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Prescribed fire lessens bark beetle impacts despite varied effects on fuels 13 years after mastication and fire in a Sierra Nevada mixed-conifer forest

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ABSTRACT

Mastication, thinning, and prescribed fire can help shift fire-prone forests to a structure and composition more resilient to wildfire, but the ability to evaluate treatment effectiveness requires monitoring forest response to disturbances over time after treatment. In this study, we investigated fuel loadings, forest structure, and tree growth to assess treatment legacies thirteen years after mastication, prescribed fire, and surface fuel pull-back from tree boles in Sierra Nevada mixed-conifer forest. An outbreak of bark beetles between 2011 and 2018 impacted all plots but burned treatments had lower overstory mortality relative to unburned treatments which experienced an 80 % decline in live tree biomass. Tree diameter, canopy density, and surface fuel loadings became similar across all treatments during the 13 year time period. Height to live crown remained elevated in burned treatments relative to the control but had lowered by an average of 1.9 ± 0.3 (SE) m across all treatments. Radial tree growth did not have a sustained response to treatment and was greater in burned treatments for only a single year, 2011, several years post-treatment. Prescribed fire decreased duff mass by 56 % relative to unburned treatments but did not affect forest floor bulk density. Downed woody fuel loadings (1-h – 1000-h) were similar across treatments. The invasive *Bromus tectorum* (cheatgrass) had uniformly high cover across treatments. Whereas treatments were largely ineffective at producing long-term reductions in surface fuel loadings, the enduring reductions in duff loadings and reduced overstory mortality support the long-term utility of prescribed fire. Cumulatively, our results highlight the potential for prescribed fire to reduce overstory mortality and duff loadings in dry mixed-conifer forests, thereby contributing more effectively to fire-resilient characteristics relative to other fuel reduction treatments.

1. Introduction

Silvicultural treatments such as thinning, mastication, or prescribed fire can restore forests to natural ranges of variability and promote resilience to disturbances (Nikinmaa et al., 2020, Long et al., 2018) but may also lead to unexpected negative outcomes such as increased risk of bark beetle attack (Maloney et al., 2008) or invasion by non-native plant species (Keeley, 2006). Such unintended consequences can alter forest structure, fuel loadings, and increase the susceptibility to undesirable fire effects. This in combination with an increasingly variable climate and altered fire regimes may cause undesirable ecosystem changes that exceed the resilience of forests (Germain & Lutz 2020, Miller et al., 2019, Reyer et al., 2015).

Forest management treatments that reduce fuel loadings and introduce spatial heterogeneity (within the stand and landscape scales) may be particularly desirable for promoting forest resilience (Odland et al., 2021) and mitigating undesirable fire effects (Stephens and Moghaddas 2005). Variability in forest structure and composition was historically high in mixed-conifer forests prior to fire suppression, land use change, and criminalization of indigenous burning practices, which together contributed to forest densification and altered fire effects (Ziegler et al., 2021, Collins et al., 2015). These changes, along with climate warming,

Abbreviations: BAF, Basal area factor; DBH, Diameter at breast height (1.37 m); FBAT, Fire Behavior Assessment Team; C, Control; M, Mastication; MB, Mastication + burn; MPB, Mastication + pull-back + burn; SPEI, Standardized precipitation-evapotranspiration index.

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have shifted the historically frequent, mixed-severity wildfires toward fires of greater size and severity (Safford and Stevens 2017, Noss et al., 2006) and increased forest susceptibility to invasive species or beetle outbreak (Kerns et al., 2020, Bentz et al., 2010). For example, high-severity fire or bark beetle infestation can open ecosystems to *Bromus tectorum L.* (cheatgrass) invasion, which can establish a continuous cover of fine fuels and promote shortened fire return intervals (Balch et al., 2013) – a particular concern in forests where it can contribute to ecosystem type conversion to non-forest stable states (Kerns et al., 2020, Peeler et al., 2018).

How fuels accumulate and vary on the landscape after silvicultural treatment has important implications for the long-term ecosystem trajectory and vulnerability to future disturbance. Mechanical treatments like mastication can be effective at altering the physical arrangement of canopy and ladder fuels (Harrod et al., 2009), but may require prescribed fire to reduce surface fuel loadings and promote resilience to wildfires (Knapp et al., 2017). While prescribed fire and mechanical treatments can dramatically reduce canopy and surface fuel loadings by 20 – 90 % in the short term (Reiner et al., 2009, Vaillant et al., 2009, Stephens and Moghaddas 2005), there is greater uncertainty in treatment effects over decadal timeframes. In particular, variable and warming climates may overcome treatment effects (Tarancón et al., 2014) and cause overstory mortality or stable state changes (Hartmann et al., 2022, Allen et al., 2010).

Monitoring forests after silvicultural treatment can help identify and evaluate how additional biotic and abiotic influences contribute to trajectories of change in forest vegetation and fuels, i.e., towards or away from desired conditions. The decadal legacy of treatments is particularly relevant for California dry mixed-conifer forests where historic fire return intervals averaged 11 years, and the enduring legacy of treatments may be sufficient to alter wildfire behavior (Hunter and Robles 2020, Van de Water and Safford 2011, Strom and Fulé 2007). Therefore, we investigated the legacy effects of mastication, prescribed fire, and their combination on (a) forest structure and fuel loadings and their variation, (b) overstory tree growth, and (c) invasive species (*Bromus tectorum*) cover and biomass in mixed-conifer forest, 13 years after treatment in a California mixed-conifer forest.

2. Methods

2.1. Site description

The study was located in the Red Mountain fuel treatment area in the Kern River Ranger District, Sequoia National Forest, California, USA (35.65° N, −118.61° W). The area was replanted with *Pinus ponderosa* Douglas ex Lawson & C. Lawson (ponderosa pine) after the Red Mountain wildfire which burned 10,316 ha in September 1970 (Wildland Fire Interagency Geospatial Services, 2023). However, isolated remnant *P. ponderosa*, *Calocedrus decurrens* (Torrey) Florin (incense-cedar), and several large *Quercus kelloggii* Newberry (black oak) were present in and around the plots. The study area consisted of 30 plots within three blocks (Fig. 1) across an area of approximately 150 ha. Elevation ranged from 1610 to 1787 m and aspect varying from South to Southeast (Table S1). Mean annual temperature (1981 – 2010) was 10.5° C ± 6.5 (SD) with total annual precipitation of 1,069 mm, of which 284 mm fell as snow (Régnière and St-Amant 2007).

