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Extreme wildfire supersedes long-term fuel treatment influences on fuel and vegetation in chaparral ecosystems of northern California, USA

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Abstract

Background Within California's chaparral ecosystems, fuel reduction treatments are commonly used to reduce the negative impacts of wildfire but the durability of fuel treatment changes to fuels and vegetation when exposed to wildfire is less well understood. This study examined the interactive effects of 15-year-old fuel treatments and an extreme wildfire on burn severity, fuel loading, and vegetation in chaparral and oak vegetation types in Whiskeytown National Recreation Area in northern California, USA. Fuel treatment types included hand thinned, mechanical mastication, mechanical mastication + prescribed burning, and prescribed burning only.

Results Vegetation and substrate burn severity was characterized as moderate across the study site and did not differ among treatments. Contrasting with higher pre-fire shrub density in the mastication + burning treatment, 2-year post-fire live shrub density did not differ among treatments. Higher pre-fire fine woody fuel loading in the mastication treatment did not correspond to post-fire fuel loading among treatments, while the hand thinned treatment was the only treatment where fine fuel loading was not significantly reduced post-fire. Total plant species richness increased in all treatment types following wildfire, largely driven by an increase in exotic species. Native cover decreased, and exotic cover increased in oak and chaparral types, but greater exotic species cover in the mastication + burning treatment in chaparral was maintained following wildfire.

Conclusions Pre-fire differences in fuel and vegetation responses among treatments largely did not persist or were not detectible 1 to 2 years following wildfire. These findings suggest that the extreme wildfire conditions superseded long-term treatment differences in many fuel and vegetation metrics observed prior to wildfire. Despite subtle treatment differences, the hand thinned treatment resulted in the lowest change in fuel loading relative to all other treatments. Lastly, pre-fire differences in exotic species among fuel treatments were retained following wildfire, suggesting some treatments may have greater potential for exotic species expansion or type conversion to exotic grasslands.

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Resumen

Antecedentes Dentro de los ecosistemas de chaparral de California, lo tratamientos de reducción del combustible son comúnmente usados para reducir el impacto negativo de los incendios, aunque la durabilidad de los cambios en los combustibles y vegetación es en general mucho menos conocida. Este estudio examinó las respuestas a la severidad de la quema, carga de combustible, y datos de vegetación, y su interacción entre tratamientos de combustible de 15 años de antigüedad en vegetación del tipo chaparral o robledales, con un fuego extremo ocurrido en el área recreativa nacional denominada Whiskeytown en el norte de California, EEUU. Los tratamientos incluyeron remoción manual (reduciendo la densidad), astillado mecánico, astillado mecánico + quema prescripta, y quema prescripta sola.

Resultados La severidad del incendio en la vegetación y en el sustrato fue caracterizado como moderado en todos los sitios de estudio y difirió entre tratamientos. Contrastando con densidades altas previas al fuego en el tratamiento de astillado mecánico + quema prescripta, dos años luego del incendio, la densidad de arbustos no difirió entre tratamientos. La carga más alta de combustible fino leñoso en el pre fuego en el tratamiento de astillado mecánico, no se correspondió con la carga de combustible en el post-fuego entre los tratamientos, mientras que la remoción manual fue el único tratamiento en el cual la carga del combustible fino no fue reducida significativamente en el post-fuego. La riqueza total de especies se incrementó en todos los tipos de tratamiento en el post-fuego, largamente influenciada por un incremento de especies exóticas. La cobertura de nativas decreció, y la de exóticas se incrementó tanto en el tipo chaparral como en los robledales, y una mayor cobertura de exóticas en el tratamiento de astillado mecánico + quema prescripta se mantuvo en el chaparral después del incendio.

Conclusiones Las diferencias en carga de combustible y vegetación previas al incendio y sus respuestas a los tratamientos no fueron detectables de uno a dos años posteriores al incendio. Estos resultados sugieren que las condiciones extremas del incendio superaron las diferencias que en el largo plazo pudieron existir entre los efectos y medidas de los tratamientos previos al incendio. Por supuesto, las unidades pequeñas que comprendían los tratamientos pueden haber contribuido a la baja posibilidad de detectar diferencias relativas a escalas operacionales, entre otros condicionantes. A pesar de las sutiles diferencias entre tratamientos, el tratamiento de remoción manual fue quien resultó en el menor cambio en carga de combustible en relación a los otros tratamientos. Por último, las diferencias en el pre fuego en las especies exóticas fueron retenidas luego del incendio, lo que sugiere que algunos tratamientos pueden tener un mayor potencial de expansión de especies exóticas o su conversión a pastizales exóticos.

Background

Fire is an important ecological process that maintains and promotes biodiversity and ecosystem services in California's chaparral shrublands (Keeley 2002). California chaparral extends along the coastal mountains and foothills of the Sierra Nevada and represents a diverse set of plant communities often characterized by the presence of the woody genera *Arctostaphylos*, *Ceanothus*, and *Adenostoma* (Keeley and Davis 2007). Vegetation associated with chaparral is both resilient to and dependent upon infrequent, high-severity wildfires, making this an important component in maintaining the high endemism found in these ecosystems (Keeley 1991; Keeley and Davis 2007). Chaparral is characterized by unique features, such as a dense contiguous shrub canopy of twigs and leaves that contain volatile oils, supporting high-intensity crown fires with rapid rates of spread (Quinn and Keeley 2006). Historical fire return interval estimates for California's chaparral range from 30 to 100 years (Keeley and Davis 2007; Van de Water and Safford 2011), and many of these shrub species rapidly regenerate following wildfires via seed or basal sprouting (Horton and Kraebel 1955).

Over the past few decades, expansion of the wildland-urban interface coupled with anthropogenically-altered fire regimes in areas containing chaparral ecosystems pose substantial challenges toward protecting ecological and human communities. In recent decades, much of the new housing development in California has occurred within the wildland-urban interface (Hammer et al. 2007), exacerbating the risks to human lives and property during wildfires (Radeloff et al. 2018). Higher human population densities are also associated with an increase in human-caused fires (Keeley 2001; Syphard et al. 2007). Warmer and drier conditions associated with climate change have increased fuel availability and the ability to ignite and spread fire (Abatzoglou and Williams 2016). These combined circumstances have contributed toward increases in wildfire size and frequency in chaparral ecosystems (Syphard et al. 2009), prompting managers to rapidly expand the implementation of fuel treatments without a sufficient understanding of their impacts.

Many fuel treatment options, such as prescribed burning, mechanical mastication, or hand-thinning, are commonly used to modify or reduce hazardous fuels, but each treatment has benefits and drawbacks that are not fully understood in chaparral ecosystems. Prescribed burning in chaparral and its effectiveness as a fuel treatment is debated (Keeley and Fotheringham 2001; Keeley 2002), partially due to the variability in fuel consumption associated with prescribed burning conditions (Knapp et al. 2005). Prescribed burning also requires highly trained staff, appropriate weather, and air quality conditions and often faces societal challenges (Yoder et al. 2004; Ryan et al. 2013). Because of these barriers to prescribed burning, managers often opt for manual thinning or mechanical mastication treatments. Mechanical mastication is an increasingly common fuel treatment in chaparral vegetation. This method uses machinery to grind and shred shrubs and small trees to reduce fuel bed depth and vertical continuity by converting the live, contiguous fuel layer to a compacted layer of dead surface fuels (Jain et al. 2007; Kane et al. 2009, Brennan and Keeley 2015). While the altered fuel structure from mastication can be effective at reducing crown fire risk (Rothermel 1991), the substantial increase in dead surface fuels can lead to undesired surface fire behavior (Bradley et al. 2006; Kreye et al. 2014). Additionally, much of the dead surface fuels generated from mastication can persist for over a decade (Reed et al. 2020; Martorano et al. 2021). Hand thinning of chaparral, which entails cutting shrubs with a chainsaw and removed off site or pile burned, can be a less disruptive option than mastication in more sensitive ecological areas. Hand-thinning is a more labor-intensive treatment in chaparral ecosystems but has shown to be effective in the short-term through substantially reducing shrub height (Kane et al. 2010).

Most fuel treatments applied in chaparral ecosystems will involve tradeoffs in their impacts on understory vegetation. For example, prescribed burning outside of historic wildfire conditions can have negative effects on species composition (Le Fer and Parker 2005). Hand-thinning is effective at reducing shrub cover in chaparral and oak woodlands while limiting ground disturbance but has also been associated with increased cover of exotic annual plants (Perchemlides et al. 2008). The deep woody fuel layer following mechanical mastication can lead to increased burn residence time with temperatures exceeding lethal limits to roots and seeds under dry soil conditions (Busse et al. 2005, 2010). Yet, mastication followed by prescribed burning can increase plant biodiversity by exposing mineral soil and increasing light availability to support plant establishment (Kane et al. 2010). Mastication treatments can maintain lower shrub cover compared to prescribed burning treatments but can also support higher densities of exotic annual grasses (Perchemlides et al. 2008; Potts and Stephens 2009; Wilkin et al. 2017).

Increases in the amount of area treated combined with increasing fire activity may contribute to the type conversion of chaparral to exotic grasslands (Keeley et al. 2005; Dickens and Allen 2014). However, fuel treatment and wildfire interactions and their effect on understory vegetation have not been adequately examined. Historically, long-unburned chaparral has largely resisted exotic species invasion by maintaining a thick, closed shrub canopy that inhibits herbaceous understory plant growth (Brooks et al. 2004; Keeley et al. 2005). Disturbances, such as wildfires or fuels treatments, that result in shrub removal in chaparral stands can increase the risk of type conversion to exotic annual grasslands if subsequent disturbances occur in short succession (Zedler et al. 1983; D'Antonio and Vitousek 1992). Once exotic annual grasses have been sufficiently established, their high surface area-to-volume ratios, earlier seasonal drying, and horizontal fuel continuity promote a positive feedback effect that increases the probability of a subsequent fire (Brooks et al. 2004). Increasing fire frequency prevents shrubs from regenerating because they require a longer recovery time than exotic annual grasses, conditions that perpetuate and self-sustain exotic annual grasses (Keeley 2001; Brooks et al. 2004; Dickens and Allen 2014).

The longer-term influence of fuel treatments on fuel and vegetation recovery in chaparral will largely vary depending on treatment type, time since treatment, and vegetation characteristics. Prescribed fire only treatments can have a slightly more rapid shrub recovery compared to mastication only treatments, although shrub cover and height for both treatments have been shown to approach untreated levels within 8 to 10 years (Brennan and Keeley 2017; Wilkin et al. 2017). However, prescribed fire that is applied with insufficient intensity may be ineffective at reducing shrub fuel height (Martorano et al. 2021). Shrub recovery of different treatments also depends on whether species are resprouters or obligate seeders. Chaparral that is primarily composed of resprouting species will recover the fastest, although substantial regeneration of obligate seeder shrub species in masticated sites followed by a prescribed burn has also been observed (Stephens et al. 2009; Kane et al. 2010; Wilkin et al. 2017; Martorano et al. 2021). This stimulation can eventually lead to live shrub recovery that may reduce treatment differences over time.

