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CASE STUDY

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Overstory retention in a managed mixed-conifer stand limits cheatgrass invasion after wildfire

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Abstract

Background Silvicultural treatments that modify forest structure and reduce fuel loads can help mitigate future wildfire effects, but treatment efficacy declines over time. In 2021, we remeasured a southern Sierra Nevada mixed conifer forest 13 years after prescribed fire, mastication, and surface-fuel pull-back treatments to assess changes in forest structure and fuels. One month after our remeasurement, the 2021 French Wildfire burned across the study site, providing a serendipitous opportunity for additional remeasurements to investigate wildfire interactions with fuel treatments, where data from original and 13-year posttreatment forest characteristics exist. Here, we report on changes in forest and fuel structure and understory plant composition 3 years after wildfire and relate wildfire outcomes to the legacy of silvicultural treatments.

Results Wildfire induced large declines in the live overstory biomass for control (47%) and prescribed fire plots (32%) though remotely sensed burn severity was lower in treated plots relative to the control. Downed woody fuels and duff were consumed equivalently in both control and treated plots, ranging from 24 to 99% consumption. Grass loading increased 78-fold in control plots and 22-fold in prescribed fire plots after wildfire, largely driven by invasive cheatgrass, which comprised 79% to 99% of grass cover. However, overstory canopy cover was negatively correlated with cheatgrass loadings ($R^2 = 0.81$) and cover ($R^2 = 0.84$).

Conclusions Prescribed fire treatments 13 years prior to the wildfire reduced wildfire effects and mitigated cheatgrass invasion where intervening drought and bark beetle outbreak had not caused high overstory mortality. In contrast, where tree mortality reduced canopy cover before wildfire, cheatgrass biomass increased to dominate the herbaceous layer. The dramatic shift in understory composition and loadings may lead to increased fire frequency and further loss of native vegetation. Cheatgrass invasions after wildfire in low-elevation, mixed conifer forests have the potential to shift fire frequencies and increase the risk of forest conversion toward alternative stable states. Interventions to increase resilience to compounding disturbances may be necessary to mitigate cheatgrass invasion, including prescribed fire and restoration of forest cover where it has been degraded by disturbances.

Keywords Mixed conifer, Cheatgrass, Sierra Nevada, *Bromus tectorum*, Reburn, Prescribed fire, Ponderosa pine, Fire Behavior Assessment Team, Mastication, Thinning

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Resumen

Antecedentes Los tratamientos silvícolas que modifican la estructura forestal y reducen la carga de combustible, pueden ayudar a mitigar los efectos de futuros incendios de vegetación, aunque la eficiencia de estos tratamientos declina con el tiempo. En 2021, remedimos un bosque de coníferas en Nevada después de 13 años de tratamientos de quema prescripta, de triturado de la biomasa superficial, y de extracción (retiro) del combustible superficial, para determinar los cambios en la estructura forestal y en los combustibles. Un mes después de nuestra remedición, el denominado Incendio Francés del 2021, quemó el sitio de estudio, lo que proveyó de una oportunidad fortuita para remedir nuevamente el sitio para investigar las interacciones con el legado de los tratamientos anteriores, en los cuales se tenían los datos originales de estructura y carga de combustible y también de los tratamientos luego de 13 años de realizados. En este trabajo, reportamos los cambios en la estructura forestal y de los combustibles, y en la composición de las especies del sotobosque 3 años después del incendio, y relacionamos los efectos de este incendio con el legado dejado por los tratamientos silvícolas.

Resultados El incendio produjo grandes disminuciones en la biomasa viva del dosel superior del bosque, tanto en el control (47%), como en las parcelas tratadas con quemas prescriptas (32%), y la severidad, registrada mediante sensores remotos, fue menor en parcelas tratadas en relación con las del control. El combustible leñoso superficial y el mantillo de hojarasca fueron consumidos de manera equivalente tanto en las parcelas tratadas como en las parcelas control, en un rango de consumo que varió entre el 24 y el 99%. La carga de biomasa de pastos se incrementó 78 veces en las parcelas control y 22 veces en las tratadas luego del incendio, mayoritariamente debido al pasto invasor cheatgrass (Bromus tectorum), que comprendió del 79 al 99% de la cobertura de gramíneas. Sin embargo, la cobertura del dosel arbóreo se correlacionó negativamente con la carga (R2=0,81) y cobertura (R2=0,84) de cheatgrass.

Conclusiones Los tratamientos de triturado y quemas prescriptas realizados 13 años antes de incendio redujeron los efectos del fuego y mitigaron la invasión de cheatgrass, mientras que la sequía y un estallido de insectos de la corteza no causaron grandes mortalidades del dosel superior del bosque. Como contraste, cuando la mortalidad redujo la cobertura del dosel antes del incendio, la biomasa del pasto cheatgrass se incrementó hasta dominar el tapiz herbáceo. El cambio dramático en la composición y carga de combustible del tapiz herbáceo del sotobosque puede conducir a un incremento en la frecuencia de los incendios y posterior pérdida de la vegetación nativa. La invasión de cheatgrass luego de incendios en tierras bajas con bosques mixtos de coníferas, tiene el potencial de cambiar las frecuencias de incendios e incrementar el riesgo de conversión hacia estadios alternativos estables. Las intervenciones para incrementar la resiliencia a los disturbios puede ser necesaria para mitigar la invasión de cheatgrass, pudiendo incluirse entre ellas a las quemas prescriptas y la restauración de la cobertura forestal, en aquellos casos en que ésta haya sido degradada por otros disturbios.

Introduction

Fire is a critical ecological process in dry, mixed conifer forests (McLauchlan et al. 2020) and strongly influences species composition, stand structure, and productivity (Sparks et al. 2018). Management actions, such as thinning, mastication, or surface-fuel pull-back from tree boles, can reduce undesirable fire effects, such as large tree mortality (Brodie et al. 2024). However, management actions may also have unintended negative consequences, such as when treatments enable invasion by undesirable species (Dodson and Fiedler 2006; Merriam et al. 2006), increase surface fuels (e.g., mastication, Reiner et al. 2009), or cause undesirable changes in overstory structure (Collins et al. 2014). Interactions between disturbances may compound these effects by reducing canopy cover (Brodie et al. 2024), inducing changes in vegetation composition (Phillips et al. 2024), or further accelerating biological invasion (Reilly et al. 2020). One critical and underexplored consequence of fuel treatments and wildfire interactions is their potential to facilitate the invasion of invasive grasses, such as the annual grass cheatgrass (*Bromus tectorum* L.), a problematic invader in western North American ecosystems (Balch et al. 2013).

