EVALUATING IMMATURITY RISK IN YOUNG STANDS OF THE SEROTINOUS

KNOBCONE PINE (*PINUS ATTENUATA*)

By

Katherine Marlin

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Forestry, Watershed and Wildland Sciences

Committee Membership

Dr. David Greene, Committee Co-Chair

Dr. Buddhika Madurapperuma, Committee Co-Chair

Dr. Jeffrey Kane, Committee Member

Dr. Erin Kelly, Graduate Coordinator

December 2021

ABSTRACT

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As wildfire becomes increasingly frequent, many plant populations risk local extirpation if fire recurs too soon, a problem dubbed "immaturity risk". We studied the regeneration of a serotinous conifer species, knobcone pine (*Pinus attenuata*), as a function of the time between high-severity fires (6-79 years). We evaluated age, cone production, and regeneration at two burned sites in northern California, the Ranch Fire (2018) in Mendocino National Forest, and the Carr Fire (2018) in Whiskeytown National Recreation Area. We found an average of 30.5 filled seeds in closed, brown cones (42% viability of filled seeds). The bulk of the older (gray) cones were partially or fully open, and thus available seed in them at the time of fire was approximately halved. Adjusting for survivorship, the estimated minimum age for knobcone pine to produce one recruit per tree (self-replacement) was 8.2 years. Characterizing the probability of burning as a negative exponential model and using an 81-year return time, we found the likelihood of reburn before 8.2 years was 0.09. Our study demonstrated the importance of understanding the size and time to reproductive maturity in serotinous tree species to adequately quantify immaturity risk. Based on our results and current estimates of return time, we suggested

that immaturity risk is very low for knobcone pine. Our approach could be broadly applied to better quantify immaturity risk in other conifer species.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Fire regime characteristics, especially the mean and variance of the return time, promote or reduce the probability of a species' persistence through a sequence of fire rotations (Bond and Keeley 2005). Climate change contributes to increased fire size, frequency, and, in some instances, severity in many fire-prone regions (Price and Rind 1994, Gillett et al. 2004, Westerling 2016), and climate-fire models predict that this trend will continue (Parks et al. 2017). While the direct impacts of changing precipitation and temperature regimes on shifting species distributions are often emphasized (Schwartz 1992, Franklin et al. 2013), climate-induced changes in disturbance regimes can overshadow physiological limits in determining a species' distribution (Keith et al. 2008, Schwilk and Keeley 2012).

Several studies demonstrate the threat of local extirpation of plant species when a fire recurs prior to the population reaching reproductive maturity, or what has been referred to as immaturity risk (Zedler et al. 1983, Keeley et al. 1999, Ne'eman et al. 1999, Westerling et al. 2011, Enright et al. 2015). Enright et al. (2015) points out that while some species may reach reproductive maturity before the mean return time for stand-replacing fire, the variance in return times can occasionally lead to sufficiently short intervals that are locally deleterious for a population. While timing of reproductive maturity is an important parameter in determining how short an interval can permit persistence (Bradstock et al. 1996, Gill and McCarthy 1998), perhaps the concept is better phrased as

the age or size at which enough seeds are available for the population to replace itself following fire.

Determining the potential immaturity risk within a population for most species is hindered by the lack of information on the timing of reproductive maturity. Of the limited studies available, most examine the age of reproductive onset, though the more causal variable of reproductive maturity appears to be plant size (Lacey 1986, Gauthier et al. 1993, Greene and Johnson 1999, Wenk and Falster 2015). Within a species, size at a particular time is a function of growth rate, which depends on site quality (Brand 1991, Yeh and Wensel 2000, Sabaté et al. 2002). Site quality varies geographically along a species' distribution, and over time due to climate variability. As climates in many regions continue to become warmer and drier due to climate change, increases in fire frequency will likely coincide with slower growth rates and thereby increase age to reproductive maturity (Enright et al. 2015).

While immaturity risk can occur in both serotinous and non-serotinous species, serotinous species are often emphasized. 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 are especially at risk from a too-brief return time since they are fire-embracing rather than fire-tolerant (Lamont et al. 1991, Greene and Michaletz 2015), with high fire-induced mortality rates (Schwilk and Ackerly 2001). In the absence of a sufficiently large seed crop at the time of a repeat fire, a serotinous population would be extirpated. Serotinous species are also advantageous to examine immaturity risk because of their assumed lower temporal variation in crop size compared to non-serotinous species

(*cf.* the coefficients of variation for serotinous and non-serotinous species in the data sets collected by Koenig and Knops (2000)). While species with high temporal variation in crop size require observation over multiple years to find a mean crop size, a serotinous species is much closer to its mean crop size in any given year. Thus, with a serotinous species, a short-term study should suffice to determine the size and age of first reproduction, or of a crop sufficient to permit self-replacement.

