

ORIGINAL RESEARCH



Prescribed fires effects on actual and modeled fuel loads and forest structure in southern coast redwood (*Sequoia sempervirens*) forests



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Abstract

Background Fire suppression, timber harvesting, and the forced removal of Indigenous burning have fundamentally changed conditions in coast redwood forests. The contemporary approach of forest preservation and fire exclusion has produced high densities of small trees, elevated fuel loads, and increased vulnerability to wildfire and climate change. Prescribed broadcast burning presents a viable treatment option to meet forest management goals, especially where mechanical treatments are not feasible. Forest and fire managers utilizing fire modeling software such as the Fire and Fuels Extension of Forest Vegetation Simulator (FFE) to predict prescribed fire effects in redwoods are limited by model accuracy due to a lack of empirical research and model verification across a breadth of site conditions.

Results We compared the difference between pre- and post-treatment conditions for two fall-season prescribed burns in Sonoma and Santa Cruz counties in California to quantify changes to forest structure, fuel loads, and modeled wildfire hazard. Observed data was used to analyze the accuracy of FFE modeled prescribed fire treatment outputs for post-treatment forest and fuel conditions. Observed burn treatments were low intensity and resulted in no significant change to forest structure and composition, but there was a reduction in seedling and sapling densities and an increase in resprout density. There was a reduction in duff and litter fuels, and litter and fine woody debris reduction was driven by pre-treatment total fuel loads. The modeled probability of torching was very low pre-and post-treatment. FFE underpredicted scorch height, duff fuel reduction, and redwood regeneration, but slightly overpredicted tree mortality and significantly overpredicted reduction of litter and fine woody debris.

Conclusion Our results highlight a need for model refinement in regard to species-specific mortality, tree regeneration dynamics, fuel recruitment and deposition, and moisture-dependent fuel consumption. In order to achieve desired forest management goals, fire practitioners may need to burn at moderate to high intensities, and potentially pair burning with mechanical thinning. Long-term health of coast redwood forests also relies on the restoration of cultural fire and stewardship partnerships that equally share decision making power between western science and Indigenous knowledge bearers.

Keywords Coast redwoods, Prescribed fire, Fuel reduction, Forest restoration, Fire effects modeling, Sonoma County, Santa Cruz County

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Resumen

Antecedentes La supresión de incendios, la tala de bosques, y la remoción forzosa de las quemas que realizaban los indígenas, han cambiado de manera fundamental las condiciones en los bosques costeros de sequoias. El enfoque contemporáneo de la preservación de los bosques y la exclusión de los incendios, ha producido una alta densidad de plántulas, cargas de combustible elevadas, y un incremento en la vulnerabilidad a los incendios y al Cambio Climático. Las quemas prescriptas se presentan como una opción de tratamiento viable para alcanzar metas de manejo forestal, en especial cuando los tratamientos mecánicos no son factibles de realizar. Los gestores de fuegos que utilizan el modelado basado en software como el Simulador de extensión de fuegos y combustibles vegetales (FFE), para predecir los efectos de una quema prescripta en bosques de sequoias, están limitados en la exactitud del modelo debido a la falta de investigaciones empíricas y verificación de ese modelo un amplio rango de condiciones de sitio.

Resultados Comparamos las diferencias entre condiciones de pre y post tratamientos de quemas prescriptas en dos otoños en los condados de Sonoma y Santa Cruz en California, sobre cambios en la estructura forestal, la carga de combustibles y el modelado del riesgo de incendios. Los datos observados fueron usados para analizar la exactitud de los resultados obtenidos mediante el tratamiento del modelado por el FFE en relación al postrataiento del bosque y las condiciones de los combustibles. Los tratamientos de quema observados fueron de baja intensidad y resultaron en cambios no significativos en cuanto a la estructura y composición el bosque, aunque hubo una reducción en la densidad de plántulas y brinzales y un aumento en la densidad de rebrotes. Hubo una reducción en la carga de man-tillo y broza (*Duff and Litter*), y la reducción de broza y material leñoso fino fue debido al pretratamiento de la carga total del combustible. La probabilidad modelada de coronamiento del fuego fue baja tanto en el pre como en el post tratamiento. El Modelo FFE subestimó la altura de chamuscado, la reducción del mantillo y la regeneración de las sequoias, aunque sobreestimó levemente la mortalidad de los árboles y sobreestimó significativamente la reducción en la broza y los residuos forestales finos.

Conclusiones Nuestros resultados resaltan la necesidad de un refinamiento del modelo relacionado con la mortalidad específica de las especies, la dinámica de la regeneración, el crecimiento y deposición de la carga de combustibles, y la dependencia de la humedad de los combustibles en el consumo de los mismos. De manera de alcanzar metas deseadas de manejo forestal, los practicantes de quemas prescriptas deberían quemar a intensidades moderadas a altas, y realizar de modo apareado las quemas junto con tratamientos mecánicos de raleos. La salud de los bosques costeros de sequoias a largo plazo también necesita la restauración de los fuegos culturales y de administradores que compartan igualmente el proceso de decisión entre la ciencia occidental y el conocimiento ancestral que poseen los indígenas.

Introduction

Prescribed broadcast burning, a growing practice in stewarding coast redwood (hereafter referred to as "redwood") forests in the central coast region (Audubon Canyon Ranch 2022), presents a financially and logistically viable treatment option to meet restoration goals. Given recent large high-severity wildfires impacting these forests, such as the 2020 Walbridge Fire and 2020 CZU Complex Fire, and changing liability laws that expand the legal protections of prescribed fire practitioners in California (Varner et al. 2021), the use of prescribed burning is increasing. This is especially the case in regions and settings where standard mechanical silvicultural methods are cost prohibitive and may not necessarily address all aspects of restoration goals (Glebocki 2015; North et al. 2015; O'Hara et al. 2010). Existing research suggests repeated prescribed burning may gradually improve the overall resilience of redwood stands to wildfire by reducing fuel loads (Finney and Martin 1992b; Biblin 2023) and small tree stand density, without adverse effects on the diversity and cover of understory species (Cowman and Russell 2021; Engber, Teraoka, and van Mantgem 2016).

Tree ring fire history studies suggest that prior to fire suppression and the cessation of Indigenous burning, southern redwood forests were characterized by a highfrequency, low-intensity surface fire regime (Appendix Table 4). Mean fire return intervals (FRIs) in inland Sonoma County redwood forests ranged between 6 and 23 years (Finney and Martin 1992b), and in coastal Sonoma County (Salt Point State Park) mean FRIs were found to be 6 (composite) and 24 years (point) (Finney and Martin 1989). For Santa Cruz and San Mateo counties, mean FRIs ranged between 9 and 16 years for inland sites (Stephens and Fry 2005) and 6.9 (composite) to 39 years (point) for coastal sites (Striplen 2014). Scars from shortinterval fires were predominantly found in latewood and dormant wood, indicating the seasonality of the burn was mid-August to late fall (Brown et al. 1999; Brown and Baxter 2003; Stephens and Fry 2005; Striplen 2014). Fire occurrence in all studies greatly decreased between 1850 and 1950 and were very uncommon after 1950, roughly coinciding with European colonization and settlement of the region, restrictions on Indigenous burning, and establishment of fire suppression policies. Common issues with complacent annual ring patterns and discontinuous rings (Stephens and Fry 2005; Brown et al. 1999) make redwood tree ring reconstructions and crossdating difficult. As a result, fire history reconstructions likely underestimate fire frequency, limiting our understanding of the true deviation from historic fire regimes and subsequent ecological impacts caused by the disruption.

The infrequent occurrence of lightning in the central coast region (van Wagtendonk and Cayan 2008), which is not sufficient to account for the high frequency of fire scars reported in fire history studies, strongly supports that fires were intentionally lit by Indigenous peoples (Lightfoot and Parrish 2009; Lightfoot et al. 2013). The evidence provided by fire scars is affirmed by Indigenous knowledge and oral histories of Southern Pomo, Coast Miwok, Ohlone, and many other Indigenous peoples in coastal California that describe the frequent, intentional use of low to moderate severity fire for a wide variety of eco-cultural and spiritual reasons (Castro, Yamane, and Lopez 2023; Long et al. 2021). Despite interruptions to the transmission of Indigenous knowledge through the dispossession of land and criminalization of burning practices, Indigenous leaders and cultural fire practitioners maintain a right and responsibility to use fire-termed "Indigenous fire sovereignty" (Lake and Christianson 2019)-in a self-governed, culturally, and place-specific manner (Martinez et al. 2023). These factors, in conjunction with the legitimate concerns about the appropriation of Indigenous knowledge, make defining specific cultural burning strategies (e.g., timing, intensity, and extent) and subsequent fire effects on vegetation dynamics (Lightfoot et al. 2013; Nelson, Peter 2017) unlikely and somewhat unnecessary. Generally, this anthropogenic-driven frequent fire regime likely maintained relatively low surface fuel loads (Jacobs et al. 1985), open and variable overstory structure (Lorimer et al. 2009), and diverse understory vegetation communities in redwood forests, amidst a heterogenous mosaic of many native plant communities (Keeley 2005). Assuming a mean FRI of 15 years, and conservatively 70 years without fire, many redwood forests in this region have now missed four to five fire events, constituting an ecologically meaningful disruption in the fire regime.

