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Long-term influence of prescribed burning on subsequent wildfire in an old-growth coast redwood forest

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Abstract

Background Prescribed burning is an effective tool for reducing fuels in many forest types, yet there have been few opportunities to study forest resilience to wildfire in areas previously treated. In 2020, a large-scale high-intensity wildfire burned through an old-growth coast redwood (*Sequoia sempervirens*) forest with a mixed land management history, providing a rare opportunity to compare early post-wildfire data between areas with and without previous application of prescribed burning. The purpose of this study was to analyze the differences between these two treatments in terms of tree mortality, stand structure, fuel composition, and post-wildfire regeneration. Field data were collected approximately 1 year after the wildfire using a total of fifty 20 m plots in three sites previously treated with prescribed fire more than 9 years prior to the wildfire, and fifty plots in three adjacent sites without a history of prescribed fire. Data regarding the influence of prescribed burning on forest structure and composition following wildfire were assessed using generalized linear mixed effects models (GLMMs).

Results Prescribed burning was positively associated with greater canopy cover, tree survival, counts of early post-fire coast redwood seedlings, and lower stand density, following subsequent wildfire. In addition, the mortality of individual trees was lower within areas treated with prescribed fire and negatively associated with tree height. Topkill was also lower within treated areas and was negatively correlated with tree diameter and tree height for all basal sprouting species combined and for *S. sempervirens* individually.

Conclusions Results suggest that prescribed fire improved coast redwood forest stand resistance and resilience to wildfire and that these benefits were maintained after a significant wildfire event in areas treated more than 9 years prior to the wildfire. Further research is recommended in areas where prescribed fire has been applied repeatedly, to better understand long-term effects and guide best practices for future prescribed fire use in coast redwood forests.

Keywords Controlled burning, Prescribed fire, Prescribed burning, Coast redwood, Topkill, Wildfire, Forest management, Resilience, Resistance

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Resumen

Antecedentes Las quemas prescriptas son herramientas efectivas para reducir los combustibles en muchos tipos forestales; sin embargo han habido pocas oportunidades para estudiar la resiliencia de los bosques a los incendios de vegetación en áreas previamente tratadas con estas quemas. En 2020, un gran incendio forestal afectó un bosque maduro de sequoias rojas de la costa (*Sequoia sempervirens*) con una historia de manejo mixta, proveyendo entonces de una rara oportunidad para comparar datos del post-fuego reciente entre áreas con y sin aplicación previa de quemas prescriptas. El propósito de este estudio fue analizar las diferencias entre estos dos tratamientos en términos de mortalidad de árboles, estructura de los rodales, composición de los combustibles, y regeneración post incendio. Datos de campo fueron colectados aproximadamente un año luego del incendio usando un total de 20 parcelas en tres sitios previamente tratados con quemas prescriptas más de nueve años antes de la ocurrencia del incendio, y 50 parcelas en sitios adyacentes sin una historia de quemas prescriptas. Los datos relacionados con la influencia de las quemas prescriptas en la estructura y composición del bosque luego del incendio fueron determinados mediante el uso del efecto de Modelos Lineales Generalizados Mixtos (GLMMs).

Resultados Las quemas prescriptas fueron positivamente asociadas con una mayor cobertura del dosel, la supervivencia de árboles, el conteo de plántulas en el postfuego temprano, y en la menor densidad de los rodales, luego del incendio subsecuente. Adicionalmente, la mortalidad de árboles individuales fue menor dentro de áreas tratadas con quemas prescriptas, y negativamente asociadas con la altura de los árboles. La muerte de ápices fue también menor dentro de áreas tratadas y fue negativamente correlacionado con el diámetro de los árboles y su altura para todas las especies rebrotantes combinadas, y para *S. sempervirens* de manera individual.

Conclusiones Los resultados sugieren que las quemas prescriptas mejoran la resistencia y resiliencia de los rodales de sequoias rojas de la costa a los incendios, y que esos beneficios perduraron luego de un evento de incendio significativo ocurrido en esas áreas luego de 9 años del tratamiento de quemas. Más investigaciones son necesarias en lugares donde las quemas prescriptas se han aplicado repetidamente, para poder entender mejor los efectos a largo plazo y poder guiar las mejores prácticas de uso de quemas prescriptas en bosques de sequoias rojas de la costa.

Background

Forests in the western United States have long been shaped by fire (Marlon et al. 2012). Yet, recent history has seen a dramatic increase in the frequency and severity of wildfires due to climate change, removal of Indigenous burning practices, and fire suppression (Westerling 2016; Steel et al. 2015). Over a century of fire suppression has resulted in live and dead fuel accumulations on landscapes historically treated with fire (Hagmann et al. 2021). In addition, increased temperatures and prolonged drought brought on by climate change paired with the expansion of the wildland-urban interface (WUI) complicates the wildfire problem (Williams et al. 2019; Radeloff et al. 2018).

Coast redwood (*Sequoia sempervirens*) forests are known for their resistance to, and resilience following wildfire (Ramage et al. 2010). Coast redwood forests are only found within a narrow band along California's central coast, extending into southern Oregon (Lorimer et al. 2009). They are found at elevations between sea level and 900 m and reside in a Mediterranean climate characterized by cool winters and dry summers with heavy fog. The preferred soil types for coast redwoods are sandstone, limestone, slate, chert, and schist (University of California Agriculture and Natural Resources 2016). In California's central coast redwood forests, Douglas-fir (*Pseudostuga menziesii*) and tanoak (*Notholithocarpus densiflorus*) are the most common associated tree species. While each species has unique adaptations to fire, coast redwoods have been found to have the lowest fire-induced mortality rates among these codominant species (Ramage et al. 2010).

Coast Redwood is host to a number of fire adaptations. As the tallest trees in the world, high canopies help coast redwoods resist most low to moderate-intensity surface fires, and thick, insulative bark helps to protect the cambium. Uncommon among conifers, coast redwoods can resprout both basally and epicormically after disturbance (O'Hara et al. 2017). Coast redwoods have also been shown to regenerate via seedlings after wildfire events, though it is a less common post-fire regeneration strategy compared to sprouting (Douhovnikoff et al. 2004). Common tree species associated with coast redwoods, while also adapted to fire, are somewhat less resistant. Tanoak is the most common sub-canopy tree species with coast redwood along California's central coast (Sawyer et al. 2000). When exposed to fire, tanoaks topkill easily, yet resprout vigorously (Donato et al. 2009). With impressive height, thick bark, and a high crown, mature Douglas-fir trees exhibit some of the same fire-resistant characteristics as coast redwoods, but to a lesser extent. However, Douglas-fir does not have the ability to resprout basally or epicormically after fire, and thus total loss of foliage ensures individual tree mortality. Since seeds are stored in the crown and regeneration can only occur through seedling dispersal, Douglas-fir exhibits some post-fire resilience under low and moderate surface fire conditions but is less resilient following high-intensity or crown fire (Hood et al. 2007).