Invasion of mixed conifer forests by cheatgrass

Cheatgrass is a fire-adapted annual grass that has invaded much of the Great Basin in Western North America and in recent decades has advanced into mixed conifer ecosystems (Peeler and Smithwick 2018; Kerns et al. 2020) following favorable climates, grazing by non-native herbivores, and disturbances that open canopy cover (Parker et al. 2006; Pilliod et al. 2017; Kerns and Day 2024). Cheatgrass was introduced to North America in the 1800s and, in many ecosystems, has successfully outcompeted native vegetation owing to early germination, prolific seeding, and by strongly competing for water during wet years (Mack and Pyke 1983; Novak and Mack 2001; Chambers et al. 2007; Pilliod et al. 2017). The early germination and senescence of cheatgrass, relative to most native vegetation, create a dry, continuous cover of fuels early in the fire season (Davies and Nafus 2013) and a commensurate shortening of the fire return interval (Bradley et al. 2018). After fire, cheatgrass often increases in abundance, relative to native vegetation, due to high propagule pressure from seed banking and prolific seeding and the ability to compete effectively in open environments (Keeley and McGinnis 2007; Peeler and Smithwick 2018; Donovan et al. 2023). Whereas cheatgrass has been a problematic species in sagebrush steppe, its recent advances in disturbed mixed conifer ecosystems may represent a new, troublesome front in its wide-ranging impacts in forest ecosystems (e.g., Nagaraja et al. 2024). Thus, understanding the conditions leading to cheatgrass invasion in mixed conifer ecosystems is critical to predicting the extent of future cheatgrass invasions and its consequences on invaded forest dynamics.

Silvicultural treatments such as prescribed fire or thinning are frequently used in mixed conifer ecosystems to manage fuel structure and reduce risks of high-severity wildfire and promoting tree resistance to bark beetle mortality (Hood et al. 2015; Bernal et al. 2023; Brodie et al. 2024). However, these treatments may also facilitate cheatgrass dominance by removing overstory cover and opening gaps in understory vegetation (Dodson and Fiedler 2006; Sutherland and Nelson 2010). For example, prescribed fire and low-intensity wildfire are unlikely to reach temperatures sufficient to kill cheatgrass seedbanks (e.g., > 120 °C for several minutes; Keeley and McGinnis 2007) may instead increase habitat openness by consuming litter and duff fuels (Pierson and Mack 1990) and enhance post-fire growth of newly germinating cheatgrass seed (Fenesi et al. 2016). McGlone et al. (2009) attributed a 90-fold increase in cheatgrass cover in a ponderosa pine forest to the combination of prescribed fire, thinning, grazing, and drought which reduced overstory cover and opened gaps in the understory for existing propagules to exploit. Therefore, understanding the conditions under which silvicultural treatments promote cheatgrass invasion is important for minimizing unintended consequences of treatments on understory communities.

Research aims

The serendipitous burning of the Red Mountain fuel treatment area (Reiner et al. 2009; Birch et al. 2023b) by the 2021 French Wildfire provided an opportunity to assess how wildfire effects and cheatgrass presence are moderated by 13-year-old fuel treatments. Between the time of treatment and burning in the 2021 French Wildfire (2008–2021), the study site had experienced concurrent drought and bark beetle outbreaks which caused widespread overstory mortality, opening of the canopy, and fuel accumulation, though these effects were greatly reduced in the areas treated with prescribed fire, but not mastication alone (Birch et al. 2023b). Here, we report on the interactions between silvicultural treatments and fire effects as measured 3 years post-wildfire (Fig. 1).

Methods

Study area and site history

The Red Mountain fuel treatment area is a *Pinus ponderosa* Douglas ex Lawson & C. Lawson (ponderosa

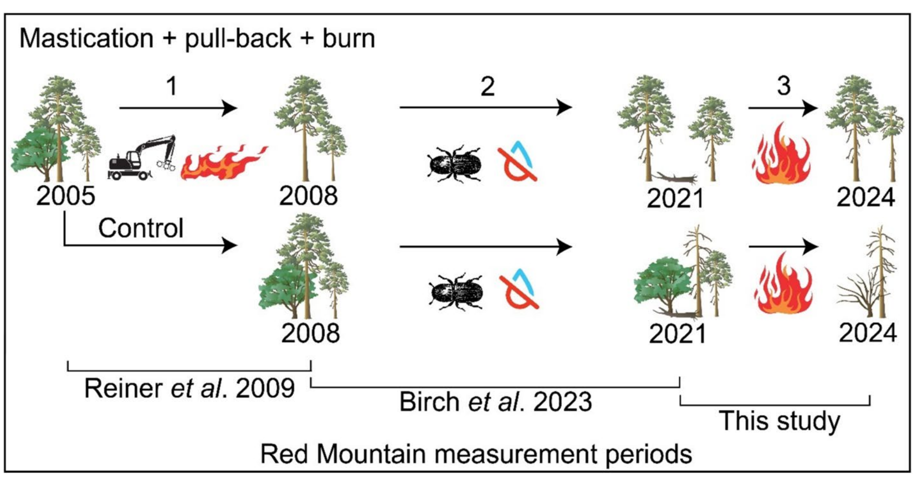

Fig. 1 Conceptual diagram of the study design and site history of the Red Mountain study site, California, USA. The site was established in 2005, treated in 2007 (1), and remeasured in 2008 (Reiner et al. 2009). Bark beetle and drought disturbances (2) between 2008 and 2021 caused substantial forest changes including fuel accumulation (Birch et al. 2023b). The 2021 French Wildfire (3) burned across a portion of the study site, enabling a post-wildfire remeasurement to assess treatment + wildfire interactions (this study)

