

ARTICLE

Assessing giant sequoia mortality and regeneration following high-severity wildfire

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Funding information

US Geological Survey Climate Research and Development; National Park Service

Handling Editor: Amy Hudson

Abstract

Fire is a critical driver of giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz) regeneration. However, fire suppression combined with the effects of increased temperature and severe drought has resulted in fires of an intensity and size outside of the historical norm. As a result, recent mega-fires have killed a significant portion of the world's sequoia population (13%–19%), and uncertainty surrounds whether severely affected groves will be able to recover naturally, potentially leading to a loss of grove area. To assess the likelihood of natural recovery, we collected spatially explicit data assessing mortality, crown condition, and regeneration within four giant sequoia groves that were severely impacted by the SQF- (2020) and KNP-Complex (2021) wildfires within Sequoia and Kings Canyon National Parks. In total, we surveyed 5.9 ha for seedlings and assessed the crown condition of 1104 giant sequoias. To inform management, we used a statistical methodology that robustly quantifies the uncertainty in inherently “noisy” seedling data and takes advantage of readily available remote sensing metrics that would make our findings applicable to other recently burned groves. A loss of giant sequoia grove area would be a consequence of giant sequoia tree mortality followed by a failure of natural regeneration. We found that areas that experienced very high-severity fire (above ~800 RdNBR) are at substantial risk for the loss of grove area, with tree mortality rapidly increasing and giant sequoia seedling density simultaneously decreasing with fire severity. Such high-severity areas comprised 17.8, 142.0, 14.6, 1.6 ha and ~90%, ~14%, ~53%, and ~27% of Board Camp, Redwood Mountain, Suwanee, and New Oriole Lake groves, respectively. In all sampling areas, we found that seedling densities fell far below the average density measured after prescribed fires, where seedling numbers were almost certainly adequate to maintain giant sequoia populations and postfire conditions were more in keeping with historical norms. Importantly, spatial pattern is also important in assessing the risk of grove loss, and in two groves, Suwanee and New Oriole Lake, the high-severity patches were not always

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contiguous, potentially making some areas more resilient to regeneration failure due to the proximity of surviving trees.

KEYWORDS

fire effects, giant sequoia, high-severity wildfire, natural regeneration, restoration management, *Sequoiadendron giganteum*, tree mortality

INTRODUCTION

Throughout western North America, changes in land use patterns combined with the effects of severe drought—specifically, over a century of fire exclusion and large-scale tree mortality events—have led to shifts in forest structure and fire regimes throughout fire-prone forest ecosystems (Hagmann et al., 2021; Parks & Abatzoglou, 2020; Stevens et al., 2017). A resultant increase in ground, surface, and standing fuels, coupled with increasing temperatures and aridity, has facilitated an increase in wildfire-affected landscapes across the western United States (Westerling, 2016), with profound fire-induced changes within forest ecosystems of California (Safford et al., 2022).

In recent years, the southern Sierra Nevada of California has been impacted by multiple wildfires of large extent that contained large patches that burned at high severity (where the majority of all trees die from fire effects; Steel et al., 2022). Two of the largest recent wildfires within the southern Sierra Nevada, the SQF-Complex fire of 2020 and the KNP-Complex fire of 2021 (hereafter referred to as the “SQF” and “KNP” fires) had cumulative burn areas of ~106,000 ha, of which ~47,000 ha were classified as “high severity” (Monitoring Trends in Burn Severity [MTBS]; www.mtbs.gov). While fire is an important and natural process in fire-adapted forest communities such as those in the Sierra Nevada (Stephens et al., 2007)—facilitating important ecosystem functions such as fuel reduction, landscape heterogeneity, and regeneration—large patches of high-severity fire are not typical for mixed conifer forests and can lead to deleterious ecological outcomes, such as reduction in seed source, biodiversity, and wildfire and climate resilience (Cova et al., 2023). Large wildfires are not absent from the fire records of California forests, but the severity and scale of recent fire events have been outside the historical range of variation (Safford et al., 2022; Stephens et al., 2022), at times facilitating vegetation type conversion from forest to shrub permanence (Coop et al., 2020; Coppoletta et al., 2016; Steel et al., 2021). As such, these fires have had negative impacts on forest structure and ecosystem services, including for species of special interest such as the giant sequoia (*Sequoiadendron giganteum*) (Shive et al., 2022).

Giant sequoia has a limited distribution, covering ~11,000 ha in fewer than 100 groves across the western slope of the Sierra Nevada (Hart, 2023). Due to their tremendous size, longevity, and limited distribution, these charismatic macroflora have inspired much public admiration and were central to the designation of state parks, national monuments, and national parks (Stephenson, 1996). Specifically, they were instrumental in enabling legislation for Sequoia and Kings Canyon National Parks and are a focal resource in the parks’ mission to “...preserve unimpaired the natural and cultural resources and values of the national park system...” (National Park Service Mission Statement).

Historically, southern Sierra Nevada wildfires tended to burn at low to moderate severities, interspersed with small patches (<0.1 ha to a few hectares) of high-severity fire (Stephenson, 1994, 1996; Stephenson et al., 1991), with a mean fire return interval at the scale of an individual tree of ~15 years (Swetnam et al., 2009). Giant sequoia possesses a number of adaptations to fire, including thick fire-resistant bark and semi-serotinous cones (Hartesveldt et al., 1975; Harvey et al., 1980). Regeneration is abundant following fires, especially within small gaps created by local high-severity fire, as the combination of exposed, friable mineral soil, canopy light penetration, and seed release from semi-serotinous cones facilitates high levels of germination (Hartesveldt et al., 1975; Harvey et al., 1980). Fire is a critical component for large-scale seed release, with the heat pulse from a fire killing, desiccating, and opening cones (Hartesveldt et al., 1975; Harvey et al., 1980). However, such seed release is predicated on episodic pulses of heat rather than direct consumption of canopy and cones by fire. Such direct burning of the forest canopy (crown fire) is a phenomenon that has been observed in high-severity burn areas within recent catastrophic wildfires, and at the individual tree scale, this phenomenon is referred to as “torching.” Indeed, postfire observations within large patches of recent high-severity wildfire (NPS communications) suggest low levels of regeneration for giant sequoia that are potentially not commensurate with grove reestablishment and resilience to future fire events. Generally, regeneration of giant sequoia in large, high burn severity patches is not yet well understood. Thus, given the high level of mortality reported in

Sierra Nevada giant sequoia groves within recent years (~13%–19% of “large” [$>1.07\text{-m}$ diameter] giant sequoias; Shive et al., 2022; Stephenson & Brigham, 2021)—a situation that is both historically unprecedented and absent from the extensive, multi-millennial sequoia tree-ring record (e.g., Stephenson, 1996; Swetnam et al., 2009)—there is uncertainty around whether large areas of high-severity fire-impacted groves will naturally regenerate to a state resembling their prefire structure (Figure 1). Natural resources managers are currently tasked with deciding whether to replant areas of groves where natural recovery without intervention is uncertain. To help inform this decision-making, we collected data on regeneration, giant sequoia mortality, and crown damage in four groves recently affected by the SQF and KNP fires. Importantly, all of these groves are candidates for intervention. Our goal was to assess overall, postfire

giant sequoia regeneration within our sampled areas and to develop the predictive models of regeneration as a function of neighborhood metrics of canopy conditions (live, scorched, and torched crown volume) and a remotely sensed metric of fire burn severity—relativized differenced normalized burn ratio (RdNBR; Miller & Thode, 2007). We predicted that giant sequoia regeneration would decline nonlinearly with high-severity-classified values of RdNBR, corresponding with an increased percentage of giant sequoia crown torch (consumption by fire) and decreased percentage of crown scorch (intact crown killed by heat), both of which would reduce the available supply of viable giant sequoia seeds. This would result in some severely burned grove areas with low probabilities of regeneration meeting the critical thresholds of concern (i.e., low probability of meeting seedling densities deemed adequate for successful natural regeneration). Our models allowed us to use our mechanistic understanding of giant sequoia ecology and regeneration to estimate seedling densities within large, contiguous high burn severity areas and subsequently scale those predictions across high-severity burn areas of recently fire-affected groves.

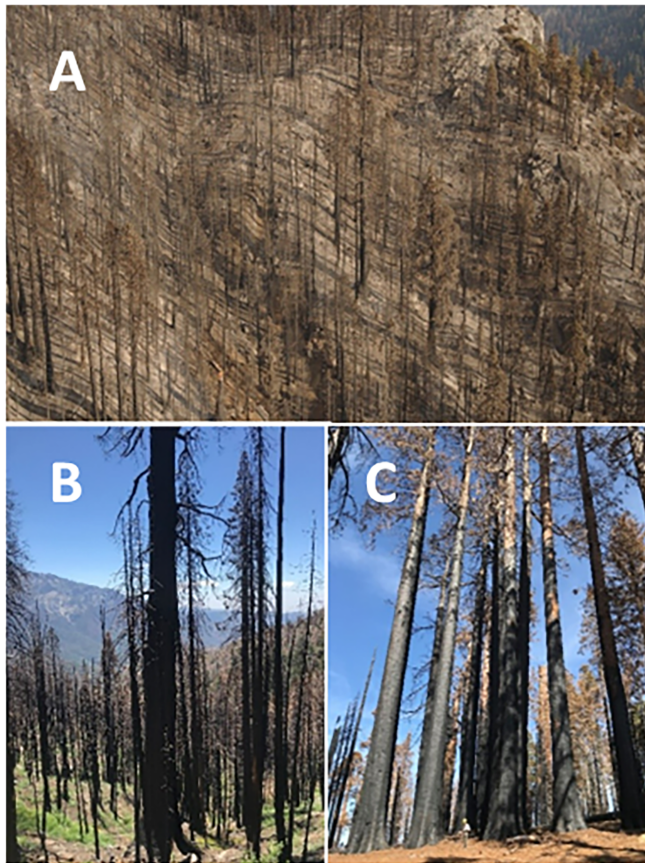


FIGURE 1 (A) Fire-killed giant sequoias (*Sequoiadendron giganteum*) and other conifers in the Board Camp Grove, Sequoia National Park. (B) Ground view of giant sequoia and other conifers in the Board Camp Grove, Sequoia National Park. Note the fire-killed “monarch” giant sequoia (~500-cm dbh) in the foreground. (C) Cluster of fire-killed giant sequoias in Redwood Mountain Grove. Photo credits: (A) Tony Caprio, NPS; (B, C) David Soderberg, USGS.