Indigenous ignitions may have been limited to periods when fuel accumulation was sufficient and fuel moisture was low enough to carry fire (Norman et al. 2009). Fire frequency in coast prairie and oak woodlands adjacent to redwood stands was much higher (2–12 years (Van De Water and Safford 2011; Fryer and Luensmann 2012)), which leaves the possibility that nearby fires spread into redwood forests from exogenous sources as soon as fuel accumulation and moisture dynamics allowed (Varner and Jules 2016; Stephens et al. 2018). Redwood forests are now ignition limited, meaning that alterations to historic fire regimes are driven more by the exclusion of fire (e.g., cultural burning practices) than the suppression of nonhuman fire starts, necessitating the active use of fire in future management (Norman et al. 2009).

Since European colonization, redwood forests have been altered by timber harvesting, fire suppression, and the related dispossession of Indigenous from their lands and stewardship practices, including burning (Brown and Baxter 2003; Finney and Martin 1992b; Martinez et al. 2023). The vast majority of old-growth redwoods have been harvested for timber, and remaining stands are primarily second- and third-growth clonal basal sprouts regenerated from cut stumps (O'Hara et al. 2017; Thornburgh et al. 2000). Currently, redwood forests owned by small private landowners, public agencies, and conservation non-profit organizations tend to be managed for non-industrial timber values (public access, biodiversity, aesthetics, etc.) (Ferranto et al. 2011). The concerns presented by legacy timber harvesting practices have been replaced by the contemporary threat of a tandem preservation and fire exclusion management approach. Despite the intent to protect forest, this management regime is proving inadequate for maintaining ecosystem resilience (Stephens and Ruth 2005), defined as a system's ability to absorb disturbance and maintain the same basic ecosystem identity and function (Holling 1973).

Second- and third-growth forests, where fire has largely been suppressed and excluded for the past 100 years, are now characterized by high stem densities (1533–5586 trees ha⁻¹), predominantly composed of small trees (<14 cm DBH) (Engber, Teraoka, and Van Mantgem 2016; Teraoka and Keyes 2011). These forests also have high accumulations of duff and litter (29–55 Mg ha⁻¹), fine woody fuels (9–22 Mg ha⁻¹), and coarse woody fuels (0–246 Mg ha⁻¹) (Finney and Martin 1992a), as well as sparse understories with limited herbaceous plant diversity and cover (Brown and Baxter 2003; Cowman 2020).

Prescribed broadcast burning in redwood forests presents a financially and logistically viable treatment option to meet restoration goals. Mechanical management practices (i.e., thinning) used to minimize the severity and spread of wildfire have high economic costs and societal objections and may not meet the need for restoring ecological processes. Non-industrial redwood forest landowners and managers are left with few scalable options to manage their forests. In light of recent large wildfires and changing liability laws (Varner et al. 2021), the use of prescribed burning is increasing in regions and settings where standard mechanical silvicultural methods may not necessarily address all aspects of restoration efforts in redwood forests (Glebocki 2015; North et al. 2015; O'Hara et al. 2010).

Prescribed burning may gradually improve the overall resilience of redwood stands to wildfire by reducing fuel loads (Finney and Martin 1992b; Biblin 2023) and stand density without necessarily reducing the diversity and cover of understory species (Cowman and Russell 2021; Engber, Teraoka, and van Mantgem 2016). While prescribed fire can reduce surface fuel loads, fuel dynamics after burn treatments are nuanced. Fine fuel conditions have been found to return to pre-treatment conditions within 7 years after burning (Engber, Teraoka, and van Mantgem 2016) and post-treatment large woody debris can vary (increase or decrease) due to log consumption and tree fall (Cowman and Russell 2021). Low-intensity fire appears to have little effect on overstory species composition and structure, with tree mortality concentrated in smaller, understory size classes (roughly < 20-30 cm DBH). Moderate to higher intensity fire is likely needed to produce meaningful effects on forest structure (Cowman and Russell 2021; Engber, Teraoka, and van Mantgem 2016; Woodward et al. 2020), though managers must consider the species-specific responses to higher fire intensity (i.e., basal and epicormic resprouting, seed regeneration) and morphological characteristics of trees within units (i.e., canopy base heights, bulk density, and basal cavities), as well as subsequent changes to forest composition.

Forest and fire managers utilizing prescribed fire in forest restoration efforts rely on fire behavior modeling software to predict fire behavior, fire effects, and fuel treatment effectiveness in mitigating modeled wildfire hazard. Modeling systems allow for simulation of fire behavior and effects at the point (e.g., BehavePlus (Andrews, Bevins, and Seli 2005)), stand (e.g., the Fire and Fuels Extension of Forest Vegetation Simulator (FFE) (Rebain et al. 2022)), and landscape scale (e.g., FlamMap (Finney 2006)). These models are made for wildfire scenarios, however, with built-in assumptions that limit their applicability to prescribed fires (Hiers et al. 2020). As a result of limited empirical research on this topic specific to redwood forests (Scanlon and Valachovic 2006), there is little verification of model projections across a breadth of weather, fuel loads, fuel moistures, and topographic conditions, especially in prescribed fire scenarios. The minimal existing research on the accuracy of fire effects models in redwood forests have focused on landscape scale fire effects using FARSITE (now part of FlamMap) (Scanlon and Valachovic 2006), but were not found to be useful in predicting post-fire effects on vegetation. As fire practitioners and resource managers increase the pace and scale of prescribed burning throughout redwood forests, more research is needed on fuels, weather, and seasonality influence on fire effects in redwood forests in order to (1) ensure treatments are meeting restoration goals and other management objectives and (2) improve fire behavior model usefulness and applicability for forest and fire managers.

Analysis of FFE modeled stand-level prescribed fire behavior and effects have been conducted for dry conifer forests in California (Noonan-Wright et al. 2014), yet model runs were not compared to observed fire behavior and post-treatment effects, providing little insight into the accuracy of model outputs. Noonan-Wright et al. and others (Hummel, Kennedy, and Steel, Ashley 2013) have found that dynamics of some fuel size classes (e.g., fine fuels and litter) are not well predicted by FFE. Most commonly, stand-level modeling using FVS is used to predict fuels and forest treatment effects on wildfire behavior and effects, especially under the hot, dry, windy conditions when fire behavior is likely to be most intense. Assessment of stand-level model performance has yet to be conducted for prescribed fire (e.g., typically, cooler, wetter conditions) in southern range of redwood forests, as best as we can tell.

The objective of this study is to analyze the accuracy of modeled fire behavior and effects using FFE for prescribed fire treatments in the southern range of redwood forests (south of Mendocino County). Model accuracy was assessed by comparing pre- and post-treatment field data from two fall-season prescribed burns in the central coast (Sonoma and Santa Cruz counties) to FFE modeled outputs. Three research questions guide the study: (1) What are the observed effects of prescribed fire treatments on fuel dynamics and forest structure and composition? (2) Do modeled prescribed fire effects in redwood forests accurately predict observed post-treatment effects (fuel load change, basal area change, and mortality of overstory trees, seedlings, and saplings)? and 3) Do prescribed fire treatments reduce modeled future potential wildfire hazard?

Methods

Site descriptions

This study analyzes the effects of two recent prescribed burns at Grove of Old Trees (GOT) west of Occidental, CA and Wilder Ranch State Park (WIL) west of Santa Cruz, CA. GOT is relatively flat and located at the top of a ridge surrounded by a mix of grassland, mixed hardwood and Douglas-fir forest, and vineyards. The primary aspects are south and northwest, with slopes ranging from 3 to 10%. The WIL burn unit is located in a midslope drainage, surrounded by coast prairie and mixed hardwood forest. The primary aspects are southeast to southwest, with slopes ranging from 8 to 55%. The burn unit at GOT is 7.7 km from the coast and 120 m in elevation, while the unit at WIL is 3.5 km from the coast and ranges from 45 to 100 m in elevation.

Weather and plant communities at both sites are characterized by the Mediterranean climate. While summers are typically long and dry, maritime influences provide some moisture during summer months via fog. Winters are relatively short, mild, and wet. Average annual precipitation is 136 cm in Occidental, CA, and 78 cm in Santa Cruz, CA (National Centers for Environmental Information, NOAA 2021), though there is a high degree of interannual variability. Overstory species at both sites are dominated by coast redwood (Sequoia sempervirens (D. Don) Endl.) and Douglas-fir (Pseudotsuga menzeseii (Mirb.) Franco), with a mixed subcanopy including species such as tanoak (Notholithocarpus densiflorus (Hook & Arn.) Rehd.), bay laurel (Umbellularia californica (Hook & Arn.) Nutt.), Pacific madrone (Arbutus menziesii Pursh), and several oak species (Quercus spp.). Understory vegetation communities are generally sparse with patchy distribution of several ferns, California blackberry (Rubus ursinus), poison oak (Toxicodendron diversilobum), California hazelnut (Corylus cornuta), and various forbs. While forest composition and structure are similar at both sites, there are a few key differences (Table 1). GOT is dominated by large, mature redwoods, with relatively few smaller diameter Douglas fir and hardwoods.

The management history of both sites represent site conditions of typical coast redwood forest in the central coast managed primarily for recreation and conservation values (as opposed to timber production). There is no recorded wildfire history in the study area at Grove of Old Trees or Wilder Ranch State Park. While there is no recent history (30+years) of forest or fuel management at Grove of Old Trees, some plots in Wilder Ranch State Park received a prescribed burn treatment in November 2005 and prior thinning treatment along control lines as part of burn unit preparations. California State Parks has a robust prescribed burn program in Santa Cruz County focused mostly on grasslands, and much of the coast prairie around the study area has been burned multiple times in the past 15-20 years. Both sites have evidence of historic timber harvests in the late 1880s or early 1900s.

