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ARTICLE

Wildfire-contingent effects of fuel treatments can promote ecological resilience in seasonally dry conifer forests

Jens T. Stevens, Hugh D. Safford, and Andrew M. Latimer

Abstract: Fire suppression has made many seasonally dry conifer forests more susceptible to high-severity wildfires, which cause large changes in forest structure and function. In response, management agencies are applying fuel reduction treatments to millions of acres of forest, with the goal of moderating fire behavior by reducing tree density and understory fuel loads. However, despite their wide application, we still lack basic information about the extent to which these treatments contribute to forest restoration by increasing forest resilience to recurring wildfire events. To address this question, we established 664 plots across 12 different sites in California, USA, where wildfire burned through fuel treatments, and measured a suite of forest characteristics relating to overstory structure, understory cover, and woody plant regeneration. We tested a "wildfire-contingency" hypothesis that there should be strong interactions between treatment and fire, specifically that the direction and magnitude of fuel treatment effects on forest characteristics will depend on subsequent disturbance. This interaction hypothesis had strong support, driven largely by effects on trees: without wildfire, live-tree cover was lower in treated stands than in untreated stands, but after wildfire, it was higher in treated stands than in untreated stands. Treated stands had higher soil moisture and more shrub seedlings than untreated stands without wildfire but had greater soil moisture and fewer shrub seedlings than untreated stands after wildfire. Conversely, litter depth, litter cover, and tree seedling abundance were lower in treated stands than in untreated stands without wildfire but higher in treated stands than in untreated stands after wildfire. Ordination revealed that the magnitude of ecological change attributable to wildfire is lower in treated stands than in untreated stands. We conclude that properly implemented treatments can promote resilience to both first-entry and subsequent wildfires.

Key words: California, forests, fuel treatments, mixed conifer, resilience, restoration, yellow pine, wildfire.

Résumé : La suppression du feu a rendu plusieurs forêts résineuses plus susceptibles aux feux de forêt durant la saison sèche entraînant d'importants changements dans la structure et la fonction de la forêt. En réaction, les organismes de gestion appliquent des traitements de réduction des combustibles sur des millions d'acres de forêt dans le but de contrôler le comportement du feu en réduisant la densité des arbres et les charges de combustibles dans le sous-bois. Cependant, malgré leur application généralisée, nous sommes toujours à court d'informations de base à savoir dans quelle mesure ces traitements contribuent à la restauration des forêts en augmentant leur résilience aux épisodes récurrents de feu de forêt. Pour résoudre cette question, nous avons établi 664 placettes dans 12 sites différents en Californie, aux États-Unis, où un feu de forêt est survenu après un traitement des combustibles et nous avons mesuré une série de caractéristiques de la forêt reliées à la structure de l'étage dominant, au couvert en sous-étage et à la régénération des plantes ligneuses. Nous avons testé une hypothèse de feu de forêt potentiel selon laquelle il devrait exister d'importantes interactions entre les traitements et le feu, spécifiquement que la direction et l'ampleur des effets du traitement des combustibles sur les caractéristiques de la forêt dépendraient de la perturbation subséquente. Cette hypothèse d'interaction était fortement supportée, surtout à cause des effets sur les arbres : sans feux de forêt, le couvert d'arbres vivants était plus faible dans les peuplements traités que dans les peuplements non traités, mais après un feu de forêt il était plus important dans les peuplements traités que dans les peuplements non traités. La teneur en eau du sol était plus élevée et il y avait plus de semis d'arbustes dans les peuplements traités en l'absence de feux de forêt, mais la teneur en eau du sol était plus élevée et il y avait moins de semis d'arbustes que dans les peuplements non traités après un feu de forêt. À l'inverse, l'épaisseur de la litière, le couvert de litière et l'abondance de semis d'arbres étaient plus faibles dans les peuplements traités que dans les peuplements non traités en l'absence de feux de forêt, mais plus élevés dans les peuplements traités que dans les peuplements non traités après un feu de forêt. L'ordination a révélé que l'ampleur du changement écologique attribuable aux feux de forêt est moins prononcée dans les peuplements traités que dans les peuplements non traités. Nous croyons que des traitements adéquatement appliqués peuvent améliorer la résilience face aux feux de forêt, lors d'un premier feu et des feux subséquents. [Traduit par la Rédaction]

Mots-clés : Californie, forêts, traitements des combustibles, forêt mélangée de conifères, résilience, restauration, pins jaunes, feu de forêt.

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J.T. Stevens. Graduate Group in Ecology, University of California, Davis, CA 95616, USA; Department of Plant Sciences, University of California, 1 Shields Ave., Davis, CA 95616, USA.
H.D. Safford. USDA Forest Service, Pacific Southwest Region, Vallejo, CA 94592, USA; Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA.
A.M. Latimer. Department of Plant Sciences, University of California, 1 Shields Ave., Davis, CA 95616, USA.
Corresponding author: Jens T. Stevens (e-mail: jtstevens@ucdavis.edu).

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Introduction

Many seasonally dry conifer forests in eastern California experienced a frequent low- to moderate-severity fire regime, with return intervals generally less than 20 years, prior to Euro-American settlement (Van de Water and Safford 2011). However, many of these forests have now experienced over 100 years of anthropogenic fire suppression, due primarily to federal fire management policy (Stephens and Ruth 2005). Fire suppression has altered forest structure in these forests, leading to an increase in stand density, an accumulation of surface and ladder fuels, and an increase in density of shade-tolerant trees that tend to be less fire tolerant (McKelvey et al. 1996; Sugihara et al. 2006; Collins and Stephens 2007). These altered structural conditions have increased the likelihood and extent of high-severity fires, which can, in turn, cause long-lasting changes to forest structure through altered successional dynamics (Savage and Mast 2005; Miller et al. 2009). Fire suppression in dry conifer forests has thus increased the probability that wildfire will result in hysteresis (Beisner et al. 2003). Specifically, fire in suppressed forests has the potential to produce a post-disturbance state much different from the pre-disturbance state, which could persist for an extended period of time as an alternate stable state (Suding et al. 2004).

Fuel-reduction treatments have been the principal management tool used to reduce the likelihood of high-severity wildfire in frequent fire adapted conifer forests (Agee and Skinner 2005). Generally, fuel treatments that include mechanical removal of smaller-diameter trees, followed by prescribed surface fire or slash-pile burns, are the most effective at reducing fuel loads and restoring forest structure found under frequent fire regimes (Stephens et al. 2009). Fire behavior models predict that such treatments will reduce wildfire severity and tree mortality (Schmidt et al. 2008; Vaillant et al. 2009), and recent empirical work across multiple sites has confirmed that fuel treatments can be highly effective in reducing wildfire severity (Pollet and Omi 2002; Ritchie et al. 2007; Lezberg et al. 2008; Prichard et al. 2010; Safford et al. 2012; Martinson and Omi 2013).

Fuel treatments can be used to reduce wildfire severity for varying reasons, depending on management priorities: treatments may be implemented as a safe access point to effectively suppress fires from spreading to untreated forest (Moghaddas and Craggs 2007; Syphard et al. 2011) or to achieve ecological benefits resulting from structural modification (Wayman and North 2007; Ryu et al. 2009; Schwilk et al. 2009). When the goal is ecological restoration, however, there is increasing evidence that fuel treatments can most effectively achieve lasting restoration when they are used as a precursor to allowing wildfire to recur naturally at lower severity, rather than simply as a tool to enable continued wildfire suppression (Reinhardt et al. 2008; North et al. 2012). Thus, fuel treatments that are designed to be restorative rather than suppressive should allow land managers to maintain desired forest structure by way of recurring managed wildfires and (or) prescribed fires, without continuous intervention in the form of repeated mechanical fuel treatments.