METHODS

Study area

California’s Sierra Nevada contains fewer than 100 giant sequoia groves, with ~40% of giant sequoia grove area within the footprint of Sequoia and Kings Canyon (SEKI) National Parks. In this study, we surveyed four groves that experienced large areas of high-severity fire during the 2020 SQF (Board Camp Grove) and 2021 KNP (Redwood Mountain, Suwanee, and New Oriole Lake groves) wildfires (Figures 1 and 2).

Seedling sampling

To survey postfire regeneration, we placed plots throughout the Board Camp, Suwanee, and New Oriole Lake groves and within high-severity burn regions of Redwood Mountain Grove (areas with $>75\%$ basal area loss, Rapid Assessment of Vegetation Condition after Wildfire [RAVG], 2022; <https://burnseverity.cr.usgs.gov/ravg/>) using the Generalized Random Tessellation Stratified (GRTS) algorithm (Stevens & Olsen, 2004) with an equal probability stratified sampling design (Figure 2). We used RAVG initial assessment (generally ≤ 45 days after fire containment) data based on the RdNBR (Miller & Thode, 2007) for the sampling design because extended

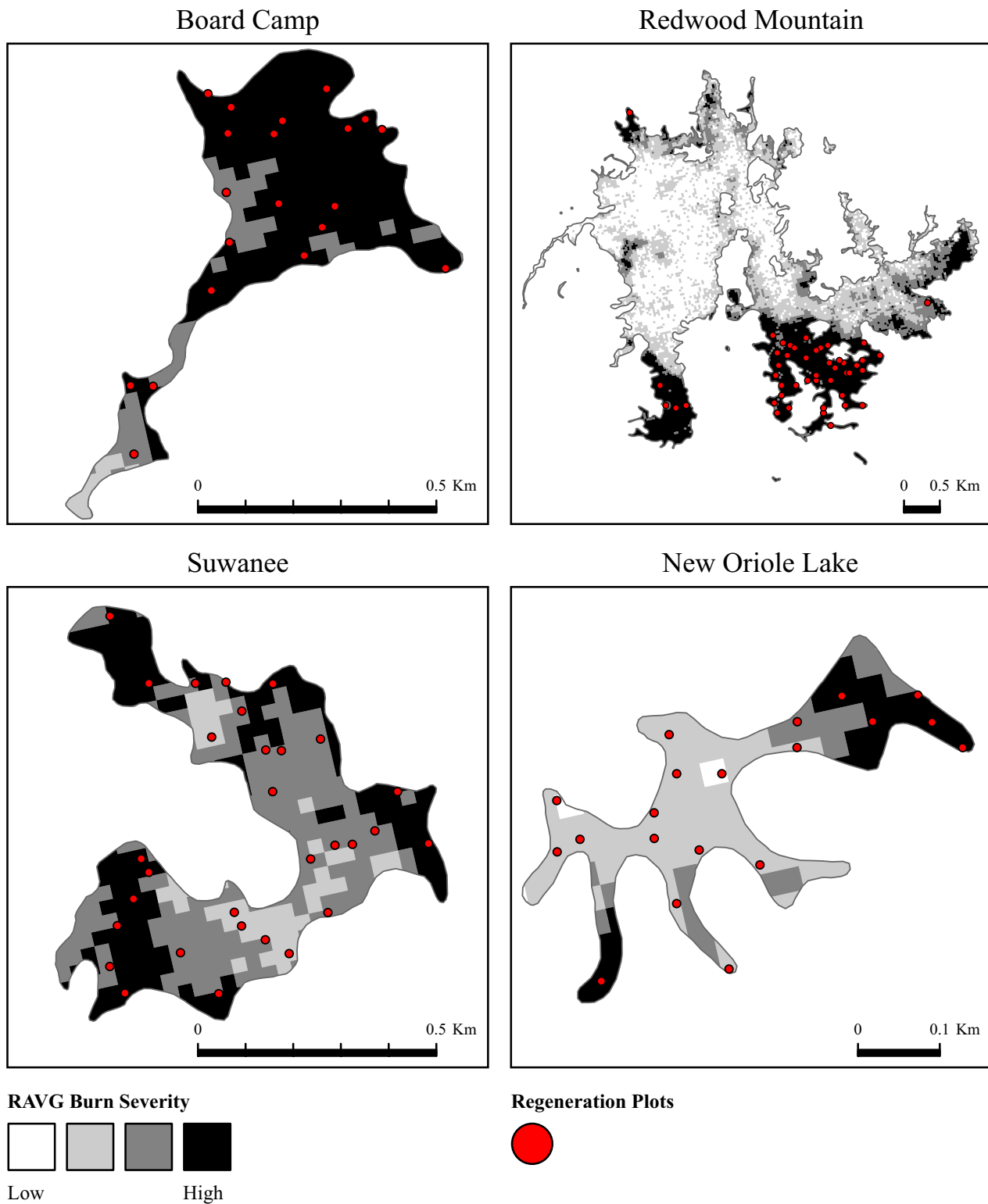


FIGURE 2 Study plot locations (red circles) within Board Camp, Redwood Mountain, Suwanee, and New Oriole Lake giant sequoia (*Sequoiadendron giganteum*) groves within Sequoia and Kings Canyon National Parks, CA. Locations were drawn using the Generalized Random Tessellation Stratified algorithm (Stevens & Olsen, 2004) using an equal probability stratified sampling design within the entirety of Board Camp, Suwanee, and New Oriole Lake groves, but confined to the “high” burn severity (>75% basal area loss; see Rapid Assessment of Vegetation Condition after Wildfire [RAVG]; <https://burnseverity.cr.usgs.gov/ravg/>) regions of Redwood Mountain Grove. Relativized differenced normalized burn ratio-categorized burn severity raster pixels are presented in grayscale (white indicates low severity, <25% basal area loss; light gray and dark gray indicate moderate severity, 26%–75% basal area loss; black indicates high severity or unburned, >75% basal area loss). Grove depictions are oriented north.

assessment data (growing season following the fire) were not available before sampling commenced. However, the two metrics are largely consistent (Miller & Quayle, 2015). Plots in Redwood Mountain Grove were limited to high-severity areas because the large size of the grove made a full sampling impractical and high-severity areas were of greater concern to resource managers based on previous studies of postfire conifer regeneration in Sierra Nevada mixed conifer forests (Shive et al., 2018). We surveyed plots in the 2020 SQF fire-affected Board Camp Grove on April 27–28, 2022. We surveyed the 2021 KNP fire-affected Redwood Mountain, Suwanee, and New Oriole Lake groves within a 6-week span on September 1–7, September 25–October 5, and October 12, 2022, respectively. In addition, all plots within three of the groves (Redwood Mountain, Suwanee, and New Oriole Lake groves) were resurveyed for seedling counts on June 22–July 7, July 9–12, and September 27, 2023, respectively. During field sampling, plot locations were found and recorded with a high-accuracy GPS device (Javad Triumph-2, Eos Arrow Gold GNSS Receivers).

At each site, we tallied seedlings within fixed radius plots (Board Camp: 17.84-m radius, 1/10 ha, 20 plots; Redwood Mountain: 11.35-m radius, ~1/25 ha, 45 plots, 17.84-m radius, 1/10 ha, 1 plot; Suwanee: 11.35-m radius, ~1/25 ha, 30 plots; New Oriole Lake Grove: 11.35-m radius, ~1/25 ha, 20 plots; total sampled area: ~6 ha). Generally, a plot radius of 11.35 m was used, with an increased radius of 17.84 m used when seedling counts were sparse (i.e., the entirety of Board Camp Grove and when ≤ 2 seedlings were counted within the initial 11.35-m plot). Any tree less than 1.37 m in height was considered a seedling, though no seedlings in these surveys exceeded 30 cm tall. Given that (1) sequoias very rarely regenerate without fire (Hartesveldt et al., 1975; Shellhammer & Shellhammer, 2006), (2) severe fire likely killed all existing prefire seedlings, and (3) the small stature of all the seedlings counted, we were confident that all seedlings had recruited postfire. In Board Camp Grove, since sampling occurred two years after the fire, existing seedlings could have been established in the first year after fire (first cohort seedlings) or in the second year after fire (second cohort seedlings). At Board Camp, we distinguished between cohorts based on the presence of cotyledon leaves, which can still be found on seedlings for some time after establishment (Hartesveldt et al., 1975). Based on the lack of cotyledon leaves on any Board Camp Grove seedlings we observed, we found no evidence of second cohort seedlings in the Board Camp Grove despite a robust sampling effort.

