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ARTICLE

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Evaluating immaturity risk in young stands of the serotinous knobcone pine (*Pinus attenuata*)

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Abstract

As wildfire becomes increasingly frequent, many serotinous plant populations risk local extirpation if fire recurs prior to sufficient seed accumulation in the canopy (i.e., "immaturity risk"). Following two 2018 wildfires in northwestern California, we studied seed viability, cone production, and postfire regeneration of a serotinous conifer, knobcone pine (*Pinus attenuata*), with stand ages (time since fire) ranging from 6 to 79 years. Cone density per tree was more strongly associated with tree diameter than age, and cone density was positively related to postfire seedling regeneration. Most of the postfire knobcone pine regeneration established during the first year with high survivorship in the following first postfire year. Adjusting for survivorship, the estimated minimum age for knobcone pine to promote self-replacement (one recruit per tree) was 9.5 years (or 4.6-cm dbh) and the probability of reburning at the modern fire rotation of 43 years was 19.8%. Based on our results, we found that immaturity risk was currently low for knobcone pine. Our approach provides a quantitative method to assess immaturity risk in knobcone pine and other serotinous conifer species that can be used to evaluate future risk under rapidly changing climate and fire conditions.

KEYWORDS
fire, interval squeeze, knobcone pine, ovulate cones, *Pinus attenuata*, recruitment, regeneration, serotiny

INTRODUCTION

Fire regime characteristics, especially the mean and variance of the probability of reburning at the stand scale, control the persistence and size of competing tree populations through a sequence of fires (Bond & Keeley, 2005). Climate change is presently contributing to increased fire size, frequency, and, in some instances, severity in many fire-prone regions (Abatzoglou & Williams, 2016; Gillett et al., 2004; Price & Rind, 1994; Westerling, 2016), and climate-fire models predict that this trend will continue (Abatzoglou et al., 2021; Parks et al., 2017). While the direct impacts of changing precipitation and temperature regimes on shifting species distributions are often emphasized (Franklin et al., 2013; Schwartz, 1992), climate-induced changes in disturbance regimes can have direct effects that outweigh physiological limits in determining a species' distribution or local

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abundance (Johnstone et al., 2016; Keith et al., 2008; Schwilk & Keeley, 2012).

Several studies demonstrated the threat of local extirpation of plant species when a fire recurs prior to the population reaching reproductive maturity, a concept referred to as immaturity risk (Brown & Johnstone, 2012; Enright et al., 2015; Keeley et al., 1999; Ne'eman et al., 1999; Zedler et al., 1983). Enright et al. (2015) pointed out that while some species may reach reproductive maturity before the next stand-replacing fire, variance in the local return time can occasionally lead to sufficiently short intervals that are deleterious for a population.

However, determining the potential immaturity risk within a population for most species is hindered by the lack of information regarding the timing of reproductive onset. Of the limited studies available, most examine reproductive maturity based on age (Bradstock et al., 1996; Gill & McCarthy, 1998), though the more causal variable of reproductive maturity appears to be plant size (Gauthier et al., 1993; Greene & Johnson, 1999; Lacey, 1986; Wenk & Falster, 2015). But clearly, this means that the time to reach this age for a species will vary with site productivity (Brand, 1991; Sabaté et al., 2002; Yeh & Wensel, 2000). Site quality in turn varies geographically along a species' distribution as well as locally, and over time due to climate variability. As climates in many regions of western North America continue to become warmer and drier due to climate change, increases in fire frequency will likely coincide with slower growth rates and thereby increase the age to reproductive maturity (Enright et al., 2015).

While immaturity risk can occur in both serotinous and nonserotinous species, serotinous species are frequently emphasized despite often reaching maturity at relatively young ages. Serotiny is defined here as the maintenance of a canopy seed bank for more than one year until an environmental factor triggers seed release (Garcillán, 2010). Serotinous species may be especially at risk from a too-brief interval between fires since they are fire-embracing rather than fire-tolerant (Greene & Michaletz, 2015; Lamont et al., 1991), with high fire-induced mortality rates (Schwilk & Ackerly, 2001). In the absence of a sufficiently large seed crop to perpetuate itself at the time of a repeat fire, a serotinous population would likely be locally extirpated. Serotinous species are also advantageous for examining immaturity risk because of their much lower temporal variation in crop size compared with nonserotinous species (Koenig & Knops, 2000; LaMontagne et al., 2021). While species with high interannual variation in cone production require observation over multiple years to find a mean crop size, crop sizes for serotinous tree species are relatively consistent over short time intervals, increasing slowly as the tree grows. Thus, with a serotinous species, a short-term study should suffice to determine the size and age of first reproduction.

Seed supply in serotinous species is not merely a function of the number of accumulated cones, however. The aerial seed bank of serotinous species is often reduced by predation (Lamont et al., 1991) and by prefire cone opening (Martín-Sanz et al., 2017; McMaster & Zedler, 1981; Tonnabel et al., 2012). Variance in the level of serotiny is well known for many species, both as a snapshot termed "apparent serotiny" and as a trend over time termed "inherent serotiny" (Lamont, 2021). Thus, immaturity risk is also a function of the degree of serotiny within a population. A low degree of serotiny within a population would lead to a low number of cones available at the time of fire. Conversely, annual cone opening in the absence of fire for an extended period allows a population to potentially recruit continuously when conditions are suitable.

Population persistence of strongly serotinous populations relies primarily on postfire regeneration. Provided there is sufficient cone accumulation, serotinous species typically have dense postfire regeneration where they are present before a fire (e.g., Greene & Johnson, 1999; Pounden et al., 2014; Turner et al., 2019). Seedling survival after establishment in the first postfire summer depends primarily on access to soil water (Greene et al., 1999), and mortality is typically highest for a seedling cohort in the interval between seed abscission and censused germinant, with subsequent age-specific mortality declining rapidly (Charron & Greene, 2002; Daskalakou & Thanos, 1996; Kolb & Robberecht, 1996). Yet, there is potentially extremely high variability in seedling survivorship between years and sites, even on the same seedbed type (e.g., Greene & Johnson, 1998). Vegetative cover has an unclear relationship with seedling survival; cover may ameliorate microclimatic conditions in Mediterranean summers for germinating seeds, but shrubs also hinder subsequent seedling height growth and survival via competition for moisture and light following germination (O'Brien et al., 2007; Rodrigeuz-Garcia et al., 2011). Thus, variability in seedling survival over time and space related to climate and the competitive environment can also contribute to differences in the probability of stand replacement.

Knobcone pine (*Pinus attenuata*) is a widespread, shade-intolerant serotinous conifer with populations extending from Oregon to Baja California (Griffin & Critchfield, 1972; Little, 1971). Because this species often regenerates at high density (Vogl, 1973), self-thinning of the growing stand along with highly flammable chaparral and resprouting vegetation on lower (drier) slopes contributes to the accumulation of fuels. Mixed stands of

knobcone pine and chaparral are associated with stand-replacing fire with an estimated pre-Euro-American settlement fire cycle ranging between 30 and 90 years (Van de Water & Safford, 2011). A recent estimate (1985–2015) of the fire rotation across the range of knobcone pine specifically was 81 years (Reilly et al., 2019), though so many large fires (>400,000 ha) have occurred since that study (e.g., 2020 August Complex and 2018 Ranch Fire) that the cycle now is presumably lower. Knobcone pine is strongly serotinous in southern California populations with only 4%–6% prefire cone opening (Keeley et al., 1999; Vogl, 1973). However, lower levels of apparent serotiny are suggested for knobcone pine in northern California (Reilly, 2019) where trees have a large fraction of their cones partially or completely open at some sites (J. Gibson, personal communication). If this premature cone opening, termed xeriscence (Nathan et al., 1999), is common for this region, then we expect the pool of seeds available for postfire regeneration in knobcone pine to accumulate more slowly with age than expected for strongly serotinous species with little premature seed release, and thus a lessened recruitment density.

