

# Tree recruitment in relation to climate and fire in northern Mexico

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**Abstract.** Extensive changes in montane forest structure have occurred throughout the U.S. Southwest following Euro-American settlement. These changes are a product of confounding effects of disturbance, climate variability, species competition, and modern land use changes. Pronounced forest reproduction events in the Southwest have generally occurred in climatically wet periods but have also followed widespread fire exclusion. Understanding the ecological processes driving such events has important implications for forest restoration, although these efforts remain difficult due to confounding factors. Separation of these interacting factors was possible in the Sierra San Luis of northern Mexico where we investigated climate, fire, and tree recruitment in areas with continued frequent fires or where fire exclusion came relatively late (1940s). Fires were strongly tied to interannual wet–dry cycles of climate, whereas recruitment peaks were more closely tied to local processes, namely, fire-free periods, than to broad-scale climatically wet conditions. The greatest pulse of tree recruitment coincided with a pronounced mid-century drought (1942–1957) and a period of reduced fire frequency. The second largest pulse of recruitment (ca. 1900) preceded a well-documented period of recruitment (and an anomalously wet period) elsewhere across the Southwest in the 1910s–1920s, and also coincided with specific fire-free periods during below-average precipitation. We also found greater spatial dependence and clustering in older age classes of trees. This spatial pattern indicates a legacy of fire-induced mortality in shaping stand structure, underscoring the importance of frequent fire effects on spatial variability in forests.

*Key words:* age structure; climate; fire history; Mexico; recruitment; spatial pattern.

## INTRODUCTION

Southwestern forest communities experience regionally synchronous, episodic recruitment and mortality (Swetnam and Betancourt 1998, Brown and Wu 2005), with striking connections to synoptically driven climate variation (Barton et al. 2001, Swetnam and Brown 2010). These trends have been proposed as evidence of broad-scale climate forcing, with anomalous climate years overriding local processes in long-term forest dynamics (Swetnam 1993, Swetnam and Brown 2010). The strong influence of climate rather than disturbance on historical recruitment of ponderosa (*Pinus ponderosa*) in the Colorado Front Range led to suggestions that the processes of mortality and regeneration there were temporally uncoupled (Boyden et al. 2005). However, in the upper montane zone of the Colorado Front Range, pulses of ponderosa establishment occurred during periods of extreme drought, following moderate to high-severity fire (Sherriff and Veblen 2006, Schoennagel et al. 2011). In southwestern Colorado, Brown and Wu (2005) attributed cohorts

of ponderosa to favorable climate conditions for recruitment pulses (wet conditions less suitable to burning) and longer intervals between surface fires, and with little evidence of episodic mortality. Discrepancies across sites in associations of recruitment to disturbance and climate are common and likely reflect spatial and temporal variation.

Similarly, in contrast to regional correlations between recruitment and climate in the Southwest, local comparisons often lack clear connections. Tree establishment before Euro-American settlement in Arizona was not easily related to climate patterns, but instead more closely aligned with reduced fire frequency, though periods of high moisture availability and low fire frequency were often linked (Mast et al. 1999, Barton et al. 2001). A peak in age structure in the late 19th and early 20th centuries in many studies of ponderosa is an extreme example of both favorable (anomalously wet) climate (Savage et al. 1996), and reduced fire frequency through anthropogenic fire exclusion. Combining climate and disturbance histories for this period may provide a more complete picture of these dynamics (Mast et al. 1999). Evaluating synchronizing effects of regional climate on forests requires assessing the degree to which local responses of tree populations are driven by large-scale controls vs. local site-specific factors (Barton et al. 2001).

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Processes influencing change in structure of forest communities operate through both time and space (Sánchez Meador et al. 2010). It follows that quantitative description of tree recruitment spatial patterns offers insight into the historical and environmental mechanisms influencing forest stand structure (Boyden et al. 2005, Sánchez Meador et al. 2010). White (1985) suggested that successful tree establishment depended on “safe sites” where seedlings could establish and grow above lethal flame heights. This implies that seedling survival is low overall, but could lead to patches of high survival in safe sites missed by fires with heterogeneous burn patterns. Such patterns might lead to a relatively flat age distribution rather than a mixed age distribution expected in an uneven-aged forest with constant mortality (Mast et al. 1999). Spatially limited recruitment could also lead to greater clumping of tree recruitment in frequent fire periods. We were interested in the spatial distribution of trees based on age class as a means to determine the relative influence of direct climate effects and competition vs. fire controls. More uniform tree recruitment is expected with climate and competition controls, vs. safe site limited recruitment where greater aggregation of trees is expected, particularly in frequent fire periods and sites (Larson and Churchill 2012).

Our research was focused on a unique area in northern Mexico, where differences in land use history among sites allowed us to separate the apparent influence of different factors in explaining patterns of tree recruitment and stand structure. Land use differences are in part a result of long Apache Indian occupation, followed by the decade-long Mexican revolution (1910–1920) and subsequent unstable land policies in the region. The result was that frequent fires continued in parts of northern Mexico long after fire frequency declined north of the border (Marshall 1957, 1963, Fulé et al. 2012). This region provided a unique opportunity to study tree recruitment in the presence of frequent fires under similar climate conditions to adjacent forests in the southwestern United States.

Our goal was to provide a more complete picture of tree recruitment dynamics by comparing areas with different fire history both locally (e.g., among study sites), and regionally (Mexico vs. United States Southwest) operating under similar climate. Our primary objectives were to (1) compare climate–fire–recruitment relationships locally within three ecologically similar sites in Mexico that have different land use, and subsequent fire, histories, (2) compare recruitment regionally between Mexico and the United States using pronounced events, such as the early 1900s recruitment event, to disentangle widespread climate and site-specific effects on tree recruitment, and (3) compare current forest spatial patterns for sites with different land use and fire histories.

## METHODS

### *Study area*

Our study sites (Table 1, Fig. 1) comprise the larger mountaintops of the Cajon Bonito Watershed in the Sierra San Luis. They included three similar physiographic areas (Appendix A) with different land use histories including (1) El Pinito Canyon (EPC), which was grazed beginning in the early 1930s but never logged, (2) Pan Duro Arroyo (PDA) grazed in a similar time period and logged ca. 1952 to 1954, and (3) Sierra Pan Duro (SPD), which had little grazing pressure and was never logged (see Plate 1). EPC included stands of Douglas-fir (*Pseudotsuga menziesii*) at the highest elevations (~2440 m), which we treated independently for analysis of plot-level data as El Pinito Mountain Top (EPMT). The high-elevation Douglas-fir stands may have also largely escaped grazing due to rugged topography and lack of water. The Sierra San Luis is an arid mountain region with few permanent water sources, though water developments (beginning in the 1930s) facilitated livestock grazing locally (e.g., EPC, PDA). Tree species composition was very similar to sites in southern Arizona and New Mexico. EPC contained mostly lower-elevation (~1800–2000 m) forests with stands limited to confines of a major canyon. Dominant overstory trees included Chihuahua (*Pinus leiophylla*) and Apache pine (*P. engelmannii*), with extensive pinyon pine (*P. cembroides*) and mixtures of Madrean oaks (*Quercus arizonica*, *Q. emoryi*, *Q. oblongifolia*) beyond the confines of the main canyon. PDA and SPD were most similar and had a greater extent of intermediate elevation (~2000–2200 m) ponderosa pine (*P. ponderosa* var. *arizonica*) with Apache pine and a few scattered Chihuahua pines.

