Post-fire reference densities for giant sequoia seedlings

Nathan L. Stephenson[1,a], Anthony C. Caprio[2], David N. Soderberg[1], Adrian J. Das[1],
Eva L. Lopez[1], and A. Park Williams[3]

[1] U.S. Geological Survey, Western Ecological Research Center, Sequoia-Kings Canyon Field Station, Three Rivers, CA 93271
[2] Division of Resources Management and Science, Sequoia and Kings Canyon National Parks, Three Rivers, CA 93271
[3] Department of Geography, University of California, Los Angeles, Los Angeles, CA 90095

[a] Corresponding author: nstephenson@usgs.gov

Abstract

In some areas burned by recent wildfires, most or all giant sequoias were killed. Sequoia managers wish to know whether post-fire seedling establishment in those areas has been adequate to regenerate the locally extirpated sequoias. To provide a yardstick for interpreting sequoia seedling densities measured after the recent severe wildfires, here we calculate mean seedling densities measured one, two, and five years after several mixed-severity fires of the past. Our analyses are based on 42 sites in eight different sequoia groves in Sequoia and Kings Canyon national parks, California, which burned in 26 different fires spanning a 48-year period. Conservatively (i.e., without correcting probable errors of underestimated densities), mean sequoia seedling density the first summer following fire was 153,278/ha (Bayesian estimated median = 173,742/ha; 95% credible interval [CI] = 63,319/ha to 850,336/ha). Mean seedling densities the second and fifth summers following fire were, respectively, 34,870/ha (Bayesian estimated median = 39,562; 95% CI = 14,181/ha to 181,011/ha), and 8,601/ha (Bayesian estimated median = 9,513/ha; 95% CI = 3,827/ha to 34,057/ha). Case-study comparisons showed that measured post-fire seedling densities across the Board Camp Grove and in the severely burned portions of the Redwood Mountain Grove were significantly lower than our second-year reference seedling densities.

Introduction

Following severe wildfires in giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz) groves in 2020 and 2021 – which killed an estimated 13% to 19% of the world's large sequoias (Shive et al. 2021) – questions have been raised about the adequacy of post-fire sequoia regeneration. For example, some grove areas burned in historically unprecedented crown fires that killed most (or all) mature sequoias and simultaneously burned cones out of the sequoias' crowns, killing most of the local seed source and potentially reducing local regeneration for centuries to come. At the same time, historically exceptional drought and warmth (e.g., Williams et al. 2022) has almost certainly reduced survival of young sequoia seedlings (Harvey et al. 1980). Finally, scientists and managers who have observed and monitored post-fire sequoia regeneration for decades have been surprised by the unusually low densities of seedlings in some of the areas burned by the recent wildfires.

In responding to the recent wildfires, sequoia managers can benefit from a key piece of information: reference seedling densities. Reference densities are the seedling densities expected to be adequate either to maintain sequoia populations that survived the wildfires, or, of more immediate interest to managers, to replace sequoia populations locally extirpated by the fires. That is, reference densities help managers judge the adequacy of post-fire sequoia regeneration, thus helping them make decisions about whether to respond, and if so, how to respond.

An independent demographic analysis has suggested that sequoia regeneration following past prescribed fires was almost certainly adequate to maintain giant sequoia populations (York et al. 2013). Thus, seedling densities measured after past prescribed fires could serve as useful reference densities, at least for the past environmental conditions under which those seedling densities were measured. Two such sources of reference densities already exist, both reporting densities during the years immediately following prescribed fires (Kilgore 1973, York et al. 2013). However, as described in Methods, a significant flaw was recently discovered in the larger of the two data sources (i.e., York et al. 2013). Consequently, York et al.'s (2013) seedling densities for at least the first two years following fire were significantly underestimated.

Here we combine, reanalyze, and interpret the Kilgore (1973) and the corrected York et al. (2013) seedling data sets. We begin with a brief review of the biology of giant sequoia reproduction; this helps provide the context and biological foundation relevant to subsequent interpretations of results. We then calculate new reference densities for the first few years following fire, explicitly addressing uncertainty in the calculated densities. Next, we quantify the mismatch between the climatic conditions that prevailed when the data underlying our new reference densities were collected, and the climatic conditions that prevailed after the recent wildfires. To illustrate potential uses of our new reference seedling densities, we present two case studies, centered on sequoia grove areas that burned severely in the recent wildfires. Finally, we broadly consider interpretation of our reference densities – which are based on mixed-severity (mostly low to moderate severity) fires that burned in the climatically more benign past – to judge the adequacy of sequoia regeneration following exceptionally severe wildfires during historically hotter, drier conditions.

Review: The biology of sequoia reproduction

Unlike other mid-elevation conifers of the Sierra Nevada, giant sequoias have persistent green cones that can retain viable seeds for decades (Buchholz 1938, Fry and White 1938, Metcalf 1948, Hartesveldt et al. 1975). In contrast, once seeds are released from the cones, seed viability can be lost in a matter of months or, in summer, a matter of weeks, mostly due to desiccation (Harvey et al. 1980). Such rapid loss of viability means that giant sequoias have no soil seed bank; instead, they depend on their remarkably persistent canopy seed bank – held in living green cones – for reproduction.

Demographic analysis has shown that in the absence of fire (or other major disturbances that expose large areas of mineral soil), successful sequoia seedling establishment has been orders of magnitude too low to maintain otherwise healthy sequoia populations (York et al. 2013). Reproduction is insufficient despite an abundant seed rain; in the absence of fire, background seed rain in sequoia groves has been estimated to be about one million seeds/ha/yr (Harvey et al. 1980). (The background seed rain results from the ongoing death, from various natural causes, of some of the green cones in sequoias' crowns [Harvey et al. 1980].) Occasionally, sequoia seeds may germinate successfully on the forest litter layer of unburned groves, but the seedlings die of desiccation as the litter layer dries during the summer (Harvey et al. 1980).

In sharp contrast, after fire sequoia seedling establishment typically increases by many orders of magnitude, and, if fires occur periodically, is sufficient to maintain sequoia populations (York et al. 2013). Although fires often induce a greatly enhanced seed rain that contributes to post-fire seedling abundance (Harvey et al. 1980, Stephens et al. 1999), other factors may be even more important. Specifically, abundant, successful sequoia germination and establishment appears to depend heavily on seeds becoming at least partially buried in exposed mineral soil that has been made soft and friable by extreme heat (Hartesveldt and Harvey 1967, Hartesveldt et al. 1975, Harvey et al. 1980). But this critical fire-induced soil friability is lost as rain and snow compact the soils over the first few years following fire, thus leaving newly fallen seeds exposed on the surface and vulnerable to desiccation (Hartesveldt and Harvey 1967, Hartesveldt et al. 1975, Harvey et al. 1980). Thus, the first cohort of new seedlings – those germinating the first spring or early summer following fire – is almost always the largest. A second cohort of new seedlings – usually smaller than the first – often germinates the second spring or early summer (Harvey et al. 1980, Harvey and Shellhammer 1991). Sometimes a very small third cohort can become established. However, given how small the third cohort is, and its near-zero survival by the end of its first summer, the third cohort, even when it does occur, apparently does not meaningfully contribute to sequoia regeneration (Harvey et al. 1980). Giant sequoia reproduction is therefore overwhelmingly dominated by seedlings that become established during the first and second years after fire.