If forest management goals include the reintroduction of a low- to moderate-severity fire regime into forests where this regime was historically present, then large areas of western US forests would benefit from active, strategic restoration of forest structure through fuel treatments (Schoennagel and Nelson 2011; Fulé et al. 2012). Restoration of these fire-prone forests aims to increase their resilience, that is, their capacity to reorganize to a pre-disturbance state and maintain characteristic ecosystem processes, following recurring wildfire events (Allen et al. 2002). We conceptualize resilience of dry conifer forests to recurring wildfire into three categories. At the overstory level, resilience to first-entry wildfires is enhanced by reducing stand density, especially of smaller trees, and canopy cover (Stephens and Moghaddas 2005; Stephens et al. 2009) while increasing the crown base height of remaining trees and retaining large fire-resistant trees and live canopy cover after wildfire. At the understory level, resilience to first-entry wildfires is enhanced by reducing litter depth and surface fuels, which can cause mortality of large trees during fires (Hood 2010), while allowing for the re-accumulation of conifer litter after fire to reduce bare soil erosion and promote subsequent low-intensity surface fires (Stephens and Moghaddas 2005; Cerda and Doerr 2008). At the regeneration level, which we distinguish from the understory level in that it concerns live potential fuels rather than dead potential fuels, resilience to first-entry wildfires is enhanced by removal of live-tree seedlings and saplings that could act as ladder fuels (Schwilk et al. 2009). Following first-entry wildfires, resilience is enhanced by the presence of naturally regenerating tree seedlings, particularly of fire-resistant tree species such as pines (Fulé et al. 2004; Schwilk et al. 2009). At each of these three levels, characteristics that foster resilience to a frequent wildfire regime are those that retain large live trees and (or) reduce the likelihood of large high-severity wildfires.

Most current research on the effects of fuel treatments on forest resilience involves comparisons of different treatment types and untreated stands in the absence of any wildfire (Schwilk et al. 2009; Stephens et al. 2012). Data comparing treated and untreated stand structure following wildfire are sparse because of the impossibility of implementing experimental prescribed burns under severe fire weather conditions (Fulé et al. 2012). However, because fuel treatments and wildfires are both increasing in frequency (Westerling et al. 2006; North et al. 2012), it will be increasingly necessary to consider the structural effects of fuel treatments in the context of naturally recurring wildfire. Comparisons of treated and untreated stands are likely to be very different after wildfire than they are in the absence of wildfire, because of the amount of structural change that occurs in untreated stands burning at high severity, particularly with respect to live-tree density. Treatments reduce live-tree density relative to untreated forest, yet post-wildfire tree survivorship in treated areas is often much higher than tree survivorship in untreated areas (Safford et al. 2012). Thus, differences between treated and adjacent untreated stands are likely to be contingent upon whether or not the forest is subsequently burned by wildfire. This "wildfire-contingency" effect has been modeled for some fuel-treatment outcomes such as carbon emissions (North et al. 2009*a*; Carlson et al. 2012; Winford and Gaither 2012) and productivity (Van Leeuwen 2008). However, the potential for wildfire-contingent differences between treated and untreated stands has not been directly assessed for characteristics relating to ecological resilience to recurring fires.

We take advantage of a series of recent wildfires that burned through fuel treatments in seasonally dry conifer forests in eastern and southern California to ask whether the occurrence of wildfire changes the direction and magnitude of structural differences between treated and adjacent untreated stands (hereafter the "wildfire-contingency hypothesis"). We specifically ask the following questions. (1) Do the effects of fuel treatments on overstory and understory structure, compared with the structure of untreated forest, depend on whether the treatment is subsequently burned in wildfire? (2) Do the effects of fuel treatments on regeneration dynamics depend on whether the forest is burned in wildfire and do they relate to overstory structure? We hypothesized that those forest dynamics that are influenced by the relative abundance of live trees would show wildfire contingency in their response to fuel treatments. We also investigate whether fuel treatments increase forest resilience to first-entry wildfire. Here we specifically test whether the magnitude of structural change in forest characteristics in response to wildfire is lower in forests that had previously been treated relative to previously untreated forests. We argue that understanding how fuel treatments interact with subsequent wildfires is critical because the most effective restoration of fire-prone forests involves repeated occurrences of fire (Reinhardt et al. 2008; North et al. 2012).

Materials and methods

Study sites and field methods

We measured overstory, understory, and regeneration characteristics of 12 recently burned, seasonally dry conifer forest sites throughout eastern and southern California, ranging from the Modoc Plateau in the north to the San Bernardino Mountains in the south. Our 12 sites were all located in montane regions with a Mediterranean climate, in forests dominated by yellow pine species (*Pinus ponderosa* Laws. and (or) *Pinus jeffreyi* Balf.) and white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.), with other species contributing to the canopy trees in varying degrees (Table 1). A map of site locations is presented in Safford et al. (2012). The 12 sites span a gradient in mean annual precipitation from 40.4–180.3 cm annually, with dry season length ranging from 3 to 5 months. The moister sites support a more notable component of shade-tolerant species such as white fir and incense cedar (*Calocedrus decurrens* (Torr.) Florin) than the drier locations (Table 1), but all sites are found within the yellow pine – dry mixed-conifer forest belt (Barbour et al. 2007). In California, these forest types historically experienced frequent surface fires and have undergone increases in tree density, shifts towards shade-tolerant understory trees, and decreases in fire frequency in response to fire suppression (Thorne et al. 2008; Mallek et al. 2013).

We selected sites where a wildfire had burned from an untreated forest stand into a treated forest stand within the previous 5 years and where the treated stand had been treated with a combination of mechanical thinning and surface fuel removal, which included prescribed fire of some sort in all but one case (Table 1). Wildfire severity varied within treated and untreated stands, but at 10 of the 12 sites, there were strong significant differences in severity between stands, with untreated stands having greater char height, crown scorch, and tree mortality (Safford et al. 2012). Because we are making inferences at the stand scale, we consider untreated stands to have higher fire severity than treated stands, while ignoring variation in severity at the substand scale. At each site, we established two to three transects that spanned the fuel treatment boundary and collected data from at least five sampling points on either side of the treatment boundary, with sampling points spaced 20–30 m apart along the transect (Safford et al. 2012). We also established two to three transects that spanned the treatment boundary in adjacent unburned forest, using either the same treatment unit as within the fire perimeter or a treatment unit of approximately the same age. We named sites after the fire name, although hereafter "sites" refers to both unburned and burned transects within a site.

