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Post-fire reference densities for giant sequoia seedlings in a new era of high-severity wildfires

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ABSTRACT

Many forests globally are experiencing increases in large, high-severity wildfires, often with increasingly inadequate post-fire tree regeneration. To identify areas that might need post-fire planting, forest managers have a growing need for seedling reference densities – the natural seedling densities expected to be adequate to regenerate a forest – to compare with observed post-fire seedling densities. The most useful reference densities will meet five criteria: they will (1) be specific to natural post-fire reproduction rather than planted seedlings (because planted seedlings can have substantially greater survival than natural seedlings, thus underestimating adequate natural reproduction), (2) apply to the first few years following fire (when management decisions and actions are most likely), (3) be specific to each of those post-fire years (because post-fire seedling densities can change rapidly with time since fire), (4) be associated with estimates of uncertainty, and (5) include consideration of novel environmental conditions during management applications (because most reference densities will be based on data collected under more environmentally benign conditions). The world's most massive tree species, the giant sequoia (*Sequoiadendron giganteum*) of California's Sierra Nevada, recently experienced historically unprecedented wildfires that killed an estimated 13–19% of mature sequoias across their native range. Seedlings germinating after these fires then experienced exceptional summer heat and the two most severe summer droughts of the 121-year historical record. To help inform management responses to these events, we used seedling censuses from past fires (mostly prescribed fires) to calculate sequoia seedling reference densities meeting the five criteria. The reference densities had three striking features, which are partly attributable to giant sequoia's status as a pioneer species. First, despite being inherently conservative, the reference densities were quite high. For example, mean first-year reference density was 172,599 seedlings ha^{-1}. Second, reference densities declined precipitously with time since fire: the mean fifth-year reference density was only 5% of the mean first-year density. Third, the reference densities were associated with relatively substantial uncertainty, a consequence of density variations among seedling plots; for example, the 95% credible interval for first-year reference density was 64,377 to 313,438 seedlings ha^{-1}. Despite this uncertainty, a case-study sequoia grove that recently burned in a high-severity wildfire had second-year post-fire seedling densities that were significantly (and dramatically) lower than the corresponding second-year reference density, suggesting inadequate post-fire reproduction. Our results highlight the value of the five criteria for reference densities – criteria that, in current practice, are rarely all met.

1. Introduction

The combined effects of a warming climate and decades of human actions, such as fire exclusion, have predisposed forests in several parts of the world to abnormally large, severe wildfires (Boer et al., 2020, Parks and Abatzoglou, 2020, Duane et al., 2021, Hagmann et al., 2021, Libonati et al., 2022, Kreider et al., 2024). Indeed, increases in both the absolute and relative areas burning at high severity (areas where most or all trees are killed) are well-documented across several regions (e.g., Singleton et al., 2019, Tran et al., 2020, Collins et al., 2021, Parks et al.,

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2023). The increasing size of high-severity fire patches, in turn, has caused an increase in the size of areas that are distant from surviving seed sources, thus contributing – along with ongoing climatic changes – to reduced post-fire forest regeneration, and potential conversion to non-forest vegetation types (North et al., 2019, Stevens-Rumann and Morgan, 2019, Coop et al., 2020, Stewart et al., 2021, Guiterman et al., 2022, Stevens-Rumann et al., 2022, Davis et al., 2023).

As managers across many different forest types increasingly respond to the effects of large, high-severity fires, they often face a basic question (Welch et al., 2016): after any given fire, is natural post-fire tree reproduction sufficient to regenerate the forest? Seedling reference densities provide a benchmark for answering this question. Reference densities reflect the densities of naturally seeded tree seedlings that can reasonably be expected to restore tree populations that were locally extirpated (or nearly extirpated). Currently used guidelines (e.g., see examples in Welch et al., 2016, Tepley et al., 2017, Povak et al., 2020, Meyer et al., 2021) often meet several but not all of five criteria that we propose might be expected to characterize the most useful reference densities specific to natural post-fire reproduction. First, reference densities should be based on densities of natural post-fire reproduction, not planted seedlings. Planted seedlings can have much higher survival rates than natural seedlings (Section 5.5), and thus silvicultural stocking densities based on planted seedlings potentially could greatly underestimate the natural seedling densities needed to regenerate a forest. Second, to the extent possible (see Section 5.6), reference densities should be applicable to the timeframes typical of post-fire management decision-making and actions – usually within the first five years following a fire, and often within the first one, two, or three years. This is often the timeframe in which emergency response funds are available, and before dense post-fire shrub growth can hamper restoration efforts and potentially diminish probability of reforestation success. Third, each of those post-fire years should have its own, year-specific reference density. This is because, for any given tree species and location, post-fire seedling densities naturally change with time since fire (often declining). For example, seedling reference densities reflecting reproduction that is adequate to restore many forests often will be higher one year after a fire than five years after a fire (e.g., Landis et al., 2005, Becker and Lutz, 2023; also see Section 4.1). Fourth, reference densities should be associated with estimates of uncertainty. The spatial distribution of natural post-fire reproduction can be quite patchy (e.g., Welch et al., 2016, Stevens-Rumann and Morgan, 2019, Fertel et al., 2022), leading to high variance among seedling census plots and thus intrinsically high uncertainty in estimated landscape-scale seedling reference densities, suggesting that a probabilistic approach may be most informative. Finally, the interpretation of reference densities should be relative to the novel environmental conditions to which they are being applied. The data that are available to estimate reference densities usually will have been collected during past environmental conditions that were more benign than current conditions. That is, while robust samples of past post-fire reproduction might reasonably be expected to provide useful reference densities for any regions that might still be experiencing similar conditions today, they cannot automatically be assumed to be appropriate to the novel conditions that are an increasing focus of concern (i.e., patches of high-severity fire of historically unprecedented scale, during historically warm – and often dry – climatic conditions). A robust understanding of species' reproductive demography, traits, and ecology will usually be the foundation of such assessments.

Here we calculate seedling reference densities for the world's most massive tree – the narrowly endemic giant sequoia (*Sequoiadendron giganteum*) of California's Sierra Nevada. Like forests in several other parts of the world, forests of the Sierra Nevada have experienced increasing total area burned at high severity and increasing sizes of high-severity patches (e.g., Stevens et al., 2017, Safford et al., 2022, Cova et al., 2023, MacDonald et al., 2023, Williams et al., 2023). In 2020 and 2021 alone, and despite the exceptional fire resistance of giant sequoias, extreme wildfires killed an estimated 13–19% of mature sequoias across their native range (Fig. 1) (Stephenson and Brigham, 2021, Shive et al., 2021, Shive et al., 2022). Some areas of sequoia forest burned in historically unprecedented crown fires that burned cones out of the sequoias' crowns, killing much of the local seed source (Soderberg et al., 2024). At the same time, historically exceptional drought and warmth (Williams et al., 2022; also see Section 4.2) almost certainly reduced survival of young sequoia seedlings (Harvey et al., 1980). Forest managers thus need sequoia seedling reference densities to help them identify which areas might have post-fire reproduction that is ultimately inadequate to restore locally extirpated or reduced sequoia populations.

First, we briefly review the ecology of giant sequoia reproduction, providing an essential foundation for understanding and interpreting the remainder of the paper. We then calculate seedling reference densities that meet all five criteria described above and illustrate their use in a case study. Finally, we consider the strengths and weaknesses of the data and discuss management implications related to our findings.