It is less well understood how fuels and vegetation in chaparral ecosystems will respond to interactions with older fuel treatments and wildfire. Prior research on the effectiveness of fuel treatments during extreme wildfire conditions has been mixed (e.g., Hunter et al. 2006, Prichard and Kennedy 2014, Lydersen et al. 2017), with limited studies that directly examine fuel and vegetation differences among treatments following wildfire in chaparral (but see Brennan and Keeley 2017). It is likely that the persistence of fuel treatment responses following wildfire will depend on the magnitude of treatment effects, time since treatment, wildfire conditions, and topographic context.

In 2018, the Carr Fire burned through a previously established experimental fuel treatment study in Whiskeytown

National Recreation Area of northern California. The original study was implemented in 2002 to examine the immediate vegetation effects of five different fuel treatment types; mechanical mastication, prescribed burning, mechanical mastication followed by prescribed burning, hand thinned, and an untreated "control" in chaparral and oak vegetation types (Bradley et al. 2006). The initial study was conducted to compare the impacts of mechanical mastication and other fuel treatments on native and exotic vegetation. In 2018, the study site was serendipitously resurveyed 15 years after fuel treatment and shortly before the Carr Fire to examine the longer-term impacts of these treatments on both fuels and understory vegetation (Martorano et al. 2021). The main findings of this prior study indicated that there were long-term tradeoffs in the impacts of fuel treatments on vegetation and fuels. All treatments, except prescribed burn only, reduced shrub height and cover compared to untreated areas. However, mastication and burning treatments also increased exotic plant richness and cover (Martorano et al. 2021).

The current study expands upon this earlier work by assessing the persistence of long-term fuel treatment effects when exposed to an extreme wildfire event. While some studies have examined short and long-term fuel and vegetation responses to treatments in chaparral or shrublands, we are unaware of studies that have examined the interaction between older fuel treatments and wildfire in chaparral ecosystems. In 2019 and 2020, the Whiskeytown National Recreation Area study site was resurveyed following the 2018 Carr Fire. Specifically, our study examined the effects of fuel treatments and wildfire interactions on (1) vegetation and substrate burn severity, (2) post-wildfire live and dead surface fuel characteristics, and (3) native and exotic plant species richness and cover. Results from this study can assist management decisions within northern California chaparral by identifying the benefits and drawbacks to fuels and vegetation associated with different fuel treatment types following an extreme wildfire event.

Methods

Site description

Our study site encompasses 18.2 ha within Whiskeytown National Recreation Area in Shasta County (40.6221° N, 122.5541° W), along the southeastern boundary of the Klamath Mountains in northern California, USA. Elevation ranges from 381 to 457 m with slopes ranging from 1 to 40%. Whiskeytown National Recreation Area has a Mediterranean climate with hot, dry summers and cool, rainy winters. Summer (May through October) temperatures are often as high as 38° C, while winter (November through March) temperatures occasionally fall below freezing. Average annual precipitation is 1,524 mm, with 70% falling between November and March (PRISM Climate Group 2019). In 2018, the year the Carr Fire burned, annual precipitation was 1101 mm, and in 2019 was 2271 mm. Soils in the study site location are either Boomer gravelly loam (15 to 30% slopes) or Neuns very stony loam (8 to 50% slopes) (USDA NRCS 2020).

The overstory of our study site was comprised primarily of California black oak (*Quercus kelloggii* Newb.) and knobcone pine (*Pinus attenuata* Lemmon), with a less common overstory of canyon live oak (*Q. chrysolepis* Liebm.), gray pine (*P. sabiniana* D. Don), and interior live oak (*Q. wislizeni* A DC). Shrubs at the site included two obligate seeder species, whiteleaf manzanita (*Arctostaphylos viscida* Parry) and Lemmon ceanothus (*Ceanothus lemmonii* Parry), as well as the resprouting species toyon (*Heteromeles arbutifolia* (Lindl.) M. Roem.), California yerba santa (*Eriodictyon californicum* (Hook. & Arn.) Torr.) and western poison oak (*Toxicodendron diversilobum* Torr. & A. Gray) (Bradley et al. 2006). Common native perennial herbaceous plants at this site included Hartweg's odontostomum (*Odontostomum hartwegii* Torr.), wild hyacinth (*Dichelostemma multiflorum* Benth. A. Heller), and Tolmie star tulip (*Calochortus tolmiei* Hook. & Arn.). The most common annual grasses were non-native and included Rattail sixweeks grass (*Festuca myuros* L.), silver hairgrass (*Aira caryophyllea* L.), and nit grass (*Gastridium phleoides* (Nees & Meyen) E.E. Hubb).

The 2018 Carr Fire, which burned through the study site, was a human-caused fire that burned 92,936 ha. Nearly all (97%) of Whiskeytown National Recreation Area burned during the fire, and the National Park Service lost numerous structures (National Park Service 2020). The Carr Fire burned through our study area during 2 of the 3 days in which fire growth was the largest. The fire spotted across a narrow finger of Whiskeytown Lake in the vicinity of the study site and spread laterally into the study area. Firefighting was conducted by handcrews and bulldozers in and adjacent to the study area in an unsuccessful attempt to hold the spot from progressing to the south but did not observably impact any of our plots.

Experimental design

In 2002, a complete randomized block design was implemented within the study site containing ten blocks (Fig. 1). Blocks were delineated based on similar slope, aspect, and vegetation characteristics, which were broadly classified as oak-dominated or chaparral-dominated vegetation types (Bradley et al. 2006). Prior to treatment, the oak vegetation type was characterized by having some California black oak and knobcone pine in the overstory and a mixed shrub component in the midstory. The chaparral vegetation type was mostly composed of mixed shrub species with the occasional knobcone pine in the overstory. There were four blocks

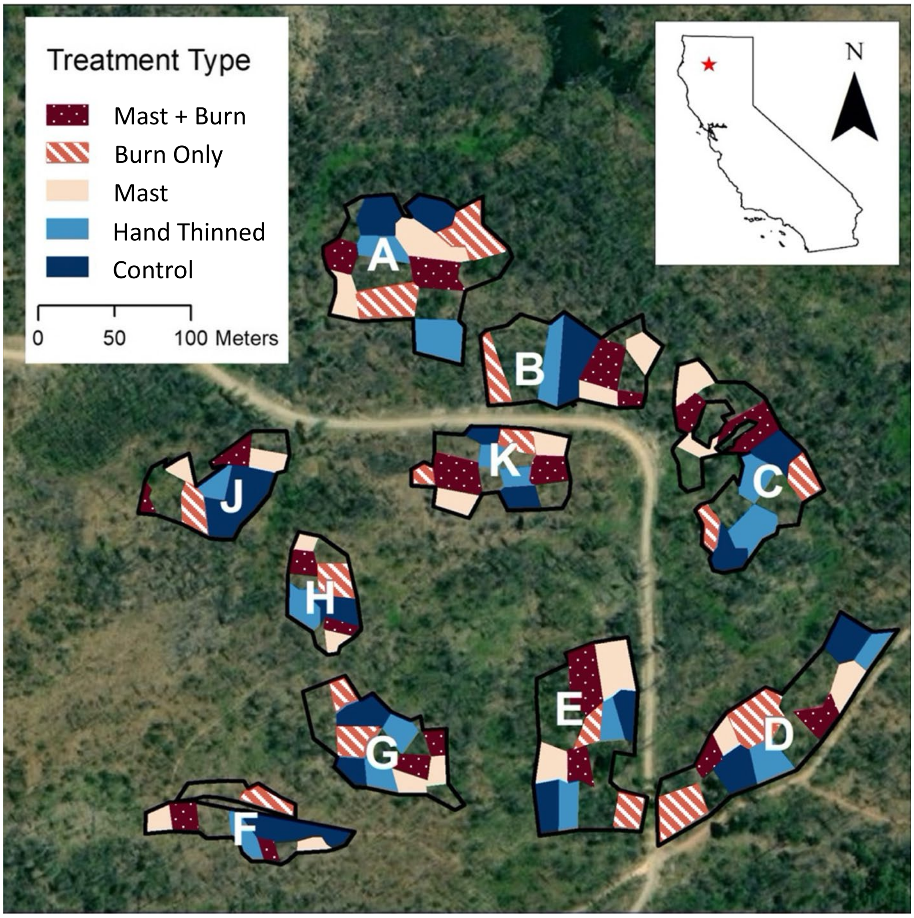

Fig. 1 Experimental fuel treatment study in Whiskeytown National Recreation Area of northern California, USA. Layout of experiment is subdivided by treatment (including untreated control (Control), hand thinned, mastication only (Mast), mastication and burning (Mast + Burn), prescribed burn only (Burn Only), and vegetation type (chaparral or oak). Chaparral-dominated vegetation type was present in blocks F, H, J, and K, while the oak-dominated type was present in blocks B, C, D, E, and G. Block A was split up into half chaparral-dominated and half oak-dominated units

with an oak-dominated vegetation type, four blocks with a chaparral-dominated vegetation type, and one block that contained both vegetation types. Each block was subdivided into units that ranged in size from 0.01 to 0.15 ha with an average size of 0.11 ha (standard error = 0.01). Within each block, one or two units were treated with one of the following five treatments: hand thinned, prescribed burned in the spring (burn only), mechanically masticated (mastication only), mechanically masticated and spring burned (mastication + burning), or an untreated control (Table 5 in Appendix 2). All units burned during the 2018 Carr Fire and there was no true control treatment that was untreated and unburned.

Mechanical mastication was completed in November of 2002 using a North Tree Fire International ASV Posi-Track with an industrial brushcutter. Machine operators attempted to minimize soil disturbance and compaction by operating the masticator over chipped surfaces only when soils were dry. It was the goal of the mastication treatments to reduce understory shrub density and small trees less than 3 or 4 m tall by 60–95% (Bradley et al. 2006). Hand thinned treatment was implemented using chainsaws in February and March of 2003. Heavy hand-thinning was conducted, to mimic the shrub reduction that took place in masticated units. Once cut, the brush was carried outside of the experimental site and pile burned.