### *Stand structure*

We characterized forest demography using an *n*-tree density-adapted sampling design (Jonsson et al. 1992, Lessard et al. 2002) to collect data from the nearest ~30 trees >7.5 cm diameter breast height (dbh measured at 1.35 m height) to each plot center. Variable radius *n*-tree sampling is a density-adapted sampling design that permits comparison of patterns within and among plots using a fixed number of trees. Plots were randomly located 500 m apart (EPC and PDA) or from a probability-based spatially balanced design (Theobald and Norman 2006, Theobald et al. 2007) for delineable stands (SPD). We sampled both living and remnant trees (stumps, logs, and snags) within plots by coring all living trees for age, and taking partial cross-sections from remnant trees and fire-scar samples at 10 cm height to determine recruitment and fire scar dates. We sampled all fire-scarred plot trees having at least three visible scars, and also collected samples from multiple-scarred trees surrounding our plots (≤200 m) to more completely reconstruct fire history for our sites.

TABLE 1. Characteristics of three study sites in the Sierra San Luis, northern Sonora, Mexico.

Study site	Site code ( <i>n</i> plots)	Elevation (m)	Species†	Trees/ha	Basal area (m <sup>2</sup> /ha)
El Pinito Canyon	EPMT (4) EPC (8)	2240–2430 2104–1815	PSME PILE/PICE	263.5 342.2	29.0 10.4
Pan Duro Arroyo	PDA (6)	2050–1959	PIPO/PIEN/PILE	163.7	16.3
Sierra Pan Duro	SPD (12)	2217–1979	PIPO/PIEN	200.8	15.4

† Species codes listed are for Douglas-fir (PSME, *Pseudotsuga menziesii*), Chihuahua pine (PILE, *Pinus leiophylla* var. *chihuahuana*), pinyon pine (PICE, *P. cembroides*), ponderosa pine (PIPO, *P. ponderosa* var. *arizonica*), and Apache pine (PIEN, *P. engelmannii*).

In the laboratory, we sanded samples until the cellular structure of the xylem was clearly visible under magnification (Grissino-Mayer and Swetnam 2000). Samples were subsequently crossdated against reference

chronologies from the nearby Animas and Chiricahua Mountains in the United States. We dated all fire scars to their exact year of formation for precisely crossdated samples (Dieterich 1983, Dieterich and Swetnam 1984).

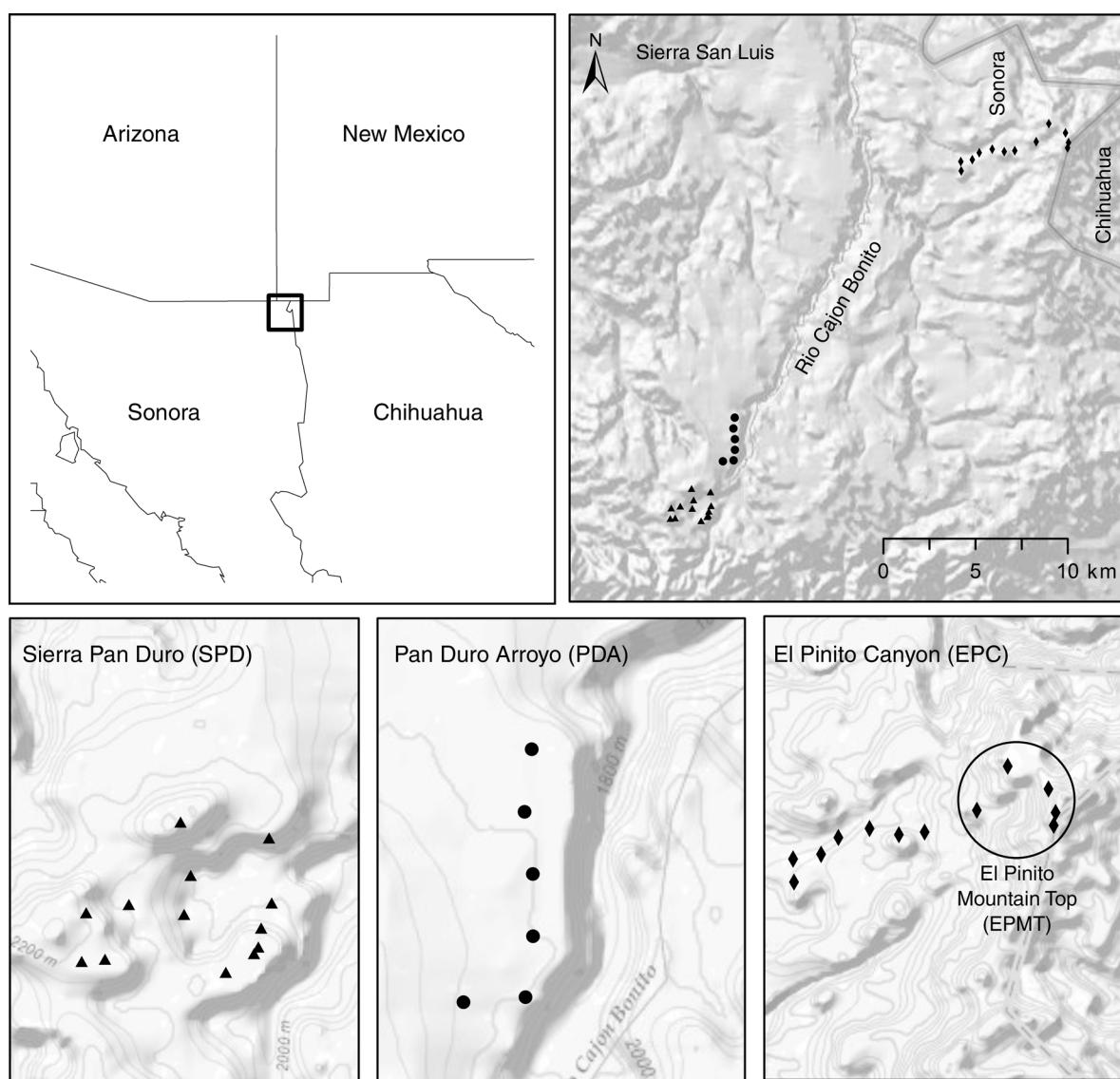


FIG. 1. Study area and sampling sites in the Sierra San Luis, Sonora, Mexico. Sites were sampled from 2008 to 2010 within randomly placed plots at three sites (from south to north): Sierra Pan Duro (SPD, little to no grazing or logging); Pan Duro Arroyo (PDA, logged and grazed after 1930); and El Pinito Canyon (EPC, grazed after 1930 but not logged).