pine)-dominated mixed conifer forest located in California, USA (35.65° N, −118.61° W) and managed by the US Forest Service Sequoia National Forest. Nondominant tree species include *Calocedrus decurrens* (Torrey) Florin (incense cedar), *Quercus kelloggii* Newberry (California black oak), and *Quercus chrysolepis* Liebmann (canyon live oak). Most of the forest regenerated naturally or was planted (*P. ponderosa*) following the 1970 French Wildfire, with isolated old-growth (150–250+ years) individuals in the study area (Birch et al. 2023b, 2023c). Mean annual temperatures (1981–2010) were 10.5 °C ± 6.5 °C (*SD*; 1981–2010) with mean annual precipitation of 1069 mm (284-mm snow, Régnière and St-Amant 2007). Cattle grazing occurred in the area annually from May 1 to August 31.

The Red Mountain fuel treatment area was originally established by Reiner et al. (2009) as a randomized complete block design to assess silvicultural treatment impacts on forest and fuel structure. The study had treatments assigned randomly to four-plot groupings, split evenly across four blocks within the Red Mountain fuel treatment area in the Sequoia National Forest, CA, USA. Each experimental block existed in a separate landscape position with homogenous within-block topography. Plots were originally established and measured in 2005, treated in 2006–2007, and remeasured in 2008 (Reiner et al. 2009) with a subsequent remeasurement in May and June of 2021 (Birch et al. 2023b). Treatments included a control (C), mastication (M), mastication and prescribed burn (MB), and mastication with a pull-back of surface fuels and subsequent prescribed burn (MPB). The mastication targeted *Abies* sp. and *Calocedrus* sp. < 38 cm in diameter at breast height (DBH) with a stand target density of 61 trees ha^{-1}. Plots treated as MPB had masticated material, and the forest floor raked away from the live stems to each tree's dripline to prevent consumption of fuels adjacent to sensitive cambial tissue and fine roots. The prescribed burn was conducted on Dec 5 and 6, 2007, using spot and strip-firing as described in Reiner et al. (2009).

A *Dendroctonus brevicomis* and *Dendroctonus ponderosae* outbreak occurred between 2008 and 2021 and, along with severe drought, resulted in widespread mortality of *P. ponderosa* at the site. Notably, overstory mortality was greatly reduced in prescribed fire treatments, relative to unburned mastication and control treatments (Birch et al. 2023b). In August of 2021, the French Wildfire burned across one of the four experimental blocks of the Red Mountain fuel treatment area (Fig. 2), providing an opportunity to study interactions between wildfire and previous fuel manipulation treatments.

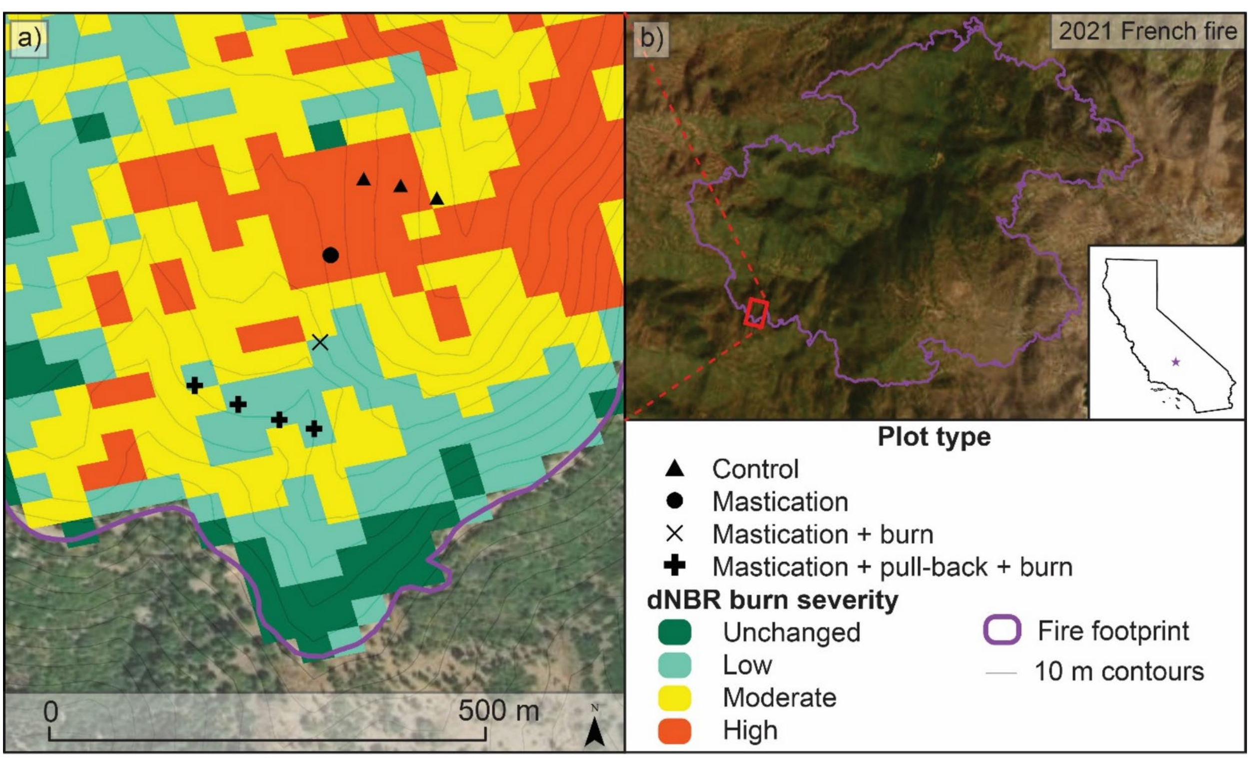

Fig. 2 Map of the study area with the 2021 French Wildfire burn perimeter. Continuous delta normalized burn severity (dNBR) is plotted as burn severity categories as defined by Miller and Thode (2007) using 30 × 30 m LANDSAT imagery

Remeasurement after wildfire

In 2024, we remeasured nine plots burned by the 2021 French Wildfire to identify changes in forest composition, structure, and fuel loadings. We did not remeasure plots that did not burn in the 2021 French Wildfire, as they were in separate experimental blocks and represented drier, lower elevation landforms. Unless otherwise noted, our remeasurement protocols in 2024 were identical to those used 2005–2008 (Reiner et al. 2009) and 2021 (Birch et al. 2023b) and follow the USFS Fire Behavior Assessment Team protocols (Fire Behavior Assessment Team 2022; Appendix S1). Our sample size for this study included three C and four MPB plots (Fig. 2) as well as one M and one MB plots that were excluded from analyses due to a lack of replication. All plots used in this study were located within a single experimental block of the original study.