Our study seeks to better understand the immaturity risk of serotinous species through the examination of seed viability, cone production, and regeneration across a tree size and age gradient for the serotinous knobcone pine at two sites in northwestern California following stand-replacing portions of the 2018 Ranch and Carr fires. We explore explanatory variables associated with population self-replacement from seed to established stand, asking:

1. What is the role of cone age and openness on seed viability?
2. Is the number of closed cones better associated with tree age or size?
3. How do seedling survivorship and shrub growth vary within the first few years following fire?
4. How extensive is premature cone ripening in our area and does the rate change with tree age?

Here, we use the negative exponential distribution to calculate the probability of a stand reburning, given the fire cycle, prior to the onset of sexual maturity (i.e., cone production). We then update the most recent estimate of the fire rotation (the single parameter of the negative exponential) within the range of knobcone pine. Finally, we propose an ecologically meaningful definition for this critical age threshold: at the stand scale, we define *effective* reproductive maturity as the age at which a canopy individual produces sufficient seeds to replace itself with a single recruit. Results from our research will provide insights into the factors that contribute to immaturity risk in knobcone pine as well as a framework for characterizing the risk in other serotinous species undergoing climate and fire regime shifts.

MATERIALS AND METHODS

Study area

We sampled two fires that occurred within the southern portion of the Klamath Mountain ecoregion: the Ranch Fire that burned a 6-year-old stand starting on August 13, 2018, and the Carr Fire that burned through a variety of stand ages (9–79 years) starting on July 27, 2018 (Figure 1). The vegetation at both sites was a mix of knobcone pine and chaparral, with few other resprouting tree species (mainly *Quercus*), on dry lower slopes of the Klamath Range. The study site (39.45222 N, −122.86166 E) at the 2018 Ranch Fire (185,800 ha) was about 13 km northeast of Ukiah, California, in the southern part of Mendocino National Forest (hereafter Mendocino). At the 2018 Carr Fire (92,937 ha), the study site (40.63840 N, −123.55946 E) was located 16 km west of Redding, California, in Shasta County within Whiskeytown National Recreation Area (hereafter Whiskeytown). Elevations at our plots ranged from 950 to 1190 m at Whiskeytown and from 700 to 1520 m at Mendocino. Soils at both sites were loams derived from sedimentary colluvium. Climate averages for both sites were derived for the past 15 years prior to 2019 using gridded climate data (PRISM, 2021). For the Ranch Fire site, the mean maximum temperature was 34.4°C and the mean annual precipitation was 819 mm. For the Carr Fire site, the mean maximum temperature was 39.4°C and the mean annual precipitation was 956 mm. Thirteen of our selected Whiskeytown plots were quite young (ages 9–10) having previously burned in the 2008 Motion Fire.

Seed viability

To calculate age-specific or cumulative juvenile survivorship from the pre-abscised seed to established seedling, we estimated the number of viable seeds at various cone ages to gain a better understanding of the prefire aerial seed bank. In September 2019, we selected trees from an unburned stand 40 km north of Redding, California, about 45 km from our Whiskeytown site (40.8473717, −122.4064005), at an elevation of 1066 m. Though it is a small area, we assume this site may represent both Whiskeytown and Mendocino since it possesses similar climatic and soil conditions.

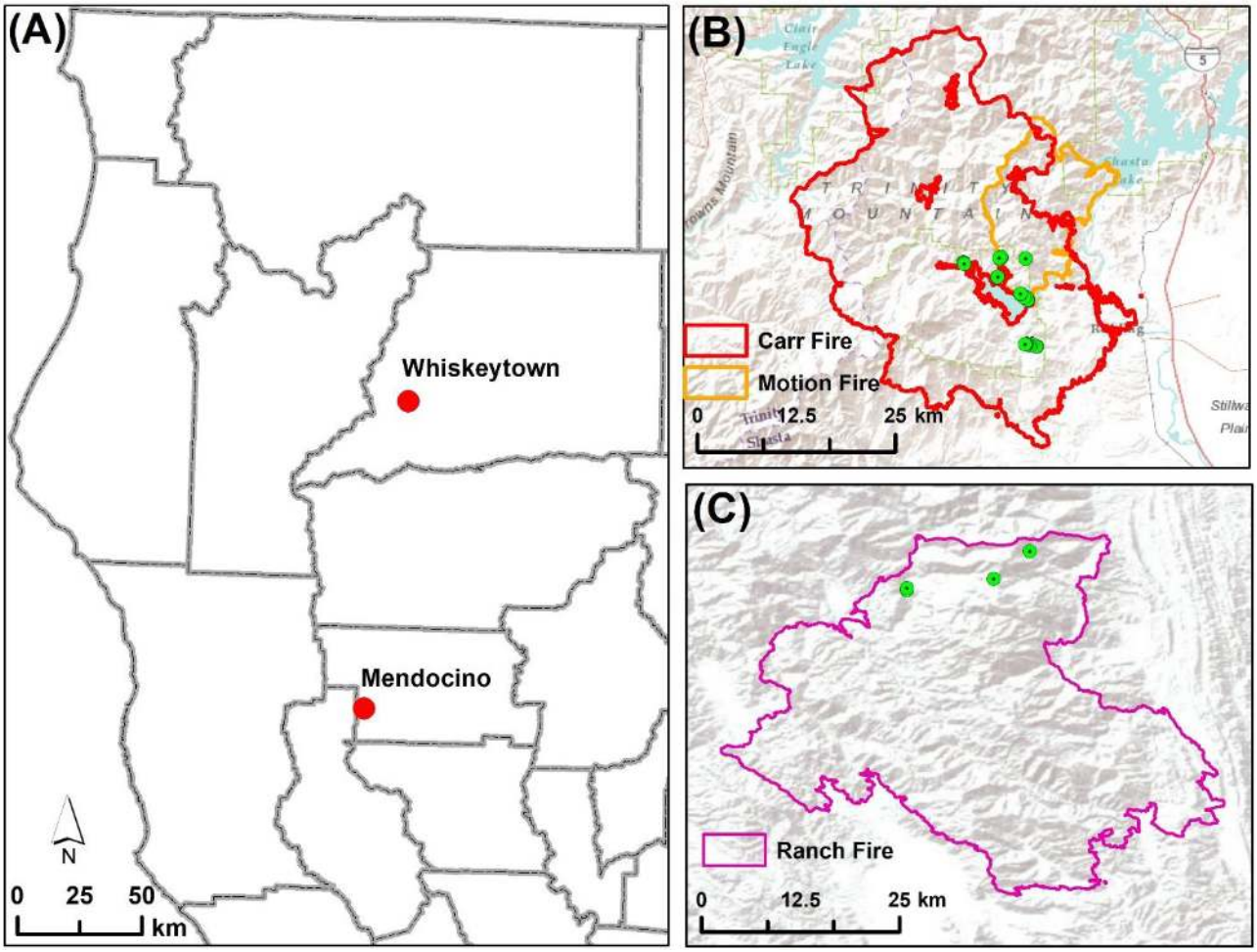


FIGURE 1 Study area map showing the location of plots: (A) location map, (B) Whiskeytown, and (C) Mendocino. The elevation for Whiskeytown plots ranged from 948 to 1191 m and Mendocino plots ranged from 763 to 1524 m.