Sequoia seedling densities decline dramatically in the years and decades following germination (Hartesveldt and Harvey 1967, Harvey et al. 1980, Harvey and Shellhammer 1991, Miller 1994, Shellhammer and Shellhammer 2006, York et al. 2013). This decline is a simple consequence of the combined effects of (1) high seedling mortality rates (Hartesveldt and Harvey 1967, Harvey et al. 1980, Harvey and Shellhammer 1991), and (2) the fact that germination and establishment of new seedlings is orders of magnitude too low to keep pace with those high mortality losses (see the preceding paragraph). Thus, even if sequoia seedlings superficially appear to be abundant soon after a fire, high mortality losses in subsequent years, decades, and centuries could mean they are insufficient to replace, for example, a single millennial-aged sequoia. This emphasizes the importance of establishing quantitative seedling reference densities – those that might best be expected to maintain a sequoia population into the future, or to replace a locally extirpated population.

Finally, local fire severity plays a strong role in sequoia seedling growth and survival. Both ancient (preceding Euroamerican settlement) and modern managed fires typically burned through sequoia groves as mixed-severity fires. Specifically, past fires were characterized by a large matrix that burned at low or moderate severity (i.e., the forest canopy remained largely intact) interspersed with small forest gaps created by local high-severity fire; those gaps typically ranged in size from hundredths of a hectare up to a few hectares (Stephenson et al. 1991, Stephenson 1994, Stephenson 1996). Compared to intact forest or small gaps (gaps less than ~0.1 ha), average seedling growth rates are higher in larger gaps (those between ~0.1 ha and several hectares) (Stephenson 1994, Demetry 1995, Meyer and Safford 2011). Seedlings with higher growth rates, in turn, have higher survival rates (Harvey et al. 1980, Harvey and Shellhammer 1991). Thus, in the past, most sequoia seedling establishment that went on to successfully produce mature sequoias occurred in forest gaps ranging from 0.1 ha to several hectares in size. Importantly, in the past many (if not most) large sequoias inside the larger gaps usually survived the fires that created the gaps, even if the co-occurring pines, firs, and incense cedars did not (Stephenson 1996).

However, given their recency, we do not yet have robust data sets on seedling growth and, most importantly, survival in the new very large gaps (e.g., >10 ha, and even >100 ha) that were created in sequoia groves by recent wildfires, and in which (unlike the past) most or all mature sequoias were killed. In the Discussion, we address whether enhanced seedling growth and survival might also be expected in these extraordinarily large gaps, and potential implications for the use of our new reference densities.

Methods

Seedling densities

We limited our data sources for giant sequoia seedling densities to those with the following six characteristics. (1) Seedling densities were reported for at least one of the first five years following fire (i.e., during the period that is most relevant to establishing reference densities for management decision-making). (2) The fires that induced seedling establishment were the first to occur after a long period of fire exclusion (usually more than a century – similar to most of the areas that burned at high severity in recent wildfires). (3) The samples were in old forest that had not previously been logged. (4) The fires spread freely through continuous (or nearly continuous) litter and duff layers and woody surface fuels (e.g., pile burns were excluded). (5) The sample design was spatially unbiased relative to seedling densities. (6) Data were from sites unaffected by the severe 2020 and 2021 wildfires (because our goal was to produce historical reference densities to compare with those wildfires).

Once potential data sources meeting these criteria were identified, we imposed a final collective criterion driven by our desire to calculate uncertainty in seedling densities and to perform other statistical analyses. Specifically, to analyze seedling densities for a given year after fire (i.e., the first, second, third, fourth, or fifth year since fire), for all data sources combined, that year needed to have data from at least 20 separate plots or transects. After imposing this and our other criteria, we were left with two data sources: Kilgore (1973), and National Park Service (NPS) fire effects monitoring data (National Park Service 2003) that were used by York et al. (2013). Although NPS fire effects data were available for sequoia groves in Sequoia, Kings Canyon, and Yosemite national parks, none of the Yosemite data met our criterion of being from areas experiencing their first fire after prolonged fire exclusion.

Kilgore (1973) – whose methods are described in Kilgore and Biswell (1971) – reported sequoia seedling densities for the first three years following prescribed fires conducted in 1969 along a ridgetop in Redwood Mountain Grove, Kings Canyon National Park. For each of three ~380-m-long transects, Kilgore counted sequoia seedlings in fifty ~1.486 m^2 (4 ft x 4 ft) quadrats distributed every ~7.6 m (25 ft) along the transect, for a total seedling count area of 74.3 m^2 per transect. During the first year post-fire (1970), sampling was conducted in “mid-summer” (Kilgore and Biswell 1971), but the seasonal timing of later samples was not reported.

Methods for the NPS fire effects monitoring plots are described in detail elsewhere (Ewell and Nichols 1985, National Park Service 1992, 2003); here we summarize the aspects most relevant to this study. The 0.1-ha (50 m x 20 m; not slope-corrected) monitoring plots were established and permanently marked before planned prescribed fires (except for two plots in our final data set that were established after a wildfire), with locations determined by restricted random sampling (an approach related to stratified random sampling). Most seedling counts in the six oldest plots (established 1982-1984) occurred in four 100 m^2 (10 m x 10 m) subplots in the corners of the larger 0.1-ha plots. In contrast, in the large majority of plots, seedling counts occurred within a single predefined 250 m^2 (25 m x 10 m) quarter of the 0.1-ha plots (the “Q1” quarter). If seedling densities (of both sequoias and other tree species) were judged to be too high to efficiently conduct full counts across the entire 250 m^2 subplot, the subplot was further subsampled with smaller quadrats of variable sizes – the smallest being 1 m^2 – that were systematically placed in standardized locations, usually in each corner of the 250 m^2 seedling subplot. Counts within quadrats were then scaled up, usually in the field, and recorded as the estimated count within the entire 250 m^2 seedling subplot. Seasonal timing of seedling counts varied from May through November (most often in July), depending on field crew schedules and priorities.

For the National Park Service (2003) fire effects data, we corrected the database error that had been a dominant contributor to the underestimated post-fire sequoia seedling densities that were reported in Figure 2 of York et al. (2013). Specifically, the standardized database used in York et al. (2013) was based on data imported from the original 1990s FMH FoxPro database (National Park Service 1992, Sydoriak 1992, 2001), which capped the number of seedlings that could be reported in a 250 m^2 subplot at 9,999. We corrected this database shortcoming, and then referred to the original paper datasheets to enter the correct seedling counts for plots where the count was greater than 9,999. Data from four sample dates in three plots were found with capped values that we then corrected.

We also discovered some National Park Service (2003) fire effects data in which first-year sequoia seedlings were apparently misidentified as white fir (*Abies concolor*) seedlings. Before sequoia seedlings develop their distinctive awl-shaped leaves late in their first summer, their cotyledon leaves and young secondary leaves are linear, and thus superficially resemble those of white fir (although several other traits easily distinguish the species at this stage; e.g., see Hartesveldt et al. 1975). Four lines of evidence led us to identify five plots in which first-year seedlings were likely misidentified. First, for those five plots, first-year sequoia seedling densities were recorded as zero, even though subsequent density records – which, biologically, are expected to be lower than (or equal to) first-year densities (see the section on the biology of sequoia reproduction, above) – were positive numbers up to 162,520/ha. Second, the reverse was true for white fir seedling densities; that is, high-density fir seedlings were recorded the first year but plummeted to 0 (or very low densities) the second year. Third, crew members who were recording second-year seedling densities in these plots explicitly commented on some of their data sheets that the first-year seedlings may have been sequoias that had been misidentified as white firs. Finally, the questionable data were temporally clustered in 1992 and 1993, suggesting that one or more crew members working during this narrow period may have been responsible for the apparent misidentifications.