Tree recruitment or establishment dates refer to the date when trees became successfully rooted as seedlings, rather than the exact date of germination (Swetnam and Brown 2010). Recruitment dates are defined as 10 cm height pith dates (Brown et al. 2008), rather than exact germination dates, as exact dates of “root–shoot” boundaries are difficult to determine without destructive sampling (Savage et al. 1996, Swetnam and Brown 2010). We measured diameters at 10 cm (diameter sample height, dsh) for all trees in addition to dbh for all living trees. Diameter at breast height of living trees was used for conversion of dsh to dbh for remnant trees. We counted the number of trees <7.5 cm dbh in each plot for which we did not collect increment cores.

We measured distance and azimuth to all sampled trees from spatially referenced plot centers and converted these measurements into  $x$ ,  $y$  coordinates for all samples. We determined the radius of each plot by calculating the distance from plot center to the center of the farthest tree sampled. Subsequently we determined plot areas as circular plots of calculated radii (Moore 1954, Lessard et al. 2002, Brown et al. 2008; see also Appendix A). Stem basal areas of living trees (measured as square meters per hectare) were determined from dbh measurements. We converted dsh for recently dead remnants (with bark) using a linear regression equation derived from dbh/dsh measurements on living trees by species ( $n = 91\text{--}299$ ,  $R^2 = 0.970\text{--}0.991$ ,  $P < 0.001$ ; Appendix B). We also corrected recently dead remnant trees with only sapwood to bark diameters using a separate regression equation for estimates of bark diameters ( $n = 17$  [Brown et al. 2008]). We used empirically derived regression equations (age vs. dbh) by species from 541 trees with pith dates to estimate age of trees we could not crossdate ( $n = 259$ ). While calculated ages for trees without pith dates were estimates, they were generally accurate enough to assign trees into one of four periods of recruitment for spatial analysis (1, pre-1885; 2, 1890–1930; 3, 1935–1975; 4, post-1975).

#### *Spatial analysis*

We examined spatial aspects of tree recruitment at the tree-neighborhood and within-patch scales for plot level data ( $n = 28$  plots, 766 trees). While plot areas were generally small (0.04–0.37 ha,  $\mu = 0.15$  ha), changes in spatial pattern at tree-neighborhood and within-stand patch scales typically are most apparent within 20 m (Frelich et al. 1998) and at scales less than 4 ha (Agee 1998, Kauffman et al. 2007, Larson and Churchill 2012), indicating utility of local pattern analysis even for small plot areas. Furthermore, we were primarily interested in relative comparisons among plots with different land use histories and distribution patterns of tree recruitment. Examples of distribution patterns include even-age cohorts of recruitment, and multiaged distributions (e.g., usually displayed as reverse-J; more numerous young trees and fewer trees in older age classes).

We used Ripley’s  $K(t)$  function (Ripley 1976, 1977) to determine how spatial interactions of recruitment change over distance for our plots. The  $K(t)$  function estimates spatial dependence between points, producing a cumulative distribution function that represents the expected number of trees within a given distance of individual trees (Ripley 1981, Boyden et al. 2005). The model tests point data for departure from a spatially random pattern, and we used an  $L(t)$  square-root transformation to stabilize variance. We computed 95% confidence intervals using a Monte Carlo simulated Poisson process with 100 simulations (Reich and Davis 1998) for an indication of statistical significance. Significant differences ( $P \leq 0.05$ ) between observed and random patterns occur where the  $L(t)$  plot falls outside of the simulated confidence envelope. We used a Cramer-von Mises goodness-of-fit test to compare simulated and observed point patterns to test for spatial randomness.

The degree to which trees within an age class tended to occur close to one another (compared with trees in other age classes) was calculated with Pielou’s index of segregation (Pielou 1961). Pielou’s index randomly selects a tree and then its nearest neighbor, recording the type or age class of each tree to test hypotheses about whether age classes were segregated or mixed using a chi-square test under the null hypothesis of no segregation (spatial independence). The test also calculates an index of segregation ( $S$ ), which is a population parameter with no sampling variance. Pielou’s index of segregation is not strongly influenced by plot size or tree spacing, making it a robust measure for plots of small and variable sizes. All spatial statistics were computed using Reich and Davis’s online spatial library (Reich and Davis 1998) in R 2.14.0 (R Development Core Team 2008).

#### *Fire, climate, and recruitment interactions*

To compare recruitment periods and fire occurrence to climate conditions we used two independently derived measures of climate; Palmer Drought Severity Index (PDSI, Cook et al. 2004), and cool-season precipitation (November–April) reconstructions (Ni et al. 2002). Both climate variables were averages of nearest tree-ring-based reconstructions. Cool-season precipitation was the average of southern Arizona and New Mexico regions (Ni et al. 2002), and PDSI was the average of four nearest grid points (105, 106, 120, 121) surrounding our study area for the North America Drought Atlas PDSI (Cook et al. 2004). PDSI is a single variable that represents precipitation and to a lesser extent temperature (Sheppard et al. 2002).

We graphically and statistically compared tree recruitment and fire year chronologies with climate to assess climate forcing of fire years and recruitment episodes (Brown and Wu 2005). We used superposed epoch analysis (SEA) in FHX2 version 3.2 (Baisan and Swetnam 1990, Grissino-Mayer 2001) to compare

climate during the smallest (fires recorded on <10% of recording trees) vs. most widespread (fires recorded on >50% of recording trees) fire years, as well as for lagged climate relationships in years prior to and following fire events. Most trees, once large enough to be protected by thick bark, are not injured by low-intensity fires; however, once injured, trees are more susceptible to repeated injury in subsequent fires and considered “recording trees” (Swetnam and Baisan 1996). Filtering, based on scarring percentage, provides a relative index of fire size (Swetnam and Baisan 1996), which is useful in considering “safe site” limited recruitment. A 10% filter, for example, will only consider fire years recorded on  $\geq 10\%$  of recorder trees, therefore eliminating fires that may have burned one or few trees in a single lightning strike or localized incident. We identify fires on  $\geq 25\%$  of recording samples as “widespread.” While defining extent or size of fires by filtering is relative, we were primarily interested in effects of fires on recruitment within sites of similar areas.

We also calculated fire return intervals within sites for all fire years, and for fire years in which  $\geq 25\%$  of recording samples were scarred for the period of adequate sample depth. We defined adequate sample depth (a way to restrict analyses, particularly beginning dates with small sample size) as the first fire year recorded by  $\geq 10\%$  of recording trees with a minimum of two trees recording the same fire, until time of sampling or major disruption of fire events was apparent. We tested for statistical difference in recruitment distribution among sites using a Kolmogorov-Smirnov test (MATLAB), and analyzed fire frequency data with FH2 software, version 3.2 (Grissino-Mayer 2001).

## RESULTS

### *Stand structure and spatial patterns*

We sampled 30 plots among three sampling sites (Table 1 and Appendix A). Plot sizes for ponderosa pine-dominated sites ranged from 0.051 to 0.374 ha; the smallest plot area was 0.036 ha, which was a mix of Chihuahua and pinyon pines. A total of 589 plot trees (73% of all trees collected) were crossdated. Trees that could not be crossdated were primarily trees with very tight ring series and too few rings (generally <100 rings) for confident crossdating with a master chronology. For crossdated samples, 545 (93%) had pith present or pith dates could be determined based on inside ring curvature (within an estimated 10 years of exact pith dates). Regression estimates of age based on dbh performed well ( $n = 22\text{--}233$ ,  $R^2 = 0.829\text{--}0.943$ ,  $P < 0.001$ ), and correctly assigned trees with known pre-1885 inner dates, but without exact pith dates, to the correct age class (age class one; pre-1885, >125 yr old). The majority of trees across all sites were relatively young with 96% under 200 years old (post-1811), and 55% under 100 years (post-1911).