Tree mortality and crown damage sampling

We took advantage of an existing spatially explicit giant sequoia stem map (Sequoia Tree Inventory 1973; “STI”) with individual tree attribute data (e.g., dbh) to assess postfire giant sequoia mortality and crown damage. We conducted a full survey of all mapped giant sequoia trees within Board Camp, Suwanee, and New Oriole Lake groves. In contrast, within the large Redwood Mountain Grove, tree mortality and crown damage data were recorded only for giant sequoias within 50 m of study plot centers. For each tree in the survey, we recorded the tree status (live/dead) and percentage of its crown that was live, scorched, or torched. We defined foliage as “live” if green, “scorched” if dead and brown (presumably killed from fire heat pulse), and “torched” if foliage was blackened from fire char or missing (e.g., blackened, bare branches) but presumably consumed during the SQF or KNP fires.

We estimated crown volumes (in cubic meters) for each giant sequoia in our dataset using diameter values from the STI and an allometric equation relating tree diameter to crown volume (in cubic meters) (Sillert et al., 2019, see Appendix S1: Figure S1). To calculate the crown volumes of live, scorched, and torched foliage, we multiplied the estimated individual tree crown volumes by the recorded proportion of crown that was live, scorched, or torched. To calculate “neighborhood” crown volumes of live, scorched, or torched canopies, we summed all tree crown volume estimates for all giant sequoia within the 50-m radius “neighborhood” (wherein a majority of the seed rain contribution from a large giant sequoia will fall, see Clark et al., 2021), of a study plot centroid.

Fire perimeters and burn severity

Burn area boundary polygons and spatially explicit severity raster data (e.g., RdNBR values) for the SQF and KNP fires were sourced from MTBS (2017; www.mtbs.gov). MTBS raster datasets are generated from Landsat (TM/EMT+/OLI) image data, which are acquired at a spatial resolution of 30 m. MTBS vector datasets (burn scar boundaries) are delineated from imagery and burn severity index data at a map scale of 1:24,000 to 1:50,000. Within Board Camp, Suwanee, and New Oriole Lake groves, our plots fell within high-severity patches roughly in proportion to the total high-severity area in the given grove (high severity: BOCA—~92% area, 90% plots; SUWA—~40% area, 37% plots; NEOL—~46% area, 50% plots).

As noted above, our study locations within Redwood Mountain Grove were specifically chosen within high-severity burn areas (high severity ~28% area, 100% plots).

Statistical analysis

To estimate the seedling densities (SDens) at each surveyed giant sequoia grove, we fit an intercept-only negative binomial count model (Equation 2 without parameters). 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 (Figure 3, Table 1), where the quantifiable uncertainty can be used to calculate the probability of the true mean being above or below specified values (see Tables 1 and 2).

To assess the spatial relationship between ground measurements and a remote-sensed measure of burn severity, we applied a negative binomial generalized additive model (GAM) to estimate seedling densities

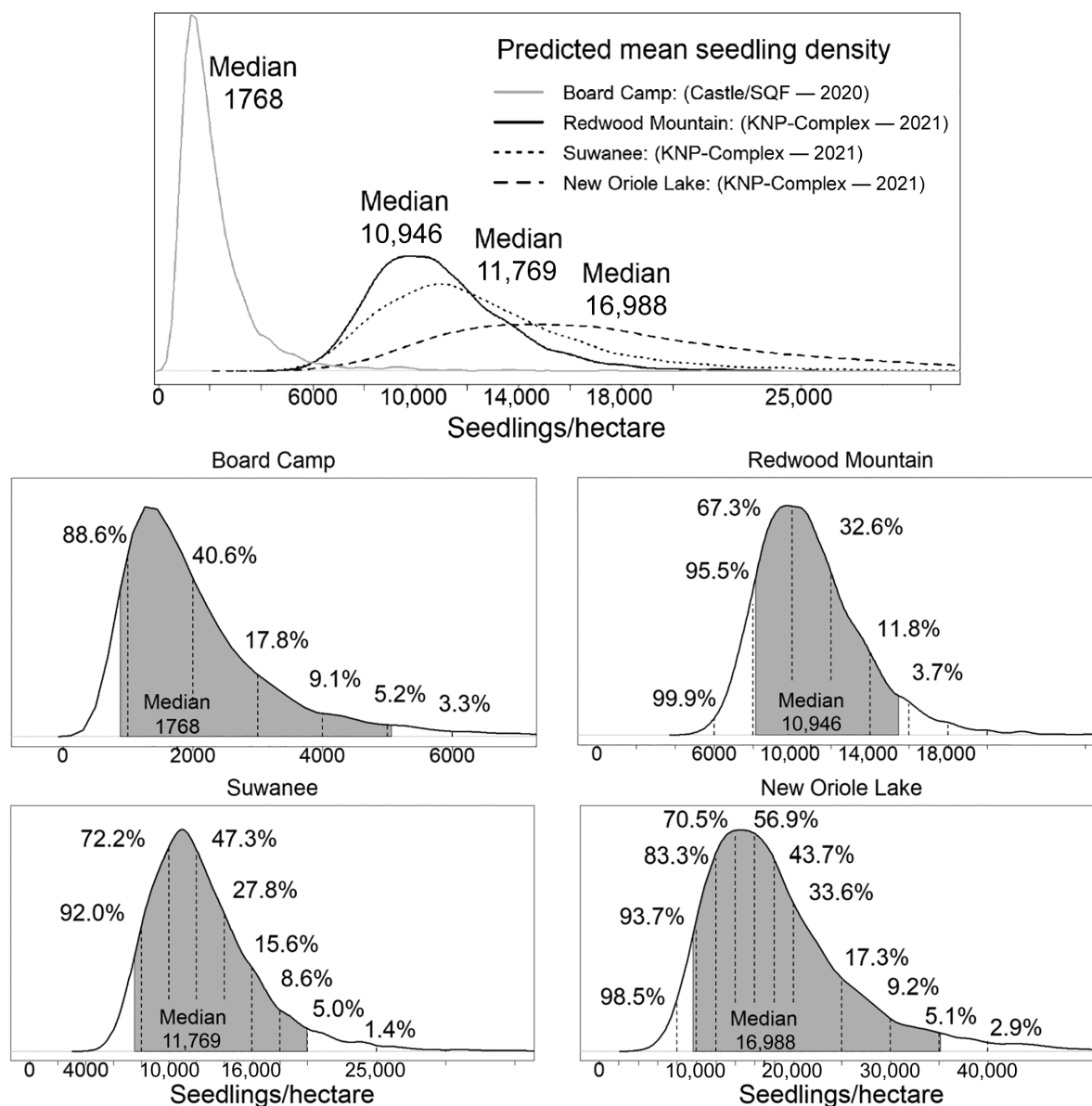


FIGURE 3 Predicted mean regeneration (seedlings per hectare) for groves affected by the 2021 KNP-Complex (i.e., Redwood Mountain, Suwane, and New Oriole Lake groves) and 2020 SQF-Complex fires (i.e., Board Camp). For each sampled grove, the probabilities of the true mean regeneration density (i.e., seedlings per hectare) being larger than specified seedling counts are shown (see Table 1). Bayesian 90% credible intervals are highlighted in gray.

TABLE 1 Mean regeneration densities and Bayesian probabilities of mean regeneration densities meeting (i.e., are greater than or equal to) the specified number of seedlings per hectare for each grove.

No. seedlings/ha	SQF 2020		KNP-Complex 2021		
	Board camp	Redwood Mountain	Suwanee	New Oriole Lake	
Raw mean	1611	10,810	11,435	16,080	
1000	87.7	100	100	100	
2000	41.6	100	100	100	
3000	18.5	100	100	100	
4000	9.8	100	100	100	
5000	5.7	99.9	99.9	100	
6000	3.4	99.5	99.5	99.9	
8000	1.5	95.5	92.0	98.5	
10,000	0.8	67.3	72.2	93.7	
12,000	0.5	32.6	47.3	83.3	
14,000	0.4	11.8	27.8	70.5	
16,000	0.3	3.7	15.6	56.9	
18,000	0.2	1.0	8.6	43.7	
20,000	0.1	0.3	5.0	33.6	
25,000	<0.1	<0.1	1.4	17.3	
30,000	<0.1	0	0.5	9.2	

Note: See [Statistical analysis](#) for details. Probabilities that are <10% are denoted in boldface. Redwood Mountain plot locations were restricted to areas of high burn severity (relativized differenced normalized burn ratio >640).

TABLE 2 Bayesian probability estimates of mean regeneration densities as a function of relativized differenced normalized burn ratio (RdNBR; Miller & Thode, 2007).

No. seedlings/ha	RdNBR						
	800	850	900	950	1000	1050	1100
SQF 2020—Board Camp ^a							
1000	45.8	29.0	17.4	12.2	10.0	10.5	10.2
2000	14.9	7.5	4.2	3.1	2.9	2.9	3.2
3000	6.8	2.9	1.7	1.3	1.3	1.4	1.5
4000	3.7	1.6	0.8	0.7	0.8	0.7	0.8
5000	2.1	0.9	0.5	0.4	0.4	0.5	0.5
6000	1.5	0.5	0.2	0.2	0.2	0.3	0.4
KNP-Complex 2021—Redwood Mountain, Suwanee, and New Oriole Lake ^b							
8000	99.7	99.4	97.5	90.5	74.5	45.7	17.0
10,000	97.4	94.7	84.6	64.2	38.2	15.6	3.6
12,000	88.5	80.6	60.8	35.9	16.3	4.7	0.8
14,000	73.4	59.2	36.6	17.9	6.0	1.3	0.2
16,000	55.1	39.1	21.0	8.2	2.3	0.4	<0.1
18,000	38.4	24.5	11.4	3.8	0.9	0.1	<0.1

Note: See [Methods](#) for details. Probability estimates represent the probability of meeting (greater than or equal to) the specified number of seedlings per hectare for a given RdNBR value. Probabilities that are <10% are denoted in boldface.