The dbh of selected trees ranged from 5 to 60 cm. We categorized cones as current (still somewhat green), brown (recently matured), or gray (older), and whether they were open or closed. These categories ignored transitional phases characterized by closed gray cones with some scales already open. Current cones were less than 1 year old, brown cones were estimated to be 1–2 years old since seed ripening, and gray cones were expected to be three or more years old (Fry & Stephens, 2013). For each sampled tree, we estimated the proportion of current, brown, or gray cones, distinguishing between trees with a dbh greater than or less than 10 cm. Throughout the collection area, we gathered 125 knobcone pine cones (20–30 cones from each cone age category) from 12 living trees. Few current cones were available. We counted filled seeds but did not include them in the viability test. To estimate seed viability in these cones, we first opened each by placing them in an oven at 50°C for 8 h until the scales reflexed, and seeds could be manually extracted. Tiny seeds lacking an endosperm were discarded. Filled seeds were then scarified with sandpaper and placed in a petri dish filled with water for 24 h. Afterwards, the seeds were transferred to a dish filled with 1% diluted 2,3,5-triphenyl-2H-tetrazolium chloride solution and kept in the dark for 24 h (AOSA, 2008). After soaking, the seeds were longitudinally cut and observed under a dissecting microscope. Viable seeds were characterized by a pink tint in the embryo. Percent seed viability by cone type was then later applied to determine stand recruitment estimates based on tree size classes (see below).

Cone production and postfire regeneration

In fall 2019, we randomly selected eight plots at the Mendocino site, each centered on a burnt knobcone pine in areas with 100% postfire tree mortality. Since knobcone pine and ponderosa pine (*Pinus ponderosa*) seedlings are difficult to distinguish, we selected plots where ponderosa pine individuals were a minimum of 1 km away. Within a 5-m radius of a fire-killed tree, we

counted the number of burnt knobcone pine seed sources within the plot, measured the dbh of each tree, and counted the number of cones. We counted all cones on the ground or appended to the trees within each plot. We did not include heavily combusted cones where only the basal scales remained (presumably these were already-opened cones). Open cones were counted if all scales were still present; these cones typically had much more char than closed cones because of the enhanced surface area of the flexed scales.

We also counted the number of 2019 germinants within each plot. These areas were quite open and recruits were highly visible within the first postfire summer environment. One exception was germinants under new asexual shrub foliage. In these cases, we simply looked carefully for knobcone germinants within the shrub's initially small crown. Within each plot, we aged 5–10 of the tallest trees by cutting the tree at its base, collecting a full cross-section of the base to estimate tree age and thus the timing of stand establishment. We progressively sanded the collected basal samples with finer grit and then counted the number of annual rings using a microscope. We took the oldest tree age to represent the stand age, though our tree age estimates were quite similar (±3 years) within a plot.

In summer 2019, we sampled 29 randomly stratified plots at Whiskeytown, selecting for a diverse range of size classes based on a detailed fire history map (wild and prescribed fires) compiled by Whiskeytown National Recreation Area. The same protocol and measurements were followed at the Mendocino site, except that at the Whiskeytown site, we used a 15-m radius for each plot because the prefire tree density was on average much lower than at the younger (6 years) Mendocino site (Table 1).

Recruit survivorship and shrub competition

We randomly selected a subset of five 15-m radius plots at the Whiskeytown site, representing the full range of stand ages that were censused in the summer of 2019, and returned to the exact location over the next two years using GPS coordinates and flagging to examine subsequent recruitment as well as survival of the previous seedling cohort. We determined the age of germinants or seedlings based on bud scale scars. In 2020, we tallied the number of new 2020 germinants, as well as the initial 2019 cohort. In 2021, we tallied the new 2021 germinants, 2020 one-year seedlings, and 2019 two-year seedlings. We also measured the height of 20 2019 seedlings, 12 2020 seedlings, and the single 2021 germinant we found. We counted all shrubs within the plot and then randomly selected 40 to measure height and search under the canopy for recruit presence. This value for the number of recruits under shrubs was then multiplied by the ratio of the total number of shrubs in the 15-m radius divided by 40 to obtain an estimate for the number of recruits under shrubs. The estimate for recruits within shrubs was then compared with the much higher, visible number of recruits in the intershrub spaces, and added together to adjust total recruit density per year for each plot. Mean percentage decline in recruit density between 2019 and 2021 was then applied to all recruitment density estimates from 2019 to achieve a cumulative recruit density (all three cohorts combined) as of 2021.

In addition to censusing 2019–2021 recruits, we visually estimated vegetative cover at the permanent plots at Whiskeytown in the summers of 2020 and 2021 as we sought to understand the crown expansion rates of the recruits' main competitors, the shrubs. Vegetative cover was expressed as the percent area of ground covered by the canopy of all plant species, in increments of 5%. In the rare case where shrub crowns overlapped, we did not double-count, and thus, canopy cover never exceeded 100%. Two field members separately evaluated vegetative cover in one quadrat (1/4 of the circular, 15-m radius plot) at a time. We averaged our estimates for each quadrat and then averaged across all estimates for the entire plot. The composition of shrubs was mainly chamise (*Adenostoma fasciculatum*), toyon (*Heteromeles arbutifolia*), poison oak (*Toxicodendron diversilobum*), yerba santa (*Eriodictyon californicum*), manzanita (*Arctostaphylos* spp.), ceonothus (*Ceonothus* spp.), and occasional, asexually reproducing hardwood tree species such as black oak (*Quercus kelloggii*).

Given the expected number of viable seeds per cone category (green, brown, or gray; open or closed) and the proportion of each cone category per tree, we estimated the total number of viable seeds per tree at the time just after the fire had passed by. Lumping all fire-killed trees within the stand, we estimated the prefire density of seeds (total number of seeds per plot area). Thus, to calculate age-specific survivorship from the fire to a

TABLE 1 Seed viability for knobcone pine cones by cone age and openness.

Cone type	Viable seed count	Viability (%)
Green closed cones	13 (2.7)	n/a
Brown closed cones	34.4 (5.2)	41
Gray closed cones	18.1 (4.8)	34
Brown open cones	12.4 (4.3)	30
Gray open cones	3.3 (1.1)	13

Note: Values for viable seed count are presented as mean with SE in parentheses.

subsequent stage (our census of recruits at the end of the first through third summers), we used the ratio of recruit density to prefire viable seed density.

Data analysis

For most statistical analyses, we used a linear regression model approach in R (R Development Core Team, 2020) with log-transformed variables when necessary to meet assumptions of normality and equal variance. We modeled recruit density as a function of cone density (cones per plot area) using logged linear regression ($n = 37$). To find the best explanatory variable for cones per tree, we considered dbh or age as independent variables in separate models. We intended to include both variables with an interaction term but had to exclude this possibility due to multicollinearity (variance inflation factor >10). For the age-only model, to calculate the age at which a tree produces its first cone or first recruit, we performed an arithmetic linear regression of age using observations from the younger stands (<30) as the independent variable ($n = 18$ for the Whiskeytown plots) because the full range of data did not meet test assumptions. In cases where the assumptions of linearity were violated, we considered a suite of potential polynomial relationships because of the likely impacts of xeriscence with tree age at our sites.