In November 2022, both prescribed burns were conducted with the primary management goals being to reduce fuel loads, kill Douglas-fir seedlings and saplings, reduce density of non-redwood overstory trees, limit large redwood tree mortality, and reduce the threat of

Pre-treatment GOT WII Variable Mean ± SE (Min-Max) Mean ± SE (Min–Max) Trees/plot $10.8 \pm 0.8 (6.0 - 14.0)$ $19.4 \pm 2.5 (8.0 - 37.0)$ Tree ha⁻¹ 265.5 ± 20.7 (148.2-345.8) 479.6±61.3 (197.6-913.9) Total BA/plot (m²) 6.7 ± 1.1 (2.2–10.9) $3.6 \pm 0.6 (1.0 - 7.0)$ Total BA ha⁻¹ (m²) 164.8±26.7 (54.5-269.9) 88.6±14.9 (25.0-172.7) Canopy Base Height (m) 12.8±2.2 (4.9-26.1) 5.3±0.9 (0.2-12.1) Canopy Bulk Density (kg m³) $0.02 \pm 0.00 (0.01 - 0.05)$ $0.03 \pm 0.00 (0.01 - 0.06)$ Relative Density (%) SESE 87.2±6.8 (50.0-100.0) 60.4±10.8 (0.0-97.3) PSME $1.0 \pm 1.0 (0.0 - 8.3)$ $6.9 \pm 3.6 (0.0 - 45.5)$ NODE3 $1.0 \pm 1.0 (0.0 - 8.3)$ $3.3 \pm 1.2 (0.0 - 11.1)$ UMCA 10.7±6.5 (0.0-50.0) 10.9±3.7 (0.0-37.5) QUAG $0.0 \pm 0.0 (0.0 - 0.0)$ $5.4 \pm 5.4 (0-64.3)$ QUWI $0.0 \pm 0.0 (0.0 - 0.0)$ $2.3 \pm 1.6 (0.0 - 16.7)$ ARME $0.0 \pm 0.0 \ (0.0 - 0.0)$ 10.9±5.4 (0.0-54.6) 62.7±11.7 (0.0-99.9) Relative Dominance (%) SESE 98.9.±0.0 (96.1-100.0) $0.0 \pm 0.0 (0.0 - 0.3)$ 9.1 ± 5.3 (0.0-55.7) PSME NODE3 $0.3 \pm 0.3 (0.0 - 2.2)$ $0.2 \pm 0.1 (0.0 - 0.7)$ UMCA $0.8 \pm 0.4 (0.0 - 3.3)$ $7.5 \pm 3.2 (0.0 - 34.4)$ QUAG $0.0 \pm 0.0 (0.0 - 0.0)$ $4.3 \pm 4.3 (0.0 - 51.6)$ QUWI $0.0 \pm 0.0 (0.0 - 0.0)$ 3.1 ± 2.9 (0.0-35.1) ARMF $0.0 \pm 0.0 (0.0 - 0.0)$ 13.2±7.5 (0.0-84.6)

Table 1 Pre-treatment live overstory forest structure and composition by site. Variables were calculated for each plot and then aggregated by site for reporting

wildfire to neighboring communities (Hyland 2022; Berleman 2022). Exact unit preparation, ignition techniques, and mop-up activities tactics were determined by the burn boss. Generally, pre-burn unit preparation consisted of fuel reduction along containment lines. There were limited fuel alterations inside the unit beyond moving large downed logs away from the base of large trees.

Sampling design

Sampling was conducted in twenty 0.04-ha circular plots that were established on a standardized 50-m grid (GOT) and 250-m grid (WIL) across the two prescribed burn units. Study plots were placed no less than 30 m from containment lines to reduce potential impacts of unit preparation and mop up efforts. In total there were eight plots at GOT and twelve plots at WIL (Fig. 1). Tree and fuel data were collected before and after burn operations at both sites. Pre-treatment data was collected in Summer 2021 (WIL) and Summer 2022 (GOT), prescribed burn treatments were conducted in November 2022, and post-treatment data was collected in Summer 2023 (8 months after burn treatments were implemented).

Field sampling

In each plot, the following data was collected utilizing California Prescribed Fire Monitoring Program (CPFM) protocols (CAL FIRE 2023): surface fuel loads, tree regeneration, overstory tree inventory, slope, and understory species cover. Four 11.3-m fuel transects (Brown et al. 1999) were installed in each plot, oriented in the cardinal directions, to measure dead and downed fuels. All 1-h (<0.64 cm) and 10-h (0.64–2.54 cm) fuels that intersected the transect between the last 2 m of the transect line (11.3 m–9.3 m) were counted, as well as all 100-h fuels (2.54–7.62 cm) that intersect the transect between the last 4 m of the transect line (11.3–7.3 m). Every 1000-h fuel (>7.62 cm) that intersected the entire 11.3-m transect



Fig. 1 Map of site and plot locations at Wilder Ranch State Parks (WIL) in Santa Cruz County and Grove of Old Trees (GOT) in Sonoma County, California. Plot locations vary slightly from standardized grid due to GPS inaccuracies under forest canopy

line was counted and its species, diameter at intersect, and decay class (1–5) were recorded. Duff, litter, and total fuel depths were sampled in two locations along each transect; at the end of the transect (outside edge of the plot) 4 m from the end of the transect (7.3 m mark). To measure total fuel depth, a 30-cm section of transect (15 cm in both directions from the sampling location) was identified. Within this 30-cm segment, the three highest dead fuels were identified. The depth from the bottom of the litter layer to the top of the three highest dead fuels were measured and the average of the three points was recorded. The slope of each transect was also recorded to allow for slope correction when calculating fuel loads for each plot.

Fuel load calculations were conducted at the plot level using the Rfuels package (Foster et al. 2018) to attain a mean fuel load in metric tons per hectare (Mg ha⁻¹) for the following fuel classes: 1-100 h (FWD), litter and FWD (Litter+FWD), sound 1000-h, rotten 1000-h, combined 1000-h (CWD), surface, and total fuels. Rfuels utilizes tree plot data (species relative dominance) to determine values for quadratic mean diameter (QMD), secant of acute angle (SEC), and specific gravity (SG), which are needed to calculate loads for 1-1000-h fuels. Rfuels includes these values for 19 Sierra Nevada tree species, only some of which occur in the coast range. Given this, Douglas fir is the only species in this study that has species-specific values assigned by Rfuels. All other species are given the QMD, SEC, and SG constant values for "Other" tree species, which may differ slightly from actual species values and thus effect on the accuracy of fuel calculations.

Duff and litter loads were not calculated using the Rfuels package due to inaccurate bulk density values. Duff and litter loads were calculated using the coast redwood bulk density equation in Finney and Martin (1993):

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CW(cumulative weight) = 6.461(depth of strata)^{1.07} - 0.254(total depth)
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Finney and Martin developed this model for duff and litter, collectively referred to as "forest floor" fuels, which describes a positive linear relationship between forest floor depth and bulk density. Given this depth-dependent bulk density, the above calculation could not be applied to the litter and duff layers individually, as it would result in underestimation of duff weight. Duff weight was calculated by first calculating the weight of the litter layer and the cumulative weight of "forest floor" layers, and then subtracting the litter weight from the cumulative weight.

Duff weight = Total CW - Litter weight

Data for overstory trees, defined as > 1.4 m tall and > 7.6 cm DBH, was collected for all live trees and snags with the bole center located within the 11.3-m radius

circular plot (0.04 ha). Overstory tree variables included species, DBH, total height, height to live crown, scorch height, bole char height, and snags were assigned a decay class (1–5). The number and species of seedlings, saplings, and resprouts (tree regeneration) were recorded within a 4.37-m circular subplot (60 m²). Seedlings were defined as trees < 1.4 m tall and saplings were trees > 1.4 m tall but <7.6 cm DBH. Resprouts were defined as any basal respout growing from a live or dead tree, regardless of size. Prior to prescribed burns, understory vegetation cover was determined using ocular estimates across the entire 0.04 ha circular plot. Understory cover estimates were only used in the process of fuel model selection (described subsequently in FVS-FFE Modeled Prescribed Burn section) and were not analyzed pre- and post-treatment.

During burn operations, flame length estimates and ignition patterns were recorded. The following data was also collected every 10 min from the nearest weather station (Occidental DW2845 and Dimeo Lane PG853) (University of Utah, n.d. "MesoWest Surface Weather Maps."): temperature, relative humidity, wind speed, and wind direction. Weather stations are 2.4 and 2.5 km from GOT and WIL, respectively, and represent unshaded conditions, which is generally warmer and drier than shaded conditions within each burn unit. Fuel moisture samples of each fuel size class were collected near plot locations every 2 h during GOT prescribed burn and the day prior. No fuel moisture samples were collected prior to or during the WIL burn operation. All fuel samples were collected, weighed, dried, and calculated using standard fuel moisture sampling methods (Zahn and Hanson 2011).

Observed prescribed burn

Overall, prescribed burn conditions were very similar between the two operations (Appendix Table 5), falling between the "Cool" and "Desired" range of the burn prescription. "Cool" conditions for GOT were generally defined as temperature 10 °C, RH 80%, wind 0 km h^{-1} , and 12% fine dead fuel moisture. "Desired" conditions were defined as 21.1 °C, RH 35%, wind 8 km h^{-1} , and 8% fine dead fuel moisture (Berleman 2022). The "Cool" end of the prescription at WIL was defined as 7.2 °C, RH 80%, wind 0 km h⁻¹, and 11% fine dead fuel moisture (Hyland 2022). Both operations included dot and strip firing techniques with 2–4 m spacing, resulting in a combination of heading, flank, and backing fire spread and flame lengths between 0.2-0.3 m (GOT) and 0.05-0.6 m (WIL). Rate of spread estimates were not recorded during burn operations, though anecdotally reports indicate fire spread was slow (Hyland 2022). At WIL, fuels in sunny, exposed areas were more available to burn than shaded areas, creating patchy fuel consumption patterns. Torching was rare in both operations. Given the similarity in weather

conditions and fire behavior, as well as the relatively small sample size, findings derived from the observed prescribed burns represents only a narrow range of possible fire effects in redwood forests.