Humans have shaped coast redwood forests with fire for thousands of years. Indigenous burning in and adjacent to central California coast redwood forests was intended to improve food gathering efficiency, exterminate insects that ate acorns, attract game to rich grasslands, encourage production of materials to construct high-quality cordage, and clear ways for travel (Anderson 2006). European colonization and removal of Indigenous people from their lands disrupted millennia of traditional practices of intentional burning. The removal of Indigenous burning from the region has resulted in longer fire return intervals and less frequent, yet more intense wildfires (Keeley 2002).

The importance of anthropogenic fire in California's forests has become more widely acknowledged within the wildfire management field in the past several decades, prompting an increased application of prescribed fire as a fuel management tool (Ryan et al. 2013). Low-intensity prescribed fires in coast redwood forests can reduce fuel loads, increase the relative dominance of coast redwoods, and reduce stand density (Teraoka and Keyes 2011). Prescribed fire has little effect on coast redwood overstory structure, and therefore can be used to reduce densities of competing species without a high risk of mortality to coast redwoods (Ramage et al. 2010). While limited research exists on the long-term effects of prescribed burning, previous research has shown prescribed fire effects in California's mixed-conifer forests extending for as much as 8 to 10 years (Brodie et al., 2024; Van Mantgem et al. 2011). Additionally, prescribed fire's effects on stand structure have been shown for up to 45 years in northern pine forests (Scherer et al. 2016). Within coast redwood forests, Cowman and Russell (2021) found that prescribed burns impacted fuel load and stand structure for up to 20 years.

Our study expands on a field of research regarding the influence of prescribed fire in coast redwood forests (Finney and Martin 1993; Ramage et al. 2010; Engber et al. 2017), and specifically examines a forest with mixed land management history that recently burned in a large-scale wildfire. In this study, we sampled the same areas as Cowman and Russell (2021), three years later and after the 2020 CZU Lightning Complex (CZU) fire. The purpose of our study was to assess the influence of prescribed burning, or the lack of it, on mortality, coast redwood forest structure, fuel load, and post-fire regeneration, following a high-intensity wildfire within an old-growth coast redwood forest, and to assess whether the long-term effects of prescribed fire found by Cowman and Russell (2021) persisted through a large-scale wildfire.

Methods

Study site

Big Basin Redwoods State Park (BBRSP) is located in the Santa Cruz Mountains of California and is home to the largest stand of old-growth coast redwoods south of San Francisco. BBRSP is within the southern end of the Marine West Coast Climatic Zone (Martin 1998). Due to its proximity to the coast, BBRSP experiences minimal seasonal variation with high relative humidity and consistent temperatures throughout much of the year (Martin 1998). Elevation ranges from sea level to about 600 m; however, the areas with old-growth coast redwoods range from approximately 300 to 600 m in elevation. Prescribed fire has been used as a management tool in BBRSP since 1978. Burns have varied in size and frequency but were predominately low-intensity understory burns.

We sampled six total sites, including three sites with and three sites without prescribed fire treatments that subsequently burned during the CZU (Cowman and Russell 2021; Fig. 1; Table 1). Environmental and biological variations between sites were limited. All sites had similar overstory and understory plant composition, topographic position, and seasonal moisture levels. All sites contained soil types predominantly composed of loam or sandy loam (Table 2).

Prior to the CZU, three of the six sites underwent prescribed burns in 1999, 2007, or 2011. Before the CZU, all six sites most recently experienced wildfires in 1936. Information on prescribed burn operations was from Cowman and Russell (2021) which were limited based on a compilation of handwritten and typed notes from spot weather forecasts on burn days, conversations with fire managers onsite, and Department of Parks and Recreation daily records of weather. All prescribed burn plans required daily conditions of air temperatures between 7.2 and 24 °C, relative humidity between 25 and 89%, wind speeds of less than 16 km per hour, and 10-h dead fuel moisture between 8 and 14%. Primary ignitions were only permitted if at least 3.8 cm of precipitation had fallen during the rainy season, or 2.5 cm if no rain had fallen prior to November 1st. Ignition patterns for the three burns typically began with perimeter ignitions along ridgetops, followed by flanking and interior strip ignition.

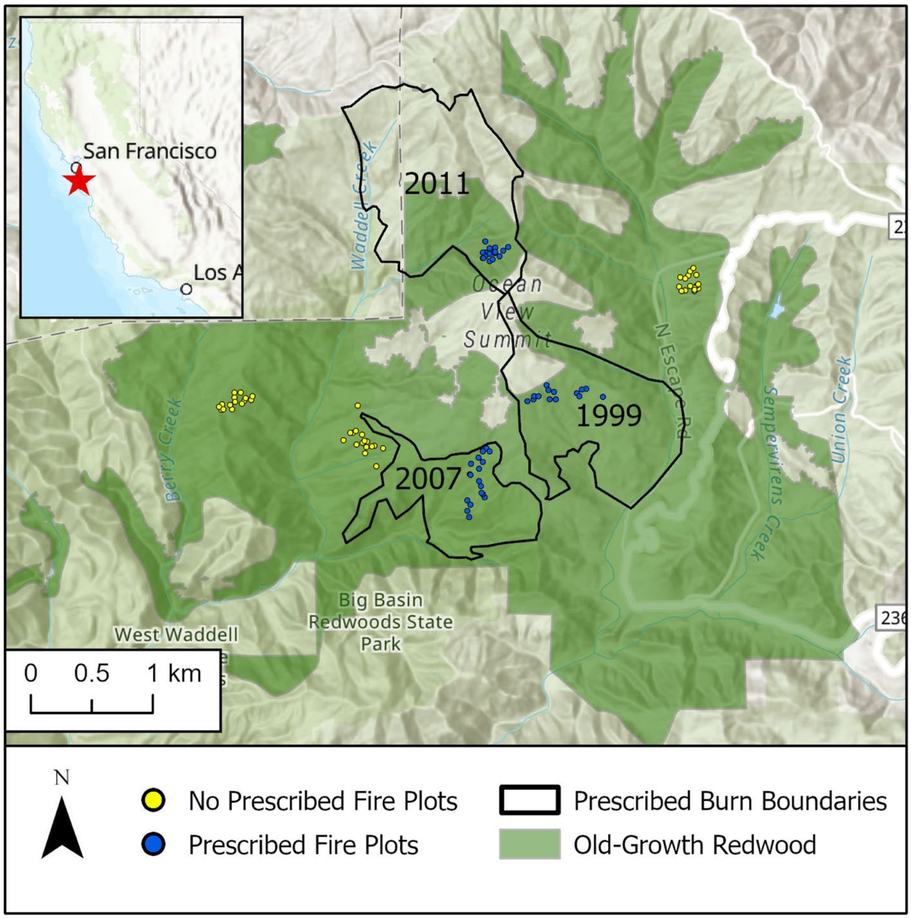

Fig. 1 Research area in Big Basin Redwoods State Park, Boulder Creek, CA, USA. The entire area was affected by the 2020 CZU Lightning Complex (CZU). Old-growth redwood boundary defined as areas without a history of timber harvest highlighted in green. Yellow dots indicate plot locations without a history of prescribed fire. Blue dots indicate plot locations with prescribed fire history. Black lines indicate prescribed fire boundaries. Listed years represent years prescribed burn projects were conducted. 2007 and 2011 prescribed burn projects represent the boundary of the achieved prescribed burn area. No spatial data for the achieved burn area for the 1999 prescribed burn project were available and the boundary represents the planned burn area. 1999 prescribed burn plot locations were based on Cowman and Russell's (2021) plot locations which were selected in consultation with California State Parks staff to ensure areas were part of achieved 1999 prescribed burn

