TITLE: Assessing giant sequoia mortality and regeneration following high severity wildfire

Authors: David N. Soderberg[1], Adrian J. Das[1], Nathan L. Stephenson[1], Marc D. Meyer[2], Christy A. Brigham[3], and Joshua Flickinger[3]

[1]U.S. Geological Survey, Western Ecological Research Center, Sequoia and Kings Canyon Field Station, Three Rivers, CA 93271, USA.

[2]USDA Forest Service, Southern Sierra Province Ecology Program, Bishop, CA 93514, USA.

[3]Sequoia and Kings Canyon national parks, Division of Resources Management and Science, Three Rivers, CA 93271, USA.

Corresponding author: David N. Soderberg (email: dsoderberg@usgs.gov).

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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 have 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 to 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) fires within Sequoia and Kings Canyon national parks. In total, we surveyed 5.9 ha for seedlings and assessed the crown condition of 1140 trees. 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 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 high severity fire (above ~800 RdNBR) are at substantial risk for 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 hectares 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 risk of grove loss, and in two groves, Suwanee and New Oriole Lake, the high severity patches were not always contiguous, potentially making some areas more resilient to regeneration failure due to the proximity of surviving trees.

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

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 (Stevens et al., 2017, Parks & Abatzoglou, 2020, Hagmann et al., 2021). A resultant increase in ground and standing fuels, coupled with increasing temperatures and aridity, have 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 mountains of California have been impacted by multiple fires of large extent that contained large patches that burned at high severity (Steel et al., 2022). Two of the largest recent fires within the southern Sierra Nevada, the SQF- 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 hectares, of which ~47,000 hectares were classified as 'high 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 fuels 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 of seed source, biodiversity, and wildfire and climate resilience (Cova et al., 2022). 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 (Keeley & Syphard, 2021, Safford et al., 2022, Stephens et al., 2022). 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 hectares in ~70 groves across the western slope of the Sierra Nevada (Stephenson & Brigham, 2021), much of which resides within the boundaries of Sequoia National Park, CA (Hart, 2023). Due to their tremendous size, longevity, and limited distribution, these charismatic macro-flora have inspired much public admiration and been central to the designation of state parks, national monuments, and national parks (Stephenson, 1996). Specifically, they were instrumental in the 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 et al., 1991, Stephenson, 1994, Stephenson, 1996), with a mean fire return interval 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, and 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 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 is referred to as 'torching'. Indeed, post-fire 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-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' [>4ft. diameter] giant sequoias; Stephenson & Brigham, 2021, Shive et al., 2022) – a situation that is likely anomalous as giant sequoia is a fire-adapted species that can live for thousands of years (Stephenson 2000, Sillett et al. 2015) and is in substantial contrast to more conservative mortality estimates from previous prescribed burns, wildfires, and tree-ring records (Stephenson 1996) – there is uncertainty around whether large areas of high-severity fire impacted groves will naturally regenerate to a state resembling their pre-fire 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, tree mortality, and tree fire damage in four groves recently affected by the SQF and KNP fires. Importantly, all these groves are candidates for intervention. Our goal was to assess overall, postfire giant sequoia regeneration within our sampled areas and to develop predictive models of regeneration as a function of neighborhood metrics of scorched crown volume and a remotely sensed metric of fire burn severity -- RdNBR (relativized differenced normalized burn ratio; 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) that would reduce the available supply of viable giant sequoia seeds. This would result in some severely burned grove areas with low probabilities of mean regeneration meeting 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.

METHODS

Study area

The California Sierra Nevada contains ~70 known 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 within 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 1,2).

Seedling sampling

To survey post-fire 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 relative differenced normalized burn ratio (RdNBR; Miller & Thode, 2007) for the sampling design because extended assessment data (growing season following the fire) was not available before sampling commenced. However, the two metrics are largely consistent (Miller & Quayle, 2015). Plots in Redwood Mountain 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 2021 SQF fire-affected Board Camp grove on April 27-28, 2022. We surveyed the 2022 KNP fire-affected Redwood Mountain, Suwanee, and New Oriole Lake groves within a 6-week span on Sept. 1-7, Sept. 25 – Oct. 5, and Oct. 12, 2022, 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: 17.84m radius, 1/10thha, 20 plots; Redwood Mountain: 11.35m radius, ~1/25thha, 45 plots, 17.84m radius, 1/10thha, 1 plot; Suwanee: 11.35m radius, ~1/25th ha, 30 plots; New Oriole Lake Grove: 11.35m radius, ~1/25th ha, 20 plots; total sampled area: ~6 hectares). Generally, a plot radius of 11.35m was used, with an increased radius of 17.84m used when seedling counts were sparse (i.e., entirety of Board Camp grove, when ≤2 seedlings were counted within initial 11.35m plot). Any tree less than 1.37m in height was considered a seedling, though no seedlings in these surveys exceeded 30cm tall. Given that (1) sequoias very rarely regenerate without fire (Harvey et al., 1975, Shellhammer & Shellhammer, 2006), (2) severe fire likely killed all existing seedlings, and (3) the small stature of all the seedlings counted, we were confident that all seedlings had recruited postfire. In Board Camp, since sampling occurred two years after the fire, existing seedlings could have 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. Based on the lack of cotyledon leaves on any Board Camp 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., diameter at breast height) to assess post-fire giant sequoia tree damage and mortality. 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 damage data were recorded only for giant sequoias within 50m of study plot centers. For each tree in the survey, we recorded the tree status (live/dead) and % 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 (m^3) for each giant sequoia in our dataset using diameter values from STI and an allometric equation relating tree diameter to crown volume (m^3) (Sillett et al., 2019, see Appendix S1: Figure S1). To calculate crown volume 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, respectively, we summed all tree crown volume estimates for all giant sequoia within the 50-meter 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 Monitoring Trends in Burn Severity (MTBS; www.mtbs.gov). MTBS raster datasets are generated from Landsat (TM/EMT+/OLI) image data which is acquired at a spatial resolution of 30 meters. 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 (Eq.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 1,2).