Seed supply is not merely a function of accumulated cones. The aerial seedbank of serotinous species is often reduced by predation (Lamont et al. 1991) and by pre-fire cone opening (McMaster and Zedler 1981, Tonnabel et al. 2012, Martín-Sanz et al. 2017). 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. Populations with lower levels of apparent or inherent serotiny will likely result in higher immaturity risk.

Stand replacement relies on post-fire regeneration. Provided that there is sufficient cone accumulation, serotinous species typically have strong post-fire regeneration (e.g., Greene and Johnson1999; Turner et al. 2007). Seedling survival after establishment in the first post-fire summer depends primarily on access to soil water and, at the germinant stage, the frequency and intensity of frost heaving (Greene et al. 1999). Mortality is typically highest for a cohort from the stage of an abscising seed to a censused germinant, with subsequent age-specific mortality declining rapidly (Daskalakou and Thanos 1996; Kolb and Robberecht 1996; Charron and Greene 2002). Within a species, there is extremely high

variability in juvenile survivorship between years and sites (Greene and Johnson 1998). Thus, variability in seedling survival over time can also contribute to differences in stand replacement.

Knobcone pine (*Pinus attenuata*) is a widespread, serotinous conifer extending from Oregon to Baja California (Little 1971, Griffin and Critchfield 1972). Because of its dense post-fire regeneration (Vogl 1973), self-thinning leads to a large accumulation of fuels. Often juxtaposed to highly flammable chaparral, knobcone pine is commonly associated with stand-replacing fire with an estimated pre-Euro-American settlement mean fire return time ranging between 30 and 90 years (Van de Water and Safford 2011). Knobcone pine is strongly serotinous in southern California populations with only 4-6% pre-fire cone opening (Vogl 1973, Keeley et al. 1999). However, lower levels of apparent serotiny is suggested for knobcone pine in northern California (Reilly 2019) and likely possesses a large fraction of its cones partially or completely open at some sites (J. Gibson, personal communication). If confirmed, we would expect the pool of seeds available for post-fire regeneration in knobcone pine to rise more slowly with time than expected for strictly serotinous species with little premature seed release.

Our study seeks to better understand immaturity risk since it is an increasingly pressing topic in the context of climate change. In this paper, we used two ecologically meaningful measures that relate to immaturity risk at both the tree and stand scale. At the tree scale, we determine minimum age or size thresholds to reach one cone per tree, or reproductive maturity. At the stand scale, we estimate the number of viable seeds within cones of varying age and openness and determine the reproductive age and size thresholds

at which a population could minimally replace itself; that is, the density of the burnt parents is equal to the density of the established recruitment. We then use the negative exponential distribution to estimate the probability of a fire occurring before this critical age threshold. Results from our research will provide much needed insights into the factors that can contribute to immaturity risk in knobcone pine but also provides information that may broadly characterize risk in other serotinous species undergoing similar climate and fire shifts.

MATERIALS AND METHODS

Study Area

We selected two fires where knobcone pine populations differed in age and stand structure for sampling: 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 to 79 years) starting on July 27, 2018. In both cases we worked only in areas of the burn where the tree mortality was 100%. 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, at an elevation between 700 and 1520 m. Soils were loams derived from sedimentary colluvium. Climate averages were extrapolated using the past 15 years prior to 2019. Mean maximum temperature was 34.4 °C and mean annual precipitation was 819 mm (PRISM 2021). At the 2018 Carr Fire (92,937 ha), the study site (41.91304 N, -123.14661 E) was located 16 km west of Redding, California in Shasta County within Whiskeytown National Recreation Area with an elevation between 950 and 1190 m. Soils were primarily stony loams. Mean maximum temperature was 39.4 °C and mean annual precipitation was 956 mm (PRISM 2021). Thirteen of our selected Whiskeytown plots (ages 9-10) were burned by the Motion Fire in 2008.

Data Collection

In fall 2019, we randomly selected eight plots at the Mendocino site, each centered on a

burnt knobcone pine. Within a 5 m radius of a burnt tree, we counted the number of dead pine seed sources within the plot, measured the diameter at breast height (DBH) of each tree, and counted the number of cones (including empty cones still appended to the tree) and the number of 2019 germinants within the plot. We defined a germinant as a stem which established from seed and is in its first growing season. Within each stand, we aged several of the tallest trees by cutting the tree at its base. We progressively sanded the collection, then counted the number of annual rings using a microscope. We took the oldest age (though collections within a stand tended to be similar) to represent the stand age.

