et al. 2004). Similarly, flower and cone surveys in conjunction with historical data may be used to forecast seed production (Barnett 1999). As underscored by Davis et al. (2019), successful regeneration may be dependent on episodic seed production coinciding with favorable weather conditions.

The sensitivity of predicted postfire regeneration to variation in seed output highlights the idea that seed production may partially determine postfire recovery. Rapid seedling establishment may be important to capitalize on the period of reduced competition from other vegetation (Gray et al. 2005, Tepley et al. 2017). Once alternative vegetation types are established they may persist, outcompeting conifer seedlings. For instance, competition from shrubs tends to slow initial conifer regeneration and may increase susceptibility to secondary stand-replacing fires that kill regenerating conifers and maintain shrub dominance (Nagel and Taylor 2005, Lauvaux et al. 2016). Regenerating trees must attain a sufficient size before they become resistant to low-severity understory fires (Larson et al. 2013). Temporal priority plays an important role in determining long-term ecosystem trajectory (Young et al. 2015). In this study, we used the 5-yr moving average of seed production across 216 seed fall traps as an estimate of variability in postfire seed production. However, for reasons discussed above, the importance of seed production to

conifer regeneration may decline each year after a fire. To the extent that successful conifer regeneration is primarily dependent on seed production during shorter time windows following fire, our projections are likely to underestimate the impact of variable seed production on postfire regeneration (i.e., variability in seed production is higher for shorter moving-average periods; Appendix S1: Fig. S2).

The modern regime shift toward large, high-severity fires with diminished postfire regeneration presents managers with critical challenges. Maintaining forests and preserving ecosystem services will require new insights and proactive management (Millar and Stephenson 2015). The models we developed here help answer the questions of when and where postfire management interventions may be necessary to maintain forests, but do not address questions of which species or local genetic varieties will be most suited to persist and maintain ecosystem services under climate change. Depending on context, appropriate strategies may involve (1) sourcing seeds from locations where populations are better adapted to current and future climate (e.g., moving seeds upslope), (2) promoting transition to desirable species compositions that may be better adapted to climate change (e.g., more drought-tolerant native conifer species), and (3) allowing ecosystems transitions to unfold on their own (e.g., natural transition to grassland, shrub, or oak dominated types). While some work provides insight into these approaches (Wang et al. 2010, Thorne et al. 2018, McWethy et al. 2019), more research is necessary to understand the context-dependent effects of these strategies and how they can be most effectively implemented.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2280/full

Data Availability

Data are available from the USGS ScienceBase repository (Stewart et al. 2020): https://doi.org/10.5066/P9CWOGXV