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 seedlings densities as a function of the burn severity metric 'RdNBR' (see Miller & Thode, 2007) (Eq. 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 (GLM) 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 50m radius of plot center) as a function of RdNBR (Eq. 2, Figure 5). Crown volumes of individual giant sequoias were calculated using an allometric equation derived from Sillett et al., (2016) (Eq. S1, Figure S1), with individual crown volumes of live, torched, and scorched 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 (i.e., 'CVS', see Harvey et al., 1980), we assessed the relationship between neighborhood crown volume scorch and RdNBR to bridge the mechanistic rationale underpinning an association between seedling density and RdNBR using the same GLM approach described above (Eq. 3 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 parameter 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 via the following link function:

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

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

where $\log(T_i)$ is an 'offset', which corrects for the variation in surveyed area amongst *i*th observations, α is the 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:

$$\mu SDens_i \sim \text{Normal } (\mu SDens, SDens\sigma^2) \quad (4)$$

$$\mu CVL_i \sim \text{Normal } (\mu CVL, CVL\sigma^2) \quad (5)$$

$$\mu CVS_i \sim \text{Normal } (\mu CV\text{T}, CVT\sigma^2) \quad (6)$$

$$\mu CVT_i \sim \text{Normal } (\mu CVS, CVS\sigma^2) \quad (7)$$

$$\mu RdNBR_i \sim \text{Normal } (\mu RdNBR, RdNBR\sigma^2) \quad (8)$$

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

$$\mu SDens, \mu CVL, \mu CVS, \mu CVT, \mu RdNBR \sim \text{Normal } (0,1000) \quad (9)$$

With the exception of the variance parameters, which were given a modest, Student-t prior distribution: Specifically:

$$SDens\sigma^2, CVL\sigma^2, CVS\sigma^2, CVT\sigma^2, RdNBR\sigma^2 \sim \text{Student-t}\ (0,3) \qquad (10)$$

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

Using Bayesian MCMC estimates, a median estimate and quantified uncertainty were derived for each model parameter. The median estimate (ME) and 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 mean estimate of a parameter (e.g., slope coefficient for the relationship between a response and predictor variable) is statistically different (greater or less than) than zero. MP was estimated by calculating the total number of parameter MCMC estimates greater (or less) than the test comparison (e.g., ‘0’), divided by the total number of MCMC estimates. 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., in prep).

RESULTS

Seedling Overview

Our seedling surveys 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, ~1.5% of the high burn severity area was surveyed. 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 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 19282 seedlings across ~1.9 ha of the ~350ha of high severity burn area. Within the 30 plots in Suwanee grove, we counted 14239 seedlings across ~1.2 ha. Within the 20 plots in New Oriole Lake grove, we counted 13025 seedlings across ~0.8 ha (Table 1). In general, seedling surveys within the KNP (2021) affected 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 exposure to mortality.

Estimating overall seedling densities

To provide conservative comparisons, we contrast second cohort reference densities presented in Stephenson et al., (in prep) 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 (2020) affected Board Camp grove, the modeled median of the probability distribution for seedling density was 1609 with a 90% credible interval (CI) of 1749 to 4709 seedlings/ha. For comparison, the estimated mean seedling density in the first year after prescribed fire (Stephenson et al., in prep) was 173742 (90% CI: 73468 – 605985) seedlings/ha with median second cohort seedling densities of 39562 (90% CI: 16357 – 133134) seedlings/ha.

We found the marginal probability of Board Camp seedling densities being equivalent to those the second year after prescribed fire was <0.1%.

For the KNP (2021) affected high burn severity area of Redwood Mountain, the modeled median of the probability distribution for seedling density was 10541 (90% CI: 7412 – 15678 seedlings/ha), with a marginal probability of Redwood Mountain seedling densities being equivalent to those the second year after prescribed fire of 1.1%. Within Suwanee grove, the median of the probability distribution for seedling density was 11769 (90% CI: 7487 – 20000 seedlings/ha), with a marginal probability of Suwanee seedling densities being equivalent to those the second year after prescribed fire of 2.4%. Within New Oriole Lake grove, the median of the probability distribution for seedling density was 16988 (90% CI: 9595 – 35181 seedlings/ha), with a marginal probability of New Oriole Lake seedling densities being equivalent to densities the second year after prescribed fire of 11.2%.

Estimating local seedling densities

We found that seedling densities increased with increasing volume of ‘neighborhood’ crown scorch. The relationship was ‘noisy’ (see Appendix S1: Figure S2), but, for both fires, marginal probabilities strongly suggest the relationship is real (100% and 93.8% marginal probability of the parameter being greater than 0 for the SQF and KNP fires, respectively). This result is 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% marginal probability of being <0) and the volume of torched foliage increased (99.9% marginal probability of being >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 (2020) affected Board Camp and KNP (2021) affected 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 probability of seedling densities reaching the average levels seen the second year after prescribed fires is very low, with the occurrence of any plots with relatively high seedling densities dropping noticeably for RdNBR values above 800 in Board Camp 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. This outlier, and high degree of data variance or 'noise', generally suggests additional mechanisms beyond local crown scorch that can affect seedling occurrence (see Discussion), but our data indicate that such mechanisms, while almost certainly causing an increase in variability, rarely result in high seedling densities in areas of very high severity fire (Figure 4).

Grove-level tree mortality

We completed a full survey of tree mortality and crown fire damage at Board Camp, Suwanee, and New Oriole Lake groves, and within 50m of each study plot center in Redwood Mountain grove. Tree mortality was 81.0% (230/284), 43.6% (144/330), and 43.1% (28/65 within the entire grove areas of Board Camp, Suwanee, and New Oriole Lake groves, respectively. However, within the high burn severity portions of each grove (>640 RdNBR, see Miller & Thode, 2007), tree mortality rates were much higher – 91.4% (169/185), 60.6% (60/99), 76.7% (23/30), and 90.5% (417/461) of Board Camp, Suwanee, New Oriole Lake, and Redwood Mountain groves. 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 4,5).

DISCUSSION

A permanent or long-term loss of 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 hectares and ~90% of the grove area in Board Camp and 142.0, 14.6, 1.6 hectares and ~13.5%, 52.7%, and ~27.0% 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 severity areas in Redwood Mountain) indicate that overall seedling densities likely fall far below those typically seen the second year after prescribed fire (Table 1 and Stephenson et al., in prep), 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 risk of regeneration failure increased with increasing fire severity, likely 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 part of the grove (Figure 6). For Redwood Mountain, 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 and the northern and southern extents of New Oriole Lake (Figure 6). Importantly, the pattern of tree mortality in Suwanee, and to a lesser extent New Oriole Lake, 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 surveyed nearly 6 ha of territory using a robust spatial sampling design) and use of statistical methods well-suited for characterizing uncertainties in an easily interpretable manner. For example, Figures 3, 4, and 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 numbers in any of the sampled areas.

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 (Stark, 1968, Hartesveldt et al., 1975, Harvey et al., 1980). 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 1: 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 1: 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 1: 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 1: Figure S2). Since 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).