Forest and fuel measurements

Within each variable radius plot, we identified all trees to species and measured diameter at breast height (DBH), height, and height to live crown (Appendix S1). For standing dead trees (hereafter "snags"), we recorded DBH, height, decay classification, and top diameter to assist with estimating mass (Appendix S1). We used three 15.24-m transects (hereafter, Brown's transects; Brown 1974) originating distal to plot center in each plot for measuring downed woody fuels (1-h to 1000-h time-lag fuels) with the planar intercept method and as the centerline of a belt transect to measure surface vegetation (Fire Behavior Assessment Team 2022). We measured tree seedlings (< 1.0-cm DBH), shrubs, grass, and forbs along the 15.24-m belt transects. We estimated cover and mean height and classified the bulk density and morphology for each species using the shrub and grass photoseries in Burgan and Rothermel (1984), with the modification of using shrub photoseries for seedlings and grass photoseries for forbs (Fire Behavior Assessment Team 2022). We used the Forest Vegetation Simulator (Dixon 2002) to estimate canopy cover across all measurement periods using stand composition and structural data from Reiner et al. (2009) and Birch et al. (2023a, b, c). We assessed remotely sensed burn severity of the 2021 French Wildfire by sourcing the delta normalized burn ratio (dNBR) from the Monitoring Trends in Burn Severity database (Key and Benson 2006; Eidenshink et al. 2007). The dNBR is a widely used metric for assessing changes in vegetation reflectance after fire and is typically assessed at 30 × 30 m scales using LANDSAT imagery (Miller and Thode 2007).

Biomass estimations

We estimated the aboveground biomass of living trees using species-specific allometric and component biomass equations (Jenkins et al. 2003; Chojnacky et al. 2013). We estimated snag mass using species-specific equations (Harmon et al. 2008; Cousins et al. 2015) and modeled snags of decay class ≥ 3 as conic frustums using the volume to estimate snag biomass with species-specific equations (Harmon et al. 2008, sensu Birch et al. 2023a). For tree seedlings, shrubs, grasses, and forbs, we used bulk density, average cover, and height to estimate biomass for each type of vegetation and averaged mass across the three transects by plot (Burgan and Rothermel 1984; Fire Behavior Assessment Team 2022). We calculated mass of 1-h to 1000-h woody fuels, litter, and duff using equations of Van Wagtendonk et al. (1998). We calculated fuel loadings (mass per unit area) by extrapolating mass estimates for each type of fuel to the nearest hectare.

Statistical analyses

We conducted all statistical analyses in R 4.2.1 using the graphical user interface R Studio 2023.06.02 (R Studio Team 2020; R Core Team 2021). We generated graphs using ggplot 3.5.1, ggpubr 0.6.0, and the viridis 0.6.5 R packages (Wickham 2016; Kassambara 2023; Garnier et al. 2024). To test for significant differences in wildfire effects on forest and fuel structure between treatments, we used an analysis of variance (ANOVA) and a before-after-control-impact (BACI) approach of the form:

$$\text{Dependent variable} \sim \text{time} + \text{treatment} + (\text{time} \times \text{treatment})$$

Significant interaction terms indicate that wildfire effects were differentially influenced by treatments. For each model, we visually checked residuals for normality and heteroscedasticity and verified that all models met statistical assumptions. We used an ANOVA to test for differences in burn severity between treatments in 2024. We do not account for a blocking factor as our 2024 measurements were entirely within a single experimental block of the original four-block design. We used linear models in base R to test for significant linear relationships between cheatgrass loadings, height, and overstory canopy cover. Because cover is a proportion bounded between 0 and 1, we used a beta regression in the betareg 3.2–1 package to assess the relationship between cheatgrass and overstory canopy cover (Cribari-Neto and Zeileis 2010). We only report values for C ($n = 3$) and MPB ($n = 4$) plots because the M and MB plots had insufficient replication ($n = 1$) in the burned study area. We report change in forest and fuel loadings in mean absolute value (Mg ha^{-1}) by treatment and as relative change in fuels (%). For relative change, we report median value, by treatment, as it is less sensitive to extreme changes in values relative to the mean. We only calculate relative change for types of fuels which had pre-fire loadings > 0 to avoid dividing by zero.

Results

Forest structure and tree mortality

The 2021 French Wildfire induced large absolute and relative shifts in forest structure across both C and MPB treatments, with smaller magnitude effects in MPB treatments, relative to C (Table 1). Remotely sensed burn severity (dNBR) was lower in MPB treatments (138 ± 18 SE), relative to C treatments (396 ± 65 SE; $P=0.007$). There were no significant interaction effects between treatment and time for any forest structure variables, indicating that treatments did not significantly alter fire effects on forest structure (Appendix S2 for full model output). Live tree biomass in the C treatment declined by a median of 47% between 2021 and 2024, whereas MPB treatments experienced a median decline of 32% (Fig. 3, Table 1, Table S1). Tree foliage in the C treatment declined by 87% between 2021 and 2024, whereas MPB treatments experienced a decline of 32% (Fig. 3, Table 1). Snag loadings in the C treatment declined by 51% between 2021 and 2024, whereas MPB treatments experienced a decline of 89% (Fig. 3, Table 1). There were no significant differences in live tree biomass, foliage, or snag loadings between C and MPB treatments in 2024. Live tree density declined by 1213 trees ha^{-1} in C and 76 trees ha^{-1} in MPB treatments (Table 1). Wildfire caused median upward shifts of 3 m in height to live crown in both C and MPB treatments.