Table 1 Prescribed burn history, including the year that the prescribed fire occurred, ignition dates, lowest and highest relative humidity (RH), and the area burned by the prescribed fire if applicable (Cowman and Russell 2021). Prescribed burn units include Ocean View Summit (OVSB), Skyline to the Sea burned (S2SB), and Johansen Road East (JREB)

	California State Parks Operational Unit		
	OVSB	**S2SB**	**JREB**
Prescribed burn year	1999	2007	2011
Area burned (ha)	109	146.2	< 206.7
Ignition dates	11/2–1/8	11/9–11/24	10/11–11/4
Lowest RH (%)	35	37	12
Highest RH (%)	100	100	100
Fire activity	Slow backing fire with intermittent runs	Backing fire with intermittent runs and torching	Backing fire with intermittent runs and torching. 0.4 ha slop-over

Table 2 Study site conditions include slope average and range, aspect average, elevation range, common soil texture, and average heat load across the management unit (McCune and Keon 2002). Sites include Ocean View Summit (OVSB), Skyline to the Sea burned (S2SB), Johansen Road East (JREB), Sunset Trail (SUNU), Skyline to the Sea unburned (S2SU), and North Escape Road (NERU)

	Prescribed burn sample sites			No prescribed burn sample sites		
	OVSB	**S2SB**	**JREB**	**SUNU**	**S2SU**	**NERU**
Plots sampled	15	18	17	17	17	16
Heat load average (unitless)	0.812	0.915	0.927	0.847	0.880	0.881
Slope average (%)	28.68	33.90	49.16	38.22	26.92	32.67
Aspect average (°)	131.07	233.28	223.12	137.0	211.94	261.31
Elevation average (m)	398.60	316.00	402.67	295.67	241.50	348.63

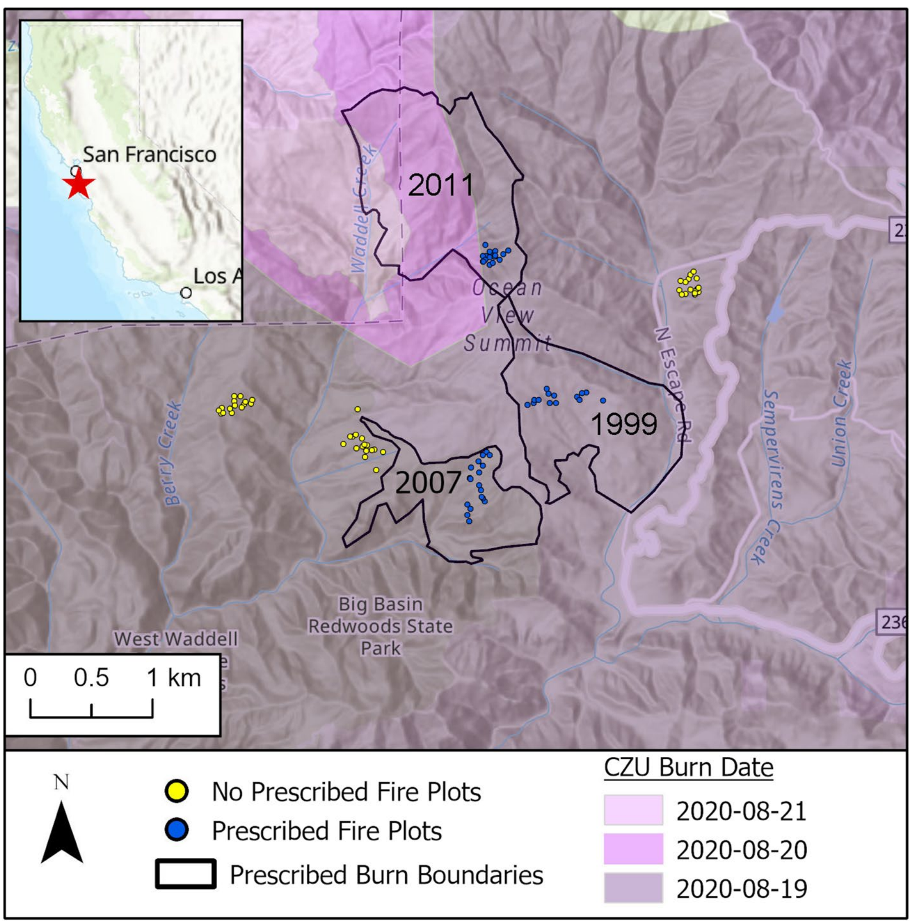

Fig. 2 Research area in Big Basin Redwoods State Park, Boulder Creek, California, USA. The entire area was affected by the 2020 CZU Lighting Complex (CZU). Yellow dots indicate plot locations without a history of prescribed fire. Blue dots indicate plot locations with prescribed fire history. CZU burn date refers to the first date of ignition based on data provided by CAL FIRE San Mateo-Santa Cruz Unit. Listed years represent years prescribed burn projects were conducted. 2007 and 2011 prescribed burn projects represent the boundary of the achieved prescribed burn area. No spatial data for the achieved burn area for the 1999 prescribed burn project were available and the boundary represents the planned burn area. 1999 prescribed burn plot locations were based on Cowman and Russell's (2021) plot locations which were selected in consultation with California State Parks staff to ensure areas were part of achieved 1999 prescribed burn

Prescribed burn ignitions were all conducted in late fall or early winter (Table 1; Cowman and Russell 2021).

All plots burned on August 18th during the CZU (Fig. 2), which affected more than (34,600 ha) between August 16 and September 22, 2020 (Santa Cruz Grand Jury Report, 2021). Due to an unusual lightning event and high winds, the CZU was unusually intense for a fire in the Santa Cruz Mountains, resulting in a high-intensity crown fire across all the study sites. Based on Landsat derived differenced normalized burn ratio (dNBR) in 2020, the CZU in BBRSP was mixed severity, that was dominated by high to moderate fire severity overall, including 77% high, 20% moderate, and just 2% low (Potter 2023). Our plots with prescribed fire had lower wildfire severities on average (Potter 2023) with high severity on 58% of prescribed fire plots and 74% on plots without prescribed fire; moderate severity on 36% of prescribed fire plots, and 26% of plots without prescribed fire; and low severity on 6% of prescribed fire plots compared to zero plots without prescribed fire (Fig. 3). This is partially explained by the lower canopy cover in prescribed fire plots (91.4%) compared to plots without prescribed fire (93.9%) found by Cowman and Russell (2021) before the CZU since dNBR does not account for pre-wildfire differences in canopy cover.