In summer 2019, we randomly stratified 29 sites at Whiskeytown, selecting for diverse size classes. The same measurements were made as the Mendocino site, except that we used 15-meter radius for each plot because the pre-fire tree density seemed much lower. We selected five plots censused in the summer of 2019 and returned to the exact location using GPS coordinates and flagging tape in following years. We determined 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 measured the height of 20 - 2019 seedlings, 12 - 2020 seedlings, and any 2021 germinant if present. We looked under the canopy of 40 random shrubs at each plot and recorded recruit presence. Mean percentage declines in recruit density between 2019 and 2021 was then applied to all recruitment density estimates from 2019 to achieve a cumulative recruit density as of 2021.

In addition to tallying 2019-2021 recruits, we visually estimated vegetative cover at the same five plots at Whiskeytown in summer 2021. Vegetative cover was expressed

as the percent area of ground covered by the canopy of all plant species, in increments of 5%. We included the influence of the stem and the outermost perimeter of foliage, ignoring gaps in the canopy and overlap. Therefore, canopy cover never exceeded 100%. Two field members separately evaluated vegetative cover one quadrat (1/4 of the circular, 15-m radius plot) at a time. We averaged our estimates for each quadrat, then averaged across all estimates for the entire plot. This competition cover was almost entirely shrubs such as 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*).

Older, prematurely opened cones were non-existent at the very young Mendocino site, but quite common at the Whiskeytown site. At this latter site, we suppose these opened cones burned intensely because of the increased surface area; typically, only the cone base (appressed tightly to the branch) remained. Such heavily combusted cones were excluded in our counts. But there were also many cones partially opened at the time of burning; we have counted these even though it is clear that parts of the cone was heavily burned and some fraction of the seeds were likely killed.

To calculate age-specific juvenile survivorship (from seed to year 2019), we analyzed seed number and viability at various cone ages. We gathered 90 knobcone pine cones from 12 living trees on September 2019 from an unburned stand 40 km north of Redding, California (about 45 km from our Whiskeytown sites). Throughout this same collection area, we selected 30 trees that were similar size classes of our burnt plots at

Whiskeytown (17 of 30 were smaller, and younger). We counted the number of cones in each cone category for 30 individuals. We categorized cones as current (still somewhat green), brown (recently matured) or gray (older), and whether they were open or closed. Brown cones were estimated to be 1-2 years since maturity and gray cones were expected to be 3 or more years old (Fry and Stephens 2013). To open and then manually extract seeds from the cones, we first dried the cones in an oven at 50 °C for 8 hours. Tiny seeds lacking an endosperm were discarded. Filled seeds were then scarified with sandpaper. The seeds were placed in a petri dish filled with water for 24 hours. Afterwards, the seeds were transferred to a petri dish filled with 1% diluted 2, 3, 5- triphenyl-2H-tetrazolium chloride solution, and kept in the dark for 24 hours (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. To estimate the initial seed supply at the time of burning in the 2018 Carr Fire at the Whiskeytown site, we used number of viable seeds per category, and the average proportion of cones in each cone category.

Data Analysis

For most statistical analyses, we used a general linear modelling approach in R (R Development Core Team 2020) with log transformed variables when necessary to meet assumptions of normality and equal variance. First, we compared cone density to recruit density using logged linear regression, where cone density was the independent variable and recruit density was our dependent variable (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, we divided the dataset into two with 30 years as our breakpoint because we did not have any observation of ages between 25 and 56 years in our dataset and the full range of data did not meet the normality assumption. Thus, we performed a non-logged linear regression analysis of age (<30) as the independent variable (n=26) and cones per tree as the dependent variable, and a second analysis with age (>30) as the independent variable (n=11). To calculate age and size to reproductive maturity, we used a non-logged linear regression equation of cones per tree on age (<30) and DBH generated above, where stand maturity was represented by one cone per tree.

We used a non-logged linear regression of recruits per tree (adjusted for second year mortality) on age (<30) to find the minimum age for the population to restock itself. Juvenile survivorship was calculated as the number of successful recruits for each viable seed from abscission to mid-summer of the year of germination. We adopted the cumulative negative exponential model ($F(t)$) to evaluate immaturity risk (Equation 1). The premise of using the negative exponential was that fire hazard is independent of stand age. In other words, we assumed a constant proportion of each cohort was burned at each time interval (Johnson and Van Wagner 1985). To calculate the probability of reburning before age (t), we used 81 years for the mean return time (RT, the single parameter of this distribution), an estimate from Reilly et al. (2019) based on the entire range of knobcone pine in northern California and southern Oregon. We also considered the minimum and

maximum return time, 30 to 90 years, provided by Van de Water and Safford (2011). The

negative exponential was expressed as:

$$F(t) = 1 - exp\left[-\frac{t}{RT}\right]$$
<div align="right">Equation 1</div>

The raw data (Excel) and R code are provided in Supporting Information and will

be permanently archived at in Dryad upon publication.

