forest ecology

Factors Associated with Establishment and Growth of *Pinus coulteri* and *Pinus sabiniana* in California's Central Coast Bioregion

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Forest inventory indicated recent decline in a *P. coulteri* population at its northern extent but live stems in sympatric *P. sabiniana* increased. Patterns of cone production, localized factors associated with regeneration, relations between wildfire and tree age distributions, and correlations between climate, seedling establishment, and tree growth were analyzed as potential mechanisms underlying unequal demographics between the two species. Four findings emerged: (1) *P. sabiniana* had a higher frequency of open cones at the time of observation, but cone production was size-biased, and cone production rates were similar for both species; (2) *P. sabiniana* seedlings were associated with a higher proportion of bare ground cover and westerly aspects, whereas establishment of *P. coulteri* seedlings was correlated with warm growing seasons and high vapor-pressure deficits, and seedlings occurred on northernly aspects; (3) age distributions of stands inside and outside a wildfire perimeter did not differ for either species, but annual growth increments of *P. coulteri* were greater within the fire perimeter; and (4) *P. coulteri* was even-aged, establishment was episodic, and occurred approximately 10 years post-wildfire. In contrast, the age distribution of *P. sabiniana* was highly variable, consistent with continuous recruitment, and establishment was not correlated with a climate signal.

Keywords: Coulter pine, gray pine, population decline, recruitment, Sabinianae

Basic ecological theory indicates that populations are in danger of extirpation when the rate of population increase (births + immigration) is consistently below population loss (mortality + emigration; Harcombe 1987, Vilà-Cabrera et al. 2013); this condition is consistent with the concept of "population decline." In long-lived tree species, recruitment events may be related to specific environmental conditions—for some tree species recruitment is closely related to climatic factors such as interannual variation in precipitation or growing season temperature (Brown and Wu 2005, Brown 2006), but in other species recruitment may be driven by disturbance events that free occupied growing space, create canopy gaps, or provide nutrient fluxes (Hubbell et al. 1999, McCarthy 2001). Regeneration of numerous tree species are associated with abiotic disturbances such as floods, wind events including hurricanes and tornados, or fires, that can create conditions favorable for rapid population recruitment through various mechanisms (Hille and den Ouden 2004, Brown 2006, Pederson et al. 2008). For example, regular flooding drives recruitment in plains cottonwood (*Populus deltoides* W. Bartram ex Marshall; Bradley and Smith

1986) by promoting seed dispersal, and the rate of floodwater abatement is closely matched with root growth rates (Mahoney and Rood 1998).

In the semi-arid forest and chaparral ecosystems of California, many woody species are "disturbance adapted" (Ackerly 2004); in particular, adaptations to fire disturbances are important for population persistence at both local and landscape scales (Zedler et al. 1983, Moreno and Oechel 1991, Hernández-Serrano et al. 2013). Serotiny, typically defined as the release of seed in response to some environmental trigger (i.e., pyriscence, Johnson and Gutsell 1993), is a common "fire-adaptive" trait of conifers in Mediterranean climates and exhibited by multiple "big cone" pine species in the Sabinianae taxonomic group such as Coulter pine (*Pinus coulteri* D. Don), gray pine (*P. sabiniana* Douglas ex D. Don), and Torrey pine (*P. torreyana* Parry ex Carr.). Cones of these species are the largest of any extant pines and are often sealed with a thick resinous layer that prevents full cone opening and seed release until exposure to very high temperatures such as those experienced in a fire event (Johnson et al. 2003). Several studies indicate that fire disturbance

is a key ecosystem process regulating population recruitment in big cone pines (e.g., Minnich 1977, Vale 1979, Borchert 1985, Johnson et al. 2003). However, increasing urbanization of the California landscape often necessitates that nonmanaged fires be rapidly suppressed to prevent losses to property and human life (Stephens et al. 2014, Steel et al. 2015); this condition may contribute to the decline of big cone pines in some areas.

Pinus coulteri is classified as a near-threatened species by conservation organizations (Walter and Gillett 1998), and the entire natural range of *P. coulteri* is narrowly restricted to the Coastal Range of California (Zobel 1952, Lanner 1999). Previous studies suggest that *P. coulteri* is likely to experience decline as a result of fire-suppression policies (e.g., Vale 1979) and a changing climate (Chardon et al. 2014), although these hypotheses have not been extensively tested. Recent reports from resource-management practitioners and aerial surveyors indicate that at the northernmost extent of the range distribution of *P. coulteri* (in proximity to Mt. Diablo State Park, CA), considerable mortality of mature trees has been observed since 2010 (California Forest Pest Conditions 2015). Aerial survey records indicated that this mortality event was because of western pine beetle (*Dendroctonus brevicomis* LeConte) populations; however, upon examination of affected *P. coulteri* stands, it was determined that pine beetle was likely not the primary cause of mature tree mortality in the area (T.S. Davis, personal observation). This decline is a significant management concern, as northern populations of *P. coulteri* represent a unique genetic and recreational resource (Zobel 1952, Ledig 2000), and cover type transition may occur if local populations are extirpated (Galiano et al. 2010). However, *P. sabiniana* is sympatric with *P. coulteri* in the region, and whereas a substantial decline in *P. coulteri* is reported, this is not the case for *P. sabiniana*. This disparity presents a unique situation for comparing drivers of recruitment in two species that share putatively similar fire-adaptive traits and ecological niches.

Multiple factors may play a role in regional decline of *P. coulteri*, including low rates of seed production, climatic unfavorability, or alteration of natural disturbance regimes. Overstory mortality and regeneration were quantified in both *P. coulteri* and *P. sabiniana* in a semi-natural northern Californian forest landscape, and population demographics were compared for evidence of decline. In addition, field surveys and dendrochronological techniques were used to compare basic factors driving abundances and growth of *P. coulteri* and *P. sabiniana* seedlings and trees. Specifically, the following research objectives were addressed: (1) to determine whether patterns of seed production differ between *P. coulteri* and *P. sabiniana*; (2) to compare how local cover conditions and climate correlate with presence and timing of recent seedling establishment in *P. coulteri* and *P. sabiniana*; and (3) to quantify the relation between growth and age distribution of mature pine cohorts with climate conditions and previous wildfire disturbance. Our study provides new information on the basic ecological characteristics of two pine species endemic to California and suggest that regional *P. coulteri* decline may be due to a combination of factors including episodic patterns of recruitment and climatic sensitivity, but do not necessarily implicate fire suppression as a primary reason for decline. These findings can provide new targets for ecosystem management strategies aimed at site-specific conservation of pines in the Sabinianae group.