Study design

A total of 100 plots were sampled, with 50 plots sampled in each of the two treatments. Plots were distributed across each treatment with an average of 17 plots per site. The time since prescribed fire varied between the three replicates (9 years, 14 years, and 21 years). However, access to the sites was restricted for safety reasons

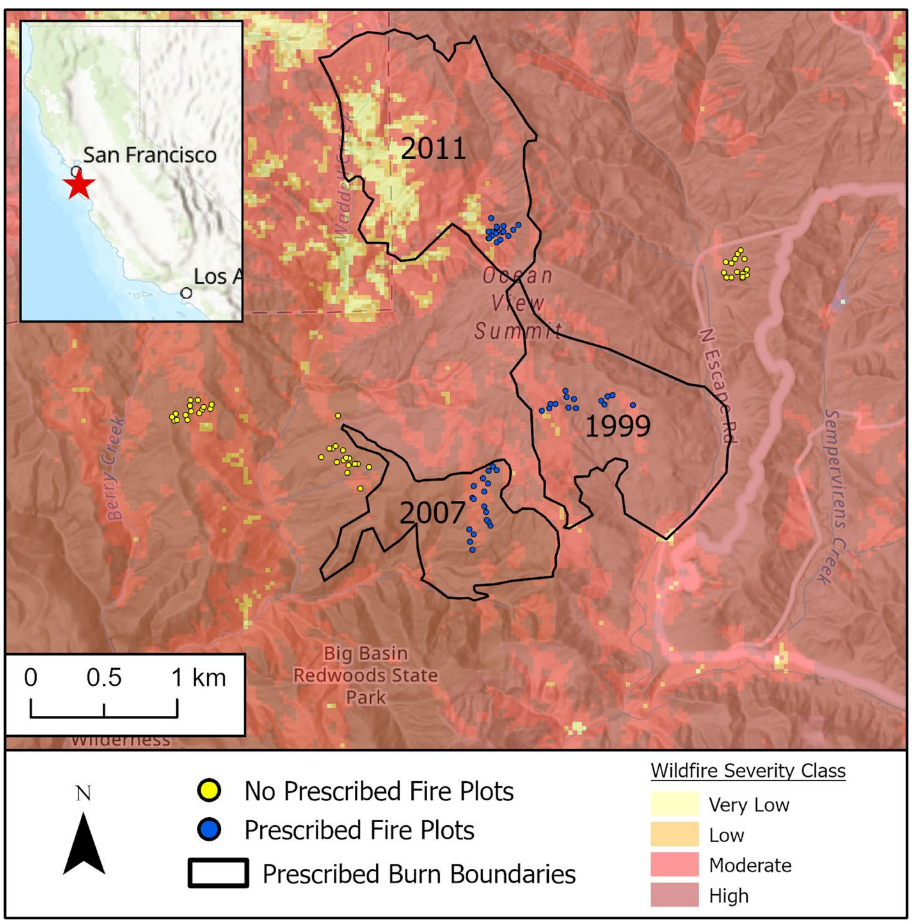

Fig. 3 Research area in Big Basin Redwoods State Park, Boulder Creek, CA, USA. The entire area was affected by the 2020 CZU Lighting Fire (CZU). Yellow dots indicate plot locations without a history of prescribed fire. Blue dots indicate plot locations with prescribed fire history. Burn severity classes based on Landsat satellite images of pre- and post-fire vegetation cover (Potter 2023). Listed years represent years prescribed burn projects were conducted. 2007 and 2011 prescribed burn projects represent the boundary of the achieved prescribed burn area. No spatial data for the achieved burn area for the 1999 prescribed burn project were available and the boundary represents the planned burn area. 1999 prescribed burn plot locations were based on Cowman and Russell's (2021) plot locations which were selected in consultation with California State Parks staff to ensure areas were part of achieved 1999 prescribed burn

at the time of sampling, so that the total number of plots sampled in each site was limited. For the purpose of this study, these three sites were treated as replicates of a single treatment (>9 years). A chronosequence approach was not employed as the number of plots, and variability between sites did not lend enough power to the analysis.

Sampling was conducted using 20 m diameter circular plots, located at least 10 m from adjacent plots and 200 m from any paved roads to avoid edge effects. Plot locations were selected based on the coordinates of randomly selected plots previously sampled by Cowman and Russell (2021). Due to the original plots not being physically landmarked, our plots are approximate locations and not a direct resampling. Measurements were limited to plots where the aspect slope from the plot center was less than 40°. Plots with evidence of more recent second burns from flare-ups following CZU containment were not sampled to maintain consistency of environmental and fire conditions across plots.

Data collection

We sampled all plots between July and November of 2021, roughly one year after the CZU wildfire, on sites that had been sampled prior to the wildfire. Slope, location coordinates, and aspect were recorded from each plot center point. Slope was measured using a Nikon Forestry Pro II Laser Hypsometer (Nikon Ltd., Tokyo, Japan). GPS coordinates were recorded with a Garmin GPSMAP 64SX (Garmin Ltd., Olathe, Kansas, USA).

Canopy cover was estimated using a concave spherical densiometer at the plot center in all four cardinal directions to increase accuracy. Tree mortality was determined by lack of residual foliage or live sprouts. Topkill was indicated by both a lack of residual foliage and epicormic sprouting, while basal sprouting may have been present (Fig. 4). All trees with a diameter at breast height (DBH) of 10 cm or greater, and at least half of the base of their trunk within the plot boundary, were measured and recorded (Busing and Fujimori 2002). Tree regeneration was measured both in terms of basal sprouts and the number of seedlings across the entire plot. Basal sprouts were counted and totaled for each plot, as basal sprouts' association with specific trees was not always possible to determine (Douhovnikoff et al. 2004; Ramage et al. 2010). Living seedlings, regardless of height, were recorded by tree species.

To measure dead and downed woody fuels, two transect lines from each plot center were employed, one along the dominant slope and the other 90° clockwise from the first transect line. To determine duff, litter, and fuel depths, measurements were taken at 1.52 m and 3.05 m from the center of each plot. Fuels were broken down into burn classes: 1-h (0–0.64 cm), 10-h (6.4–2.54 cm), 100-h (2.54–7.62 cm), and 1000 + h (7.6 + cm). On each transect line, fuels were counted for 1-h fuels between 0 and 1.52 m, 10-h and 100-h fuels between 0 and 3.05 m, and 1000-h fuels between 0 and 11.34 m (J. K. Brown 1974). 1000-h fuels were categorized as either "sound" or "rotten" (Cowman and Russell 2021). Fuel calculations were based on methods first described in J.K. Brown (1974) (Appendix 1). Understory herbaceous and shrub cover were identified to species following the Jepson Manual (Baldwin et al. 2012) and their cover was ocularly estimated with cover

