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ARTICLE

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Climate and fire impacts on tree recruitment in mixed conifer forests in northwestern Mexico and California

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Abstract

Frequent-fire forests were once heterogeneous at multiple spatial scales, which contributed to their resilience to severe fire. While many studies have characterized historical spatial patterns in frequent-fire forests, fewer studies have investigated their temporal dynamics. We investigated the influences of fire and climate on the timing of conifer recruitment in old-growth Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir (SSPM) and the eastern slope of the Sierra Nevada. Additionally, we evaluated the impacts of fire exclusion and recent climate change on recruitment levels using statistical models with realized as well as fire suppression and climate change-free counterfactual scenarios. Excessive soil drying from anthropogenic climate change resulted in diminished recruitment in the SSPM but not in the Sierra Nevada. Longer fire-free intervals attributable to fire suppression and exclusion resulted in greater rates of recruitment across all sites but was particularly pronounced in the Sierra Nevada, where suppression began >100 years ago and recruitment was 28 times higher than the historical fire return interval scenario. This demonstrates the profound impact of fire's removal on tree recruitment in Sierra Nevada forests even in the context of recent climate change. Tree recruitment at the SSPM coincided with the early-20th-century North American pluvial, as well as a fire-quiescent period in the late 18th and early 19th centuries. Episodic recruitment occurred in the SSPM with no "average" recruitment over the last three centuries. We found that temporal heterogeneity, in conjunction with spatial heterogeneity, are critical components of frequent-fire-adapted forests. Episodic recruitment could be a desirable characteristic of frequent-fire-adapted forests, and this might be more amenable to climate change impacts that forecast more variable precipitation patterns in the future. One key to this outcome would be for frequent fire to continue to shape these forests versus continued emphasis on fire suppression in California.

Scott L. Stephens and Zachary L. Steel contributed equally to this work.

KEYWORDS
climate change, forest restoration, regeneration, resilience, Sierra Nevada, Sierra San Pedro Martir, wildfire

INTRODUCTION

Managing frequent-fire-adapted forests (those with fire return intervals <35 years) to increase their resistance and resilience in the face of changing climate and fire regimes is a major challenge (Hessburg et al., 2021; Stephens et al., 2013). In western North America, frequent, low- to moderate-intensity fires were once a fundamental component of many pine-dominated ecosystems (Hessburg et al., 2019). However, fire in the western United States has been essentially excluded for more than a century, resulting in substantially altered forest conditions (Hagmann et al., 2021). Recent and accelerating climate change has also impacted western US forests, including through exacerbation of regional drying, which may impact forest productivity and recruitment (Stewart et al., 2021). An improved understanding of dual drivers of fire and climate on tree recruitment is needed to accurately predict future trajectories of western US forests and successfully manage these ecosystems in the coming decades.

Considerable research confirms that frequent-fire forest landscapes were characterized as highly heterogeneous with regard to both structure within individual forest stands and composition among vegetation patches prior to the period of fire exclusion and suppression (Carey, 2003; Fertel et al., 2022; Hessburg et al., 1999, 2015; North, Stine, et al., 2009). This heterogeneity was an important driver of the resilience to disturbance of these ecosystems (Churchill et al., 2013; Murphy et al., 2021; Steel et al., 2021). While many studies have investigated the spatial patterns of reference forests (Churchill et al., 2017; Clyatt et al., 2016; Fry et al., 2014; Larson & Churchill, 2012; Lydersen et al., 2013), fewer studies have investigated the temporal dynamics of these ecosystems (but see Brown, 2006; Brown & Wu, 2005).

Overstory recruitment in many dry ponderosa pine (*Pinus ponderosa*) forests was highly episodic, related both to optimal climate conditions for seed production, seedling germination, and sapling growth (Pearson, 1933; Savage et al., 1996) and to occasional longer intervals between surface fires, which allowed more seedlings and saplings to reach a stage where they were fire resistant (Brown & Wu, 2005). In open-canopy or climatically marginal forests and savannas, episodic recruitment often occurs as a result of transient moisture or temperature conditions optimal for new recruitment (Peet, 1981). With continued climate warming, southwestern North America is expected to become drier (Williams et al., 2020), potentially affecting tree recruitment, especially within already climatically marginal forests (Davis et al., 2019).

The objectives of this study were to quantify temporal patterns of forest structure and the corresponding factors (fire, climate, soil) that shaped them at three old-growth Jeffrey pine (*Pinus jeffreyi*)-mixed conifer forests in the Sierra Nevada (SN) of eastern California, USA, and the Sierra San Pedro Martir (SSPM) in northern Baja California, Mexico. These sites differ primarily in the timing and intensity of fire suppression efforts and fire exclusion, but they also provide contrasts of productivity driven by differences in annual precipitation and edaphic conditions. We addressed the following question: What was the relative influence of fire occurrence and climatic conditions (i.e., soil moisture) on tree recruitment in frequent-fire forests? Our hypotheses were that the SN forests would have higher tree densities and less variation in tree establishment due to cessation of fire for over a century. In contrast, the forests in the SSPM are expected to have a more complex temporal structure because the impacts of more recent fires (fire suppression did not begin until 1970) and greater aridity due to underlying edaphic conditions and recent drought. Information from this study could assist in the development of desired conditions in similar forests in the western United States and possibly other pine-dominated forests that are adapted to frequent, low- to moderate-intensity fire regimes.

METHODS

To evaluate the impacts of fire and climate on tree recruitment, we leveraged long-term fire history and recruitment data from three sites in southwestern North America and reconstructed soil moisture climate data from the region. One site was located in the SN of California, where fire suppression and exclusion have been in place for over a century. Two sites were located in the SSPM of northern Baja California and continued to experience relatively frequent fire until the mid-20th century (Stephens et al., 2003). This contrast in fire history allowed us to test the "treatment" effect of suppression/exclusion on conifer recruitment. Further, recruitment data precede and include the early effects of climate change as well as centuries of natural climate variability, allowing for an assessment of soil moisture effects and recent climate change-related soil drying on conifer recruitment. Specifically, statistical models were constructed to estimate the effects of fire-free interval and preceding soil moisture anomaly on conifer recruitment cohort size. Counterfactual model scenarios were subsequently estimated to assess the relative impacts of fire suppression/exclusion and climate change on tree recruitment of the study sites.

Study areas

Our study was located within dry conifer forests in southwestern North America (Figure 1). Two study sites were located in the SSPM National Park in the Peninsular Range in Baja California, Mexico (115.98° W; 31.62° N), and one study site was located in the Humboldt-Toiyabe National Forest near Lost Cannon Creek on the eastern slope of the SN, California, USA (119.47° W; 38.40° N). None of the study sites have been harvested.