Despite our confidence that, in these five plots, the reported first-year sequoia seedling densities of zero resulted from seedling identification errors, we conservatively chose to retain the zero values in one set of analyses (thus erring on the side of underestimating first-year sequoia seedling densities). In separate analyses, we converted first-year white fir seedling densities to first-year sequoia seedling densities in the five plots.

In addition to calculating simple mean seedling densities, we used a Bayesian negative binomial count model (described in Appendix 1) to calculate estimates of seedling density (see Soderberg et al. *in review*). This is conceptually equivalent to a simple average, although using a negative binomial distribution to determine the density is more appropriate for count data and our Bayesian methodology also allowed us to directly describe the uncertainty in our estimate as a probability distribution, where the quantifiable uncertainty can be used to calculate the probability of the true mean being above or below specified values.

We then assessed differences in post-fire seedling densities between years one and two, and between years two and five (the only years with sufficient data for analyses; see Results). Finally, we assessed the difference between year two seedling densities and those of the entire post-fire Board Camp Grove, and those parts of Redwood Mountain Grove that burned at high severity (see *Case studies*, below). We calculated marginal probabilities that our comparison estimates were the same, and the median effect size as the ratios of medians between compared estimates. Details can be found in Soderberg et al. (*in review*).

Climate

For a 236,600-ha quadrilateral – ranging from 210 m to 3820 m elevation (mean ~1700 m) – encompassing all sequoia groves within Sequoia and Kings Canyon national parks, we broadly followed the methods of Williams et al. (2022) to calculate: (1) average summer temperature (June through August), (2) water-year precipitation (1 October through 30 September), and (3) summer (June through August) re-standardized, self-calibrated Palmer Drought Severity Index (PDSI). We focused on summer temperature and PDSI because the Sierra Nevada's characteristic hot, dry summers (North et al. 2016) can be a dominant limiting factor for giant sequoia seedling establishment and survival (Harvey et al. 1980). Values were calculated for 1902-2022, using precipitation data from the NOAA ClimGrid dataset (Vose et al. 2014) and temperature data from TopoWx (Oyler et al. 2015), which corrects for known biases in high-elevation temperature records. For years that lacked TopoWx temperature data (i.e., preceding 1948 and after 2016) we used NOAA ClimGrid temperature calibrated to match the TopoWx monthly climatological means and variances. Potential evapotranspiration was calculated using the Penman-Monteith approach, with vapor pressure estimated from monthly mean dew points from the PRISM dataset (Daly et al. 2008) and wind speed and solar radiation inputs compiled from the following sources. For September 1950–August 2021, we used the new UCLA dynamically downscaled version of the ERA-5 reanalysis for the western United States developed by Rahimi et al. (2022). For months before and after the period of coverage of the UCLA product, we calibrated the Princeton Climate Forcing dataset (Sheffield et al. 2006) and the GridMet dataset (Abatzoglou et al. 2013), respectively, to match climatological monthly means and variances of the UCLA product. As in Williams et al. (2015), our summer PDSI metric was standardized to have a standard deviation of two during a 1921–2000 baseline period.

For the 33 plots with records of seedling densities during the first summer after fire – when seedlings are both most abundant (Table 1) and most vulnerable to drought (Harvey et al. 1980) – we calculated average climatic conditions for the first year following fire.

Case studies

Our first case study centered on Board Camp Grove (Sequoia National Park), 92% of which burned at high severity in the Castle wildfire in early October of 2020. On 27-28 April 2022, about one year after initial post-fire seedling germination in the grove, all living sequoia seedlings were counted in each of 20 circular 0.1-ha plots (total sample area [not slope-corrected] = 2.0 ha). Plot locations were chosen *a priori* using the Generalized Random Tessellation Stratified algorithm (GRTS), with an equal probability stratified sampling design, which provides a spatially balanced sample that has a true probability design allowing valid inference for the entire study area (Stevens and Olsen, 2004). Further details on the sampling design and data can be found in Soderberg et al. (*in review*).

Conservatively, we chose to compare Board Camp seedling densities with our second-year reference seedling densities. Mean and median data collection dates for our second-year reference densities were in late July (see Results), three months later in the second summer than the April 2022 Board Camp sample dates. That is, relative to the Board Camp data, our reference densities would be reduced by, on average, an additional three months of spring and summer seedling mortality.

Our second case study centered on those portions of the Redwood Mountain Grove (Kings Canyon National Park) that burned at high severity in the KNP Complex wildfire, in early October of 2021. High-severity burn areas were defined as those with estimated >75% basal area loss based on the satellite-derived Rapid Assessment of Vegetation Condition after Wildfire (RAVG) Composite Burn Index (https://burnseverity.cr.usgs.gov/ravg/) (see Soderberg et al. [*in review*]). On 1-7 Sept. 2022, at the end of the first summer of post-fire seedling germination, all living sequoia seedlings were counted in each of 45 circular 0.0405-ha plots, and (in one area of particularly low sequoia seedling densities) a single circular 0.1-ha plot (total Redwood Mountain sample area [not slope-corrected] ≈ 1.92 ha). As with Board Camp Grove, plot locations were chosen *a priori* using the previously described GRTS sampling procedure (Stevens and Olsen, 2004). Further details on the sampling design and data can be found in Meyer et al. (2023) and Soderberg et al. (*in review*).

As with Board Camp Grove, we conservatively chose to compare Redwood Mountain Grove's post-fire seedling densities with our second-year reference densities. The Redwood Mountain data were collected in late summer of the first year of post-fire establishment. Relative to these data, the second-year reference densities were thus reduced by, on average, more than an additional ten months of seedling mortality.

For both Board Camp and Redwood Mountain groves, we calculated the marginal probabilities that their post-fire seedling densities were the same as our second-year reference densities.

Results

Seedling densities

Standard NPS fire effects monitoring protocols only called for seedling censuses during the first, second, and fifth years post-fire. Consequently, sample sizes for the third and fourth years post-fire were far too small for analysis (i.e., not approaching our 20-plot threshold); we thus analyzed data only from the first, second, and fifth years post-fire.

The combined Kilgore (1973) and NPS fire effects data that met our basic criteria comprised 42 plots (or transects) in eight different sequoia groves, which burned in 26 different fires (Appendix 2). The fires burned in 16 separate years spanning a 48-year period from 1969 to 2016. Mean and median fire years were both 1990. Seedling census dates ranged from 28 May to 9 November, with mean census dates of 1 August, 30 July, and 5 August for the first, second, and fifth years post-fire, respectively (with corresponding median census dates of 13 July, 24 July, and 28 July, respectively). Mean seedling census areas were 169 m^2, 175 m^2, and 195 m^2 for the first, second, and fifth years post-fire, respectively; median plot census area was 250 m^2 for all three years.