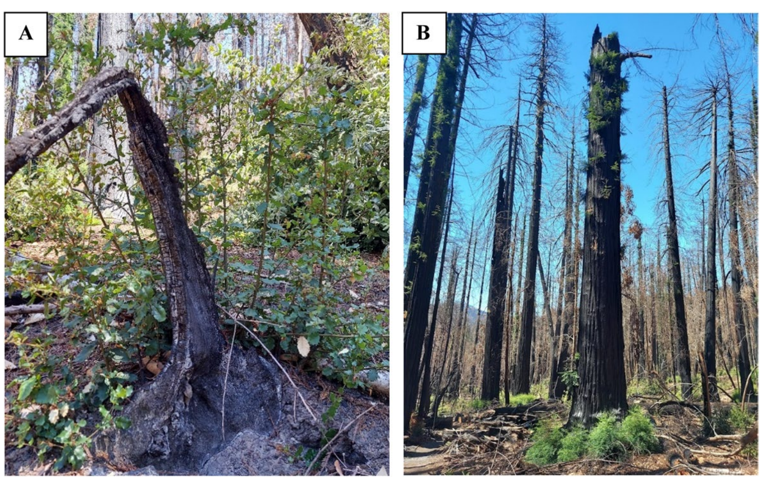

Fig. 4 Trees impacted by 2020 CZU Lightning Complex in Big Basin Redwoods State Park, Boulder Creek, California, USA. Image **A** (*Notholithocarpos densiflorus*) depicts a tree with post-wildfire basal sprouting, but neither epicormic sprouting nor retained bole foliage was classified; it was classified as both topkilled and dead. Image **B** (*Sequoia sempervirens*) depicts a tree with both epicormic and basal sprouting; it is classified as alive, e.g., not suffering either mortality or topkilled

classes (Braun-Blanquet 1932). To improve estimations, each plot was broken into four quadrants.

Statistical analyses

We analyzed data in R software version 4.3.2 (R Core Team 2023) with generalized linear mixed effect models (GLMMs). Analysis was conducted for both individual trees, and at the plot level using the model packages "lme4" and "glmmTMB" (Brooks et al. 2017, 2023). Model package and model family varied between response variables based on type of data and its distribution (Appendix 2). Candidate variables were based on our ecological hypothesis, and all candidates were included in the models. Since the three prescribed fire units varied in their time since the prescribed fire, we did not have replication for time since the prescribed fire which resulted in a weak chronosequence. Therefore, we chose to only include prescribed fire as present or absent. For tree level analysis, fixed effect variables included prescribed fire, heat load, height, and DBH; plot nested under site was included as a random effect variable. For plot level analysis, fixed effect variables included prescribed fire and heat load with the site included as a random effect variable. For individual tree analysis, an optimizer, "BOBYQA" was used in all models. For the tree level analysis, we used the "car" package (Fox and Weisberg 2023) to assess the variance inflation factor (VIF) to detect multicollinearity since we included both DBH and height as fixed effects. Nearly all tree models had VIFs less than three except the Douglas-fir mortality model. Since the Douglas-fir mortality model had a VIF of four, we removed DBH from the model. Both Douglas-fir mortality models lacked statistically significant results. Continuous variables were scaled in all models. Residuals were checked using the "DHARMa" package (Hartig 2022) to ensure appropriate distributional choices were made. When appropriate for the model family, models were checked for overdispersion using a nonparametric dispersion test of the standard deviation of fitted vs. simulated residuals based on a 95% confidence interval (Hartig 2022) (Appendix 3).

Results

Individual tree analysis

For all tree species combined, individual trees had lower rates of mortality and topkill following wildfire in areas previously treated with prescribed fire compared to areas without prescribed fire ($0.01 < P < 0.03$, $0.79 < R^2\text{m} < 0.6$, Table 3). The average percent morality from wildfire for all tree species combined was 8.6% (SE: ± 1.4) with prescribed fire and 13.2% (SE: ± 1.4) without prescribed fire ($R^2\text{m} = 0.60$, $P = 0.03$). Furthermore, for all basal sprouting tree species combined, topkilled was 57.8% (SE: ± 2.6) with prescribed fire and 76.4% (SE: ± 1.9) without prescribed fire ($R^2\text{m} = 0.79$, $P = 0.01$). For tanoak, average topkill was 97.4% (SE: ± 15.9) with prescribed fire and 100% (SE: ± 0.0) without prescribed fire ($R^2\text{m} = 0.02$, $P < 0.01$). Despite the model explaining little of the observed variation in tanoak topkill, the magnitude of the impact at 2.5% persisting tanoaks is ecologically significant as it denotes a small persistence of understory trees. Additionally, for all tree species combined, trees that were taller, or larger diameter, were less likely to be topkilled. ($R^2\text{m} = 0.0$, $P < 0.01$). Similarly, taller, and larger diameter coast redwood were less likely to be topkilled ($R^2\text{m} = 0.78$, $P < 0.01$).

Table 3 Analysis of individual tree survival data (mortality and topkill) following wildfire on sites previously treated with prescribed fire (Rx) and sites not treated with prescribed fire. Species include *Sequoia sempervirens* (Sese), *Notholithocarpus densiflorus* (Node), *Pseudotsuga menziesii* (Psme), all species combined (All), and all species with the ability for basal resprouting (All Resprout). The total number of trees per species category is indicated (n). Percent mortality/topkill, *p*-values for all explanatory variables tested, and marginal R^2 (R^2m) are included for each species category

	All (*n* = 963)	All Resprout (*n* = 856)	Sese (*n* = 383)	Node (*n* = 451)	Psme (*n* = 107)
% Mortality	11.21	–	2.04	1.77	88.79
Rx (*p*-value)	0.03*	–	0.88	0.95	0.91
DBH (*p*-value)	0.30	–	0.23	0.13	-
Height (*p*-value)	< 0.01*	–	0.10	0.22	0.70
R^2m	0.60	–	0.02	0.02	< 0.01
% Topkill	–	66.71	30.27	97.34	–
Rx (*p*-value)	–	0.01*	0.18	< 0.01*	–
DBH (*p*-value)	–	< 0.01*	< 0.01*	0.08	–
Height (*p*-value)	–	< 0.01*	< 0.01*	0.95	–
R^2m	–	0.79	0.78	1.00	–

For each explanatory variable, statistical association with prescribed fire is indicated by an asterisk; *P*-value ($\alpha < 0.05$)

Dash (-) indicates no recorded instances for listed variables in the column category

Plot level analysis

At the plot level, GLMM results show that the presence/absence of prescribed fire influenced average percent canopy cover, tree survival, tree density, fuel depth, and coast redwood seedling density ($0.04 > P > 0.01$, $0.85 > R^2\text{m} > 0.01$, Table 3).

Following wildfire, the average percent canopy cover was higher on plots previously treated with prescribed fire compared to untreated plots with 84.3% (SE: ± 0.8) canopy cover with prescribed fire and 79.2% (SE: ± 0.9) canopy cover without prescribed fire ($R^2\text{m} = 0.09$, $P = 0.03$). Despite a low $R^2\text{m}$, the fit with the model was significant, and the magnitude was ecologically important; prescribed fire areas had about 5% greater canopy cover than areas without prescribed fire (Fig. 5). Prescribed fire treatment also resulted in significantly higher average percent survival of trees, compared to areas without prescribed fire ($R^2\text{m} = 0.06$, $P = 0.04$). The average percent of trees that were living was 41.6% (SE: ± 11.5) with prescribed fire and 22.1% (SE: ± 6.1) without prescribed fire. Again, despite a low $R^2\text{m}$, the magnitude was ecologically important wherein prescribed fire areas had nearly 20% more living trees than areas without prescribed fire. A weak correlation was also detected between prescribed fire and average total tree density; areas with prescribed fire had lower average total tree density following wildfire with 245 (SE: ± 21.7) stems/ha in areas with prescribed fire compared to 319 (SE: ± 27.0) stems/ha without prescribed ($R^2\text{m} < 0.01$, $P = 0.03$).