At each plot, we collected data on the condition of the overstory environment, understory environment, and woody plant regeneration. The overstory variables that we measured were basal area (BA), tree density, crown base height, canopy closure, and live-tree cover. All five overstory variables were measured at each sampling point in the study; however, the different data required collection at different plot scales. We calculated BA using a plotless BA factor gauge (Cruz-All, Forestry Suppliers Inc., Jackson, Mississippi) and measured density of trees with diameter at breast height (dbh) > 10 cm within 8 m radius (201 m^2) plots centered at each sampling point, which we scaled up to per-hectare estimates ($m^2 \cdot ha^{-1}$ and trees$\cdot ha^{-1}$ for BA and density, respectively) for both live and dead trees. We measured the crown base height on four nearby trees using the point-centered quarter method (Safford et al. 2012) and aggregated those measurements into a single plot-level mean. For plots in post-wildfire stands, we measured the pre-fire height of the lowest residual branches that survived the fire. As most fires were sampled 2–3 years after the fire, most trees still had residual low branches even when all live foliage had been torched. Canopy closure is a measure of the light environment at a single location, which takes into account the plot surroundings in addition to the light environment directly above the plot, whereas canopy cover estimates the proportion of an area of ground surface covered by live canopy (Jennings et al. 1999). We estimated local canopy cover as the percentage of live-tree cover directly above a 2 m radius (12.57 m^2) plot centered around the sampling point by looking up from plot center and estimating the percentage of the plot covered by live foliage. This small-scale plot was necessary for both improved accuracy and rapid assessment. We calculated the percent canopy closure at each sampling point using a spherical densiometer (Forest Densiometers, Rapid City, South Dakota).

The understory variables that we measured were bare ground cover, woody debris cover, litter (needle) cover, litter depth, and soil moisture. Understory measurements were all taken within the 2 m radius plots. At each plot, we estimated percent cover for each ground cover class, which included basal vegetation, litter, bare ground, rocks, and woody debris (>2 cm diameter). We estimated litter depth to the O horizon, taking the average of three depth measurements made randomly within the circular plot where litter was present. We measured soil moisture using a Field-scout TDR 100 probe (Spectrum Technologies, Plainfield, Illinois), taking the average moisture reading from three random locations within the plot, each integrated across a soil depth of 12 cm. In addition, we estimated cover of all understory (non-tree) vegetation less than 1.4 m in height and divided that estimate into shrub, forb, and graminoid functional groups.

We measured three variables relevant to woody plant regeneration: tree seedling abundance, shrub seedling abundance, and shrub cover. We counted the number of tree and shrub seedlings within each 2 m radius plot. We defined tree seedlings as less than 1.4 m in height and identified them to species following Franklin (1961). We defined shrub seedlings as less than 0.5 m in height, not re-sprouting from the base of a fire-killed shrub, and (for prostrate shrubs) with fewer than five major branching nodes. Shrub seedlings were identified to species, and we also considered shrub cover (described above) to be an indicator of shrub regeneration. We collected data on tree regeneration at the species level, because the resilience of frequent-fire mixed-conifer forests is thought to be enhanced by the regeneration of fire-tolerant pine species relative to fire-intolerant fir and cedar species (Stephens et al. 2008). Tree regeneration is affected by the distance to potential seed sources, which is generally increased by fuel treatments and especially by wildfire (Shive et al. 2013). To relate tree regeneration data to the proximity to potential seed sources, we measured the distance to the nearest adult tree of the same species. We only measured distances for those species that were (*i*) present at the site in question and (*ii*) one of the seven most common species in our study, all of which were found at more than one site. The species were as follows: *A. concolor*, *C. decurrens*, *P. jeffreyi*, *Pinus lambertiana* Douglas, *P. ponderosa*, *Pseudotsuga menziesii* (Mirb.) Franco, and *Quercus kelloggii* Newb. Within a 50 m search radius, we used a laser rangefinder (Tru Pulse 200, Laser Technology Inc., Centennial, Colorado) to measure distances when possible, and a tape measure when our view was obscured. We marked the nearest seed tree as being 50 m when we did not find a tree during our search, unless the topography allowed us to get a rangefinder estimate of a tree that was within view but greater than 50 m. Our search radius was limited because of time constraints; however, in cases where no trees were found within 50 m, a distance estimate of 50 m biases our results in a conservative direction.

Data analysis

To standardize the analysis, to the extent possible, we used data collected 2 years after the year of the fire. For two sites (Harding in 2005 and Grass Valley in 2007), we did not begin data collection until 2010, so data for these two sites are from 5 and 3 years after fire, respectively. At all other sites, all overstory measurements are from 2 years after fire except tree density and canopy closure, which were measured in 2011. All understory and regeneration

Table 1. General information from the sampled fuel treatments, including number of treatments and sampling points, treatment completion date, date burned, and dominant tree species. Modified in part from Safford et al. (2012).

				Fuel treatment						
Fire Name	Stand wildfire status	No. of transects	No. of sample points[a]	Name	Type[b]	Year	Date burned by wildfire	Latitude (N), Longitude (W)	MAP[c]	Dominant tree spp.[d]
American River Complex	Unburned	3	30	Texas Hill–Texas Hill Roadside	1/3	1999?–2008	—	39.211°, 120.588°	180.3	PIPO, ABCO, PILA, CADE
	Burned	3	30	Texas Hill–Dawson Spring	1/2	1999?	30 June–1 July 2008			
Angora	Unburned	3	25	Various	3	2005–2007	—	38.887°, 120.039°	90.7	PIJE, ABCO
	Burned	6	88				24 June 2007			
Antelope Complex	Unburned	2	20	Stony Ridge DFPZ	10	2004	—	40.14°, 120.582°	63.2	PIJE, PIPO, ABCO
	Burned	3	30	Antelope Border DFPZ	4,5	2006	7 July 2007			
Cascadel	Unburned	1	10	Whiskey	9	2002	—	37.249°, 119.444°	106.2	ABCO, PIPO, PILA, CADE
	Burned	1	10				12 September 2008			
Cougar	Unburned	2	20	Unnamed	5	2004	—	41.65°, 121.43°	40.4	PIPO
	Burned	2	20				8 June 2011			
Grass Valley	Unburned	3	30	Tunnel 2	8	2005–2006	—	34.265°, 117.187°	69.3	QUKE, ABCO, QUCH, PIJE, PIPO
	Burned	3	30				22 October 2007			
Harding	Unburned	2	20	Antelope Valley	5	2001	—	39.635°, 120.314°	65.0	PIJE, ABCO, JUCA
	Burned	3	30				26 August 2005			
Milford Grade	Unburned	2	20	Last Chance	4	2005	—	40.109°, 120.389°	51.8	PIJE, ABCO
	Burned	2	19				22 April 2009			
Peterson	Unburned	3	33	Pittville DFPZ	4	2004	—	40.917°, 121.335°	47.2	PIJE, ABCO, JUCA
	Burned	3	45	Pittville DFPZ	6, 7	2006	23–24 June 2008			
Piute	Unburned	2	19	Kelso	7	1999	—	35.502°, 118.337°	57.9	PIJE, ABCO
	Burned	3	35	Kelso	5	1999	8–9 July 2008			
Rich	Unburned	2	30	Kingsbury-Rush	4, 5	2005	—	40.041°, 121.135°	116.6	PIJE, ABCO, PILA, CADE
	Burned	3	20				29 July 2008			
Silver	Unburned	2	30	Meadow Valley	4	2004	—	39.949°, 121.09°	106.4	PIPO, ABCO, CADE, PILA
	Burned	3	20				19 September 2009			
Total		62	664							

[a]Sample points were split approximately equally between treated and untreated stands.