Study areas were located in the North American Mediterranean climate zone (Dunbar-Irwin & Safford, 2016; Skinner et al., 2008). There was no long-term climate information from the SSPM study area; the closest weather data (1960–2004) come from the Santa Cruz Station (980 m elevation, 16 km away), where average annual precipitation was 33 cm, 48% of which occurred

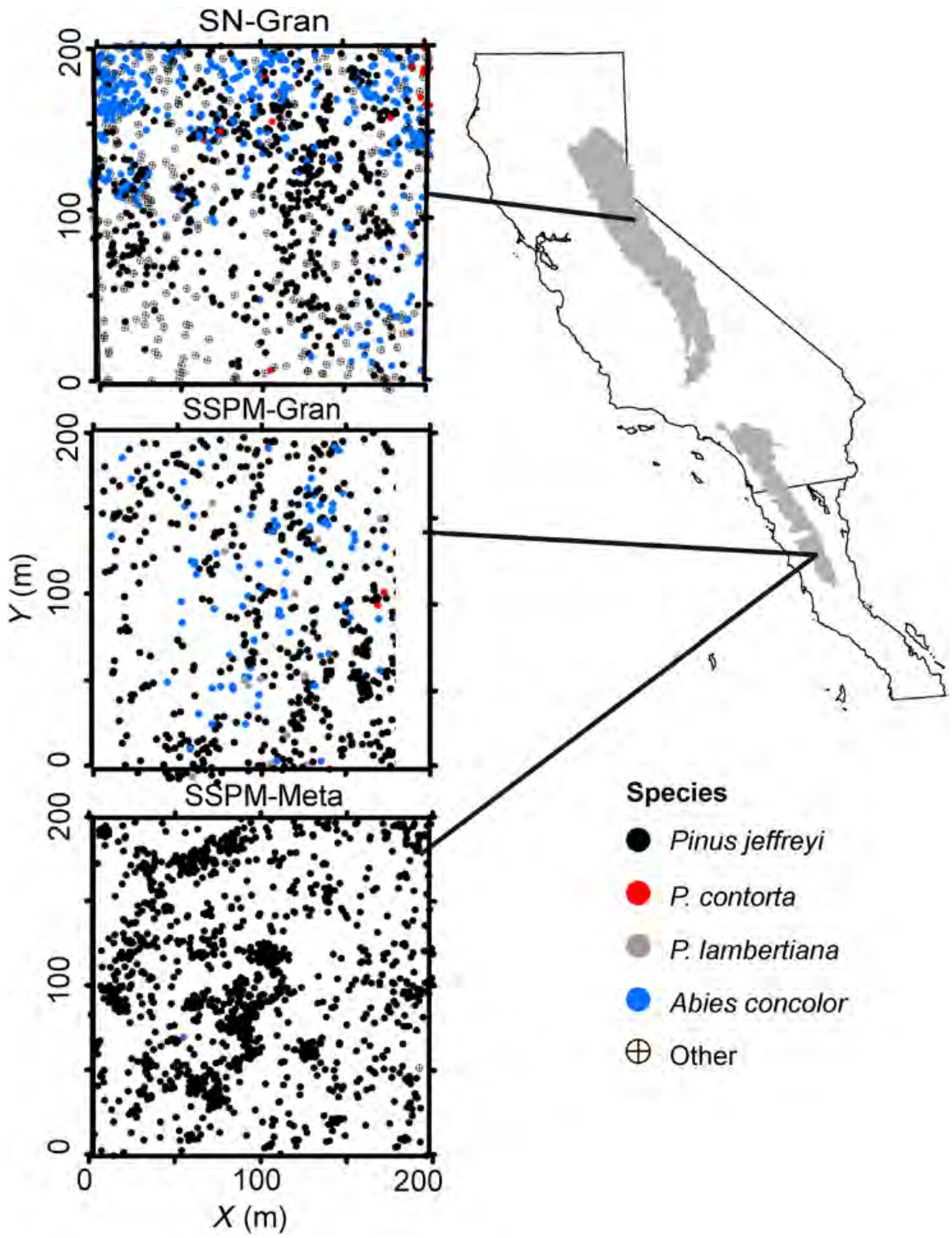

FIGURE 1 Stem maps of three study sites in southwestern North America. SN, Sierra Nevada in California; SSPM, Sierra San Pedro Martir in northern Baja California, Mexico.

during the winter months. Average annual summer and winter temperatures at this site are 25 and 12°C, respectively. Average precipitation measured with temporary weather station on the northern SSPM plateau (2400 m; 1989–1992), 1.5 km southeast of the study areas, was 55 cm (Minnich et al., 2000). For the SN site, average annual precipitation at the closest weather station in the town of Bridgeport approximately 530 m lower in elevation was 25.4 cm, 46% of which occurred during the winter. Average annual summer and winter temperatures were 15 and 3°C, respectively.

While Jeffrey pine dominates all sites, edaphic conditions are distinguishing characteristics of species composition (Table 1, Figure 2). The SN site (SN-Gran) is a Jeffrey pine-mixed conifer forest on shallow loamy coarse sand soils with granitic parent materials, and quacking aspen (*Populus tremuloides*) is common on more mesic, lower slopes (Fry et al., 2014). The Jeffrey pine-mixed conifer forests of the SSPM granite site (SSPM Gran) are similar to portions of the eastern SN, Lake Tahoe Basin, and southern California mountains (Barbour et al., 2002; Dunbar-Irwin & Safford, 2016; Minnich et al., 1995). Soils are shallow, well to excessively drained, and relatively acidic, with diorite parent material (Stephens & Gill, 2005); chemical and textural properties are similar to typical granite-derived soils in comparable forests in California (Potter, 1998). The SSPM metamorphic site (SSPM-Meta), approximately 2 km north of SSPM-Gran, is a monotypic stand of Jeffrey pine (Table 1, Figure 2) on shallow sandy loams soils derived from quartz schist parent materials (Fry et al., 2018).

Fire has been an important ecological process in Jeffrey pine-mixed conifer forests, occurring relatively frequently prior to fire suppression and exclusion. Reconstructed fire return intervals ranged from 4 to 24 years in areas in and adjacent to the three study sites (North, Van de Water, et al., 2009; Skinner et al., 2008; Stephens et al., 2003; Taylor, 2004). Fire cessation at SN-Gran began in the early 20th century, following several decades of sawmill and mining operations in this part of the SN (North, Van de Water, et al., 2009). At the SSPM, lengthened fire intervals have occurred in most forested areas, beginning in the 1960s with road construction and limited fire suppression efforts (Skinner et al., 2008; Stephens et al., 2003) and a reduction in Indigenous burning with the creation of the SSPM Mission in the 1790s (Evett et al., 2007a); changes in SSPM fire patterns from fire suppression and exclusion are shown in Stephens et al. (2003) (Figure 1).