In terms of surface fuels, areas with previously prescribed fire had lower surface fuel heights than areas without prescribed fire ($R^2\text{m} < 0.11$, $P = 0.03$). Specifically, the average fuel depth was 2.8 cm (SE: ± 0.8) with prescribed fire and 6.0 cm (SE: ± 1.7) depth without prescribed fire. It is also notable, but not surprising, that the duff layer was entirely absent from both treatment areas.

Statistical differences between the two treatments in regard to tree regeneration were only found for coast redwood seedlings, with remarkably greater numbers found in prescribed fire areas compared to untreated areas ($R^2\text{m} = 0.99$, $P < 0.01$). Despite the model explaining the majority of the variation (e.g., incredibly high $R^2\text{m}$ of 0.99) and highly significant results (e.g., $P < 0.01$), these results should be viewed cautiously. Extremely high counts of seedlings were recorded in a few plots and all seedlings were counted regardless of height at the time of sampling. Areas with prescribed fire had on average 6,750 (SE: ± 2520) coast redwood seedlings/ha compared to 120 (SE: ± 40.0) without prescribed fire. Clonal sprouting was prolific across sites and treatments for both coast redwood and tanoak.

Discussion

Prescribed fire has the potential to reduce the severity of future wildfires (Stephens et al. 2009). However, opportunities to test this theory are rare, as the incidence of wildfires is unpredictable. As a result, this is the only known study to examine the longer-term effects of prescribed fire on wildfire in coast redwood forests. While coast redwood forests are known for their resistance to wildfire (Woodward et al. 2020; Ramage et al. 2010; Stephens and Fry 2005), wildfire proliferation and climate change pose new risks for the ability of coast redwood forests to survive changing fire regimes. Our findings suggest that prescribed burning may be an effective tool to mitigate wildfire risks to coast redwood forests.

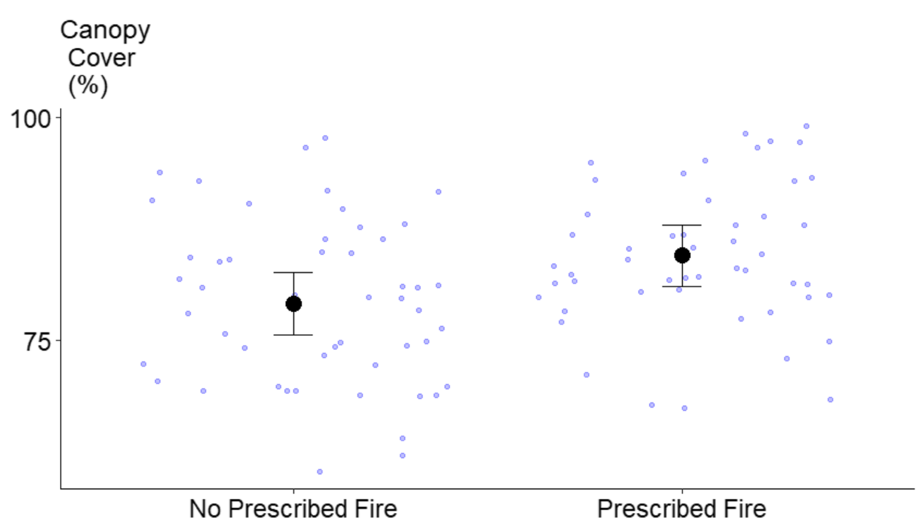

Fig. 5 Post-wildfire canopy cover response in areas treated with and without prescribed fire. Black dots indicate the model estimates, whiskers indicate 95% confidence interval, and blue dots are field observations

Additionally, prescribed fire effectiveness was prolonged, and its effects persisted even after a wildfire event. This suggests that prescribed burn projects may have surprisingly long-term and sustained benefits, even more than nine years after they were implemented. Further research is needed where (1) repeated prescribed fire treatments have been applied to the same location to better understand prescribed burning's additive effects and (2) in areas with a robust chronosequence to specifically determine how long prescribed fire effects persist in coast redwood forests.

Results from our study indicate that rates of post-wildfire canopy loss, tree mortality, and topkill were lower in areas with prescribed fire compared to areas without prescribed fire. Our results are supported by dNBR vegetation fire severity extracted to our plots as well: areas with prescribed fire had lower burn severity during the CZU: 58% of plots with prescribed fire and 74% of plots without prescribed were high severity (Potter 2023; Fig. 3). This result is not surprising given Cowman and Russell's (2021) findings that, prior to the CZU, downed woody fuel, duff depth, litter depth, and density of live woody fuels were statistically lower in areas treated with prescribed fire compared to areas without prescribed fire. Fewer surface fuels in areas with prescribed fire may have contributed to the lowered wildfire severity. However, prescribed fire's effects on lowering stand density and changing its composition likely played a more pronounced role in why the wildfire outcomes were different for areas with and without prescribed fire. These forest structure and composition differences are a potential reason why we found prolonged benefits of prescribed fire to mitigate wildfire. Cowman and Russell (2021) found that areas with prescribed fire had lower overall stand density, but they also found that treated areas had lower relative dominance of tanoaks. Tanoaks are less fire-resistant compared to other coexisting species in coast redwood forests (Lazzeri-Aerts and Russell 2014). Therefore, areas where stand composition was altered toward more fire-resistant species (e.g., fewer tanoak), would likely have lower severity wildfire. This helps to explain why prescribed burns may have had such long-lasting effects since changes to stand composition would likely have a greater duration than reduced surface fuels which can reaccumulate without repeated treatment.