2. Review: the ecology of sequoia reproduction

Giant sequoia grows naturally only on the western slope of California's Sierra Nevada, occurring in <100 scattered populations ("groves") that collectively occupy $<11{,}000$ ha. Sequoia is a long-lived pioneer species (Stephenson, 1994), typically reproducing profusely from small, abundant, primarily wind-dispersed seeds in small fire-created forest gaps. Sequoias are well adapted to frequent surface fires, having a thick, fire-resistant bark, a height to live crown base that usually exceeds 20 m, fire-dependent reproduction, and an ability to survive substantial crown scorch (Schubert and Beetham, 1962, Hartesveldt et al., 1975, Harvey et al., 1980, Stephens and Finney, 2002, Sillett et al., 2015, York et al., 2021, Shive et al., 2022). However, unlike their relatives the coast redwoods (*Sequoia sempervirens*), which can resprout epicormically after 100% crown loss, giant sequoias that have suffered $>85\%$ to $>95\%$ foliage loss to scorch or combustion will usually die (e.g., Stephens and Finney, 2002, Shive et al., 2022). All post-fire sequoia regeneration is thus from seed.

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). However, once seeds are released from the cones and lie exposed on the soil surface, their viability can be lost in a matter of months or, especially in the Sierra Nevada's characteristic hot, dry summers, in a matter of weeks, mostly due to desiccation (Hartesveldt and Harvey, 1967, Harvey et al., 1980). Such rapid loss of viability means that 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 grove areas where fire has been excluded for a century or more, successful sequoia seedling establishment has been orders of magnitude too low for the long-term maintenance of otherwise healthy sequoia populations (York et al., 2013). Reproduction in such areas is insufficient despite a background seed rain estimated to be about one million seeds ha^{-1} year^{-1} (Harvey et al., 1980). The background seed rain results from (1) the ongoing death, from various natural causes, of some of the green cones in sequoias' crowns each year, causing the cones to open and release their seeds (Harvey et al., 1980), and apparently also (2) late summer or autumn diminished water content in living, green cones, causing shrinkage of some cone scales and consequent release of some seeds from between the scales (Buchholz, 1938, Fry and White, 1938). Occasionally, sequoia seeds may germinate on the forest litter layer of unburned groves, but the seedlings die of desiccation as the litter and duff layers dry during the summer (Harvey et al., 1980).

In sharp contrast, broad-scale sequoia seedling establishment after fire typically increases by many orders of magnitude and, if fires occur periodically, is sufficient to maintain sequoia populations (York et al.,

Fig. 1. A severely burned portion of the Board Camp Grove of giant sequoias, about one month after the 2020 Castle wildfire. The largest trees in the photo – some with trunks exceeding 4 m diameter at breast height – are giant sequoias. Smaller trees are a mixture dominated by white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), incense-cedar (*Calocedrus decurrens*), and smaller giant sequoias. (Photo by A. C. Caprio.).

2013). This is because (1) the heat pulse from surface fires can cause sequoia cones to open, inducing a greatly enhanced seed rain that contributes strongly to post-fire seedling abundance (Harvey et al., 1980, Stephens et al., 1999), (2) fire exposes the bare mineral soil conducive to germination and establishment (Hartesveldt and Harvey, 1967, Hartesveldt et al., 1975, Harvey et al., 1980), and (3) all else being equal, seedling growth (hence survival; Harvey et al., 1980, Harvey and Shellhammer, 1991) is highest on burned compared to unburned mineral soil (York et al., 2009, York et al., 2013), although this generalization may depend on the magnitude and duration of soil heating (Donaghey, 1969).

Importantly, the most abundant, successful post-fire germination and establishment depends on seeds becoming at least partly buried in exposed mineral soil, particularly soil that has been made soft and friable by extreme heat, such as where logs or stumps have burned (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, 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 – probably averaging <20% the size of the first cohort (Section 5.2) – often germinates the second spring or early summer (Harvey et al., 1980, Harvey and Shellhammer, 1991). Sometimes a very small third-year cohort germinates. However, given the small size of the third cohort, and its near-zero survival by the end of its first summer, even when it occurs the third cohort 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 – a shorter period of post-fire seedling establishment than is typical for many other coniferous species, which may become established over several years and sometimes even decades (e.g., Tepley et al., 2014, Harvey et al., 2016, Tepley et al., 2017, Hankin et al., 2019, Becker and Lutz, 2023).

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 et al., 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, after the first one or two years post-fire, germination and establishment of new seedlings is orders of magnitude too low to keep pace with those high mortality losses (see the preceding paragraph). The especially high rates of seedling mortality in the first few years, in turn, is likely a consequence of the small size of recently germinated sequoia seedlings (Fig. 2A), which ultimately is a consequence of the small size of sequoia seeds (sequoia seeds average ~0.005 g, which is only ~2–17% the mass of seeds of co-occurring coniferous species [Burns and Honkala, 1990]). That is, sequoias fit the broader global pattern of smaller seeds being associated with higher seedling mortality rates (Moles and Westoby, 2004, Moles and Westoby, 2006). Small, young sequoia seedlings are especially vulnerable to desiccation, heat, insect predation, and being buried by twigs and leaf litter (Fig. 2B) (Harvey et al., 1980, Miller et al., 1994). Thus, even if sequoia seedlings superficially appear to be abundant soon after a fire, the cumulative effects of high losses to mortality over time could mean they are insufficient to replace millennial-aged sequoias killed in the fire.

At intermediate spatial scales (i.e., within a given fire in a sequoia grove), local surface fire severity plays a dominant role in sequoia seedling germination, establishment, and survival. Importantly, both ancient fires (preceding Euroamerican settlement) and modern managed fires typically burned through sequoia groves as mixed-severity fires. Specifically, both kinds of 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, with a modal gap size perhaps on the order of 0.1 ha (Stephenson et al., 1991, Stephenson, 1994, Stephenson, 1996, Stephenson, 1999, Hurstak, 2001).

At one extreme, those areas that burned at low severity usually experienced low germination, establishment, and survival (Kilgore and Biswell, 1971, Harvey et al., 1980, Stephenson, 1994, Mutch, 1994, Mutch and Swetnam, 1995, Meyer and Safford, 2011). First, without the

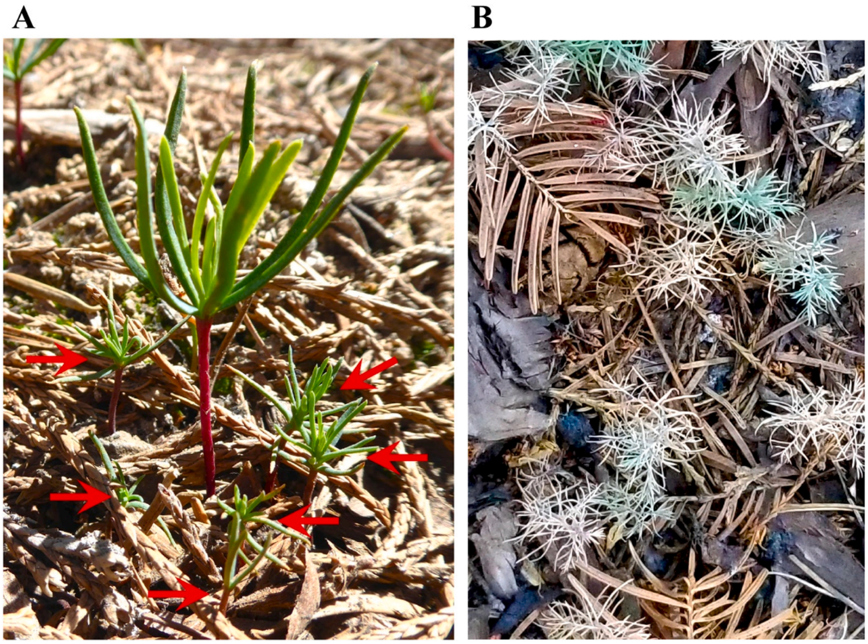

Fig. 2. Young sequoia seedlings are small and vulnerable. **(A)** Several recently germinated, naturally seeded sequoia seedlings (indicated by red arrows) near a much larger but also recently germinated white fir seedling. **(B)** Dead and dying sequoia seedlings – probably dying from desiccation – late in their first summer. Photos: (A) N. L. Stephenson, (B) A. C. Caprio.