FVS-FFE modeled prescribed burn

Stand-level prescribed fire effects were modeled using FFE. The Inland California and Southern Cascades CA variant was used for model runs (FVS Staff 2023). While it does not match the exact geographic locations of study sites, it is the best variant given the tree species present in forest plots. In order to match the years of pre- and post-treatment field data collection and prescribed fire implementation, the common starting date was set to 2021, prescribed fire treatments occurred in 2022, and common ending date was set to 2023, with the growth and reporting interval set to every 1 year. While FVS is a growth and yield model that can project changes in forest structure and growth decades into the future, outputs were only projected out to 2023 to maintain consistency with observed field data. FFE outputs (hereafter referred to as "modeled post-treatment") for fuels and forest structure conditions were compared to posttreatment field-derived conditions (hereafter referred to as "observed post-treatment"). See Fig. 2 for conceptual framework of dataset comparison.

For modeled prescribed fire treatment runs, input data included the observed pre-treatment fuels, tree data, and slope for each plot, and weather data derived from burn operations. Initial fuel loads in FVS modeling were defined using observed pre-treatment fuel loads to ensure baseline conditions were consistent between observed and modeled datasets. Each plot was assigned a Scott and Burgan fuel model (Scott and Burgan 2005). Using the assigned fire-carrying fuel type, we selected fuel models that represented the climatic conditions (dry) and were likely to produce fire behavior similar to that observed during prescribed burn operations. We used a custom decision matrix based on understory species cover, dominant tree species, fine fuel loads, and coarse woody fuel loads (Appendix Fig. 8). Similar to Stephens et al. (2024), model selection breaks were determined based on each plot's Litter+FWD and CWD fuel loads relative to the median value (50% percentile) for the group. Plots with loads below the median value were assigned the fuel model with lower fuel loads, and those greater than the median were assigned the model with the greater fuel load. GOT plots included fuel models TU5, TL3, and TL4 and WIL plots included fuel model TU1, TU5, TL3, TL4, TL6, TL7, and TL9. Fuel moisture values for GOT were assigned using the median value for each fuel class, calculated from field fuel moisture samples. GOT fuel moisture values were as follows: duff 117.8%, 1-h 13.9%, 10-h 17.6%, 100-h 16%, and 1000-h 18.8%. WIL fuel moisture values were established using the "Moist" fuel moisture scenario in FFE based on weather data for the site: duff 125%, 1-h 12%, 10-h 12%, 100-h 14%, and 1000-h 25%. Temperature (max) and 6.1 m winds (median) during both burn operations were sourced from the nearest weather station to each burn unit. GOT was set to 15.5 $^{\circ}$ C with 3.2 km h⁻¹ wind speed and WIL was set to 21.1 $^{\circ}$ C with 5.6 km h⁻¹ wind speed. The slope for each plot was included. Modeled prescribed fire treatments at both sites were set to occur in Fall and burn 100% of the stand, though this area burned value likely oversimplifies the variability in fuel consumption. Even when 100% of area is burned, fuel consumption is not uniform and complete due to variation in fuel moisture. Modeled outputs for probability of torching, fuel load, and forest structure and composition were generated for each plot using FVS_PotFire, FVS_Fuels, FVS_Regen_Sprouts, and StdStk outputs tables. Modeled post-treatment data outputs were generated for 1-year after the prescribed fire to match post-treatment field data collection dates.



Fig. 2 Conceptual framework for comparison of observed and modeled change in forest fuel dynamics. Modeled treatments utilized observed pre-treatment fuels and forest conditions and prescribed fire operation weather and fuel moisture conditions

Modeled wildfire hazard

To determine prescribed fire treatment effectiveness in reducing future wildfire hazard, FFE was used to model probability of torching (P-torch). These FVS PotFire outputs tables were generated using two sets of trees and fuel input data. Data collected prior to the prescribed burn treatments was used to simulate "untreated" site conditions and post-treatment data was used to simulate "treated" conditions. Outputs were derived for "severe" fire weather conditions, defined in FFE as: 35 °C, 64.3 km h⁻¹ wind speed, fall season, 17% duff fuel moisture (FM), 4% 1-h and 10-h FM, 5% 100-h FM, 10% 1000-h FM, 70% live herbaceous and woody FM. Weather and fuel moisture variables were derived from RAWS weather station (BNDC1) data during the 2020 CZU Lightning Complex Fire, which burned near the WIL study site. Fuel moisture values reflect the standard "Very Dry" and "Dry" moisture scenarios within FFE. Mean P-torch values were compared between pre-treatment and post-treatment conditions using Welch's T-tests.

Data analysis

Statistical analyses were performed using RStudio software version 2022.12.0 + 353 (R Development Core Team 2023) with an alpha level of 0.05 used to determine statistical significance for all statistical testing. Welch's T-tests were used to compare mean pre- and post-treatment variables including: overstory tree density and basal area for each species, regeneration (seedling, sapling, and resprout) stem density for each species, fuel loads of each fuel class and probability of torching. Welch's T-tests were also used to compare the mean observed and modeled post-treatment variables as listed above in order to determine the accuracy of FFE modeled outputs. A linear regression model was constructed for observed change in Litter + FWD after the prescribed burn treatment. The full suite of independent variables included slope, aspect, pre-treatment fuel loading, and stem density of overstory trees and regeneration (seedling, saplings, resprouts) for each species. We used the randomForest package to reduce the number of independent variables to a parsimonious list by generating Mean Decrease Accuracy scores for relevant forest, fuels, and site variables, then only selected those with positive %IncMSE scores. Models were fit using lm function in base R. Model variables were tested for normality within the data and residuals using Shapiro Wilk's (Srivastava and Hui 1987) tests and density distribution plots, respectively.

Results

Observed trees

Due to limited overstory mortality, and the fact that mortality primarily occurred in smaller DBH classes, there was no significant change in overstory forest structure, species composition, or basal area. Prior to burn treatments, mean stand density at GOT was 10.8 trees per plot (265.5 trees/ ha⁻¹), mean basal area per plot was 6.7 m² (164.8 m²/ha⁻¹), mean canopy base height was 12.8 m, and redwood relative dominance was 98.9%. WIL was characterized by a greater number of smaller trees with lower canopy base heights. While redwood was still the dominant species, hardwoods occupied a greater portion of the forest, as shown by their combined relative dominance of 28.2%. Mean stand density at WIL was 19.4 trees per plot (479.6 trees/ ha⁻¹), mean basal area per plot was 3.6 m² (88.6 m^2/ha^{-1}), mean canopy base height was 5.3 m, and redwood relative dominance was 62.7%. Overstory mortality was dominated by redwoods < 25 cm DBH (Fig. 3), accounting for 13 of 20 total overstory trees killed across all plots, nearly all of which were only top-killed and subsequently sprouted from the base. The largest overstory tree killed was a 129 cm DBH Douglas-fir at WIL, which snapped after having its basal cavity burned out. The mean total overstory stand density (>1.4 m tall and >7.6 cm DBH) was 317.4 stems ha⁻¹ pre-treatment and 302.5 stems ha⁻¹ post-treatment (P = 0.7). The mean redwood overstory stand density was 228.4 stems ha⁻¹ pre-treatment and 218.6 stems ha⁻¹ post-treatment (P = 0.9). Similarly, there was no observed change in overstory tree density (stems ha⁻¹) for bay laurel, tanoak, and coast live oak, and only slight decreases for canyon live oak (1.2 stems ha^{-1}), madrone (2.5 stems ha⁻¹), and Douglas-fir (1.2 stems ha⁻¹). Given this limited overstory mortality, and the fact that mortality primarily occurred in smaller DBH classes, there was no significant change in overstory forest structure, species composition, and basal area.

Modeled trees

Both observed and modeled datasets showed tree mortality as a result of prescribed fire treatments, though posttreatment tree densities differed among datasets (Fig. 4). Mean modeled total live tree density was 262.9 trees ha⁻¹, while observed total live tree density was 302.5 trees ha^{-1} (P=0.3). Mean modeled live redwood density was 201.3 trees ha⁻¹ and observed live redwood density was 218.6 trees ha^{-1} (*P*=0.7). Mean modeled live bay laurel density was 10.2 trees ha⁻¹ and observed live bay laurel density was 19.8 trees ha^{-1} (P=0.2). Observed live tree densities were slightly higher than modeled live tree densities for all other species, though no findings were significant $(P \ge 0.19)$. Given that observed post-treatment data and FFE modeled data showed overstory mortality concentration in smaller DBH classes (<25 cm), there was very little difference between observed and modeled live basal area



Fig. 3 Density distribution (stems ha.⁻¹) of redwood (SESE) and all other overstory tree species by DBH class (cm) before (Pre) and after (Post) prescribed fire treatment. DBH class labels denote the upper limit of class. DBH class "10" includes trees between 4 and 10 cm. All other species (Douglas-fir, tanoak, madrone, bay laurel, and oaks spp.) are grouped as "Other". Trees under 4 cm DBH (seedling, saplings, and resprouts) are shown in Appendix Fig. 9



Fig. 4 Comparison of live overstory tree density (stems ha⁻¹) and basal area (m² ha.⁻¹) between observed pre-treatment, observed post-treatment, and modeled (FFE) post-treatment. Redwood (SESE) has the highest tree density and basal area values. All other species (Douglas-fir, tanoak, madrone, bay laurel, and oaks spp.) are grouped as "Other"

across species. Mean modeled scorch height was 1.4 m and observed scorch height was 3.2 m (P=0.051).