Sites demonstrated some similarities in distributions of tree recruitment over time (Fig. 2), with the only

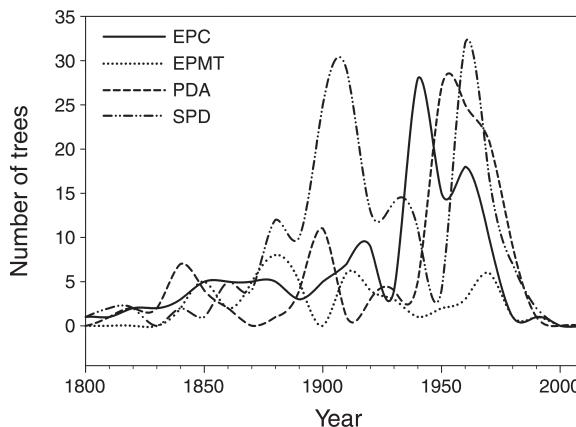


FIG. 2. Tree recruitment by site for both live and remnant trees (>7.5 cm dbh) with accurate pith dates,  $n = 545$ . Recruitment is defined as 10 cm pith dates. El Pinito Mountain Top (EPMT) consists of Douglas-fir stands and is separated from El Pinito Canyon (EPC) and other pine-dominated sites (Pan Duro Arroyo [PDA], Sierra Pan Duro [SPD]) for comparison by species.

significant differences in distribution being between the Douglas-fir stands of EPMT and the SPD pine stands ( $\alpha = 0.05$ ). Two periods of high recruitment occurred across all pine-dominated sites in the 1890s–1910s and 1940s–1960s; however, there was considerable variability among plots. Age structure tended to follow one of three distributions; (1) uneven age structure, which is expected with continuous recruitment and frequent fire disturbance, (2) a flat even-age cohort establishing around 1900, or (3) a flat even-age cohort establishing around 1950, or some combination of these three (Appendix C). The majority of plots with a strong 1900 recruitment pulse were in SPD. The 1950s recruitment pulse was more common within plots in PDA, while uneven age distributions were primarily limited to EPC.

Spatial patterns of trees varied among plots and by demographic patterns of recruitment with general agreement between Ripley’s  $K(t)$  and the Cramer-von Mises test for complete spatial randomness. Slight clustering of trees was apparent in the older tree age classes at scales up to 9 m (Fig. 3). Clustering disappeared entirely for plots with an uneven age distribution, which were spatially random. Likewise, most plots with a strong 1950s age class were also spatially random, with only one plot showing evidence of clustering. Conversely, older age classes (pre-1895 and 1890–1930) were spatially clumped at near distances ( $\leq 6$  m), with only one spatially random plot. Spatial aggregation ( $S$  values close to 1 indicate high levels of aggregation within age classes) of trees was also mostly limited to older age classes (pre-1895 and 1890–1930, e.g., trees in the pre-1895 age class were more likely to be aggregated with other trees also in the pre-1895 age class), and was only found in the high-elevation plots of EPC (EPMT) and in SPD, although in general we observed only weak evidence of spatial aggregation. We

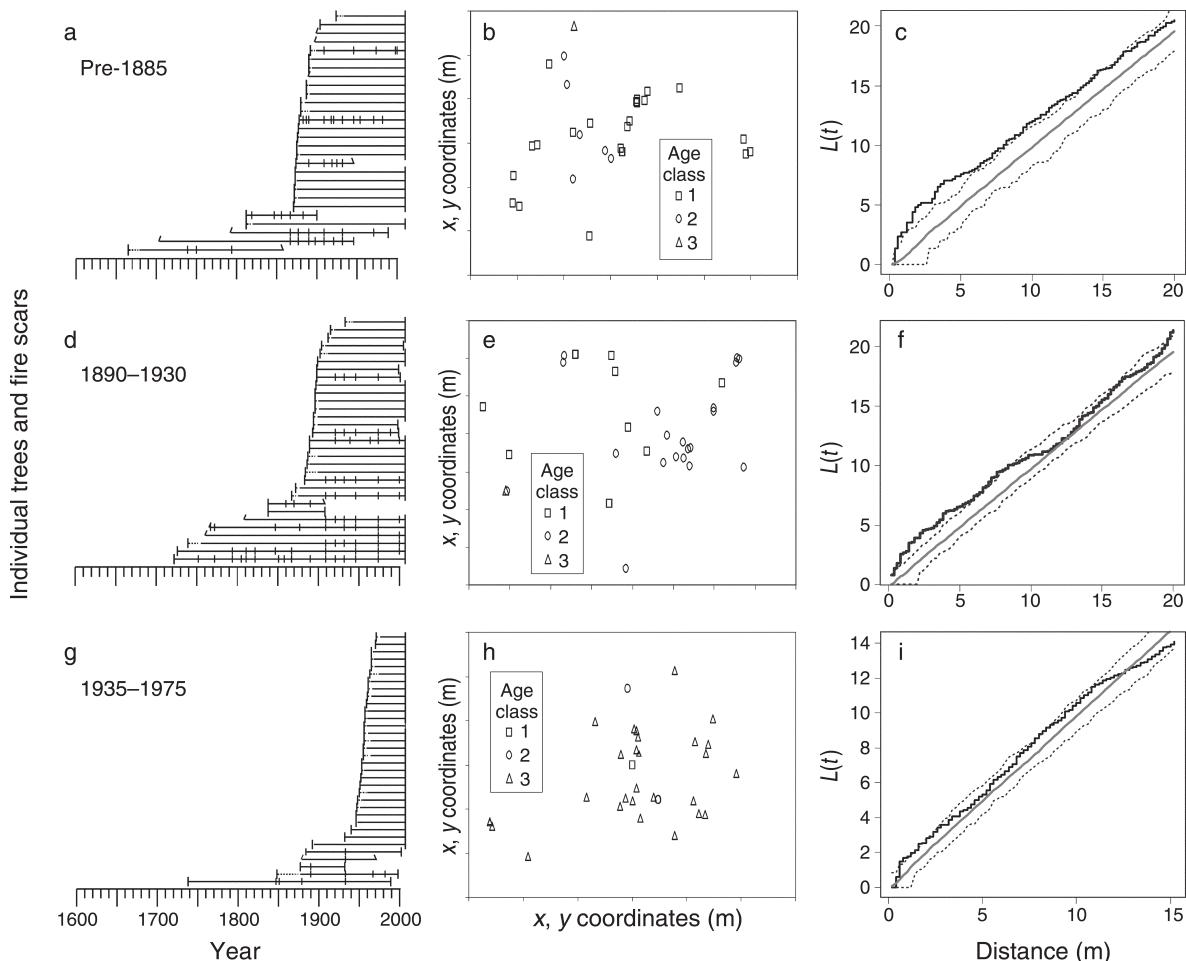


FIG. 3. Comparison of tree demography, spatial distribution, and spatial patterns of trees for three different plots (SPD8b, SPD5a, and EPC6) dominated by recruitment in age classes: 1 (a–c, SPD8b) pre-1895, 2 (d–f, SPD5a) 1890–1930, or 3 (g–i, EPC6) 1935–1975. (For site abbreviations, see Fig. 1.) Tree demography (a, d, g) includes live and remnant plot trees and additional fire scar samples within 200 m of plots. Horizontal lines are life spans of individual trees, and bold short vertical lines are fire scars. Spatial distributions (b, e, h) are  $x$ ,  $y$  coordinates of individual trees by age class, and spatial pattern results (c, f, i) are from Ripley's  $K(t)$  (original units in meters) with an  $L(t)$  square-root transformation for variance stabilization. The 95% upper and lower confidence envelopes (hashed lines) for a Poisson model are plotted as a function of lag distance from an arbitrary individual. Data above the upper limit (heavy line) indicate spatially clumped data.