RESULTS

Seed Viability

Knobcone pine seed viability varied with cone age and openness. Near the Whiskeytown site, we found closed brown (younger) cones had an average of 30.5 filled seeds and, in turn, these had 42.0% viability. All other cones, gray or partially open (older) or open (very old), had an average of 10.4 filled seeds and 24.2% viability. By contrast, young, greenish closed cones (that is, cones still maturing at the time of collection) only averaged about 13 viable seeds. We qualitatively observed that smaller trees had mostly closed brown cones, whereas trees beyond a certain size (>30 years) had a fixed maximum of closed, brown cones, and a progressively higher proportion of closed gray cones. Our average percentages of cone type were 33% closed brown, 58% closed gray, 7% open brown, and 2% open gray.

Regeneration and Survivorship

Post-fire 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 an non-logged linear regression (Figure 1; $p<0.0001$, $R^2=0.38$). These differences in cones/area for the stands resulted in a wide range of recruitment densities. Average recruits per cone ranged from 0.26 at the Mendocino site to 1.39 at the Whiskeytown stand (Table 1).
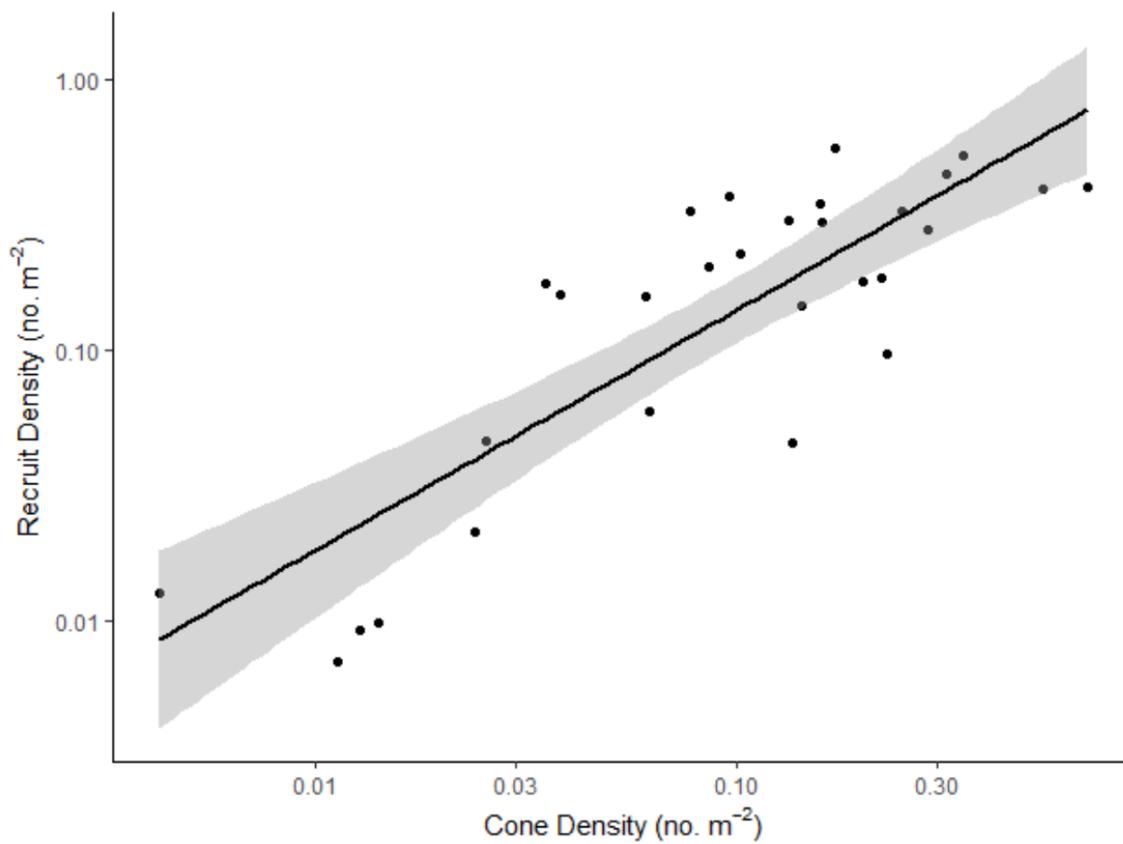
Figure 1 Effect of log cone density on log recruit density (p<0.0001, R^2=0.83) for two knobcone pine sites following fire in northwestern California.