In short, our results indicate that RdNBR can be used to estimate seedling density within high severity areas of Board Camp, Redwood Mountain, Suwanee, and New Oriole Lake groves. Similarly, RdNBR was highly effective at 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 powerful tool for assessing the 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 (Hoy et al., 2008, Verbyla et al., 2008, Fassnacht et al., 2021). 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 (<640), leading to greater uncertainty in densities in low to moderate severity burn patches – although, arguably, these areas are of less concern to resource managers since 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 post-fire 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

There are mechanisms beyond local crown scorch that 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 et al., 2022), soil characteristics

(Gates, 1982, Certini, 2005), fuels-mediated microsites (Gray & Spies, 1997), local climates (e.g., aspect-driven) (Helgerson, 1990, Wolf et al., 2020) 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 (Hartesveldt & 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 water 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 pre-fire fuels can mediate post-fire seedling densities. Such mechanisms likely help explain the substantial variability in seedling occurrence, even in areas which otherwise appeared to have enough crown scorch 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 densities can occur even when local crown conditions indicate otherwise. For example, one of the sampling plots in the Board Camp grove had a particularly high seedling density, having more than double (~2.2x) the count of any other plot, despite local crown scorch 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 upslope seed rain dispersal. The 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., in prep) 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 1st and 3rd hottest (mean °C), and 1st and 2nd 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 ~10x increase in giant sequoia seed fall relative to the annual mean of the prior 22 years (Stephenson et al., in prep). 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 (*Phymatomes nitidus*) and/or squirrels (e.g., *Tammiasciurus douglasii*) (Harvey et al., 1980), such an uptick in seed release in the absence of fire-related stimuli is unprecedented. While 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 caused the depletion of a significant portion of the seed stock before the ensuing KNP wildfire.

Given the extremely hot and dry climate window, when post-fire seed stock may have been low, postfire seedling densities in the groves sampled here could be relatively low compared to what might be found in cooler and wetter conditions and absent 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 post-fire 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 levels of 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. Given the decades of maturation required for sequoias to produce seed (Harvey et al., 1980; see Sillett et al., 2019, Clark et al., 2021), 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). Even in typical conditions, natural regeneration is subject to very high mortality, especially compared to nursery-grown seedlings, which tend to survive at much higher rates, in part because they are planted at a maturation stage which is less vulnerable to mortality from desiccation or erosion (York et al., 2007, Ouzts et al., 2015, Marsh et al., 2021).

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 (Harvey et al., 1980, Stephenson et al., 1991, Demetry, 1995, Meyer & Stafford, 2011, 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., 2022). 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 Stevens, 2017, Smoot & Gleason 2021) 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 or not to plant after a fire involves a nuanced assessment of seed tree mortality, post fire 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 (Kilgore and Biswell, 1971, Harvey et al., 1980, 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. Now, groves that haven't burned in well over a century are experiencing fires of a severity well outside the historical norm, and our research suggests that such fires have a substantial probability of resulting in loss of grove area. In other words, managers may now be asking whether giant sequoia conservation might best involve, not only prescribed burning, but also planting. 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 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., in prep) 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 regeneration 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 tradeoffs 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 helpful 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 and 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 efforts 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 post-fire regeneration within four different giant sequoia groves significantly affected by the SQF- (2020) and KNP-Complex (2021) fires. We found significant spatial relationships between giant sequoia seedling densities, neighborhood crown 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 post-fire 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 to are 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.

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FIGURES

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 (~500cm diameter at breast height) in the foreground. C) Cluster of fire-killed giant sequoias in Redwood Meadow Grove. Photo Credits: (A) Tony Caprio, NPS; (B,C) David Soderberg, USGS.

Figure 2. Study plot locations (red circles, triangles*) 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 (GRTS) 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. RdNBR-categorized burn severity raster pixels are presented in greyscale (white = low severity, <25% basal area loss; light and dark grey = moderate severity, 26-75% basal area loss; black = high severity or unburned, >75% basal area loss).
* Plots in Board Camp, Suwanee, and New Oriole Lake groves are scaled to represent the actual area surveyed. Plots in Redwood Mountain grove (triangles) are, for visibility, scaled larger than their actual sizes.
** Redwood Mountain map includes US Forest Service and state land that was not part of our sampling area.

Figure 3. Predicted mean regeneration (seedlings/hectare) for groves affected by the 2021 KNP-Complex (i.e., Redwood Mountain, Suwanee, 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/ha) being larger than specified seedling counts are shown (see Table 1). Bayesian 90% credible intervals are highlighted in grey.

Figure 4. Top panels: predicted mean regeneration (seedlings/hectare) for groves affected by the 2021 KNP-Complex (i.e., Redwood Mountain, Suwanee, and New Oriole Lake) and the 2020 SQF-Complex fires (i.e., Board Camp) as a function of RdNBR values (first row). Bottom panels: predicted mean regeneration densities (seedlings/ha) at specified RdNBR values (see Table 2).

Figure 5. Neighborhood crown volumes (within 50 meters of plot center) of giant sequoia live, scorched, and torched foliage as a function of remote-sensed derived RdNBR 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.

Figure 6. Giant sequoia stem map and categorized RdNBR areas for 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: Black = live, white = dead (individual giant sequoia within Redwood Mountain not visualized due to grove size). Grove regions with RdNBR values > 800 are colored in red, with increasingly dark color tone with increasing RdNBR values.