observed aggregation in four plots for the pre-1895 age class, three plots in 1890–1930 age class, and only two plots within the 1935–1975 age class. In most plots age classes were spatially independent ( $S$  values close to zero). Average segregation index values were negative (aggregation between different age classes) in EPC ( $S = -0.053$ ) and PDA ( $S = -0.062$ ), though not statistically significant, and positive (aggregated) in SPD ( $S = 0.170$ ) and EPMT ( $S = 0.273$ ).

#### Fire, climate, and recruitment interactions

Fires burned relatively frequently, with mean fire return intervals ranging from 6 (PDA) to 10 (EPC) years for all fires (Table 2). Maximum intervals between fires differed among sites. In EPC, prior to 1933, the maximum interval was 14 years (1890–1904) for all fires. In PDA, which generally had more frequent fires

and also more widespread scarring (Figs. 4–6), the maximum interval was 12 years (all fires, 1819–1831), and 17 years for fires scarring  $\geq 25\%$  of recorder trees (1766–1783). SPD had longer intervals, from 17 years (1954–1971) for all fires to 28 years (1946–1974) for fires recorded on  $\geq 25\%$  recorder trees.

Analyses of PDSI by fire size (SEA) indicate very different interactions between small and large events (Fig. 7). The smallest fire years (fires recorded on  $< 10\%$  of recorder trees) were significantly dry years, while the years with the most abundant evidence of burning ( $> 50\%$  scarred: 1794, 1811, 1819, 1847, 1867, 1877, 1890, 1909, 1921, and 1932) were not significantly droughty, but antecedent conditions were significantly wet (95% confidence level) for two years prior to these large fires. Four of these large fires years also covered the early (age class 1) recruitment period.



PLATE 1. Remote landscape of the Sierra Pan Duro, northeastern Sonora, Mexico. Photo credit: J. Paul White.

Comparisons of tree recruitment, fire, and climate by site indicate that fire intervals  $>10$  years were important for successful establishment of tree recruits, while climate did not appear to directly influence recruitment aside from effects on fire occurrence (Figs. 4–6). The most obvious manifestation of this was the large spike in recruitment following reduced fire frequency in the mid 20th century, which was also centered on a severe 1950s drought. This period of increased recruitment was closely aligned with changes in fire frequency, which varied by site. In SPD a pulse of recruitment occurred around 1955, with the last widespread fire ( $\geq 25\%$  recorder trees) occurring in 1946 and the next widespread fires not until 1974. In PDA this pulse of recruitment began around 1945, the last widespread fires occurring in 1932. Similarly, recruitment in EPC spiked in 1935 following the last widespread fire year in 1933.

#### DISCUSSION

Our research in northern Mexico suggests strong site-specific, local controls on forest structure, in contrast to

many studies that showed legacies of anomalous climate years (Swetnam 1993, Kitzberger et al. 1997, Brown and Wu 2005, Swetnam and Brown 2010). We found that fire-free intervals, which varied locally within and across sites, had the strongest influence on successful tree recruitment. Recruitment at a local scale was largely independent of broad-scale climate conditions. The greatest pulse of tree recruitment, for example, coincided with the most extreme drought in over 400 years (1942–1957 [Swetnam and Betancourt 1998, Sheppard et al. 2002]). Recruitment spikes in both EPC and PDA were approximately centered on this drought, and though delayed in SPD (by a fire in 1946), there was still overlap. Similarly, the second largest pulse of recruitment in our sites largely coincided with below-average precipitation conditions prior to 1900, and preceded an anomalously wet period in the 1910s–1920s when pronounced recruitment occurred elsewhere throughout western North America.

Recruitment pulses aligned strongly with periods of reduced fire frequency, with site-specific differences.

TABLE 2. Fire interval metrics (years) for three study sites in the Sierra San Luis, Sonora, Mexico.

Site (no. ha), analysis period	Category of analysis	Mean fire interval	Minimum	Maximum	Maximum interval period
El Pinito Canyon (45 ha), 1847–1933	all scars	10	4	14	1890–1904
	25% scars	17	4	43	1890–1933
Pan Duro Arroyo (63 ha), 1745–1932	all scars	6	1	12	1819–1831
	25% scars	8	3	17	1766–1783
Sierra Pan Duro (63 ha), 1794–2008	all scars	7	2	17	1954–1971
	25% scars	12	3	28	1946–1974

*Notes:* The analysis period was from the first fire year recorded by  $\geq 10\%$  of recording trees at each site until time of sampling or disruption of fire events was apparent. Analyses were further restricted to fires recorded by a minimum of two trees.