The majority of plots were dominated by an overstory of *P. ponderosa* with sporadic *Abies concolor* (Gordon & Glendinning) Hildebrand (white fir), *C. decurrens*, *Quercus chrysolepis* Liebmann (canyon live oak), and *Q. kelloggii*. The understory consisted of a diverse community of forbs and shrubs with *Bromus tectorum* L. (cheatgrass), and *Ribes roezlii* Regel (Sierra gooseberry) dominating across many plots in 2021.

2.2. Original study design and treatments

Treatments included a control (C), mastication (M), mastication + burn (MB), and a mastication + pull-back + burn (MPB) and were implemented by USFS personnel. The study was designed as a randomized complete block design with treatments randomly assigned to four randomly located blocks within the larger Red Mountain Study Area (Reiner et al., 2009).

Each treatment was replicated in 16 plots distributed evenly across

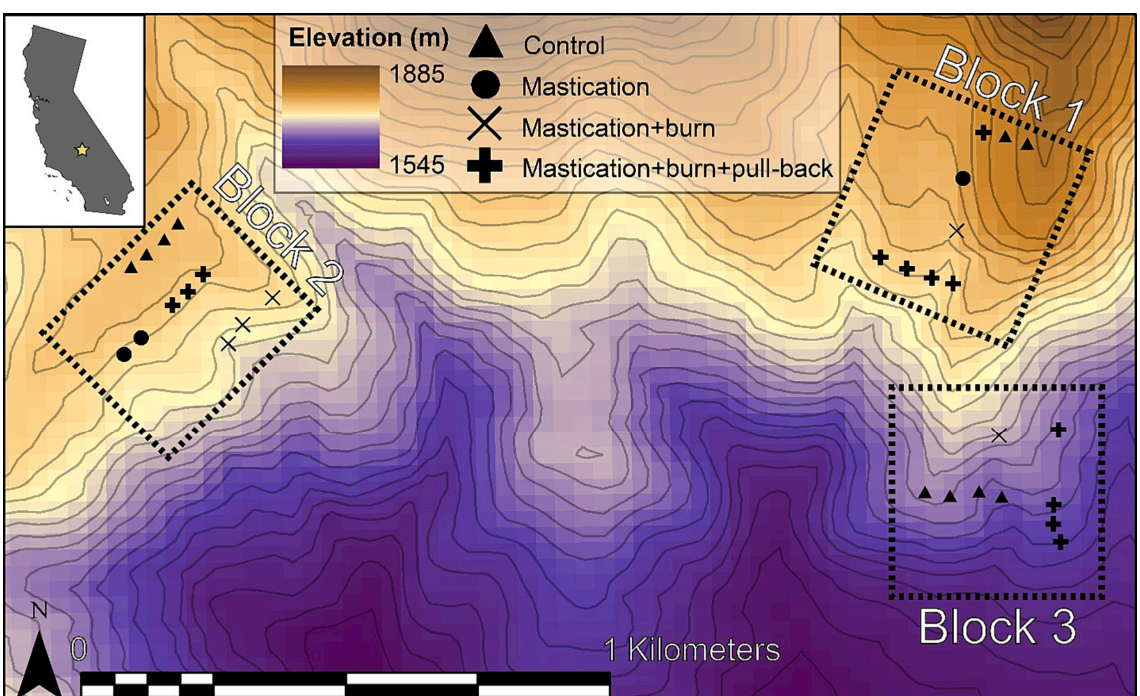

Fig. 1. Red Mountain study site location. Elevation contour intervals are 10 m and derived from 1 × 1 degree 1/3 arc-second digital elevation models (United States Geological Survey, 2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

four blocks. Block and plot locations were randomly assigned in ArcMap software (ESRI, Redlands, CA, USA) before establishment. Some treatments were not completed which resulted in an unbalanced randomized block design within the original study (Reiner et al., 2009). Plots were originally established and measured in 2005, treated in 2006 – 2007, and remeasured for forest composition, fuel loadings, and structure in 2008.

Mastication was performed using a vertical shaft mastication head on an excavator boom and targeted trees < 38 cm in diameter and a prescribed density of 61 trees ha^{-1}. *Quercus* and *Pinus* species were the highest value leave trees whereas *Abies* and *Calocedrus* trees were preferentially masticated. The 'pull-back' treatment consisted of masticated material being raked away from each tree bole out to each tree's dripline to minimize cambial heating and fine root mortality from the prescribed burn. Finally, a prescribed burn was implemented in the MB and MPB plots on December 5 – 6th 2007 using spot and strip-firing methods. Forest measurements in 2005 and 2008 were implemented by the USDA Fire Behavior Assessment Team (FBAT) which primarily assesses fuels and fire behavior on active wildland fire incidents in western U.S. forests. Full details on the original treatments are described in Reiner et al. (2009).

2.3. Remeasurement methods

Summer 2021 we remeasured a subset of the Red Mountain plots originally described in Reiner et al. (2009) (Fig. 2). Road and forest closures at the time of sampling prevented access to Block 4. We omitted parts of Blocks 1 – 3 that had been compromised by post-treatment salvage logging. Our final sample size included 11 C plots, 3 M plots, 5 MB plots, and 11 MPB plots (Table S1). Our methods in 2021 were comparable to the 2005 and 2008 survey methods of Reiner et al. (2009) with the addition of tree ring and forest floor sampling and the use of variable radius plots following then-standard FBAT protocols (Fire Behavior Assessment Team, 2022).