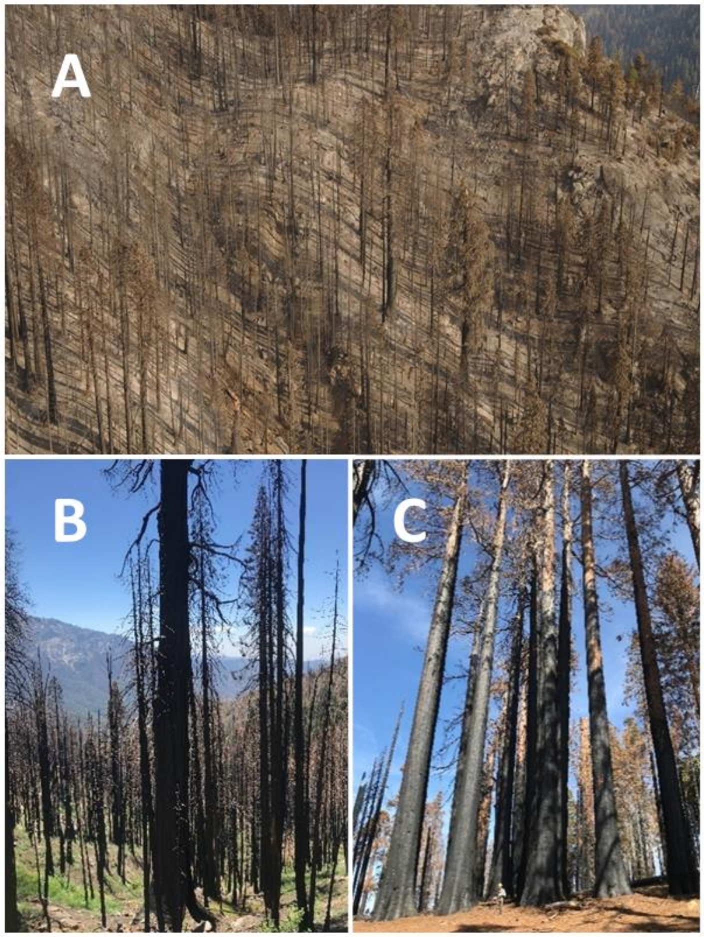
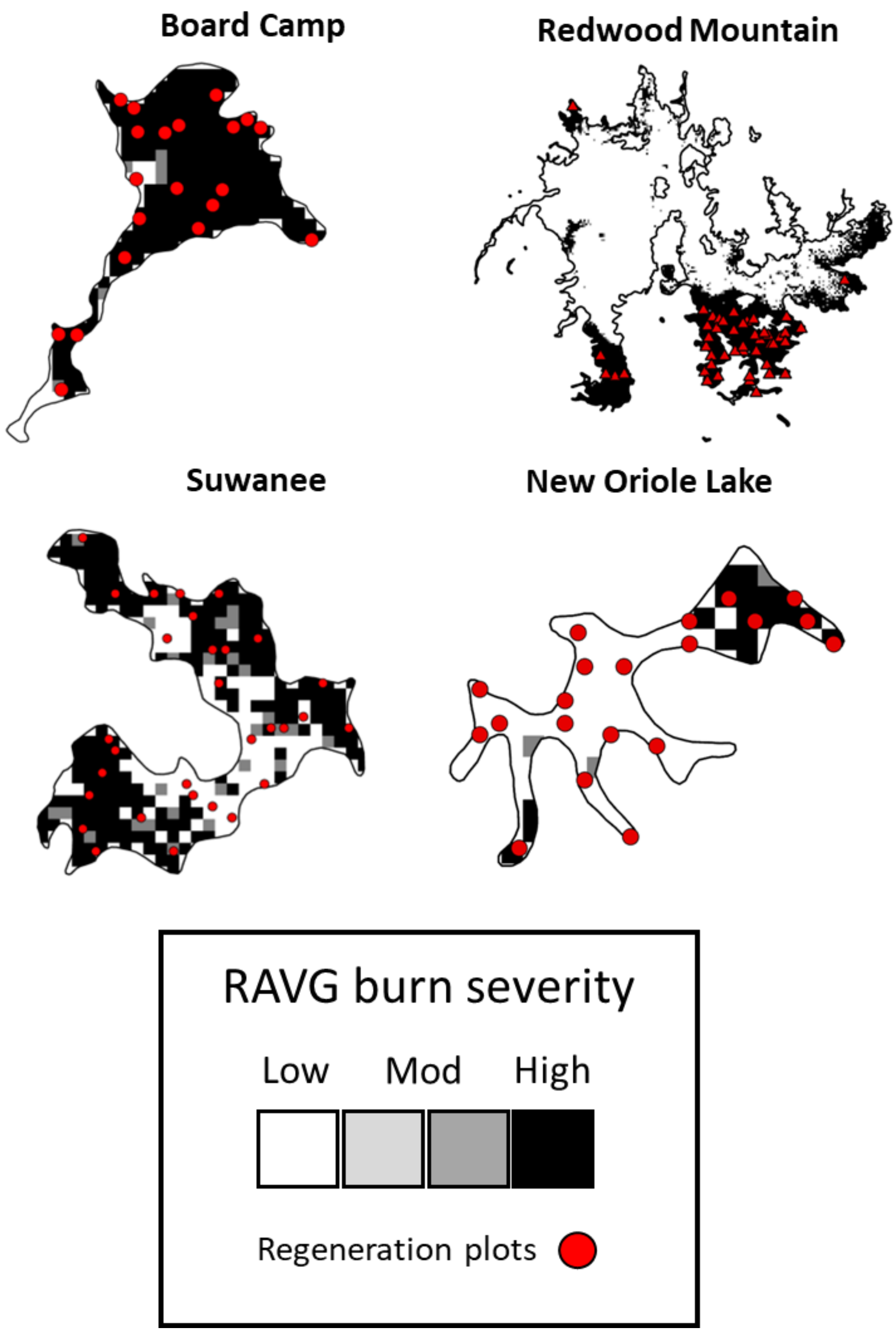