Methods and Materials

Study System

The study took place within the boundaries of Mt. Diablo State Park, a ~7,600-hectare landscape nested within the wildland–urban interface of Contra Costa county, California. Overstory vegetation throughout much of the park primarily consists of oak woodlands represented by blue oak (*Quercus douglasii* Hook. & Arn.), coast live oak (*Q. agrifolia* Née), and canyon live oak (*Q. chrysolepis* Liebm.) intermixed with expanses of chamise–redshank chaparral (*Adenostoma fasciculatum* Hook. & Arn., *A. sparsifolium* Torr.). In the northern region of the park, isolated coastal pine stands consisting of *P. sabiniana* and *P. coulteri* can be found, representing one of the northernmost natural populations of *P. coulteri*; our study area was concentrated in a ~500-hectare area predominated by these pine stands (Figure 1). The preponderance of these stands occurs as pure pine stands containing both *P. coulteri* and *P. sabiniana* with occasional intermixing of *Q. agrifolia* and *Q. douglasii*.

The fire history of the study area is well documented; wildfires occurred on the landscape in both July 1931 and July 1977, with high mortality reported for much of the *P. coulteri* during those events. However, accounts indicate that the 1977 Mitchell Canyon fire event was more intense and severe than the 1931 event, and some studies have concluded that high-intensity fires are likely to be damaging to the species, whereas low-intensity fires may be associated with reproduction (Vale 1979). Accordingly, the perimeter of the 1977 Mitchell Canyon fire is used to examine *P. coulteri* and *P. sabiniana* age distributions in an effort to determine whether years of probable stand establishment differ within and external to fire-disturbed habitats.

Vegetation Sampling

In March to May 2017, overstory and understory trees were sampled across five 1 km × 20 m belt transects (2 hectares per transect, 10 hectares total sample area). On each transect, overstory trees were sampled by recording the diameter at breast height (dbh,

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Management and Policy Implications

For several years, a decline in Coulter pine (*Pinus coulteri*) populations has been reported at the northern extent of its natural range. This decline is a pressing management concern, as Coulter stands in the region have substantial recreational, genetic, and aesthetic value; but effective intervention is difficult without an understanding of potential drivers of population recruitment. In this study, we investigate factors associated with seedling presence and both recent and previous establishment of *P. coulteri* and an ecologically similar co-occurring species, gray pine (*Pinus sabiniana*). We determined that *P. coulteri* establishment is likely "climate sensitive" and occurs episodically whereas establishment of *P. sabiniana* is relatively continuous and "climate insensitive." Recent establishment of seedlings is associated with warmer-than-average growing seasons and occurs primarily on northerly aspects. Previous studies suggest that *P. coulteri* may be unlikely to regenerate under fire suppression policies; however, our study indicates that extant stands established regardless of wildfire, but trees within a fire perimeter were faster-growing. Knowledge of the different conditions associated with establishment of these two closely related species can be used to design and implement practical strategies for their retention on the landscape.

Figure 1. Location of the study area within California and specific study region within boundaries of Mt. Diablo State Park. The dark gray polygon denotes sympatric *P. coulteri* and *P. sabiniana* populations, and cross-hatching denotes the perimeter of the 1977 Mitchell Canyon fire.

1.3 m height) of *P. coulteri* and *P. sabiniana* greater than 2.5 cm dbh, and each tree was determined to be living or dead. The dbh was also recorded for dead trees. Seed-bearing status (yes or no) was also recorded for each tree and was categorized as "no cones," "open," "closed," or "mixed," which was used to indicate a combination of open and closed cones. To analyze species-specific relations between tree size and cone production, cone production at the time of the study was quantified by counting the number of mature cones present on branches and stems for a random subset of recorded overstory trees (*N* = 49 *P. coulteri* and *N* = 47 *P. sabiniana*).

Pine seedlings of both species were recorded on each transect, and for each seedling, age was approximated by counting the number of terminal bud scars (whorls) (Urza and Sibold 2013). Although not a perfect predictor of seedling age, recent studies indicate that the whorl count method is strongly predictive of seedling age in California and explains ~85 percent of the variation in seedling ages of congeneric *P. ponderosa* (Hankin et al. 2018). For each seedling, multiple variables were recorded, including distance to nearest mature individual of the same species (m), aspect (0–360°), and hillslope (percent). Canopy closure estimates (0–100 percent) were made using a spherical densiometer (Model C, Forestry Suppliers, Bartletsville, OK) at each cardinal direction, and a single canopy closure value was derived from the average of canopy closure estimates for each seedling. Ground cover adjacent to each seedling was also

measured within a 1 × 1 m quadrat divided into 25 equal grid cells (4 percent classes), and the predominant cover in each cell was recorded as grass, woody material (stems, branches, and coarse woody debris), bare ground, herbaceous, or litter (needles, leaves, duff). Since few *P. coulteri* seedlings were recorded within belt transects, additional seedlings of *P. coulteri* were selectively located and the above parameters recorded in order to generate a sample size sufficient for making comparisons between the two species, but these were not included in per-area estimates of population recruitment.