Prescribed burning was independently applied to the burn only and mastication + burning treatments in the spring (i.e., early growing season) within each designated unit and burning conditions were recorded as part of a previous study (Bradley et al. 2006). Approximately half of the prescribed burning was conducted from 8 April 2003 to 10 April 2003, while the remaining burns were completed on 15 May 2003. All prescribed burn treatment units were ignited using drip torches with strip and spot ignition patterns. Soil moisture during the burns was recorded as "very high" (0.3–0.4 kPa tension). Air temperature ranged from 15 °C to 22 °C, while relative humidity ranged from 34 to 73%. Wind speed averaged about 3 km h^{-1} with maximum speeds of 10 km h^{-1}. Prescribed fires in the burn only treatment were generally low-intensity surface fires with limited mortality and consumption of shrubs (Bradley et al. 2006; Martorano et al. 2021). In the mastication + burning treatment, surface fires were much hotter resulting in higher mortality in the overstory.

Within each unit, two 2 × 2-m (4 m^2) vegetation plots were randomly assigned and established. In total, there were 88 units with 176 vegetation plots (Table 5 in Appendix 2). The southwest corner of each unit was established as the starting coordinate. Random numbers were generated to establish vegetation plot locations using an x and y coordinate system and were used to calculate the distance to the edge of the treatment unit for each vegetation plot. Each vegetation plot was oriented to the north and was marked using plastic stakes. Most plastic stakes were consumed in the Carr Fire, so their locations were estimated using the original coordinates and replaced in 2019 with new stakes. Data used for the study included fuels and vegetation immediately before the fire (2018) and post-fire (2019 and 2020).

Data collection and analysis

The effect of fuel treatment type on vegetation burn severity and substrate burn severity was examined along each 4.6 m fuel transect positioned at the base of the vegetation plot and running north through the center of the vegetation plot. Examination of relative normalized burn ratio (RdNBR) severity map of the study site following the Carr Fire indicated that most of the site burned at high severity with patches of moderate severity intermixed (mtbs.gov). Given the resolution of the RdNBR severity mapping relative to our treatment unit size, we elected to categorize severity using the National Park Service Fire Monitoring Handbook (form FMH-21; National Park Service 2003; Table 4 in Appendix 1) except that the order of burn severity classifications was reversed so that they logically ranged from 1 (unburned) to 5 (high severity). During post-fire data collection, we quantified and recorded the proportion of each transect by burn severity classification. We summarized burn severity data by calculating a weighted value proportional to the distance of each burn severity category along each transect to represent the average burn severity for each vegetation plot.

To examine the post-fire shrub response to wildfire among fuel treatment types, we recorded all live shrub stems (resprouts and seedlings) with distinct bases that were rooted within the first 1 m^2 quadrat of each vegetation plot. Additionally, each shrub species was classified by their regeneration strategy (resprouter or obligate seeder). Shrub heights were measured for the first five individuals of each species closest to the southwest corner of the quadrat. Average shrub height for each vegetation plot was determined as a weighted average based on the shrub density of each species present in the plot.

We used the planar intercept method (Brown 1974) to estimate dead surface fuel loading before and after the wildfire. Along the same 4.6 m transect used to collect burn severity data, we also collected fuel loading and depth data. We measured and recorded litter depth at 0 m, 1.8 m, 3.7 m, and 4.6 m along the transect from the plot origin. We counted 1 h fuels (dead woody material with a diameter less than 6.35 mm) and 10 h fuels (dead woody material with a diameter between 6.35 and 25.4 mm) along the first 1.8 m of the transect. We counted 100 h fuels (dead woody material with a diameter between 2.54 and 7.62 cm) along the first 3.7 m of the transect. We measured the diameter of all 1000 h fuels (dead woody material with a diameter greater than 7.62 cm) along the entire transect and recorded the decay class (sound or rotten) and species.

We calculated fuel loading for each time-lag class separately for fine woody fuels (1–100 h; Eq. (1)) and coarse woody fuels (1000 h; Eq. (2)) (Brown 1974). We used Eq. (3) to calculate the slope correction factor (c).

$$1-100\ h\ fuel\ load\ (Mg\ ha^{-1}) = \frac{1.234 \times n \times d^2 \times s \times a \times c}{l} \quad (1)$$

$$1000\ h\ fuel\ load\ (Mg\ ha^{-1}) = \frac{1.234 \times \Sigma d^2 \times s \times a \times c}{l} \quad (2)$$

$$c = \sqrt{1 + (\frac{Percent\ slope}{100})^2} \quad (3)$$

We utilized preexisting values from Brown (1974) to complete fuel loading calculations. The variable n refers to the number of woody particles (total count) that intersected the transect for a given time-lag class. For specific gravity (s), we used a value of 0.48 for 1 and 10 h fuels, 0.40 for 100 h fuels, 0.40 for sound 1000 h fuels, and 0.30 for rotten 1000 h fuels. For squared average diameters (d^2), we used a value of 0.1 cm, 2.5 cm, and 25.8 cm for 1 h, 10 h, and 100 h fuels, respectively. Values for the non-horizontal correction factor (a) were 1.13 for 1 h, 10 h, and 100 h and 1.00 for rotten and sound 1000 h fuels. Fine woody fuel loading for each transect was calculated by taking the sum of 1 h, 10 h, and 100 h fuels.

To study understory vegetation response to wildfire among fuel treatment types, we identified all herbaceous plants and woody shrubs within a 2 × 2-m vegetation plot in 2020, which was further subdivided into four 0.5 × 1-m quadrats. We used the Jepson Manual (Baldwin et al. 2012) and local plant lists from Whiskeytown National

Recreation Area to help with identification to species. We estimated and recorded percent cover to the nearest 1% for each understory species within each quadrat, along with lifeform (forb, grass, shrub) and nativity (exotic or native). Estimates of cover (%) and richness (species m^{-2}) at the plot-level were based on an average across the four quadrats. We also estimated tree and shrub canopy cover using a densiometer held at hip height in the center of the vegetation plot. We counted the number of points intercepted by the canopy and recorded canopy cover estimates in each cardinal direction, averaged them, and then multiplied by 1.04 (Lemmon 1956).

We conducted all statistical analyses in the R environment (R Development Core Team 2021). We used a linear mixed effects modeling approach with the *lme4* (Bates et al. 2015) package to test each response variable including vegetation and substrate burn severity, litter and fine woody fuel loading, shrub density and height, and species richness. Fixed effect variables included treatment type (mastication, mastication + burning, hand thinned, burn only, control), year (pre-fire or post-fire), and vegetation type (oak or chaparral). Litter and fine woody fuel loading response variables required square root transformation to meet model assumptions. Shrub density and height models also considered regeneration strategy (resprouter or obligate seeder) as a fixed effect. Burn severity and shrub models did not have year as a fixed effect factor in candidate models, since we only examined post-fire measures. All species richness and plant cover candidate models included a distance to edge variable to account for possible edge effects due to the relatively small unit size. We also separately modeled exotic species richness and cover. The random effects structure of all candidate models included unit nested within block. All analysis was completed at the vegetation plot level, and we compared models of each fixed effect variable individually, as well as all possible additive and interactive models. We also examined the relationship of plant species richness with canopy cover, burn severity, and litter depth using a linear regression approach.

We calculated Akaike information criteria (AIC) for all candidate mixed effects models to select the best explanatory and least complex model (Burnham & Anderson 1998). We considered the model with the lowest AIC value as the top model. If the top models were within 2 AIC, we selected the model that contained the fewest explanatory variables as the most informative. We report significant ($\alpha = 0.05$) fixed effects and interactions based on the Anova function in the *car* package (Fox & Weisberg 2019) and report the χ^2 statistic and P values in the top model. If we detected a significant fixed-effect, we performed a post hoc pairwise analysis using a Tukey HSD test in the *emmeans* package (Lenth 2018) to examine specific differences between treatment types within selected models and report the t-ratio and P value.

Results

All treatments experienced moderate burn severity (Table 1), with no significant effect of treatment on vegetation burn severity ($\chi^2 = 4.5$, $P = 0.341$) or substrate burn severity ($\chi^2 = 4.5$, $P = 0.339$). Vegetation type was also not associated with vegetation burn severity ($\chi^2 = 0.1$, $P = 0.765$) or substrate burn severity ($\chi^2 = 0.4$, $P = 0.533$) (Tables 6, 7, 8 and 9 in Appendix 3). While not statistically significant, hand thinned treatment in chaparral had the lowest substrate burn severity (2.8) and vegetation burn severity (3.1), while the mastication only treatment had the highest (substrate = 3.8, vegetation = 3.9). Severity estimates among treatments within the oak vegetation type were similar with no noteworthy trends.

Treatment had no effect on post-fire live shrub density (new seedlings and resprouts) and limited influences on shrub height (Fig. 2). While there were no significant differences among treatments compared to the untreated control, shrub density differed by vegetation type ($\chi^2 = 6.3$, $P = 0.013$) and regeneration strategy ($\chi^2 = 29.8$, $P < 0.001$) (Tables 6, 7, 8 and 9 in Appendix 3). Average shrub density was 7.4 shrubs m^{-2} within the chaparral vegetation type and 12.2 shrubs m^{-2} in the oak vegetation type. The density of obligate seeder shrubs was 0.8 and 1.5 times more than resprouter species in the oak and chaparral vegetation types, respectively. The most informative model for post-fire shrub height included treatment ($\chi^2 = 15.5$, $P = 0.004$) and vegetation type ($\chi^2 = 11.6$, $P < 0.001$). The only treatment difference in post-fire shrub height was limited to the mastication only

Table 1 Substrate and vegetation burn severity (mean ± SE) one year following the 2018 Carr Fire by treatment, including untreated control (Control), hand thinned, masticated only (Mast), masticated and burned (Mast + Burn), and prescribed burn only (Burn Only) and vegetation type (chaparral or oak). Burn severity values ranged from unburned (1) to heavily burned (5). See Table 4 in Appendix 1 for detailed burn severity category information

Vegetation type	Burn severity	Control	Hand thinned	Mast	Mast + Burn	Burn Only
Chaparral	Substrate	3.7 (0.3)	2.8 (0.3)	3.8 (0.2)	3.6 (0.2)	3.6 (0.3)
	Vegetation	3.5 (0.3)	3.1 (0.2)	3.9 (0.2)	3.8 (0.2)	3.8 (0.3)
Oak	Substrate	3.9 (0.2)	3.7 (0.2)	3.9 (0.3)	3.5 (0.2)	3.8 (0.3)
	Vegetation	3.7 (0.3)	3.4 (0.3)	3.6 (0.3)	3.3 (0.4)	3.8 (0.3)