Figure 1



876
877 **Figure 2**

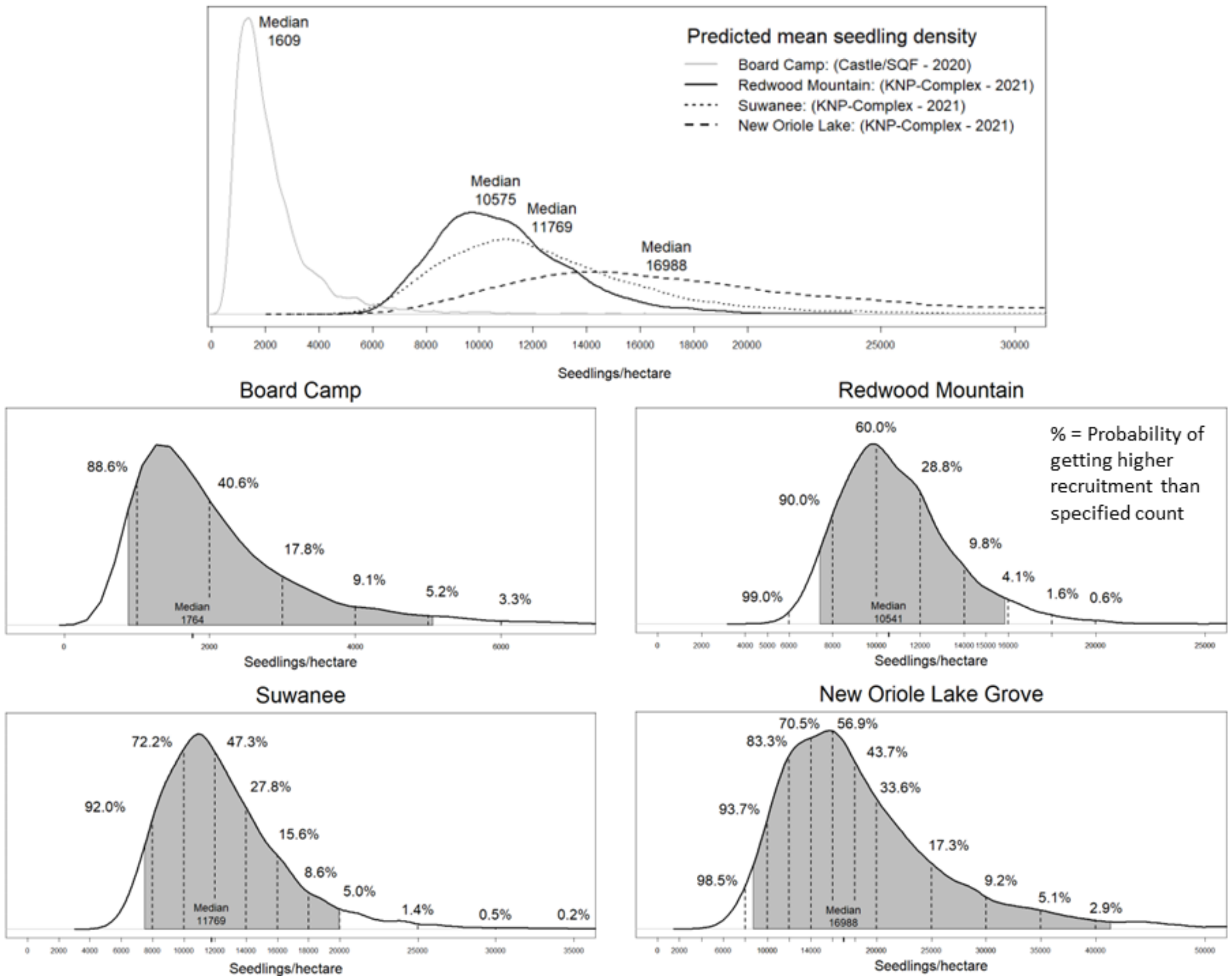
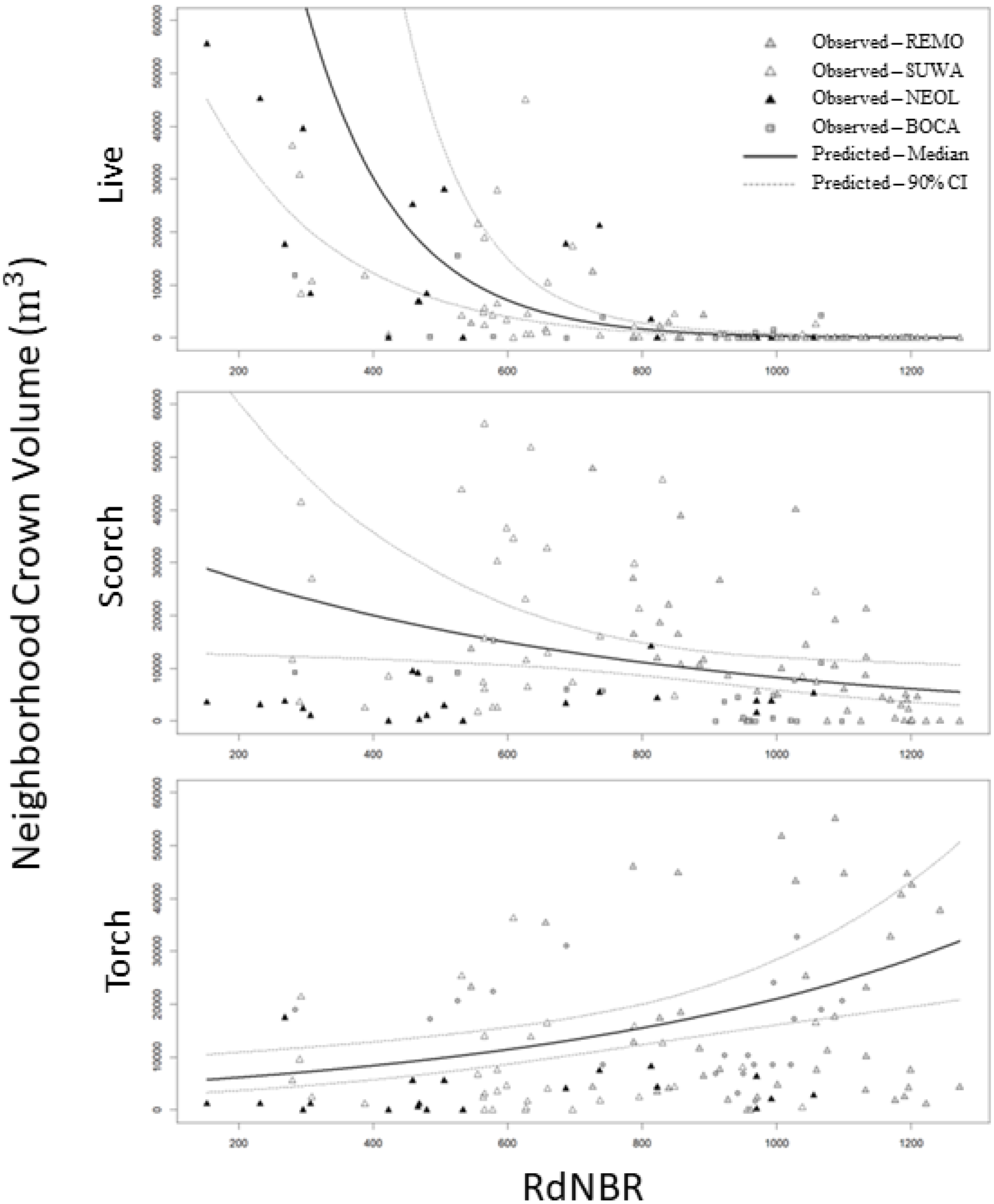