FFE overpredicted overstory dead tree densities for redwoods and bay laurels when compared to observed posttreatment forest conditions. There was no significant difference in modeled and observed dead overstory densities for other species. Modeled total dead tree density was 62.1 trees ha⁻¹, while observed total dead tree density was 35.8 trees ha⁻¹ (P=0.09). Modeled dead redwood density was 33.8 trees ha⁻¹ was greater than the observed post-treatment dead redwood density of 14.8 trees ha⁻¹ (P=0.04), both of which were greater than the observed pre-treatment dead redwood density of 8.7 trees ha⁻¹. Modeled dead bay laurel density was 9.5 trees ha⁻¹ was also greater than observed post-treatment dead bay laurel density was 1.3 trees ha⁻¹ (P=0.02). Observed pre-treatment dead bay laurel density was 1.3 trees ha⁻¹, so there was no bay laurel mortality in the observed dataset. FFE, however, predicted an increase of 8.2 dead bay laurel trees ha⁻¹, which accounts for a 41% reduction in live bay laurel tree density.

Tree regeneration

Tree seedlings, saplings, and resprouts, collectively referred to as "regeneration", were mostly top-killed by the prescribed fire treatments, but many individuals resprouted vigorously within 8 months post-treatment. Redwoods, bay laurels, and tanoak were the most common pre-treatment regeneration species in all classes and the most affected (Appendix Fig. 9) by the prescribed fire treatment. Mean density of resprout of redwood and all hardwood species increased post-treatment except for coast live oak, which were absent in post-treatment surveys. Redwood resprout densities increased after the burn treatment from 657 stems ha⁻¹ to 3372 stems ha⁻¹ (P=0.03). There was also a subtle increase in tanoak respout densities, which were 778 stems ha⁻¹ pre-treatment and 1444 stems ha⁻¹ post-treatment (P=0.29). Mean seedling density of all species decreased post-treatment. There was a reduction in seedling density for bay laurel from 977 stems ha⁻¹ to 354 stems ha⁻¹ (P=0.002) and tanoak from 977 stems ha⁻¹ to 147 stems ha⁻¹ (P=0.047). Mean sapling density of each species also decreased posttreatment, though no findings were significant ($P \ge 0.091$).

FFE outputs group regeneration classes into one single "regeneration" group, limiting the detailed comparisons between observed and modeled seedling, sapling, and resprouts data. When grouped, however, FFE underestimated the density of live regeneration for redwood. When regeneration classes were grouped, the observed post-treatment density of live redwood stems after was 3595.2 stems ha⁻¹ and modeled was 1158.1 stems ha⁻¹ (P=0.058). However, FFE tended to overestimate the density of live regeneration for all other species, though findings were not significant (P≥0.33).

Observed fuels

Prescribed burn treatments were effective in reducing fuel loads across plots at both sites (Table 2, Appendix Table 6). Fuel loads were significantly reduced for duff ($P \le 0.001$), litter and fine woody fuels (Litter+FWD) ($P \le 0.001$), and surface fuels ($P \le 0.001$). Coarse woody debris (CWD) was unchanged (P = 0.56). These results

Table 2 Fuel load values (Mg ha⁻¹) across all plots. Pretreatment data is from 2021/22, post-treatment is from 2023, and prescribed burn treatments occurred Fall 2022. Welch's two-sample *t*-tests compare the difference between observed pre- and post-treatment fuel loads

Fuel variable	Observed pre- treatment Mean±SE (Mg ha ⁻¹)	Observed post- treatment Mean±SE (Mg ha ⁻¹)	t	df	Ρ
Duff	48.3 ± 3.0	23.4 ± 3.4	-5.5	37.6	≤0.001
Litter	55.5 ± 3.4	26.0 ± 2.4	-7.1	34.2	≤0.001
FWD	6.1 ± 0.5	6.4 ± 0.7	0.3	34.5	0.79
Litter + FWD	61.7 ± 3.4	32.3 ± 2.2	-7.2	32.9	≤0.001
1000-h (s)	7.9 ± 2.4	11.2 ± 4.4	0.7	29.7	0.52
1000-h (r)	8.1 ± 4.6	0.8 ± 0.5	- 1.6	19.5	0.13
CWD	16.0 ± 5.4	11.9 ± 4.3	-0.6	36.2	0.56
Surface	77.7 ± 7.0	44.3 ± 5.4	- 3.8	35.7	≤0.001
Total	125.9 ± 6.7	67.7 ± 5.3	-6.8	36.1	≤0.001

become more nuanced as we look at the fuel load dynamics of fuel classes within these groups. Mean duff loads were reduced from 48.3 Mg ha⁻¹ to 23.4 Mg ha⁻¹ ($P \le 0.001$). Within Litter + FWD, mean litter loads were reduced from 55.5 Mg ha⁻¹ to 26 Mg ha⁻¹ ($P \le 0.001$), but mean FWD loads did not change. Mean FWD loads were 6.1 Mg ha⁻¹ pre-treatment and 6.4 Mg ha⁻¹ post-treatment (P=0.79). Similarly, within the CWD group, the mean load of rotten 1000-h fuels decreased from 8.1 Mg ha⁻¹ to 0.8 Mg ha⁻¹ (P=0.13), yet there was no difference in sound 1000-h fuels before (7.9 Mg ha^{-1}) and after (11.2 Mg ha^{-1}) treatment (P=0.52). These results suggest that much of the reduction in surface fuel loads from 77.7 Mg ha⁻¹ to 44.3 Mg ha⁻¹ was driven by consumption of litter and rotten 1000-h logs. Reported fuel loads should not be interpreted as fuel consumption due to the 8-month lag time between prescribed burn treatment and post-treatment fuel data collection and likely post-treatment fuel accumulation.

Independent variable selection for the linear regression model using Mean Decrease Accuracy values found that pre-treatment loads of litter, Litter + FWD, surface, and total fuels were the strongest influence on model accuracy. Due to strong collinearity ($r \ge 0.7$) between these variables, only total fuel load was selected. Model results (Fig. 5) revealed a significant negative relationship between pre-treatment total fuel load and relative change in Litter + FWD ($R^2 = 0.41 \pm 0.15$, P = 0.002). For every one Mg ha⁻¹ increase in pre-treatment total fuels, the model predicts a 0.55% relative reduction in Litter + FWD fuel load.



Fig. 5 Observed litter and fine woody debris relative change (%) as a function of pre-treatment total fuel load ($R^2 = 0.41 \pm 0.15$). Prediction line is shown for both sites grouped; points are colored by site

Modeled fuels

Overall, FFE overpredicted fuel load reduction across fuel size classes, especially fine woody fuels (Table 3, Fig. 6). FFE predicted a 56.4 Mg ha⁻¹ reduction in litter and fine woody fuels (Litter + FWD), which was greater than the observed 29.3 Mg ha⁻¹ reduction in Litter + FWD ($P \le 0.001$). FFE also predicted a 62.6 Mg ha⁻¹ reduction in surface fuels, which was nearly double the observed 33.4 Mg ha⁻¹ reduction of surface fuels ($P \le 0.001$). Observed total fuel loads were reduced 58.2 Mg ha⁻¹, whereas modeled total

fuels were reduced 76.5 Mg ha⁻¹ (P=0.08). The model also predicted a 5.1 Mg ha⁻¹ reduction in coarse woody debris load, which was slightly greater than the 4.1 Mg ha⁻¹ observed reduction (P=0.88). Observed change in coarse woody debris varied across plots. While rotten 1000-h fuels were generally consumed, some plots experienced an increase in CWD load due to recruitment of downed logs (sound 1000-h). Modeled CWD change, however, showed little variation. This general trend of FFE model overprediction, however, did not occur with duff. There was an

Table 3 Absolute change in observed and modeled fuel loads (Mg ha⁻¹) across all sites. Observed values are derived from Brown's transects. Modeled change is derived using a FFE simulated prescribed fire treatment. Pre-treatment data is from 2021/22, post-treatment is from 2023, and prescribed burn treatments occurred Fall 2022. Welch's two-sample *t*-tests compare absolute change in observed and modeled fuel load post-treatment

Fuel variable	Observed change Mean ± SE (Mg ha ⁻¹)	Modeled change Mean ± SE (Mg ha ⁻¹)	t	df	Р
Duff	-24.9±3.4	-15.0 ± 1.0	2.8	22.6	0.01
Litter	-29.5 ± 4.2	-53.4 ± 3.5	-4.4	36.6	≤ 0.001
FWD	0.2 ± 0.7	-3.0 ± 0.4	- 3.8	30.6	≤ 0.001
Litter + FWD	-29.3 ± 4.2	-56.4 ± 3.5	- 5.0	36.6	≤ 0.001
CWD	-4.1 ± 6.1	-5.1 ± 2.1	-0.2	23.2	0.88
Surface	-33.4 ± 8.8	-61.4 ± 4.7	- 2.8	28.7	0.009
Total	-58.2 ± 8.9	-76.5 ± 4.7	- 1.8	28.4	0.08



Fig. 6 Observed pre-treatment, observed post-treatment, and modeled post-treatment fuel load by fuel size class—duff, litter and fine woody debris, and coarse woody debris. Dark red dots signify mean values

observed 24.9 Mg ha⁻¹ reduction in duff fuel loads, which was greater than the modeled 15 Mg ha⁻¹ reduction in duff fuel loads (P=0.01).