Table 1 Average age, diameter at breast height (DBH), cone density per tree, cone density, recruit density, recruits per cone and tree density calculated from all of our plots at each of our study sites. Standard error is provided in parentheses for all categories except age, and age-specific survivorship. Age-specific survivorship refers to the interval from seed to 2019 for the 2019 cohort.

Site	Age (years)	DBH (cm)	Cone density ($\#/m^2$)	Recruit density ($\#/m^2$)	Pre-fire Tree Density (stems/m^2)	Cones per Tree	Age-specific survivorship	Recruits per cone	Recruits per tree
Whiskeytown	9-79	14.7	0.16	0.17	0.07	8.9	0.08	1.39	15.02
		(2.85)	(0.03)	(0.02)	(0.03)	(2.73)		(0.19)	(4.8)
Mendocino	6	4.0	0.07	0.06	0.24	0.2	0.07	0.26	0.06
		(0.28)	(0.03)	(0.005)	(0.07)	(0.07)		(0.2)	(0.05)

The majority of seedlings established successfully in spaces between the shrubs and seldom (15% of recruits) established under a shrub unless at the edge of the shrub's crown. Of the 893 recruits censused in the permanent plots in 2021, there was only a single 2021 germinant (0.1%), 6.4% were 2020 stems, and 93.5% were from the initial cohort of 2019. On average, 2019 seedlings were 0.64 m tall, 2020 seedlings were 0.27 m tall, and the single 2021 germinant was 0.11 m tall. We estimated the average height of the shrubs in summer 2021 as 0.7 m tall. Shrub cover increased nearly two-fold between 2019 and 2021, from 28% to 51% canopy cover.

Given the number of recruits and our estimate of initial viable seed supply, we found age-specific juvenile survivorship to be 0.07 or 0.08 for Mendocino and Whiskeytown sites, respectively (Table 2). Between 2019 and 2021, the number of recruits of the first cohort at the five permanent plots in Whiskeytown decreased by an average 20.8%. Age-specific survivorship for this initial cohort was an order of magnitude higher (0.8) from mid-summer 2019 to mid-summer 2021 in the permanent plots at Whiskeytown. The cumulative survivorship from abscised seed to third summer recruit then was 0.064 for Whiskeytown (Mendocino was never recensused).

Table 2 Estimated thresholds for reproductive maturity based on a regression of cones or recruits on tree age or size for Whiskeytown and Mendocino data. Reproduction is expressed as a mean of one cone per tree (stand maturity), or one recruit per tree (stand replacement). Recruits/cone includes 2019-21 mortality within the 2019 cohort.

Tree age/size	Stand Maturity	Replacement
Age (years)	8.2	8.2
Size (cm)	4.7	4.6
Probability of a re-burn at a given age	0.096	0.097

Adjusting for 3rd year survivorship (i.e., applying the observed cumulative survivorship over three years to all the plots that had not been recensused since 2019), 69% of our Whiskeytown plots had recruitment greater than required for self-replacement with stand-wide densities as high as 93 recruits per tree. Averaging across stands, there were about 15 recruits per tree at Whiskeytown but only 0.06 recruits per tree at the very young Mendocino site (Table 1).

Reproductive Maturity

Using non-logged linear regressions, the number of cones per tree increased with age (Figure 2; $p<0.0001$, $R^2=0.34$), yet diameter had a stronger significant positive correlation with cone density per tree ($p<0.0001$, $R^2=0.73$) than did age. Based on a non-logged regression between cone number and DBH, the size threshold for achieving one

cone per tree was 4.7 cm DBH. Using the regression results between recruit number and DBH, one recruit per tree occurs at 4.6 cm DBH.

Our age distribution at Whiskeytown fell under two distinct classes, below 30 years and above 30 years. Non-logged linear regression of stands with age <30 years with cones per tree had a stronger positive relationship (p=0.002, R^2=0.33) than age >30 years. Similarly, non-logged linear regression of stands with age >30 years was unrelated to the number of recruits per tree (p=0.8, R^2=-0.11). Non-logged linear regression of age (<30 years) with recruits per tree had a stronger relationship (p<0.0001, R^2=0.76) than cones per tree (p=0.95, R^2=-0.11).

The non-logged linear regression of cones per tree and age (for the stands with <30 years) from Whiskeytown and Mendocino yielded an intercept of -2.08 and a slope of 0.38. For a mean of one cone per tree, the age for stand maturity was 8.2 years. An arithmetic regression of recruit density per tree (adjusting, as explained in the methods, for the cumulative survivorship ascertained in the permanent plots) and age (<30 years) yielded an intercept of -5.97 and a slope of 0.85. We found that one recruit per tree (our definition of stand replacement) would occur at 8.2 years (Table 1). The two estimated ages were necessarily similar because there was essentially one recruit per cone.