2.3.1. Tree measurements and tree ring sampling

We used a Spiegel Relaskop (Silvanus Inc.; Salzburg, Austria) to select trees for measurement within a variable radius plot. We used a basal area factor (BAF) of 5 to characterize pole-sized trees (1 – 15.0 cm diameter at breast height, DBH), and BAF of 10 or 20 to select 5 – 10 overstory trees (>15.0 cm DBH) within each plot. At establishment, all overstory trees were measured within 17.85 m of the plot center and all pole-sized trees within 8.92 m (Reiner et al., 2009). Variable radius plots with 5 – 12 trees per plot are similar to fixed radius plots in estimating basal area and trees per hectare (Piqué et al., 2011; Bitterlich 1984). We assessed the selected trees for diameter at breast height (1.37 m above ground level), height and height to live crown. Height to live crown was defined as the height from the ground to the first live branch that spanned ≥30° of the crown circumference and had continuous cover (Fire Behavior Assessment Team, 2022). We documented the presence of beetle galleries, pitching, fire scars, and mechanical damage in living and standing dead trees. We present the results for pole and overstory trees together unless otherwise noted. Live trees were denoted as 'trees' whereas standing dead trees were denoted as 'snags'. During tree measurements, we discovered indicative galleries from *Curculionidae Dendroctonus ponderosae* Hopkins (mountain pine beetle) and *Curculionidae Dendroctonus brevicomis* (western pine beetle) and active pitching within a large portion of the study area. As a result, we conducted ad-hoc measurements of beetle gallery presence on trees and traumatic resin ducts in tree rings as indicators of beetle attack (DeRose et al., 2017; Birch et al., 2019a). Traumatic resin duct bands and blue-staining of the wood can indicate attack by bark beetles and are visible as a semi-continuous band of ducts within an annual ring.

To characterize the age and radial growth trends of *P. ponderosa* we collected tree increment cores within a subset (n = 21) of plots (4.3 mm increment borer; Haglöf Sweden; Mora, Sweden) (Table S1), prioritizing plots with multiple live overstory trees. Within these plots we selected 3 – 5 trees without visible damage (e.g. rotten or broken-top) from among those previously measured in the variable radius plot. Because most standing dead trees were rotten, we favored sampling live trees ≥10 cm DBH to avoid causing damage to small diameter trees. We measured 2,614 tree rings from 64 intact cores collected from 56 trees with an average tree age of 41 years ± 4 (SE) that did not significantly vary across treatments. To compare tree-ring growth with drought we calculated the standardized precipitation-evapotranspiration (SPEI) index using 1.8.1 package (Beguería et al., 2014; Beguería and Vicente-Serrano, 2023) using default settings.

2.3.2. Tree core preparation and measurement

We sanded increment cores with increasingly fine-grit sandpaper up to 400 grit. We scanned at 1200 DPI (EPSON 630 Pro Photo Scanner) and measured tree ring widths using CDendro 9.5 software (Larsson 2018). We verified visual crossdating using COFECHA 6.06P (Holmes 1983).

2.3.3. Surface and ground fuel measurements

To estimate understory vegetation mass (including shrubs, seedlings, forbs, and grasses) we estimated vegetation cover and recorded height, bulk density classification, and morphology along a 1-m belt transect centered on each of the three 15.24 m transects (Burgan and Rothermel 1984) that converged at plot center. We estimated the bulk density for each species using the morphological grass and shrub photoseries classifications of Burgan and Rothermel (1984) and multiplied these by the average height (cm) and cover (%) for each plant species. We used the closest representative shrub photoseries for tree seedlings, and the closest representative grass photoseries to estimate forb bulk density. Because crew training in botanical identification and phenology differed among years, we do not assess vegetative diversity across survey years.

We assessed all size classes of downed woody fuels (1 – 1000-h), and litter and duff using three 15.24 m Brown's transects (Brown 1974).

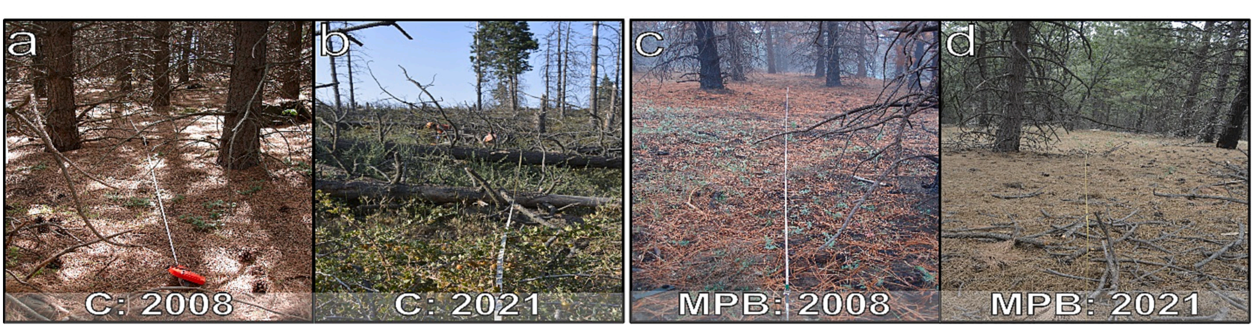

Fig. 2. Photos illustrating changes in forest structure and fuels from 2008 to 2021 at the Red Mountain plots, California, USA. Paired photos were taken at a representative control (C) and mastication + pull-back + burn (MPB) plots in 2008 (a, c) and 2021 (b, d). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Each transect originated distal to the plot center to minimize disrupting surface fuels. We measured 1-h (0.0 – 0.6 cm diameter) and 10-h (0.6 – 2.54 cm) fuels from 0.0 to 1.82 m along the transect, 100-h fuels (2.54 – 7.6 cm) from 0.0 to 3.65 m, and 1000-h fuels (>7.6 cm) along the full 15.24 m Brown's transect. We measured litter and duff depths at 0.3, 1.8, and 4.8 m from the transect origin.

To calculate the bulk density of the forest floor (litter and duff), we sampled from three 30 cm diameter circular sampling frames, each placed 1.0 m from the origin of a fuel transect. Within each sampling frame, we collected and pooled the litter and duff and measured the depth of the litter and duff to the nearest 0.10 cm at three equidistant locations at the interior edges of the sampling frame. We removed stones before weighing samples to the nearest 0.01 g.