Predicted mean seedling density
Board Camp: (Castle/SQF - 2020)
Redwood Mountain: (KNP-Complex - 2021)
Suwanee: (KNP-Complex - 2021)
New Oriole Lake: (KNP-Complex - 2021)
Median 1609
Median 10575
Median 11769
Median 16988
Seedlings/hectare
Board Camp
88.6%
40.6%
17.8%
9.1%
5.2%
3.3%
Median 1764
Seedlings/hectare
Redwood Mountain
% = Probability of getting higher recruitment than specified count
60.0%
28.8%
90.0%
9.8%
4.1%
99.0%
1.6%
0.6%
Median 10541
Seedlings/hectare
Suwanee
72.2%
47.3%
27.8%
92.0%
15.6%
8.6%
5.0%
1.4%
0.5%
0.2%
Median 11769
Seedlings/hectare
New Oriole Lake Grove
70.5%
56.9%
83.3%
43.7%
33.6%
93.7%
17.3%
98.5%
9.2%
5.1%
2.9%
Median 16988
Seedlings/hectare

Figure 3



Neighborhood Crown Volume (m^3)
Live
Scorch
Torch
RdNBR
Observed – REMO
Observed – SUWA
Observed – NEOL
Observed – BOCA
Predicted – Median
Predicted – 90% CI

Figure 4

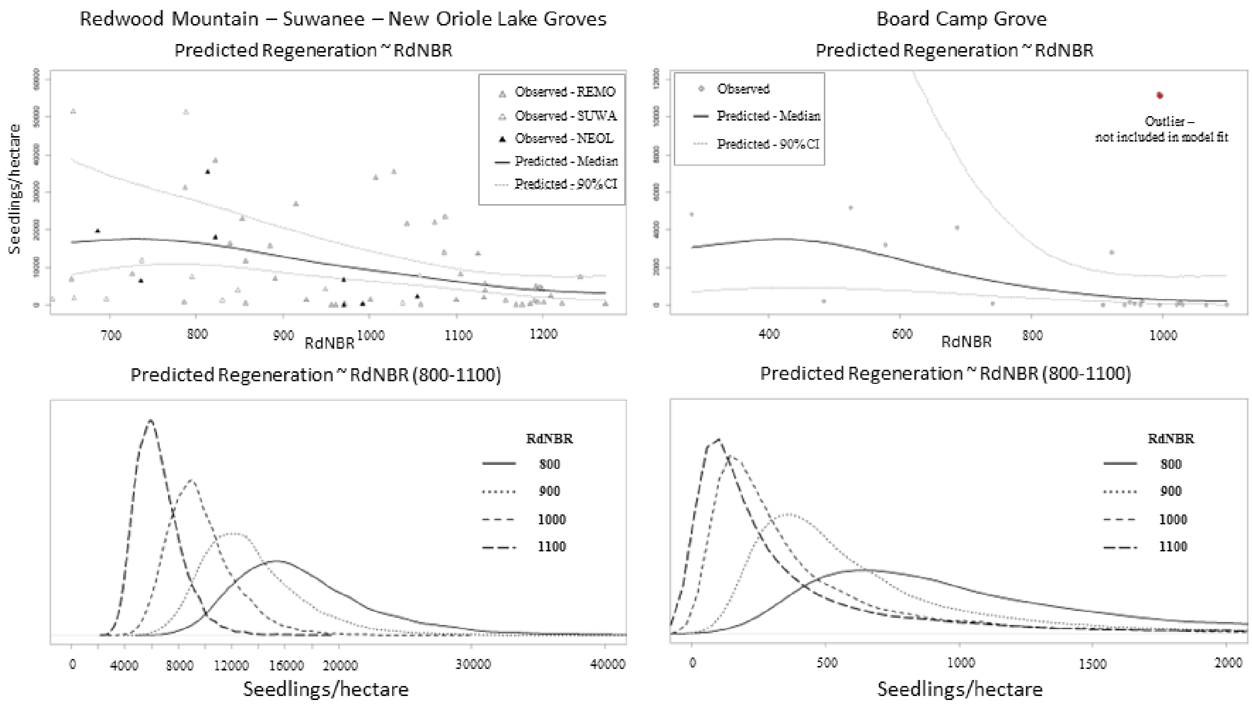

Redwood Mountain – Suwanee – New Oriole Lake Groves
Predicted Regeneration ~ RdNBR
Observed - REMO
Observed - SUWA
Observed - NEOL
Predicted - Median
Predicted - 90%CI
Seedlings/hectare
RdNBR
Board Camp Grove
Predicted Regeneration ~ RdNBR
Observed
Predicted - Median
Predicted - 90%CI
Outlier – not included in model fit
RdNBR
Predicted Regeneration ~ RdNBR (800-1100)
RdNBR
800
900
1000
1100
Seedlings/hectare
Predicted Regeneration ~ RdNBR (800-1100)
RdNBR
800
900
1000
1100
Seedlings/hectare