To assess growth-climate relations and the probability of recruitment because of fire disturbance, cores were collected from a subset of both species inside and outside the perimeter of the 1977 Mitchell Canyon fire using an increment borer (20.32 cm bit length, 5.15 mm diameter, Haglöf, Sweden); core samples were collected at the base of the stem and at a random aspect. Cores were air-dried and prepared for analysis by mounting and progressively sanding to a fine grit using standard dendrochronological techniques (Fritts 1976, Stokes and Smiley 1996). Cores were then visually cross-dated among one another, as no master tree ring chronology was available, and all growth increments were counted and measured to 0.001 mm using a sliding stage micrometer (Velmax, Bloomfield, NY) to estimate tree age and probable year of establishment, as well as yearly and mean growth increment for each sample. We confirmed visual cross-dating statistically using the

program COFECHA ([Holmes 1983](#)) and omitted any tree cores that were weakly correlated ($r \leq .20$) with the other tree cores of that species or that had less than 15 years of growth data from all subsequent growth analyses. Of the 61 *P. coulteri* and *P. sabiniana* trees sampled, 11 *P. coulteri* cores and 10 *P. sabiniana* cores were omitted, leaving a total of 50 *P. coulteri* trees and 51 *P. sabiniana* trees used for growth analyses. The mean series intercorrelation for *P. coulteri* and *P. sabiniana* is 0.65 and 0.56, respectively.

Climate Data

Surface meteorological data including mean annual temperature, mean growing season temperature (April to October), total annual precipitation, and mean growing season vapor pressure deficit (VPD) were extracted and summarized from the Precipitation-elevation Regressions on Independent Slopes model (i.e, PRISM model; [PRISM Climate Group, Oregon State University, 2018](#); [Daly et al. 1994](#)) for use in regression analysis. All predictor variables were summarized for each complete year of observation in the publicly available dataset (1981–2017).

Data Analysis

Unless otherwise stated, all parametric and nonparametric statistical tests were implemented using the statistical software JMP 13.0 (SAS Institute, Cary, NC) and incorporate a Type I error rate of $\alpha = 0.05$ for assessing statistical significance. Differences in instantaneous population growth rates of *P. coulteri* and *P. sabiniana* were estimated on each transect by subtracting overstory mortality (dead trees per hectare) from understory regeneration (seedlings per hectare) and dividing this difference by the total number of stems in the overstory (live trees per hectare) (i.e., $\frac{\#\ \text{seedlings}-\#\ \text{dead stems}}{\#\ \text{living stems}+\#\ \text{dead stems}}$) ([Harcombe 1987](#), [Sheil et al. 1995](#)), and differences in normalized growth rates (percent) were analyzed using a two-sample Student t-test to test the hypothesis that *P. coulteri* in the study area is undergoing a population decline.

Objective 1: Determine whether patterns of seed production differ between P. coulteri *and* P. sabiniana. To test the hypothesis that rates of cone production differ between the two focal species, species-specific relations between tree size (dbh) and cone production were analyzed using least-squares linear regression. Cone counts were log-transformed prior to regression fitting to conform to assumptions of heteroscedasticity. The proportions of trees with cones that were "open," "closed," "mixed," or "no cone" were also compared between the two species using a chi-square test.

Objective 2: Compare how local cover conditions and climate correlate with presence and timing of recent seedling establishment in P. coulteri *and* P. sabiniana. To test the hypothesis that localized differences in cover drive differential seedling recruitment, differences in the factors associated with *P. coulteri* and *P. sabiniana* seedling occurrence including canopy closure, distance to nearest conspecific, ground cover (grass, bare, litter, woody, and herbaceous), slope, and aspect were compared using a two-sample Student t-test.

To test the hypothesis that seedling establishment of *P. coulteri* and *P. sabiniana* is associated with different climatic conditions, relations between climate and probability of seedling establishment were analyzed using a multivariate correlation analysis. As above, the probable year of establishment for each recorded seedling was determined using terminal bud scars, and the number of individuals of each species establishing in each year was determined. Climate metrics including mean growing season temperature (April to October; ° C), mean annual temperature (° C), total annual precipitation (mm), and mean growing season VPD (kPa) were correlated with the number of seedlings establishing in each year. Correlations between climate metrics in year $t-1$ (i.e., the year prior to seedling establishment) were also evaluated.

Objective 3: Quantify the relation between growth and age distribution of mature pine cohorts with climate conditions and previous wildfire disturbance.

Prior to implementing a linear modeling approach, climate variables most strongly associated with annual growth increment of each species were identified. To do this, tree ring width data from each tree were standardized to remove growth patterns resulting from tree age and local stand dynamics, which yields a unitless ring width index (RWI). RWI was calculated by fitting a cubic smoothing spline with a 50 percent frequency response at wavelength of 20 years, and then dividing the actual growth by the expected growth for each year using the dplR packing in the R-statistical program (see [Bunn 2008](#) for details; [R Core Team 2016](#)). Pearson's correlation coefficients were assessed between seasonal precipitation and temperature (calculated using PRISM climate data) and detrended ring width data (RWI) for each tree of each species. For these analyses, seasons were defined as: winter (December [year prior], January, February), spring (March to May), summer (June to August), and fall (September to November). The percentiles of trees that were significantly correlated with each climate variable among each species are reported. For these analyses, growth data from 1981 to 2017 were used. The variables most strongly correlated with annual growth increment were subsequently used to inform a linear mixed effects model (discussed below) and included mean monthly temperature in spring, and total precipitation in winter, spring, and summer (Supplement 1).

Interactions between Climate Conditions, Previous Wildfire, and Annual Growth Increments

To test the hypothesis that growth rates differed between *P. sabiniana* and *P. coulteri* and among trees growing inside and outside the 1977 fire, linear mixed effect modeling was used. For these analyses, raw ring width was the response variable, which was log-transformed to meet model assumptions. To account for changes in tree growth with tree age, tree ages of the current year of each growth measurement (both linear and quadratic terms) as fixed-effect variables in our model ([Redmond et al. 2017](#)) were included. Species (*P. coulteri* or *P. sabiniana*) and fire location (inside versus outside the 1977 fire) and their interaction were also included as predictor variables, as it was hypothesized the effects of fire may differ by species. Interactions between species and the climate variables were also included, as it was hypothesized that the relation between climate may differ among species. An intercept for tree was included as a random effect in all models, and a first-order autoregressive correlation structure ("AR1" in function *lme* in the R package "nlme"; [Pinheiro et al. 2018](#)) was also included. The R add-on package data.table ([Dowle and Srinivasan 2019](#)) was implemented to organize tree ring data, and the "lme" function in the R add-on package "nlme" was used for analyses ([Pinheiro et al. 2018](#)). All continuous predictor variables were scaled to a mean of 0

and a standard deviation of 1 before analyses, and thus standardized regression coefficients are reported.