2.3.4. *Biomass calculations*

We used allometric equations from Chojnacky et al. (2014) to estimate aboveground biomass of living trees (Table S2), and we used component parameters from (Jenkins et al., 2003) to estimate tree foliage biomass. For snags of decay class 1 or decay class 2 we used species-specific conversion factors from Cousins et al. (2015) and general decay coefficients from Harmon et al. (2008). We modeled snags of decay class ≥3 as conic frustums using ocular estimation of the top diameter. The volume of each frustum was used to calculate mass following species-specific and general density values from Harmon et al. (2008). We estimated the mass of 1-h – 1000-h fuels, litter, and duff following van Wagtendonk et al. (1998) but modifying to use site-specific litter and duff bulk density values derived from the 2008 plot measurements (Reiner et al., 2009). We did not use the 2021 bulk density measurements to assess litter and duff mass because the litter and duff were physically pooled together in 2021. To ensure consistency across years, we re-calculated the overstory and 1–1000-h fuel mass of the 2005 and 2008 surveys using the data collected by Reiner et al. (2009) following the allometric equations used for the 2021 measurements. We calculated canopy bulk density (2005, 2008, and 2021) using the Forest Vegetation Simulator (FVS) version 20200903 (Dixon 2002) with default settings for the Sierra Nevada ecoregion with the modification that we used the 'all species' canopy bulk density formula available in the Fire and Fuels Extension for FVS (Reinhardt 2003). The 'all species' option included *Calocedrus decurrens* and *Quercus Kelloggii* canopies in bulk density estimations.

2.4. *Statistical analysis*

All statistical analyses were conducted using the graphical user interface R Studio 1.4.1106 (R Studio Team, 2021) and the statistical program R 4.1.2 (R Core Team, 2023). We used the R packages ggplot2 3.3.5 (Wickham 2016) and ggpubr 0.4.0 (Kassambara 2020) to visualize data. We created maps using ArcGIS 10.8.1 software (ESRI, Redlands, CA, USA) and 1 × 1 degree 1/3 arc-second digital elevation models (United States Geological Survey 2020).

To analyze differences in 2021 forest characteristics and fuel loadings, we used a linear mixed-effect model in the lme4 1.1–34 package (Bates et al., 2015) with treatment as a fixed effect and a random blocking factor. We calculated pairwise comparisons using the emmeans 1.8.8 package (Lenth 2023). When comparing 2008 to 2021 changes by treatment we used year as a fixed effect with a random blocking effect, excepting the mastication (M) treatment where we had a single replicate across each of the three blocks and did not include block as an independent variable and instead used an analysis of variance (ANOVA) approach. We did not compare 2005 to 2021 data as treatments were implemented in 2006 – 2007 with initial treatment effects previously evaluated by Reiner et al. (2009). For each test, we analyzed model assumptions by plotting residuals to assess normality and homogeneity. Plots were located at sufficient distances (mean distance = 46.6 m) from one another for independence, as the range at which trees are autocorrelated and influence one another typically varies on scales of 10–40 m (Birch et al., 2023a; Furniss et al., 2017; Lutz et al., 2012). Because we wanted to identify if mastication resulted in unequal fuel deposition, we calculated the within-plot variation (e.g., across transects) of all downed woody fuel, litter, and duff loadings by calculating the plot-level standard error for each fuel stratum and testing using the methods detailed above.

2.4.1. *Chronology development*

To remove ontogenetic trends within the growth of all *P. ponderosa* we detrended each tree-ring series using a 20-yr cubic spline with a 0.5 stiffness in dplR 1.7.2 (Bunn et al., 2020). The 20-yr spline with 0.5 stiffness follows Klesse (2021) and represents two-thirds of the average sequence length across all plots. All chronologies were assembled from *P. ponderosa*, the dominant tree species. We assessed differences in both absolute tree growth (mm yr^{-1}) and standardized growth, which accounts for confounding trends from ontogenesis and tree size. We present standardized growth trends among treatments because results were similar for both absolute and standardized growth (See Supplemental Information 1).

3. Results

3.1. *Tree biomass, canopy structure, and growth*

Tree and snag biomass were not significantly different in 2021 across treatments. Live tree biomass in the C treatment declined by 170.3 Mg ha^{-1} ± 60.3 (SE) ($p = 0.011$) between 2008 and 2021 while there was no significant change 2008 – 2021 for the live tree biomass in the M, MB, and MPB treatments (Fig. 3a). Snag biomass significantly increased 2008 – 2021 for the C, M, and MPB treatments (Table 1; Fig. S1a; $p < 0.05$). The density of overstory trees did not differ by treatment in 2021 ($p > 0.05$) and both M ($p = 0.012$) and C ($p < 0.001$) tree density declined from 2008 to 2021 (Table 2; Fig. 3b). The density of pole trees was not significantly different across treatments in 2021 and did not change 2008 – 2021 (Table 2).

There were no significant differences in live tree diameter at breast height (DBH; 1.37 m) among treatments in 2021 (Fig. S1b; Table 2). Tree DBH significantly increased in MB and MPB treatments from 2008 to 2021 (Fig. S1b; $p < 0.05$). Tree height in 2021 was lower in the C (mean = 9.9 m ± 6.3 SE) relative to MPB (mean = 18.2 m ± 5.3; $p = 0.004$), whereas M and MB treatments were similar to C (Table 2). Tree height increased by 6.1 m ($p < 0.001$) in the MPB treatment from 2008 to 2021. Height to live crown in 2021 were significantly lower in C and M relative to MB and MPB treatments (Table 2; Fig. 3c). Height to live crown of all trees decreased by an average of 1.9 m ± 0.3 (SE) from 2008 to 2021 across treatments (Table 2). Canopy bulk density did not significantly differ by treatment ($p > 0.05$) and had a mean decline of 69 % from 2008 levels (Fig. 3d). Tree foliage (Mg/ha) did not significantly differ by treatment in 2021, except for MPB which was greater than C ($p = 0.017$) and only C changed relative to 2008, with a decline of 5.7 Mg ha^{-1} ($p < 0.001$; Fig. S1c). In 16 (53 %) plots we detected evidence of attack by bark beetles, including entry-exit holes and galleries indicative of *Dendroctonus* species and isolated *Ips* spp. galleries. Beetle galleries and exit-entry holes were present on 57 % of all snags and 6 % of all living trees across all plots. The proportion of beetle-attacked snags did not vary by treatment ($p = 0.245$).