While we were unable to resample exact plot locations from Cowman and Russell (2021) since original plots were not physically landmarked, there are interesting trends when pre-CZU data (Cowman and Russell 2021) is compared to our post-CZU data (Table 4). More canopy cover was retained following the CZU in areas with prescribed fire than untreated areas. While canopy cover was reduced by the CZU in both treated and untreated plots, the loss of canopy in the untreated area appeared to be higher (14.7%) versus the loss of canopy in the treated

Table 4 Comparison of response variables between two treatments; prescribed fire (Rx) vs. no prescribed fire (no Rx). *P*-values for influence of prescribed fire, sample means, standard error, marginal *r*-squared (R^2m), and conditional r-squared (R^2c) are provided for prescribed fire presence and absence for each response variable. Species include *Sequoia sempervirens* (Sese), *Notholithocarpus densiflorus* (Node), and *Pseudotsuga menziesii* (Psme). Statistical association with prescribed fire is indicated by an asterisk; *P*-value (α < 0.05). Dashes (–) indicate the model was zero-inflated; only mean and standard error are reported for these response variables

	P	No Rx, means (SE)	Rx, means (SE)	R^2m	R^2c
Stand Structure					
Canopy cover (%)	0.03*	79.20 (± 0.93)	84.34 (± 0.80)	0.09	0.16
Living trees (%)	0.04*	22.08 (± 6.08)	41.63 (± 11.47)	0.06	0.06
Total tree density (stems/ha)	0.03*	319 (± 27.00)	245 (± 21.67)	< 0.01	< 0.01
Fuels					
Duff depth (cm)	–	0.00 (± 0.00)	0.04 (± 0.02)	–	–
Litter depth (cm)	0.27	5.48 (± 0.39)	6.72 (± 0.46)	0.04	0.25
Fuel depth (cm)	0.03	6.00 (± 1.69)	2.78 (± 0.78)	0.11	0.26
Fine woody fuels (Mg/ha)	0.85	2.51 (± 0.40)	2.77 (± 0.37)	0.01	0.01
Coarse woody fuels (Mg/ha)	0.09	52.93 (± 9.74)	27.04 (± 6.66)	0.09	0.2
Regeneration					
Percent understory cover (%)	0.54	3.72 (± 0.69)	4.88 (± 0.98)	0.02	0.22
Douglas-fir seedling density (1000/ha)	0.92	1.69 (± 0.56)	0.47 (± 0.25)	0.05	0.58
Redwood seedling density (1000/ ha)	< 0.01*	0.12 (± 0.04)	6.75 (± 2.52)	0.85	0.99
Tanoak sprouts density (1000 stems/ha)	0.13	11.12 (± 0.58)	8.70 (± 0.66)	0.01	0.01
Redwood sprouts density (1000 stems/ha)	0.41	11.19 (± 1.31)	14.04 (± 1.24)	0.05	0.05

areas (7.1%) (Fig. 6). Our findings on the retention of canopy support previous studies which indicate that prescribed fire is an effective management tool for mitigating crown mortality and crown fires in other forest types (Pollet and Omi 2002; Brodie et al. 2023). Canopy retention protects valuable and unique arboreal habitat (Sillett and Van Pelt 2007), including that of the marbled murrelet, a threatened species in the region that requires intact crowns for nesting (Baker et al. 2006). Additionally, retained canopy following wildfire provides more shade, which can increase fuel moisture and help prevent fire regime shifts toward more frequent and severe wildfires in the future (Kane 2021; Ellis et al. 2022).

The most pronounced difference between pre-CZU and post-CZU fuel data was for duff depth, which not surprisingly was reduced nearly to zero by the wildfire. Post-CZU average fuel depth was lower in areas previously treated prescribed fire, which may have been influenced by lower fire severity compared to untreated areas which may have accumulated more downed fuels from dead and topkilled trees. This trend may continue as more dead and topkilled trees fall and accumulate as surface fuels. The reduction in other fuel types was pronounced following the wildfire but was relatively consistent between treatments (Table 4).

Another pronounced difference between treated and untreated areas was related to the post-wildfire regeneration of dominant tree species, particularly in regard to coast redwood seedling production. Both coast redwoods and tanoaks are inherently resilient following fire events due to their propensity for clonal regeneration (Ramage et al. 2010); and as expected, both species produced abundant sprouts across treatments one year after the CZU. Douglas-fir, on the other hand, is limited to reproduction through seed and had produced a limited number of seedlings at the time of sampling. No discernable difference was found between treatments in terms of the number of Douglas-fir seedlings. The density of coast redwood seedlings had a strong association with prescribed fire. While this is an interesting finding, the results should be treated cautiously as extremely high counts of seedlings were recorded in a few plots and all seedlings were counted regardless of height, meaning that many of the recorded seedlings are not likely to survive long term. Generally, reproduction through seed is considered ancillary for coast redwood; however, sexual reproduction can help to promote genetic diversity within a stand (Douhovnikoff et al. 2004; Douhovnikoff and Dodd 2015). This is especially important in the coast redwoods' southern range, where coast redwoods typically exhibit low genetic diversity (Brinegar 2012). In addition, genetic diversity may prove increasingly important as the species needs to adapt to a changing climate (Schierenbeck 2017; Razgour et al. 2019). A similar dense and patchy distribution of coast redwood seedlings was recorded following a previous wildfire in the southern range (Lazzeri-Aerts and Russell 2014), and further research is needed to understand this phenomenon.

Following wildfires, land managers are faced with the question of how to deal with standing dead trees, which can pose public safety risks due to falling. BBRSP is a heavily used recreation area with public access trails,

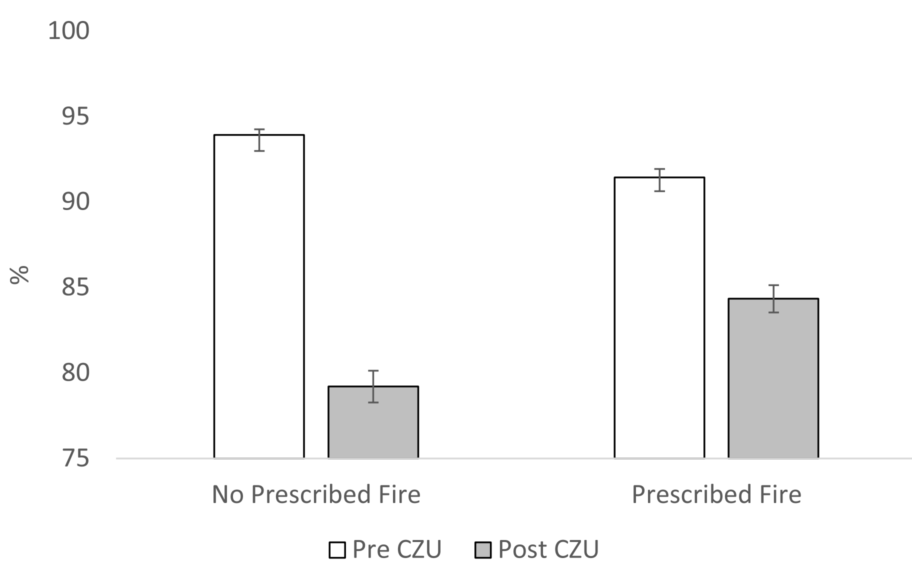

Fig. 6 Comparison of percent canopy cover before and after the 2020 CZU Lightning Complex (CZU) in the Santa Cruz Mountains of California on sites that had previously been treated with prescribed fire, and plots that had not previously been treated with prescribed fire. Data from before the CZU was retrieved from Cowman and Russell (2021)

many of which have yet to reopen since the CZU. Our finding that topkill with prescribed fire was 57.8% (±2.6) and 76.4% (±1.9) without prescribed fire indicates that previously treated areas have fewer standing dead trees after the CZU. This reduction in post-wildfire standing dead trees may have benefits for land managers balancing access to recreation with public safety. Additionally, when these trees fall over, they will contribute to the already relatively high levels of surface fuel loading in all treatments following wildfire. The relatively high post-CZU surface fuel loading across treatments suggests that the risk of repeated wildfire in redwood forests is a serious concern. Further research into the efficacy of implementing prescribed fire after wildfire events to reduce the risk of repeated wildfires is recommended.