We adopted the cumulative negative exponential model to evaluate immaturity risk in knobcone pine (Equation 1). To calculate the probability of reburning before age ($F(t)$), we separately used the modern mean fire cycle and potential historical fire cycle (RT), for the entire range of knobcone pine in northern California and southern Oregon. Age (t) was determined based on our estimate of reproductive maturity for knobcone pine across our sites. The two assumptions of this model are that (1) the annual fire probability is independent of stand age, and (2) the fire regime was stable during the period when the fire cycle was calculated. In other words, we assumed a constant proportion of each cohort was burned at each time interval (Johnson & Van Wagner, 1985). Some of the limitations of these assumptions are addressed in the *Discussion*.

$$F(t) = 1 - \exp\left[-\frac{t}{RT}\right]. \quad (1)$$

To estimate the modern fire rotation for knobcone pine, we acquired perimeters of all fires >400 ha occurring between 1984 and 2021 from the Monitoring Trends in Burn Severity (MTBS) program (www.mtbs.com; Eidenshink et al., 2007) and clipped them to the range of knobcone pine as mapped by E.L. Little's *Atlas of United States Trees* (USGS, 1999). We used the fire perimeter data to calculate the fire rotation for the 25-year period preceding each year from 2009 to 2021 following Reilly et al. (2019). Fire rotation was calculated as the 25-year time period divided by the proportion of the total range of knobcone pine that burned during that time period. We also considered the historical estimation of the minimum and maximum fire cycle, 30–90 years, provided by Van de Water and Safford (2011) for chaparral and knobcone pine (those authors lumped the two types together). We then used the inverse of the fire rotation as the single parameter in the negative exponential fire cycle (Johnson, 1996).

RESULTS

Seed viability

Knobcone pine seed viability varied with cone age and openness (Table 1). Young, greenish closed cones (i.e., cones having completed maturation by the time of collection in early September) averaged about 13 viable seeds. Gray cones made up a much larger fraction of the cone crop of large trees compared with small trees. We visually estimated about 75% of the cones appended to large trees (>10-cm dbh) were gray, but half or less for the cones on small trees (<10-cm dbh). Open gray cones had few seeds, and thus, a low viability rate.

Cone production and postfire regeneration

Postfire regeneration varied between the two sites, reflecting differences in stand ages and cone production. Across both sites, cone and recruit density were positively correlated based on a log–log regression (Figure 2; $p < 0.0001$, $R^2 = 0.7$). Differences in cone density among plots resulted in an order of magnitude difference in average recruitment densities ranging from 0.26 recruits per cone at the 6-year-old Mendocino site to 1.39 recruits per cone at the Whiskeytown site (Table 2). Across all plots at both sites, we averaged approximately one recruit per cone (Table 2). Based on the average across plots within each site, there were about 15 recruits per tree at Whiskeytown but only 0.06 recruits per tree at the younger Mendocino site.

Recruit survivorship and shrub competition

The age structure of the recruits as of 2021 was heavily slanted toward the 2019 cohort. Of the 893 recruits

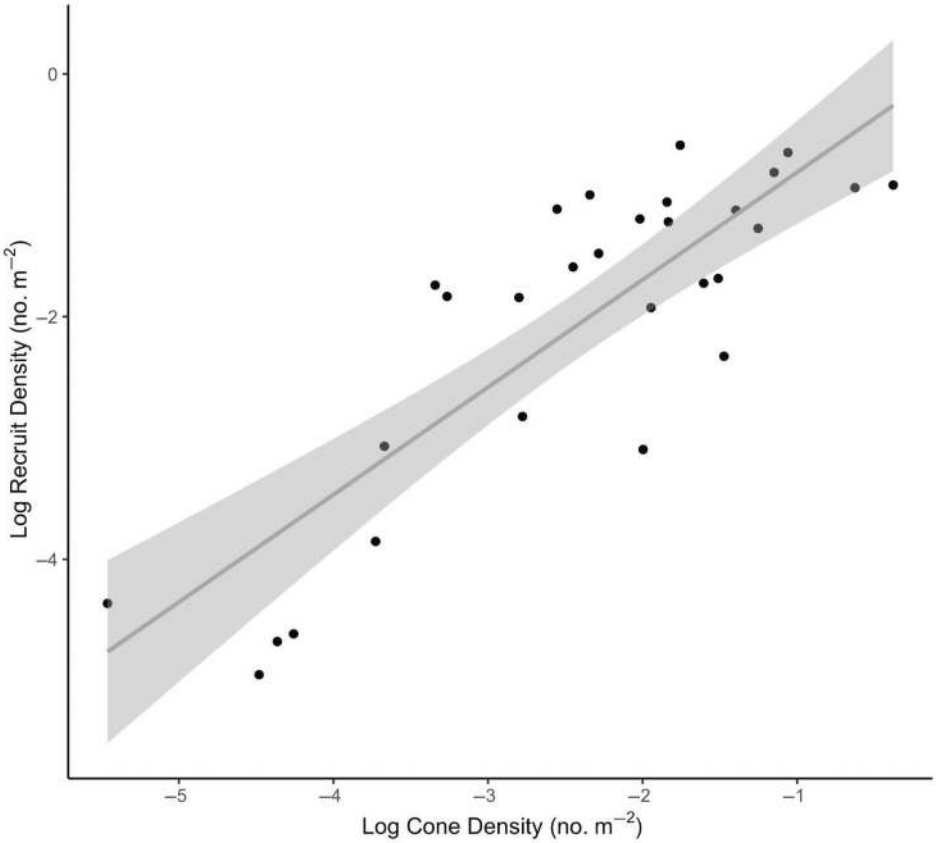


FIGURE 2 Effect of log cone density on log recruit density ($p < 0.0001$, $R^2 = 0.7$) for two knobcone pine sites following fire in northwestern California. Each black dot represents one plot, the gray line represents the log-linear relationship, and gray shading represents a 95% CI.

TABLE 2 Stand, tree, and postfire recruitment characteristics measured and calculated across all plots for each of our two knobcone pine study sites in northwestern California.

		Whiskeytown	
Recruitment characteristic	**Mendocino**	**XXX**	**XXX**
Stand age classes (years)	6	9–25	56–79
dbh (cm)	3.0 (0.28)	8.6 (1.3)	28 (54.7)
Cone density (no./m^2)	0.07 (0.03)	0.13 (0.04)	0.26 (0.06)
Recruit density (no./m^2)	0.07 (0.005)	0.21 (0.06)	0.25 (0.03)
Prefire tree density (no. stems/m^2)	0.24 (0.07)	0.02 (0.01)	0.02 (0.01)
No. cones per tree	0.2 (0.07)	4.5 (1.5)	19.4 (6.0)
No. recruits per cone	0.26 (0.2)	1.7 (0.4)	1.4 (0.3)
No. recruits per tree	0.06 (0.05)	15.0 (4.8)	33.4 (10.8)

Note: Values are presented as mean with SE in parentheses for all characteristics except for stand age classes.

censused in the permanent plots in 2021, there was only a single 2021 (the third postfire cohort) germinant (0.1%), 6.4% were established in 2020 (the second postfire cohort), and 93.5% were from the initial cohort of 2019. The number of germinants dropped 26% from 2019 to 2021. On average, the 2019 seedlings were 0.64 m tall, 2020 seedlings were 0.27 m tall, and the single 2021 germinant was 0.11 m tall. Most seedlings (85%) established in the spaces between shrubs. We estimated the average shrub height in summer 2021 as 0.7 m tall. Shrub cover increased nearly twofold within the permanent plots from 28% to 51% between the first (2019) and third (2021) postfire years.