Given an average return time of 81 years (Reilly et al. 2019), the probability of fire occurring prior to the capacity for stand replacement (8.2 years; one recruit per tree) age was 0.097. For the range of return times given by Van de Water and Safford (2011), 30 to 90 years, the probabilities of fire occurring before a stand reaches one recruit per tree were 0.24 to 0.087 (Figure 3).
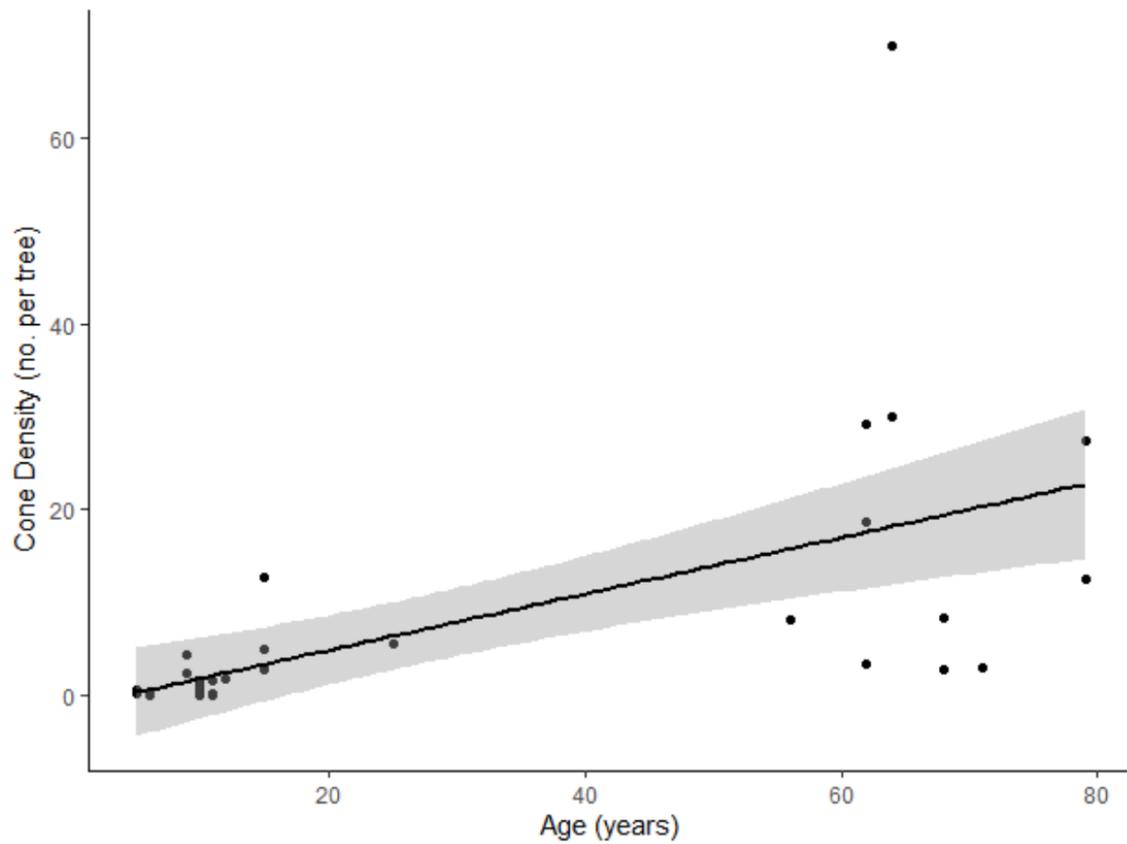
Figure 2 Effect of age on cone density (p<0.0001, R^2=0.34) based on burnt knobcone pine (*Pinus attenuata*) stands in Whiskeytown and Mendocino sites.
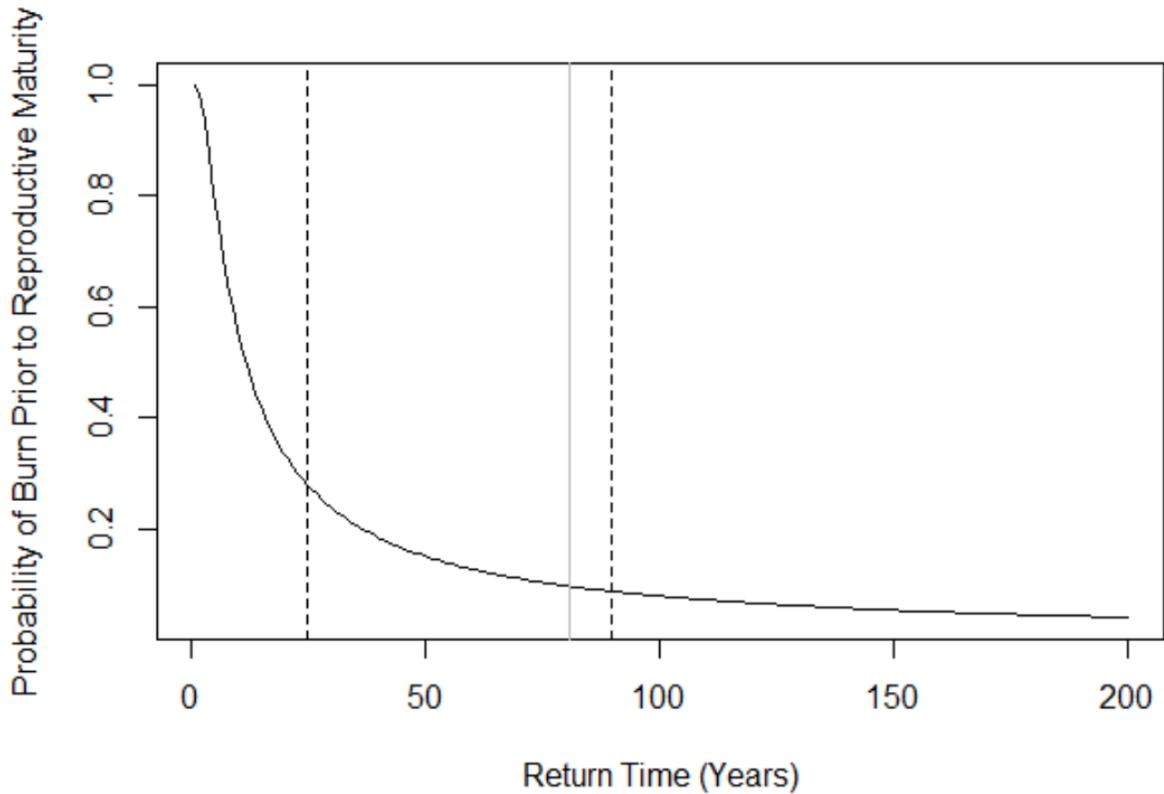
Figure 3. The relationship bewteen return time and the probability of a fire recurring before the age (8 years) for self-replacement has been reached. The probability distribution of the fire interval is experssed as the negative exponential. The modern fire return time estimate of Reilly et al. (2019) is illustrated by the solid gray line. The range of the estimated historical return times from studies of the chapparal-knobcone vegetation type is in dashed black (Van de Water and Safford 2011).