For our conservative first-year data (i.e., not correcting the five plots for which first-year sequoia seedlings were likely misidentified as white fir seedlings) (n = 33 plots), simple mean sequoia seedling density was 153,278/ha. The Bayesian median was 173,742/ha, with a 95% credible interval of 63,319/ha to 850,336/ha (Table 1, Appendix 3). When we corrected the five plots that had probable seedling misidentification errors, simple mean sequoia seedling density rose to 172,599/ha; the corresponding Bayesian median was 197,079/ha, with a 95% credible interval of 78,312/ha to 806,076/ha.

Mean seedling densities the second (37 plots) and fifth (36 plots) years after fire were 34,870/ha and 8,601/ha, respectively. Bayesian median densities were 39,562/ha and 9,513/ha, respectively, with 95% credible intervals of 14,181/ha to 181,011/ha for the second year and 3,827/ha to 34,057/ha for the fifth year (Table 1, Appendix 3).

Table 1 further quantifies uncertainty in our reference densities, showing Bayesian probabilities that the actual population-wide seedling densities that our plots and transects sampled meets or exceeds specified thresholds. Appendix 3 shows the probability distributions.

Seedling densities declined through time (Table 1). The marginal probability that post-fire seedling densities were the same for years one and two was 5.1% (uncorrected for apparent species misidentifications; median effect size = 4.39) or 3.6% (corrected for the apparent species misidentifications; median effect size = 4.98). The marginal probability that seedling densities were the same for years two and five was 4.2% (median effect size = 4.16).

Table 1. Simple mean seedling reference densities, Bayesian median reference densities, and associated uncertainties, by year post-fire.

Year post-fire	Simple mean density (seedlings/ha)	Bayesian median density (seedlings/ha)	Bayesian percentage probability (italics) of actual landscape-scale seedling density meeting or exceeding specified thresholds (seedlings/ha) (bold)											
			10k	**20k**	**30k**	**40k**	**50k**	**100k**	**150k**	**200k**	**250k**	**300k**	**400k**	**500k**
1	153,278	173,742	*100*	*100*	*100*	*99.9*	*99.3*	*84.2*	*59.7*	*41.0*	*29.1*	*21.0*	*12.0*	*7.9*
1*	172,599*	197,079*	*100*	*100*	*100*	*99.9*	*99.9*	*91.9*	*70.0*	*48.9*	*33.9*	*23.6*	*12.3*	*7.4*
2	34,870	39,562	*99.7*	*89.3*	*67.7*	*49.3*	*35.7*	*9.2*	*3.8*	*2.1*	*1.1*	*0.7*	*0.4*	*0.3*
5	8,601	9,513	*46.2*	*11.1*	*3.6*	*1.5*	*0.8*	*<0.1*	*0*	*0*	*0*	*0*	*0*	*0*

* With first-year densities corrected for apparent species misidentification in five plots (see the text).

Climate

For the 33 plots with records of seedling densities during their first summer after fire – when seedlings are both most abundant (Table 1) and most vulnerable to drought (Harvey et al. 1980) – mean and median climate was comparable to that of the entire 121-year record (Table 2). In contrast, sequoia seedlings that germinated in 2021 – in response to the 2020 Castle wildfire – were subjected to the hottest and driest summer of the 121-year record (Table 2). Seedlings germinating in 2022 – in response to the KNP Complex wildfire – were subjected to the third hottest summer and second most severe summer drought (by PDSI) on record.

Table 2. Climatic summaries for 1902-2022, for the first years post-fire in our reference density data, and for 2021 and 2022 (the first years after the Castle and KNP Complex wildfires, respectively).

		1902-2022	**Seedling plots, 1st years post-fire**	**2021**	**2022**
JJA* mean temperature (C)	**Mean**	17.9	17.8	20.6 (**1st hottest** in 121 years)	20.0 (**3rd hottest** in 121 years)
	Median	17.9	17.5		
	Range	15.7 to 20.6	16.4 to 19.8		
Water year ** precipitation (mm)	**Mean**	976	1087	311 (**1st lowest** in 121 years)	680 (**22nd lowest** in 121 years)
	Median	899	899		
	Range	311 to 2097	584 to 1967		
JJA* Palmer Drought Severity Index (PDSI) ***	**Mean**	-0.28	-0.52	-6.08 (**1st driest** in 121 years)	-5.40 (**2nd driest** in 121 years)
	Median	-0.54	-1.23		
	Range	-6.08 to 5.71	-3.86 to 5.43		

* JJA = June, July, and August.
** Water year = 1 October through 30 September.
*** Negative values of PDSI indicate drought.

Case studies

Bayesian median post-fire sequoia seedling densities at Board Camp Grove (1,768/ha), measured on 27-28 April 2022, were significantly lower than the Bayesian median second-year reference densities (39,562/ha) (median effect size = 22.4, marginal probability = 0.0%). Likewise, median post-fire densities in the severely burned portions of Redwood Mountain Grove (10,541/ha), measured on 1-7 Sept. 2022, were significantly lower than the median second-year reference densities (median effect size = 3.75, marginal probability = 0.8%). The associated probability distributions are shown in Appendix 3.

Discussion

Seedling densities

The nature of our data gives us confidence that our seedling densities are broadly representative of post-fire sequoia regeneration conditions of the recent past. First, our seedling census locations were unbiased (either determined *a priori* by restricted random sampling, or, in the case of Kilgore [1973], by systematic sampling of long line transects). Second, our samples were widely distributed in both space and time (42 plots and transects; eight different sequoia groves; 26 different fires; and 16 separate fire years spanning a 48-year period). Finally, mean and median climate of the critical first summers following our fires were comparable to that of our entire 121-year climate record (Table 2).

A previous demographic analysis suggested that sequoia regeneration following prescribed fires was almost certainly adequate to maintain otherwise healthy giant sequoia populations into the future (York et al. 2013). Thus, the results we present here can be expected to serve as meaningful reference seedling densities, at least for the past environmental conditions under which those seedling densities were measured, and perhaps also for the recent, severe wildfires (see discussion under *Case studies*, below).

Our data vividly illustrate the well-documented role of fire in giant sequoia reproduction (Harvey et al. 1980). Pre-fire seedling censuses were conducted in 37 of our plots, but the >1 ha of combined pre-fire seedling census area yielded only a single sequoia seedling. In sharp contrast, average sequoia seedling density in the first summer following fire was more than five orders of magnitude greater (Table 1).

As previously reported by others (Hartesveldt and Harvey 1967, Harvey et al. 1980, Harvey and Shellhammer 1991, Miller 1994, Shellhammer and Shellhammer 2006, York et al. 2013), after the initial post-fire burst of sequoia reproduction, seedling densities decline rapidly (Table 1). As described earlier, this is a consequence of the combined effects of high seedling mortality rates that are not matched by subsequent new seedling germination and establishment (i.e., virtually all post-fire reproduction occurs in the first two years post-fire, and most of it in the first year).

Reference densities for the first year post-fire comprise only the first seedling cohort. In contrast, reference densities for the second year comprise both surviving first-cohort seedlings, plus new second-cohort seedlings (those germinating in the second year). We can thus set some rough bounds on the probable average size of the second cohort. At one extreme, if we assume (absurdly) that mortality of the first cohort during its first year of life is 100%, then seedlings in the second year would comprise entirely second-cohort seedlings. Because the mean density of seedlings the second year was 23% that of the first year (based on our conservative data, which likely underestimate the size of the first cohort [see Methods]), our upper bound on the average size of the second cohort must be 23% the size of first cohort. At the opposite extreme, the lower bound for the second cohort would be 0%. Thus, we estimate that the average size of the second cohort may fall somewhere between the extremes of 0% and 23% the size of the first cohort.