[b]Treatment types: 1, commercial thin + pre-commercial thin + unknown; 2, commercial thin (whole-tree yarding); 3, commercial thin + pre-commercial thin + hand pile + pile burn; 4, pre-commercial thin + hand pile + underburn; 5, commercial thin (whole tree) + underburn; 6, commercial thin + pre-commercial thin + underburn; 7, pre-commercial thin; 8, salvage harvest + pre-commercial thin + chipping + underburn; 9, commercial thin + machine pile + pile burn; 10, underburn only.

[c]Mean annual precipitation, in cm.

[d]ABCO, *Abies concolor*; CADE, *Calocedrus decurrens*; JUCA, *Juniperus californica*; PIJE, *Pinus jeffreyi*; PILA, *Pinus lambertiana*; PIPO, *Pinus ponderosa*; QUCH, *Quercus chrysolepis*; QUKE, *Quercus kelloggii*.

data are from 2 years after fire except for soil moisture, which was measured at all sites in 2012.

Treatment interactions with wildfire

We assessed the independent and interactive effects of treatments and fire using linear mixed-effects models. We modeled the effects of fire and treatment on each of the 13 variables described in the previous section representing characteristics of the overstory, understory, and regeneration. We used mixed models because of the nested grouping structure inherent in the way in which the data were collected — rather than being independent, the plots are nested within transects, which are in turn nested within sites (Gilks et al. 1993; Pinheiro and Bates 2000; Cam et al. 2002). Accordingly, all of the models described in this section contain an identical random effects structure, with a random intercept for transect nested within site. For each response variable, we first assessed the effect of treatment separately in burned and unburned stands by comparing two mixed-effects models: an "intercept-only" null model and a treatment model that also contained fuels treatment as a fixed effect. For each response variable y, the general form of the treatment effects model separated into burned and unburned stands was

$$(1) \qquad y \sim \mathrm{N}(\mu, \sigma);\ \mu = \beta_0 + \beta_1 \times \mathrm{Treatment} + \beta_\mathrm{R}|\mathrm{Site/Tr}$$

where Site is an index for each of the 12 fires, Tr is the transect number nested within a given site, β_0 is the fixed intercept parameter, β_1 is the treatment effect parameter, and β_R is the random intercept parameter. We confirmed that model residuals were approximately normally distributed around their fitted means using quantile–quantile plots; for woody debris cover, the removal of four outlier points strongly improved the normality of the model residuals.

For two variables, the counts of shrub and tree seedlings, we modeled y in a generalized linear mixed model using a Poisson distribution with a log link function:

$$(2) \qquad y \sim \mathrm{Pois}(\lambda);\ \log(\lambda) = \beta_0 + \beta_1 \times \mathrm{Treatment} + \beta_\mathrm{R}|\mathrm{Site/Tr}$$

where the parameter λ describes both the mean and variance of the Poisson distribution and all other terms are as in eq. 1. Parameter estimates were made via maximum likelihood estimation using the LaPlace approximation (Bates et al. 2013). We compared the fits of the two candidate models, treatment and null, using values from Akaike's information criterion corrected for small sample size ($\mathrm{AIC_c}$) (Burnham and Anderson 2004). When the model including treatment was preferred over the null by this criterion, i.e., $\mathrm{AIC_c}$ at least two points smaller, we concluded that fuel treatments played a meaningful role in explaining variation in our response variable of interest (Bolker 2008). Though $\Delta\mathrm{AIC_c}$ values > 2 indicate a detectable fixed effect of treatment on the variable of interest, while accounting for variability across different sampling locations, we note that the magnitude of this difference between $\mathrm{AIC_c}$ values further informs the strength of the treatment effect and is not equivalent to a "statistically significant effect" that would be interpreted from a frequentist hypothesis test (Bolker 2008; Bolker et al. 2009).

After describing the separate effects of fuel treatments in burned and unburned stands, we pooled the burned and unburned data and tested the wildfire contingency hypothesis for each response variable using a mixed-effects model with an interaction term between wildfire and treatment:

$$(3) \qquad y \sim \mathrm{N}(\mu, \sigma);\ \mu = \beta_0 + \beta_1 \times \mathrm{Treatment} + \beta_2 \times \mathrm{Fire} + \beta_3 \times \mathrm{Treatment} \times \mathrm{Fire} + \beta_\mathrm{R}|\mathrm{Site/Tr}$$

where β_2 is the wildfire effect parameter, β_3 is the interaction parameter, and $y \sim \mathrm{Pois}(\lambda)$ in the case of the seedling count variables, as described in eq. 2. We compared this wildfire-contingency model with the same model without the interaction term. In this case, when the model with the interaction term was preferred, as indicated by $\Delta\mathrm{AIC_c} > 2$, we concluded that the effect of treatment on the variable in question was different following wildfire compared with the effect of treatment without wildfire.

Tree regeneration responses to treatment

We analyzed the effect of treatments on tree seedling abundance at the species level and evaluated whether the distance to the nearest live adult tree could explain potential wildfire-contingent effects of treatment. Our approach was to (1) model the effect of treatments on seedling abundance for each species, (2) model the effect of treatments on average distance to the nearest live adult tree for each species, and (3) look for a direct effect of distance without incorporating information on treatments into the model. In each case, we separated the data into burned and unburned forest stands. We modeled the effect of treatment on the per-plot seedling count using the mixed-effects model described in eq. 2. We then estimated the effects of treatment on the distance to the nearest live adult tree separately for burned and unburned stands. We used a Gaussian mixed-effects model with a square-root link function to stabilize the variance in the distance data y:

$$(4) \qquad y \sim \mathrm{N}(\mu, \sigma);\ \sqrt{\mu} = \beta_0 + \beta_1 \times \mathrm{Treatment} + \beta_\mathrm{R}|\mathrm{Site/Tr}$$

where μ is the predicted distance in either burned or unburned stands, and β_1 is the effect of fuel treatments on distance. We compared this model with a null model without a treatment effect using $\mathrm{AIC_c}$ values. When the treatment model had the most support ($\Delta\mathrm{AIC_c} > 2$), we interpreted this to mean that fuel treatments modified the average distance to a potential seed source. We finally modeled the effect of nearest live adult tree distance on seedling abundance for each species:

$$(5) \qquad y \sim \mathrm{Pois}(\lambda);\ \log(\lambda) = \beta_0 + \beta_1 \times \mathrm{Distance} + \beta_\mathrm{R}|\mathrm{Site/Tr}$$

Comparing this model with a null model of seedling abundance allowed us to evaluate whether distance to potential seed source had a direct influence on abundance ($\Delta\mathrm{AIC_c} > 2$) without using treatment as a proxy variable. We expected that for species where treatment affected both seedling abundance and distance, that distance would be able to directly explain variation in seedling abundance.

Multivariate ordination

To distill the variation in overstory, understory, and regeneration parameters in our dataset into fewer dimensions, we used nonmetric multidimensional scaling (NMDS) as implemented in the vegan package in R (Oksanen et al. 2011). Our objective was to categorize each of our 664 sample plots along two composite axes of variation and then compare the centroids of the data for each of four forest types representing a factorial combination of burned–unburned and treated–untreated to determine the structural similarity of the four forest types. We included all data described above, including data on the overstory, understory, and woody plant regeneration, as well as forb cover and graminoid cover, which were not included in the analyses above. We excluded crown base height, canopy closure, and soil moisture data from the analysis because we did not have complete data for these variables at all sites. The analysis included a total of 13 variables describing forest characteristics, which were aligned into two NMDS axes for visualization. In addition, we overlaid a matrix of predictor variables on top of the ordination space to explain

Table 2. Model comparison and parameter estimates of treatment effects on each measured variable.