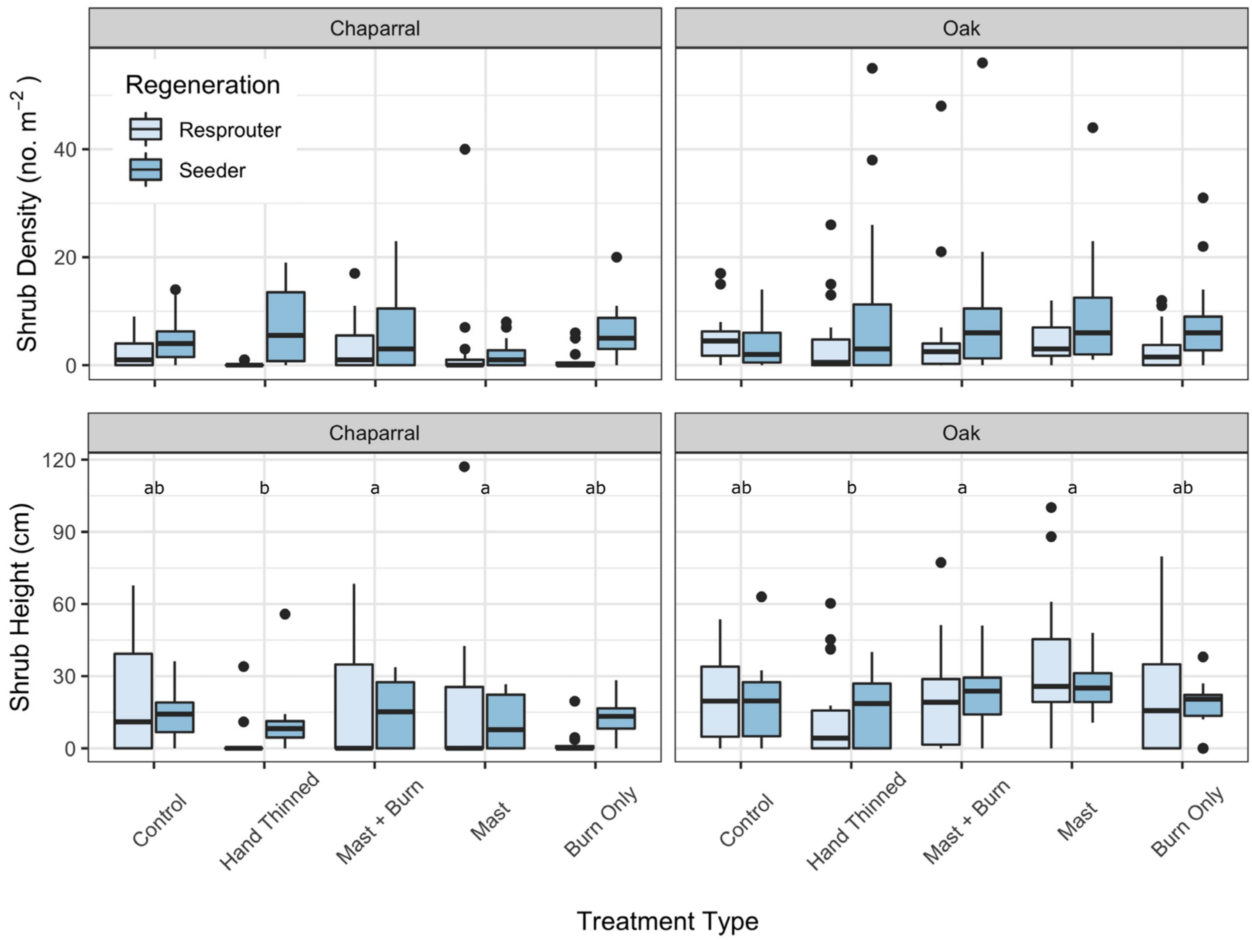

Fig. 2 Average live shrub density (upper panels) and shrub height (lower panels) two years after the 2018 Carr Fire in Whiskeytown National Recreation Area, California, USA, by regeneration type (resprouter or seeder), vegetation type (chaparral or oak), and treatment type including untreated control (Control), hand thinned, mastication only (Mast), mastication and burning (Mast + Burn), and prescribed burn only (Burn Only). Superscripted letters reflect statistically significant differences in shrub height among treatment types (independent of regeneration type) when treatment was a significant factor in the top model. See Table 10 in Appendix 4 for the model structure of each shrub response variable

treatment (29.4 cm) which had double the height of shrubs than the hand thinned treatment (14.7 cm). The oak vegetation type (20.8 cm) had 64% taller shrubs than the chaparral vegetation type (12.7 cm).

Surface fuels expectedly decreased following wildfire and initial pre-wildfire differences among treatments were not maintained or weak one year after wildfire (Table 2). The most informative model for fine woody fuel loading included treatment ($\chi^2=6.5$, $P=0.172$), year ($\chi^2=66.9$, $P<0.001$) and the interaction of treatment and year ($\chi^2=17.3$, $P=0.001$), with similar findings for woody fuels by time-lag category (Tables 6, 7, 8 and 9 in Appendix 3). Prior to wildfire, fine woody fuel loading was higher in the mastication only treatment than in hand thinned ($t=-1.2$, $P<0.001$) or mastication + burning ($t=-2.9$, $P=0.029$) treatments, but there were no differences among treatments in fine woody fuel loading following wildfire. All treatments significantly decreased in fine woody fuel loading (39 to 87%; $P<0.033$) following wildfire except for the hand thinned treatment (14 to 20%, $t=1.32$, $P=0.190$). The most informative litter depth model included year ($\chi^2=334.9$, $P<0.001$), vegetation type ($\chi^2=21.9$, $P<0.001$), and treatment ($\chi^2=11.6$, $P<0.019$). Litter depths were generally higher in the oak than in the chaparral vegetation type and litter depth declined across all treatments and vegetation types following wildfire (Table 2). Treatment differences while significant were more subtle with the mastication only treatment having greater litter depths than the untreated control ($t=-2.9$, $P=0.029$), largely driven by pre-wildfire differences.

Plant species richness increased following wildfire across all treatments but differences among treatments were limited and varied between vegetation types (Table3). We identified 63 species across all treatments, vegetation

Table 2 Litter depth and fine woody fuel loading (mean ± SE) by time-lag class (1–100 h) before (pre-fire; 2018) and after (post-fire; 2019) the Carr Fire by treatment type, including untreated control (Control), hand thinned, mastication only (Mast), mastication and burning (Mast + Burn), and prescribed burn only (Burn Only) and vegetation type (chaparral or oak). *FWF*, fine woody fuels. Superscripted letters reflect statistically significant differences among treatment types when treatment was a significant factor in the top model. See Tables 6, 7, 8 and 9 in Appendix 3 for the model structure of each fuel category

Vegetation type	Category	Control	Hand thinned	Mast	Mast + Burn	Burn Only
Pre-fire (2018)						
Chaparral	Litter (cm)	2.0 (0.3)^{b}	1.9 (0.6)^{ab}	2.4 (0.3)^{a}	1.8 (0.2)^{ab}	2.8 (0.5)^{ab}
	1 h (Mg ha^{-1})	0.4 (0.1)^{a}	0.2 (0.1)^{b}	0.3 (0.1)^{ab}	0.2 (0.0)^{b}	0.2 (0.0)^{ab}
	10 h (Mg ha^{-1})	2.1 (0.6)^{b}	1.7 (0.4)^{bc}	5.6 (1.3)^{a}	2.1 (0.5)^{b}	2.8 (0.8)^{ab}
	100 h (Mg ha^{-1})	1.6 (0.9)	1.6 (0.6)	7.5 (2.5)	3.8 (1.2)	3.9 (2.2)
	FWF (Mg ha^{-1})	4.1 (1.1)^{ab}	3.5 (0.9)^{b}	13.4 (3.5)^{a}	6.1 (1.4)^{b}	7.0 (2.7)^{ab}
Oak	Litter (cm)	2.5 (0.3)^{b}	3.2 (0.5)^{ab}	4.0 (0.3)^{a}	3.1 (0.3)^{ab}	3.4 (0.3)^{ab}
	1 h (Mg ha^{-1})	0.5 (0.1)^{a}	0.3 (0.1)^{b}	0.3 (0.1)^{ab}	0.2 (0.1)^{b}	0.3 (0.1)^{ab}
	10 h (Mg ha^{-1})	4.4 (0.8)^{b}	1.8 (0.3)^{bc}	4.2 (0.7)^{a}	2.4 (0.5)^{b}	3.4 (0.5)^{ab}
	100 h (Mg ha^{-1})	7.1 (2.0)	3.6 (1.0)	5.9 (1.2)	5.2 (1.7)	5.0 (1.4)
	FWF (Mg ha^{-1})	12.0 (2.5)^{ab}	5.7 (1.2)^{b}	10.4 (1.7)^{a}	7.9 (1.9)^{b}	8.8 (1.7)^{ab}
Post-fire (2019)						
Chaparral	Litter (cm)	0.8 (0.2)^{b}	0.5 (0.1)^{ab}	0.5 (0.1)^{a}	0.4 (0.1)^{ab}	0.4 (0.1)^{ab}
	1 h (Mg ha^{-1})	0.2 (0.1)^{a}	0.1 (0.0)^{b}	0.1 (0.0)^{ab}	0.1 (0.0)^{b}	0.2 (0.1)^{ab}
	10 h (Mg ha^{-1})	1.0 (0.3)^{b}	1.1 (0.4)^{bc}	0.9 (0.3)^{a}	1.0 (0.3)^{b}	2.2 (0.9)^{ab}
	100 h (Mg ha^{-1})	0.5 (0.4)	1.6 (0.7)	0.7 (0.3)	0.0 (0.0)	1.8 (0.6)
	FWF (Mg ha^{-1})	1.7 (0.5)	2.8 (1.0)	1.8 (0.5)	1.1 (0.3)	4.3 (1.3)
	Litter reduction (%)	60.0	73.6	79.1	77.8	85.7
	FWF reduction (%)	58.5	20.0	86.6	82.0	38.6
Oak	Litter (cm)	0.7 (0.2)^{b}	1.1 (0.2)^{ab}	1.1 (0.2)^{a}	1.1 (0.1)^{ab}	1.1 (0.2)^{ab}
	1 h (Mg ha^{-1})	0.2 (0.1)^{a}	0.2 (0.0)^{b}	0.3 (0.0)^{ab}	0.2 (0.0)^{b}	0.2 (0.0)^{ab}
	10 h (Mg ha^{-1})	1.2 (0.3)^{b}	1.0 (0.3)^{bc}	1.5 (0.3)^{a}	1.4 (0.4)^{b}	1.7 (0.4)^{ab}
	100 h (Mg ha^{-1})	2.6 (0.7)	3.7 (1.2)	0.3 (0.3)	2.5 (0.7)	3.5 (1.1)
	FWF (Mg ha^{-1})	3.9 (0.9)	4.9 (1.3)	2.1 (0.4)	4.1 (0.9)	5.4 (1.4)
	Litter reduction (%)	72.0	65.6	72.5	64.5	74.2
	FWF reduction (%)	67.5	14.0	79.8	48.1	38.6

types, and years (Table 10 in Appendix 4). Total species richness varied by year ($\chi^2 = 306.7$, $P < 0.001$), the interaction of treatment and year ($\chi^2 = 30.1$, $P < 0.001$), and the interaction of vegetation type and year ($\chi^2 = 86.9$, $P < 0.001$) (Tables 6, 7, 8 and 9 in Appendix 3). Changes in species richness following wildfire ranged from two fewer species m^{-2} in the hand thinned treatment of the chaparral vegetation type to 13 more species m^{-2} in the burn only treatment in the oak vegetation type. Prior to the wildfire, species richness only differed among treatments in the chaparral vegetation type, with the mastication + burning treatment having more species than other treatments. After wildfire, the only observed treatment difference in species richness following wildfire was between the hand thinned (13 species m^{-2}) and untreated control treatments (18 species m^{-2}) in the chaparral vegetation type ($t = 3.54$, $P = 0.004$). Exotic species richness after fire was greatest in the untreated control for both chaparral and oak vegetation types. Following fire, the mastication + burning treatment had fewer exotic species than the untreated control in oak vegetation ($t = 2.75$, $P = 0.049$), while the other treatments did not differ from the untreated control.