^aModel estimates calculated with outlier removed. See Figure 5 for all data visualization.

^bModel estimates calculated within areas of high burn severity (RdNBR >640).

as a function of the burn severity metric “RdNBR” (see Miller & Thode, 2007) (Equation 2). As seedling densities are considerably influenced by mortality rates over time, we fit a separate model for data from groves affected by the 2020 SQF (i.e., Board Camp Grove) and the 2021 KNP fires (i.e., Redwood Mountain, Suwanee, and New Oriole Lake groves) (Figure 4).

To assess the relationship between our ground-based measurements of giant sequoia crown conditions, we used negative binomial generalized linear models (GLMs) to assess the relationship between seedling density and “neighborhood” crown volumes of live (CVL), scorched (CVS), and torched (CVT) foliage (aggregate live, scorched, and torched crown volumes within a 50-m radius of plot center) as a function of RdNBR (Equation 2, Figure 5). Crown volumes of individual giant sequoias were calculated using an allometric equation derived from Sillett et al. (2015) (Appendix S1: Equation S1, Figure S1), with individual crown volumes of live, scorched, and torched foliage proportionally allocated based on our field measurements.

Additionally, given our mechanistic assumptions of giant sequoia cone semi-serotiny and observed relationship between regeneration and heat pulse-induced crown scorch (see Harvey et al., 1980), we assessed the relationships between RdNBR and neighborhood crown volumes live, scorched, and torched foliage (“CVL,” “CVS,” and “CVT,” respectively) to bridge the mechanistic rationale underpinning an association between seedling density and RdNBR using the same GLM approach described above (Equations 3–5; Appendix S1: Figure S2).

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

$$y_i \sim \text{NB}(m, q), \quad (1)$$

where y_i is the seedling count for the i th observation and m and q are the mean and the shape parameters of the negative binomial distribution, respectively. The mean parameters are related to the variables X_i (i.e., SDens, CVL, CVS, CVT, RdNBR) for i th observations using the following link function:

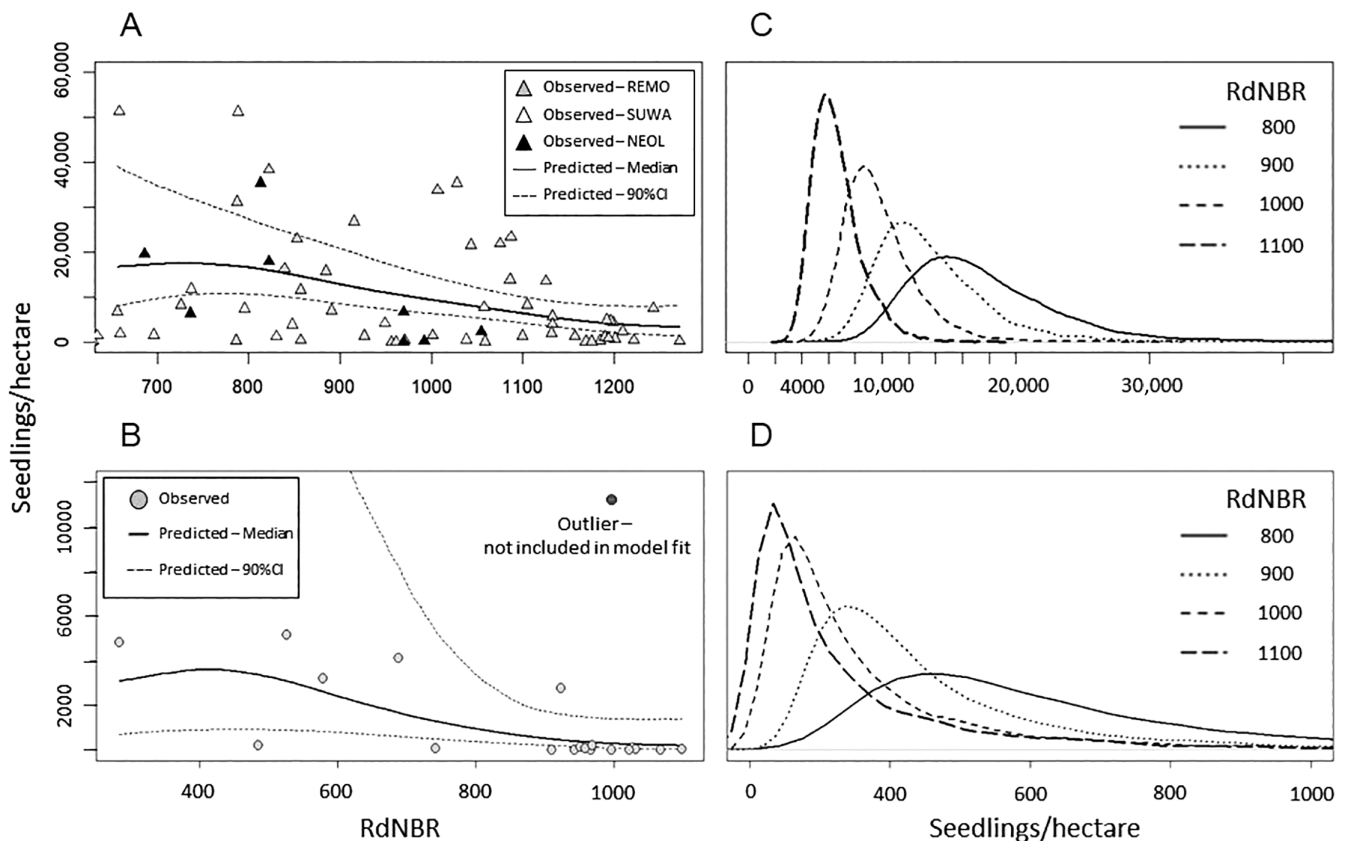


FIGURE 4 Predicted mean regeneration (seedlings per hectare) for groves affected by (A) the 2021 KNP-Complex (i.e., REMO, Redwood Mountain; SUWA, Suwanee; and NEOL, New Oriole Lake) and (B) the 2020 SQF-Complex fires (i.e., Board Camp) as a function of relativized differenced normalized burn ratio (RdNBR) values. (C, D) Predicted mean regeneration densities (seedlings per hectare) at specified RdNBR values (see Table 2).

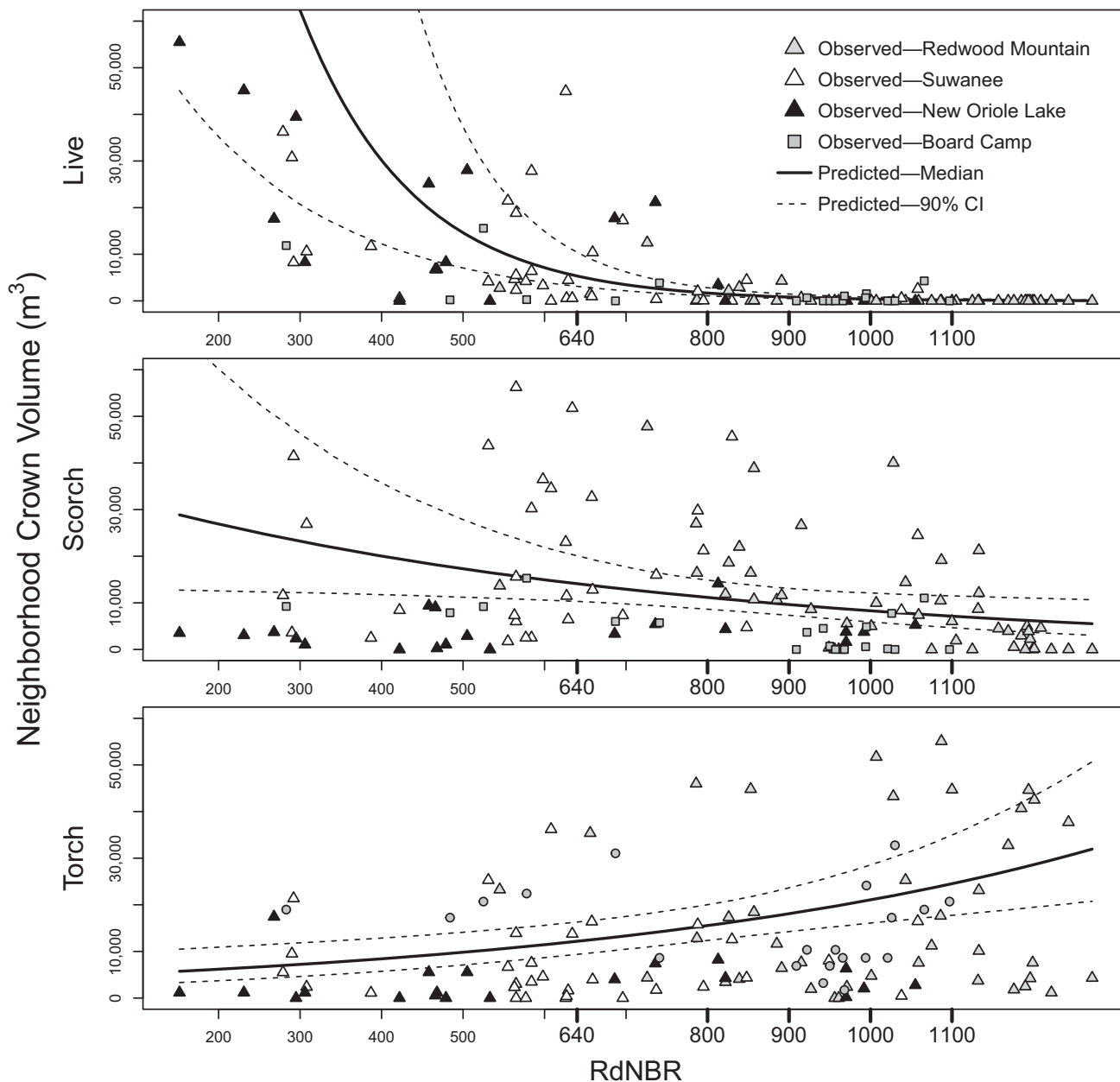


FIGURE 5 Neighborhood crown volumes (within 50 m of plot center) of giant sequoia live, scorched, and torched foliage as a function of remote-sensed derived relativized differenced normalized burn ratio values. Individual tree crown volumes were calculated using allometric equations derived from Sillett et al. (2019) measurements (see Appendix S1: Equation S1) and calculated using observed crown proportion of live, scorch, and torch and location data from this study.

$$\log(m_i) = \alpha + \log(T_i) + (X_i)\beta + e_i, \quad (2)$$

$$CVL_i = \alpha + (RdNBR_i)\beta + e_i, \quad (3)$$

$$CVS_i = \alpha + (RdNBR_i)\beta + e_i, \quad (4)$$

$$CVT_i = \alpha + (RdNBR_i)\beta + e_i, \quad (5)$$

intercept, β is the parameter estimate, and e_i is the residual error associated with the i th observation.