Effects of Wildfire on Tree Age Distribution

The age distributions of trees of each species were compared for individuals inside and outside the 1977 fire perimeter, in order to test the hypothesis that fire events promote establishment of *P. coulteri* in the study area. Accordingly, if fire were associated with a regeneration event, the alternate hypothesis would be that tree age distributions should differ inside and outside the fire perimeter. The following comparisons were made: (1) *P. coulteri* age distribution was compared inside and outside the fire; (2) *P. sabiniana* age distribution was compared inside and outside the fire; (3) *P. coulteri* age distribution inside the fire was compared to *P. sabiniana* age distribution inside the fire; and (4) *P. coulteri* age distribution outside the fire was compared to *P. sabiniana* age distribution outside the fire. Empirical cumulative probability functions constructed from age distributions were analyzed using a two-sample Kolmogorov–Smirnov test (Kolmogorov 1933, Smirnov 1948) implemented in the R-statistical programming environment and with a Type I error rate equivalent to α = 0.05 for assessing statistical significance. To test for even- versus uneven-aged cohorts, a normal distribution was fitted to age-distribution data, and statistical significance was analyzed with a Shapiro–Wilk test (*W*-statistic).

Results

Population demographics of *P. coulteri* and *P. sabiniana* in the study area differed considerably. On average, *P. coulteri* experienced a 34.3 percent decline in population size, whereas *P. sabiniana* experienced an average increase of 61.9 percent in population size, and this difference was statistically significant ($t_8 = 4.937$; $P = .001$; Supplement 2). A comparison of mortality counts to living stem counts indicated that *P. coulteri* has recently experienced a loss of ~38 percent of live overstory stems in the study area, whereas *P. sabiniana* has only experienced a loss of ~4 percent of live overstory stems (Figure 2), which was more than replaced by regenerating seedlings.

Objective 1: Determine whether patterns of seed production differ between P. coulteri *and* P. sabiniana. Evaluation of cone production revealed that cone production rates increased significantly along with tree size in both *P. coulteri* ($F_{1, 47} = 36.492$; $P < .0001$, equation: [log] number of cones = −0.804 + 1.282[log dbh]; $R^2 = .437$) and *P. sabiniana* ($F_{1, 45} = 41.033$; $P < .0001$; equation: [log] number of cones = −0.448 + 1.168[log dbh]; $R^2 = .476$; Figure 3A). Moreover, there was a significant difference between the two species in terms of the proportions of trees with open cones, closed cones, mixed open and closed cones, or no cones ($\chi^2 = 16.699$; $P = .0008$; df = 3, N = 909); *P. coulteri* had approximately 10 percent fewer trees with open cones than *P. sabiniana*, although the proportion of trees with no cones was similar for both species (Figure 3B).

Objective 2: Compare how local cover conditions and climate correlate with presence and timing of recent seedling establishment in P. coulteri *and* P. sabiniana.

The local topographical and cover factors associated with the occurrence of seedlings of each species differed for some, but not all, factors. Distance to nearest mature tree of the same species was on average 37 percent greater for *P. coulteri* than for *P. sabiniana*, *P. coulteri* were found on ~5 percent less steep slopes

than *P. sabiniana*, and *P. coulteri* were associated with ~5 percent less bare ground cover than *P. sabiniana*. In addition, most *P. coulteri* were recorded on northerly aspects, whereas most *P. sabiniana*s were recorded on westerly and northwesterly aspects, and this difference was statistically significant ($t_{146} = 3.812$; $P = .0002$; Figure 4). The approximate age of *P. coulteri* seedlings also differed from that of *P. sabiniana* (Table 1), with most recent seedling establishment occurring within the last 5 years (Figure 5).

There were significant correlations between recent establishment of *P. coulteri* seedlings (as measured by whorl counts) with climate conditions; however, there was no evidence that climate conditions were correlated with *P. sabiniana* seedling establishment (Table 2). Specifically, years with greater establishment of *P. coulteri* seedlings were associated with warm mean annual (>15.3° mean annual temperature) or growing season temperatures (April to October; >18.3° C mean growing season temperature); there was a corresponding positive correlation between probability of seedling establishment and VPD. There were no significant correlations between climate conditions in year $t − 1$ and the probability of tree establishment for either species (data not shown).

Objective 3: Quantify the relation between growth and age distribution of mature pine cohorts with climate conditions and previous wildfire disturbance.

Interactions between Climate Conditions, Previous Wildfire, and Annual Growth Increments of *P. coulteri* and *P. sabiniana*

There was significant variation in mean annual growth increment because of the main effects of tree age ($\beta_{std} = -0.44$, $P < .0001$), spring temperature ($\beta_{std} = -0.11$, $P < .0001$), December through August precipitation ($\beta_{std} = 0.10$, $P < .0001$), and the interaction between fire status and species ($P = .003$; Table 3). Growth rates of *P. sabiniana* and *P. coulteri* were similarly strongly negatively associated with spring temperature and positively associated with December through August precipitation (Figure 6; Table 3). *Pinus sabiniana* and *P. coulteri* had similar growth rates inside the fire (1.88 and 2.02 mm year^{-1}, respectively). However, *P. coulteri* annual growth increment was 1.5 times higher inside the fire perimeter, whereas *P. sabiniana* growth rates were not significantly affected by wildfire (Table 3). As a result, *P. coulteri* radial annual growth increments were substantially lower than *P. sabiniana* outside the fire, with *P. coulteri* growth averaging 1.34 mm year^{-1} (95 percent CI = 1.16–1.56 mm year^{-1}) and *P. sabiniana* radial growth averaging 1.93 mm year^{-1} (95 percent CI = 1.68–2.20 mm year^{-1}; Figure 7).