Modeled wildfire hazard

Prescribed fire treatments implemented at GOT and WIL were effective in mitigating modeled wildfire hazard at both sites, though forest and fuel conditions were such that modeled wildfire behavior was unlikely to be extreme even prior to treatments. The mean probability of torching (P-torch) was 14% (\pm 7%) prior to prescribed fire treatments and 6% (\pm 5%) post-treatment (P=0.38). Under pre-treatment conditions, FFE projected passive crown fire for only two of the 20 plots. Under post-treatment conditions, no plots were anticipated to experience passive or active crown fire. Overall, FFE outputs suggest that the prescribed fire treatment slightly moderated behavior of a potential future wildfire, though the modeled probability of torching was very low prior to the prescribed fire treatments.

Discussion

Observed prescribed burn, tree, and fuels

Mild burning conditions in the prescribed fires studied here resulted in relatively little change in overstory structure and composition, similar to past research (Cowman and Russell 2021; Engber, Teraoka, and van Mantgem 2016; Finney and Martin 1992a). The minimal tree mortality that did occur was concentrated in smaller, understory, and mid-canopy redwoods and Douglasfirs (< 30 cm DBH), which means the burn treatments did not meet their management objectives of reducing the density of non-redwood species. This limited tree mortality highlights the importance of fire intensity in effecting change in forest structure. Tree mortality may be expected to increase with fire intensity, but top killing and resprouting dynamics of redwood appear to also be related to other factors such as tree diameter, tree vigor, origin (e.g., seed germination vs stump sprout), growth structure (e.g., single tree vs clump), and fuel consumption (Finney and Martin 1992a). As with past research (Lazzeri-Aerts and Russell 2014), observed mortality in seedlings and saplings was greatest in redwoods, tanoak, and bay laurel, but post-treatment resprout densities were also greatest for redwood, tanoak, and bay laurel, all of which increased after burning. While overstory and regeneration data was collected in all plots, the size and condition of trees from which resprouts originated was not recorded as part of the regeneration data, limiting analysis of conditions affecting resprouting rates by species (e.g., bole char and scorch height, mortality). Though we did not observe this, fire-excluded secondgrowth stands may be less tolerant of fire due to high consumption of stumps and underground root networks (Brown et al. 1999). There is evidence for stump, root, and "basal hollow" consumption resulting in a loss of structural integrity of mature basal sprouts, ultimately leading to tree fall (Lorimer et al. 2009).

Observed fire effects fall short of being an effective forest restoration treatment, defined as "establishing the composition, structure, pattern, and ecological processes necessary to facilitate terrestrial and aquatic ecosystems sustainability, resilience, and health under current and future conditions" (Stephens et al. 2021; USDA Forest Service 2012). Functionally, these burns would have been considered forest restoration treatments had there been significant progress in reducing forest density and increasing structural complexity. Stand density in mature redwoods forests range from 50 to 100 trees ha⁻¹ (Lorimer et al. 2009; O'Hara et al. 2010), yet restoring structural complexity of mature redwood forests requires centuries of frequent fire to develop (Lorimer et al. 2009; Norman et al. 2009). Reduction in stand density provides an achievable, short-term objective that can be met through various treatments (Porter et al. 2007). These findings suggest that in order for prescribed fire to create meaningful reductions in stand density, fire practitioners likely need to burn at moderate to higher intensities (e.g., lower fuel moisture conditions), and potentially conduct mechanical thinning treatments (O'Hara et al. 2010) prior to prescribed burns. Fire practitioners may be able to achieve moderate to high fire intensities by burning under drier condition, altering firing patterns to encourage heading and flanking fire, intentionally creating fuel "jackpots" from pre-fire understory thinning, and using topographic (i.e., slope and aspect) and forest characteristics (i.e., canopy cover, composition) to target areas with more receptive fuel beds.

While stand density was not significantly reduced, prescribed fire treatments did achieve the objectives of reducing duff loads 0-30% and litter loads 30-70% (Berleman 2022), which is similar to short-term responses reported in related studies (Engber, Teraoka, and van Mantgem 2016; Finney and Martin 1992a). The observed mean FWD in this study remained unchanged post-treatment, but Engber et al. (2016) reported a 40% decrease in FWD loads 1-year post-treatment and 23% increase to above pre-treatment condition within 7 years after low-intensity burning. Observed CWD in this study decreased 26%, while Engber et al. (2016) reported a 21% reduction in CWD 7 years after burning. This suggests that perhaps the burns observed here consumed a similar amount of FWD and CWD, but FWD deposition occurred more rapidly after burn treatments in this study. Finney and Martin's (1992a) findings make comparison difficult because no mean values are provided. Rather, a min-max range is provided for pre-treatment load of each fuel size class and well as a min-max range for absolute change in fuel load after the burn treatment. Finney and Martin (1992a) reported a range 14-53 Mg ha⁻¹ reduction in litter and duff and a 1-15 Mg ha⁻¹ reduction in FWD, which is comparable to the 54.4 Mg ha⁻¹ mean reduction in litter and duff and 0.2 Mg ha^{-1} mean increased in CWD observed here. They also reported wide variability in CWD responses to burning, ranging from a 205 Mg ha^{-1} reduction to a 245 Mg ha^{-1} increase. This range includes the observed change in this study (4.1 Mg ha⁻¹ reduction), but far exceeds the variability observed at GOT and WIL. Despite relatively high moisture content in both duff (79-206%) and litter (15-50%), loads of both layers were significantly reduced. While we do not have fuel moisture samples from WIL, we estimate surface and ground fuels were slightly drier since WIL had experienced a longer dry period since the last rain event (17 days) and low relative humidity on the first day of burn operations. Fuel reduction only occurred in duff and litter layers at GOT, while at WIL there was an observed reduction in duff, litter, FWD, and CWD loads. This likely difference in fuel moisture content between sites could explain the differing trends in fuel loads (Appendix Table 6), though this could be cofounded by variability in fuel deposition that occurred prior to post-treatment data collection. This further supports the concept that fuel reduction could be enhanced by burning under drier conditions.

In contrast to duff and litter, there was an observed increase in mean FWD and sound 1000-h loads. This could be due, in part, to fuel deposition resulting from nine large storms (e.g., "atmospheric rivers") during winter 2022–23 (DeFlorio et al. 2024) that affected the California coast-line, which included several periods of very high winds (>60 km h⁻¹) (University of Utah, n.d.). These storms occurred between the prescribed burn treatments and post-treatment data collection (Nov 2022–June 2023) and likely deposited considerable amounts of FWD and sound 1000-h fuels from the forest canopy onto the forest floor. Variability in storm-intensity and subsequent fuel deposition between the two sites could also, in part, explain the differing trends in fuel between the two sites.

While conducting multiple prescribed fire treatments may provide a means of reducing fuels in the long term, linear regression results suggest this may not yield intended results unless sufficient time is allowed for fuel accumulation. Total pre-treatment fuel load was the strongest predictor of relative change of Litter+FWD after prescribed burn treatments. Based on this, as pre-treatment total fuel load increases, consumption of Litter+FWD also increases, which is consistent with similar analyses in dry conifer forests (Levine et al. 2020). Total fuel load increases in productive forests over long periods without fire, which leads to greater horizontal continuity of fuels (Miller and Urban 2000). This increased fuel continuity allows for continued combustion of available fuels. We did not quantify fuel continuity, but this relationship between fuel load and continuity could, in part, explain observed relative change in Litter+FWD, as opposed to absolute total fuel load. As prescribed burn treatments consume fuels, overall fuel continuity decreases, thereby limiting fuel consumption in subsequent burn treatments (Levine et al. 2020). Additionally, if fuels are discontinuous and patchy, combustion is more likely to be halted and result in lower fire intensity (Loudermilk et al. 2012). Increases in total fuel load generally results in greater heat generation when burning, which dries out and increases the availability of wetter fuels to burn and results in greater fuel consumption. Therefore, without adequate accumulation of surface and ground fuels, future prescribed burn treatments lack the fuel needed to produce higher intensity fire behavior that can achieve desired fuel consumption and tree mortality objectives. Burning under hotter, drier conditions will likely produce more desirable effects, especially for follow-up burns, though adequate time between burn treatments is needed in order to allow for sufficient surface fuel accumulation. Once structural objectives are met, follow-up burns conducted at a frequency (~15-year intervals) and severity (low-moderate) consistent with the historic fire regime (Finney 1990; Striplen 2014) can serve as an effective treatment in maintaining low fuel loads and stand densities.

While this study did not look into fire effects on understory vegetation communities, soil dynamics, cultural resources, or water or air quality, these are all important considerations in determining how and when fire is used in coast redwood forests, and present valuable routes for future research (Fig. 6). These findings also highlight a clear need for additional research on the relationship between fuel moistures, firing patterns, fuel consumption and accumulation, scorch and bole char, and species-specific tree mortality and morphological responses (i.e., epicormic an basal resprouting) when using prescribed fire in these forests. Additionally, future applied studies would benefit from analyzing and clarifying vegetation and fuel responses to a prescribed fire implemented across a breadth of intensities and seasons.