Response variable	Burned	Treatment effect	95% Confidence interval	ΔAIC_c[a]	ΔAIC_c interaction[b]	Wildfire contingent treatment effect[c]
Total basal area	No	−8.07	−11.66, −4.48	16.48	8.439	Yes
	Yes	−1.26	−3.72, 1.2	1.05		
Total density	No	−245.36	−302.4, −188.32	60.39	8.146	Yes
	Yes	−129.67	−173.31, −86.03	30.54		
Crown base height	No	0.62	0.04, 1.2	1.88	0.044	No
	Yes	0.27	−0.2, 0.74	−0.78		
Canopy closure	No	−5.43	−10.09, −0.77	5.42	58.755	Yes
	Yes	18.68	15.06, 22.3	88.07		
Tree cover	No	−19.44	−27.22, −11.66	20.86	52.717	Yes
	Yes	13.22	8.55, 17.89	27.20		
Litter depth	No	−0.85	−1.28, −0.42	12.75	36.820	Yes
	Yes	0.5	0.31, 0.69	22.40		
Litter cover	No	0.26	−5.04, 5.56	−2.07	10.802	Yes
	Yes	14.79	9.46, 20.12	26.51		
Bare ground	No	1.08	−3.12, 5.28	−1.82	8.118	Yes
	Yes	−9.84	−14.57, −5.11	14.28		
Woody debris	No	−2.72	−6.22, 0.78	0.24	0.052	No
	Yes	−0.67	−2.12, 0.78	1.87		
Soil moisture	No	0.74	0.06, 1.42	2.38	17.27	Yes
	Yes	−1.39	−2.01, −0.77	16.61		
Tree seedlings	No	−0.2	−0.33, −0.07	7.6	84.038	Yes
	Yes	0.53	0.44, 0.62	143.19		
Shrub seedlings	No	0.26	−0.06, 0.58	0.59	24.123	Yes
	Yes	−0.59	−0.67, −0.51	196.29		
Shrub cover	No	1.54	−3.15, 6.23	1.67	10.197	Yes
	Yes	−8.36	−11.83, −4.89	19.63		

[a]ΔAIC_c values show the change in support based on the AIC value for the treatment model (eq. 2) minus the AIC value for the null model.

[b]ΔAIC_c values for the interaction model show the change in support based on the AIC value for the interaction model (eq. 3) minus the AIC value for the treatment model with a wildfire parameter.

[c]A meaningful contribution of interaction term based on $\Delta AIC_c > 2$, supporting wildfire contingency hypothesis.

variation in plot data using fire (1/0), fuel treatment (1/0), and mean annual precipitation from 1981–2010, because our sites spanned a strong precipitation gradient from 40.4 cm·year^{-1} (Cougar) to 180.3 cm·year^{-1} (American River). We compared differences among four disturbance classes representing the factorial combination of the two disturbance regimes (burned–unburned and treated–untreated) using a multivariate analysis of variance (ANOVA) using the adonis R function in the vegan package (Oksanen et al. 2011). We compared individual disturbance classes with each other by creating subsets of the data to include all possible pairwise forest type comparisons and re-running the multivariate ANOVA.

Results

Wildfire contingency in treatment effects: overstory and understory

Models that included an interaction between fuel treatments and wildfire effects had the most support ($\Delta AIC_c > 2$) for 11 of the 13 response variables that we examined, providing strong support for the wildfire-contingency hypothesis (Table 2). We found support for wildfire-contingent effects of treatments for four of the five overstory-structure variables that we modeled. Treatments reduced total basal area and tree density in the absence of wildfire, as they are designed to do (Table 2; Fig. 1). In burned forest, a much higher proportion of basal area and tree density were in live biomass (Fig. 1) due to the ameliorating effects of treatments on tree mortality. Although total basal area was comparable across treatment boundaries in burned stands, total tree density after wildfire was detectably lower in treatments (Table 2), indicating that the surviving trees in the treatments were generally large-diameter trees (Fig. 1). Pre-fire live crown base height was the only variable for which the interaction model did not have the most support (Table 2). It is possible that our estimates of pre-fire crown base height were biased in post-wildfire stands by incineration of lower branches or that treatment effects were underestimated by using mean heights instead of lower quantiles (e.g., Fulé et al. 2002), yet the results trend in the direction that we expect, given that the data were based on pre-fire estimates. Canopy closure and live-tree cover both showed strong effects of treatment: without wildfire, treatments reduced closure and cover by an average of 5.43% and 19.44%, respectively, whereas with wildfire, closure and cover were higher in treated areas by an average of 18.68% and 13.22%, respectively (Table 2; Figs. 2*b*, 2*c*).

Most understory characteristics also exhibited wildfire-contingent treatment effects (Table 2; Fig. 3). Importantly, treated forest exhibited greater similarity between burned and unburned areas for each of these understory characteristics. Changes in litter depth were largely expected based on patterns of live-tree density: in unburned areas, treated stands had shallower litter layers than untreated stands, but in burned areas, treated stands had deeper litter layers than untreated stands (Fig. 3*a*). Unburned stands did not exhibit detectable treatment effects on litter cover or bare ground cover, and burned stands had less litter and more bare ground than unburned stands, as expected (Figs. 3*b*, 3*c*). However, the magnitude of reduction in litter cover, and increase in bare ground cover, caused by wildfire was much greater in untreated stands (Figs. 3*b*, 3*c*). Treated stands had slightly lower woody debris both with and without wildfire, but these differences had very weak support in our model (Table 2). Finally, treated stands had higher soil moisture than untreated stands in the absence of wildfire but had lower soil moisture than untreated stands following wildfire, a pattern likely tied to live tree density (Fig. 3*e*).

Wildfire contingency in treatment effects: regeneration

The effects of fuels treatments on woody plant regeneration were also contingent on whether or not wildfire occurred (Table 2).

Fig. 1. Combined treatment and wildfire effects on the overstory variables (*a*) basal area and (*b*) stand density. Dark and light gray bars represent the fraction of the total stand comprised of dead and live biomass, respectively. Bars represent mean values, and error bars represent ±1 SE around the mean for a particular mortality class.

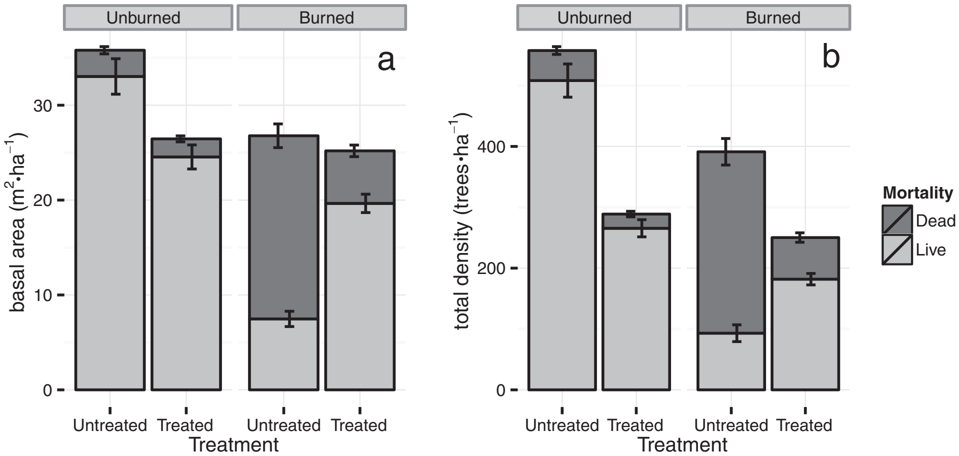


Fig. 2. Combined treatment and wildfire effects on the overstory characteristics (*a*) height to live crown base, (*b*) canopy closure, and (*c*) canopy cover. Bars indicate mean values for untreated (gray) and treated (white) stands, and error bars represent ±1 SE around the mean. Asterisks represent detectable differences between treated and untreated stands, based on ΔAIC_c values > 2 when the treatment model had the most support (Table 2).