Recruitment, fire history, and climate data

To assess conifer recruitment and fire history, one 4-ha plot was randomly located on a uniform slope and aspect at each of our three study sites. A 4-ha plot was selected to incorporate the heterogeneity of these forest types since previous studies indicated that pine-dominated forests that had once experienced frequent, low- to moderate-intensity fires regenerated in small patches (Boyden et al., 2005; Sánchez Meador et al., 2009; Stephens & Fry, 2005). The species, size (dbh), and location (*X* and *Y* coordinates) of all live stems were recorded. Tree locations were mapped using the Laser Tech TruPulse with an attached electronic compass, which has a reported accuracy of <15 cm. Mapping was done relative to monumented points (10–15 total) within each 4-ha study area. At each of these monumented points we collected differentially corrected GPS coordinates with an approximate accuracy of 0.5 m.

In each plot, all trees above 2.5 cm dbh were cored to determine tree age. Trees were cored on the downhill side of the tree within 20 cm of ground surface, with an

TABLE 1 Site and forest characteristics from three old-growth Jeffrey pine-dominated forests in California and northwestern Mexico.

Site	Elevation (m)	Soil type	Species composition (stems >2.5 cm dbh)	Density (stems ha^{-1})		
				Live	Snag	Seedling
SN-Gran	2500	Decomposed granitic rock, typic cryop-xeropsamments, loamy coarse sand	JP: 40.7%, SJ: 17.1%, WF: 10.2%, QA: 10.2%, LP: 1.3%, WP: 1.2%, PM: 0.1%	428.3	21.5	198.5
SSPM-Gran	2410	Decomposed granitic rock, typic xeropsamments, mostly loamy sands (Stephens & Gill, 2005).	JP: 83.7%, WF: 13.4%, SP: 2.2%, LP: 0.8%	193	3.5	176
SSPM-Meta	2440	Quartz schist rock, mostly sandy loams (Fry et al., 2018).	JP: 99.3%, CO: 0.6%, EO: 0.6%, WF: 0.1%	373.8	9.8	153.8

Abbreviations: CO, *Quercus chrysolepis* (Liebm.); EO, *Q. emoryi* (Torr.); JP, *Pinus jeffreyi* (Grev. & Balf.); LP, *P. contorta var. murrayana* (Dougl. Ex. Loud.); PM, *P. monophylla* (Torr. & Frém.); QA, *Populus tremuloides* (Michx.); SJ, *Juniperus occidentalis* (Hook.); SN, Sierra Nevada; SP, *P. lambertiana* (Dougl. Ex. Loud.); SSPM, Sierra San Pedro Martir; WF, *Abies concolor* (Gord. & Glend. Lindl.); WP, *P. monticola* (Douglas ex D. Don).

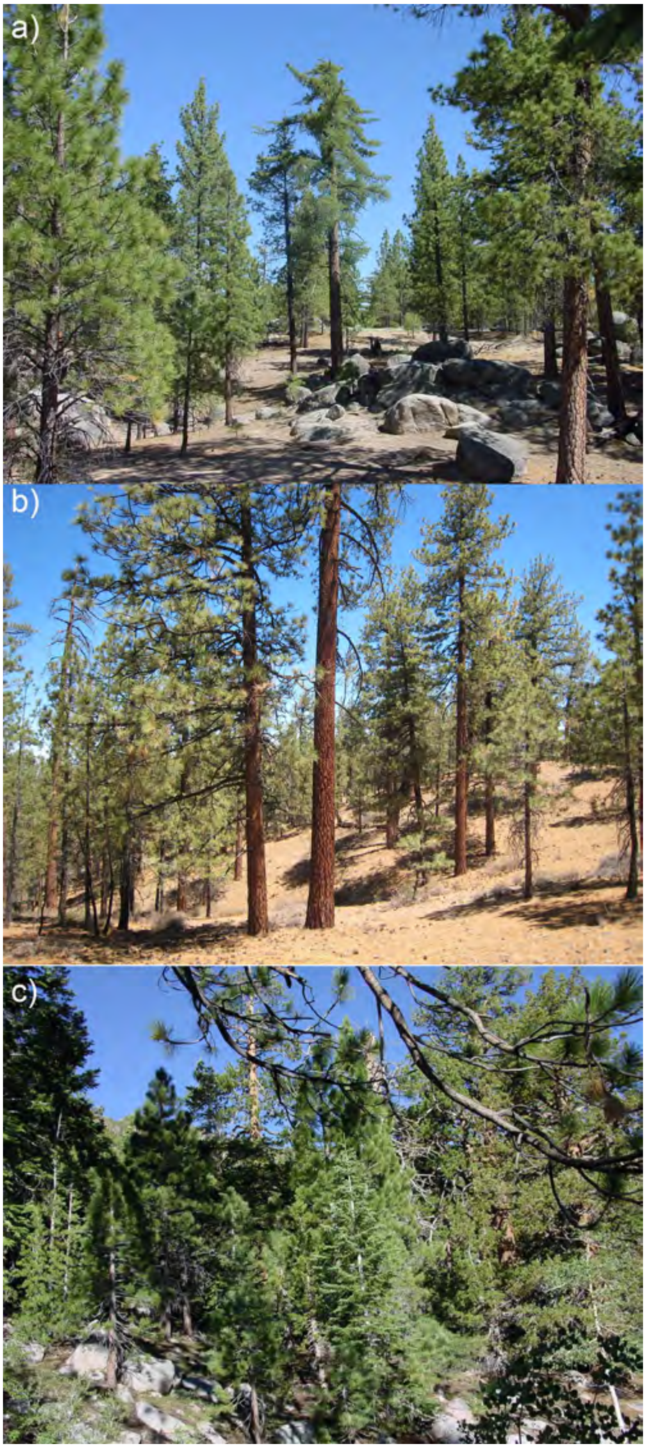

FIGURE 2 Forest conditions at (a) Sierra San Pedro Martir (SSPM) granite site in Baja California, (b) SSPM metamorphic site in Baja California, and (c) Sierra Nevada granite site in California. Photo credits: Scott L. Stephens.

increment borer, either by hand (smaller trees) or by an auger mounted to a chain saw (larger trees). If the pith was missed, trees were cored up to three times and the best core was selected. Cores were prepared and crossdated using standard dendrochronological techniques (Dieterich, 1980). Out of a total of 3477 cored trees, 12% had missing piths and were excluded from analysis, resulting in a total sample size of 3070 cores. Recruitment cohorts were calculated as the tally of trees that shared a pith year for each plot.