DISCUSSION

On-going and predicted climate and fire regime changes throughout many fire-prone ecosystems have raised concerns about the increased risk of extirpation for tree populations following short-interval fires. Here we demonstrated that while the extirpation of knobcone pine populations in northern California is possible, the risk is likely quite low based on our observations of recently burned young stands and current fire regime patterns. Additionally, we provided a framework for quantifying a meaningful measure relating immaturity risk at both the tree and stand scale that can be used to evaluate and characterize risk in other serotinous species.

The density of the post-fire regeneration of young knobcone pine stands in northern California was relatively low compared to other serotinous species. Average knobcone pine recruit density varied from 0.01 per m^2 (Mendocino, a very young site and dependent solely upon partially matured current cones) to 0.17 per m^2 (a site at Whiskeytown; Table 1). Keeley et al. (1999) reported much higher densities of 1 to 2 seedlings per m^2 for a very dense eight-year-old knobcone pine population that burned in southern California. Our reported recruitment densities were also somewhat lower than other serotinous species after intense fire (e.g., Greene and Johnson 1999, de Groot et al. 2004, Turner et al. 2007). For example, Greene and Johnson (1999), collating data from several studies, found an average post-fire density of 1.7 (*Picea mariana*) or 3.9 stems per m^2 (*Pinus banskiana*). As another example, in the Rocky Mountains, post-fire seedling densities of lodgepole pine (*Pinus contorta* var. *latifolia*) varied between 1.5 and 6.7 seedlings per m^2 (Horton 1955). Our

estimates of post-fire recruitment densities in knobcone pine, while still providing fully-stocked stands in most cases, were on the lower end of the reported range of serotinous species. Thus, while nonetheless providing fully-stocked stands in most cases in the areas we examined, these values for knobcone pine tended to be at the lower end of the reported range for serotinous species. Lower recruitment in our study presumably stemmed from our focus on young stands, many of them at low pre-fire density with one site (Whiskeytown) with a high rate of xeriscence (heat- or drought-induced premature cone opening).