Figure 5

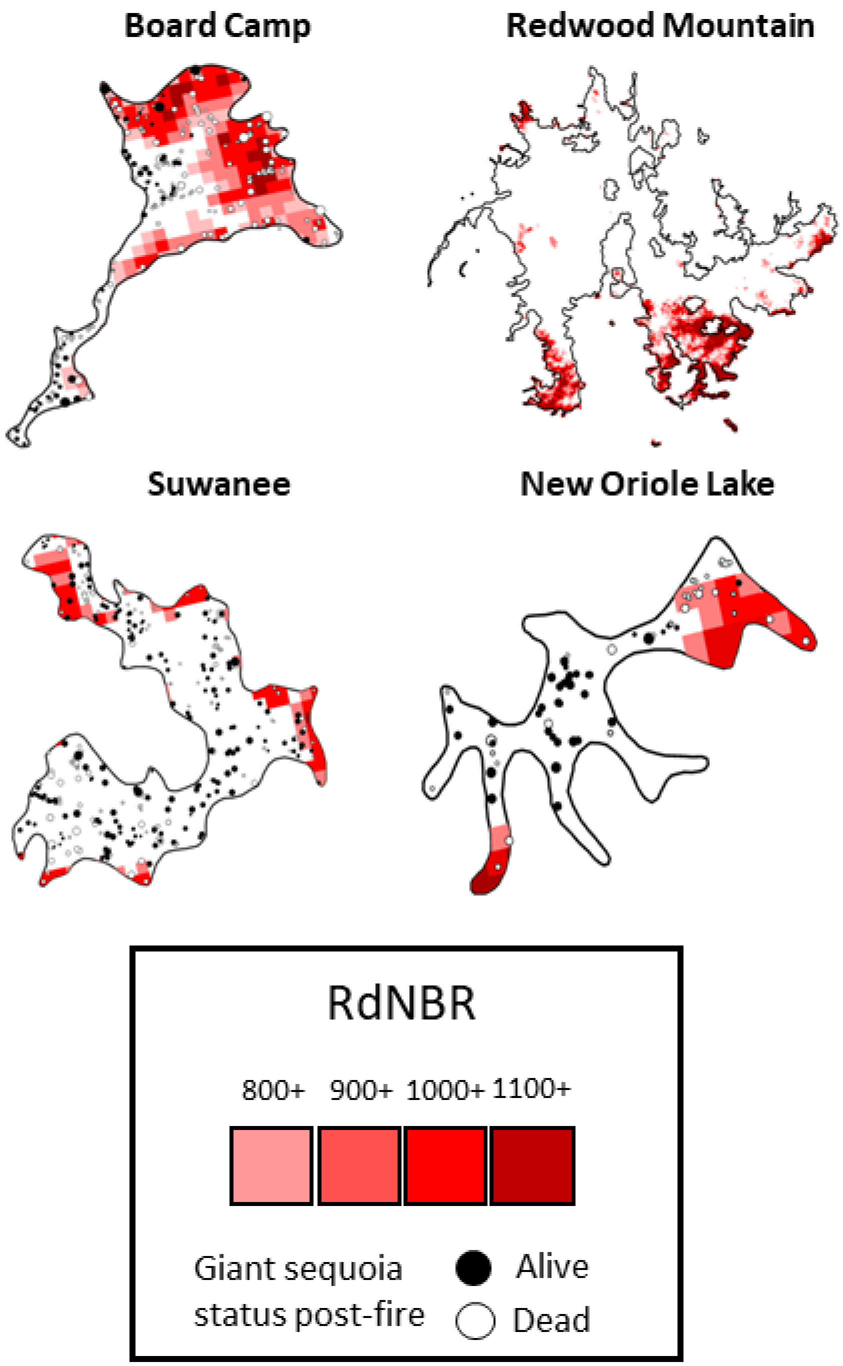

Board Camp
Redwood Mountain
Suwanee
New Oriole Lake
RdNBR
800+
900+
1000+
1100+
Giant sequoia status post-fire
Alive
Dead

Figure 6

TABLES

Table 1. Mean regeneration densities and Bayesian probabilities of mean regeneration densities meeting (i.e, are greater than or equal to) the specified seedlings/hectare for each grove. See *Methods – Statistical Analysis* for details. Probabilities that are <10% are highlighted in grey.

		Raw data	Bayesian probabilities (italics) of mean regeneration densities meeting specified seedlings/hectare (bold) for each grove								
Fire/year	Grove		Seedlings/hectare								
SQF 2020		Mean	**1000**	**2000**	**3000**	**4000**	**5000**	**6000**	**8000**	**10000**	**12000**
	Board Camp	1611	*87.7*	*41.6*	*18.5*	*9.8*	*5.7*	*3.4*	*1.5*	*0.8*	*0.5*
			8000	**10000**	**12000**	**14000**	**16000**	**18000**	**20000**	**25000**	**30000**
KNP Complex 2021	Redwood Mountain*	10363	*90.0*	*60.0*	*28.8*	*9.8*	*4.1*	*1.6*	*0.5*	*<0.1*	*0*
	Suwanee	11435	*92.0*	*72.2*	*47.3*	*27.8*	*15.6*	*8.6*	*5.0*	*1.4*	*0.5*
	New Oriole Lake	16080	*98.5*	*93.7*	*83.3*	*70.5*	*56.9*	*43.7*	*33.6*	*17.3*	*9.2*

* Redwood Mountain plot locations were restricted to areas of high burn severity (RdNBR >640)

Table 2. Bayesian probability estimates of mean regeneration densities as a function of RdNBR (relativized differenced normalized burn ratio; Miller & Thode, 2007). See *Methods* for details. Probability estimates represent the probability of meeting (greater than or equal to) the specified seedlings/hectare for a given RdNBR value. Probabilities that are <10% are highlighted in grey.

			Bayesian probabilities (italics) of mean regeneration densities meeting specified seedlings/hectare (bold) as a function of RdNBR values					
Fire/year	Grove	RdNBR	Seedlings/hectare					
			1000	**2000**	**3000**	**4000**	**5000**	**6000**
SQF 2020	Board Camp (w/o outlier*)	800	*45.8*	*14.9*	*6.8*	*3.7*	*2.1*	*1.5*
		850	*29.0*	*7.5*	*2.9*	*1.6*	*0.9*	*0.5*
		900	*17.4*	*4.2*	*1.7*	*0.8*	*0.5*	*0.2*
		950	*12.2*	*3.1*	*1.3*	*0.7*	*0.4*	*0.2*
		1000	*10.0*	*2.9*	*1.3*	*0.8*	*0.4*	*0.2*
		1050	*10.5*	*2.9*	*1.4*	*0.7*	*0.5*	*0.3*
		1100	*10.2*	*3.2*	*1.5*	*0.8*	*0.5*	*0.4*
			8000	**10000**	**12000**	**14000**	**16000**	**18000**
KNP Complex 2021	Redwood Mountain - Suwanee - New Oriole Lake (combined**)	800	*99.7*	*97.4*	*88.5*	*73.4*	*55.1*	*38.4*
		850	*99.4*	*94.7*	*80.6*	*59.2*	*39.1*	*24.5*
		900	*97.5*	*84.6*	*60.8*	*36.6*	*21.0*	*11.4*
		950	*90.5*	*64.2*	*35.9*	*17.9*	*8.2*	*3.8*
		1000	*74.5*	*38.2*	*16.3*	*6.0*	*2.3*	*0.9*
		1050	*45.7*	*15.6*	*4.7*	*1.3*	*0.4*	*0.1*
		1100	*17.0*	*3.6*	*0.8*	*0.2*	*<0.1*	*<0.1*

* Model estimates calculated with outlier removed. See Figure 5 for all data visualization.
** Model estimates calculated within areas of high severity (RdNBR >640).

APPENDIX S1

We used a negative binomial count model to calculate estimates of the relationship between diameter breast height (cm) and crown volume (m^3) based on data published in Sillett et al., 2019 (Figure S1). The median estimate for the modeled relationship is described with the following:

$$\log(y) = 6.953 + 0.00547*(\text{diameter in centimeters}) \qquad \text{(S1)}$$

and was used as an allometric equation for estimating crown volumes for the giant sequoia assessed within our study.