Given the number of 2019 recruits and our estimate of initial viable seed supply, we found age-specific survivorship (defined as the proportion of censused recruits to viable seeds) from abscission to mid-summer of the year of germination for the initial (2019) cohort to be 0.07 and 0.08 for the Mendocino and Whiskeytown sites, respectively (Table 1). Age-specific (first to third postfire summer) survivorship of the first cohort subsequently increased by an order of magnitude to 0.8 between 2019 and 2021 at the five permanent plots in Whiskeytown. The cumulative survivorship from abscised seed to third summer recruit was 0.06 for Whiskeytown. Adjusting for survivorship since 2019, 69% of our Whiskeytown plots had recruitment greater than that required for self-replacement, with a maximum density as high as 93 recruits per tree.

Reproductive maturity

The number of cones per tree increased with age ($p < 0.0000001$, $R^2 = 0.62$; Figure 3), yet diameter had a much stronger positive correlation with cone density per tree ($p < 0.0000000001$, $R^2 = 0.74$; Figure 4) than did age. Since we selected our plots based on dbh, age did not have a continuous distribution (Figure 5). Based on an arithmetic regression using only the 18 Whiskeytown plots younger than 30 years old, the size threshold for achieving one cone per tree (i.e., stand maturity) was 4.7-cm dbh. Using the regression results for size, one recruit per tree (i.e., self-replacement) occurred at 4.6-cm dbh. These two diameter minima are almost identical because we averaged about one recruit per cone. The density of recruits increased with stand age ($R^2 = 0.498$, $p = 0.00013$; Figure 6). Note in Figure 6 the seeming asymptote created by xeriscence, with younger stands steadily increasing the available seed bank up to 30 years old but a flat to declining relationship for stands older than 30.

Linear regression of cone production (cones per tree) with tree age for young stands (age <30 years) had a strong positive relationship ($p = 0.002$, $R^2 = 0.33$) but the relationship between tree age and recruit density (recruits per tree) was much stronger ($p < 0.0001$, $R^2 = 0.76$). By contrast, regression indicated that age in older stands (>30 years) was unrelated to the number of recruits per tree ($p = 0.8$, $R^2 = 0.11$).

At what size and age do knobcone pine produce their first cone or first recruit? Based on the 18 youngest plots at Whiskeytown, the age to produce the first cone was 8.8 years. Likewise, we found that the age to produce a single recruit per tree (our definition of stand replacement) was similar, 9.5 years. The two estimated ages were necessarily similar because there was essentially one recruit per cone (Table 3).

To account for the very large amount of burning within the knobcone range over the last few years, we updated the previous estimation of the modern fire

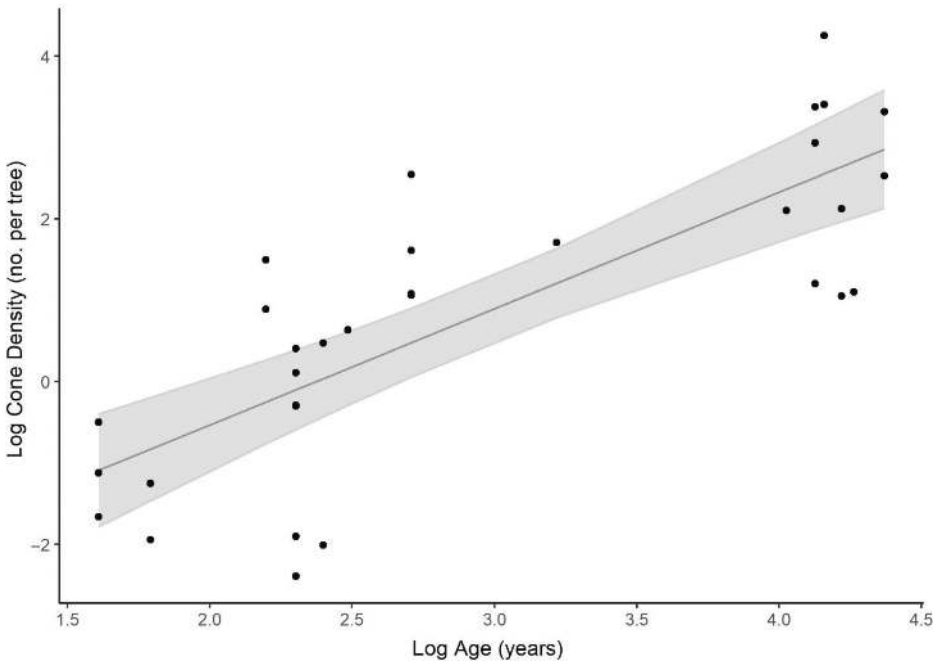


FIGURE 3 Effect of age on cone density ($p < 0.0001$, $R^2 = 0.34$) for two knobcone pine sites in northwestern California. Each black dot represents one plot, the gray line represents the log-linear relationship, and gray shading represents a 95% CI.

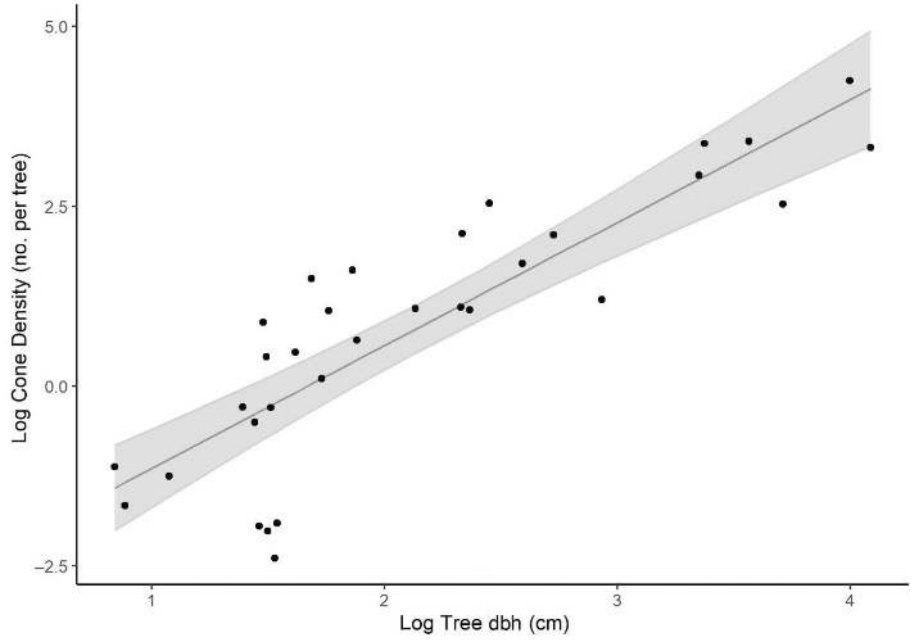


FIGURE 4 Effect of log dbh on log cone density ($p < 0.0000000001$, $R^2 = 0.74$) for two knobcone pine sites in northwestern California. Each black dot represents plot, the gray line represents the log-linear relationship, and gray shading represents a 95% CI.