Seedling, shrub, and herbaceous vegetation

Tree seedlings declined in abundance in C treatments by 100% and by 76% in MPB treatments (Table S1; Fig. 3). We detected 4 *P. ponderosa* seedlings in a single MPB plot (54 seedlings ha^{-1}) and 13 *Q. kelloggii* seedlings in a single C plot (178 seedlings ha^{-1}), with all other plots having no tree seedlings in vegetation transects. Shrub loadings decreased by 97% in C treatments and by 53% in MPB treatments. Forb loadings increased markedly in both C treatments (432%) and MPB treatments (191%, Table S1, Fig. 3).

Grass loadings increased markedly in both C treatments (7853%) and MPB treatments (2277%, Fig. 4, Table 1), relative to 2021. Increases in grass loadings were overwhelmingly from cheatgrass, which comprised 79 ± 11% of grass loadings in C and 99 ± 1% of loadings in MPB. Cover, height, and loadings of cheatgrass were greater in 2024, relative to 2021 (Fig. 5, Table S2, Appendix S2), though no significant differences existed between C and MPB treatments in 2024. Overstory canopy cover (%) in 2024 was negatively associated with cheatgrass cover ($P=0.005$, Fig. 5d) and biomass ($P<0.001$, Fig. 5e), but had no significant relationship with cheatgrass height ($P=0.144$, Fig. 5f).

Downed woody fuels, litter, and duff

Each type of downed woody fuel loading (1 to 1000 h) was reduced in 2024, relative to 2021 in both C and

Table 1 Mean forest structural values and fuel loadings (Mg ha^{-1}) ± 1 SE for 2021 and 2024 for control (C) and mastication + pull-back + burn (MPB) treatments in California, USA. Values reported for 2021 were taken before the 2021 French Wildfire. We used an ANOVA to test for significant differences ($P<0.05$) between C and MPB treatments in 2024 and denote significantly different values with an asterisk ("*")

Variable	C		MPB	
	2021	2024	2021	2024
Live trees per hectare	1255.6 ± 874.8	41.1 ± 24.6	219.2 ± 73.7	143.2 ± 95.9
Canopy cover (%)	69.3 ± 16.1	44.0 ± 28.2	71.0 ± 7.5	62.5 ± 9.5
Diameter at breast height (cm)	21.9 ± 15.0	15.0 ± 13.1	46.2 ± 2.8	45.6 ± 2.7
Live tree height (m)	8.2 ± 4.6	7.4 ± 3.8*	20.2 ± 0.8	19.9 ± 0.5*
Height to live crown (m)	1.3 ± 1.3	4.0 ± 0.3*	5.8 ± 1.1	9.3 ± 0.9*
	Fuel loadings (Mg ha^{-1})			
Live tree	42.03 ± 9.62	27.14 ± 15.20	188.81 ± 53.57	146.28 ± 72.51
Snag	74.96 ± 15.30	35.26 ± 2.35	52.58 ± 30.69	29.85 ± 16.96
Shrub	0.04 ± 0.10	0.00 ± 0.00	0.01 ± 0.00	0.02 ± 0.02
Seedling	0.02 ± 0.00	0.03 ± 0.02	0.00 ± 0.00	0.00 ± 0.00
Forbs	0.01 ± 0.00	0.07 ± 0.03	0.03 ± 0.01	0.09 ± 0.02
Grass	0.02 ± 0.01	1.66 ± 0.64	0.02 ± 0.01	0.51 ± 0.25
1000-h fuels	104.44 ± 72.43	9.74 ± 3.99	32.31 ± 6.87	1.77 ± 1.45
100-h fuels	7.83 ± 2.59	2.17 ± 1.11	4.62 ± 1.79	2.99 ± 2.07
10-h fuels	2.05 ± 0.53	1.51 ± 0.21	3.69 ± 1.36	1.07 ± 0.61
1-h fuels	0.39 ± 0.07	0.20 ± 0.11	0.24 ± 0.08	0.02 ± 0.01
Litter	0.68 ± 0.26	1.56 ± 0.30*	1.17 ± 0.49	3.80 ± 0.38*
Duff	37.50 ± 7.31	3.34 ± 1.64	28.36 ± 5.31	14.58 ± 5.70