In addition, we calculated estimates of the relationships between regeneration density (seedlings/hectare) and neighborhood crown volume scorch (first row) and neighborhood crown volume scorch and RdNBR (second row), separating analyses by groves that were affected by different fires/years (column 1: KNP-complex [2021] affected Redwood Mountain, Suwanee, and New Oriole Lake groves); column 2: SQF-complex [2020] affected Board Camp grove) (Figure S2). Models were checked graphically for convergence and the Rhat ($\hat{r}$) value was equal to 1. *See Methods: Statistical Analysis* for details.

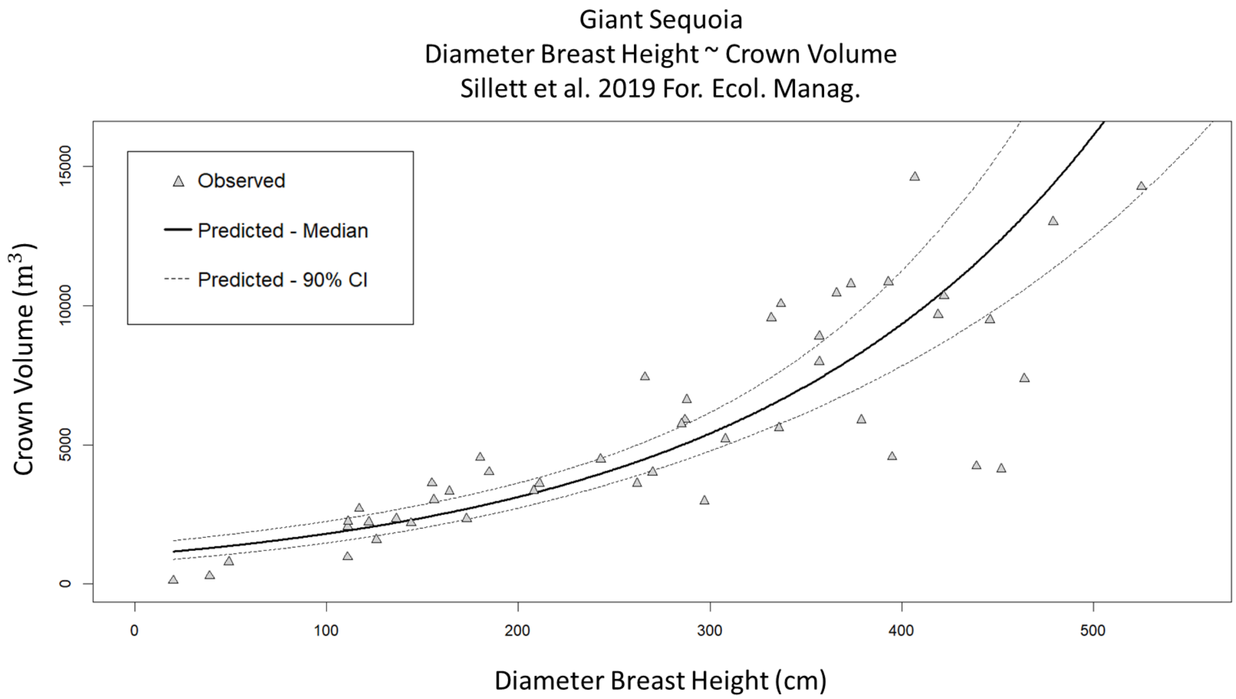


Figure S1. Modeled relationship between giant sequoia (*Sequoiadendron giganteum*) diameter at breast height (cm) and crown volume (m^3) based on data published in Sillett et al., 2019.

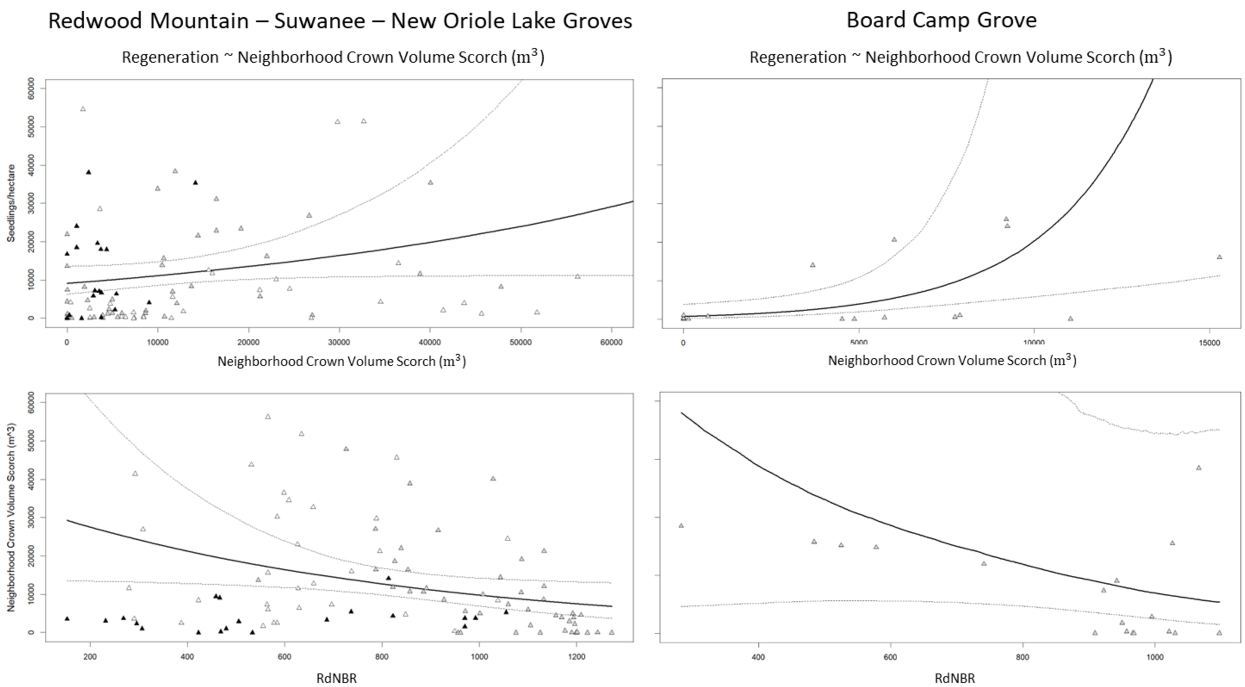


Figure S2. Visualizing the relationships between regeneration density (seedlings/hectare) and neighborhood crown volume scorch (top panel) and neighborhood crown volume scorch and RdNBR (bottom panel). Analyses are separated by groves that were affected by different fires/years (column 1: KNP-complex [2021] affected Redwood Mountain, Suwanee, and New Oriole Lake groves); column 2: SQF-complex [2020] affected Board Camp grove).