Effects of Wildfire on Tree Age Distribution

There was no evidence that the age distribution of *P. coulteri* within the 1977 fire perimeter differed from that of *P. coulteri* outside the 1977 fire perimeter ($D = 0.292$, $P = .131$), nor was there any evidence that the age distribution of *P. sabiniana* within the fire perimeter differed from that of *P. sabiniana* outside the fire perimeter ($D = 0.189$, $P = .540$). However, the *P. coulteri* age distribution did differ significantly from that of the *P. sabiniana* age distribution both within ($D = 0.467$, $P = .001$) and outside the fire perimeter ($D = 0.400$, $P = .006$; Supplement 3). The overall age distribution of *P. coulteri* was even-aged, with a single cohort both within and outside the fire perimeter (median age = 30, Shapiro–Wilk $W = 0.971$, $P = .153$), consistent with the hypothesis that
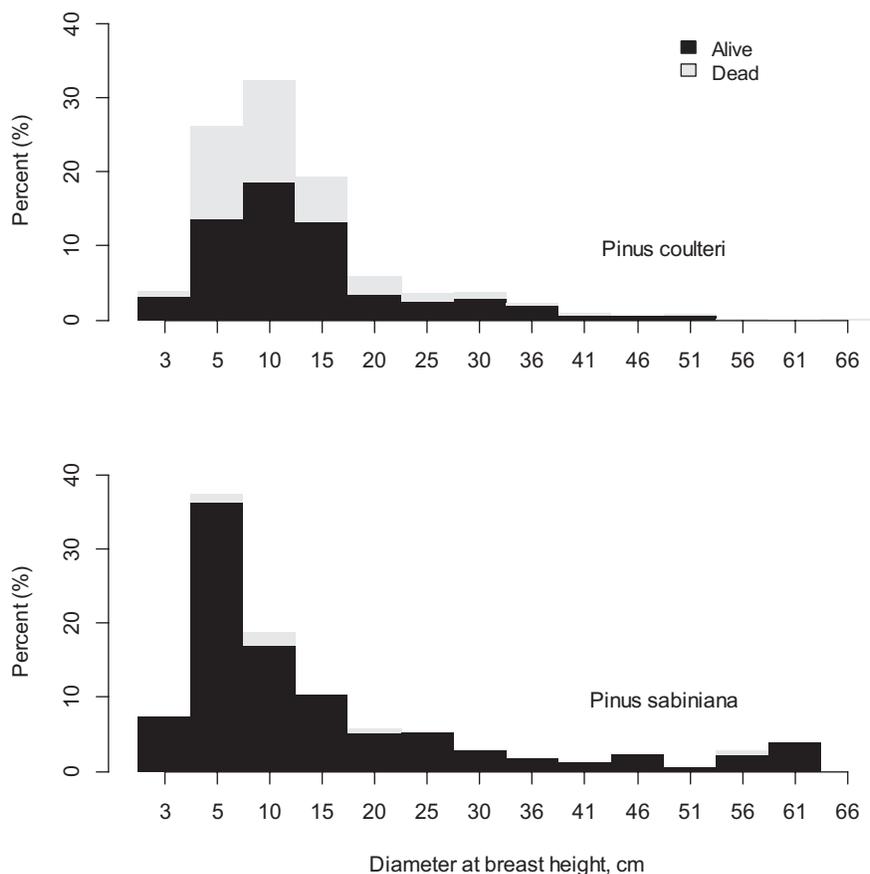
Figure 2. Histogram of diameter at breast height for *P. coulteri* and *P. sabiniana* measured along 1-km belt transects (*n* = 5), relative to mortality status.
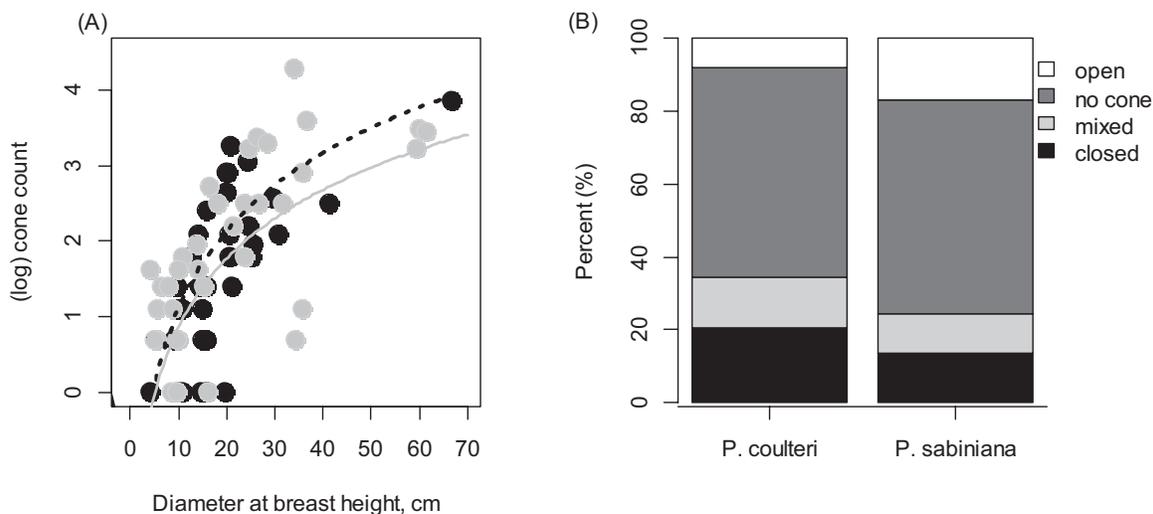
Figure 3. (A) Least-squares relation between tree size (diameter at breast height) and cone production at the time of observation (log-transformed); black points and dotted line denote *P. coulteri*, and gray points and solid line denote *P. sabiniana*. (B) Proportion of *P. coulteri* and *P. sabiniana* trees with open cones, closed cones, a mix of open and closed cones, or no cones at the time of survey.

population recruitment is episodic, but not necessarily regulated by fire disturbances. In contrast, the overall age distribution of *P. sabiniana* was uneven (median age = 25.5, Shapiro–Wilk *W* = 0.913, *P* < .0001), indicating that the probability of establishment for *P. sabiniana* remains relatively constant from year to year (Figure 8).