At each site, we sampled the 4-ha plot, including a 100-m buffer for fire-scarred trees, snags, and logs, preferentially selecting trees that appeared to record multiple fires (Swetnam & Baisan, 2003) and larger trees that potentially had a longer record. We dated all fire scars using standard crossdating procedures (Dieterich, 1980). The FHX2 software (Grissino-Mayer, 2001) was used to record and analyze fire scar data. To exclude highly localized fires, we considered fire years to be those where a minimum of two trees recorded a scar. By this definition, the first recorded fire year was 1673 for the SN-Gran site, 1584 for SSPM-Gran, and 1685 for SSPM-Meta.

To assess long-term variation in climatic conditions we used soil moisture anomaly data published by Williams et al. (2022). Soil moisture data were reconstructed using a composite tree-ring database (independent of the tree-ring data used in this study) and interpolated across North America at a resolution of 0.5° for the years 800–1983 CE. Soil moisture data were reported as summer (June, July, and August) anomalies relative to the 1950–1999 mean, with negative values representing drier than average years and positive numbers wetter than average years (Williams et al., 2020, 2022). Williams et al.'s choice of reference period would influence the absolute value of calculated soil moisture anomalies but not the relative effect of changes in soil moisture on conifer recruitment, which is of interest here and estimated using standardized predictor values (see *Statistical Analysis* in what follows). To assess the contribution of realized anthropogenic climate change on conifer recruitment, we used Williams (2022) observed and counterfactual soil moisture anomaly data spanning 1901–2021. The counterfactual data developed by Williams et al. (2020) represent a modeled expectation of soil moisture anomalies in the absence of anthropogenic climate change using a 29-climate-model ensemble mean. Reconstructed, observed, and counterfactual summer soil moisture anomalies were extracted for our SN and SSPM locations using the terra R package (Hijmans, 2022). The soil moisture index was selected over other climate indices (e.g., PDSI) due to its long temporal extent and the availability of the climate change-free counterfactual scenario.

Statistical analysis

We modeled annual conifer recruitment cohort size as a function of preceding soil moisture anomaly (smz_i) and fire-free interval length (ffi_i) for cohort i. Cohort size followed a zero-inflated Poisson distribution with mean annual recruitment of 3.0 trees per 4-ha site (0.75 trees ha^{-1}), with 42% of years recording zero recruitment among the three sites. Data were both spatially and temporally structured among the three sites and across years. Thus, we allowed all predictor variables to vary by site (k) as random intercepts and slopes (Equation 1). We also included a first-order temporal autoregressive term to account for serial nonindependence on consecutive recruitment years:

$$\begin{aligned} y_i &\sim ZI\text{Poisson}(p_i, \lambda_{i,k}). \\ \text{logit}(p_i) &= zi_p, \\ \log(\lambda_{i,k}) &= \alpha_k + \beta 1_k \times smz_i + \beta 2_k \times ffi_i. \end{aligned} \tag{1}$$

We assessed recruitment rather than germination because the latter is uncertain without destructively sampling to obtain the pith at the root/shoot boundary. For example, Puhlick et al. (2012) found that it took 7 years on average for a ponderosa pine to reach 10 cm in height. The unavoidable measurement error with respect to tree age at pith year likely resulted in greater model uncertainty and wider parameter credible intervals. Both the initial germination and establishment/survival during the subsequent years are affected by a multiyear period of climate and fire occurrence (Puhlick et al., 2012). For each recruitment year, the fire-free interval was calculated as the difference between the year of the next fire and the last fire recorded for a given plot. For relatively recent pith years where a plot had not yet experienced a subsequent fire, the year of the next fire was assumed to be the year following sampling. Mean soil moisture anomaly was calculated for a moving 5-year window at different starting points (lags) prior to the recorded pith year. For example, a lag of 1 represents the mean of Years 1–5 before the pith year. We tested candidate models with different soil moisture lags from 1 to 10 using leave-one-out information criteria (Vehtari et al., 2017) and found a lag of 7 (7–11 years before pith) created the best-performing model (Appendix S1: Figure S1 and Table S1). Aside from lag year, candidate models were identical, and results from this final model are reported. Continuous predictor variables were standardized with a mean of zero and a SD of one. Models were estimated using Hamiltonian Monte Carlo sampling in Stan via the BRMS package and program R (Bürkner, 2017; R Core Team, 2021; Stan Development Team, 2020). Models were run with four chains, each for 2000 samples with a warmup of 1000. Trace plots and R-hat values were assessed for proper mixing and model convergence.

To evaluate the impacts of fire exclusion and climate change on recruitment levels, predictions were made using the final statistical model with realized and counterfactual scenarios. The climate counterfactual scenario used soil moisture anomaly values with the estimated effect of climate change removed (Williams et al., 2022), as described previously, and observed fire-free intervals. Annual recruitment predictions from this climate change-free scenario were subtracted from a scenario with realized climate change effects on soil moisture retained to generate expected mean annual recruitment anomaly attributable to climate change for the years 1912–2021. Predictions were limited to the soil moisture data provided by Williams (2022) and the relatively recent and accelerating impacts of climate change. We extended predictions to 2021 to illustrate the potential effect of recent drought conditions in the region and the implications of likely further drying due to worsening climate change. For the fire regime counterfactual, we fixed fire-free interval predictor values to 14 years (the median of the 4- to 24-year range of historical estimates) and used observed soil moisture anomalies for the full range of the observed recruitment record (1584–1982) to create a fire exclusion-free scenario. We used the fire frequency median to construct this scenario rather than attempting to iterate over a distribution of historical fire frequency (e.g., using a Monte Carlo approach) since the central tendency of this distribution is better understood than the shape of the distribution's dispersion. This methodological choice was intended to avoid bias in model predictions but might have underestimated uncertainty in recruitment departure attributable to fire exclusion. Annual recruitment predictions from this fire exclusion-free scenario were subtracted from predictions using observed fire-free interval and soil moisture anomaly values to generate expected mean annual recruitment anomaly attributable to fire exclusion/suppression.