The model parameters were drawn from normal distributions centered around the mean and estimated variances of our data. Specifically:

$$\mu SDens_i \sim \text{Normal}(\mu SDens, SDens\sigma^2). \quad (6)$$

$$\mu CVL_i \sim \text{Normal}(\mu CVL, CVL\sigma^2). \quad (7)$$

$$\mu CVS_i \sim \text{Normal}(\mu CVT, CVT\sigma^2). \quad (8)$$

where $\log(T_i)$ is an “offset,” which corrects for the variation in surveyed area among i th observations, α is the

$$\mu\text{CVT}_i \sim \text{Normal}(\mu\text{CVS}, \text{CVS}\sigma^2). \quad (9)$$

$$\mu\text{RdNBR}_i \sim \text{Normal}(\mu\text{RdNBR}, \text{RdNBR}\sigma^2). \quad (10)$$

The model parameters were given normal, diffuse priors with wide distributions. Specifically:

$$\mu\text{SDens}, \mu\text{CVL}, \mu\text{CVS}, \mu\text{CVT}, \mu\text{RdNBR} \sim \text{Normal}(0, 1000). \quad (11)$$

With the exception of the variance parameters, which were given a modest, Student's t prior distribution: Specifically:

$$\text{SDens}\sigma^2, \text{CVL}\sigma^2, \text{CVS}\sigma^2, \text{CVT}\sigma^2, \text{RdNBR}\sigma^2 \sim \text{Student}(0, 3). \quad (12)$$

We conducted all analyses in R version 4.3.2 (R Core Team, 2022) by computing Bayesian parameter estimates using 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 2000 iterations, discarding the first 1000 iterations as burn-in and sampling each iteration thereafter. All models were checked graphically for convergence and Rhat (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 mean estimate and quantified uncertainty were derived for each model parameter. The mean estimate (ME) and 90% Bayesian credible intervals were then calculated as the median model parameter, bounded by the range of values indicating the equal-tail 90% credible interval of the true parameter estimate. The marginal probability (MP) is the probability that the ME 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. To provide a reference for managers, we also used MP to compare seedling densities estimated in this study with those estimated from seedling data collected after prescribed fires (Stephenson et al., 2023).

RESULTS

Seedling overview

Our seedling counts covered ~10.0%, ~4.3%, and ~5.5% of the total area in Board Camp, Suwanee, and New Oriole Lake groves, respectively. Within the much larger Redwood Mountain Grove, seedlings were counted in ~0.5% of the high burn severity area. Within the 20 plots in the SQF (2020) fire-affected Board Camp Grove, we counted 3221 seedlings across ~2.0 ha of census area. None of the seedlings were identified as the second cohort (germinated the second year following fire), strongly suggesting very little additional regeneration in the second year after the fire. Within the 46 plots in Redwood Mountain Grove, we counted 19,282 seedlings across ~1.9 ha of the ~350 ha of high-severity burn area. Within the 30 plots in Suwanee Grove, we counted 14,239 seedlings across ~1.2 ha. Within the 20 plots in New Oriole Lake Grove, we counted 13,025 seedlings across ~0.8 ha (Table 1). In general, seedling surveys within the KNP-affected (2021) Redwood Mountain, Suwanee, and New Oriole Lake groves yielded substantially higher numbers than those at Board Camp, as expected given that Board Camp only had first cohort seedlings that had experienced at least an additional 6 months of potential mortality.

Estimating overall seedling densities

To provide conservative comparisons, we contrast second-year reference densities presented in Stephenson et al. (2023) with giant sequoia seedling densities measured within Board Camp, high burn severity portions of Redwood Mountain, Suwanee, and New Oriole Lake groves. For the SQF-affected (2020) Board Camp Grove, the ME of the probability distribution for seedling density was 1768, with a 90% credible interval (CI) of 816–5174 seedlings/ha. For comparison, the estimated mean seedling density in the first year after prescribed fire (Stephenson et al., 2023) was 129,816 (90% CI: 71,023–267,045) seedlings/ha, with a second-year seedling density ME of 24,134 (90% CI: 11,887–59,100) seedlings/ha. We found the MP of Board Camp seedling densities being equivalent to those observed in the second year after the prescribed fire was 0.1%.

For the KNP-affected (2021) high burn severity area of Redwood Mountain Grove, the first-year postfire (2022) ME of the probability distribution for seedling density was 10,946 (90% CI: 7641–15,479 seedlings/ha), with an MP of Redwood Mountain Grove seedling densities being equivalent to the second year after prescribed

fire of 4.9%. Within Suwanee Grove, the ME of the probability distribution for seedling density was 11,769 (90% CI: 7487–20,000 seedlings/ha), with an MP of Suwanee Grove seedling densities being equivalent to those observed in the second year after prescribed fire of 9.2%. Within New Oriole Lake Grove, the ME of the probability distribution for seedling density was 16,988 (90% CI: 9,595–35,181 seedlings/ha), with an MP of New Oriole Lake Grove seedling densities being equivalent to those observed in the second year after prescribed fire of 27.2%.

We found similar results from our 2023 seedling count resurvey for all previously sampled plots within Redwood Mountain, Suwanee, and New Oriole Lake groves. The second-year (2023) seedling density ME for Redwood Mountain Grove was 9,572 (90% CI: 6,718–13,419 seedlings/ha), with an MP of seedling densities being equivalent to those observed in the second year after prescribed fire of 2.6%. Similarly, the second-year (2023) seedling density ME for Suwanee Grove was 7803 (90% CI: 5532–11,688 seedlings/ha), with an MP of seedling densities being equivalent to those observed in the second year after prescribed fire of 1.0%. The second-year (2023) seedling density ME for New Oriole Lake Grove was 3058 (90% CI: 1805–5872 seedlings/ha), with an MP of seedling densities being equivalent to those observed in the second year after prescribed fire of <0.1%.

Estimating local seedling densities

We found that giant sequoia seedling densities increased with increasing volumes of “neighborhood” canopy that was live and scorched (see Appendix S1: Figure S2). The relationship was “noisy,” but, for both fires, marginal probabilities strongly suggest the relationships between seedling densities and live canopy (98.6% and 87.8% marginal probability of the parameter being greater than 0 for the SQF and KNP fires, respectively) and scorched canopy (100% and 93.8% MP > 0) are real. Not surprisingly, we did not find a relationship between seedling densities and torched canopy (55.8% and 68.6% MP < 0), as we presume crown torching results in the combustion of seed-bearing cones. These results are consistent with scorched giant sequoia crowns having intact, heat-killed cones that release abundant viable seed, thus yielding higher local seedling densities (see *Introduction* and *Discussion*). We also found that across groves, the volume of scorched foliage decreased (97.8% MP < 0) and the volume of torched foliage increased (99.9% MP > 0) with increasing RdNBR (Figure 5), indicating that RdNBR was sensitive to an increasing percentage of torched foliage (i.e., as fire severity increased, more of the crown was

directly consumed by fire, leaving less scorched foliage and cones).

Not surprisingly, we also found a strong relationship between seedling density and RdNBR in both the SQF-affected (2020) Board Camp and KNP-affected (2021) Redwood Mountain, Suwanee, and New Oriole Lake groves (Figure 4), with seedling densities and the variability in seedling densities decreasing with increasing RdNBR. In general, across our sampled range, the probabilities of seedling densities reaching the average levels seen the second year after prescribed fires are very low, with the occurrence of any plots with relatively high seedling densities dropping noticeably for RdNBR values above 800 in Board Camp Grove and above 1100 in the other groves (Figure 4, Table 2). For our fitted seedling density to RdNBR relationship within Board Camp Grove, we excluded one outlier plot that had a very high density of seedlings in an area with a relatively low volume of local crown scorch and a relatively high value of RdNBR (note: these data are included in our ME of seedling density for the grove). This outlier, which was observed within a drainage bottleneck that captured water washed seed fall, along with a high degree of data variance or “noise,” generally suggests additional mechanisms beyond local crown scorch that can affect local seedling occurrence (see *Discussion*), but our data indicate that such mechanisms, while almost certainly causing an increase in variability, rarely result in high local seedling densities in areas of very high-severity fire (Figure 4).