cone-opening canopy heat pulse associated with higher-severity fire, far fewer seeds are released in areas of low-severity fire (Harvey et al., 1980, Stephens et al., 1999). Indeed, the critical role of post-fire seed release has been demonstrated in mechanically created canopy gaps in which pile burns prepared a burned mineral soil seedbed. Without an abundant post-fire seed release triggered by scorch to nearby sequoia crowns, few or no seedlings became established (Stephens et al., 1999, York et al., 2011). Second, low-severity fire is often associated with incomplete log combustion, meaning less soil area experiences the extreme heat that yields the friable soils that yield the highest rates of germination, establishment, and growth. Third, Hartesveldt and Harvey (1967) suggested that shade also plays a role in low seedling establishment rates: "If seeds germinate [in shady areas], they generally die aborning, or shortly thereafter." Finally, those seedlings that do become established usually have low growth rates – a consequence of shading and moisture competition from surrounding vegetation. Low growth, in turn, is associated with low survival in subsequent years (Harvey et al., 1980, Harvey and Shellhammer, 1991).

At the opposite extreme, forest gaps created by local high-severity fire usually experienced abundant seedling germination and establishment, and higher average seedling survival (Kilgore and Biswell, 1971, Harvey et al., 1980, Stephenson, 1994, Mutch, 1994, Mutch and Swetnam, 1995, Meyer and Safford, 2011). Sequoia cones opened by the heat pulse from a local high-severity surface fire release abundant seeds (Kilgore and Biswell, 1971, Harvey et al., 1980, Stephens et al., 1999), and many of those seeds fall on soils that have been made soft and friable by extreme heat (e.g., where logs or stumps have burned). Demetry (1995) and Demetry and Duriscoe (1996) found that sequoia seedling densities reached their maximum between about 11 m to 19 m from the edges of fire-created gaps and speculated that this zone reflected the intersection of gradients of increasing water availability toward gap centers (Ziemer, 1964, York et al., 2011) and of decreasing seed rain toward gap centers (i.e., there were no sequoia seed trees inside of their gaps [Demetry and Duriscoe, 1996]). The relatively short distance to maximum seedling density also highlights limitations to sequoia seed dispersal. Seedling height, in turn, usually increased dramatically up to roughly 10 m to 15 m from gap edges and then increased more gradually up to >30 m from gap edges (Demetry, 1995, York et al., 2004). Thus, when considering gap-wide averages, those gaps large enough to receive greater direct sunlight and to suffer less root competition from surrounding vegetation (i.e., gaps ranging from roughly 0.1 ha to a few hectares) typically experienced greater average seedling growth rates (Stephenson, 1994, Demetry, 1995, Demetry, 1998, York et al., 2003, York et al., 2004, York et al., 2007, Meyer and Safford, 2011, York et al., 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 seedlings that went on to successfully produce mature sequoias occurred in forest gaps ranging from 0.1 ha to a few hectares in size. Importantly, in the past the gaps were created by the local deaths of most pines, firs, and incense-cedars but usually not large sequoias, which are more resistant to locally intense surface fires (Mutch and Swetnam, 1995, Stephenson, 1996).

While the studies cited above reported that seedling densities increased with fire severity, recent wildfires have burned with unprecedented severity, including crown fire. At these recent, new extremes of high severity, sequoia seedling densities have declined (Soderberg et al., 2024), suggesting that the relationship between severity and seedling density is hump-shaped, peaking at the lower levels of severity (i.e., without crown fires) that were typical of the past (other Sierra Nevada tree species show a similar pattern; Welch et al., 2016). One likely mechanism contributing to declining seedling densities at the most extreme severities is fire consuming cones that have been burned out of sequoia crowns by crown fires (Soderberg et al., 2024).

Although, at the intermediate scales discussed in the preceding paragraphs, areas of typically low and high fire severity had, respectively, low and high average post-fire seedling densities, fine-scale variation (e.g., <1 m to 10 m) in seedling densities is pronounced in all burned areas (Demetry, 1995; Fig. 40 of Harvey et al., 1980; Appendix D of Demetry and Duriscoe, 1996). Causes of fine-scale seedling patchiness include things like distance to mature, cone-bearing sequoias, prevailing wind directions during seed release, seed transport by seasonal water flow, and fine-scale variation in site favorability (such as determined by severity of soil heating, localized variation in soil moisture and nutrients, and presence or absence of sheltering objects) (Hartesveldt and Harvey, 1967, St. John and Rundel, 1976, Harvey et al., 1980, Gebauer, 1992, Demetry, 1995, Soderberg et al., 2024). The often extreme fine-scale spatial variation in seedling densities means that a randomly placed seedling census plot may contain few or no seedlings even though seedlings are abundant a few meters away, or vice versa. Consequences of this variation for analysis and interpretation are addressed in subsequent sections.

3. Methods

3.1. Data

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). This suggests that seedling densities measured after past prescribed fires should serve as useful reference densities, at least for the past environmental conditions under which those seedling densities were measured. Our analyses are therefore predominantly based on censuses of naturally seeded sequoia seedling following prescribed fires.

We limited our data sources to those with the following six characteristics. (1) Seedling densities were reported for at least one of the first five years following fire. (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). After imposing these criteria, we were left with two data sources: Kilgore (1973) and the 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 census 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, National Park Service, 2003); here we summarize the aspects most relevant to this study. The 0.1-ha (50 m x 20 m; not slope-corrected) fire effects plots were established and permanently marked before planned prescribed fires (except for two plots in our final data set that were established after a 1987 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 NPS fire effects data, we corrected a database error that was a dominant contributor to the underestimated post-fire sequoia seedling densities that were reported in Fig. 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, Sydoriak, 2001), which capped the number of seedlings that could be reported in a 250 m^2 subplot at 9999. 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 9999. Data from four sample dates in three plots were found with capped values that we then corrected.

We also discovered some NPS 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 (typically 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 Fig. 2A, and Hartesveldt et al. (1981)). Four lines of evidence led us to identify five plots in which first-year seedlings were 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 first-year densities (Section 2) – were positive numbers up to 162,520 ha^{-1}. 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, field crew members who recorded second-year seedling densities in these plots explicitly commented on their data sheets that the first-year seedling counts may have been sequoias that had been misidentified as white firs. Finally, the questionable data were temporally clustered in 1992 and 1993, suggesting that a crew member working during this narrow period may have been responsible for the apparent misidentifications. In these five plots, we thus converted first-year white fir seedling densities to first-year sequoia seedling densities. Regardless, mean first-year density without this correction was nearly as high (89%) as the corrected value (Stephenson et al., 2023).

3.2. Analyses

Because standard NPS fire effects monitoring protocols only called for seedling censuses during the first, second, and fifth years post-fire, very few data were available for the third and fourth years (Appendix B). Specifically, seedling density data for the first, second, and fifth years post-fire came from 33, 37, and 36 plots (or transects), respectively, and 20, 23, and 24 different fires. In sharp contrast, data from the third year post-fire came from only three transects and a single fire, and data for the fourth year came from only two plots and a single fire. We thus took different approaches to estimating reference densities for the three data-rich years and the two data-poor years.