RESULTS

The SSPM sites continued to experience periodic fires into the 20th century with multiple fires (three in SSPM-Gran and two in SSPM-Meta) between 1900 and the time of writing in 2022 (Figure 3a,b); the SN site, in contrast, experienced its last fire in 1896, reflecting effective fire exclusion in California (Figure 3c). Tree recruitment was fairly continuous throughout the period of record (1584–1982) at each site, but the timing and magnitude of recruitment pulses differed among sites (Figure 3a–c). Both SSPM sites had distinct pulses in the early 1900s, but the SSPM-Gran pulse was at a lower overall magnitude. This pulse was the only noticeable one over the period of record for SSPM-Gran, while SSPM-Meta had two earlier pulses at lower magnitude (Figure 3a,b).

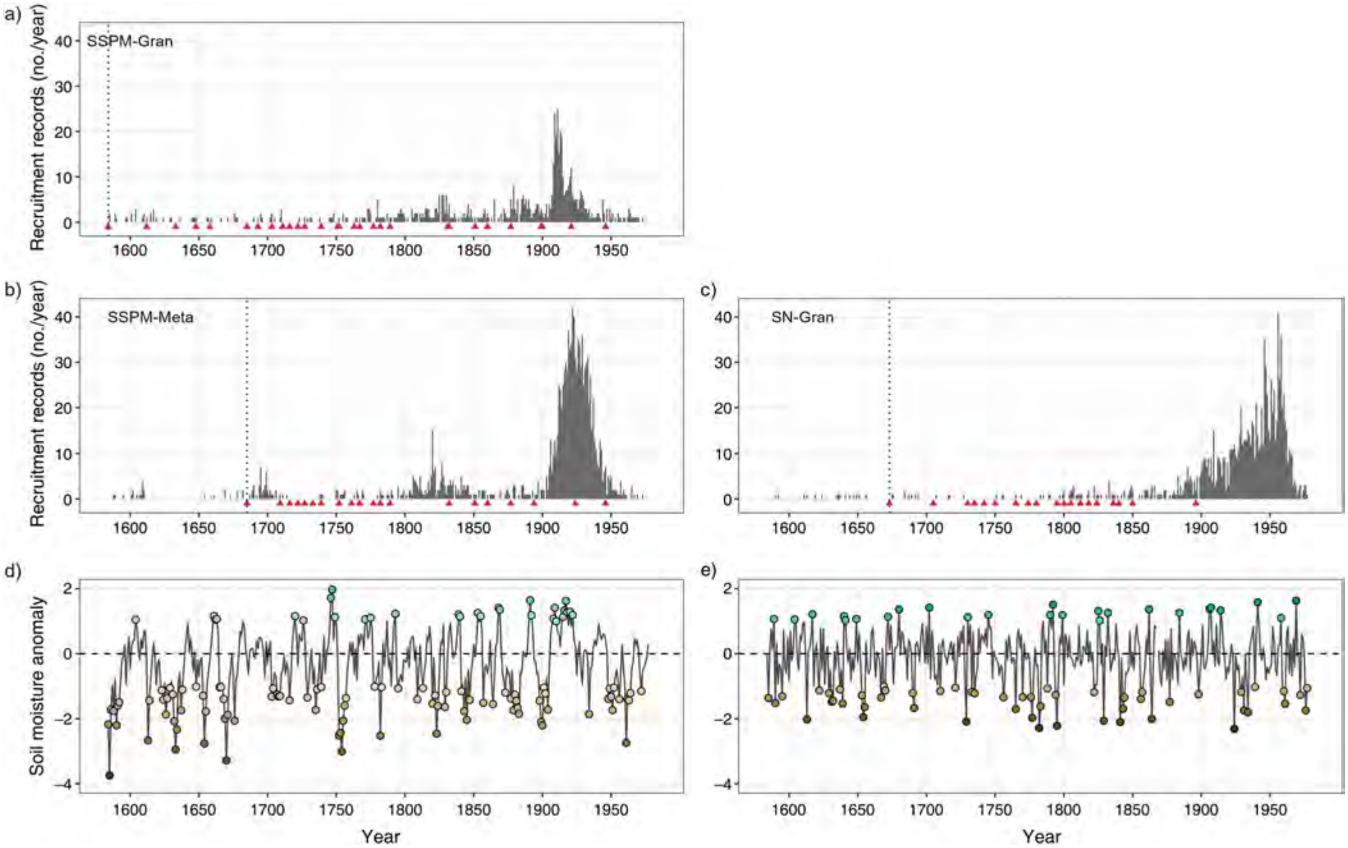

FIGURE 3 Conifer recruitment, soil moisture anomaly, and fire history data. Fires (recorded by at least two scarred trees) are noted as red triangles. Vertical dotted lines indicate the first fire year and the first year included in statistical analysis for each site. Extreme soil moisture years (>1 SD from mean) are indicated by colored circles in panels (d) and (e). SN, Sierra Nevada; SSPM, Sierra San Pedro Martir.

SN-Gran had only one large and lengthy recruitment pulse, which began in the late 1800s and peaked in the mid-1900s (Figure 3c). Within our study period, the soil moisture record showed greater variability in the SSPM (0.97 SD; Figure 3d) than SN-Gran (0.82 SD; Figure 3e).

The final model suggests soil moisture is positively associated with recruitment in the SSPM, with the metamorphic site showing a stronger association (log mean effect [μ] = 0.40; 90% credible interval [CI90] = 0.25, 0.56) than the granite site (μ = 0.26; CI90 = 0.13, 0.38). The model estimated a weak and uncertain effect of soil moisture anomaly for the SN site (μ = −0.14; CI90 = −0.41, 0.11). Longer fire-free intervals were also positively associated with recruitment, especially for the SN site (μ = 1.03; CI90 = 0.91, 1.16), where fire exclusion and suppression policies have been implemented longer. Longer fire-free intervals were also associated with greater recruitment for both the SSPM-Meta (μ = 0.40; CI90 = 0.16, 0.64) and SSPM-Gran (μ = 0.35; CI90 = 0.12, 0.59) sites, although the effect size was smaller than the SN site (Figures 4 and 5; Appendix S1: Table S2).

Soil drying associated with anthropogenic climate change resulted in less than expected annual recruitment in the SSPM by the turn of the 21st century based on the differences between observed climate and modeled climate change-free counterfactual (Figure 6). Between 2000 and 2021, 3.5 fewer trees ha^{-1} (90% prediction interval [PI90] = 1.6, 7.4) were predicted to have recruited in total at the SSPM-Meta site due to climate change, constituting a 17% reduction (PI90 = 11, 23) relative to the non-climate change scenario. For the SSPM-Gran site this predicted climate change-associated reduction in recruitment was 1.2 trees ha^{-1} (PI90 = 0.5, 2.8), an 11% reduction (PI90 = 6, 16). Predicted percentage declines in recruitment on an annualized basis were similar but less precise. Climate change-driven soil drying likely resulted in 16% (PI90 = 35, −5) lower recruitment at the SSPM-Meta site and 11% (PI90 = 25, −3) lower recruitment at the SSPM-Gran site per year since 2000, although 90% prediction intervals include zero. There was no obvious climate change signal on tree recruitment at the SN-Gran site (Figure 6).