Grove-level tree mortality

We completed a full survey of giant sequoia mortality and crown fire damage at Board Camp, Suwanee, and New Oriole Lake groves, and within 50 m of each study plot center in Redwood Mountain Grove. Tree mortality was 81.5% (198/243), 48.1% (163/339), and 45.3% (29/64) within the entire grove areas of Board Camp, Suwanee, and New Oriole Lake groves, respectively (see Appendix S2 for details). However, within the high burn severity portions of each grove (>640 RdNBR, see Miller & Thode, 2007), sequoia mortality rates were much higher—96.8% (153/158), 62.7% (69/110), 84.8% (28/33), and 92.8% (425/458) in Board Camp, Suwanee, New Oriole Lake, and Redwood Mountain groves, respectively. We found a very strong relationship between RdNBR and tree mortality (Figure 5), and, as expected, mortality was high across the high-severity zones. Specifically, across all groves, the majority of sampled plots within areas of ~800 or greater RdNBR had 0 surviving sequoias and/or the “neighborhood” volume of live foliage dropped precipitously to near 0

(e.g., a single live “neighborhood” giant sequoia with 10% remaining live foliage) (Figure 5). This relationship, combined with the negative relationship between RdNBR and seedling density, allows us to produce a RdNBR-based heat map (Figure 6) indicating areas with a high probability of both complete tree mortality and low levels of regeneration (Figures 4 and 5).

DISCUSSION

A permanent or long-term loss of the giant sequoia grove area would be a consequence of giant sequoia tree mortality followed by a failure of natural regeneration. In that context, our results suggest that areas that experienced high-severity fire in both the SQF-affected Board Camp Grove and KNP-affected Redwood Mountain, Suwanee, and New Oriole Lake groves appear to be at substantial risk for loss of grove area. Mortality was very high in the high burn severity patches in all groves sampled, and high-severity areas comprise 17.8 ha and ~92% of the grove area in Board Camp Grove and 142.0, 14.6, and 1.6 ha and ~28%, ~40%, and ~46% of Redwood Mountain, Suwanee, and New Oriole Lake groves, respectively. Furthermore, our data (sampled grove-wide at Board Camp, Suwanee, and New Oriole Lake, and in high burn severity areas in Redwood Mountain groves) indicate that overall seedling densities likely fall far below those typically seen the second year after prescribed fire (Table 1; Stephenson et al., 2023), where regeneration was almost certainly adequate to maintain giant sequoia populations (York et al., 2013) and postfire conditions were more in keeping with historical norms (Stephenson, 1996).

More in-depth analyses suggest that the risk of regeneration failure increases with increasing fire severity, at least partly as a function of reduced seed availability due to direct consumption of cones during the fire. In Board Camp Grove, mortality and high probability of regeneration failure covered much of the northern and eastern parts of the grove (Figure 6). For Redwood Mountain Grove, areas at highest risk for grove loss occurred mostly in the southern part of the grove. Within Suwanee and New Oriole Lake groves, inadequate natural regeneration and loss of parent seed trees was not as severe, comparatively, but still showed a substantial risk of some grove area loss in several portions of Suwanee Grove and the northern and southern extents of New Oriole Lake Grove (Figure 6). Importantly, the pattern of tree mortality in Suwanee Grove, and to a lesser extent in New Oriole Lake Grove, was less contiguous—often leaving some live and mature giant sequoia trees in or near high-severity

patches. In such cases, regeneration failure should be less likely to lead to permanent loss of grove area, as existing seed trees remain as a source of replenishment after future fires—so long as those fires are in keeping with the heterogeneous, mixed-severity fire regimes within which giant sequoias evolved.

As is common with regeneration data, there is considerable variability or “noise” in the dataset. This argues strongly for robust data collection (e.g., we collectively counted all seedling across nearly 6 ha of territory using a robust spatial sampling design) and the use of statistical methods well-suited for characterizing uncertainties in an easily interpretable manner. For example, Figures 3–5 illustrate how data depth and inherent variability affect the confidence in our estimates. Nevertheless, it is clear that natural regeneration is very unlikely to reach historical densities in any of the sampled areas.

Moreover, while the assessment of overall seedling densities can help managers determine the extent to which a grove is regenerating postfire, the spatial distribution of seedlings will play an important role in determining the extent to which those seedlings result in successful recruitment across the affected area. Given the significant space required for a giant sequoia to grow and mature, the number of giant sequoias that can be recruited at a particular site will be limited, especially with higher postfire seedling densities. As is reflected in our data, and within the literature on giant sequoia regeneration, the spatial distribution of seedlings is highly clumped (Harvey et al., 1980). This functionally translates to postfire areas with sparse or no seedlings interspersed with occasional high-density seedling patches. In a low- or moderate-severity fire, where the vast majority of adult trees survive, such regeneration is likely adequate for replacing lost trees and a return to a state resembling the previous grove structure. However, in the context of a large, high-severity burn where the vast majority of large trees have died, the clumped nature of giant sequoia seedlings might be highly concerning, possibly resulting in isolated patches of successful recruitment rather than the more widely distributed recruitment that would be required to restore the affected grove area to its pre-disturbance structure and function. In other words, for large, high-severity burn patches, the mean number of seedlings alone probably overestimates the potential for long-term postfire recovery. As such, the decision-making criteria of managers interested in restoring severely affected grove areas would likely benefit from also considering the spatial distribution of the regeneration (i.e., data skewness or clumped spatial distribution).

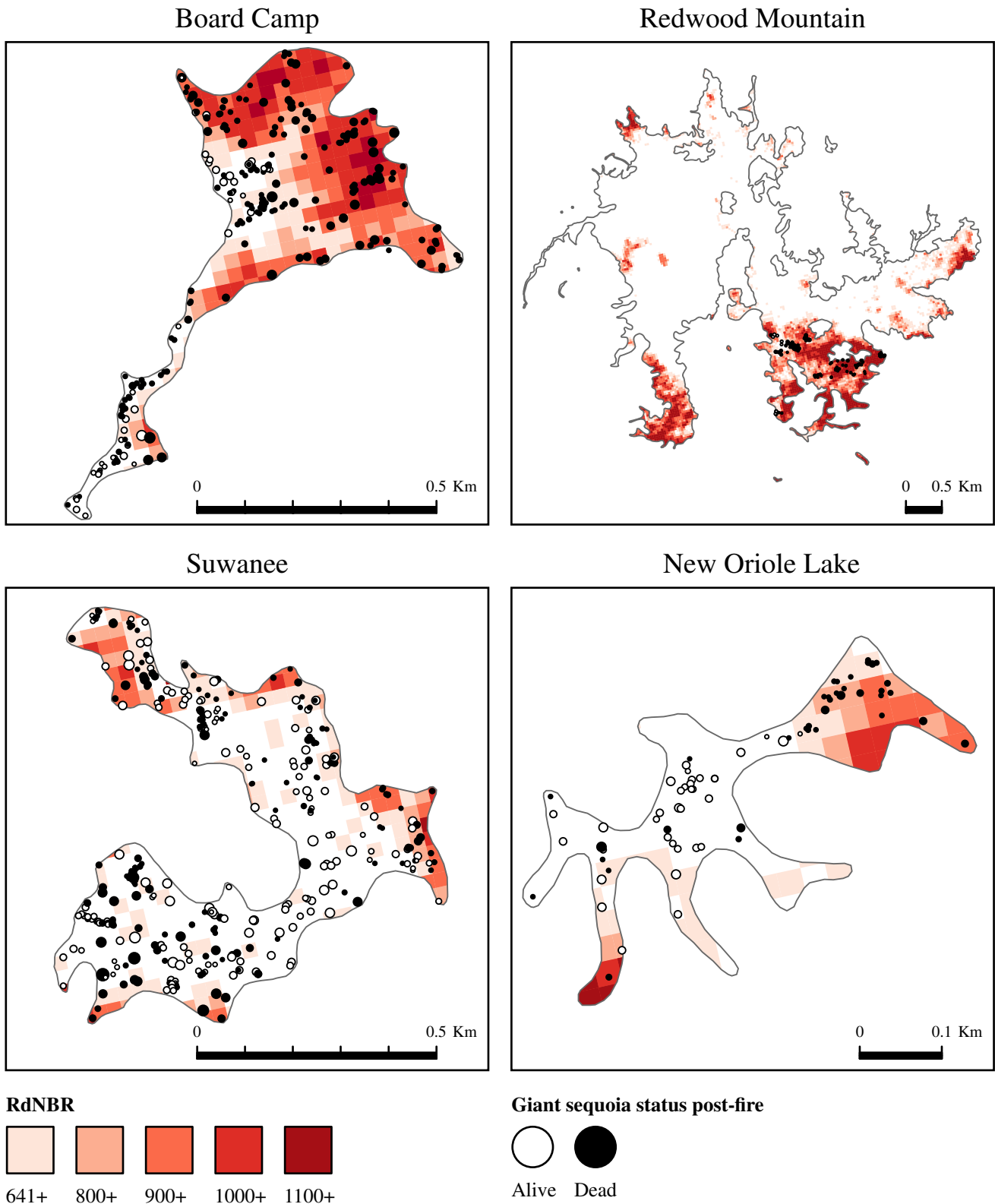


FIGURE 6 Giant sequoia stem map and categorized relativized differenced normalized burn ratio (RdNBR) within high burn severity (>640 RdNBR) areas within surveyed groves: Board Camp, Redwood Mountain, Suwanee, and New Oriole Lake groves, Sequoia and Kings Canyon National Parks, CA. Mapped giant sequoias are color coded by live/dead status. High-severity burn areas are presented in red tone, with increasingly dark color tone indicating increasing burn severity categorization. Grove depictions are centered on the north.