For each of the three data-rich years, in addition to calculating arithmetic mean seedling density, we used a Bayesian negative binomial count model (described in Appendix A and in Soderberg et al. (2024)) to calculate estimated mean seedling density. This approach is conceptually equivalent to calculating a simple arithmetic mean, although using a negative binomial distribution to determine mean density is appropriate for count data and our Bayesian methodology also allowed us to directly describe the uncertainty in our mean estimate as a probability distribution. We recently discovered that in our preprint analysis (Stephenson et al., 2023) we mistakenly used a Poisson model even though the preprint said we used a negative binomial. Although Poisson models are commonly used in applications like ours, they assume that mean and variance are equal which, in our data, they are not. Thus, a negative binomial model is both more appropriate and gives a better fit to the data. The probability distributions presented here therefore differ from those in Stephenson et al. (2023); however, the differences result in no changes in conclusions.

In contrast, for the two data-poor years we used a flexible generalized additive model (GAM), using a negative binomial count distribution, to interpolate year three and four values and their associated uncertainties, as described in Appendix A.

For our data-rich plots, we used a paired approach to test whether temporal differences in seedling densities were significant (Appendix A). Specifically, to detect density differences between the first and second years post-fire, we used the subset of 29 plots that had records of seedling densities for both the first and second years post-fire. To detect differences between the second and fifth years, we used the subset of 33 plots that had records for both the second and fifth years post-fire.

3.3. *Climate*

We wished to quantify the mismatch between the climatic conditions that prevailed when the data underlying our reference densities were collected and the climatic conditions that prevailed after the recent wildfires. 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, Mutch, 1994, Mutch and Swetnam, 1995). 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.

3.4. *Case study*

Our case study centered on the small (19.5 ha) Board Camp Grove of giant sequoias (Sequoia National Park), 92% of which burned at high severity in the Castle wildfire in early October 2020 (Soderberg et al., 2024). On 27–28 April 2022, about one year after initial post-fire seedling germination in the grove (and early in the second growing season post-fire), all living sequoia seedlings were counted in each of 20 circular 0.1-ha plots (total sample area [not slope-corrected] = 2.0 ha). Thus, ~10% of grove area was censused for seedlings. 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).

We calculated the marginal probability that post-fire seedling densities at Board Camp Grove equaled or exceeded our second-year reference densities and calculated effect size as the ratios of compared estimates. Further details on case-study sample design, data, and analyses can be found in Soderberg et al. (2024).

4. Results

4.1. *Seedling densities*

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 B). The fires burned in 16 separate years spanning a 48-year period from 1969 to 2016. Mean and median fire years were both 1990.

Comparisons of sample dates and sizes of census areas contribute to interpretations of results (Sections 5.1 and 5.4). For the three data-rich years, 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 161 m^2, 168 m^2, and 188 m^2 for the first, second, and fifth years post-fire, respectively.

Arithmetic mean seedling densities for the first, second, and fifth years post-fire were 172,599 ha^{-1}, 34,870 ha^{-1} and 8601 ha^{-1}, respectively (Table 1; Fig. 3). The corresponding Bayesian mean estimated densities were 129,816 ha^{-1}, 24,134 ha^{-1}, and 6700 ha^{-1}, respectively, with 95% credible intervals of 64,377 ha^{-1} to 313,438 ha^{-1} for the first year, 10,419 ha^{-1} to 73,895 ha^{-1} for the second year, and 3067 ha^{-1} to 18,555 ha^{-1} for the fifth year.

Our GAM-interpolated Bayesian mean estimated seedling densities

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

Year post-fire	Arithmetic mean density (seedlings ha^{-1})	Bayesian mean estimated density (seedlings ha^{-1})[**]	Bayesian percentage probability (italic) of actual landscape-scale seedling density meeting or exceeding specified thresholds (seedlings ha^{-1}, bold)											
			1k	**5k**	**10k**	**20k**	**30k**	**40k**	**50k**	**100k**	**150k**	**200k**	**250k**	**300k**
1	172,599	129,816	*100*	*100*	*100*	*100*	*100*	*99.9*	*99.6*	*75.6*	*36.7*	*15.5*	*6.5*	*3.1*
2	34,870	24,134	*100*	*100*	*97.9*	*66.2*	*33.1*	*15.8*	*8.1*	*0.9*	*0.1*	*< 0.1*	*0*	*0*
3	–[*]	16,344	*99.9*	*95.4*	*77.4*	*37.1*	*14.6*	*6.0*	*2.7*	*0.1*	*< 0.1*	*< 0.1*	*< 0.1*	*0*
4	–[*]	10,818	*99.9*	*90.7*	*56.2*	*14.4*	*4.3*	*1.8*	*0.8*	*< 0.1*	*0*	*0*	*0*	*0*
5	8601	6700	*100*	*74.4*	*19.7*	*2.0*	*0.4*	*0.1*	*0.1*	*0*	*0*	*0*	*0*	*0*

[*] For the data-poor years 3 and 4 post-fire, arithmetic means were not calculated (Section 3.2).

[**] For the data-rich years 1, 2, and 5 post-fire, Bayesian mean estimates and probabilities of meeting or exceeding specified thresholds were produced using the single-year analyses (Section 3.2). For the data-poor years 3 and 4, GAM interpolations were used (Section 3.2). Details can be found in Appendix A.