Neither absolute (mm yr^{-1}) nor standardized radial tree growth (1980 – 2020) varied between treatments except in 2008 and 2011 (Fig. 4; Fig. S2). In 2008, the year following treatment, the C and M had greater growth than MPB and MB treatments ($p < 0.001$; Fig. 4). In 2011, the MB and MPB had greater growth than the M and C treatments ($p < 0.001$). There were no distinct patterns of traumatic resin ducts on tree rings associated with attack by bark beetles; however, bark-beetle associated blue-staining occurred in the 2011 and 2018 rings.

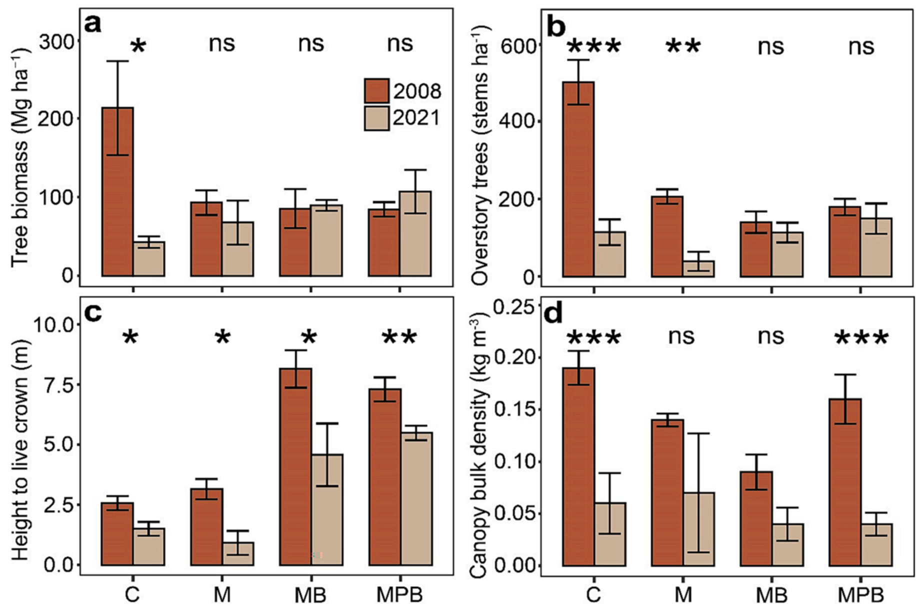

Fig. 3. The mean biomass (±1 SE; Mg ha^{-1}) (**a**), trees per hectare (**b**), height to live crown (**c**), and canopy bulk density (**d**), for all living trees in the Red Mountain plots, California, USA. The treatments are: control (C), mastication (M), mastication + burn (MB), and mastication + pull-back + burn (MPB). Significant differences are denoted between 2008 and 2021 values as: * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Mean loadings (Mg/ha ± 1 SE) for each fuel component by treatment for the Red Mountain study site, California, USA. The treatments are: Control (C), mastication (M), mastication + burn (MB), and mastication + pull-back + burn (MPB). Different lowercase letters indicate differences among treatments in 2021.

Year	Treatment	Tree	Snag	Shrub	Seedling	Grass	Forb	1000-hr	100-hr	10-hr	1-hr	Litter	Duff
2005*	C	195.7 (56.4)	0.4 (0.2)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	57.9 (28.3)	1.2 (0.6)	1.1 (0.4)	0.0 (0.0)	1.6 (0.2)	22.9 (3.5)
	M	128.9 (15.5)	0.0 (0)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	21.5 (18.7)	0.0 (0.0)	0.2 (0.2)	0.1 (0.1)	1.4 (0.1)	35.3 (8.5)
	MB	151.3 (41.1)	0.6 (0.6)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	24.3 (14.9)	0.5 (0.5)	0.2 (0.1)	0.0 (0.0)	0.9 (0.1)	22.5 (5.5)
	MPB	119.5 (6.4)	0.8 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	13.9 (8.7)	1.2 (0.5	0.6 (0.2)	0.0 (0.0)	1.4 (0.1)	21.8 (4.1)
2008	C	213.2 (59.7)	3.6 (2.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	64.0 (30.0)	4.4 (2.2)	3.1 (1.0)	0.2 (0.1)	2.2 (0.2)	16.1 (4.8)
	M	93.0 (15.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	30.5 (30.5)	4.5 (4.5)	1.0 (1.0)	0.2 (0.0)	1.8 (0.1)	20.6 (4.1)
	MB	85.3 (24.7)	9.2 (3.1)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	2.2 (1.5)	0.6 (0.6)	0.6 (0.3)	0.0 (0.0)	0.6 (0.0)	3.2 (1.3)
	MPB	84.4 (9.1)	5.8 (2.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.0 (1.0)	1.7 (1.0)	1.3 (0.3)	0.1 (0.0)	0.6 (0.0)	2.7 (1.2)
2021	C	42.8 (7.2)a	42.8 (10.7)a	0.6 (0.4) a	0.0 (0.0) a	0.0 (0.0) a	0.0 (0.0)a	68.5 (20.0)a	8.1 (1.2)a	4.5 (0.8)a	0.5 (0.1)a	1.2 (0.2) a	28.3 (4.6) a
	M	67.6 (27.8) a	49.9 (13.8)a	0.1 (0.0) a	0.0 (0.0) a	0.2 (0.1) a	0.0 (0.0)a	57.3 (27.3)a	7.1 (2.2)a	4.2 (1.0)a	0.1 (0.0)a	2.1 (0.5) a	26.8 (2.1) ab
	MB	89.5 (6.8)a	25.1 (21.7)a	0.0 (0.0) a	0.0 (0.0) a	0.1 (0.0) a	0.0 (0.0)a	19.1 (4.5) a	3.5 (0.6)a	2.8 (0.8)a	0.1 (0.0)a	1.0 (0.2) a	8.6 (3.1)b
	MPB	107.0 (27.6)a	35.7 (12.6)a	0.0 (0.0) a	0.1 (0.0) a	0.1 (0.0) a	0.0 (0.0)a	30.4 (5.9) a	6.9 (1.5)a	3.8 (0.8)a	0.2 (0.0)a	1.0 (0.1) a	13.8 (3.9) b

*Treatments were implemented in 2006 – 2007.