Case studies

Our case study comparisons were purposely conservative; that is, our comparisons were biased toward finding that post-fire Board Camp and Redwood Mountain seedling densities were not lower than our (second-year) reference densities. Specifically, Board Camp seedling densities were measured in late April of the second spring following fire, whereas our reference density had mean and median measurement dates in late July of the second summer. If the Board Camp seedling densities had instead been measured in late July (like our second-year reference densities), the Board Camp densities would have been further reduced by an additional three months of spring and summer seedling mortality. The difference was more extreme in our Redwood Mountain comparison. Redwood Mountain seedling densities were measured in early September of the first summer post-fire, but were compared with second-year reference densities with mean and median measurement dates more than ten months later. Furthermore, there can be little expectation of a meaningful second seedling cohort germinating at Redwood Mountain in the spring of 2023 (just as none was found at Board Camp in the spring of 2022). In areas of Redwood Mountain where all sequoias were killed, the dead trees have already released their seeds. Sequoia seeds rapidly lose their viability once released – mainly through desiccation – meaning no seeds carry over as part of a soil seed bank (Harvey et al. 1980). In high-severity areas of Redwood Mountain where some scattered green sequoia crowns might remain, we still expect no significant second cohort of seedlings. Even before the KNP Complex wildfire began, and for reasons that are currently unknown, in the summer of 2021 we observed a widespread and apparently spontaneous opening of giant sequoia cones in the southern Sierra Nevada, so that few mature green cones capable of releasing viable seed remained in their crowns.

In spite of the conservative nature of our comparisons, both the Board Camp and Redwood Mountain groves had seedling densities that were significantly lower than our second-year reference density. We propose that at least two mechanisms contributed to the difference. First, the first-year germinants in Board Camp Grove were subjected to the hottest and driest summer of our 121-year record, while those in Redwood Mountain Grove were subjected to the third hottest and second driest (by PDSI) summer on record (Table 2). Such hot, dry conditions undoubtedly contributed to unusually high seed and seedling death by desiccation (Harvey et al. 1980). Second, in those parts of the Board Camp and Redwood Mountain groves that burned in crown fires, we observed that most cones were burned out of the sequoias' crowns, killing much of the local seed source. These same mechanisms – drought, heat, and loss of local seed source – have been implicated in limiting the regeneration of dominant coniferous species across western North America following severe fires (Shive et al 2018, Coop et al. 2020, Stewart et al. 2021, Stevens-Rumann et al. 2022, Davis et al. 2023).

Do our reference densities – which, of necessity, reflect the effects of past mixed-severity fires during a more climatically benign period – provide a useful yardstick for judging seedling densities observed after historically large and severe wildfires? More specifically, considering the high death rates of sequoia seedlings during their first years and decades after germination (Harvey et al. 1980, Harvey and Shellhammer 1991, Shellhammer and Shellhammer 2006, York et al. 2013), do we have reason to believe that the low seedling densities found in the severely burned portions of Board Camp and Redwood Mountain groves might still be adequate to eventually replace the sequoia populations that were locally extirpated by the wildfires? We address this question by considering expected sequoia seedling survival relative to (1) the size of fire-created forest gaps, (2) the presence or absence of a post-fire leaf litter mulch, and (3) a warming climate.

Relative to small fire-created gaps (<0.1 ha), Demetry (1995) found that sequoia seedlings had greater average size (and thus growth rates) in progressively larger gaps, up to ~1.2 ha in size (the largest gap she sampled). Seedlings with higher growth rates, in turn, have higher survival rates (Harvey et al. 1980, Harvey and Shellhammer 1991). Relative to mixed-severity fires of the past, can we thus expect higher average seedling survival within the very large (e.g., >10 ha, and even >100 ha) gaps created by recent wildfires? Not necessarily. Snow accumulation and retention are usually maximized in forest gaps of intermediate sizes (e.g., up to ~1 to 5 ha) (Golding and Swanson 1978, Troendle and Meiman 1984, Stevens 2017), which in turn maximizes snowmelt moisture available to sequoia seedlings. In contrast, gaps that are larger than ~1 to 5 ha, and particularly the very large gaps created by recent severe wildfires, retain less snow and melt out earlier (Stevens 2017, Gleason et al. 2019, Smoot and Gleason 2021, Hatchett et al. 2023), lengthening and deepening the summer drought experienced by the sequoia seedlings that germinate in those gaps. The earlier snowmelt in these very large gaps will likely be amplified by a warming climate (see below). The more severe summer drought in very large gaps – induced by earlier snowmelt – could be further exacerbated by the reduced relative humidity and increased temperature, solar radiation, and wind speed found in gaps (Ma et al. 2010, Bigelow and North 2012, Wolf et al. 2021). Certainly, within the very large gaps created by recent wildfires there will be many scattered microsites capable of supporting rapid seedling growth and high survival rates, but this does not mean that, at the scale of the entire landscape, seedling densities lower than our reference densities can be assumed to be adequate to regenerate the locally extirpated sequoias.

Sequoia seedling survival is lower when the soil surface lacks a layer of leaf litter (Stark 1968). In the absence of litter, soil temperatures can be up to 10ºC to 15ºC higher, and soil moisture at 10 cm depth as much as 25% to 60% lower – conditions that will typically contribute to increased sequoia seedling deaths related to soil fungi, heat canker, and desiccation (Stark 1968, Harvey et al. 1980). In forest gaps created by crown scorch – that is, where most trees were killed by the convective heat of a surface fire – the dried leaves (needles) of the dead trees quickly begin to fall and create a new litter layer that contributes to seedling survival. These were the typical post-fire conditions in the plots used to derive our reference densities. In contrast, during the recent wildfires some areas of sequoia groves burned in large, historically unprecedented crown fires that consumed most of the forest canopy. In these crown fire areas, reduced post-fire litter accumulation could contribute to reduced seedling survival relative to the post-fire conditions upon which our reference densities were based (cf. Welch et al. 2016).

Finally, temperatures have been rising in the southern Sierra Nevada (Edwards and Redmond 2011, Das and Stephenson 2013) and are expected to continue to rise (Gonzalez 2012). Even in the absence of directional shifts in precipitation, warming has already contributed to earlier snowmelt at the elevations where giant sequoias occur (Andrews 2013, Mote et al. 2018), which in turn lengthens the summer drought experienced by sequoia seedlings. In addition to lengthening the summer drought, rising temperatures increase the atmosphere's evaporative demand for water, thus increase drought severity (Williams et al. 2015, Williams et al. 2022). Young sequoia seedlings today and in the future are thus expected to experience, on average, longer and more severe drought periods – and associated reductions in survival – than those that were censused for our reference densities.

Given the preceding considerations, and until any new, compelling evidence might suggest otherwise, we find no reason to believe that the Board Camp Grove and Redwood Mountain Grove seedling densities, which are significantly lower than our reference densities, can be assumed to be adequate to regenerate the locally extirpated sequoia populations.