Discussion

Recent mortality events reported from northern populations of *P. coulteri* prompted significant public interest in the factors underlying population decline. *Pinus coulteri* and *P. sabiniana* occur in sympatry throughout much of their respective ranges and are putatively ecologically similar, but our studies suggest several differences

between the two species that may contribute to the observed disparity in population dynamics in northern California: (1) although rates of cone production were similar between the two species, localized biotic and landscape factors associated with seedling occurrence differed, especially distance to nearest conspecific and aspect; however, cone production was size-biased for both species; (2) correlations between age distributions of seedlings and climate factors indicated that recent patterns of *P. coulteri* establishment may be "climate sensitive," whereas patterns of *P. sabiniana* establishment may be "climate insensitive;" and (3) annual growth increment is responsive to climate for both species, yet unlike *P. sabiniana*, radial growth of *P. coulteri* appears to be reduced when growing in areas that have not burned within the last 40 years. However, establishment patterns were not clearly associated with a fire perimeter for either species. Collectively, these findings are important for understanding key differences between ecologically similar species that may contribute to differential population recruitment and can be used for developing implementation strategies aimed at the retention of forest cover on the landscape.

Both *P. coulteri* and *P. sabiniana* have physical traits that are interpreted as consistent with fire serotiny, including very large and resinous cones that are often stored in the canopy, closed, for many years (Borchert 1985). However, both species exhibit substantial phenotypic variation in this habit, and the nature of fire serotiny in *P. coulteri* specifically has been a subject of research effort for decades. For instance, some fire prone populations of *P. coulteri* exhibit synchronous establishment following fire events (Minnich 1977, Griffin 1982), which is hypothesized to be linked with variability in cone habit (Borchert 1985)—consequently, there has been concern among authors (e.g., Franklin et al. 2006) that policies of fire suppression could be detrimental to stand establishment of *P. coulteri* in some areas, particularly if long-term suppression efforts create highly flammable forest structures because of a lack of natural fuel reduction. However, the majority of cone production (~76 percent) occurred in trees ≥75th percentile dbh, which corresponded to 20 and 25 cm dbh for *P. coulteri* and *P. sabiniana*, respectively. Accordingly, management practitioners can target the abundance of these size classes, and rate of recruitment into these size classes, to control species-specific regeneration rates and achieve desired species composition conditions.

In our study area, regeneration of *P. coulteri* following the 1977 Mitchell Canyon fire was apparently synchronous (Figure 8A); however, previous reports indicate that a majority of *P. coulteri* regeneration following fire disturbance typically occurs within 1–2 years following fire (Minnich 1977, Borchert et al. 2003). In the present study, age distributions of mature trees within the fire perimeter were nearly identical to age distributions outside the fire

Figure 4. Radar graph showing relation between aspect (in degrees) and proportion of *P. coulteri* (•) and *P. sabiniana* (▪) seedlings recorded from belt transect surveys.
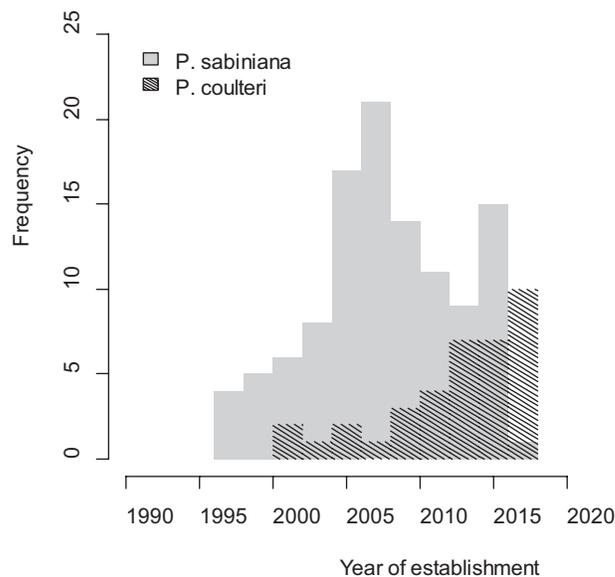
Figure 5. Age frequency distribution of *P. coulteri* and *P. sabiniana* seedlings, based on whorl counts, within the Mt. Diablo study area.

Table 1. Comparison of local topographical, biotic, and cover factors associated with *P. coulteri* and *P. sabiniana* seedling occurrence.

Variable	Tree species		t_{146}	P
	P. coulteri	*P. sabiniana*		
Canopy cover (percent)	55.7 ± 4.9	60.4 ± 2.8	0.840	.402
Distance to nearest conspecific (m)	18.5 ± 1.9	11.7 ± 1.1	−3.005	**.003**
Slope (percent)	19.1 ± 1.0	23.1 ± 0.6	3.191	**.001**
Grass cover	32.5 ± 4.1	26.0 ± 2.3	−1.363	.174
Herbaceous cover	23.8 ± 3.0	19.1 ± 1.7	−1.350	.178
Woody cover	12.3 ± 2.8	10.9 ± 1.6	−0.370	.712
Litter cover	25.4 ± 4.0	32.8 ± 2.3	1.572	.117
Bare ground cover	6.1 ± 2.4	10.8 ± 1.4	1.665	**.049**
Seedling age (whorl count)	5.0 ± 0.8	9.8 ± 0.4	5.125	**<.0001**

Note: Significant parameters are shown in bold.

Table 2. Summary of correlation analysis examining relations between climate conditions and year of seedling establishment, as estimated from whorl counts.

Species	Variable	Correlation	P
P. coulteri	Mean growing season temperature (° C)	**0.646**	**.017**
	Mean annual temperature (° C)	**0.589**	**.034**
	Total annual precipitation (mm)	0.380	.200
	Mean vapor pressure deficit (kPa)	**0.641**	**.018**
P. sabiniana	Mean growing season temperature (° C)	−0.351	.108
	Mean annual temperature (° C)	−0.285	.197
	Total annual precipitation (mm)	−0.287	.195
	Mean vapor pressure deficit (kPa)	−0.098	.663

Note: Values are Pearson's correlation coefficient, r, and statistically significant correlations are shown in bold.