3.2. Understory vegetation & downed woody fuels

There were no effects of treatment on shrub, seedling, grass, or forb loadings in 2021 (Table 1). Shrub loadings in 2021 was largely driven by *Ribes roezlii* ($mean_{total}$ = 0.37 Mg ha^{-1}; 96 % of shrub biomass) while grass loadings were driven by the invasive *B. tectorum* ($mean_{total}$ = 0.07 Mg ha^{-1}; 50 % of grass biomass). Shrub loadings increased from 2008 to 2021 in M (0.11 Mg ha^{-1}; 507 %; $p = 0.018$) and MPB (0.05 Mg ha^{-1}; 772 %; $p = 0.004$) while seedling loadings increased in only M treatments (0.02 Mg ha^{-1}; 16 %; $p = 0.022$; Fig. S3a:b). Grass loadings increased 2008 – 2021 in C (0.08 Mg ha^{-1}, 463 %; $p = 0.005$) whereas forb loadings increased in the MPB treatment (0.06 Mg ha^{-1}, 12 %; $p = 0.022$; Fig. S3c:d). Neither cover ($mean_{total}$ = 17.8 %; $p = 0.435$) nor loadings ($p = 0.225$) of *B. tectorum* varied among treatments (Fig. S4).

The mass of downed woody fuels (1 – 1000-h) did not vary by treatment in 2021 (Table 1). There was no difference in any size class of downed woody fuels from 2008 to 2021 for the C and M treatments. In contrast, the loadings of all size classes of downed woody fuels increased for both MB and MPB treatments (Table 1; Fig. S5). Within-plot variation (SE) of fuel loadings across transects did not vary for any size classes of downed woody fuels among treatments.

Table 2
The mean per hectare values ± 1 SE, by treatment, for overstory tree diameter at breast height (DBH), overstory tree basal area (m^2), overstory trees (>15 cm DBH, "Trees") per hectare, pole trees (<15 cm DBH) per hectare, tree height (m), height to live crown (HLC), canopy bulk density (CBD), and overstory foliage (Mg/ha) for forest plots in California, USA. The treatments are: Control, mastication (M), mastication + burn (MB), and mastication + pull-back + burn (MPB). Standard error values are provided in parenthesis. Different lowercase letters indicate differences across treatments in 2021.

Year	Treatment	DBH (cm)	Basal area (m^2)	Trees (ha^{-1})	Pole trees (ha^{-1})	Height (m)	HLC (m)	CBD (kg m^{-3})	Foliage (Mg/ha)
2005*	C	25.7 (1.3)	30.7 (3.8)	529 (55)	334 (101)	7.9 (1.3)	2.3 (0.2)	0.201 (0.015)	8.4 (1.1)
	M	26.7 (4.1)	26.6 (2.6)	510 (140)	416 (132)	8.2 (2.5)	2.1 (0.1)	0.159 (0.006)	7.4 (0.5)
	MB	26.6 (2.7)	25.9 (3.9)	452 (63.9)	360 (91)	7.8 (2.3)	1.9 (0.2)	0.170 (0.009)	7.3 (1.0)
	MPB	25.7 (1.4)	25.7 (3.8)	488 (63)	185 (82)	9.1 (1.6)	2.6 (0.1)	0.238 (0.008)	7.0 (0.4)
2008	C	26.4 (1.2)	28.0 (1.6)	501 (57)	432 (122)	9.1 (2.2)	2.5 (0.2)	0.190 (0.015)	7.9 (0.3)
	M	31.7 (2.0)	17.7 (3.0)	206 (18)	66 (47)	12.0 (2.7)	3.1 (0.4)	0.141 (0.005)	4.9 (0.9)
	MB	32.0 (3.4)	13.3 (4.6)	140 (27)	8 (7)	12.4 (4.0)	8.1 (0.7)	0.090 (0.016)	3.9 (1.4)
	MPB	31.3 (1.2)	15.1 (2.3)	179 (20)	50 (43)	12.1 (2.1)	7.3 (0.4)	0.162 (0.023)	4.2 (0.6)
2021	C	27.0 (4.9)a	7.2 (1.5)a	114 (32)a	400 (246)a	9.9 (1.8)a	1.5 (0.2)a	0.068 (0.028)a	2.2 (0.4)a
	M	53.2 (11.1)b	7.4 (2.6)ab	39 (24)a	361 (275)a	11.0 (0.1)ab	0.9 (0.4)a	0.076 (0.005)a	2.6 (0.8)ab
	MB	42.4 (2.1)ab	15.8 (1.6)ab	113 (25)a	148 (148)a	14.8 (0.0)ab	4.5 (1.2)b	0.049 (0.015)a	4.9 (0.4)ab
	MPB	42.3 (2.3)b	19.7 (5.0)b	149 (39)a	0 (0)a	18.2 (1.5)b	5.4 (0.3)b	0.043 (0.010)a	6.0 (1.5)b

*Treatments were not implemented until 2006 – 2007.

3.3. Forest floor biomass and bulk density

Litter loadings did not differ by treatment in 2021 and decreased by 46 % (1.05 Mg ha^{-1}; $p = 0.004$) in the C from 2008 to 2021. Duff loadings in 2021 was lower in MB and MPB relative to the C (Fig. 5a). Duff increased by 400 % (11.08 Mg ha^{-1}) in the MPB treatment ($p = 0.014$) from 2008 to 2021 (Fig. 5b). Within-plot variation of litter loadings in 2021 was greatest in M treatments (SE = 6.6; $p < 0.05$) relative to all other treatments (mean SE = 0.9) which were similar ($p > 0.05$). In contrast, there were no differences in within-plot variation of duff loadings among treatments. Mean forest floor (litter + duff) bulk density in 2021 was 44.27 ± 4.7 kg m^{-3} and did not vary among treatments ($p > 0.05$; Table S3; Fig. S6).