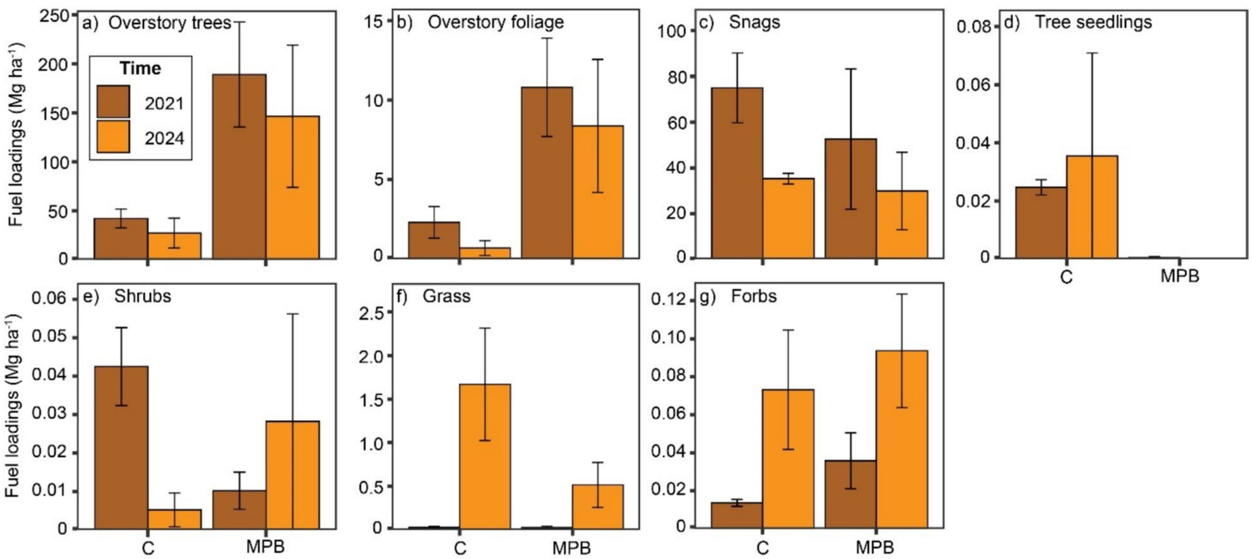

Fig. 3 Mean ± 1 SE change in loadings (Mg ha^{-1}) by type of fuel and between control (C) and mastication + pull-back + burn (MPB) treatments between 2021 and 2024 in California, USA. **a** Overstory trees. **b** Overstory foliage. **c** Snags. **d** Understory tree seedlings. **e** Shrubs. **f** Grass. **g** Forbs. There were no significant differences between C and MPB treatments in 2024 for the types of fuel plotted. See Birch et al. (2023b) for a comprehensive description of differences between treatments in 2021

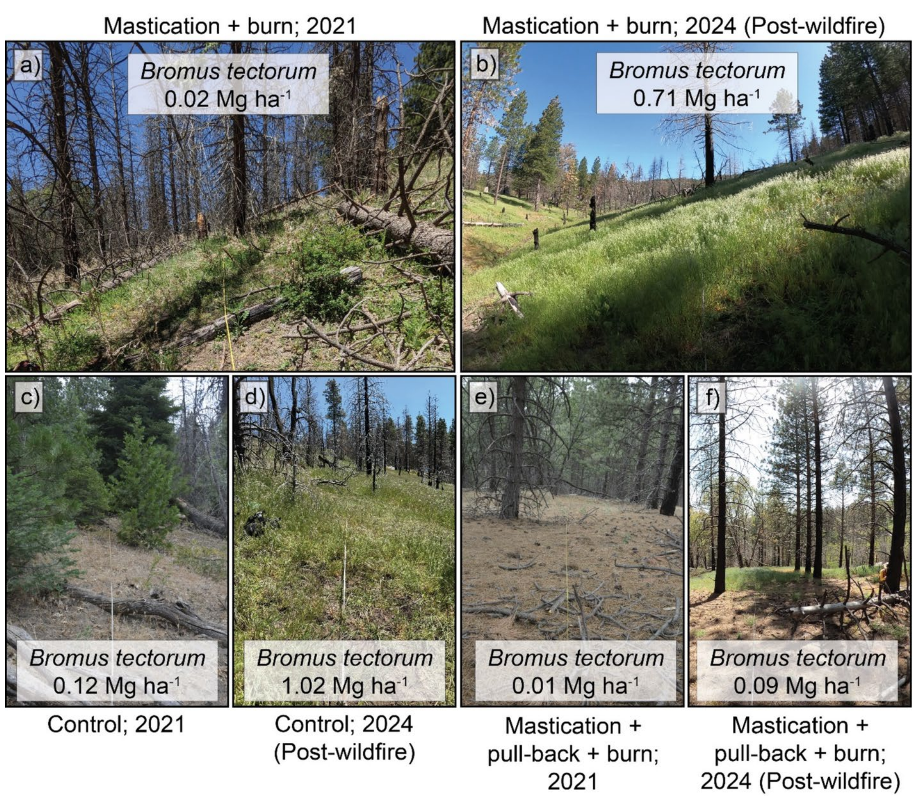

Fig. 4 Paired pre-wildfire and post-wildfire images of plots from the Red Mountain site, California, USA. **a** and **b** Mastication + burn plot. **c** and **d** Control (untreated) plot. **e** and **f** Mastication + pull-back + burn plot. Cheatgrass (*Bromus tectorum*) loadings (Mg ha^{-1}) are described in each photo