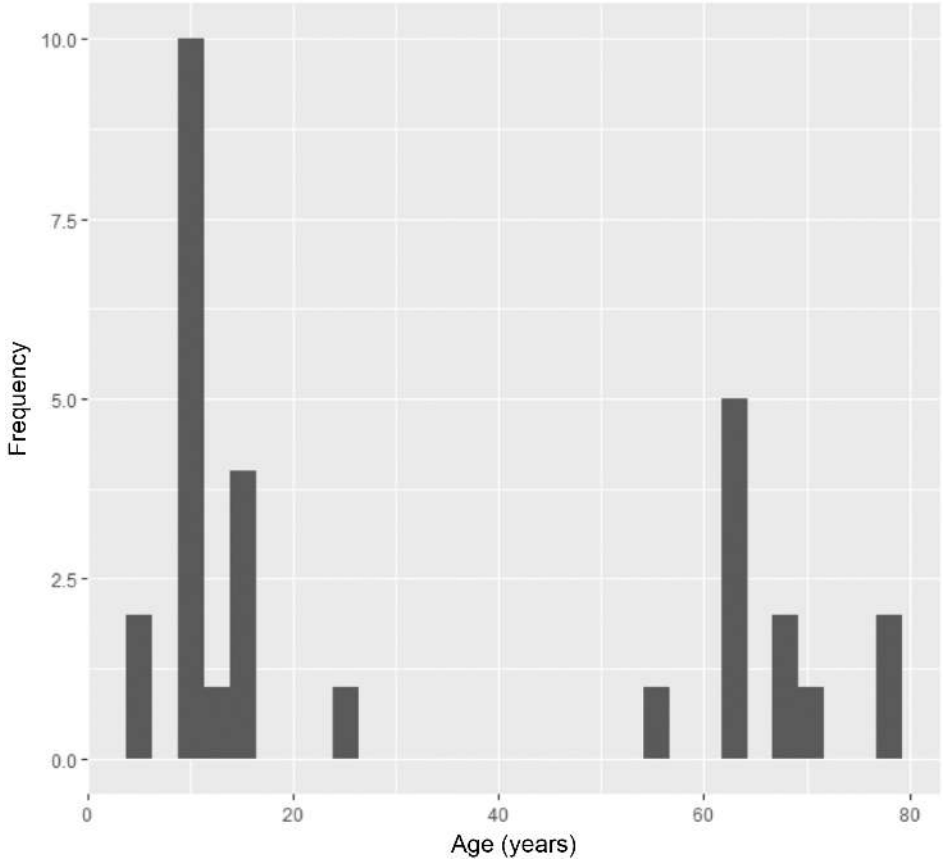


FIGURE 5 Age distribution of sampled stands from both Mendocino and Whiskeytown, a total of 37 plots. Intermediate ages were rare because of a local paucity of fire from 1960 to 2000.

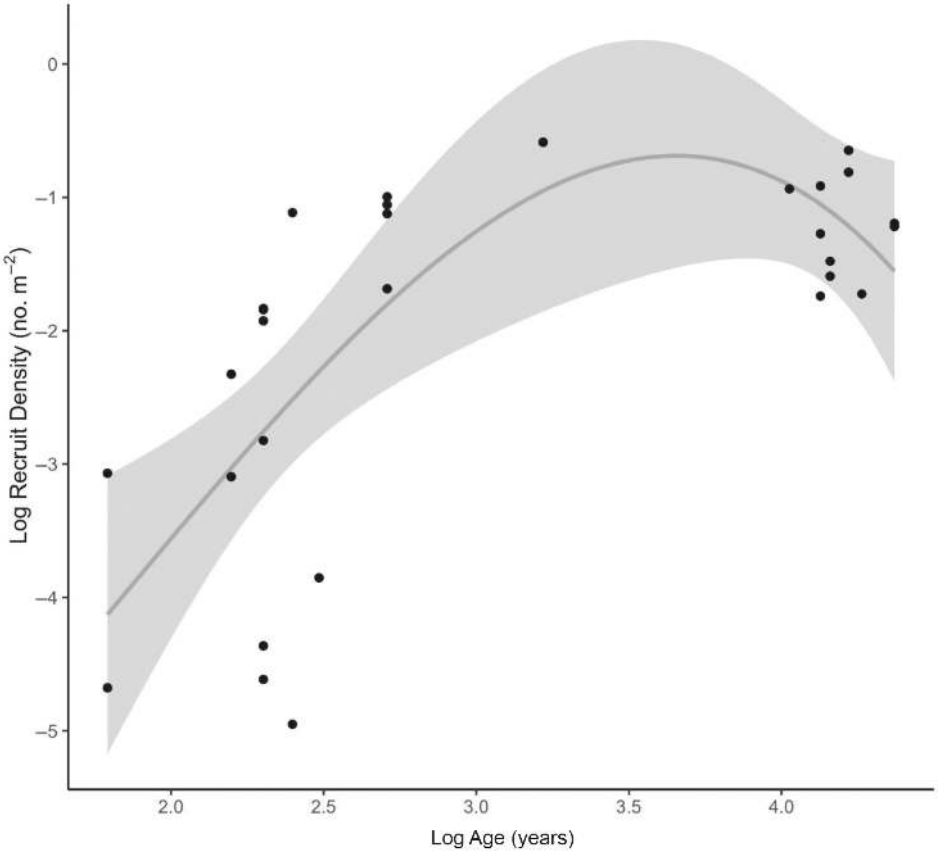


FIGURE 6 A polynomial relationship between recruit density and stand age for the Whiskeytown and Mendocino plots. Each black dot represents one 30-m^2 plot, the gray line represents the log-linear relationship, and gray shading represents a 95% CI.

TABLE 3 Estimated thresholds for reproductive maturity based on a regression of cones or recruits on tree age or size for Whiskeytown and Mendocino sites.

Tree age/size	Stand maturity	Self-replacement
Age (years)	8.8	9.5
Diameter (cm)	4.7	4.6
Reburn probability	0.096	0.097

Note: Reproduction is expressed as a mean of one cone per tree (stand maturity) or one recruit per tree (self-replacement). Reburn probability is the probability of a reburn at the given age.

rotation within the range of knobcone pine, for 1984–2015 (Reilly et al., 2019), and extended this dataset to 2021. The fire rotation from adding these additional years was reduced from 81 to 43 years (Figure 7). Using the negative exponential distribution and given an average fire cycle of 54 years, the probability of fire occurring prior to the age (9.5 years = one recruit per tree) for stand replacement was 19.8% (Figure 8). For the approximate fire rotation range of 30–90 years given by Van de Water and Safford (2011) for knobcone pine/chaparral vegetation, the probabilities of fire occurring before a stand reaches one recruit per tree were 27%–10%, respectively (Figure 8).