4. Discussion

After 13 years, the initial differences in fuel loadings and forest structure among treatments had diminished, due to high overstory mortality apparently resulting from bark beetle attack. Although mastication and prescribed fire appeared to reduce the severity of bark beetle induced mortality, all treatments were ineffective at stimulating sustained increases in radial tree growth. Overall, prescribed fire treatments had the lowest mortality from bark beetles, suggesting that prescribed fire may have long-term viability as a means of increasing resistance and resilience to bark beetles and fires, two important and interacting disturbances in the Sierra Nevada mixed-conifer ecoregion (Bernal et al., 2023, Westlind and Kerns 2021, Hood et al., 2015).

4.1. Tree mortality, growth, and canopy structure – Legacies from treatments

The extensive overstory tree mortality between 2008 and 2021 was likely due to the local bark beetle outbreak as evidenced by the galleries on most snags. Similar outbreaks occurred during this time within the broader geographic region (Fettig et al., 2019). Although we did not detect differences in the proportion of bark beetle galleries on snags among treatments, only the unburned treatments experienced significant overstory mortality from 2008 to 2021. This difference may be attributable to stand density, as the greatest overstory density in 2008 occurred in the C treatment. This is supported by other reports showing positive associations between forest density and mortality from bark beetles (Furniss et al., 2022, Birch et al., 2019b), which likely arise from competition-induced stress that increases tree vulnerability to detection and attack from bark beetles. Thinning and prescribed fire may protect from attack by bark beetles by stimulating induced tree defenses and promoting resin duct production (Hood et al., 2016, but see Steel et al., 2021). Though the bark beetle outbreak partially obscured the long-term effects of the treatments, such outbreaks are increasing across North America and, when combined with drought and fire, are likely to continue causing substantial mortality in western forests (Buotte et al 2019, Bentz et al., 2010).

Though thinning treatments can improve tree growth responses under drought (Vernon et al., 2018, Kolb et al., 2007, but see Lydersen et al., 2019), there were no sustained changes in tree growth among treatments. It is likely that thinning to 61 trees ha^{-1} (Reiner et al., 2009) did not sufficiently alleviate density-dependent competition for water among overstory trees. Interestingly, the comparatively wet year (2011) was the only year in which burn treatments had greater growth than the unburned (C, M) treatments. The bark beetle induced mortality may have provided equivalent thinning post-drought in the unburned (C, M) treatments and reduced density-dependent competition for water. A reduction in density-dependent competition from mastication, fire, or bark beetle-induced mortality may explain the lack of consistent differences in growth among treatments. Our sampling of live trees represents a survivorship bias by not fully assessing the growth of trees that died pre-2021 and may represent only those trees with the greatest growth, a bias that may have increased apparent growth rates in untreated (C) and unburned (M) treatments. Though bark beetle associated mortality thinned the C to equivalent densities as the other treatments, the unburned treatments may have greater risk from wildfire owing continued fuel depositions from snags and lowered canopy base heights (Hicke et al., 2012). As standing snags fall in the next decade (Lutz et al., 2020, their Fig. 7) we expect downed woody fuels to increase, particularly in the unburned treatments whose snag loadings nearly equal live tree biomass (Table 1). Similar proportions of beetle mortality have been associated with extreme fire behavior (e.g., firestorms) and high severity in the southern Sierra Nevada (Stephens et al., 2022) and additional treatments are likely needed to reduce fire risk in unburned stands that experienced high beetle associated mortality.

4.2. Changes in vegetation, downed woody fuels, litter, and duff

The uniform *B. tectorum* (cheatgrass) cover across all treatments will likely promote more frequent surface fires and further proliferate *B. tectorum* (Kerns et al., 2020, Balch et al., 2013). Cheatgrass invasions are more likely when canopy cover is <30 % (Peeler et al., 2018), and the outbreak of bark beetles and subsequent decline in overstory cover likely facilitated the invasion of *B. tectorum* into the system. As well, a combination of treatments and bark beetle induced mortality may have reduced competition from overstory trees and enabled vigorous populations of *R. roezlii* (Quick 1954). The continued prevalence of *R. roezlii* may slow the recruitment of shade-intolerant species, such as *P. ponderosa* and increase competition for growth-limiting resources.

The convergence of all size classes of woody fuels among treatments

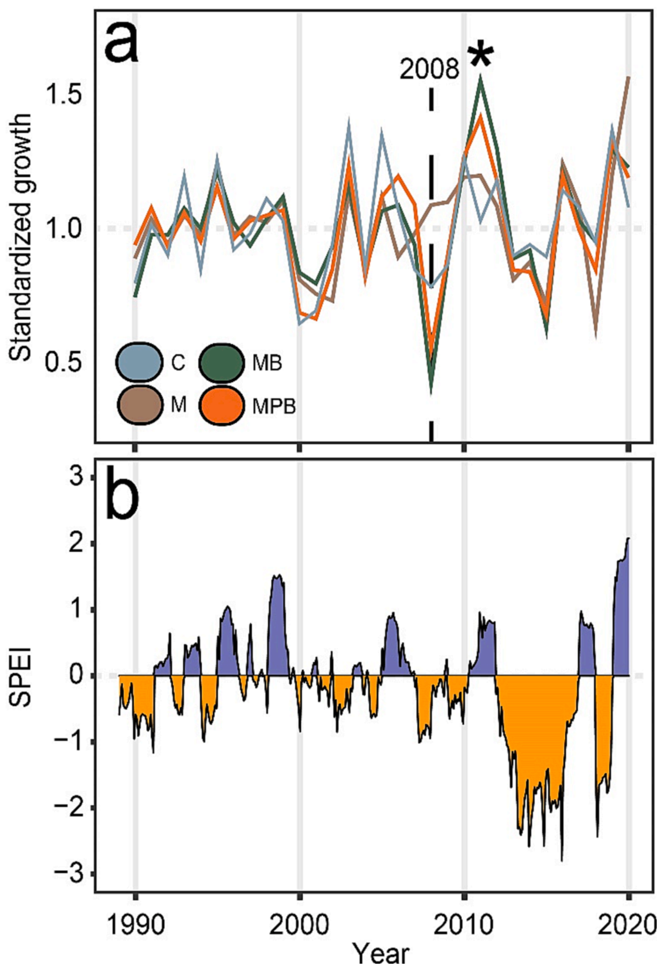

Fig. 4. The (**a**) standardized tree growth and (**b**) standardized precipitation-evapotranspiration index (SPEI) from 1989 to 2020 at the Red Mountain plots, California, USA. The time period 1989 – 2020 is plotted as the period with the greatest sample depth over the measurement period (1734 – 2021) across all treatments. (**a**) The standardized growth for *P. ponderosa* in each treatment. The treatments are: control (C), mastication (M), mastication + burn (MB), and mastication + pull-back + burn (MPB). A vertical dashed line marks 2008, the first growing season following treatment implementation and the only year in which unburned treatments (C, M) had greater growth ($p < 0.05$) than burned treatments (MB, MPB). An asterisk marks 2011, the only year in which burned plots had greater relative growth than the unburned treatments ($p < 0.05$). (**b**) The SPEI index from 1989 to 2020. Values above (below) '0' are associated with wetter (drier) conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