Longer fire-free intervals attributable to fire suppression and exclusion of Indigenous burning resulted in greater rates of expected annual recruitment across all sites during the 20th century (1900–1982), which was particularly pronounced at the SN site. During

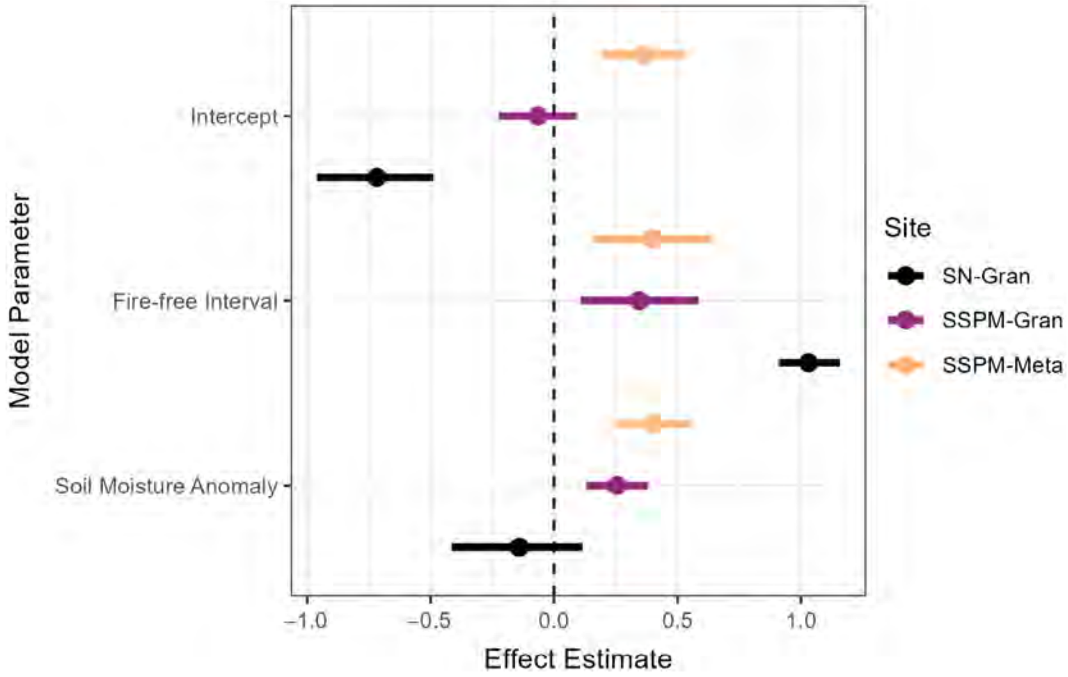

FIGURE 4 Standardized model coefficient estimates on log scale for recruitment of old-growth Jeffrey pine-mixed conifer forests in SSPM in Mexico and SN in California, USA. Gran, granite site; Meta, metamorphic site; SN, Sierra Nevada; SSPM, Sierra San Pedro Martir.

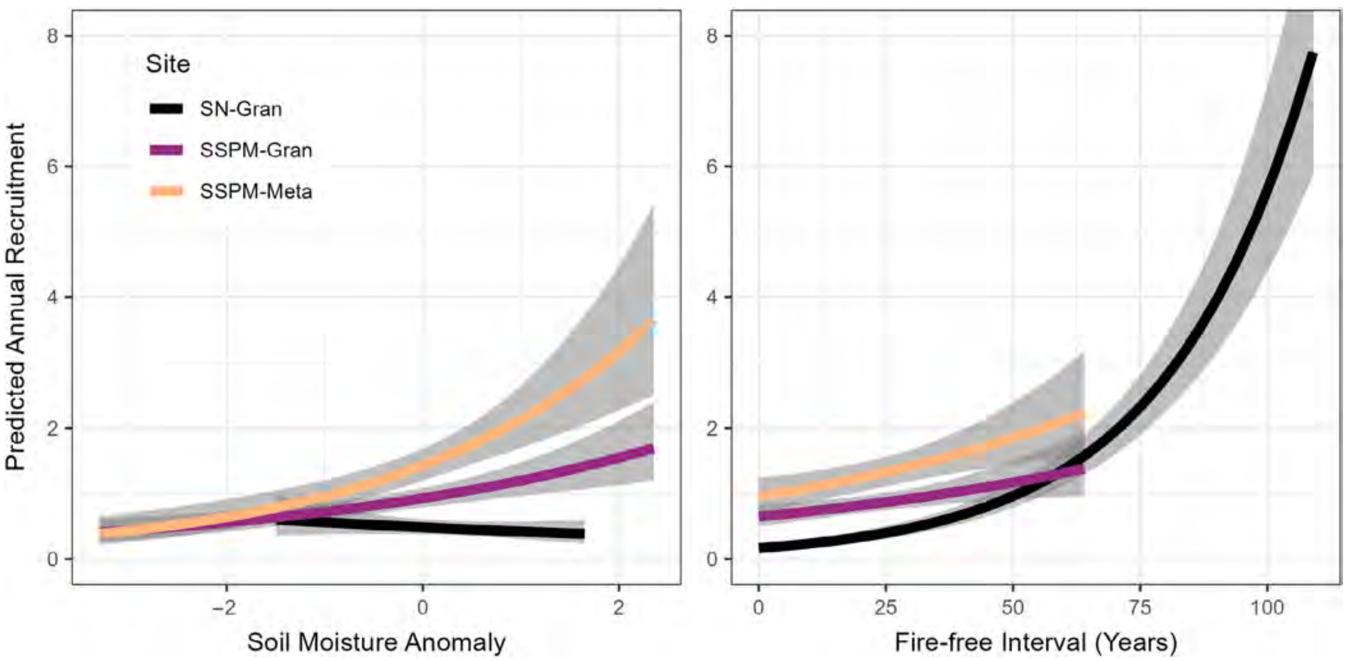

FIGURE 5 Conditional marginal effects of soil moisture and fire-free interval when other predictor is held at its mean value. Gran, granite site; Meta, metamorphic site; SSPM, Sierra San Pedro Martir; SN, Sierra Nevada.