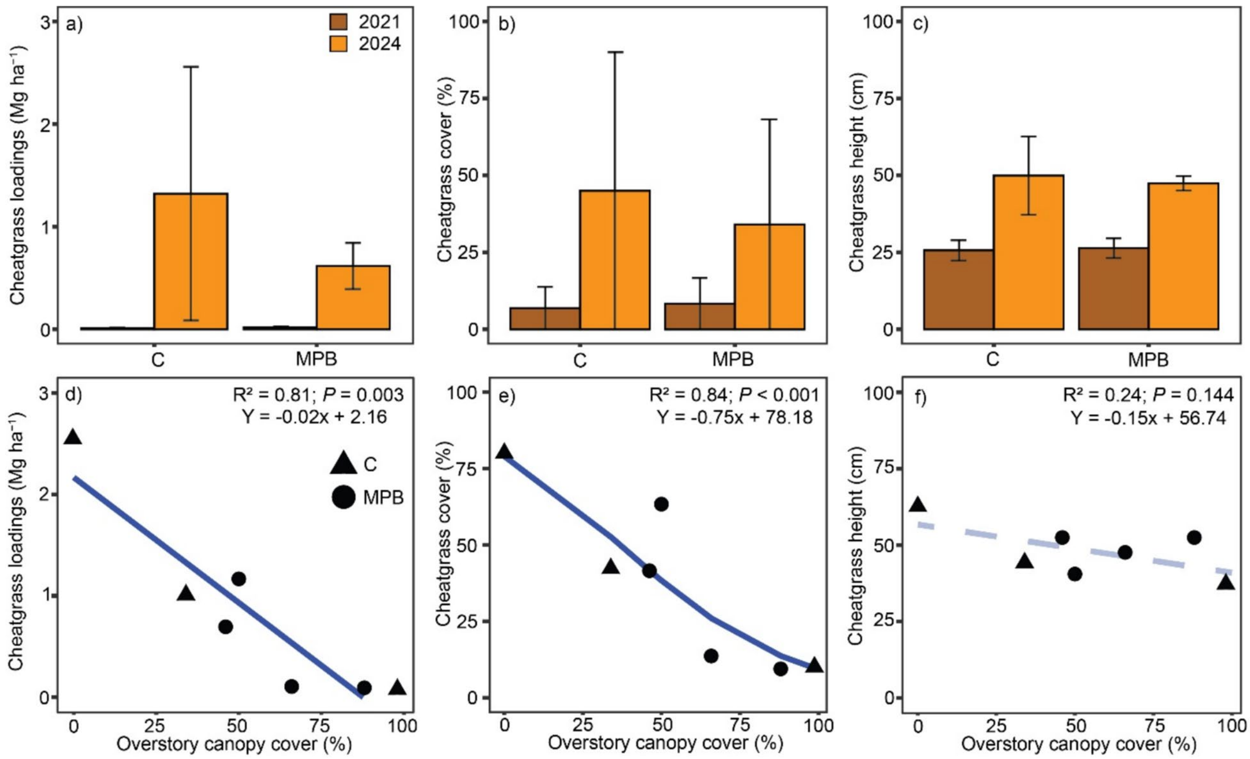

Fig. 5 Cheatgrass characteristics between control (C) and mastication + pull-back + burn (MPB) treatments between 2021 and 2024 in California, USA. Cheatgrass (*Bromus tectorum*) **a** loadings (Mg ha^{-1}), **b** cover (%), **c** height (cm) in 2021 and 2024, and the relationship with overstory canopy cover (**d**, **e**, **f**) in 2024. There were no significant differences in cheatgrass characteristics between C and MPB treatments in 2024

MPB treatments (Appendix S1: Fig. S1). There were no significant differences in downed woody fuels between C and MPB treatments in 2024. Litter loadings in 2024 increased by 174% in C treatments and 318% in MPB treatments, relative to 2021, and were significantly elevated ($P = 0.007$) in MPB, relative to C treatments (Table S1, Appendix S1 Fig. S1). Duff loadings decreased by 94% in C treatments and 56% in MPB treatments, relative to 2021 (Table 1, Fig. 4), and were not significantly different between treatments in 2024.

Discussion

Legacy-prescribed fire treatments reduced tree mortality and fuel consumption during wildfire

Despite difficulty in assigning significance due to the limited sample size, the MPB treatments had lower overstory mortality and fuel consumption than the C treatments, indicating more favorable fire effects. Prior to the 2021 French Wildfire, the plots treated 13 years prior with prescribed fire had lower overstory mortality, elevated canopies, and lower duff fuels (Birch et al. 2023b), and these differences in stand structure and fuel loadings were likely contributors to differential wildfire effects between treatments in 2024 (Larson et al. 2022). Whereas other studies have identified prescribed fire as effective at reducing wildfire severity (Walker et al. 2018; Cansler et al. 2022; Brodie et al. 2024), the Red Mountain site had reduced treatment efficacy owing to increased fuels caused by compounding bark beetle and drought disturbances that resulted in widespread tree mortality in the intervening period (e.g., 2007–2021; Birch et al. 2023b). Whereas low replication (e.g., $n = 7$) and limited spatial coverage constrain both statistical inference and geographic generalization, the overall trends suggest that fire effects associated with MPB treatments are typically more desirable than those observed in the C treatments.

The treatments at the Red Mountain site may have long-term legacies by promoting differential tree recruitment and species assemblages on the landscape. Tree recruitment was minimal in both MPB and C plots in 2024, except for vigorous post-fire sprouting of *Q. kelloggii* and *Q. chrysolepis*, concentrated around *Quercus* spp. which had aboveground stem mortality (i.e., "top-killed") due to the 2021 French Wildfire. The greater pre-fire abundance of *Quercus* spp. in C plots may aid in the post-fire regeneration of new cohorts regenerating from surviving pre-fire root crowns (Hammett et al. 2017). In contrast, *P. ponderosa* was the only species regenerating in the MPB plots; this species may fail to reach a sufficient size for resisting fire if future fires occur on short return intervals (e.g., a "fire trap"; Peeler and Smithwick 2018; Hoffmann et al. 2020). Because low-severity fires — whether natural or prescribed — can enhance resistance to future bark beetle attacks (Hood et al. 2015, 2016; Birch et al. 2023b), mature *P. ponderosa* may be able to persist on the landscape in areas experiencing low to moderate severity fire. In contrast, non-conifer species (e.g., *Quercus* sp. or *Calocedrus decurrens*) and invasive grasses may compete more effectively in unburned refugia where *Pinus* spp. are vulnerable to bark beetle outbreaks or in areas that burn under high severity (Dudney et al. 2021; Smith et al. 2023).

Wildfire-facilitated dominance of cheatgrass

The most dramatic change after wildfire in our study site was the shift in understory vegetation from 2005 (no cheatgrass, Reiner et al. 2009) to a near-complete dominance of the invasive grass in C treatments in 2024, highlighting a gradual invasion in the past 20 years that was fully catalyzed by the 2021 French Wildfire. Cattle grazing at the site may have facilitated the initial invasion of cheatgrass into the site by transporting seeds, reducing native plant cover, and by disturbing soil through trampling (Young et al. 1987; Leffler et al. 2016). However, grazing was present in the site prior to the 2021 French Wildfire when cheatgrass maintained relatively low cover (1–21% cover, Birch et al. 2023b) — suggesting that grazing was not a primary cause of the change in cheatgrass dominance 2021–2024.

Cheatgrass was present pre-fire in 2021, but the surge in cheatgrass loadings and cover 2021–2024 represents a dramatic change in fuel continuity and a decline in native vegetation at the site (Fig. 4). The bark beetle and drought-induced overstory mortality of 2008–2021 opened the canopy, which likely facilitated the gradual invasion of cheatgrass over time (Peeler and Smithwick 2018; Dudney et al. 2021; Birch et al. 2023b). These results are consistent with other studies in forest and chaparral finding a negative correlation between invasive species cover and overstory cover (Keely et al. 2003, Dodson and Fiedler 2006; Merriam et al. 2006). Additionally, strongly above-average precipitation in 2023 (133%–212% of average; DeFlorio et al. 2024) may have facilitated cheatgrass invasion and reduced competition with native plants, which are generally weaker competitors during wet years, relative to cheatgrass (Prevéy and Seastedt 2015; Pilliod et al. 2017). Whereas future climates are generally expected to be hotter and drier, increased variability may also include above-average precipitation events from atmospheric rivers (Gershunov et al. 2019), such as those during the 2023 water year. It is uncertain if cheatgrass dominance at the site will persist at high levels or if a sufficient period without disturbance may allow native communities and the overstory to re-establish and shift understory vegetation toward conditions similar to before the 2021 French Wildfire.