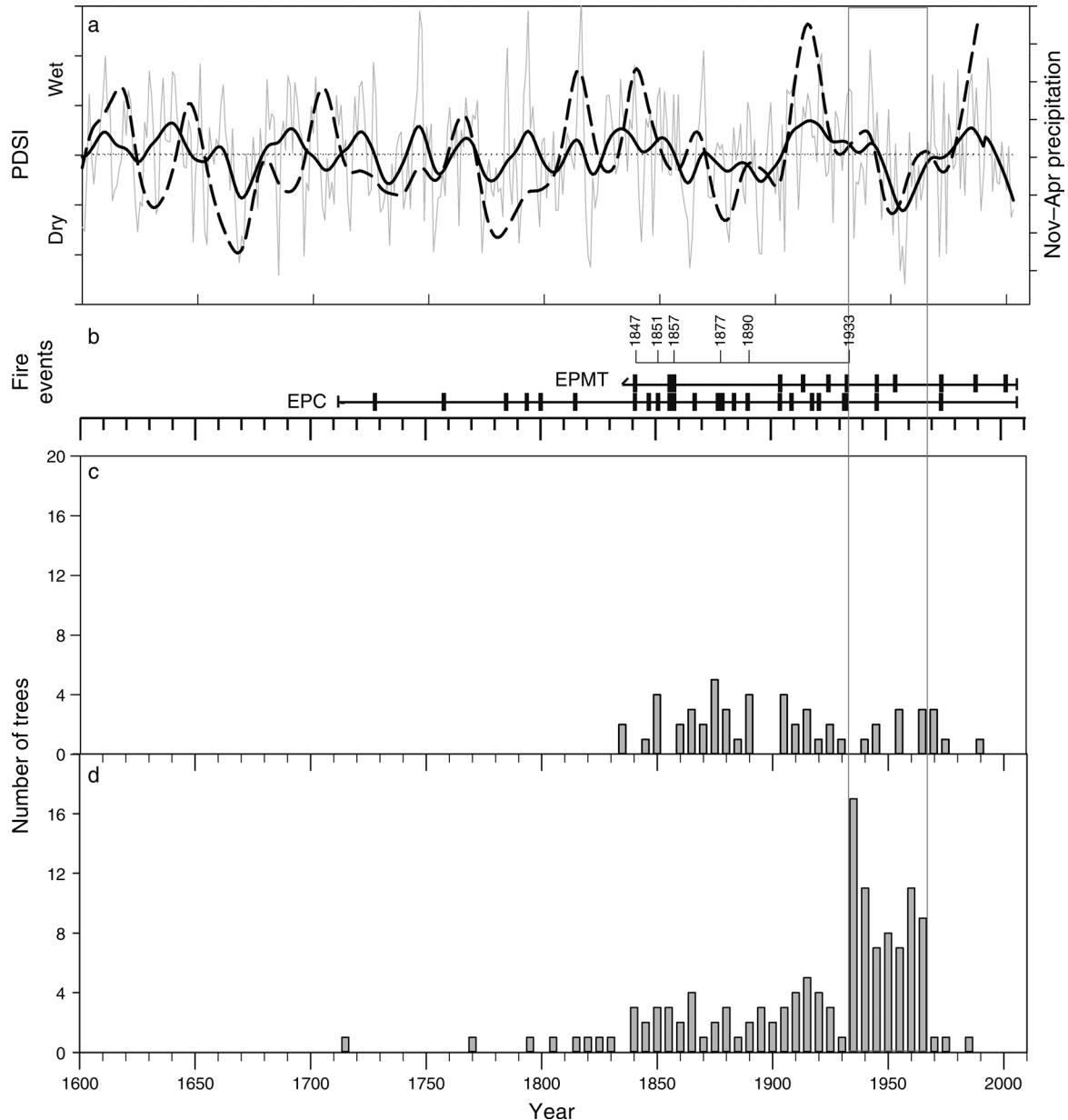


FIG. 4. Comparison of climate, fire year, and tree recruitment chronologies for El Pinito Canyon. (a) Reconstructed climate time series; the light gray line shows Palmer drought severity index (PDSI) for the nearest four grid points (Cook et al. 2004), and the solid line is smoothed PDSI. The heavy dashed line is cubic spline smoothed cool-season precipitation (November–April) for southeast New Mexico and southwest Arizona (Ni et al. 2002). (b) Composite fire year chronologies of all plots for El Pinito Mountain Top (EPMT) and El Pinito Canyon (EPC); horizontal lines represent composited plots tree time spans, and heavy, short vertical lines are fire scars; dates are fire years with  $\geq 25\%$  recorder trees scarred. Note that plots often had few or no fires recorded, so site composite fire chronologies are somewhat different from Figs. 5 and 6. (c, d) Tree recruitment dates by five-year periods for (c) high-elevation Douglas-fir stands (EPMT) and (d) EPC.

Amplified recruitment in EPC and PDA with the onset of grazing (1930s) and cessation of widespread fires is perhaps the most obvious example. This is similar to findings throughout the United States Southwest, where the onset of grazing, and subsequent reduction in fine fuels, was concurrent with widespread cessation of fires, though occurring approximately seven decades later in

this part of Mexico. Differences in recruitment around the turn of the 20th century within the ponderosa-dominated sites (PDA and SPD) also illustrate alignment between recruitment and reduced fire frequency. In SPD the greatest magnitude of recruitment began in 1900 and dropped precipitously in 1910 following a widespread fire year in 1909. There was a 19-year