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Appendix 1. Statistical details, model equation, and Bayesian prior distributions.

Our models are structured with normal prior distributions and are described as follows:

$$y_i \sim \mathrm{NB}(m,q) \qquad (1)$$

where $y_{i,}$ is the seedling count for the ith observation and m and q are the mean and the shape parameter of the negative binomial distribution, respectively.

The model parameter ($S"Dens" - \text{seedling density}$) was drawn from normal distributions centered around the mean and estimated variance of our data. Specifically:

$$\mu SDens_i \sim \mathrm{Normal}\ (\mu SDens,\ SDens\sigma^2) \qquad (2)$$

The model parameter was given a normal, diffuse prior with a wide distribution:

$$\mu SDens \sim \mathrm{Normal}\ (0{,}1000) \qquad (3)$$

The variance parameter was given a modest, Student-t prior distribution:

$$SDens\sigma^2 \sim \text{Student-t}\ (0{,}3) \qquad (4)$$

We conducted all analyses in R version 4.3.2 (R Core Team 2022) by computing Bayesian parameter estimates via Markov chain Monte Carlo (MCMC) sampling. Statistical package "rstanarm" (Goodrich et al. 2022, Stan Development Team 2023) was used to compute 4 MCMC chains for 2,000 iterations, discarding the first 1,000 iterations as burn-in and sampling each iteration thereafter. All models were checked graphically for convergence and Rhat ($\hat{r}$) values (i.e., the Gelman–Rubin convergence diagnostic [Gelman & Rubin 1992]), a ratio of variation within and between MCMC chains, were less than 1.01, indicating thorough MCMC sampling and convergence of the posterior distributions.

Using Bayesian MCMC estimates, a median estimate and quantified uncertainty were derived for each model parameter. The median estimate (ME) and 95% Bayesian credible intervals were then calculated as the median model parameter, bounded by the range of values indicating the equal-tail 95% credible interval of the true parameter estimate. The marginal probability (MP) is the probability that the mean estimate of a parameter (e.g., slope coefficient for the relationship between a response and predictor variable) is statistically different (greater or less than) than zero. MP was estimated by calculating the total number of parameter MCMC estimates greater (or less) than the test comparison (e.g., '0'), divided by the total number of MCMC estimates.

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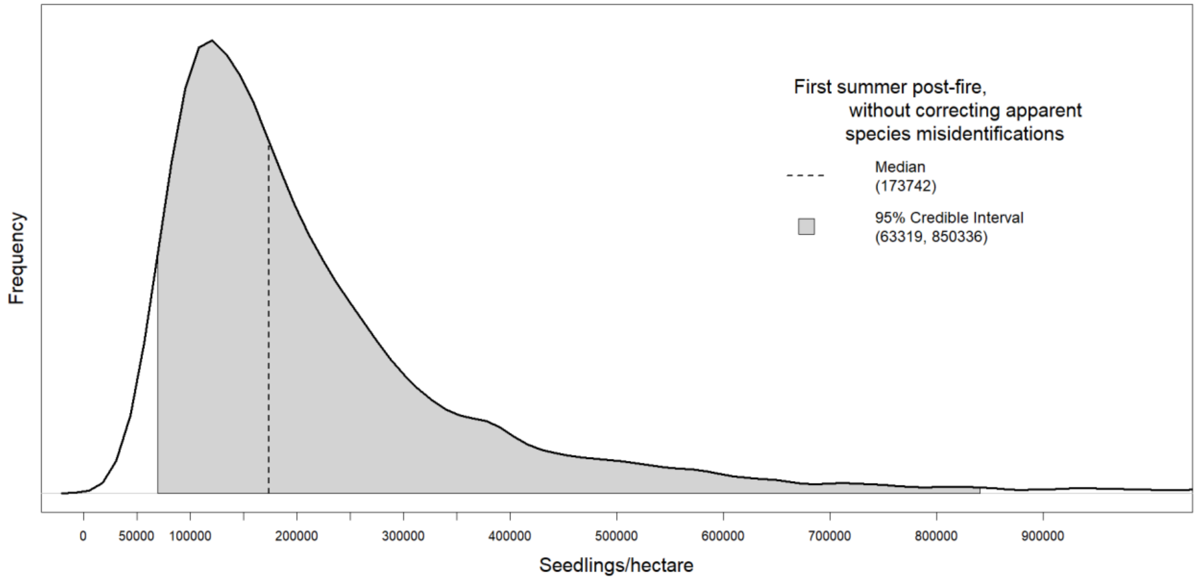
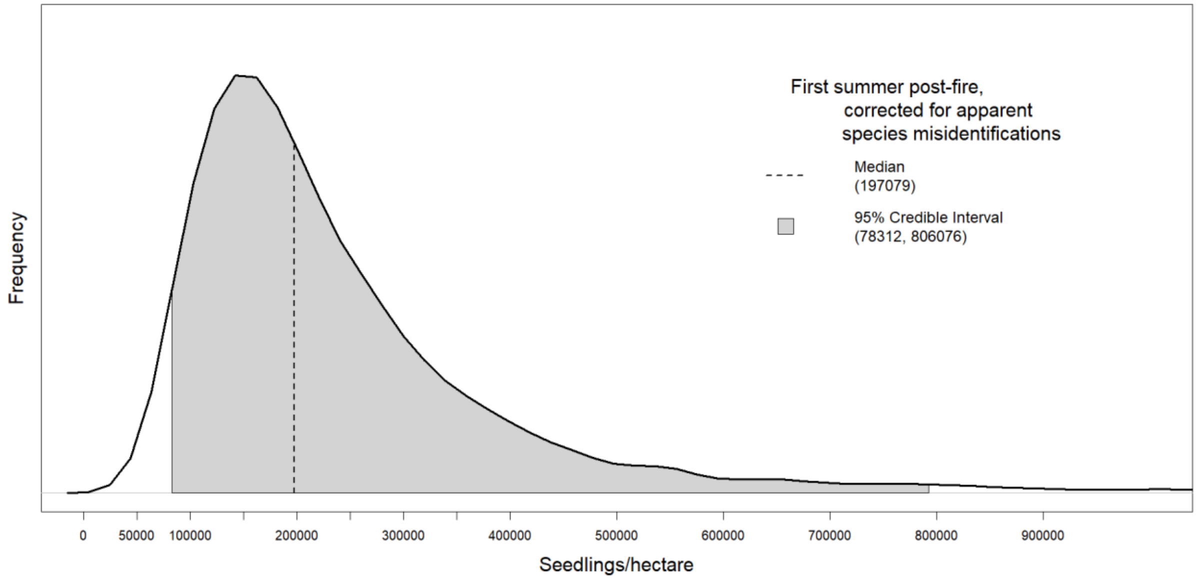
Appendix 2. The seedling census data.