supports previous work that repeated applications of mastication and prescribed fire are needed to reduce woody fuel accumulations and promote resilient forest structure and composition (Knapp et al., 2017, Schwilk et al., 2009). The fuel accumulation from 2008 to 2021 is similar to post-wildfire forests where pre-fire fuel loadings match pre-fire levels in six to seven years, though duff recovers over longer periods in dry mixed conifer systems (Eskelson and Monleon, 2018, Lutz et al., 2020).

Although overall forest floor bulk densities were similar across the treatments, duff loadings were substantially lower in the burned treatments even 13 years after fire, highlighting the utility of prescribed fire for reducing duff loadings. Forest floor bulk density is inversely related to combustion rates (Dickinson et al., 2013, Wilson, 1990) and we may expect similar rates of combustion among treatments. Notably, the mastication treatment may have more variable fire behavior, owing to the increased within-plot variability of litter loading. This small-scale pyrodiversity may be desirable and lead to unburned refugia or variable fire effects (Jones and Tingley, 2022, Blomdahl et al., 2019, Ryan et al., 2013).

4.3. Implications for forest health and resilience

The burned treatments improved forest resistance to attack by bark beetles, thereby safeguarding carbon retention in live biomass pools, and reducing overstory vulnerability to future wildfire, relative to unburned treatments. The conversion of the majority of ecosystem biomass from live to dead pools in the unburned treatments may see substantial carbon emissions with future wildfires. Carbon emissions from fires can intensify climate change (Liu et al., 2014) and lead to a positive feedback of warming temperatures altering disturbance regimes and causing greater carbon emissions from forests (Barbero et al., 2015, Kurz et al., 2008).

Though litter and duff comprise a small proportion of overall ecosystem carbon (10–22 %; Birch et al., 2023b) wildfire consumption is often greatest in these strata (Miesel et al., 2018). Based on the greater duff loading (and therefore biomass carbon content), the unburned treatments likely store more carbon in the forest floor layer compared to burned treatments (Maestrini et al., 2017), and will thus likely produce greater carbon emission in future wildfire. In all treatments the prevalence of *R. roezlii* and *B. tectorum* will likely challenge tree seedling recruitment, and create a readily available surface fuel bed for future fires. Treatments aimed at reducing the cover of *R. roezlii* and *B. tectorum* may enhance seedling regeneration and reduce the continuity of fine surface fuels. Ingrowth of ladder fuels lowered the height to live crown across all treatments and increases the risk of crown fire (Cruz et al., 2004) unless new treatments are implemented.

5. Conclusions

Burned plots maintained their treatment level overstory densities and biomass despite the outbreak of *D. ponderosae*, suggesting that the prescribed fire provided protection against the outbreak despite not inducing enduring growth advantages. Although effects were limited, the treatments with prescribed fire had enduring duff reductions and more fire-avoidant canopies, relative to the unburned plots. Our results suggest that desirable forest outcomes at this site would require more frequent implementation of treatments to maintain elevated crown structure and enduring reduction of woody surface fuels. Cumulatively, our results inform management practices by contrasting the initial and long-term efficacy of common silvicultural treatments and highlighting the potential of prescribed fire to mitigate mortality from bark beetle attacks in dry mixed conifer ecosystems.

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CRediT authorship contribution statement

Joseph D. Birch: Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Formal analysis, Software. **Alicia Reiner:** Conceptualization, Data curation, Investigation, Methodology, Writing – review & editing. **Matthew B. Dickinson:** Writing – review & editing, Project administration. **Jessica R. Miesel:** Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

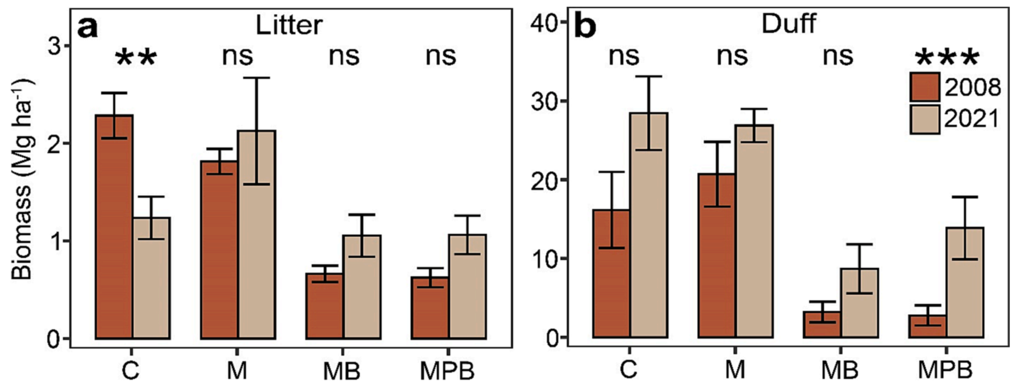

Fig. 5. Distribution of mean biomass (±1 SE; Mg ha^{-1}) of (**a**) litter and (**b**) duff loadings by treatment at Red Mountain, CA, USA. The treatments are: control (C), mastication (M), mastication + burn (MB), and mastication + pull-back + burn (MPB). Significant differences are denoted between 2008 and 2021 values as: ** = p < 0.01, *** = p < 0.001, and 'ns' as non-significant. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data collected by the Fire Behavior Assessment Team (FBAT) is publicly available through frames.gov. Tree ring data available at the International Tree-Ring Data Bank (CA726). Analytical code available upon request from the authors.

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Appendix A. Supplementary data

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