Post-fire plant species richness decreased with increasing canopy cover, but the strength of this relationship varied by vegetation type (Fig. 3). Species richness was best informed by canopy cover ($t = -2.67$, $P = 0.009$), vegetation type ($t = 4.68$, $P < 0.001$), and the interaction of canopy cover and vegetation type ($t = -5.23$, $P < 0.001$). Canopy cover had a negative relationship with species richness in the oak vegetation type ($r^2 = 0.29$, $P = 0.002$) and no relationship in the chaparral type ($r^2 = 0.01$, $P = 0.720$). Other potential factors, such as litter depth ($P = 0.291$) or either measure of burn severity (vegetation severity: $P = 0.760$ or substrate severity: $P = 0.448$), were not informative and relationships did not improve if vegetation type or treatment type were considered.

Table 3 Plant species richness (mean ± SE) per m^2 by origin, treatment type, including untreated control (Control), hand thinned, mastication only (Mast), mastication and burning (Mast + Burn), and prescribed burn only (Burn Only) and vegetation type (chaparral or oak), immediately before (pre-fire) the Carr Fire (2018) and two years after (post-fire; 2020) in Whiskeytown National Recreation Area, California, USA. Superscripted letters reflect statistically significant differences among treatment types when treatment was a significant factor in the top model. See Tables 6, 7, 8 and 9 in Appendix 3 for the model structure of each fuel category

Vegetation type	Origin	Control	Hand thinned	Mast	Mast + Burn	Burn Only
Pre-fire (2018)						
Chaparral	Native	8.2 (0.7)	11.1 (0.6)	10.7 (0.6)	10.5 (0.6)	9.7 (0.6)
	Exotic	2.9 (0.7)	4.0 (0.3)	2.9 (0.4)	3.9 (0.3)	2.7 (0.7)
	Total	11.1 (1.1)	15.1 (0.7)	13.6 (0.8)	14.5 (0.7)	12.3 (1.1)
Oak	Native	7.4 (0.6)	8.1 (0.7)	8.1 (0.9)	7.4 (0.5)	6.1 (0.6)
	Exotic	1.3 (0.4)	1.7 (0.5)	1.8 (0.4)	1.8 (0.4)	0.6 (0.3)
	Total	8.6 (0.9)^{ab}	9.8 (1.1)^{ab}	9.9 (1.2)^{a}	9.2 (0.8)^{ab}	6.7 (0.8)^{b}
Post-fire (2020)						
Chaparral	Native	12.2 (0.7)	9.3 (0.8)	10.8 (0.8)	10.9 (0.8)	12.1 (0.9)
	Exotic	5.9 (0.5)^{a}	3.7 (0.3)^{c}	4.6 (0.4)^{abc}	4.0 (0.4)^{bc}	5.4 (0.4)^{ab}
	Total	18.1 (1.0)^{a}	13.0 (0.9)^{b}	15.4 (1.0)^{ab}	14.9 (1.0)^{ab}	17.5 (1.0)^{a}
Oak	Native	13.3 (0.7)	13.4 (0.7)	12.6 (0.6)	12.3 (0.5)	13.6 (0.7)
	Exotic	6.3 (0.4)^{a}	5.6 (0.2)^{ab}	5.7 (0.3)^{ab}	5.0 (0.3)^{b}	6.2 (0.4)^{ab}
	Total	19.6 (0.8)	18.9 (0.7)	18.2 (0.7)	17.3 (0.6)	19.8 (0.8)

Total plant cover varied by treatment ($\chi^2 = 11.8$, $P = 0.018$), year ($\chi^2 = 17.5$, $P < 0.001$) and vegetation type ($\chi^2 = 22.1$, $P < 0.001$) (Tables 6, 7, 8 and 9 in Appendix 3). Treatment differences were limited to hand thinned units having more plant cover than burn only units across both years and vegetation types ($t = 2.8$, $P = 0.041$). Shifts in plant cover over time differed by lifeform category (Fig. 4). Across treatments, average shrub cover after the fire decreased by 56% in the chaparral vegetation type and by 13% in the oak vegetation type. Grass cover increased after wildfire by 117% compared to pre-fire levels in the chapparal vegetation type and by > 500% in oak vegetation types. Forb cover increased by 166% in the oak vegetation type and decreased slightly by 6% in the chaparral type.

Native and exotic cover were strongly influenced by wildfire (Fig. 5). Prior to wildfire, native cover was 6.6% to 8.1% greater than exotic species cover in chaparral and 6.2% to 11.2% greater in the oak vegetation type. Exotic species cover after wildfire ranged from 9.6% to 25.1% greater than native species cover in chaparral and from 0.4 to 8.3% in the oak vegetation type. Exotic species cover, when analyzed separately, differed significantly by treatment ($\chi^2 = 27.3$, $P < 0.001$), vegetation type ($\chi^2 = 27.5$, $P < 0.001$), year ($\chi^2 = 165.0$, $P < 0.001$) (Tables 6, 7, 8 and 9 in Appendix 3), and the interaction of treatment and vegetation type ($\chi^2 = 10.5$, $P = 0.032$). Chaparral had about 10% greater exotic species cover than the oak vegetation type. Across both vegetation types and years, the burn only ($t = 0.84$, $P = 0.919$) and mastication only ($t = -2.09$, $P = 0.227$) treatments did not have significantly more exotic cover compared to the untreated control. The hand thinned ($t = 3.76$, $P = 0.002$) and mastication + burning ($t = 4.162$, $P < 0.001$) treatments both had more exotic cover than the burn only treatment across both years and vegetation types. Post-fire exotic cover within the chaparral type was greatest in mastication and mastication + burning treatments (32.8% and 32.1%, respectively) and least in the burn only and the untreated control treatments (19.5% and 21.6%, respectively).

Discussion

To our knowledge, this study represents the first to observe the effects of wildfire following commonly used fuel treatments that were implemented 15 years prior in chaparral ecosystems. Pre-wildfire differences in fuels and vegetation among treatments did not result in consistent treatment effects following an extreme wildfire based on multiple measures of fuels and vegetation. Differences in burn severity, fuel loading, and vegetation were often more distinct between vegetation type (chaparral or oak) or year than by treatment type. Our findings suggest that extreme wildfire conditions can supersede fuel and vegetation differences following fuel treatments implemented 15 years in northern California chaparral ecosystems. It is possible that pre-wildfire treatment differences may be more persistent under more moderate wildfire conditions or with larger treatment units. Additionally, the relatively small scale of treatment units may have limited our ability to detect

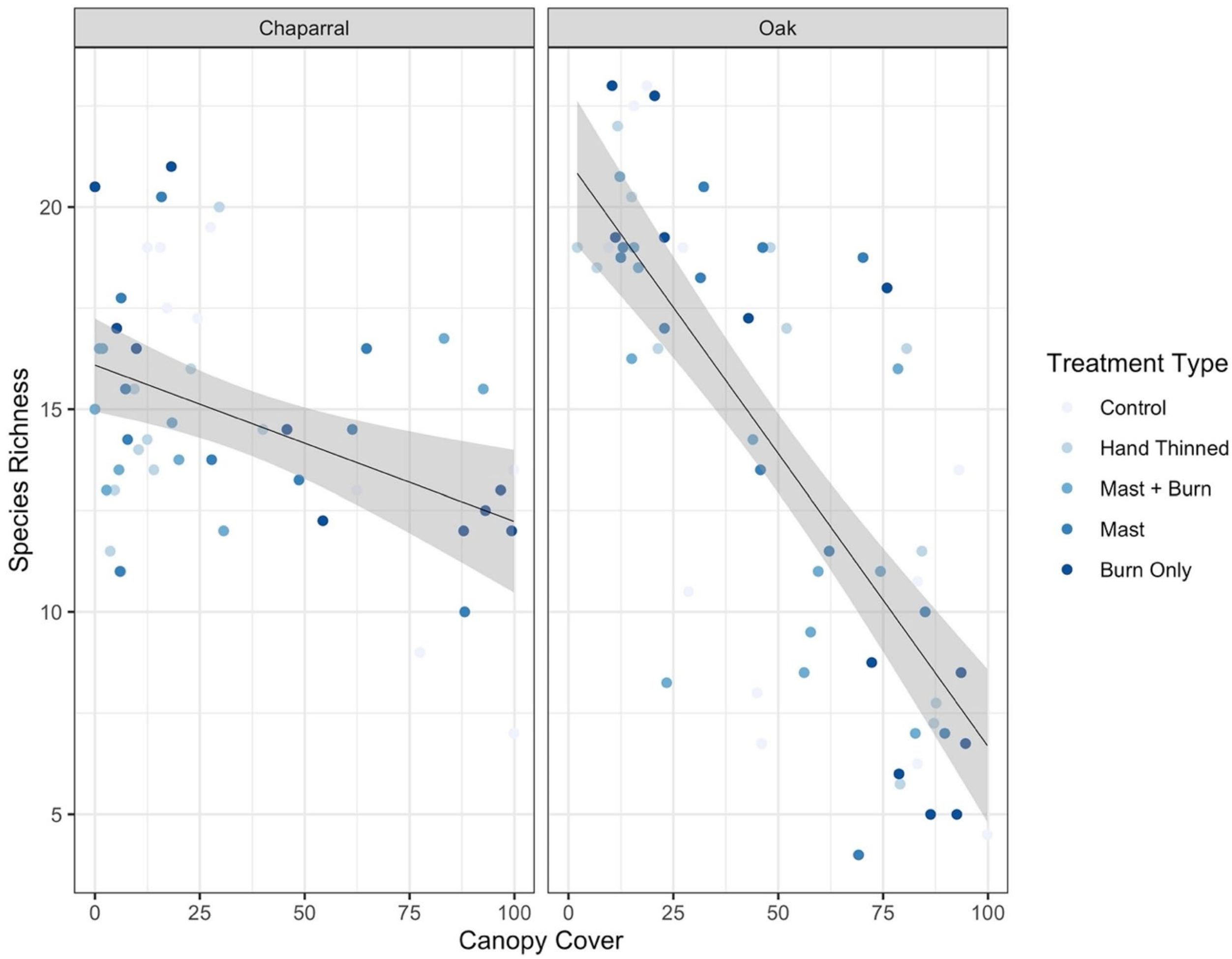

Fig. 3 Relationship between average species richness (per m^2) and canopy cover (%) by treatment type (including untreated control (control), hand-thinned, mastication only (mast), mastication and burning (mast + burn), and prescribed burn only (burn only) for both chaparral ($r^2 = 0.01$, $P = 0.720$) and oak ($r^2 = 0.29$, $P = 0.002$) vegetation types two years after the 2018 Carr Fire in Whiskeytown National Recreation Area, California, USA. Canopy cover was measured at ~ 1 m height and included both shrub and tree canopy cover