Mechanisms

We hypothesized, based on previous research, that seedling densities would in part be a function of the availability of seeds from giant sequoia cones killed by a heat pulse into the crown, as such cones are known to be an important source of seed release postfire (Hartesveldt et al., 1975; Harvey et al., 1980; Stark, 1968). Due to the great height of giant sequoia tree canopies, there was no practical way to count cones directly. We therefore further hypothesized that scorched foliage—foliage killed by a heat pulse into the crown—should be associated with heat-killed cones, and therefore, subsequent seedling densities. Though the relationships have substantial inherent variability, our results were generally consistent with this hypothesis (Figure 4, Appendix S1: Figure S2), with our remote sensing analysis providing further support (see below).

The noise in the scorch-seedling density relationship is likely the result of a variety of factors, including tree-to-tree variation in cone crops among sequoias, as well as inherent error in our dbh-based crown volume allometry and in visual estimations of crown conditions from ground observations. This may explain why the relationship between RdNBR and seedling density (Figure 4) was less noisy than relationships derived from ground-based measures (Appendix S1: Figure S2). In addition, our approach assumed crown scorch volume was linearly related to heat-killed cones, an assumption that may not hold in practice, and our method would also not capture tree-to-tree variability in cone load, which can be substantial (Sillett et al., 2019). Finally, and perhaps most importantly, there are additional ecological “filters” between seed fall and seedling establishment—with a variety of factors that might weaken the relationship between local seed production and local seedling establishment (see *Uncaptured mechanisms*).

Extrapolating within and across groves using remote sensing

Our analysis supports the hypothesis that greater scorched crown volume results in increased seed rain, and therefore, higher seedling densities (Appendix S1: Figure S2). In addition, our results show that, within high-severity areas (RdNBR > 640), RdNBR values reflect the level of crown scorch and torch (Figure 5). As noted above, the relationships between RdNBR and seedling density were in fact less noisy than those developed using ground-based measures (Figure 4, Appendix S1: Figure S2). Because the majority of our data were collected in areas classified as having experienced high-severity fire

(i.e., most, if not all, of the standing trees were killed in the fire), relatively lower RdNBR values in the context of our samples meant that dead trees had retained more scorched foliage while higher RdNBR values indicated that an increasing percentage of the crowns, and therefore cones, had been torched (i.e., consumed directly by fire).

While the effects of wildfire severities are often classified into broad categories (e.g., low, moderate, high), our data highlight the importance of using more interpretive nuance within the high-severity burn category (also see “Composite Burn Index,” Key & Benson, 2006 and “Relativized Burn Ratio,” Parks, Dillon, & Miller, 2014). In the context of giant sequoia regeneration and resilience, the canopy conditions generally created by the lower end of high burn severity (e.g., ~641–800 RdNBR), where the crowns of large sequoias are intact, have significantly different facultative effects on postfire regeneration and stand resilience—specifically, the retention of seed source and live mature trees—relative to the higher ends of the high-severity gradient (i.e., “very high-severity fire”), where increases in canopy torching and large tree mortality affect the ability to regenerate in both the near and long term (Figure 5; Appendix S2: Figure S2).

In short, our results indicate that RdNBR can be used to estimate seedling densities within high-severity areas of Board Camp, Redwood Mountain, Suwanee, and New Oriole Lake groves. Similarly, RdNBR was highly effective in detecting adult giant sequoia mortality (Figure 5) within all sampled groves. Given that RdNBR is a standardized measure used across fires, one would expect these relationships to be effective across other burned groves. This suggests RdNBR—taken as a continuous variable rather than by broad fire severity categories—is a useful tool for assessing the likely adequacy of sequoia regeneration in any giant sequoia grove after a wildfire.

Using RdNBR to estimate giant sequoia regeneration densities does have limitations. RdNBR values can be influenced by shadows, clouds, and other atmospheric disturbances (Fassnacht et al., 2021; Hoy et al., 2008; Verbyla et al., 2008). Also, as RdNBR does not distinguish between giant sequoias and other canopy vegetation, spectral changes in other parts of the canopy and/or understory could give misleading results. For example, RdNBR from a relatively open patch dominated by shorter canopy trees or shrubs and possessing relatively few giant sequoias might indicate a high-severity burn even if the fire did not do substantial damage to taller giant sequoias. Additionally, RdNBR-derived estimates of giant sequoia regeneration densities are highly variable at lower values (<641), leading to greater uncertainty in densities in low- to moderate-severity burn patches—although, arguably, these areas are of less concern to resource managers because canopy tree mortality

is lower. Finally, other factors particular to a given fire and time period might affect the relationship between RdNBR and seedling densities (see “Large-scale and anomalous drivers of regeneration”). For these reasons, we strongly suggest pairing RdNBR-based regeneration estimates with field validation to provide more reliable estimates of postfire giant sequoia regeneration densities for a given fire and year. For example, how might these relationships change in relatively large groves that burned primarily at high severity? How do differences in local factors (see *Uncaptured mechanisms*) scale for groves with different topographic profiles?

Uncaptured mechanisms

Mechanisms beyond local crown scorch can affect interannual seedling abundances within and between giant sequoia groves. In addition to among-tree variation in seed release, variability in abiotic factors such as topography (Marsh, Krofcheck, et al., 2022), soil characteristics (Certini, 2005; Gates, 1982), fuel-mediated microsites (Gray & Spies, 1997), local climates (e.g., aspect-driven) (Helgerson, 1990; Wolf et al., 2021), and moisture conditions (Stielstra et al., 2015) can either facilitate or impede germination success—especially during the summer immediately following wildfire when seedlings are most vulnerable to abiotic stressors (Hartseveldt & Harvey, 1967; Harvey et al., 1980).

Anecdotal observations by our field crews indicated that high-density patches of seedlings within a plot often occurred within watercourse bottlenecks, which function as moist deposition sites for seeds caught in runoff. In addition, high-density patches were common within soil compressions where a log was partially or fully combusted (see Harvey et al., 1980), suggesting that prefire fuels can mediate postfire seedling densities. Such mechanisms likely help explain the substantial variability in seedling occurrence, even in areas that otherwise appeared to have enough live and scorched canopy to result in higher levels of seed release and subsequent high seedling densities. Importantly, these highly local effects might also have bearing on the eventual success of maturing seedlings. For example, there is reason to question the viability of even high-density patches of seedlings that occur near creek bottoms, as such areas are likely to experience substantially increased stream flow, and subsequent mortality of initially established seedlings, in high precipitation years.

Our data also indicate that—on rare occasions—patches of high seedling density can occur even when local crown conditions indicate otherwise. For example, one of the sampling plots in Board Camp Grove had a

particularly high seedling density, having more than double (~2.2×) the count of any other plot, despite local live and scorch crown and RdNBR values indicating that the availability of seeds should have been limited. Plausible explanations include the transport of seeds from an area with higher seed production via seasonal stream flow and downslope seed rain dispersal. Board Camp Grove is on a particularly steep slope (mean slope within grove: 27.7°) and is riddled with numerous drainages. Our “outlier” plot was located within one of these drainages (mean slope within plot: 34.4°) and downslope of trees with enough remaining scorched crown volume to have potentially produced large numbers of viable seeds.

Large-scale and anomalous drivers of regeneration

Our results suggest that the burn severity metric RdNBR can be predictive of giant sequoia seedling densities following wildfire. However, in addition to small-scale drivers facilitating regeneration success, the magnitude of the relationship between burn severity and seedling densities can be additively, and perhaps substantially, influenced by variation in more global conditions such as trends in regional climate (see Avery et al., 2023) and their potential interactions with giant sequoia ecology (Harvey et al., 1980). A recent climate assessment encompassing all giant sequoia groves within Sequoia and Kings Canyon National Parks (Stephenson et al., 2023) found that the meteorological summers (June, July, August) following the SQF and KNP wildfires were anomalously hot and dry, suggesting that seedlings that germinated in 2021 and 2022—in the summers following the 2020 SQF and 2021 KNP wildfires—were subject to the first and third hottest (mean degrees Celsius), and first and second driest (Palmer Drought Severity Index, PDSI; Palmer, 1965) summers within the 121-year record.

Moreover, seed trap data from giant sequoia groves within Sequoia National Park (Wright et al., 2021), along with NPS communications, suggest there was a region-wide seed release event (non-masting) before the KNP wildfire, with >10× increase in giant sequoia seed fall relative to the annual mean of the prior 22 years (see Stephenson et al., 2023). While giant sequoias release viable seed year-to-year (Harvey et al., 1980; van Mantgem et al., 2006; Wright et al., 2021), possibly triggered by the ambient feeding of Cerambycid beetles (*Phymatodes nitidus*) and/or squirrels (e.g., *Tamiasciurus douglasii*) (Harvey et al., 1980), such an uptick in seed release in the absence of fire-related stimuli is unprecedented.

Although the causal mechanisms of the seed release event are unknown, the extreme heat and aridity of the 2020 and 2021 meteorological summers may have induced a physiological response to release seed en masse. Moreover, the mid-summer seed release in the absence of fire-mediated bare mineral soil would not favor germination (Hartesveldt & Harvey, 1967; Stohlgren, 1993) and may have contributed to a depletion of the seed stock before the ensuing KNP wildfire.

Given the extremely hot and dry climate window, when postfire seed stock may have been low, postfire seedling densities in the groves sampled here could be relatively low compared with what might be found in cooler and wetter conditions and in the absence of a prior large-scale and likely unproductive seed release. As such, as noted above, it is important that any remote sensing analysis is paired with robust ground data collection to provide an accurate quantification of giant sequoia postfire regeneration after a given fire.