We found a higher slope for closed cone accumulation in younger trees than for older trees. We ascribe this to the effect of xeriscence; a large fraction of the cones at Whiskeytown were open at the time of the fire, reduced almost completely to ash when burned, and therefore not counted in the field. Any seeds abscising from them in the months before the fire would have been killed by smoldering in the duff. In summary, the premature emptying of cones was the main reason that our reported recruit densities, while adequate for self-replacement, are lower than found with other serotinous species.

The lower densities of knobcone pine regeneration we observed cannot be due to unexpectedly low survivorship at Whiskeytown as they had juvenile survivorship values within 60% of the predicted value based empirically on many other species germinating on mineral soil with 100% light receipt (Greene and Johnson 1998). Keeley et al. (1999) did not provide an estimate of viable seeds/cone at their burned 8-year old knobcone pine site, but if we substitute our viability values then they found a knobcone survivorship of 0.028, similar to the Mendocino site in our study (if we calculate Mendocino survivorship using

values within their standard errors, we can yield the same value), but somewhat lower than the Whiskeytown juvenile survivorship. We found few filled seeds per cone in green cones (current) and it may be because many of the green cones were from the Mendocino site and were picked in mid-August; perhaps seed maturation was not yet complete for the entire complement of developing seeds. As we saw, the very young Mendocino site, which was almost entirely green cones at the time of the fire, had the lowest number of recruits per cone.

Our results showed that size was a better predictor for cone production than age. Burczyk et al. (1996) found a similarly strong correlation between size and cone production in knobcone pine, though tree height was the proxy for size rather than DBH. Likewise, basal area was highlighted by studies in other coniferous species as a good predictor of cone number (Turner et al. 2007; Andrus et al. 2020). At Whiskeytown and Mendocino, there appeared to be no salient differences in productivity or site conditions. Size or cone production in young individuals were similar at each of the sites, and the estimated age-specific survivorship values were almost identical.

Knobcone pine cones emptied quickly 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, four months after the fire. Thus, the size of the second 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 2021 cohort constituted only 0.1% of all recruits. Rapid post-fire seed abscission is perhaps a consistent feature of serotinous pines although there are very few studies that

have examined this (but see Greene et al. 2013). We presume there will be no fourth cohort at our sites.

Cover of the asexually recruiting shrubs doubled between 2019 and 2021. It is likely that much of the 26% loss of the 2019 cohort from 2019 to 2021 was due to this increase in shrub cover. Further, we suppose the competition for water and light led to poorer growth; recruits among marginal branches of shrubs (about 15% of all recruits as of 2021) were only half the height of conspecifics in the areas between shrubs. The seedlings well away from shrubs were about 60 cm in height, almost as tall as most of these competing shrubs, and thus very unlikely to be shaded out by the still-expanding shrub stems given their present growth rates compared to the rate of shrub crown expansion. Based on our 2021 census of each age class, these recruits outside the shrub crowns nearly doubled their height each summer. Rarely, there were recruits extending above the crown of a shrub; but we presume most germinants died under these crowns from the paucity of light. Thus, without further shade-induced mortality, we expect that seedlings with full sun exposure should persist until the onset of the self-thinning stage. Regarding abiotic factors, as reported by Charron and Greene (2002) for much more humid conditions of the western boreal forest in Canada, the root systems of seedlings in full sun in their second year were usually sufficiently deep that there was little additional mortality due to soil moisture constraints or frost heaving events after their second summer of growth. In short, we assume a few decades from now the Whiskeytown area will consist of well-stocked stands almost everywhere that this species had burned.

The risk of a fire before a knobcone pine population can replace itself was low. Our estimate for the age before replacement can occur was ~8 years. Keeley et al. (1999) reported that on average the recruits in their 8 years old stand were about twice as dense as the parents in the burned stands, with cones initiated at ages as young as 3 years old. This threshold of about 8 years for self-replacement was similar to the few other serotinous species for which there are reports. 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 and 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), seed viability, and the return time for fire. Our estimate of 8 years for the self-replacement threshold, when coupled with the current return time of 81 years for severe fires in *knobcone-dominated sites only* estimated by Reilly et al. (2019), meant there is only a 10% chance of a fire reducing the density of a knobcone pine stand rather than increasing it. When using the minimum historical return time 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, 24%. However, this minimum was extrapolated from the

entire landscape, which includes completely chapparal-dominated sites. Thus, given the expected decrease in the length of a fire rotation due to warming, our optimism about the resilience of this species must be guarded.

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