A critical missing aspect to many prescribed fire treatments is the persistent lack of collaboration with cultural fire practitioners and tribal communities, risking the continued appropriation of traditional ecological knowledge as a means of improving the health of ecological communities and addressing wildfire hazard (Martinez et al. 2023). Given the continued legacy of criminalizing cultural burning practices (Cuthrell 2013), and persistent risk of high severity fire due to high fuel loads and dense forest conditions, stewardship partnerships that equally share power and decision making between western science and Indigenous knowledge are needed to make meaningful contributions to the health of humans and landscapes, including coast redwood forests.

Modeled trees and fuels

Overestimation of overstory tree mortality by FFE is likely driven by underlying model assumptions. The largest overestimation in overstory tree mortality occurred for redwoods, bay laurel, coast live oak, and madrone. Similar to observed post-treatment effects on forest structure, FFE predicted most overstory tree mortality occurring in smaller size classes (>50 cm DBH). Based on the underlying tree mortality equation (Ryan and Reinhardt 1988), tree diameter, bark thickness, and percent crown scorch drive tree mortality. Douglas-fir is the only species with a defined bark thickness parameter (0.0665), whereas the remaining species were designated the "other species" bark thickness parameter of 0.033, making them all more susceptible to fire-caused mortality within FFE. When considering the more appropriate bark thickness value utilized by other fire effects models (i.e., FOFEM) for redwood (0.081) (Reinhardt, Keane, and Brown 1997), it is reasonable to conclude that FFE's underestimate of redwood bark thickness is likely a major driver of mortality overestimates for that species. Correcting these bark thicknesses to accurate species-specific values in FFE provides an actionable update to future versions of FFE modeling software that would improve the accuracy of fire-caused tree mortality. These overestimates could also be due to the observed lowintensity burning conditions and the possibility of patchy, discontinuous burn patterns, whereas model inputs were set to have 100% of the stand burn. Curiously, while tree mortality was generally slightly overestimated by FFE, scorch heights were underestimated. Scorch height underestimates could be due to the prevalence of fire climbing up the fibrous redwood bark and thus scorching nearby needles, which is not well represented by FFE. FFE also underestimated redwood regeneration. Underlying species-specific algorithms used in FFE to estimate resprouting responses are based on the quantity and diameter of parent trees within each plot (FVS Staff 2023). Consistent with other research (Lazzeri-Aerts and Russell 2014; Woodward et al. 2020), FFE's sprouting probability for redwood increases with DBH of the parent tree, but this equation does not incorporate fire damage, which have been found to affect redwood basal resprouting responses (Engber, Teraoka, and van Mantgem 2016), potentially explaining the large difference between observed and modeled redwood regeneration stem densities.

FFE model inaccuracies in predicting changes of duff, litter, and FWD loads indicate key limitations in using the software to model prescribed fire effects on fuel load dynamics in redwood forests. Fuel reduction in most fuel classes (except duff) was generally overestimated by FFE and variability among classes was not well predicted. These inaccuracies could be due to two different sets of model assumptions: (1) Overestimation of fuel consumption (litter, FWD, and CWD) due to consumption being independent of moisture content in FFE, and (2) Underestimation of canopy fuel deposition (crown lifting, crown breakage, snag fall, and litter fall), which could be accentuated by increased deposition of woody canopy fuels associated with winter storms.

FFE underestimated duff fuel reduction when compared to observed post-treatment duff loads. In Douglas-fir forests, when duff fuel moisture content is between 30 and 120%, heating from the burning surface fuels is required for combustion. Above 120%, combustion is nearly impossible (Sandberg 1980). Given high observed duff fuel moisture content, duff consumption may appear unlikely, if not impossible, but combustion of litter layers during the burn operations may have effectively pre-heated duff layers enough to allow for slow smoldering combustion (Frandsen 1987). As upper strata of litter combust, radiant, and conductive heat dries lower strata, consuming deeper layers of litter and duff as long as moisture conditions permit continued smoldering combustion. FFE assigns a single moisture value to the entire duff layer (Rebain et al. 2022), simplifying the moisture gradient present in redwood duff fuels. According to FFE, in order to achieve the observed reduction in duff loads (~50%), duff moisture would need to be ~ 80%, which is 37% lower than our median observed duff moisture content. Model overestimation of litter fuel reduction is entirely explained by the fact that FFE assumes 100% consumption of litter fuels independent of their moisture content (Rebain et al. 2022).

Similar to litter, FFE assumes a constant consumption rate for FWD independent of fuel moisture content: 90% for 1-h and 10-h fuels, and 65% for 100-h fuels. CWD consumption is based on fuel class size and moisture content, which is generally higher for dry, smaller diameter CWD (7.6–15.2 cm) and lower for wet, larger diameter CWD (> 30.5 cm). Based on observed fuel data, these FWD consumption rates were significantly overestimated, but FFE estimates for change in CWD load were relatively accurate.

The difference between observed and modeled posttreatment FWD loads that we demonstrated is somewhat confounded by heightened deposition of canopy fuel associated with winter storms that affected both study sites. This influence of storm activity on accumulation of limb wood is likely not captured in FFE model runs. FFE estimates woody fuel deposition from crown material using crown lifting, background crown breakage, and species-specific snag breakage rates. FFE may accurately model accumulation of FWD on a "typical" year, while observed data represents an "atypical" year with elevated fuel accumulation rates. This hypothesized influence of winter storms may not accurately explain post-treatment FWD and CWD dynamics, however, as observed increases in FWD and CWD post-treatment were not consistent across both sites. At GOT, we observed a mean increase in both observed FWD (1.3 Mg ha^{-1}) and CWD (1.2 Mg ha^{-1}) while FFE predicted a mean decrease in FWD (4.1 Mg ha⁻¹) and CWD (1.7 Mg ha⁻¹), supporting the hypothesis that "atypical" winter storms could account for high CWD accumulation rates due to winter storms and inaccurate FFE fuel change predictions. At WIL, however, we observed a mean decrease in FWD (0.5 Mg ha^{-1}) and CWD (7.6 Mg ha^{-1}), which was similar to the modeled decrease in FWD (2.2 Mg ha^{-1}) and CWD (7.3 Mg ha^{-1}), suggesting that the large winter storms did not undermine the predictive accuracy of FFE at WIL.

It may seem reasonable to speculate that FFE model overestimation of FWD and CWD reduction could also

be due to mop-up activities conducted after firing operations that interrupted combustion of fuels, limiting consumption of fuel classes with high fuel moisture contents (e.g., 100-h and sound 1000-h fuels). This is not a likely explanation however, because under these circumstances, we would expect to see more consumption in the litter and FWD fuels, given their high surface area to volume ratio and ability to quickly respond to fluctuations in relative humidity and heating from adjacent burning fuels, and less consumption in duff and CWD that had recorded fuel moisture contents greater than the moisture of extinction. This explanation does not accurately describe observed changes in fuel load dynamics.

While our fuel moisture sample dataset lacks robustness across and within sites, low-intensity prescribed fire treatments created a patchy mosaic in which fine-scale fuel moisture variability may have driven fire effects and fuel consumption (Finney and Martin 1992a), rather than weather, fuel load, forest structure, or topographic variables. This fuel moisture variability, paired with potentially elevated canopy fuel deposition rates, and underlying assumptions within FFE, likely all contributed to inaccuracies in modeled fuel reduction outputs when compared with observed fuel data.

Modeled wildfire hazard

While prescribed burn treatments were effective in reducing future wildfire hazard, key metrics for wildfire hazard-probability of torching (P-torch)-signified that pre-treatment conditions were not conducive to high intensity fire behavior. Under severe weather conditions, mean P-torch values decreased from 16 to 4% after the burn treatments. Given the dry, hot, and windy conditions defined under the "severe" weather scenario, we surmise that fuel conditions, slope, canopy cover, and canopy base height were not conducive to torching within FFE (Rebain et al. 2022). However, observations from 2020 CZU Complex Fire in redwood forest found significant portions (>60%) burned at high severity (("CZU Lightning Complex Map-Preliminary Vegetation Burn Severity" 2023; Potter 2023)). Probability of torching is only one metric of treatment effectiveness, and future research would benefit from considering other metrics of success, including fire behavior (e.g., flame lengths, rate of spread, and fireline intensity), fire effects (tree mortality, soil impacts), and suppression efficiency. Large-scale high severity fire effects appear to be uncommon within the historic fire regimes of redwood forests (Agee 1993; Stephens et al. 2018), but passive crown fire activity in warmer, drier, open sites such as ridges has been observed in prior wildfires (Scanlon and Valachovic 2006). This suggests that FFE may underestimate fire behavior under severe weather conditions. One potential explanation for this may be the flammability of redwood bark. Fire readily climbs up the fibrous bark, which can carry fire>50 m into

the canopy (Lazzeri-Aerts and Russell 2014) and allow for pre-heating and drying of live canopy fuels via convective heat (Fig. 7), potentially making them more available to burn. This phenomenon is compounded by the common occurrence of basal cavities and casting embers into the forest canopy. Taken together, these unique characteristics could allow for the possibility of vertical fire spread through both convective heating and spotting, even under mild burning conditions (e.g., nighttime), which are not well represented by FFE's underlying fire spread models (Rothermel 1972; Scott and Reinhardt 2001). As such, FFE outputs for probability of torching may not accurately describe on-the-ground fuel hazard conditions in redwood forests. Further empirical investigation on the interaction between surface, ladder, and canopy fuels is needed in these forests to determine the driver of high severity fire effects. Warming and drying climatic conditions (Williams et al. 2019) may continue to elevate the risk of high severity fire for ecological and human communities in and around these forests (Hagmann et al. 2021; Prichard et al. 2021). Continued fire exclusion may increase the likelihood of passive and active crown fire (van Wagtendonk et al. 2018) over time due to elevated loading and continuity of surface and ladder fuels.