1900– 1982, 149 (PI90 = 113, 198) more trees per hectare were predicted to have recruited at the SN site due to fire exclusion, 28 (PI90 = 20, 44) times higher than the historical fire return interval scenario. Twelve (PI90 = 5, 21) more trees were predicted at the SSPM-Meta site and 6 (PI90 = 2, 13) more at the SSPM-Gran site, 1.44 (PI90 = 1.15, 1.85) and 1.38 (PI90 = 1.10, 1.80) times more, respectively, than the historical reference. On an annualized basis, the SN site saw an equivalent 28-fold or 2800% increase (PI90 = 1860, 4520) per year, an absolute recruitment increase from an average of 0.07 (PI90 = 0.5, 0.9) to 1.9 (PI90 = 1.3, 2.7) trees ha^{-1} $year^{-1}$.

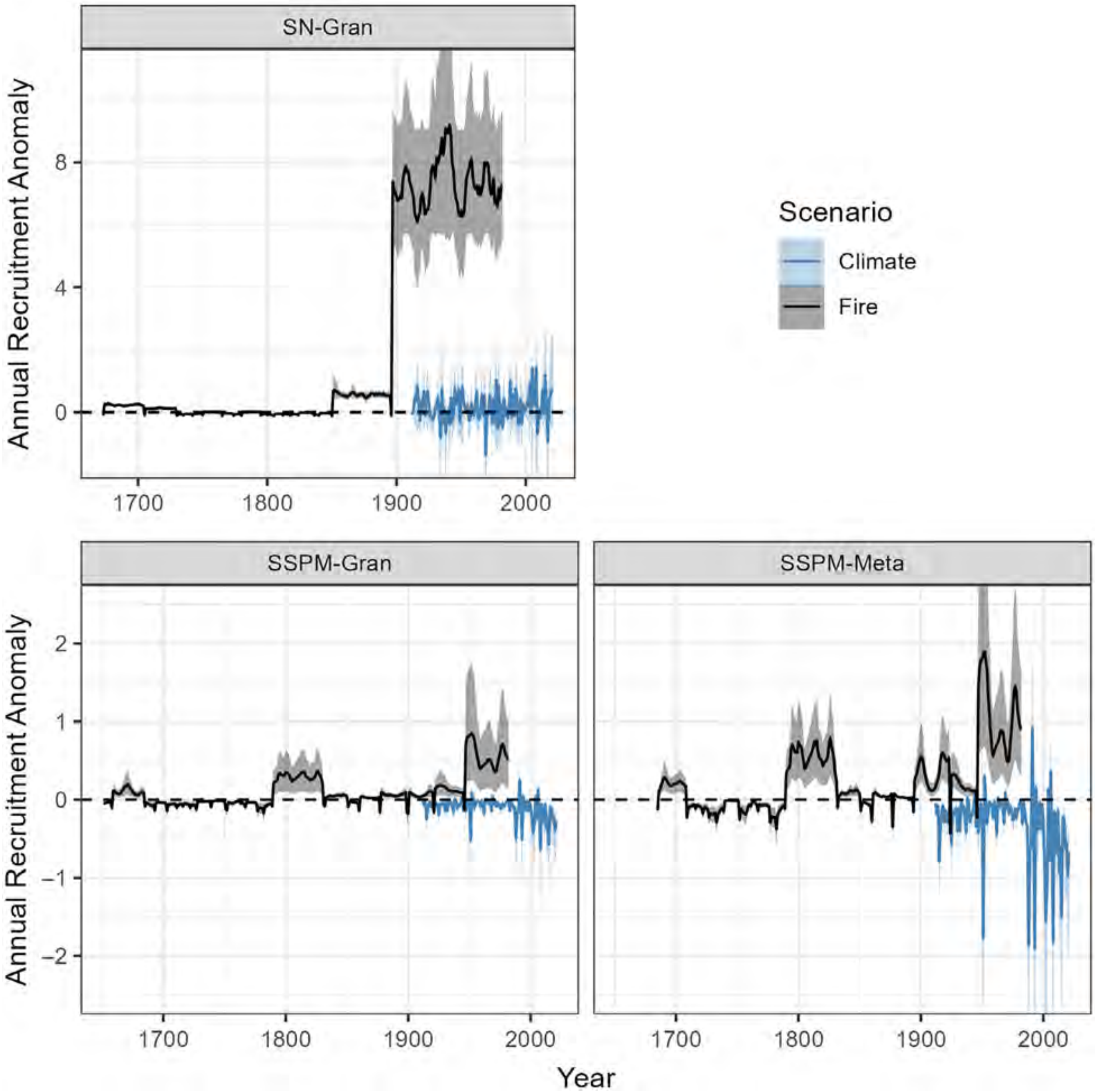

FIGURE 6 Expected annual recruitment difference between realized and counterfactual scenarios. Black lines: predicted recruitment departures relative to 14-year fire return interval up to 1982; blue lines: predicted recruitment departures attributable to climate change-associated soil moisture declines for 1912–2021. Gran, granite site; Meta, metamorphic site; SSPM, Sierra San Pedro Martir; SN, Sierra Nevada.

The SSPM-Meta site saw an increase of 0.53-fold or 53% (PI90 = 6, 160), and the SSPM-Gran site saw an increase of 0.45-fold or 45% (PI90 = 3, 147) per year attributable to increased fire-free intervals.

DISCUSSION

Climate directly affects forest age structure through favorable conditions for tree establishment or through unfavorable conditions (droughts, high temperatures) that can result in seedling death. In addition, climate indirectly affects age structure through control of both disturbance severity, which influences the scale and magnitude of mortality, and disturbance frequency, which limits establishment to longer periods between disturbance events (Brown & Wu, 2005). Disturbances of varying scales are crucial processes in many forests to create canopy gaps and expose bare mineral soil for seedling establishment (Biswell, 1989; Brown & Wu, 2005).

However, climatic anomalies at relatively short time scales (several years to decadal length), such as droughts, can also result in broad-scale mortality that have persistent impacts on forest structure (Brown & Wu, 2005; Steel et al., 2022; Swetnam & Betancourt, 1998).

During the 1900–1982 period, 597 more trees were predicted to have recruited at our SN site (SN-Gran) due to fire suppression and exclusion (average of 150 trees ha^{-1}), while drying effects due to climate change impacts were minimal. The current inventory of the SN site includes 955 trees with pith dates later than 1900, indicating 52% of them would not have established there if the site had continued to experience frequent fire into the 20th century. This demonstrates both the profound impact of fire removal in frequent-fire-adapted forests and minimal climate change impacts thus far on tree recruitment in this area of California (Figure 6).