That said, we would expect RdNBR to remain a useful planning tool, regardless of other factors. RdNBR should still be indicative of increasing giant sequoia mortality. In addition, the metric should still have a relationship with tree scorch and torch, and therefore, local seed availability. In other words, for any fire, we expect increasing RdNBR, at least within the range of high severity, will be associated with increasing risk of grove area loss, with only the degree of that risk varying with other conditions.

Assessing long-term resilience

While assessing seedling densities and the drivers of postfire regeneration is important for understanding the immediate trajectory of potential grove recovery, natural resource managers are also understandably concerned with long-term grove resilience (DeRose & Long, 2014). Arguably, one of the best indicators of such resilience is the retention of seed-producing trees, which allow for “second chances” when a given regeneration cohort fails.

For example, high burn severities can facilitate conditions favorable for seed release and soil conditions for germination, while simultaneously killing a large proportion of the seed-producing parent trees, resulting in a lack of resilience to future disturbance. Figure 4 shows that high local postfire seedling germination can occasionally occur within high burn severity areas (~800 RdNBR), while Figure 5 indicates that, at around the same RdNBR, the volume of remaining live foliage and the probability of remaining live sequoias drops precipitously to near zero. In general, giant sequoias require decades of maturation before producing seed (Harvey et al., 1980), with the majority of seed produced by centuries old trees (Sillett et al., 2019, see Clark

et al., 2021). As such, large grove areas with high levels of seedling germination but low levels of remaining live seed trees may not be resilient to near-term natural disturbances (e.g., fire, drought, high precipitation). Moreover, stand long-term resilience can be negatively affected by fuel conditions following high-severity burns. Resultant shrub dominance interspersed with snags and logs (Coppoletta et al., 2016; Parks, Miller, et al., 2014) can facilitate a feedback loop of sequential high-severity fires (Holden et al., 2010; van Wagtenonk et al., 2012) that inhibit postfire recovery through continued reduction in seed availability (Davis et al., 2023), short-interval reburning that eliminates postfire regeneration (Coop et al., 2020), and microsite refugia within which seedling establishment is dependent (Blomdahl et al., 2019; Kolden et al., 2012). Even in typical conditions, natural regeneration is subject to very high mortality (Harvey et al., 1980), especially compared with nursery-grown seedlings, which tend to survive at much higher rates, in part because they are planted at a maturation stage that is less vulnerable to mortality from desiccation or erosion (Marsh, Crockett, et al., 2022; Ouzts et al., 2021; York et al., 2007).

The location and size of fire-caused gaps in the context of the broader grove is also an important consideration. Giant sequoia seedling germination and survivorship have been associated with canopy gaps (Demetry, 1995; Harvey et al., 1980; Meyer & Safford, 2011; Stephenson et al., 1991; York et al., 2011); however, it is uncertain whether this association holds for the large canopy gaps produced by the large high-severity burn areas of recent fires (e.g., Cova et al., 2023). Fire-produced gaps can facilitate germination and survivorship (Hartesveldt et al., 1975; Harvey & Shellhammer, 1991; Shellhammer & Shellhammer, 2006) through increased understory light penetration, exposed mineral soil, and removal of shade-tolerant competitors from the forest understory (Harvey et al., 1980; Stephenson, 1994). However, larger gaps (e.g., more than a few hectares) contain areas considerably distant from the bulk of the seed shadow of living sequoias (Clark et al., 2021), with these larger areas potentially experiencing a more severe set of environmental conditions (e.g., reduced snow retention, see Smoot & Gleason, 2021; Stevens, 2017) that may have a negative, rather than positive, effect on giant sequoia seedling germination and establishment. Moreover, gaps created at the edge of a grove boundary have less perimeter adjacent to sequoias relative to gaps created internal to the grove boundary and are less likely to receive giant sequoia seed. In short, deciding whether to plant after a fire involves a nuanced assessment of seed tree mortality, postfire regeneration, probability of long-term seedling survival, topography, and their spatial characteristics.

Informing management

Giant sequoias present an interesting case study of how management challenges can evolve through time and how science informs decision-making. Decades ago, robust research on giant sequoias led to the realization that over a century of fire suppression had resulted in regeneration failure across much of the species' natural range (Harvey et al., 1980; Kilgore & Biswell, 1971; Stephenson, 1994). This led managers to implement prescribed burning programs to try to restore historical conditions and encourage more giant sequoia recruitment (Stephenson, 1996). Ultimately, many groves were not reached by these programs due to limited restoration treatment rates in Sierra Nevada forests (e.g., North et al., 2012). Now, groves that have not burned in well over a century are experiencing fires of a severity well outside the historical norm (Williams et al., 2023), and our research suggests that such fires are resulting in substantially reduced ecosystem resilience (i.e., failure of giant sequoia to regenerate following high-severity fire) and loss of grove area. In other words, managers may now be asking whether giant sequoia conservation and restoration might best involve not only prescribed burning, but also planting to concurrently reduce fuels and reestablish regeneration. As such novel conditions occur, managers often have an increased need for real-time data and comparisons with past conditions to inform management decisions.

In deciding whether to intervene, managers may balance agency management goals, directives, and budgets against the risk of permanent giant sequoia grove loss, and they may have only limited time to do so, as the growth of shrubs in high-severity burn patches could rapidly make proposed replanting areas inaccessible. For an agency like the National Park Service, especially managing within designated wilderness areas, this may include balancing goals and directives to maintain giant sequoia groves unimpaired for future generations with a desire to minimize human intervention. This decision-making is complicated by the fact that there is not enough information to set a precise minimum threshold that will guarantee regeneration success, and, even if there were, the inherent uncertainty in sampling seedling densities will always leave uncertainty in whether any given threshold has actually been met.

Traditional statistical approaches, which test mean estimates against a particular threshold at an arbitrary level of confidence, are not ideally suited to such situations. First, in a circumstance without definitive thresholds, managers are best served by approaches that allow simultaneous consideration of a variety of potential thresholds that can be determined based on the management context (e.g., the level of seed tree mortality or the

degree of public resistance to intervention). Furthermore, in a conservation context, managers are more likely to ask, "What is the probability that there are plenty of seedlings?" rather than "Can I prove with 95% confidence that my seedling densities are not high enough?"

In this study, we used a Bayesian statistical framework that allows us to assess probabilities of meeting any given management-relevant threshold (see Stephenson et al., 2023) while also explicitly quantifying the uncertainty (which is affected both by data variability and richness). Moreover, Bayesian modeling offers a more flexible and interpretable tool for managers to use in the context of conservation, where decision-making can be inherently subjective and challenging. Such an approach allows managers to explore a range of risk tolerances. For example, do we only want to intervene if there is less than a 25% probability that the mean seedling density falls above the threshold for successful regeneration, or would we choose a higher threshold because we consider the consequences of regeneration failure and the lost opportunity to act within the natural regeneration window of giant sequoia too great? Decisions regarding what risk level to set can involve trade-offs between costs of action versus costs of inaction made in the context of agency mandates, law, policy, and budgets. Having clearly identified probabilities regarding whether the mean is likely to meet an identified target can be very useful in these contexts. Managers may find this level of explicit risk analysis helpful in tackling these difficult conservation and management decisions.

Conclusion

Increasingly, forests in the Sierra Nevada are experiencing wildfires well outside the historical norm, with such fires affecting vast landscapes and potentially leading, without intervention, to permanent changes in vegetation composition and structure (Safford & Stevens, 2017). Managers are faced with responding to these events and deciding whether to intervene—often with only short windows in which action can be implemented practically and in the face of enormous uncertainty and public concern. Such circumstances demand robust data collection combined with analyses designed to quantify uncertainty in a way that is usable and informative for managers who must make pragmatic assessments about whether to act.

Here, we assessed postfire regeneration within four different giant sequoia groves significantly affected by the SQF- (2020) and KNP-Complex (2021) wildfires. We found significant spatial relationships between giant sequoia seedling densities, neighborhood canopy conditions, and the remotely sensed burn severity metric, RdNBR, and used those relationships to scale predictions of giant sequoia mortality and regeneration across unsampled

grove areas along a gradient of high burn severity. To help inform natural resource managers, we developed a Bayesian probabilistic modeling approach that directly quantifies the uncertainty surrounding modeled estimates of postfire regeneration that could potentially be scaled across groves and different fires.

Overall, this study advances our understanding of giant sequoia ecology and provides a statistical tool for informing management decisions regarding postfire restoration following severe, large wildfires. Going forward, if we are to gain a deeper understanding of giant sequoia regeneration in this new era, we will need to tease apart the relationships that drive high heterogeneity of seed germination on the landscape and gain a far better handle on the likely survivorship of such seedlings in the long term.

ACKNOWLEDGMENTS

We thank the many people involved in collecting field data, specifically the U.S. Geological Survey, Sequoia and Kings Canyon National Parks, and University of California, Davis field crews, and those maintaining the critical information used in this study. We also thank the Sequoia and Kings Canyon National Parks and the University of California, Merced Science & Conservation (SCICON) Field Stations for logistical support, and Martin Holdrege for statistical help. We are continually appreciative of the Sequoia and Kings Canyon National Parks' staff for decades of invaluable cooperation. This research was funded by the NPS and the US Geological Survey Climate Research and Development programs. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Soderberg & Das, 2023) are available from ScienceBase: <https://doi.org/10.5066/P96Z1PBK>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Soderberg, David N., Adrian J. Das, Nathan L. Stephenson, Marc D. Meyer, Christy A. Brigham, and Joshua Flickinger. 2024. "Assessing Giant Sequoia Mortality and Regeneration Following High-Severity Wildfire." *Ecosphere* 15(3): e4789. <https://doi.org/10.1002/ecs2.4789>