post-fire severity and fuels differences 1 to 2 years post-fire. While somewhat unexpected, our study provides additional information for managers and analysts to assess the potential utility of older fuel treatments to meet management goals and inform wildfire response. However, further research is needed that examines interactions of fuel treatments across a range of ages and fire weather conditions.

Vegetation and substrate burn severity estimates were consistent across all treatments. This finding was unexpected at our site since pre-wildfire fuel structure and loading for some treatments were far below untreated control levels (Martorano et al. 2021). It is possible that fire weather can be more important than fuels and vegetation, particularly at finer scales, during extreme fire weather conditions (Lydersen et al. 2017). The treatment area of our study burned during two of the three largest fire-growth days within the park and coincided with a large fire-generated vortex that formed near our study site (Lareau et al. 2018). It is also possible that the prolonged time since treatment (15 years) sufficiently diminished treatment effects to limit any observable reduction in fire severity under extreme wildfire conditions. The small scale of treatment units may have also played a role. The lack of a fuel treatment effect to modify fire in chaparral has been suggested, with previous observations of fires carrying easily through young chaparral stands (Dunn 1989; Conrad and Weise 1998; Moritz et al. 2004). While we were unable to detect significant trends in burn severity across treatments, it is possible there were differences in fire behavior (e.g., flame length and rate of spread) between treatments and untreated areas that are difficult to detect in our post-fire fuel surveys and point to the need for more real-time fire behavior research during wildfires.

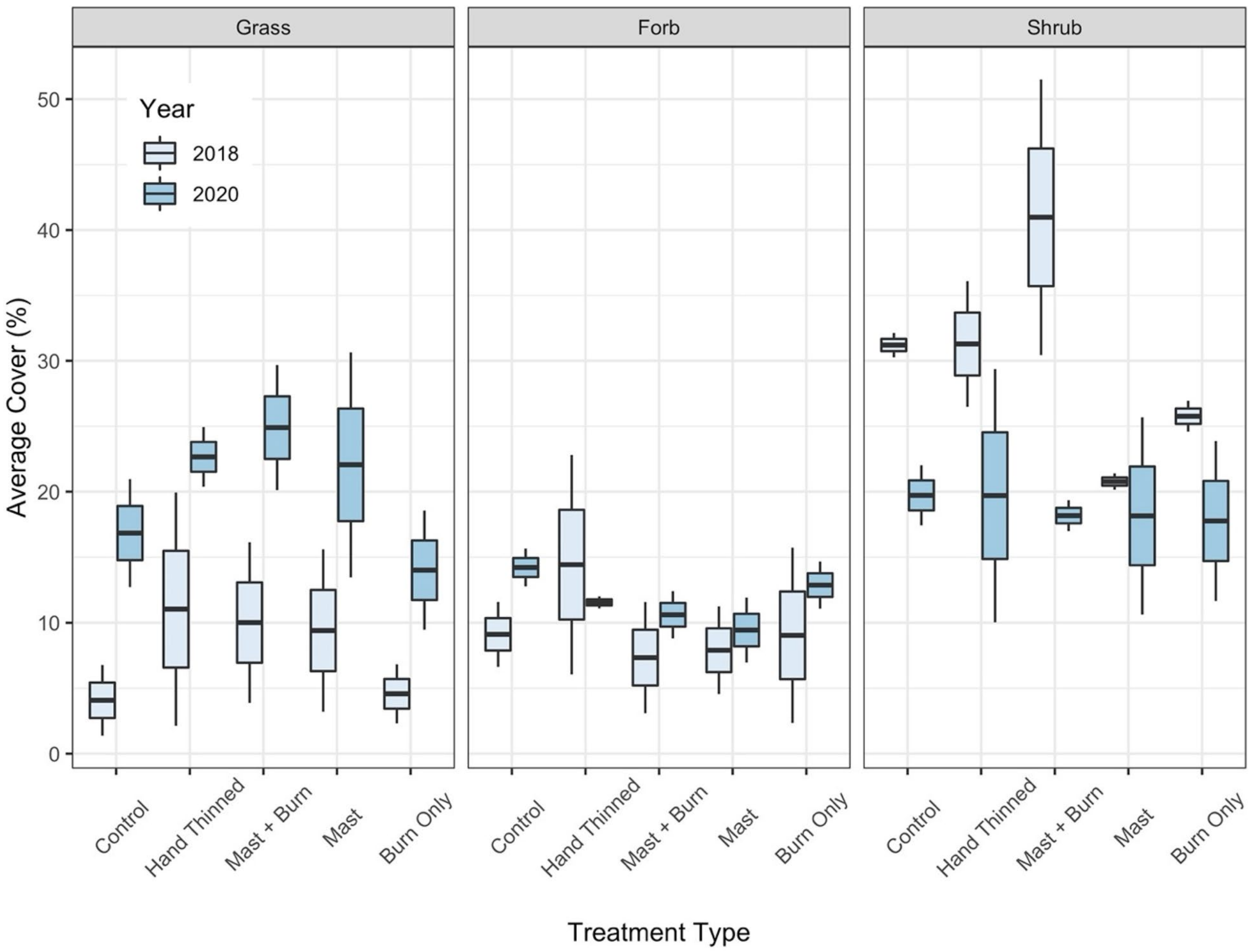

Fig. 4 Average percent cover (per m^2) of grass, forb, and shrub lifeforms by treatment including untreated control (Control), hand thinned, mastication only (Mast), mastication and burning (Mast + Burn), and prescribed burn only (Burn Only), immediately before and two years after the 2018 Carr Fire in Whiskeytown National Recreation Area, California, USA

Pre-fire treatment differences in shrub height and density prior to wildfire did not correspond to post-fire shrub responses among treatments. Prior to wildfire, the burn only and untreated control treatments had greater shrub height than all other treatments in the chaparral vegetation type (Martorano et al. 2021). Following wildfire, however, differences were limited to lower shrub height in the hand thinned treatment compared to the burn only treatment. Consistent with the shrub height results, higher pre-fire shrub density in the mastication + burning treatment compared to other treatments in the chaparral vegetation type (Martorano et al. 2021) did not correspond to post-fire differences in shrub density. We had anticipated that the mastication + burning treatment would result in lower obligate seeder shrub densities following wildfire due to the depletion of the seed bank following prescribed fire. But the recovery of the seed bank appeared to have been sufficient to promote shrub seed regeneration in this treatment.

Post-wildfire fine woody fuel loading differences among treatments did not correspond well to pre-wildfire differences. Before wildfire, the mastication only treatment in the chaparral vegetation type had higher fine woody fuel loading compared to other treatments. After wildfire, fine woody fuel loading was only greater in the burn only treatment compared to either the mastication or mastication + burning treatments. Greater fine woody fuels following the wildfire in the burn only treatment of chaparral was likely due to the promotion of a mixture of live and dead shrubs following the initial prescribed burning treatment in 2003, as demonstrated by Martorano et al. (2021), that potentially provided higher fine woody fuel inputs shortly following the wildfire. However, we expected that the untreated control would similarly have higher post-wildfire fine woody fuel recruitment. Reduced consumption of fine woody fuels in the hand thinned treatment of chaparral vegetation types coupled with relatively (but not significantly) lower fire severity levels, may indicate the