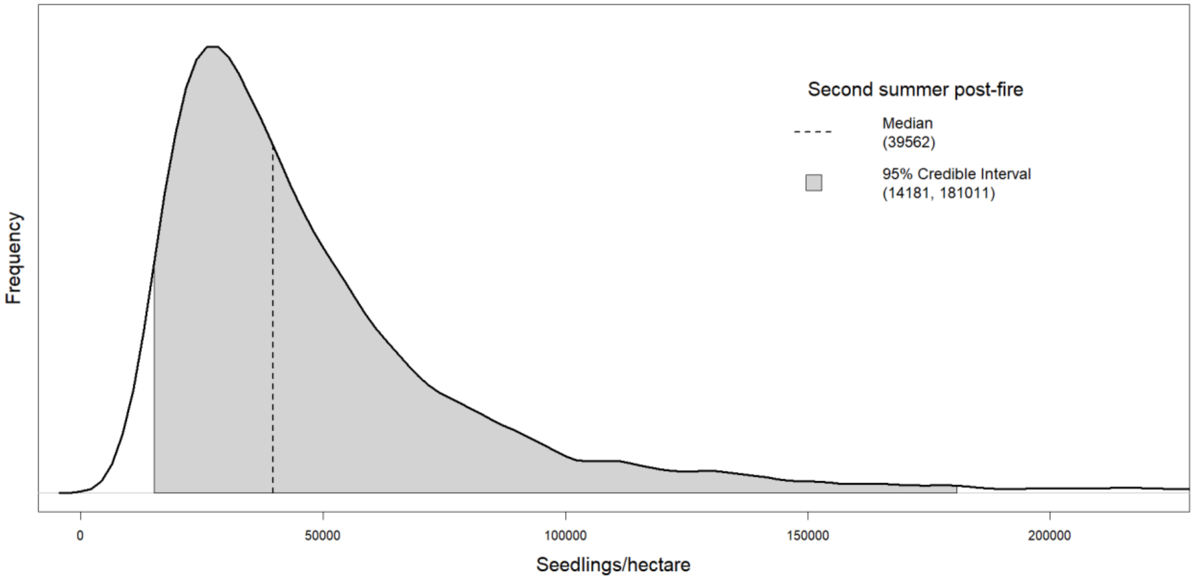
					Pre-fire	Date of seedling census			Seedling census area (m^2)			Number of live seedlings / ha			
Plot Name	Fire Type	Fire name	Fire year	Grove name	seedling count	Year 1	Year 2	Year 5	Year 1	Year 2	Year 5	Year 1 uncorrected	Year 1 corrected	Year 2	Year 5
B:FCADE1T09:063	Prescribed	Grant West #2	1992	Gen. Grant	0	7/29/1993	7/22/1994	8/15/1997	250	250	250 & 4	797520	797520	522500	145760
B:FSEGI1T08:001	Prescribed	Hercules	1982	Giant Forest	0	10/4/1983	8/25/1984	7/13/1987	400	400	250	30450	30450	6300	80
B:FSEGI1T08:002	Prescribed	Hercules	1982	Giant Forest	0	10/21/1983	8/25/1984	7/15/1987	400	400	250	350	350	200	120
B:FSEGI1T08:003	Prescribed	Hercules	1982	Giant Forest	0	10/27/1983	10/27/1984	7/17/1987	400	400	250	16050	16050	11025	4520
B:FSEGI1T08:004	Prescribed	Hercules	1982	Giant Forest	0	10/24/1983	8/25/1984	7/20/1987	400	400	250	6750	6750	3675	120
B:FSEGI1T08:011	Prescribed	Nichols' Folly	1984	Giant Forest	0	9/22/1985			400			5200	5200		
B:FSEGI1T08:012	Prescribed	Nichols' Folly	1984	Giant Forest	0	9/22/1985			400			4475	4475		
B:FSEGI1T08:022	Prescribed	Garfield	1985	Garfield	0			11/9/1990			250				0
B:FSEGI1T08:023	Prescribed	Garfield	1985	Garfield	0	6/24/1986		11/9/1990	4		250	1605000	1605000		320
B:FSEGI1T08:024	Prescribed	Keyhole	1987	Giant Forest	0		7/25/1989	6/16/1992		250	250			0	400
B:FSEGI1T08:030	Prescribed	Muir Grove	1986	Muir	0		8/15/1988	7/15/1991		250	250			0	0
B:FSEGI1T08:032	Prescribed	Camp Creek	1986	Garfield	0		7/6/1988			250				40	
B:FSEGI1T08:042	Prescribed	Keyhole	1987	Giant Forest	0		7/23/1989	6/16/1992		250	250			0	0
B:FSEGI1T08:043	Prescribed	Tharp's 1	1987	Giant Forest	0		8/1/1989	7/16/1992		250	250			0	40
B:FSEGI1T08:050	Wildfire	Pierce	1987	Redwood Mtn.			7/31/1989	7/23/1992		250	4			45680	62520
B:FSEGI1T08:051	Wildfire	Pierce	1987	Redwood Mtn.			7/30/1989	7/22/1992		250	250			0	0
B:FSEGI1T08:052	Prescribed	Huckleberry	1989	Giant Forest	0	7/6/1990	6/19/1991	6/22/1994	250	250	250	1200	1200	0	440
B:FSEGI1T08:068	Prescribed	Tharps 90	1990	Giant Forest	0	7/10/1991	6/8/1992	6/27/1995	250	50	50	0	0	0	0
B:FSEGI1T08:069	Prescribed	Suwanee Rx 1990	1990	Suwanee	0		7/9/1992	7/14/1995		250	250			80	120
B:FSEGI1T08:070	Prescribed	Suwanee Rx 1992	1992	Suwanee	0	7/21/1993	7/27/1994	7/26/1997	50	250	250	400	400	0	0
B:FSEGI1T08:071	Prescribed	Suwanee Rx 1992	1992	Suwanee	0	7/21/1993	7/19/1994	7/25/1997	4	4	50	1172720	1172720	217520	36000
B:FSEGI1T08:072	Prescribed	Grant West #2	1992	Gen. Grant	0	7/15/1993	7/20/1994	8/8/1997	25	4	250	0	77,600	162520	3600
B:FSEGI1T08:073	Prescribed	Grant West #2	1992	Gen. Grant	0	7/15/1993	7/22/1994	8/8/1997	250	250	250	0	1,600	1640	600
B:FSEGI1T08:074	Prescribed	Grant West #1	1990	Gen. Grant	0	7/2/1991	7/12/1992	7/18/1995	250	4	50	0	0	0	800
B:FSEGI1T08:075	Prescribed	Grant West #2	1992	Gen. Grant	0	7/19/1993	8/9/1994	8/7/1997	1	4	250	0	162,400	32520	0
B:FSEGI1T08:079	Prescribed	Highway II	1990	Giant Forest	0	7/3/1991	6/26/1992	9/6/1995	250	250	250	0	0	0	0
B:FSEGI1T08:080	Prescribed	Highway II	1990	Giant Forest	0	7/3/1991	6/26/1992	9/8/1995	250	250	250	0	0	0	40
B:FSEGI1T08:081	Prescribed	President	1991	Giant Forest	0	6/19/1992	7/8/1993	6/17/1996	4	4	4	0	380,000	102520	1160
B:FSEGI1T08:082	Prescribed	Tharps IV	1991	Giant Forest	0	6/24/1992	7/30/1993	8/20/1996	250	4	4	0	16,000	5000	0
B:FSEGI1T08:085	Prescribed	Wallspring	2007	Giant Forest	0	7/8/2008	7/9/2009	7/30/2012	250	250	250	0	0	0	200
B:FSEGI1T08:086	Prescribed	Wallspring	2007	Giant Forest	0	7/8/2008	7/9/2009	8/2/2012	4	4	250	177520	177520	0	4640
B:FSEGI1T08:087	Prescribed	Deer Creek	1991	East Fork	0	5/28/1992	10/5/1993	10/1/1996	4	4	50	335000	335000	0	0
B:FSEGI1T08:088	Prescribed	Deer Creek	1991	East Fork	1	10/20/1992	10/1/1993	10/1/1996	4	4	4	135000	135000	42520	32560
B:FSEGI1T08:093	Prescribed	Mineral 1	1995	Atwell	0	7/2/1996	7/10/1997	9/16/2000	50	50	50	176600	176600	11600	7600
B:FSEGI1T08:095	Prescribed	Mineral 2	1995	Atwell	0	7/10/1996	7/24/1997	8/3/2000	250	250	250	0	0	0	0
B:FSEGI1T08:106	Prescribed	Giant Forest Restoration	1999	Giant Forest	0	9/14/2000	8/30/2001	8/5/2004	250	250	250	0	0	440	480
B:FSEGI1T08:115	Prescribed	Hart	2009	Redwood Mtn.	0	9/3/2010	7/27/2011	8/14/2014	4	4	250	342520	342520	97520	4320
C:FSEGI1T08:005	Prescribed	Goliath	2016	Redwood Mtn.	0	7/11/2017		8/20/2021	24		250	80833	80833		3200
C:FSEGI1T08:008	Prescribed	Whitaker RX	2012	Redwood Mtn.	0	6/11/2013	8/12/2014	7/13/2017	24	250	250	7500	7500	7500	0
Kilgore Burn 1	Prescribed	Kilgore's ridge Rx	1969	Redwood Mtn.		"mid-summer" 1970	1971		74.3	74.3		32560	32560	5382	
Kilgore Burn 2	Prescribed	Kilgore's ridge Rx	1969	Redwood Mtn.		"mid-summer" 1970	1971		74.3	74.3		31350	31350	3230	
Kilgore Burn 3	Prescribed	Kilgore's ridge Rx	1969	Redwood Mtn.		"mid-summer" 1970	1971		74.3	74.3		99161	99161	10764	