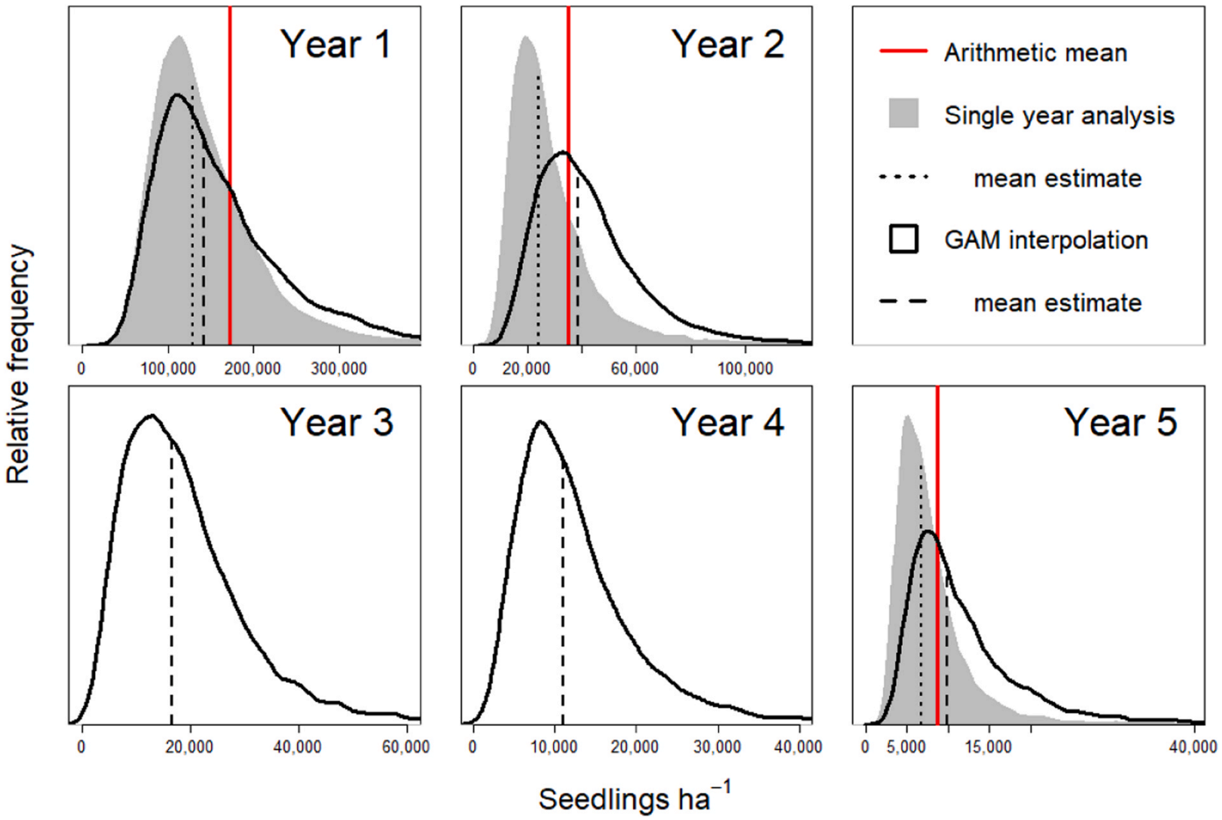

Fig. 3. Probability distributions for giant sequoia seedling reference densities for each of the first five years after fire. The probability distributions for single year analyses (for the data-rich years 1, 2, and 5) are shown in grey-filled polygons, and GAM interpolated distributions (all years) are shown in black-outlined polygons with mean estimates depicted with dashed vertical lines. The arithmetic means (for the data-rich years 1, 2, and 5) are shown with red vertical lines. See Sections 3.2 and 4.1 for details.

for the third and fourth years post-fire were 16,344 ha^{-1} and 10,818 ha^{-1}, respectively, with 95% credible intervals of 4000 ha^{-1} to 48,862 ha^{-1} and 3241^{-1} to 34,358 ha^{-1} (Table 1; Fig. 3).

As expected, seedling densities declined through time (Table 1; Fig. 4). Despite a somewhat reduced sample size for the paired test (Section 3.2) and changes in plot sizes that likely weakened our test (Section 5.1), our paired analysis showed that the marginal probability that year 1 post-fire seedling density was less than year 2 was 0.034 (median effect size = 3.36). The marginal probability that year 2 post-fire seedling density was less than year 5 was 0.035 (median effect size = 3.5).

4.2. *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). Sequoia seedlings that germinated in 2021 (including our case study seedlings) – in response to the 2020 Castle wildfire – were subjected to the hottest and driest summer of the 121-year record (Table 2). Seedlings that germinated in 2022 – in response to the KNP Complex and Windy wildfires (Soderberg et al., 2024) – were subjected to the third hottest summer and second most severe summer drought (by PDSI) on record.

4.3. *Case study*

The Bayesian mean estimate of second-year sequoia seedling density at Board Camp Grove (1768 ha^{-1}) was significantly lower than our second-year Bayesian mean estimated reference density (24,134 ha^{-1})

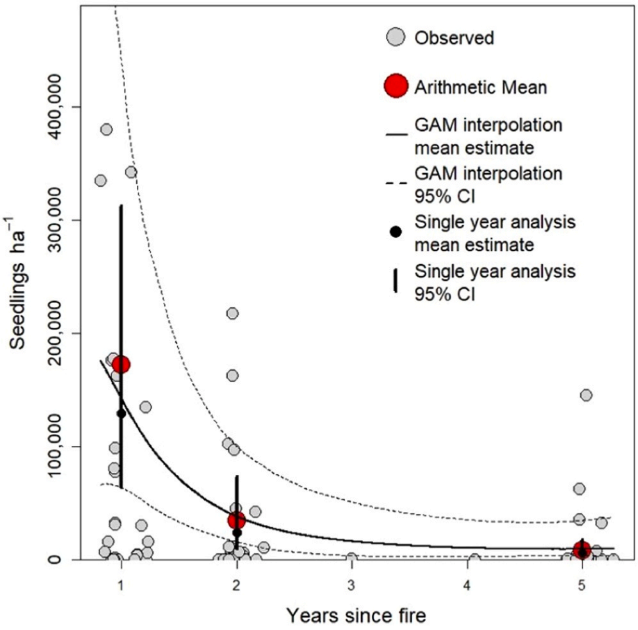

Fig. 4. Generalized additive model (GAM) fit to our reference density data (see Appendix A). Tick marks for years since fire indicate 1 August of the indicated years. Red dots show the arithmetic mean sequoia seedling densities for the data-rich first, second, and fifth years post-fire. For the first year, three observed density values (797,520 ha^{-1}, 1,172,720 ha^{-1}, and 1,605,000 ha^{-1}) exceed the graph's vertical scale; for the second year, one value exceeds the scale (522,500 ha^{-1}). All third, fourth, and fifth year observed values are shown.

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

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

(marginal probability that it was not lower = 0.0011, effect size = 13.7). The associated probability distributions are shown in Fig. 5.

5. Discussion

5.1. Strengths and weaknesses of the data

The nature of our reference data suggest that our seedling densities are broadly representative of post-fire sequoia reproduction 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 the fires were comparable to that of our entire 121-year climate record (Table 2).

However, plot-to-plot variation in seedling densities was substantial (e.g., among individual plots, first-year seedling densities ranged from 0 to 1,605,000 ha^{-1}; Appendix B), contributing to relatively large uncertainty in our final estimates of mean seedling densities at a landscape scale (Figs. 3 and 4). Much of this substantial variance is almost certainly a consequence of highly variable local fire severity in the vicinities of our plots. For example, nearly one half (45%) of first-year plots recorded fewer than 10,000 seedlings ha^{-1} (mean = 1832 ha^{-1}). Most of these areas probably burned at low severity, resulting in little seed release and poor initial seedling establishment and survival (Section 2). At the opposite extreme, two first-year plots had densities exceeding 1,000,000 seedlings ha^{-1}, almost certainly a consequence of local high-severity fire that created ideal seed beds and triggered heavy seed fall.

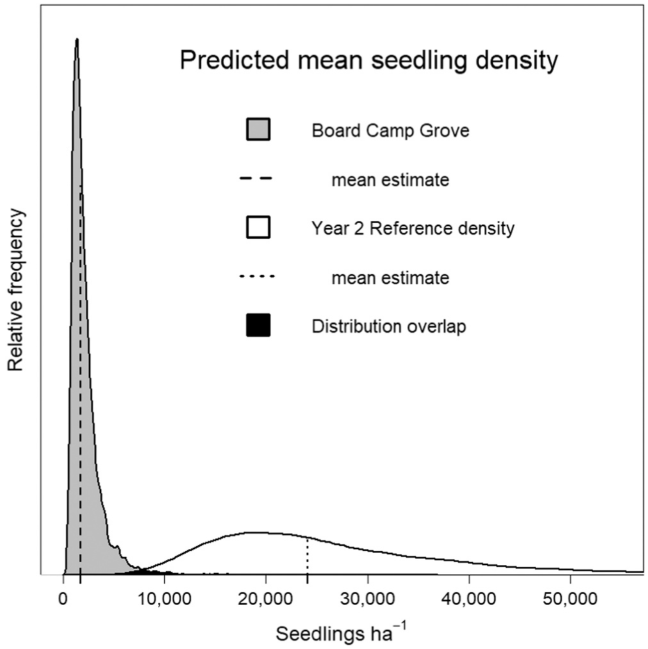

Fig. 5. Probability distributions of seedling densities the second year after fire, both for the case study (Board Camp Grove) and for seedling reference density. Mean estimated values of the distributions (dashed vertical lines) are Board Camp Grove = 1768 ha^{-1} and reference density = 24,134 ha^{-1}.