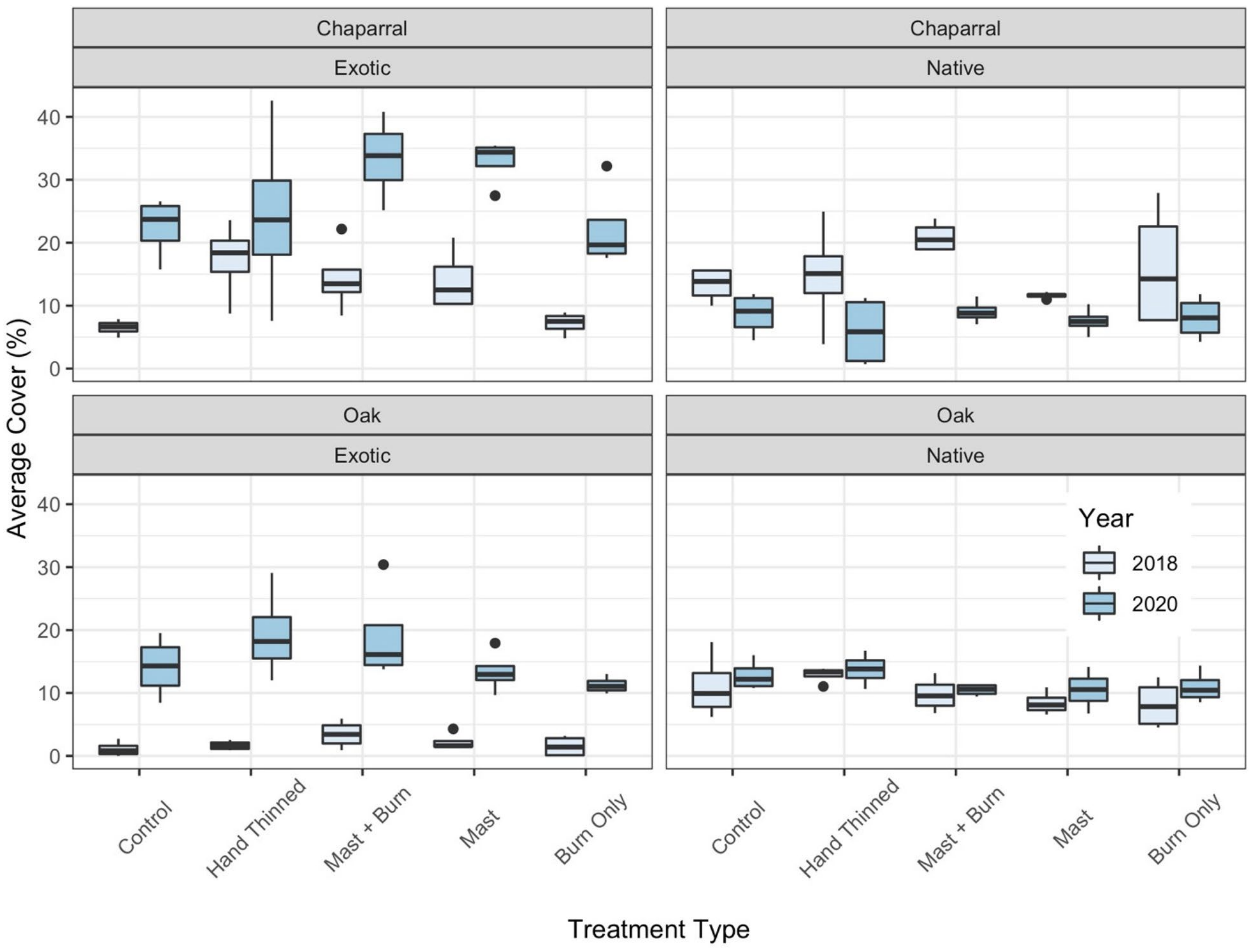

Fig. 5 Average percent cover (per m^2) of exotic species and native species by treatment including untreated control (Control), hand thinned, mastication only (Mast), mastication and burning (Mast + Burn), and prescribed burn only (Burn Only) and vegetation type (chaparral or oak) immediately before and two years after the 2018 Carr Fire in Whiskeytown National Recreation Area, California, USA

potential ability to reduce fire behavior and effects more so than other treatments, but this likely requires more thorough examination.

Plant species richness following wildfire in our study similarly increased across most treatments and did not coincide with pre-fire differences in species richness. The limited treatment effect on species richness was likely related to the wildfire burning under extreme fire weather conditions that resulted in consistent fire severity. Significant increases in plant richness following wildfire coincided with an increase in exotic plant species richness and a noticeable decline in native species richness. The general warming trend and prolonged drought prior to the Carr Fire in northern California may have contributed to the weaker native plant species response in our study, as has been found in other chaparral systems (Werner et al. 2022). Furthermore, the year following the Carr Fire, annual precipitation was 49% above average, possibly supporting an even stronger exotic species response.

The increase in exotic species cover following wildfire was expected, since exotic species often colonize burned areas more quickly than native species (Dickens and Allen 2014), especially in areas that burn with higher severity (Hunter et al. 2006). Increased exotic annual grass cover may lead to shorter fire return intervals and subsequent reductions in shrub cover over time with increased vulnerability to type conversion to exotic annual grasslands, as has been found by previous studies in chaparral (Zedler et al. 1983; Dickens and Allen 2014; Syphard et al. 2019). However, our study indicated that type conversion risk was not uniform across all treatments and vegetation types. In the oak vegetation type, treatments did not differ in exotic cover before or after wildfire. In the chaparral vegetation type, hand thinned and mastication + burning treatments in the chaparral vegetation type prior to wildfire had the greatest exotic species cover 15 years following treatment (Martorano et al. 2021). Following wildfire, exotic species cover was greatest in the mastication and mastication + burning treatments, despite richness being greatest in untreated controls. The prescribed burn only treatment within the chaparral vegetation type was the only treatment that had significantly lower exotic species cover compared to most other treatments before and after wildfire. This was unexpected given that previous studies have observed prescribed fire only treatments resulting in more exotic cover 10 years following treatment compared to mastication only (Wilkin et al. 2017). The lower exotic species cover in the prescribed burn only treatment, could be related to the low reduction of shrub cover compared to the other treatments following the initial prescribed fire (Martorano et al. 2021), but we would have expected to see a similar low exotic species response in untreated controls given similar pre-fire shrub heights and cover to the prescribed burning only treatment.

Vegetation dominance at our study site shifted from shrubs to exotic grasses after wildfire. A previous study in southern California chaparral recorded over 75 species of exotic plants during the first 5 years after wildfire and exotic plant cover peaked in the second year after wildfire (Keeley et al. 2005). The strongest factor that affected the presence of exotic plants following wildfire was woody plant canopy recovery. In the chaparral vegetation type of our study, the hand thinned treatment resulted in the smallest increase in exotic grass cover following wildfire, while the prescribed burn only treatment had the lowest overall post-fire exotic grass cover. Our study found that decreased tree and shrub canopy cover was associated with increased species richness (including exotic species). These results suggest that chaparral vegetation types are possibly more vulnerable than oak vegetation types to post-wildfire exotic species invasion and that both mastication and mastication + burning treatments may negatively impact the native chaparral plant communities more so than hand thinned and prescribed burn only treatments. It is likely that reduced canopy cover promotes exotic invasion when disturbed (Keeley et al. 2005). Similar post-fire shrub density responses across all fuel treatments in our study indicate that exotic cover should decline over time as shrub cover increases (Brennan and Keeley 2017), assuming it does not burn again at a short interval. It is also unclear, how northern California chaparral will respond to short-interval fires, given the greater precipitation of this region. Other ecosystems in this region that experienced repeated fires showed lower levels of exotic species following the second fire (McCord et al. 2020).

While extreme fire conditions or fuel treatment age may have limited differences in fire severity, fuels, and vegetation responses among treatments, the small treatment units utilized in our study may have also contributed to our lack of strong post-fire treatment effects. Treatment sizes used for this study, which averaged 0.11 ha, may have been too small to influence fire behavior and effects regardless of treatment type under the extreme Carr Fire conditions. Information on the size of treatments necessary to influence fire behavior and effects is generally limited, and even more so in chaparral ecosystems. Previous studies examining the effectiveness of larger treatments (5–194 ha) in forested areas found that interior areas of treatments were effective but that the edge areas of treatments experienced similar fire effects to untreated areas following wildfire (Agee and Skinner 2005; Safford et al. 2009). If fuel treatments are not sufficiently large enough, they may be ineffective at altering fire behavior and effects (Graham et al. 2004; Agee and Skinner 2005). Further research is needed that examines interactions between fuel treatment age and wildfire at larger operational scales, and experimental units that capture initial fuels treatment effects may not be sufficiently scaled to detect treatment effects during larger-scale wildfire events.

Conclusions

We found limited persistence of fuel treatment effects on fuels and vegetation when subject to an extreme wildfire in chaparral and oak vegetation types of northern California. We suspect that the muted or altered treatment differences following fire can be attributed to extreme wildfire conditions coupled with fuel treatment age (i.e., 15 years). The relatively small scale of treatment units may have also limited our ability to detect fine-scale differences in treatment effects following extreme wildfire conditions.

Unfortunately, our findings somewhat complicate management recommendations regarding the interactions of older fuel treatments and extreme wildfire in chaparral ecosystems. By most measures of fuel and vegetation in our study, we did not find that pre-wildfire differences translated to post-wildfire differences among treatments, although some treatments did have lower levels of fine fuel consumption (e.g., hand thinned treatments). These findings suggest that selection of fuel treatments to maximize desirable management outcomes in chaparral ecosystems may not be upheld following an extreme wildfire, especially in older treated areas. Conversely, our findings also indicate that some fuels treatments, such as mastication and mastication followed by prescribed burning, did have persistent effects on increasing exotic grass cover compared to untreated controls following and extreme fire. Treatments or vegetation types that retain canopy cover and reduce ground disturbance may limit the spread of exotic species, even after wildfire. While our study aids management decision-making, future work examining larger treatment units that represent operational scales and real-time fire behavior monitoring within and adjacent to fuels treatments during wildfires in chaparral across a range of wildfire conditions will advance understanding and better inform management decisions.

Appendix 1

Table 4 National Park Service form FMH-21 was used to standardize burn severity. Values were reversed for this study with heavily burned as 5 and unburned as 1

	Unburned (1)	Scorched (2)	Lightly burned (3)	Moderately burned (4)	Heavily burned (5)
Substrate	Not burned	Litter partially blackened; duff nearly unchanged; wood/leaf structures unchanged	Litter charred to partially consumed; upper duff layer may be charred but the duff layer is not altered over the entire depth; surface appears black; woody debris is partially burned; logs are scored or blackened but not charred; rotten wood is scorched to partially burned	Litter mostly to entirely consumed, leaving coarse, light colored ash; duff deeply charred, but underlying mineral soil is not visibly altered; woody debris is mostly consumed; logs are deeply charred, burned-out stump holes are common	Litter and duff completely consumed, leaving fine white ash; mineral soil visibly altered, often reddish; sound logs are deeply charred, and rotten logs are completely consumed. This code generally applies to less than 10% of natural or slash burned areas
Vegetation	Not burned	Foliage scorched and attached to supporting twigs	Foliage and smaller twigs partially to completely consumed; branches mostly intact	Foliage, twigs, and small stems consumed; some branches still present	All plant parts consumed, leaving some or no major stems/trunks; any left are deeply charred

Appendix 2

Table 5 Sample size information by vegetation type and treatment including the number of units and vegetation plots. Treatments included an untreated control (control), hand thinned, mastication only (mast), mastication and prescribed burning (mast + burn), and prescribed burn only (burn only). Vegetation types included chaparral- or oak-dominated types. Note: one sample block was split to include both vegetation types, otherwise blocks were separated by vegetation type

Vegetation type	Treatment	Units (*n*)	Vegetation plots (*n*)
Chaparral *n* = 4.5 blocks	Control	6	12
	Hand thinned	6	12
	Mast	9	18
	Mast + burn	9	18
	Burn only	6	12
Chaparral *n* = 5.5 blocks	Control	10	20
	Hand thinned	10	20
	Mast	11	22
	Mast + burn	11	22
	Burn only	10	20

Appendix 3

Mixed-effects model selection results for the top five performing models of each severity, fuels, and vegetation variables examined. Each model included a random effect term of plot nested within unit. Richness and cover data also included an additional variable of distance to edge. The top models selected had the lowest Akiake's information criterion (AIC). When one or more models had a Δ AIC within 2 of the top model, we selected the model with the least number of parameters (k). Treatments included an untreated control, hand thinned, mastication only, mastication and burning, and prescribed burn only treatments. Vegetation types included chaparral or oak-dominated types. Year refers to immediately before (2018) and after (2019–2020) the 2018 Carr Fire in Whiskeytown National Recreation Area, California, USA. Regen = shrub regeneration strategy that included either obligate seeders or resprouting shrub species.