Table 3. Parameter estimates for the linear mixed effect model of annual growth increment responses of *P. coulteri* and *P. sabiniana*.

Parameter	Estimate	SE	*t*-value	*P*
Intercept	7.64	0.07	109.23	**<.0001**
age	−0.44	0.02	−18.1	**<.0001**
age2	0.01	0.01	0.83	.40
species [*P. sabiniana*]	−0.10	0.10	−0.97	.34
fire [outside]	−0.40	0.10	−3.89	**.0002**
spring temperature	−0.11	0.01	−11.94	**<.0001**
precipitation (Dec. to Aug.)	0.10	0.01	10.01	**<.0001**
species [*P. sabiniana*] * fire [outside]	0.44	0.15	3.01	**.003**
species [*P. sabiniana*] * spring temperature	0.01	0.01	0.59	.55
species [*P. sabiniana*] * precipitation	0.02	0.01	1.66	.10

Note: The marginal (fixed effects only) R^2 of the model was 0.37, and the conditional R^2, which incorporates both fixed and random effects, was 0.51 (Nakagawa and Schielzeth 2013). Continuous predictor variables were scaled to a mean of zero and a standard deviation of 1, and thus standardized parameter estimates are reported. Significant parameters are shown in bold.
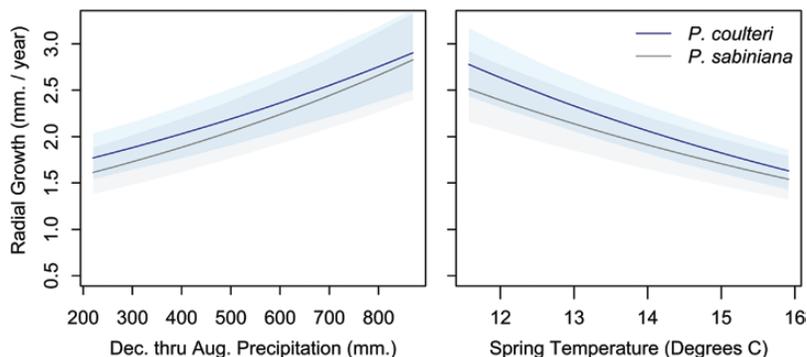
Figure 6. Predicted mean effect of December to August precipitation and spring temperature on *P. coulteri* (blue line) and *P. sabiniana* (gray line) radial growth among trees growing within the wildfire perimeter. Shading denotes the 95 percent confidence interval, with light blue shading corresponding to *P. coulteri* growth, and light gray shading corresponding to *P. sabiniana* growth.
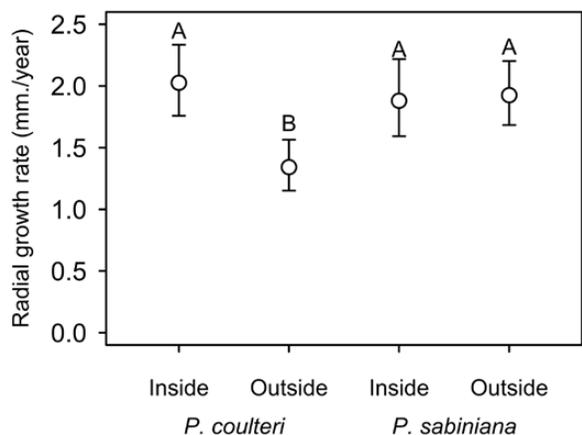
Figure 7. Predicted mean growth rates of *P. coulteri* and *P. sabiniana* located within the fire perimeter (inside) and outside the fire perimeter (outside). Brackets show the 95 percent confidence interval, and different letters denote significant differences in growth rates as detected by Tukey's HSD.

perimeter, indicating that stand establishment in the study area was neither hindered nor promoted by the Mitchell Canyon fire. These results parallel those of Borchert et al. (2003), who found that seedling recruitment was unrelated to burn severity in central California. Establishment of *P. sabiniana*, in contrast, was continuous but similarly showed no clear association with fire. *Pinus sabiniana* recolonized burned areas more rapidly than *P. coulteri*

(Figure 8B) and may be important as a postfire pioneer species in this ecosystem. However, although radial growth increments of both species were similar within the fire perimeter, trees growing outside the fire perimeter had reduced radial growth among *P. coulteri*, but not *P. sabiniana* (Figure 7). The mechanisms underlying enhanced growth within the fire perimeter among *P. coulteri* were not evaluated in the present study, but could be due to reduced stand densities or shifts in soil nutrient composition (Johnson and Curtis 2001, Nave et al. 2011). These results suggest that *P. coulteri* may not be as competitive in unburned areas and could partially explain why there have been recent declines in *P. coulteri* populations associated with fire suppression.