Some among-plot density variation was also likely attributable to climatic conditions during the first one or more years post-fire, with drought years expected to result in lower seedling germination and survival (Section 2). But because very few plots were sampled per fire (mean = 1.6, median = 1, range = 1–4), we could not partition density variation according to that caused by within-fire variation (such as caused by local fire severity and proximity of seed trees) and that caused by among-fire variation (e.g., related to different seasons of burns, weather, and average fuel moistures).

Variation in growing-season census dates (Section 4.1) also may have contributed to among-plot density variation. Previous work has demonstrated that live seedling densities decline substantially over the course of their first summer (Hartesveldt and Harvey, 1967, Harvey et al., 1980). Although about one half of our first-year seedling census dates were in July, dates ranged from late May (soon after germination, when seedling densities are expected to be greatest) to late October (when seedling densities will have been reduced substantially by summertime mortality). Similar (although perhaps less dramatic) reductions in seedling densities are also likely to have occurred over the course of subsequent summers (second through fifth).

Our paired comparisons of seedling densities one, two, and five years after fire (the data-rich years) may have been weakened by the fact that in about one third of cases, the sizes of seedling subplots changed between sample years (Appendix A). For example, if a given subplot expanded between years 2 and 5, and if that expansion was into an area of much higher seedling densities than was found in the smaller year 2 subplot, seedling densities could appear to increase between years 2 and 5 even when they actually declined. Conversely, subplot expansion into areas of very low seedling densities could cause an apparently steeper decline in seedling densities than actually may have occurred between years 2 and 5. However, our data suggest that any collective effects of changing subplot sizes on our broad results and conclusions were almost certainly quite small (Appendix A).

5.2. Reference density characteristics and post-fire seedling dynamics

Our reference densities have three striking features. First, despite being inherently conservative (Section 5.3), the densities are very high.

For example, mean fifth-year sequoia seedling densities are more than an order of magnitude greater than the corresponding minimum U.S. Forest Service regional seedling stocking standards for similar Sierra Nevada forest types (Welch et al., 2016, Meyer et al., 2021). These high densities also vividly illustrate the well-documented role of fire in giant sequoia reproduction (Section 2). 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 (<1 seedling ha^{-1}). In sharp contrast, average sequoia seedling density in the first summer following fire was more than five orders of magnitude greater (Table 1).

Second, and as previously reported by others (Section 2), seedling densities decline precipitously with time since fire (Table 1; Fig. 4). For example, fifth-year densities are only 5% of first-year densities. This is a consequence of the combined effects of high seedling mortality that is not matched by subsequent new seedling germination and establishment (Section 2).

Third, the densities were associated with relatively substantial uncertainty – a consequence of intermediate- and fine-scale spatial variation in seedling densities (Section 5.1). Yet despite this uncertainty we detected, with high certainty, that reproduction in our severely burned case study sequoia grove was lower than our reference density (marginal probability that it was not lower = 0.0011), strongly suggesting inadequate post-fire regeneration.

Our data allow us to estimate rough bounds on the average magnitude of the second seedling cohort (the cohort that often germinates the second spring and early summer after a fire). 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. 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 entirely comprise second-cohort seedlings. Because the arithmetic mean density of seedlings the second year was 20% that of the first, our upper bound on the average size of the second cohort would be 20% 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 is likely <20% the size of the first cohort.

During specific sequences of years, it may be possible for the second seedling cohort to exceed the first. For example, the first year following a fire could be characterized by extreme heat and drought that desiccates most seeds and kills most germinants, whereas the second year could be unusually wet, allowing the establishment and survival of a relatively large proportion of second-cohort seedlings despite reduced seed fall and reduced soil favorability (Section 2). However, our data suggest such events are rare. Twenty-two of our plots had seedling census areas that remained unchanged between the first and second years post-fire (thus avoiding the potentially confounding effects of changing census areas; Section 5.1 and Appendix A). Of those 22, only two (9%) showed an absolute increase in seedling densities between years 1 and 2. In both cases, seedling densities were quite low and showed only small increases – the equivalent of 1 and 11 seedlings within the 250 m^2 census areas. We suspect that the small increases are most likely a consequence of small seedlings being overlooked in the first census, then being counted in the second census after they had grown larger and become more visible. But even if the increases did at least partly reflect proportionally larger second cohorts, the absolute magnitude of the second cohorts remained quite small.

5.3. Interpreting the reference densities under novel environmental conditions

Do our reference densities – which are based on sequoia reproduction following mixed-severity surface fires and during more benign climatic conditions of the past – provide a meaningful yardstick for judging the adequacy of seedling densities after historically severe wildfires – including historically unprecedented crown fires – in a warmer climate? To address this key question, we first consider the effects of the following factors on seedling density and survival: (1) severity of the fires that trigger seedling establishment, (2) size of fire-created forest gaps, (3) presence or absence of a post-fire leaf litter mulch, (4) a warming climate, and (5) frequency and severity of future fires that will affect established seedlings. We then additionally consider the paleoecological evidence of sequoia responses to a warm period of the past, and interpret the collective evidence.

The prescribed fires underlying our reference densities were of mixed severity, generally comprising a matrix of forest that burned at low to moderate severity (leaving the forest canopy largely intact) interspersed with patches that burned at high severity (creating small forest gaps) (Section 2). Our seedling plots – the large bulk of which were established *a priori* using restricted random sampling – can be expected to have proportionally sampled this full range of fire severity in the prescribed fires. Our sample areas that burned at low severity would, on average, be expected to yield relatively few sequoia seedlings, whereas those that burned at high severity (resulting in crown scorch but not crown combustion) would, on average, be expected to yield abundant seedlings (Section 2). Our average seedling reference densities therefore can be expected to be lower than they would have been if we had only sampled patches that burned at high severity. Thus, all else being equal, our reference densities are likely to be conservative – substantially lower than they should be for comparisons with areas that have burned predominantly at high severity (as in our case study).

Although past work showed greatest sequoia seedling growth and survival in what, in the past, were considered to be large fire-created gaps (those on the order of 1 ha; see Section 2), the same cannot automatically be assumed to apply to the novel, very large gaps (>10 ha, and even >100 ha) created by recent wildfires. Snow accumulation and retention are usually maximized in forest gaps of intermediate sizes (e.g., up to ~1–5 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 ~1–5 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), thus 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 exacerbated 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, we can assume that patchily distributed seedling survival in very large gaps will somehow compensate for low seedling densities (i.e., those lower than our reference densities).

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 than with litter, and soil moisture at 10 cm depth as much as 25–60% lower – conditions that will typically contribute to increased sequoia seedling deaths related to pathogenic 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 likely contributes to seedling survival (see Fig. 2A, which shows a new litter layer already in place the first spring following a fire). These were the typical post-fire conditions in the occasional "hot spots" in the plots used to derive our reference densities. In contrast, during the recent wildfires some areas of sequoia groves burned in historically unprecedented crown fires that consumed most of the forest canopy. In these crown fire areas, reduced post-fire litter accumulation (e.g., Welch et al., 2016) could contribute to reduced seedling survival relative to the post-fire conditions upon which our reference densities were based.