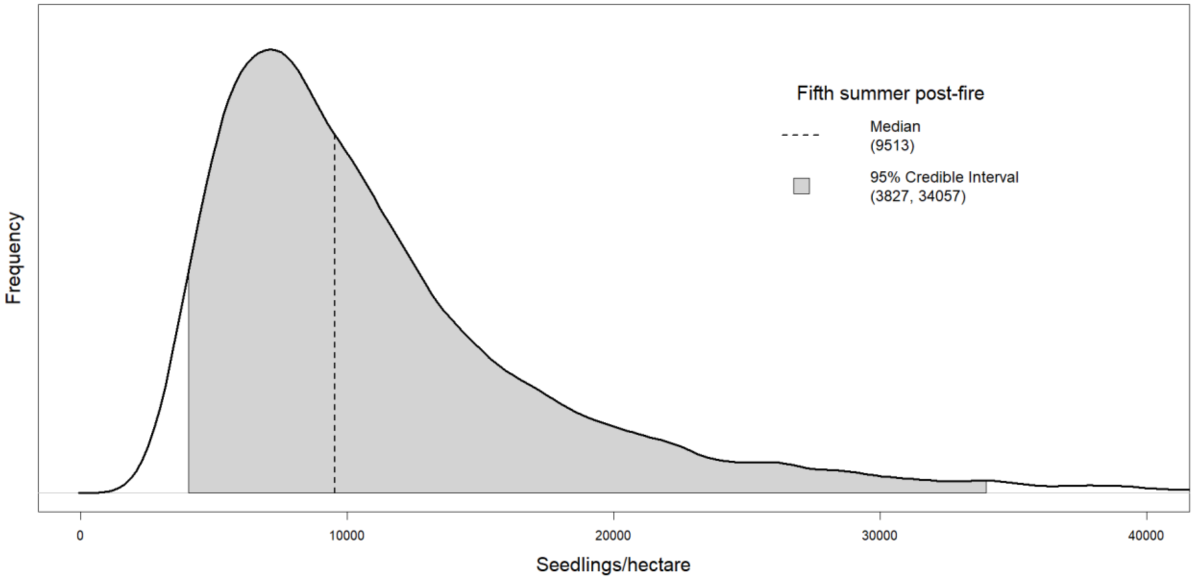
Note: Yellow shading indicates the five instances when Year 1 sequoia seedlings were apparently misidentified as white fir seedlings (see the text), and their corrected values.

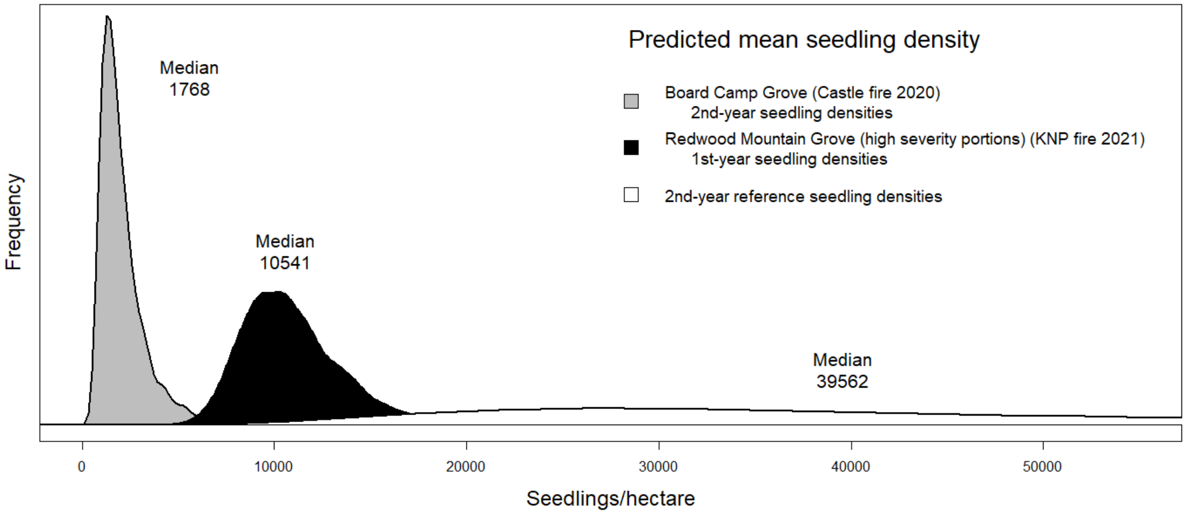
Appendix 3. Bayesian probability distributions for estimated landscape-scale sequoia seedling densities.






Second summer post-fire
Median
(39562)
95% Credible Interval
(14181, 181011)
Frequency
0
50000
100000
150000
200000
Seedlings/hectare


Fifth summer post-fire
Median
(9513)
95% Credible Interval
(3827, 34057)
Frequency
0
10000
20000
30000
40000
Seedlings/hectare


Predicted mean seedling density
Board Camp Grove (Castle fire 2020)
2nd-year seedling densities
Redwood Mountain Grove (high severity portions) (KNP fire 2021)
1st-year seedling densities
2nd-year reference seedling densities
Median
1768
Median
10541
Median
39562
Frequency
0
10000
20000
30000
40000
50000
Seedlings/hectare