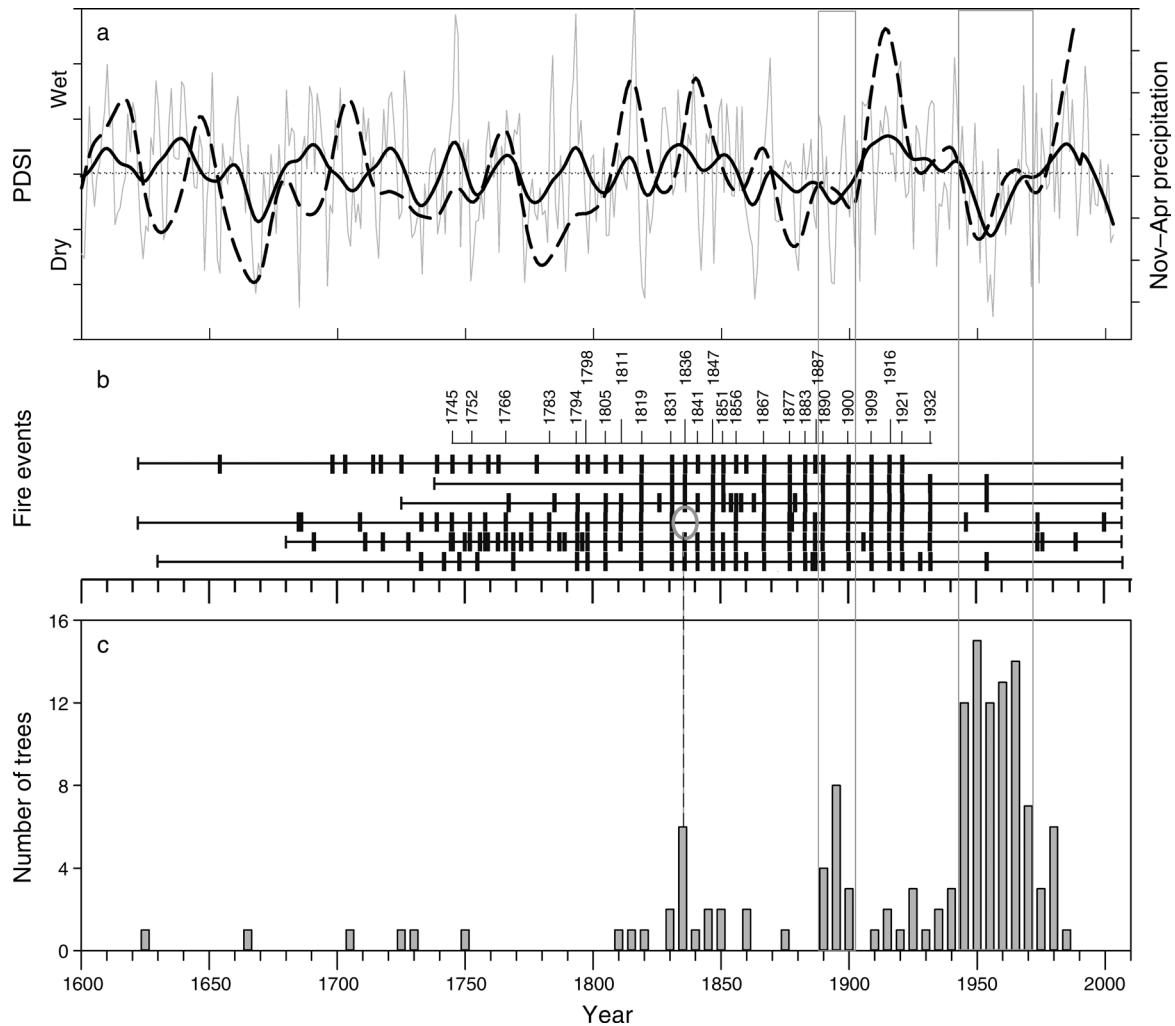


FIG. 5. Comparison of climate, fire year, and tree recruitment chronologies for Pan Duro Arroyo. (a) Reconstructed climate time series; the light gray line shows Palmer drought severity index (PDSI) for the nearest four grid points (Cook et al. 2004), and the solid line is smoothed PDSI. The heavy dashed line is cubic spline smoothed cool-season precipitation (November–April) for southeast New Mexico and southwest Arizona (Ni et al. 2002). (b) Composite fire year chronologies for all fire scar trees scarred, by plot. Horizontal lines represent composited tree time spans for each plot, and heavy, short vertical lines are fire-scars; dates are fire years with  $\geq 25\%$  recorder trees scarred. (c) Tree recruitment dates by five-year periods.

interval between fires in 1890 and 1909. PDA shows a recruitment spike also following a fire in 1890, but this recruitment pulse dropped off with another widespread fire in 1900, a fire year not recorded in SPD. The turn of the century recruitment pulse in PDA was limited to a 10-year fire interval (vs. 19-year in SPD), and was a smaller recruitment event overall. It is noteworthy that this turn-of-the-century recruitment pulse occurred prior to an exceptionally wet period in the 1910s–1920s when climate presumably would have been favorable for recruitment, but was also a period of widespread fires in 1909, 1916, and 1921.

Within periods of frequent widespread fire there was evidence that “safe sites” could allow for limited recruitment within sites. In PDA recruitment from 1830–1840, for example, was limited to one plot where

there was not evidence of a fire in 1836 that was found in surrounding plots (Fig. 5). Greater synchrony of burning among plots in PDA was likely a result of less topographic relief than the other sites and more contiguous forest stands. EPC had less synchrony in recruitment and fewer fires overall prior to 1935 compared to PDA and SPD. However, EPC also shows a spike in tree recruitment in 1935 following the last fire recorded on  $\geq 25\%$  recorder trees in 1933. In EPMT more continuous tree recruitment and few fires were evident, which was expected for higher-elevation Douglas-fir sites that have different life history attributes than the lower-elevation pine sites.

Climate–fire interactions may help explain an apparent lack of relationship between timing of recruitment peaks and climate. Climate is a forcing agent for fire

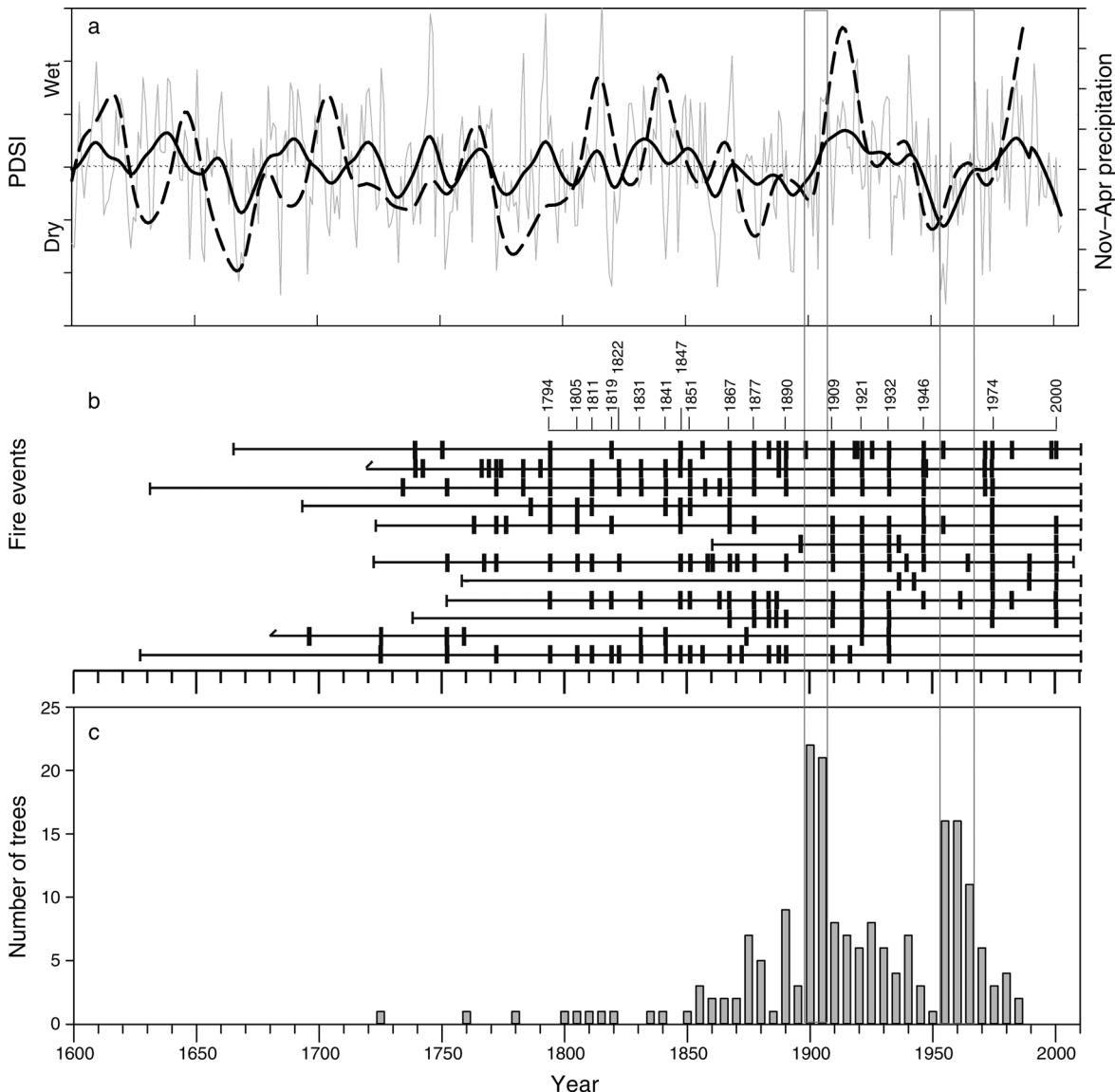


FIG. 6. Comparison of climate, fire year, and tree recruitment chronologies for Sierra Pan Duro. See caption of Fig. 5 for details of analysis.

occurrence, with a notable importance of antecedent conditions for fire years. The same multiple-year wet conditions that typically facilitate tree recruitment may have in fact limited recruitment by promoting fire occurrence. This is especially notable in the largest fire years (fires recorded on >50% of recorder trees), where there was no apparent relationship to drought in year of fire occurrence, but two significantly wet years prior to widespread fire years (Fig. 7). These climate–fire relationships may help explain why there are not greater magnitudes of recruitment during wet periods such as the 1910s–1920s that are prevalent in sites without evidence of fire. Strong associations of wet–dry cycles in promoting fire occurrence may be more limiting to successful recruitment in fuel-limited systems of the arid

Southwest, where significant moisture events are often followed by fire.