Temperatures and climatic water deficits (drought) have been rising in the Sierra Nevada (Edwards and Redmond, 2011, Das and Stephenson, 2013, Tercek et al., 2021) 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 seedlings (Harpold and Molotch, 2015) and potentially increases seedling mortality. In addition to lengthening the summer drought, rising temperatures increase the atmosphere's evaporative demand for water, thus increasing drought severity (Williams et al., 2015, Tercek et al., 2021, Williams et al., 2022), which can be expected to further increase seedling mortality (Harvey et al., 1980, Mutch and Swetnam, 1995). Furthermore, and like the effects of higher temperatures on other western North America conifer seedlings (e.g., Moran et al., 2019, Rank et al., 2022, Crockett and Hurteau, 2024; also see Still et al., 2023), increased sequoia seedling mortality related to longer and more severe summer drought is likely to be exacerbated by the direct effects of higher temperatures (Stark, 1968, Moran et al., 2019). Thus, young sequoia seedlings today and in the future might reasonably be expected to experience reduced survival compared to those that were censused for our reference densities.

Finally, sequoia seedlings that became established after the recent high-severity wildfires will inevitably face more fires in the future. Fuels for those fires will include abundant logs and snags (from the trees killed by the initial high-severity fires) and shrubs, whose germination from a persistent soil seed bank was triggered by the fires (Knapp et al., 2012, Collins and Roller, 2013, Coppoletta et al., 2016, Lydersen et al., 2019, North et al., 2019). Within the small forest gaps created by locally severe "hot spots" during past prescribed fires, subsequent prescribed fires have generally burned through such fuels with patchy mixed intensity, killing some of the young sequoia seedlings (especially the smallest) while leaving others alive (ACC and NLS, personal observations; also see York et al. (2021)). We presume similar dynamics may have been common during the centuries and millennia preceding fire exclusion. However, especially during extreme fire weather in California, areas that previously burned at high severity have a very high probability of reburning at high severity (Coppoletta et al., 2016, Harris and Taylor, 2017, Lydersen et al., 2017, Lydersen et al., 2019, Taylor et al., 2021), with indications that the severity of a reburn can exceed the severity of the original burn (Taylor et al., 2022). Extreme fire weather, in turn, has been increasing in the Sierra Nevada and is projected to continue increasing as regional temperatures rise (Collins, 2014, Williams et al., 2019, Goss et al., 2020, Gutierrez et al., 2021, Rother et al., 2022, Brown et al., 2023). It is thus reasonable to anticipate that future wildfires, increasingly burning under extreme conditions through grove areas that had already recently burned at high severity, could reburn those same areas at high severity, killing a greater proportion of young sequoia seedlings than would have been killed in the past. If the severely reburned areas are distant from surviving seed trees, a type conversion to shrub fields with few surviving sequoia seedlings would be possible and perhaps even probable (e.g., North et al., 2019, Coop et al., 2020). All else being equal, our reference densities thus may inadequately reflect densities needed to replace sequoia populations that were locally extirpated by recent fires.

Paleoecological records from sedimentary pollen and macrofossils are consistent with the preceding evidence suggesting potential warming- and wildfire-induced loss of sequoia grove area. In the early and middle Holocene (roughly 11,000 to 4500 years ago), sequoias were much rarer than they are today (Anderson, 1994, Anderson and Smith, 1994), probably living only along some moist creek and meadow edges. This may have been a period of generally higher global summertime temperatures and prolonged summer drought in California (Anderson and Smith, 1994; but see Osman et al., 2021). The cooling and shortening of summer droughts that began about 4500 years ago then allowed sequoias to expand out to their contemporary grove boundaries (Anderson, 1994; Anderson and Smith, 1994). A persistent return to warmer conditions in the future thus might be expected, over time, to shrink sequoia populations again, with one possible mechanism being inadequate seedling establishment and survival following severe wildfires.

Collectively, the weight of evidence suggests that our reference densities are likely conservative, underestimating the seedling densities needed to regenerate sequoia populations killed in high-severity areas of recent wildfires. The probable underestimation is a consequence of (1) our reference data included large areas that burned at low and moderate severity, not just high severity, and (2) our data being from a climatic period more benign than that which prevailed during and after the recent wildfires and more benign than is expected for the future.

5.4. *Case study*

For reasons presented in Section 5.3, our case study comparison was almost certainly conservative (i.e., biased toward finding that post-fire Board Camp seedling densities were not lower than our second-year reference densities) and was also conservative based on the timing of its seedling census relative to those of the reference densities. Regarding the latter, the case study 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 case study seedling densities had instead been measured in late July (similar to our second-year reference densities), they would have been further reduced by some additional summertime seedling mortality.

Despite the conservative comparison, Board Camp Grove had an overall second-year seedling density that was significantly lower than our second-year reference density. Two mechanisms likely contributed to the difference (Soderberg et al., 2024). First, the first-year germinants in Board Camp Grove were subjected to the hottest and driest summer of our 121-year record (Table 2). Such hot, dry conditions undoubtedly contributed to unusually high seed and seedling death by desiccation (Harvey et al., 1980, Mutch and Swetnam, 1995). Second, in those parts of the Board Camp Grove that burned in crown fires, most cones were burned out of the sequoias' crowns and fell into the fire below, 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 much of 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).

5.5. *Management implications*

In the face of rapid and historically unprecedented changes, public land stewards are increasingly making decisions within the Resist-Accept-Direct (RAD) framework (Schuurman et al., 2022), choosing among resisting, accepting, or directing change. Decisions within this framework will necessarily be limited by the range of potential responses that are both physically possible and practical (e.g., North et al., 2019, Long et al., 2023) and further guided and constrained by a complex interplay of the enabling legislation for specific land units, other applicable laws and policies, management goals, and societal expectations and desires (e.g., Clifford et al., 2022, Crausbay et al., 2022, Lynch et al., 2022, Magness et al., 2022).

Considering possible sequoia management responses to large, high-severity fires within the RAD framework (also see Stevens-Rumann and Morgan, 2019, Guiterman et al., 2022), "resist" might entail replanting seedlings from local seed sources (i.e., local genotypes) in selected high-severity burn areas within grove boundaries. "Accept" would simply mean not responding to any observations of low sequoia seedling densities, thereby accepting the risk of an ultimate net loss in sequoia grove area. “Direct” options might include responding to expectations of continued climatic warming by (1) planting sequoia seedlings at higher elevations, above groves’ current boundaries (i.e., assisted migration), and (or) (2) planting inside grove boundaries with drought-tolerant genotypes brought in from other populations (De La Torre et al., 2022, Valness et al., 2023). Importantly, managers might choose to implement a mix of resist-accept-direct responses, depending on goals, site-specific conditions, and practicality. Regarding the two classes of active responses (resist and direct), we are unaware of any current post-fire management proposals for assisted migration. We thus limit our remaining discussion to planting of sequoia seedlings within grove boundaries (whether with local genotypes, drought-tolerant genotypes, or both), which has already been completed in some areas and has been proposed for others.

Managers who are considering planting sequoia seedlings might first wish to consider the paleoecological record, which suggests that sequoias were much rarer than today – perhaps only existing along stream and meadow edges – during a warmer, drier period from ~11,000 to ~4500 years ago (Section 5.3). In the face of expectations of continued warming, does the paleoecological record suggest that planting seedlings is thus inherently futile and that doing nothing – i.e., passively accepting change – is the most sensible option? Or, given the inherent unpredictability of the future (e.g., potential mitigations of climatic warming), is planting a sensible option, even if its future success is uncertain? Further considerations can help inform this decision.