While some of our models explained little of the total variation observed, they still had high results whose magnitudes were ecologically significant. We designed our models to detect the effect of prescribed fire with a limited data set. So, finding any positive effects of prescribed burns conducted more than 9 years previously provides support for the use of prescribed fire to increase wildfire resistance of coast redwood forests. Furthermore, our results suggest more research on prescribed fire's long-term benefits should be examined, especially beyond 9 years with a robust chronosequence.

Conclusions

Recent years have been marked by record-breaking wildfires as our landscapes continue to reconcile accumulated fuel loads resulting from over a century of fire suppression, compounded with the impacts of climate change. Coast redwood forests are highly resistant to low and moderate-severity fires and are even resilient following severe wildfires. However, a predicted increase in high-intensity fires puts these forests at risk. Prescribed fire is one possible method for reducing the impacts of wildfire, and we demonstrate some of the benefits of the treatment in the face of a high-severity crown fire. Following wildfire, we found that areas previously treated with prescribed fire had higher percent canopy cover and coast redwood seedling recruitment, lower percent mortality and topkill, lower stand density, and reduced surface fuel depth, compared to areas without prescribed fire. Overall, our results suggest that previous prescribed fires in BBRSP mitigated the severity of the CZU wildfire. Benefits of prescribed burns shown in this study add support to the use of this land management tool and indicate that those benefits can be sustained for an unexpectedly prolonged period, even though in the event of a wind-driven, and high-intensity wildfire.

Additional research is needed to better understand the duration of prescribed fire effects, including in areas with repeated prescribed fire, to inform prescribed fire best practices in coast redwood forests.

Appendix 1

Fuel load methods and calculations

Fuel Data Collection—To measure dead and downed woody fuels, two transect lines from each plot center were sampled, one along the dominant slope and the other 90° clockwise from the first transect line. To determine duff, litter, and fuel depths, measurements were taken at 1.52 m and 3.05 m from the center of each plot. Fuels were broken down into burn classes: 1-h (0–0.64 cm), 10-h (6.4–2.54 cm), 100-h (2.54–7.62 cm), and 1000+h (7.6+cm). On each transect line, fuels were counted for 1-h fuels between 0 and 1.52 m, 10-h and 100-h fuels between 0 and 3.05 m, and 1000-h fuels between 0 and 11.34 m (J. K. Brown 1974). 1000-h fuels were categorized as either "sound" or "rotten" (Cowman and Russell 2021).

Fuel calculations—Fuel load was broken into fine woody fuels (FWF) and coarse woody fuels (CWF) based on calculations first described in Brown (1974) to calculate mean fuel load. Mean fuel load was first calculated in tons per acre and then converted to metric tons per hectare (Mg ha^{-1}). Fuel load calculated as FWF and CWF for each transect line was averaged to have one (Mg ha^{-1}) measurement for each plot.

Fine woody fuels in (1-h, 10-h, and 100-h fuels) were calculated using Equation A.1, based on J. K. Brown (1974) where k is a constant of 11.64, n represents the number of FWF individual intersections counted in each size class, $d2$ is the square of the quadratic mean diameter of each size class, soc is the composite specific gravity, a is the composite angle correction factor for each size class, c is the average transect slope correction factor, and Nl is the transect length. The slope correction factor (c) calculated based on the percent slope of each transect line using Equation A.2 ($d2$, a, and soc), were constant values for non-slash, conifer, and Western species found in J. K. Brown (1974).

$$\textit{Fine Woody Fuel Load}\left(\text{Mg ha}^{-1}\right) = \frac{sknd^2 s_{oc} ac}{Nl} \tag{A.1}$$

$$c\sqrt{1 + \left(\frac{\textit{percent slope}}{100}\right)^2} \tag{A.2}$$

Calculations for CWF (≥1000-h fuels) were conducted separately for sound and rotten thousand-hour fuels

(Cowman and Russell 2021; Glebocki, 2015). CWF calculations were made using Equation A.3 from J. K. Brown (1974). ∑d2 is the sum of the diameters of particles in each decomposition class squared, and all other terms are the same as defined for Equation A.2.

$$\mathit{Coarse\ Woody\ Fuel\ Load}\left(\mathrm{Mg\ ha^{-1}}\right) = \frac{k(\sum d^2)s_{oc}ac}{Nl} \tag{A.3}$$

Appendix 2

Statistical approach and modeling

Response variable	Data type	Distribution	Package	Model family
Individual trees				
Total mortality	Binomial	Binary	lme4	Binomial
Redwood mortality	Binomial	Binary	lme4	Binomial
Tanoak mortality	Binomial	Binary	lme4	Binomial
Douglas-fir mortality	Binomial	Binary	lme4	Binomial
Sprouting species topkill	Binomial	Binary	lme4	Binomial
Redwood topkill	Binomial	Binary	lme4	Binomial
Tanoak topkill	Binomial	Binary	lme4	Binomial
Stand structure				
Canopy cover	Continuous, 0–100	Normal	glmmTMB	gaussian
Living trees	Proportion	Discrete proportion	glmmTMB	Binomial
Total tree density	Count	Right skewed	lme4	nbinom2
Fuels				
Duff depth	Continuous	Zero inflated	-	-
Litter depth	Continuous	Right skewed	glmmTMB	ziGamma(link = "log"), ziformula = ~ 1
Fuel depth	Continuous	Right skewed	glmmTMB	ziGamma(link = "log"), ziformula = ~ 1
Fine woody fuels	Continuous	Right skewed	glmmTMB	ziGamma(link = "log"), ziformula = ~ 1
Coarse woody fuels	Continuous	Right skewed	glmmTMB	ziGamma(link = "log"), ziformula = ~ 1

Response variable	Data type	Distribution	Package	Model family
Regeneration				
Understory cover	Continuous, 0–100	Right skewed	glmmTMB	ziGamma(link = "log"), ziformula = ~ 1

Appendix 3

Heat load index calculations

Calculations for heat load were based on methods outlined by McCune and Keon (2002) which rely on tables of incident radiation using slope, aspect, and latitude. Aspect was "folded" on the Northeast-Southwest line so Northeast equals 0° and southwest becomes 180° using Equation B.1. Equation (B.1) Folded aspect = | 180 – |aspect – 225| | Latitude, slope, and folded aspect were all converted into radians and entered into a formula provided by McCune and Keon (2002) using Microsoft Excel. Estimates are made by least-squares multiple regression using trigonometric functions of latitude, slope, and aspect (McCune, 2007). Results for heat load are considered unitless as there is not a basis for converting the results into a measure of temperature (McCune, 2007).

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Authors' contributions
WR and SB designed the study and worked to obtain funding. SB and WR oversaw data collection. KW and SB developed and implemented the analysis. WR and SB drafted the manuscript. WR, SB, and KW contributed editorial input during manuscript preparation. The authors read and approved the final manuscript.

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Data availability
The datasets used and/or analyzed here are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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