Our analysis also provided evidence that both local variation in cover and physiography, as well as climatic factors, are potentially linked to recent establishment events of *P. coulteri* in the northern extent of its range. For instance, *P. coulteri* seedlings occurred primarily on northern aspects, flatter slopes, and further from conspecifics than *P. sabiniana* seedlings. In addition, probable timing of recent *P. coulteri* seedling establishment was associated with warmer growing seasons and mean annual temperatures, whereas *P. sabiniana* seedling establishment was not significantly correlated with any climatic conditions. Climate conditions were also associated with growth of established trees, and the annual growth increment of both *P. coulteri* and *P. sabiniana* appears to be similarly affected by climate. Radial growth of both species was negatively associated with warmer spring temperatures and positively associated with December through August precipitation, suggesting
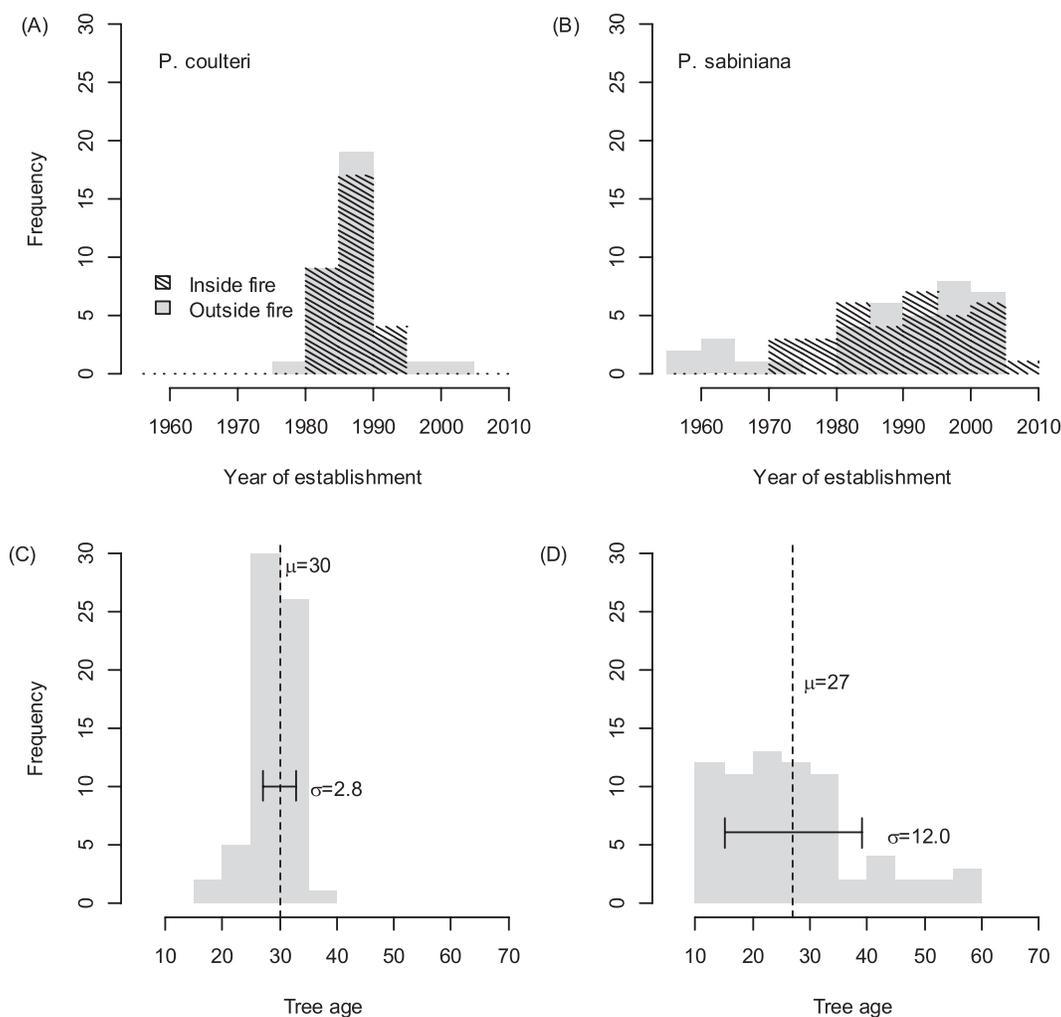
Figure 8. Frequency distribution of tree age for mature **(A)** *P. coulteri* and **(B)** *P. sabiniana* relative to perimeter of the 1977 Mitchell Canyon fire and combined (inside and outside fire perimeter) tree age distributions for **(C)** *P. coulteri* and **(D)** *P. sabiniana*. Dashed vertical lines denote the mean (μ), and horizontal solid bars denote the standard deviation (σ) of each age distribution.

water stress strongly limits the annual growth increment of both species, which is similar to reports from other Mediterranean climates (e.g., Sarris et al. 2007, Martín-Benito et al. 2008).

At its northern extent, *P. coulteri* is genetically distinct, and northernmost populations contain unique alleles that are only also found in the southern extreme of the range (Ledig 2000), potentially indicating that establishment processes of northern *P. coulteri* are associated with specific environmental conditions. Although populations exhibit variation in traits associated with serotiny (Borchert et al. 1985), it remains unknown whether genetic groups are also associated with varying environmental tolerances, but this is an important consideration for conservation of the species under ongoing climate change (Ledig 1988). Further research on the response of *P. coulteri* genotypes to environmental variation is warranted in this regard. Although *P. sabiniana* exhibits a larger range than *P. coulteri* (Powers 1990), the genetic distance between populations appears to be very low (Ledig 2001), indicating that *P. sabiniana* maintains a consistent degree of genetic diversity across its range. These patterns of genetic diversity may be related to the observed "climate sensitivity" in *P. coulteri* establishment and the observed "climate insensitivity" in *P. sabiniana* establishment. However, recent studies indicate that *P. coulteri* populations at the

northern extent of the species range are not necessarily limited by climate conditions (Chardon et al. 2014).

In our field surveys, a substantial decline in *P. coulteri* live stems and a corresponding increase in *P. sabiniana* live stems were observed; these population demographics are consistent with decline of natural *P. coulteri* stands in the northern California landscape. Our analyses suggest that this could be due to correlations between stand establishment processes and site or environmental conditions; however, there was no clear evidence that a fire disturbance was associated with establishment of either pine species in the study area. Collectively, these findings have several implications for the management and conservation of Sabinianae pine stands in northern California: (1) maintaining a mix of overstory species (in this case, both *P. coulteri* and *P. sabiniana*) is likely to favor both continuous and episodic strategies of stand establishment, which may contribute to long-term retention of forest cover in mixed pine–chaparral ecosystems; (2) fire disturbance may not be required for recruitment of *P. coulteri* or *P. sabiniana* in northern California landscapes; and (3) counterintuitively, warm or dry years may be positively associated with recruitment of some species. Several additional research directions could enhance the management and retention of Sabinianae pines in northern California including

information on the specific conditions required for seed germination *in situ* and a basic understanding of the effects of stand density, intraspecific resource competition, and species composition on the demography of *P. coulteri* and *P. sabiniana*.

Supplementary Materials

Supplementary data are available at *Forest Science* online.

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