For example, once sequoias have passed their vulnerable seedling stage and have become well established, they have proven to be quite resistant to extreme drought – more resistant than neighboring coniferous species (Ambrose et al., 2018, Nydick et al., 2018, Stephenson et al., 2018; also see Ambrose et al., 2015). Seedlings planted sooner rather than later likely have a greater chance of becoming well established before potential continued warming further reduces chances of successful establishment (cf. Davis et al., 2023). Additionally, seedlings can be selectively planted in favorable sites, such as in moister areas and away from competing shrubs, ensuring more rapid height growth (Heald and Barrett, 1999, York et al., 2003, York et al., 2004, York et al., 2006, York et al., 2007, York et al., 2009). For example, York et al. (2004) reported a six-year-old planted sequoia seedling that was already an astounding 4.41 m tall. Rapid height growth, in turn, rapidly increases seedlings’ resistance to subsequent fires (York et al., 2021).

If seedling planting is accepted as an option, a next step would likely include identifying thresholds for action. Our case study illustrated a probabilistic approach, which calculated the probability that broad-scale seedling densities within severely burned areas were lower than our inherently conservative reference densities (especially see Soderberg et al. (2024) for example applications). Importantly, the conservative statistical thresholds that are typically used by scientists may not be suitable for managers who are using a probabilistic approach to aid conservation decisions. For example, do we need to be 95% confident (i.e., $P<0.05$) that a societally valuable species is in danger before we act? Or would 70% confidence ($P<0.30$), or even less, be enough to trigger action? Many factors beyond probability thresholds will likely help define thresholds for action, such as the magnitude of the difference between reference densities and observed seedling densities in severely burned areas, the expected directions and magnitudes of ongoing environmental changes, and the implications of inherently patchy sequoia reproduction in areas where all mature sequoias have been killed (Soderberg et al., 2024).

While they can help managers decide whether to plant, reference densities should not be interpreted as target planting densities. Given the higher growth and survival rates expected from planted sequoia seedlings relative to naturally established seedlings, final seedling density (planted + natural) is likely to be much lower than our reference densities. Specifically, although some natural seedlings can show exceptional growth and survival (e.g., Stephenson, 1994, Shellhammer and Shellhammer, 2006), the bulk of natural seedlings have quite low growth and survival in their early years (Hartesveldt and Harvey, 1967, Harvey et al., 1980, Harvey and Shellhammer, 1991). In contrast, planted sequoia seedlings have average growth and survival rates that are typically orders of magnitude greater (e.g., Heald and Barrett, 1999, York et al., 2007, Perraca and O’Hara, 2008, Cox et al., 2021). This suggests that lower densities of planted seedling might ultimately be able to restore mature sequoia densities. However, interpretation of the growth and survival difference between natural and planted sequoia seedlings is confounded by the fact that, in most studies of planted seedlings, the seedlings were evenly spaced (unlike clumped natural reproduction) and competing vegetation was controlled during the first few years (but see York et al., 2011). Regardless, several mechanisms seem likely to contribute to higher growth and survival of planted seedlings (e.g., North et al., 2019). First, nursery-grown seedlings have been grown under ideal conditions and thus have a remarkable head start in size, root system development, carbohydrate reserves, and health (e.g., Grossnickle, 2012, Grossnickle and Ivetic, 2022). Second, planted seedlings immediately have their roots inserted at soil depths where water may be more available. Third, field crews conducting the planting can select sites that are more conducive to seedling growth and survival, or at a minimum can avoid obviously poor sites. Fourth, planting spades may locally breach the shallow hydrophobic layer that is often present in post-fire soils of the Sierra Nevada (e.g., Samburova et al., 2023, Sion et al., 2023). This layer likely affects the growth and survival of natural sequoia seedlings (Donaghey, 1969), although further research is needed. Importantly, most of the preceding advantages will typically have their greatest effect for seedlings planted the first or second year after a fire, with advantages expected to diminish for seedlings planted in later years when competition from post-fire shrubs and forbs may become substantial (but see Werner et al., 2019).

Finally, given the novelty of rapid, ongoing changes in climate and fire regimes, surprises seem inevitable (Doak et al., 2008). In the face of uncertainty and surprises, progress will almost certainly be most rapid if management decisions are supported by robust monitoring of the survival and growth of both natural and planted seedlings.

5.6. *Conclusions*

The three striking features of our sequoia seedling reference densities – namely, that the densities are very high, decline precipitously with time, and are associated with relatively substantial uncertainty (Section 5.2) – may at least partly be attributable to giant sequoia’s status as a pioneer species (cf. Swaine and Whitmore, 1988, Stephenson, 1994). That is, sequoias typically release profuse, small seeds into small fire-created forest gaps, resulting in extremely abundant, small seedlings within the gaps (and usually far fewer seedlings outside the gaps), which are then quickly reduced by high mortality. However, even for non-pioneer tree species, the challenges of high seedling spatial variation and rapid temporal changes in post-fire seedling densities are generally recognized (e.g., Welch et al., 2016, Stevens-Rumann and Morgan, 2019, Meyer et al., 2021). Thus, we suggest there may be broader value in (1) explicitly addressing uncertainty by taking probabilistic approaches to using reference densities, and (2) developing and using reference densities that are unique to individual years post-fire.

In our experience working with forest managers, the need for reference densities specific to each year post-fire has been acute. Managers often must plan and execute their responses to large, high-severity fires within the first few years following the fires and thus must sometimes judge the adequacy of reproduction that has been measured just one, two, or three years after the fire (Soderberg et al., 2024). In the U.S., a potential source of seedling density data for the first several years post-fire, potentially spanning several different forest types and tree species, is the NPS fire effects monitoring program (National Park Service, 2003) – the data source we used for this paper. Other data sources are likely to be available in the U.S. and elsewhere.

However, the reproductive ecology of individual tree species should be assessed to determine whether post-fire seedling densities measured during the first few years after a fire are likely to meaningfully reflect the adequacy or inadequacy of natural reproduction. The case is relatively straightforward for giant sequoia, for which seedling establishment is effectively limited to the first two summers post-fire, and mostly to the first summer. But assessments may become more difficult for any species that might be capable of both (1) successful seedling establishment for many years following a fire, and (2) dispersing abundant seeds far into large high-severity forest gaps, especially during occasional mast years. These factors may not automatically preclude decisions based on early seedling censuses, but they do argue for caution and case-specific study.

New seedling reference densities will typically be derived from data collected during environmentally more benign conditions of the past. Thus, application of past reference densities to judge the adequacy of seedling densities measured under novel conditions – i.e., after historically large high-severity fires, under historically warm (and often dry) conditions – will likely need to be assessed on a case-by-case basis (Stevens-Rumann and Morgan, 2019). Such assessments will benefit from a detailed understanding of species' reproductive demography, traits, and ecology.

In the face of ongoing environmental changes, the need for robust seedling reference densities only seems likely to increase. As suggested by our development and application of reference densities for giant sequoia seedlings (also see Soderberg et al. 2024), our five criteria for useful reference densities seem likely to apply broadly.

CRediT authorship contribution statement

Anthony C. Caprio: Writing – review & editing, Validation, Supervision, Software, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Nathan L. Stephenson:** Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Formal analysis, Conceptualization. **Adrian J. Das:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **David N. Soderberg:** Writing – review & editing, Visualization, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Eva L. Lopez:** Writing – review & editing, Investigation, Data curation. **A. Park Williams:** Writing – review & editing, Software, Methodology, Funding acquisition, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Seedling reference density data are available in Appendix B. Case study data are available in Soderberg and Das (2023).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121916.

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