The increase in tree recruitment at the two SSPM sites (Figure 6) coincides with the early-twentieth-century North American pluvial (TCNAP) (1905–1917), one of the more extreme wet periods of the last 500 years (Cook et al., 2011). Allowing for a slight difference in actual establishment to age at coring height, the peak at SSPM-Gran is similar to the timing of the TCNAP (Figure 3). Though increased tree recruitment begins at a similar time at SSPM-Meta, the period of elevated recruitment continues for several decades after the TCNAP. The timing of tree establishment at SN-Gran appears to be more associated with the onset of fire suppression/exclusion in the early 20th century than to any particular climatic event.

Optimal climatic conditions for ponderosa pine (*Pinus ponderosa*) regeneration and establishment in the early 20th century across much of the southwestern United States contributed to denser forests, especially in 1919, when a tremendous pulse of seedlings established (Pearson, 1933; Savage et al., 1996). The second largest pulse of ponderosa pine recruitment from a study in Northern Mexico also occurred in the 1910–1920s during very wet conditions (Meunier et al., 2014). Interestingly, a pulse of tree regeneration among Jeffrey pines, which have a life history strategy similar to that of ponderosa pine and are closely related genetically (Barbour et al., 2007; Burns & Honkala, 1990), occurred in both SSPM sites around 1919, even though fire suppression had not begun but fire frequency was reduced from the elimination of Indigenous burning (Evett et al., 2007a; Stephens et al., 2003).

Very few ponderosa pine trees predate a multiyear megadrought centered in the 1580s in the southwestern United States (Brown & Wu, 2005), and this pattern exists in the SSPM and California sites as well, with few trees predating this time period (Figure 3). This prolonged drought, the most severe in at least the last 1000 years in this region (Grissino-Mayer, 1996), has been identified in tree-ring chronologies from throughout the western United States and northern Mexico (Stahle et al., 2000). Another interesting regeneration pattern is evident in the late 18th and early 19th centuries, when a period of no fires was recorded in the SSPM (Figure 6). Previous studies documented tree recruitment during periods when surface fires were restricted by climate conditions less conducive to burning (i.e., safe periods, Brown & Wu, 2005), which we observed in the SSPM. During periods of more frequent fire, many seedlings and saplings could be killed before they had a chance to produce bark thick enough to resist heat and crowns high enough to reduce needle scorch (White, 1985).

CONCLUSIONS

This study revealed the importance of fire and climate in structuring old-growth forests in northern Baja California and the eastern SN. While climate was an important factor in northern Baja California (Figure 6), the elimination of fire early in the 20th century was the dominant factor influencing tree recruitment in the eastern SN (Figures 3 and 6). The additional trees and subsequent fuels they contributed have resulted in increased fire hazards and forest structure more vulnerable to severe wildfire and bark beetle mortality (Steel et al., 2022; Stephens et al., 2018), highlighting the need for restoration in these forests (North et al., 2022). The fact that fire continued to burn into the 20th century in northern Baja California reduced overall tree recruitment. Yet we still saw evidence of tree recruitment in the late 18th and early 19th centuries, during a period that had eliminated fires for approximately 30 years, and around 1919 when conditions were favorable to conifer establishment coincident with a larger area of the southwestern United States. At the SSPM sites we see more negative climate influences on recruitment in the last 30 years (Figure 6), and this will likely continue as climate continues to warm into the 21st century (Williams et al., 2019). Whether and when this climatic effect will be observed further north in areas such as the eastern SN will depend on the magnitude of continued climate change and its effects on regional weather patterns.

Although the SSPM sites exhibit a great deal of structural diversity (Murphy et al., 2021; Stephens, 2004; Stephens et al., 2007; Stephens & Gill, 2005), the continued presence of frequent, low- to moderate-severity fires (Rivera-Huerta et al., 2016) likely limited tree recruitment (White, 1985). In the mountains of central-northern Mexico, where fire continued into the 20th century, forest structure is less a reflection of previous episodes of suitable climate for seedling establishment than of local survival of seedlings in sites missed by lethal fires (Meunier et al., 2014). Fires would not burn uniformly in frequent-fire forests since many openings would be fuel limited until trees grew sufficiently to generate enough leaf litter to carry a fire. This fuel limitation control would be more pronounced in forests lacking substantive understory vegetation cover (i.e., grasses), which is the case in the less productive SSPM sites (Evett et al., 2007b). In more productive mixed conifer forests, the top-down effects of fire and climate on recruitment are mediated by different species responses to these effects and within-stand differences in where species are located adding further complexity to these ecosystems (North et al., 2005).

Research has demonstrated the importance of heterogeneity in tree spatial patterns for producing resilient frequent-fire-adapted forests (Churchill et al., 2013; Knapp, Lydersen, et al., 2017; Murphy et al., 2021; North, Stine, et al., 2009). Such patterns can provide discontinuities to fire and reduce the spread of tree-killing insects and pathogens that are frequently species specific. Indeed, the pattern of individual trees, clumps, and openings (also known as ICO) has shown that average forest spatial patterns at the stand level were rare in intact old-growth frequent-fire forests (Rodman et al., 2017; Stephens & Fule, 2005) and that spatial heterogeneity should be used in formulating restoration prescriptions (North, Stine, et al., 2009; Stephens et al., 2021).

Here we demonstrated that temporal heterogeneity in tree recruitment is also a critical component of frequent-fire-adapted forests. Indeed, recruitment has been mostly episodic at the two intact SSPM sites over the last 300 years (Figure 3); this would also add to the structural diversity of these forests. There is no "average" recruitment that occurred in the SSPM over the last three centuries but mostly episodic recruitment coincident with favorable climate and/or the cessation of fire for one to three decades. More episodic recruitment could be a desirable characteristic in the restoration of frequent-fire-adapted forests, and this might be more amenable to climate change impacts that forecast more wet and dry years in the future (Knapp, Avolio, et al., 2017). Recruitment might happen every few decades when fire, climate, and seed crops align, producing the needed regeneration to conserve frequent-fire forests into the future. One key to this outcome would be for frequent fire to continue to shape these forests versus what has happened in our SN site, where fire's removal produced a dense forest vulnerable to high-severity fire and drought/bark beetle attack.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Steel, 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.7730693. Soil moisture anomaly data (Williams, 2022) are available from the NOAA National Centers for Environmental Information at https://doi.org/10.25921/8pt9-hz08.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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