Conclusion

As the pace and scale of prescribed fire is increasing in the range of coast redwood forests, managers are right to consider the reintroduction of fire a success in and of itself, but there are critical ecological and social aspects of such treatments that dictate whether they are making meaningful strides toward long-term restoration efforts. This study, along with past research, suggests low severity prescribed



Fig. 7 Fire climbing redwood bark and basal cavities during burn operations at Grove of Old Trees in November 2023. Note this fire behavior was observed overnight when burning conditions were mild (temperature 7.2–10 ℃, RH 45–50%). Trees in the photos are ~ 200–300 cm DBH and 50–60 m tall. Photo credit: Ryan Klausch, California Department of Parks and Recreation, Sonoma-Mendocino Coast District

fires may be able to meet some fuel reduction goals, but forest structure and composition changes likely require more mixed or moderate severity fire effects. That said, the prescribed burn treatments here represent only a narrow range on low severity fire effects and do not cover all forest, fuels, or potential burn conditions experienced across the coast redwood range. Furthermore, post-treatment forest and fuel conditions reported here were likely affected by an 8-month delay in post-treatment data collection, during which several major winter storms likely accelerated fuel deposition. In many circumstances, mechanical thinning will likely be needed prior to burning to meet forest structure restoration goals, and additional research is needed to quantify the effects of combined mechanical and fire treatments. This research also provides regionally specific feedback to fire practitioners for the refinement of prescribed fire prescriptions to more effectively meet forest structure and composition and fuel reduction goals in redwood forests.

With few empirical studies on the effects of prescribed fire, there has been limited verification and calibration of fire effects modeling software (e.g., FFE) for redwood forests. If modeling products do not accurately account for the unique traits of redwoods including morphology (e.g., bark structure and flammability), disturbance responses (basal and epicormic resprouting), and small-scale variability in fuel load and moisture dynamics, they will be less effective in the planning and prioritization of fuel reduction projects in the region. Further research is needed on how prescribed fire conducted under a broad range of weather conditions affects fuel dynamics, forest structure and composition, and wildfire resilience. On the whole, FFE modeling software was designed to account for wildfire effects that typically burn in warmer, drier conditions, but these low intensity prescribed fire treatments may begin to highlight the limitations of FFE in relatively mild burning conditions. That said, underlying fire spread models used in FFE are based on assumptions of ignition, heat transfer, and fire spread processes that are not based on experimental research, signaling a vast oversimplification of fire behavior and effects (Finney et al. 2013).

As managers move to restore heterogeneity and historic fire regimes in redwood forests, prescribed burn operations must be used as opportunities to analyze and understand how fuels, weather, and seasonality contribute to treatment effectiveness in meeting goals for biodiversity, ecosystem health and resilience, and community safety. Simultaneously, the same prescribed burns can be used to verify the accuracy of fire effects models in order to improve their operational applicability for forest and fire managers. In assessing the relative success of FFE in predicting fuels and forest dynamics after a prescribed burn treatment, and characterizing drivers of inaccuracy within the modeling software, we have identified a clear need for fire effects model refinement in redwood forests.

Appendix

Table 4 Tree ring fire history studies in the southern range of Coast Redwood forests. Note the short fire return intervals and seasonality of fire events

Study	Location (County)	Scar Date Range	Mean Fire Interval Yrs (Range)	Study Type	Fire Scar Seasonality	Notes
Jacobs et al (1985)	Muir Woods NM (Marin)	~1400-1850	22–27 (2–98)	Point	-	Longer intervals near coast
Finney and Martin (1989)	Salt Point SP (Sonoma)	1200-1950	7 (6–9) (comp) 24 (21–29) (point)	Composite / Point	-	Coast redwood and Bishop pine
Finney (1990)	Bolinas Ridge (SW Marin)	1450–1945	8–20	Point	-	-
Finney and Martin (1992a, b)	Annadel SP (Sonoma)	Prior to early 1800s	6–23 (2–131)	Point	-	Dry inland site
Brown et al (1999)	Point Reyes NS (Marin)	1722–1973	8–13 (1–18)	Composite	Dormant and Late (Aug–March)	Coast redwood and Douglas-fir
Brown and Baxter (2003)	Jackson Demo SF (Mendocino)	1505–1933	6–22 (3–34)	Composite	Dormant and Late (Aug–March)	Longer intervals near coast
Stephens and Fry (2005)	(NE Santa Cruz and SW San Mateo Co.)	1615–1884	9–16 (2–58) (int) 12 (2–58) (point)	Interval / Point	Dormant and Late (Aug–March)	Longer intervals near coast
Striplen (2014)	(NE Santa Cruz and SW San Mateo Co.)	1600–2013	5 (1–29) (comp) 39 (1–167) (point)	Composite / Point	Dormant or Late (Aug–March)	-

Table 5 Site characteristics, weather conditions, fuel moistures, fire behavior, and fire effects observed at both sites. All values are shown as median (min-max range). No fuel moisture samples were collected at WIL

Site	GOT	WIL	
Dates	Nov 19–20, 2022	Nov 25–27, 2022	
Area Burned (ha)	3.6	~81	
Slope %	6 (3–10)	31 (8–55)	
Aspect	S and NW	SW, S, and NE	
Days Since Rain (> 0.64 cm)	10	17	
Temp (F)	53 (46–60)	54 (45–70)	
RH (%)	42 (35–53)	56 (15–98)	
Wind Direction	N-NE-E	N-NE-SE-S-SW	
Wind Speed ($km h^{-1}$)	3.2 (0–4.8)	5.5 (0–16.4)	
Gust Speed (km h ⁻¹)	4.8 (0–6.4)	8.2 (0–23.5)	
Duff FM (%)	117.8 (79–206)	-	
Litter FM (%)	19.7 (15–50)	-	
1 h FM (%)	13.9 (12–41)	-	
10 h FM (%)	17.6 (11–19)	-	
100 h FM (%)	16 (15–20)	-	
1000 h FM (%)	18.8 (17–23)	-	
Firing Patterns	Dots / Strips	Dots / Strips	
Fire Spread	Heading / Backing	Heading / Backing	
Flame Length (m)	0.2–0.3	0.05–0.6	
Bole Char Ht (m)	1.1 (0–7.5)	1.3 (0–10)	
Scorch Ht (m)	2.7 (0–11)	3.5 (0–28)	



Fig. 8 Fuel Model selection decision matrix. Fuels models include Timber-Understory 1 (Low Load Dry Climate Timber-Grass-Shrub), Timber-Understory 5 (Very High Load, Dry Climate Timber-Shrub), Timber-Litter 3 (Moderate Load Conifer Litter), Timber-Litter 4 (Small downed logs), Timber-Litter 7 (Large downed logs), Timber-Litter 6 (Moderate Load Broadleaf Litter), and Timber-Litter 9 (Very High Load Broadleaf Litter)

Table 6	Fuel load values (Mg ha-	1) grouped by site (GOT)	WIL, and All) pre- and pos	t-treatment. All values showr	n as Mean±SE
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	GOT		WIL		ALL	
Fuel Variable	Pre	Post	Pre	Post	Pre	Post
Duff	51.7 ± 5.6	28.6 ± 6.5	46.0±3.5	20.0 ± 3.4	48.3±3.0	23.4 ± 3.4
Litter	53.7 ± 5.4	25.2 ± 3.7	56.8 ± 4.5	26.6±3.2	55.5 ± 3.4	26 ± 2.4
FWD	7.3±1	8.6±1.3	5.4 ± 0.5	4.9±0.6	6.1 ± 0.5	6.4 ± 0.7
Litter + FWD	61.0 ± 5.4	33.9 ± 2.9	62.1±4.5	31.4±3.2	61.7 ± 3.4	32.4±2.2
1000-h (s)	3.4±2	4.0±1.6	10.9±3.6	15.9±7	7.9 ± 2.4	11.2±4.4
1000-h (r)	0.0 ± 0.0	0.6±0.6	13.5±7.3	0.9 ± 0.8	8.1 ± 4.6	0.8 ± 0.5
CWD	3.4±2	4.6±1.5	24.4±8.2	16.8±6.9	16.0±5.7	11.9±4.3
Surface	64.4 ± 5.8	38.5 ± 2.7	86.5 ± 10.4	48.2±8.7	77.7±7.0	44.3 ± 5.4
Total	116.1±6.5	67.0±7.7	132.5±10.1	68.2 ± 7.5	125.9±6.7	67.7±5.3



Fig. 9 Regeneration (seedling, saplings, and resprouts) density of all tree species (stems ha-1) before and after prescribed fire treatment across all plots. Note, one outlier was removed from the above graphs to more clearly communicate results, though this outlier was included in the dataset for statistical testing. The outlier was 21,958.3 live redwood response ha-1 in plot GOT-37 post-treatment. Y-axis range differs among graphs

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Authors' contributions

TAK: Methodology, Investigation, Formal analysis, Software, Resources, Data curation, Visualization, Writing—original draft, Writing—review & editing, Project administration, Funding acquisition. BMC: Conceptualization, Methodology, Writing—review & editing, Funding acquisition. SLS: Conceptualization, Writing—review & editing, Funding acquisition.

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Data availability

Data will be made available by SS on reasonable request.

Declarations

Competing interests

The authors declare that they have no competing interests.

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