How problematic is increased fire frequency from cheatgrass in mixed conifer forests? Despite large increases in area burned, western forests still present with a 44–88% fire deficit, relative to pre-1880 (Parks et al. 2025), and increased fire frequency in cheatgrass-invaded ecosystems will likely result in increases in area burned. However, if cheatgrass induces similar increases in fire frequency in mixed conifer forests as it has in other invaded ecosystems, the resulting fire return intervals (e.g., 3–5 years; Stewart and Hull 1949; Fusco et al. 2019; Kerns et al. 2020) would be much shorter than the natural range of variability for mixed conifer ecosystems (7–16 years fire return interval; Safford and Stevens 2017). Further studies are needed to identify how cheatgrass invasion alters fire behavior, burn severity, and resulting long-term ecosystem consequences in mixed conifer ecosystems. As wildfire and concomitant disturbances (e.g., drought or bark beetles) continue to cause overstory mortality and open the canopies of mixed conifer forests, it is likely that we will see continued expansion of cheatgrass and subsequent alteration of fire frequency and effects.

Management implications and conclusions

Our results suggest that management actions that promote and maintain overstory cover may indirectly reduce cheatgrass dominance by minimizing favorable conditions for cheatgrass. In a previous study at this experimental site, Birch et al. (2023b) found that prescribed fire minimized overstory mortality from fire and bark beetles and may be an appropriate tool to minimize canopy gaps while providing for fuel reductions. High severity fire is likely to favor forest structural characteristics that promote cheatgrass persistence, whereas low severity prescribed or wildfire may maintain sufficient overstory cover so as to limit favorable cheatgrass habitat. In dry, low-elevation forests, reducing impacts of invasive annual grasses would require that land management strike a balance between maintaining wildfire-resistant forests and fuel structures and minimizing opening canopy gaps into which cheatgrass may readily invade and outcompete local vegetation (Peeler and Smithwick 2018). Additional grass-focused treatments, including herbicide applications and annual monitoring, may be needed to fully eradicate cheatgrass or reduce its prevalence in mixed-conifer forests.

Positive-feedback loops between invasive annual grasses (including cheatgrass) and fire frequency are very well-supported by studies in dry forest and shrubland ecosystems (Balch et al. 2013; Peeler and Smithwick 2018; Kerns et al. 2020 and citations therein), but cheatgrass is equally capable of invading ecosystems in the absence of fire provided that moisture, light, and space requirements are satisfied (Smith et al. 2023). Restoration and monitoring of native vegetation and maintaining large diameter overstory trees may be desirable to reduce the risk of high-severity wildfire and preempt the conversion of nascent cheatgrass populations into monocultures following disturbance (e.g., bark beetles or wildfire). Cheatgrass increases the homogeneity of fire behavior and consumption (Balch et al. 2013; Harrison et al. 2024), which may be undesirable because variation in fire behavior and effects is a natural component of mixed-severity fire regimes (Kolden et al. 2012; Ziegler et al. 2021) and can promote greater landscape species diversity (Meddens et al. 2018; Birch et al. 2025). Therefore, treatments that increase spatial variability of fuels, such as mastication (Reiner et al. 2009) or seeding with competitive native species (Csákvári et al. 2023), may be desirable to counteract monocultures of cheatgrass

Wildfire-facilitated invasion by annual grasses is likely to become more widespread and alter fire regimes in low-elevation mixed conifer forests. In cases where invasive grasses sufficiently shorten fire regimes, it may result in failure of tree recruitment and ultimate type conversion. Despite a limited sample size and a single location, our study suggests that overstory cover may limit cheatgrass invasion in mixed conifer forests. More research is needed across a broader range of forests to understand the long-term dynamics and persistence of post-fire cheatgrass invasions and their potential to alter fire behavior and frequency. Our study joins a larger body of work indicating the continued invasion of low-elevation, post-fire western North American forests by invasive annual grasses and highlights the challenges of managing overstory cover that promotes fire-resilient structure while minimizing cheatgrass invasion.

Abbreviations

DBH	Diameter at breast height (1.37 m)
FBAT	Fire Behavior Assessment Team
M	Mastication
MB	Mastication + burn
MPB	Mastication + pull-back + burn

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-025-00445-5.

Supplementary Material 1: Appendix S1. Table S1. Median relative change (%) by type of fuel between 2021 and 2024 for control (C) and mastication + pull-back + burn (MPB) treatments in California, USA. Table S2. Mean ± 1 SE values of cover (%), height (cm), and loadings (Mg ha^{-1}) of *Bromus tectorum* (cheatgrass) in 2021 and 2024 for control (C) and mastication + pull-back + burn (MPB) treatments in California, USA. Values reported for 2021 were taken before the 2021 French Wildfire. Values correspond with Fig. 5 in the main manuscript file. There were no significant differences in cheatgrass characteristics between C and MPB treatments in 2024. Figure S1 Mean ± 1 SE change in loadings (Mg ha^{-1}) by type of fuel and between control (C) and mastication + pull-back + burn (MPB) treatments between 2021 and 2024 in California, USA. (a) 1-h time-lag fuels. (b) 10-h time-lag fuels. (c) 100-h time-lag fuels. (d) 1000-h time-lag fuels. (e) Litter. (f) Duff. There were significant ($P < 0.05$) differences between treatments in 2024 for litter fuels only (Table 1) and no significant differences for all other types of fuel. See Birch et al. (2023a, b, c) for a comprehensive description of differences between treatments in 2021.

Supplementary Material 2: Appendix S2. Full model output.

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Authors' contributions

JDB and MDB collected the data. JDB and EKB analyzed the data. All authors contributed to the synthesis and read and approved the final manuscript.

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Data availability

Data from this study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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