Table 6 Burn severity model selection results. Type = vegetation type

Response variable	Model structure	*k*	AIC	ΔAIC
Vegetation severity	Null (random effects only)	3	219.1	0
	Type	4	221	1.9
	Treatment	7	222.5	3.4
	Treatment + type	8	224.4	5.3
	Treatment × type	12	228.2	9.1
Substrate severity	Null (random effects only)	3	236.8	0
	Type	4	238.3	1.5
	Treatment	7	240.1	3.3
	Treatment + type	8	241.5	4.7
	Treatment × type	12	246.2	9.4

Table 7 Fuel loading model selection results for the top five performing models and the null model for each fuel component. Type = vegetation type

Response variable	Model structure	*k*	AIC	ΔAIC
Litter depth	Treatment + type + year	9	367.9	0
	Treatment × type + year	13	366.3	-1.6
	Treatment + type × year	10	369.2	1.3
	Type + year	5	371.5	3.6
	Type × year	6	372.9	5
	Null (random effects only)	3	610.4	242.5
1 h loading	Treatment + type + year	9	6.5	0
	Treatment + type × year	10	8.2	1.7
	Type × year	12	8.4	1.9
	Treatment + year	8	9.1	2.6
	Type + year	5	12.5	6
	Null (random effects only)	3	31.7	25.2
10 h loading	Treatment + year	8	836.3	0
	Treatment × year	12	835.3	-1
	Treatment + type + year	9	837.2	0.9
	Treatment + type × year	10	838.9	2.6
	Treatment × type + year	13	843.0	6.7
	Null (random effects only)	3	902.0	65.7
100 h loading	Type + year	5	1191.7	0
	Treatment × type × year	22	1191.9	0.2
	Treatment × year	12	1192.5	0.8
	Type × year	6	1193.6	1.9
	Year	4	1197.2	5.5
	Null (random effects only)	3	1228.8	37.1
FWF loading	Treatment × year	12	1140.6	0
	Treatment × type × year	22	1144.2	3.6
	Type + year	5	1144.3	3.7
	Treatment + type + year	9	1145.8	5.2
	Type × year	6	1146.1	5.5
	Null (random effects only)	3	1204.6	64.0

Table 8 Post-fire shrub density and height model selection results for the top five performing models and the null model for each shrub measure. Type = vegetation type, regen = shrub regeneration type (seeder or resprouter)

Response variable	Model structure	*k*	AIC	ΔAIC
Shrub Density	Regen + type	5	1228.2	0
	Regen × type	6	1229.2	1
	Regen	4	1232.4	4.2
	Treatment × regen + type	13	1234.0	5.8
	Treatment × regen × type	22	1237.5	9.3
	Null (random effects only)	3	1258.8	30.6
Shrub Height	Treatment + type	8	1599.5	0
	Treatment × regen + type	13	1601.1	1.6
	Regen + type	5	1604.3	4.8
	Treatment × regen × type	22	1605.2	5.7
	Regen × type	6	1605.3	5.8
	Null (random effects only)	3	1613.7	14.2

Table 9 Plant species richness and cover model selection results for the top five performing models and the null model for each richness measure. Type = vegetation type

Response variable	Model structure	*k*	AIC	ΔAIC
Total richness	Treatment × year × type	23	1891.7	0
	Treatment × year + type	14	1963.5	71.8
	Year	5	1975.2	83.5
	Treatment + year	9	1982.5	90.8
	Treatment + year + type	10	1983.1	91.4
	Null (random effects only)	3	2145.9	254.2
Exotic richness	Treatment × year × type	23	1315.7	0
	Treatment × year + type	14	1369.4	53.7
	Year	5	1387.7	72
	Treatment + year + type	10	1393.7	78
	Treatment + type	9	1393.8	78.1
	Null (random effects only)	3	1580.9	265.2
Total cover	Treatment + type + year	10	17,913	0
	Treatment + type × year	14	17,918	5
	Treatment × year + type	14	17,920	7
	Treatment × type × year	23	17,922	9
	Treatment + type	9	17,926	13
	Null (random effects only)	3	17,940	26.7
Exotic cover	Treatment × type + year	14	2985.3	0
	Treatment + year + type	10	2987.9	2.6
	Treatment × type × year	23	2988.2	2.9
	Treatment × year + type	14	2992.2	6.9
	Treatment + year	9	3004.4	19.1
	Null (random effects only)	3	3018.1	32.8

Appendix 4

Table 10 Plant species list for the study and their associated nativity, lifeform, and life cycle. Scientific names were based on prior version of Jepson for consistency with the original study

Family	Species code	Scientific name	Nativity	Lifeform	Life cycle
Anacardiaceae	TODI	*Toxicodendron diversilobum*	Native	Shrub	Perennial
Apiaceae	SABI	*Sanicula bipinnatifida*	Native	Herb	Perennial
Apiaceae	TOAR	*Torilis arvensis*	Exotic	Herb	Annual
Asteraceae	AMPS	*Ambrosia psilostachya*	Native	Herb	Perennial
Asteraceae	COCA	*Conyza canadensis*	Native	Herb	Biennial
Asteraceae	ERLA	*Eriophyllum lanatum*	Native	Herb	Perennial
Asteraceae	FIGA	*Filago gallica*	Exotic	Herb	Annual
Asteraceae	GNCA	*Gnaphalium canescens* ssp. *beneolens*	Native	Herb	Perennial
Asteraceae	HYGL	*Hypochaeris glabra*	Exotic	Herb	Annual
Asteraceae	LASE	*Lactuca Serriola*	Exotic	Herb	Perennial
Asteraceae	MAMI	*Madia minima*	Native	Herb	Annual
Asteraceae	MICA	*Micropus californicus*	Native	Herb	Annual
Asteraceae	MINU	*Microseris nutans*	Native	Herb	Perennial
Asteraceae	SEVU	*Senecio vulgaris*	Exotic	Herb	Annual
Caprifoliaceae	LOIN	*Lonicera interrupta*	Native	Vine	Perennial
Convolvulaceae	CAOC1	*Calystegia occidentalis*	Native	Vine	Perennial
Ericaceae	ARVI	*Arctostaphylos viscida*	Native	Shrub	Perennial
Fabaceae	CEOC	*Cercis occidentalis*	Native	Tree	Perennial
Fabaceae	LOMI	*Lotus micranthus*	Native	Herb	Annual
Fabaceae	LOPU	*Lotus purshianus*	Native	Herb	Annual
Fagaceae	QUCH	*Quercus chrysolepis*	Native	Tree	Perennial
Fagaceae	QUKE	*Quercus kelloggii*	Native	Tree	Perennial
Hydrophyllaceae	ERCA	*Eriodictyon californicum*	Native	Shrub	Perennial
Hypericaceae	HYCO	*Hypericum concinnum*	Native	Herb	Perennial
Hypericaceae	HYPE	*Hypericum perforatum*	Exotic	Herb	Perennial
Liliaceae	ALSA	*Allium sanbornii*	Native	Herb	Perennial
Liliaceae	CATO	*Calochortus tolmiei*	Native	Herb	Perennial
Liliaceae	CHPO	*Chlorogalum pomeridianum*	Native	Herb	Perennial
Liliaceae	DIMU	*Dichelostemma multiflorum*	Native	Herb	Perennial
Liliaceae	ODHA	*Odontostomum hartwegii*	Native	Herb	Perennial
Linaceae	HEMI	*Hesperolinon micranthum*	Native	Herb	Annual
Onagraceae	EPBR	*Epilobium brachycarpum*	Native	Herb	Annual
Onagraceae	EPFO	*Epilobium foliosum*	Native	Herb	Annual
Orchidaceae	PITR	*Piperia transversa*	Native	Herb	Perennial
Pinaceae	PIAT	*Pinus attenuata*	Native	Tree	Perennial
Pinaceae	PISA	*Pinus sabiniana*	Native	Tree	Perennial
Poaceae	ACLE	*Achnatherum lemmonii*	Native	Graminoid	Perennial
Poaceae	AICA	*Aira caryophyllea*	Exotic	Graminoid	Annual
Poaceae	BRMA	*Bromus madritensis* ssp. *rubens*	Exotic	Graminoid	Annual
Poaceae	BRMI	*Briza minor*	Exotic	Graminoid	Annual
Poaceae	ELEL	*Elymus elymoides*	Native	Graminoid	Perennial
Poaceae	GAVE	*Gastridium ventricosum*	Exotic	Graminoid	Annual
Poaceae	MECA	*Melica californica*	Native	Graminoid	Perennial
Poaceae	POMO	*Polypogon monspeliensis*	Exotic	Graminoid	Annual
Poaceae	VUBR	*Vulpia bromoides*	Exotic	Graminoid	Annual
Poaceae	VUMI	*Vulpia microstachys*	Native	Graminoid	Annual
Poaceae	VUMY	*Vulpia myuros*	Exotic	Graminoid	Annual
Polemoniaceae	COHE	*Collomia heterophylla*	Native	Herb	Annual
Polygalaceae	POCO	*Polygala cornuta*	Native	Herb	Perennial
Primulaceae	DOHE	*Dodecatheon hendersonii*	Native	Herb	Perennial
Rhamnaceae	CELE	*Ceanothus lemmonii*	Native	Shrub	Perennial
Rosaceae	ADFA	*Adenostoma fasciculatum*	Native	Shrub	Perennial
Rosaceae	HEAR	*Heteromeles arbutifolia*	Native	Shrub	Perennial
Rubiaceae	GAAP	*Galium aparine*	Native	Herb	Annual
Rubiaceae	GABO	*Galium bolanderi*	Native	Herb	Perennial
Rubiaceae	GAPA	*Galium parisiense*	Exotic	Herb	Annual
Rubiaceae	GAPO	*Galium porrigens*	Native	Herb	Perennial
Santalaceae	COUM	*Comandra umbellata ssp. californica*	Native	Shrub	Perennial
Scrophulariaceae	PEDE	*Pedicularis densiflora*	Native	Herb	Perennial
Solanaceae	SOPA	*Solanum parishii*	Native	Shrub	Perennial
Sterculiaceae	FRCA	*Fremontodendron californicum*	Native	Shrub	Perennial

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Authors' contributions
JK, EE and JG conceived of the project idea and procured funding to support the work. AJ and JK analyzed the data, interpreted the findings, and wrote the major portions of the manuscript. All authors read and reviewed earlier drafts of the manuscript and approved the final version.

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