DISCUSSION

Our study provides important insights into characterizing the factors effecting regeneration following stand-replacing fires in the serotinous knobcone pine and develops methods to quantify potential risks of population loss due to short-interval fires (i.e., immaturity risk). Here we provided evidence that (1) prefire seed abundance and viability varied with cone age and openness; (2) cone density generally increased with tree size and tree age, but tree size was more strongly associated; (3) cone density was positively related to postfire regeneration, but we observed static or declining regeneration with tree age in older stands; (4) majority of postfire recruitment (>90%) occurred in the first year with most seedlings (85%) establishing in the intershrub spaces; (5) reproductive maturity was reached at 9.5 years or 4.5-cm dbh; and (6) current estimates of the fire cycle for fire in knobcone pine decreased to 43.2 years (a decrease by almost 50 years since 2013), resulting in a 19.8%

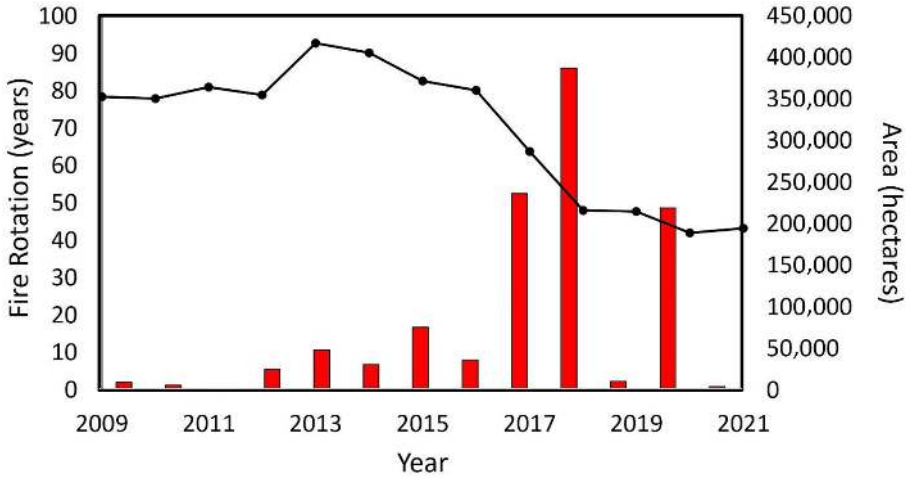


FIGURE 7 Temporal trends in fire rotation and area burned between 2009 and 2021 within the range of knobcone pine.

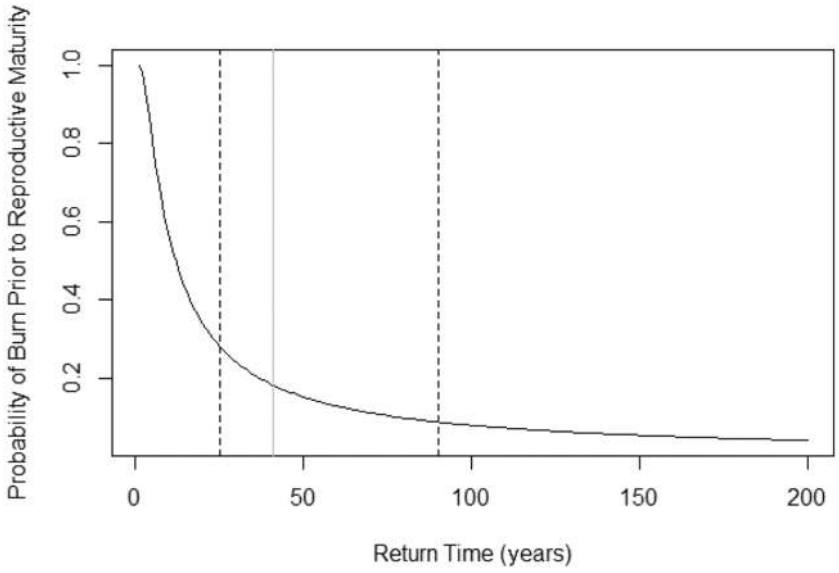


FIGURE 8 The relationship between the return time (fire cycle) and the probability of a fire recurring before the age (9.5 years) for self-replacement has been reached. The probability distribution of the fire interval is expressed as the negative exponential. The modern fire cycle estimate of Reilly et al. (2019) is shown by the solid gray line. The range of the estimated historical fire cycles from studies of the chaparral–knobcone vegetation type is shown by dashed black lines (Van de Water & Safford, 2011).

probability of reburning prior to reproductive maturity. Given the relatively young time to reproductive maturity and low probability or reburning in knobcone pine, we conclude that immaturity risk currently remains relatively low and that most stands would likely experience replacement or population growth following repeated fires. However, given ongoing changes in climate and fire activity in the region, we recommend that immaturity risk continue to be appraised over the coming decades.

The postfire regeneration density in knobcone pine stands in northwestern California varied with tree and stand characteristics. In our study, average knobcone pine recruit density varied from 0.066 recruits/m^2 at the Mendocino site, a very young site with partially immature cones at the time of burning (mid-August), to 0.17 recruits/m^2 (one plot at Whiskeytown; Table 1). Our findings were within the range (0.025 and 11.8 recruits/m^2) observed in a recent study of knobcone pine regeneration in northern California and southern Oregon which included a portion of one of our Whiskeytown sites (Agne, Fontaine, Enright, & Harvey, 2022). For example, they found 0.025 recruits/m^2 for a reburn interval of 6 years whereas we found 0.066 recruits/m^2. However, both of these results were lower than the 1–2 recruits/m^2 reported much higher density for a very dense 8-year-old knobcone pine population that burned in southern California. Thus,

while our older burnt knobcone pine stands (>9 years) usually regenerated sufficiently to increase the density relative to that of the prefire cohort, our overall regeneration was lower than in other studies on knobcone pine. We assume this result was primarily due to (1) our focus on relatively young and sparse stands and (2) the low number of viable seeds per cone, which in turn was likely due to the high level of xeriscence (premature cone opening), especially in the older stands. Xeriscence at our site is likely controlled by water receipt via the cone peduncle as argued by Martín-Sanz et al. (2017). A third explanation for decreased regeneration relative to earlier studies is that increased warming presumably has reduced germination success via less available soil moisture on these lower elevation slopes.

The low densities of knobcone pine regeneration we found cannot be due to unexpectedly low survivorship from viable seed to germinant. Survivorship at Whiskeytown from seed to the first mid-summer census was 8% (Mendocino was 7%), a value within 60% of the predicted seed mass-based value found empirically using a wide range of species germinating on mineral soil with 100% light receipt (Greene & Johnson, 1998). Keeley et al. (1999) did not provide an estimate of viable seeds per cone at their burned 8-year-old knobcone pine site, but if we substitute our viability values, then they saw a knobcone pine survivorship of 2.8% whereas our 2019 cohort had a cumulative survivorship of 6.4% halfway through its third growing season.

Our finding of, on average, one knobcone pine recruit per cone was similar to that of Agne, Fontaine, Enright, Bisbing, and Harvey (2022), and is potentially a useful measure of regeneration potential for other studies of serotinous species with similar age structure and climatic conditions. As mentioned, our recruit densities are lower than other reports on postfire knobcone pine regeneration because of our focus on young stands while our survivorship values were more typical. That is, other serotinous species will probably also provide around one or two recruits per cone, but with denser stands and thus far more cones (and recruits) per square meter. Indeed, as more researchers census not just recruits but also cones, it will be interesting to see if a value of one recruit per cone is generally correct for small-seeded species with mineral soil seedbeds and ample light. Certainly, for knobcone pine, someone conducting a field survey immediately after fire can make an estimate of subsequent regeneration density by making cone counts on both the branches of the burned serotinous trees and on the ground.