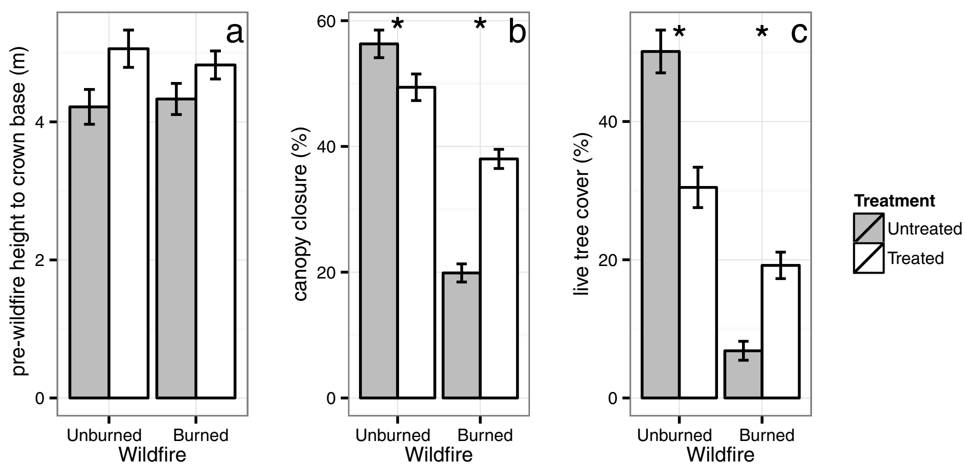


Fig. 3. Combined treatment and wildfire effects on the understory characteristics (*a*) litter depth, (*b*) litter cover, (*c*) bare ground cover, (*d*) woody debris cover, and (*e*) soil moisture. Bars indicate mean values for untreated (gray) and treated (white) stands, and error bars represent ±1 SE around the mean. Asterisks represent detectable differences between treated and untreated stands based on ΔAIC_c values > 2 when the treatment model had the most support (Table 2).

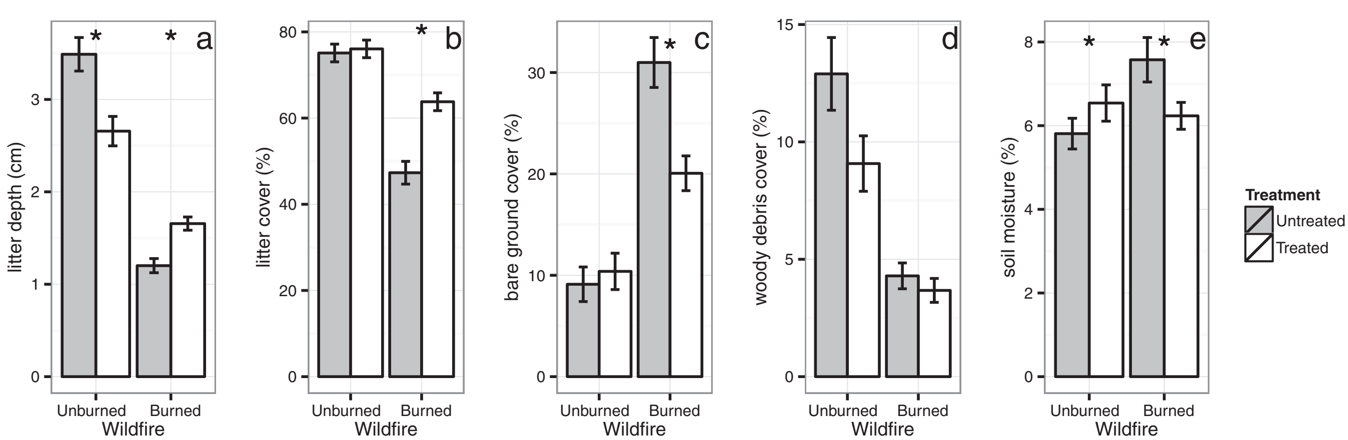


Fig. 4. Combined treatment and wildfire effects on the regeneration characteristics (*a*) tree seedlings·ha⁻¹, (*b*) shrub seedlings·ha⁻¹, and (*c*) shrub cover. Bars indicate mean values for untreated (gray) and treated (white) stands, and error bars represent ±1 SE around the mean. Asterisks represent detectable differences between treated and untreated stands based on ΔAIC_c values > 2 when the treatment model had the most support (Table 2).

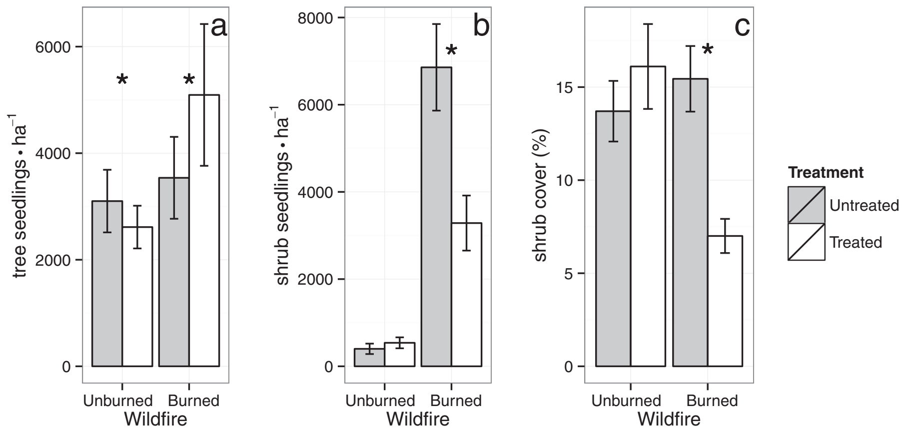


Table 3. Treatment effects on seedling counts and nearest-tree distances, for the seven most common species in this study.