While active fire suppression remains untenable in northern Mexico, fire exclusion has begun to occur (e.g., cessation of widespread fires with onset of grazing in EPC and PDA). It remains to be seen if frequent fires in isolated forests like SPD will continue despite disrupted fuel continuity on the larger landscape matrix via effects of grazing and drought. Our results primarily compare recruitment among relatively small areas, and caution is needed when applying these findings to landscape scale patterns, but our findings do suggest that tree recruitment and mortality are coupled processes controlled largely by fire occurrence. Current forest structure in the United States Southwest may primarily be a result of fire

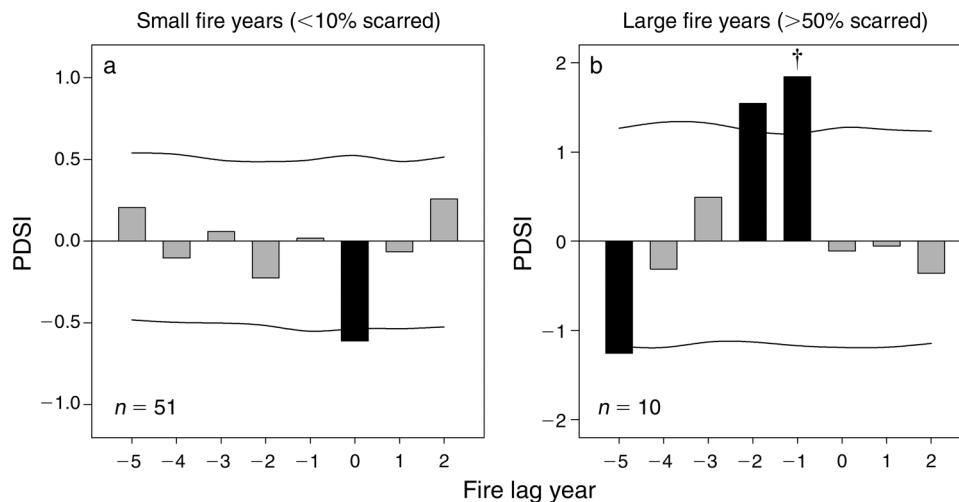


FIG. 7. Results of superposed epoch analysis (SEA) of tree ring reconstructions of Palmer Drought Severity Index (PDSI 1650–2003 [Cook et al. 2004]) for years prior and subsequent to event years (year 0). Positive PDSI values indicate wet conditions, and negative values represent dry conditions. Data shown are for (a) small fire years when fires were recorded on <10% of samples and (b) large fires recorded on >50% of recorder trees. Solid bars indicate PDSI values outside a 95% confidence interval (depicted by wavy lines); the dagger symbol (†) indicates a value outside a 99% CI. All CI's are based on 1000 Monte Carlo simulations of random distributions of annual PDSI. Sample sizes are identified for the number of fire events tested against PDSI data.

exclusion, justifying restoration efforts (e.g., thinning and burning) aimed at creating heterogeneous forest structure more representative of pre-Euro-American settlement.

Spatial dependence among trees was primarily limited to plots dominated by older trees that recruited into plots prior to 1895 (age class 1) or from 1890 to 1930 (age class 2) within  $\sim 9$  m. This pattern was more apparent in SPD, which also had a greater number of plots dominated by age classes 1 and 2. This finding offers limited support for increased levels of clustering in older trees that recruited during periods of frequent fires and limited to “safe sites” (White 1985). It follows that plots dominated by the younger 1935–1975 age class, when fires were less frequent, would demonstrate little clustering, as was our observation. Recruitment in this time period was likely influenced to a greater extent by climate and competition, more universal controls that result in random spatial patterning.

Harvesting has also been found to increase aggregation of trees (Sánchez Meador et al. 2009), and stand density (Naficy et al. 2010). Interestingly, effects of tree harvest may vary by location. In southwestern ponderosa pine, Fulé et al. (2002) suggest that historical logging may not produce as strong long-term density feedbacks as observed elsewhere (Naficy et al. 2010). This appears to be the case in our sites as well where PDA (harvested in early 1950s), for example, had lower tree density (164 trees/ha) and slightly higher basal area (16.3 m<sup>2</sup>/ha) than similar unharvested sites in SPD (201 trees/ha, 15.4 m<sup>2</sup>/ha). This difference could also be in part a result of more frequent fires from 1890 to 1930 in PDA that limited tree recruitment in this time period and affected current forest structure.

Measuring spatial aggregation of trees within age classes was another way to investigate if broad climate effects resulted in widespread recruitment independent of local site-specific factors. In most plots, trees within age classes were spatially independent with segregation values ( $S$ ) close to zero, but again we found differences, particularly in older age classes (1–2) where trees in age class 1 and 2 were more likely to be aggregated with themselves (e.g., trees in age class 2 aggregate with other trees in age class 2), while trees in age class 3 were spatially independent. In general, segregation values were highest (more aggregated) in SPD (mean  $S = 0.170$ ) and EPMT (mean  $S = 0.273$ ), although there was high variability among plots. Comparisons were limited to  $\sim 30$  trees, which limits the ability for interpretation aside from relative comparisons. However, this suggests that not only are trees in plots dominated by older trees (>80 years, age class 1–2) clustered in space at near distances, but they are clustered with each other more often than for tree recruitment after 1935 (age class 3). These differences would not be expected from effects of competition or climate, but could be with heterogeneous fires. We found few trees that recruited after 1975 (age class 4), which is partially a result of sampling only trees >7.5 cm dbh, but generally we observed few plot trees <7.5 cm dbh.

Forest structure is a result of tree recruitment and survival over long time periods. In the mountains of northern Mexico, the forest structure that we observe today 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. The importance of fire-induced mortality in shaping stand structure underscores the spatial variability in forests and helps explain even-age patches in forests, not as a

product of rare stand-replacing fire, but patch survival of seedlings that recruit into the overstory. Recruitment peaks here were tied directly to local processes, notably fire-free periods within and across sites, rather than broad-scale regional climate conditions. However, the importance of antecedent wet conditions promoting fire occurrence raises the possibility that in arid regions of the Southwest, anomalously wet years, still functioning under frequent fire occurrence, may further limit recruitment by promoting extensive fires.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Plots sampled to construct stand structure and fire history in the Sierra San Luis, northern Sonora, Mexico ([Ecological Archives E095-018-A1](#)).

### Appendix B

Scaling relationships for predicting diameter at breast height (dbh) from measurements of diameter sample height (dsh, 10 cm) for remnant wood ([Ecological Archives E095-018-A2](#)).

### Appendix C

Examples of age structure distribution for three different plots that demonstrate (a) uneven age structure, (b) a flat even-age cohort establishing around 1900, and (c) a flat even-age cohort establishing around 1950 ([Ecological Archives E095-018-A3](#)).