Our results showed that size was a better predictor for cone production than age. Agne, Fontaine, Enright, Bisbing, and Harvey (2022) found a similarly strong correlation between size and cone production in knobcone pine. Likewise, basal area or diameter was highlighted by studies in other coniferous species as a good predictor of cone number (e.g., Andrus et al., 2020; Calogeropoulos et al., 2003; Turner et al., 2007). The fact that size is the driver means that age at first reproduction for a species necessarily will vary with site productivity. While our study only examined two sites with similar soils and climate, soil clay content has been positively associated with cone production in knobcone pine (Agne, Fontaine, Enright, & Harvey, 2022). However, additional research that more deeply examines the variation in reproductive onset with site productivity is needed.

Knobcone pine cones dispersed seeds promptly following the late July 2018 fire at Whiskeytown. Cursory examination of one cone from each of five trees in November 2018 indicated that all cones had their scales flexed open and were largely empty of seeds three months after the fire. Thus, the size of the second recruit cohort (2020) was 15 times smaller than that of the first (2019) simply because there were few seeds left to form a second age class. The third cohort (2021) constituted only 0.1% of all recruits. Rapid postfire seed abscission is perhaps a consistent feature of serotinous pines (Greene et al., 2013), although there are very few studies on this. We presume there will be effectively no fourth cohort at the Whiskeytown site.

The 2019 cohort suffered a loss of 26% from 2019 to 2021. We assume most of these deaths were simply due to inadequate soil moisture receipt; the bulk of these dead recruits were easily seen as yellowed stems in the intershrub spaces. Nonetheless, shading by shrubs likely played some role in mortality as the percentage of living recruits within a shrub crown was about half of the proportion of ground occupied by those crowns, implying recruit mortality due to shading. By contrast, a recent study on this species did not find a relationship between shrub cover and knobcone pine recruitment (Agne, Fontaine, Enright, Bisbing, & Harvey, 2022).

We presume there will be little subsequent mortality among the recruits until the thinning stage, and thus our results provide a potential guide to what the future stand will look like (Gill et al., 2017). The recruits averaged 0.37 m/year in height growth from summer 2020 to summer 2021. Given that the shrubs in this area seldom become much taller than 1.5 m, we think that in the absence of other disturbances, the great majority of the pine recruits will be above the shrub crowns within three years, and thus there will be little diminishment in recruit density for the next few years, especially for the tallest recruits.

The risk of fire before a knobcone pine population can replace itself was low at our two study sites. Our

estimate for the age before replacement can occur was about 9 years. Keeley et al. (1999) reported that on average the recruits in their 8-year-old stand were about twice as dense as the parents in the burned stands (i.e., two recruits per tree whereas we would predict slightly less than one recruit per tree for their study), with cones initiated at ages as young as 3 years old. This threshold of about 9 years for self-replacement was similar to Agne, Fontaine, Enright, Bisbing, and Harvey (2022). For Aleppo pine (*Pinus halepensis*) in the Mediterranean region, the age when half of the population was reproductive varied between 7 and 15 years (Thanos & Daskalakou, 2000). At lower elevations in Wyoming, Rocky Mountain lodgepole pine initiated cone production 9–10 years after the previous fire (Turner et al., 2007). It makes sense that a serotinous species would need to achieve reproductive onset as early as possible precisely to minimize the risk of short-interval burns, but more research is needed to examine the generality of this trait among serotinous species.

Clearly, the risk of burning prior to the age of first reproduction was a joint function of the reproductive onset of a species (dictated in turn by site conditions and characteristic growth rates in full sun), the number of available viable seeds, and the fire cycle. Our estimate of 9 years for the self-replacement threshold, when coupled with the estimate of a 43-year fire cycle, means that there is only a 19.8% chance of a fire reducing the density of a knobcone pine stand rather than stabilizing or increasing it. When using the minimum fire cycle of 30 years provided by Van de Water and Safford (2011), the probability of reburn prior to the capacity for stand replacement was much higher at 27%. Their maximum fire cycle (about 90 years) would lead to a 10% chance of premature extirpation by fire. Therefore, the range of probabilities is 10%–27% given the range of fire cycles we entertained. Van de Water and Safford's minimum fire cycle was extrapolated from the entire landscape, which includes chaparral-dominated sites, and this may result in an overestimate. Furthermore, a fire history study in mixed-conifer forests upslope to one of our Whiskeytown study sites had a much shorter fire cycle of 8 years (Fry & Stephens, 2006), which may indicate a higher probability of more frequent fires in the adjacent knobcone pine ecosystems in this region. It is important to point out our sample size was relatively small and does not accurately represent the full variability of knobcone pine across its entire range, but it fits the findings of Ramiadantsoa et al. (2023), who report that the risk of extirpation in serotinous conifers drastically decreases between a 20- and 50-year fire cycle. Finally, given that the fire cycle is predicted to shorten in the western United States, inspection of Figure 8 means that our optimism about the resilience of this species must be guarded. More pointedly, the great increase in area burned in the last 15 years in northern California and southern Oregon means that the fire rotation, as we reported with the reanalysis of the Reilly et al. (2019) dataset, is certainly shortening.

We should discuss two problematic assumptions in our use of the negative exponential to predict immaturity risk. The first assumption of this one-parameter distribution is that the hazard of burning is independent of stand age. While there are many reports arguing that the accumulation of fuel (and thus burning hazard) rises with stand age, increasing rapidly through the first decade (reviewed in Prichard et al., 2017), multiple studies have shown that dead surface fuel loading was greatest within the first few years after stand-replacing fire (e.g., Agee & Huff, 1987; Dunn & Bailey, 2015; McNamara et al., 2019). Likewise, in spite of the rapid recovery of shrubs following fire in in chaparral ecosystems, studies have demonstrated that the probability of burning was independent of stand age (Moritz, 2003; Moritz et al., 2004). In any case, it seems likely that young stands do have a lessened risk of burning but it is not clear that the risk difference with age is dramatic after the first few years. Thus, this assumption with the negative exponential must be exaggerating the risk at the very young ages where serotinous species reach reproductive onset. But how much of an exaggeration is unclear, and it may well be small. The second problem is the assumption that the fire cycle, necessarily inferred from past fire activity, is a reasonable description of the future fire regime. Given warming, we expect the fire cycle to become shorter and thus the future risk must be greater than we predict. We can merely say that our estimate represents a lower limit on the current risk of this species. Interestingly, Ramiadantsoa et al. (2023) developed a simulation of serotinous species persistence in a stand-replacing fire regime and found that monocultures were extirpated at a fire rotation of around 20 years, not much less than the minimum cycle estimate we examined here. Nonetheless, a comparison of the likelihood of persistence across sites and species clearly depends on the time to reach reproductive maturity, which in turn depends on site productivity. Whether there are also inherent differences in time to first reproduction among serotinous species is simply unknown at this time.

In conclusion, we see that, empirically, knobcone stands as young as 9 years can currently maintain or increase their abundances following a repeat fire. Mortality (seed to censused germinant) is high initially for an early-arriving cohort, but age-specific survivorship subsequently increases by an order of magnitude after the first year. At present, the risk of a repeat fire prior to reproductive maturity is low.

As the fire cycle decreases, the incidence of immaturity risk will necessarily increase (Figure 8), but we point out this would not preclude an increase in knobcone range or density because the bulk of the fires experienced by knobcone across its range in a period of increasing severe fire frequency will be well-regenerated, including many stands where it was previously a minor component. Thus, it may well be that even as immaturity risk increases, the species is nonetheless not only expanding its range but also, on average, densifying within it (Reilly et al., 2019).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Marlin et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.x3ffbg7k8.

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