		Treatment effect on log(seedling abundance)		Treatment effect on √(distance to nearest tree)		Distance effect on log(seedling abundance)	
Species[a]	Burned	Coefficient[b]	ΔAIC_c[c]	Coefficient[b]	ΔAIC_c[c]	Coefficient[b]	ΔAIC_c[c]
ABCO	No	**−1.05**	24.96	0.46	1.89	0.00	−2.1
	Yes	**0.71**	115.54	**−2.28**	90.42	**−0.08**	1471.98
CADE	No	**−0.37**	6.99	0.13	−1.80	**−0.07**	69.87
	Yes	**1.51**	124.42	**−0.74**	7.32	**−0.07**	172.9
PIJE	No	**−1.65**	12.57	0.11	−1.91	−0.10	1.5
	Yes	**1.80**	95.9	**−1.66**	56.50	**−0.14**	213.02
PILA	No	**−0.67**	11.79	0.32	−0.87	0.05	1.89
	Yes	**1.43**	107.55	**−1.02**	11.18	**−0.05**	101.77
PIPO	No	−0.56	1.15	0.06	−2.06	0.00	−2.07
	Yes	**0.37**	2.76	**−1.68**	39.41	**−0.04**	36.47
PSME	No	**0.76**	9.35	0.42	1.08	−0.02	−0.89
	Yes	**−0.98**	29.79	−0.31	−1.16	0.01	−1.54
QUKE	No	**−2.46**	40.06	0.67	0.83	−0.01	−1.14
	Yes	1.53	0.42	−0.50	1.68	−0.01	−1.87

[a]Species codes are as in Table 1.
[b]Non-zero coefficients, determined by $\Delta AIC_c > 2$, are shown in bold.
[c]ΔAICc is change in Akaike's information criterion, corrected for small sample sizes, between candidate model and null model, where candidate models were as shown in eq. 2 (treatment effect on seedling abundance), eq. 4 (treatment effect on distance), or eq. 5 (distance effect on seedling abundance).

In forests without wildfire, mean tree seedling abundance in treated stands compared with untreated stands was reduced by 925 tree seedlings·ha⁻¹, but with wildfire, mean tree seedling abundance increased in treatments by approximately 1556 seedlings·ha⁻¹ relative to untreated stands (Fig. 4*a*). The opposite pattern was observed for shrubs: in forests without wildfire, treatments did not have a detectable effect on shrub seedling abundance, whereas in post-wildfire forests, shrub seedling abundance was greater in untreated stands by over 3272 seedlings·ha⁻¹ relative to treated stands (Fig. 4*b*). Similarly, treatments did not have a detectable effect on shrub cover in unburned forest, whereas in burned forest, shrub cover in untreated stands was 8.4% higher than in treated stands (Table 2; Fig. 4*c*).

When we examined species-specific tree regeneration responses to treatment, we found a similar pattern for the majority of the species: ΔAIC_c comparisons supported a negative effect of treatment on tree seedling abundance in unburned forest and a positive effect of treatment on tree seedling abundance in burned forest (Table 3). Treatments decreased seedling abundance for five of the seven most common species in unburned forest (ABCO, CADE, PIJE, PILA, and QUKE; species codes are given in Table 1), whereas in burned forest, five species (ABCO, CADE, PIJE, PILA, and PIPO) had higher seedling abundance in treated stands (Figs. 5*a*–5*e*). Douglas-fir (PSME) showed the opposite pattern (Fig. 5*f*), while black oak (QUKE) had very low seed regeneration after fire.

As we expected, the patterns in species-specific seedling abundance were related to patterns of distance to the nearest potential seed source. For each of the five species that had more seedlings in treated stands than untreated stands following wildfire, based on ΔAIC_c comparisons, there was also a detectably shorter average distance to the nearest live adult tree in treated stands (Figs. 5*h*–5*l*; Table 3). For each of these species, there was also a direct effect of distance on seedling abundance in the burned stands (Table 3). For Douglas-fir and black oak, there was neither a detectable difference in distance between treated and untreated stands nor a detectable effect of distance on seedling abundance, based on ΔAIC_c comparisons (Table 3; Figs. 5*m*, 5*n*). In both the treated and untreated stands that had burned, seedlings of the two fire-tolerant yellow pine species (PIJE and PIPO) had the shortest average

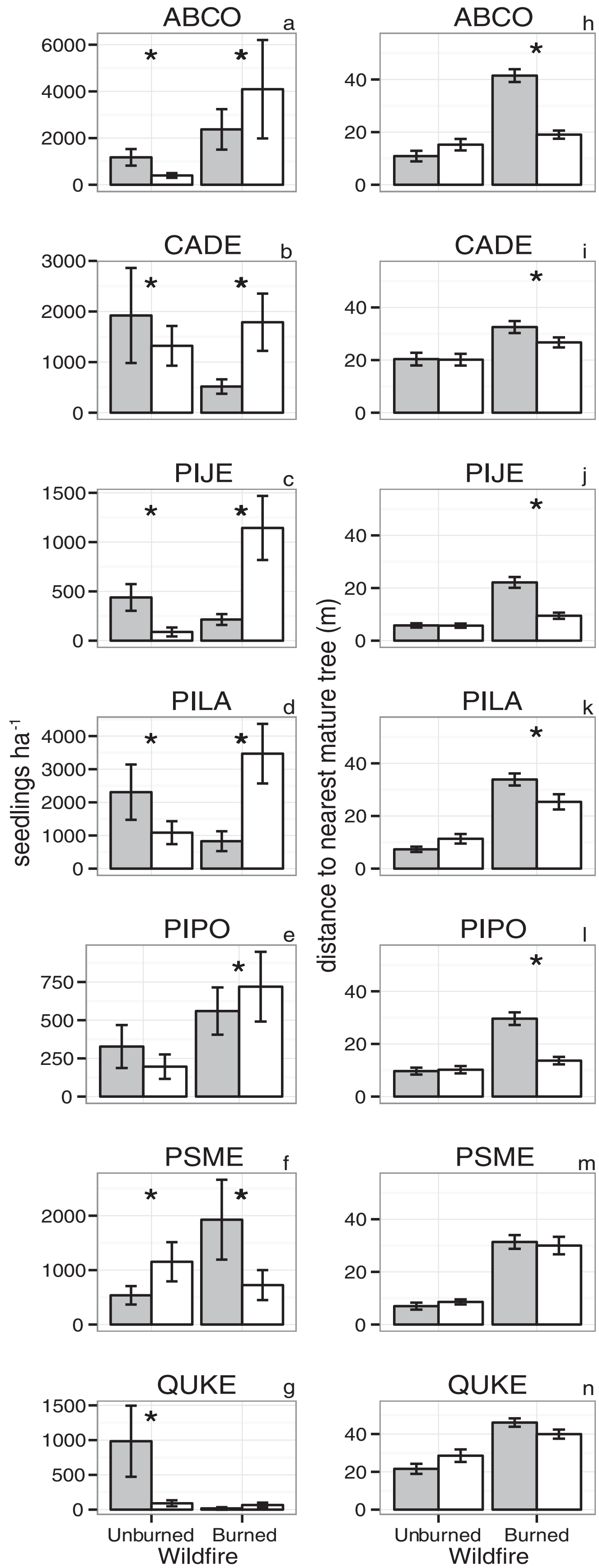


Fig. 5. Combined treatment and wildfire effects on seedling counts (left column) and distances to the nearest live adult tree (right column) for the seven most common tree species observed in this study. Bars indicate mean values for untreated (gray) and treated (white) stands, and error bars represent ±1 SE around the mean. Asterisks represent detectable differences between treated and untreated stands based on ΔAIC_c values > 2 when comparing the model in eq. 2 with a null model for seedling counts (left column) or when comparing the model in eq. 4 with a null model for distances to the nearest live adult tree (right column). Species: ABCO, *Abies concolor*; CADE, *Calocedrus decurrens*; PIJE, *Pinus jeffreyi*; PILA, *Pinus lambertiana*; PIPO, *Pinus ponderosa*; PSME, *Pseudotsuga menziesii*; QUKE, *Quercus kelloggii*.

distances to potential seed sources, yet they also had among the lowest seedling abundances of all of the species (Fig. 5). Within unburned stands, treatment did not have a detectable effect on distance to the nearest live adult tree for any species (all $\Delta AIC_c < 2$), suggesting that in unburned sites, the direct removal of seedlings by the treatment is responsible for the decrease in seedling abundance rather than an indirect effect on seed dispersal.

Multivariate ordination

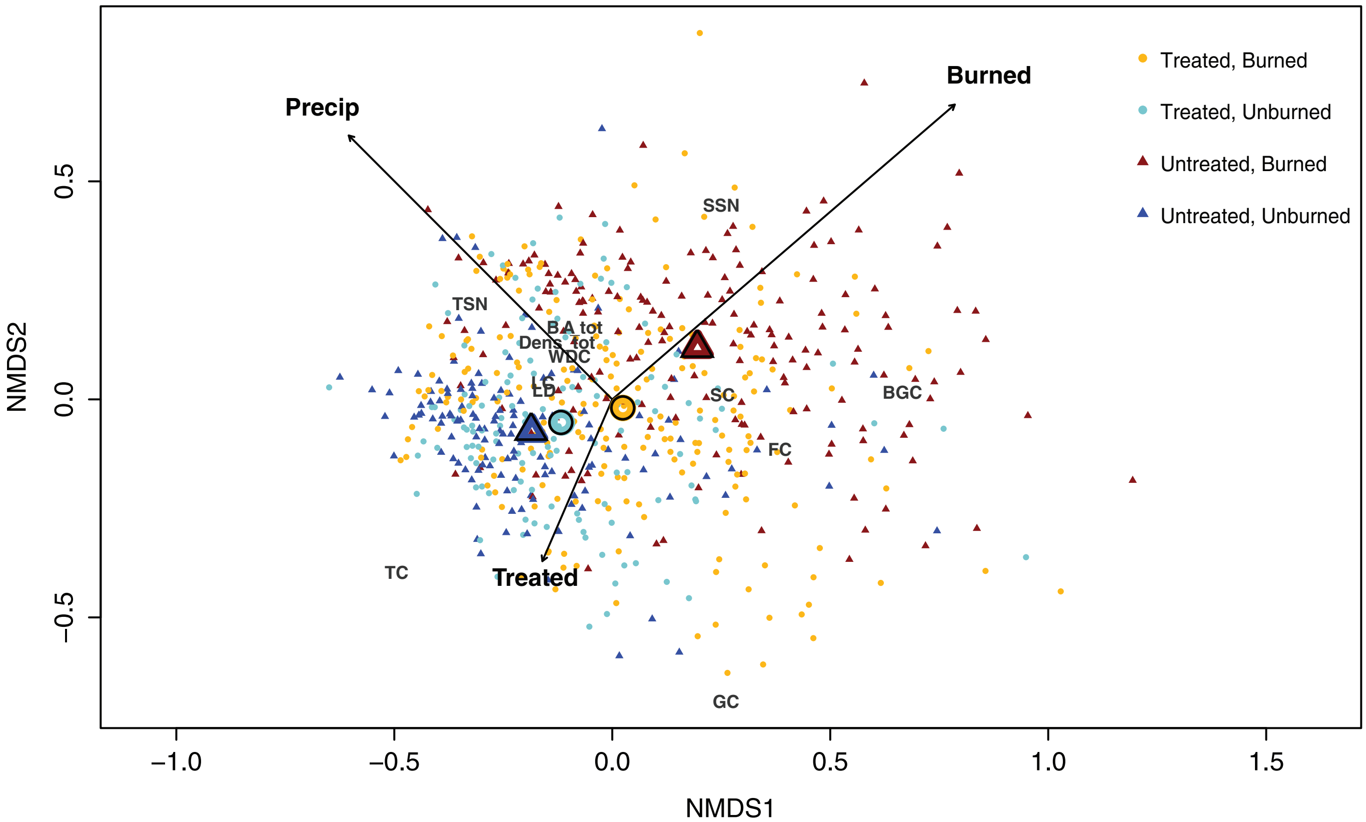
The occurrence of wildfire was the strongest predictor of plot characteristics, although treatment and mean annual precipitation were also important (Fig. 6). The centroids of the four forest types (untreated–unburned, treated–unburned, treated–burned, and untreated–burned) aligned roughly along the axis explained by fire in two-dimensional space (Fig. 6). The relative positioning of the data centroids for each forest type indicated that the magnitude of change in burned stands compared with unburned stands was much greater in forest that had not been treated. The average positions of the four forest types in multivariate space were significantly different from each other ($F = 23.25$, $P < 0.001$). Post hoc comparisons of the data subset into different pairwise combinations of the four forest types confirmed that each group was significantly different from all others ($F > 6.61$, $P < 0.001$). Much of the variation that is orthogonal to the burned-treated axis is explained by precipitation, with drier sites having greater herbaceous cover and wetter sites having greater tree density and basal area and more tree seedlings.

Discussion

We draw two principal conclusions from this work, which both indicate that fuel treatments are an important precursor to restoring an active fire regime in seasonally dry forests that historically experienced frequent fires. First, differences in forest structure and regeneration between treated and adjacent untreated stands are strongly contingent on whether the forest subsequently burns in a wildfire, driven largely by differences in live-tree density before and after wildfire. Second, resilience of fire-suppressed forests to first-entry wildfires is demonstrably increased by fuel treatments. We argue that the initial structural differences caused by treatments are the reason for the observed resilience to first-entry wildfires. Furthermore, we predict that the structural differences between treated and untreated forest stands following wildfire will contribute to the continued resilience of treated stands to future wildfires.

Most of the wildfire-contingent differences in structure between treated and untreated forest stands are attributable to differences in live-tree density in untreated stands before and after wildfire (Fig. 1*b*). That untreated stands have lower density of live trees following wildfire relative to treated stands is the direct result of the moderating effect of fuel treatments on fire severity (Safford et al. 2012; Martinson and Omi 2013). It follows that canopy cover and closure will be highest in untreated stands before

Fig. 6. Nonmetric multidimensional scaling of sample plots across all fires. Points represent individual sample plots, and their colors correspond to the disturbance status of each plot: untreated–unburned (dark blue), treated–unburned (light blue), treated–burned (orange), and untreated–burned (dark red). The data centroids of these four forest types are shown as large hollow symbols in ordination space. Vector arrows and associated variable names in bold indicate the location and magnitude of independent variable effects. Plain-text variable names indicate the spatial orientation of plot-level dependent variables used in the ordination: TC, live-tree cover; GC, grass cover; FC, forb cover; SC, shrub cover; BGC, bare ground cover; LC, litter cover; LD, litter depth; WDC, woody debris cover; Dens_tot, stand density of live + dead trees; BA_tot, stand basal area of live + dead trees; TSN, tree seedling number; SSN, shrub seedling number (all units are given in the text).



wildfire and lowest in untreated stands after wildfire. The greater litter depth in treated stands than in untreated stands after wildfire is most likely due to continued needle cast by surviving trees, which are more abundant in treated areas where fire severity tends to be low (Hall et al. 2006), whereas the reduced litter depth in treated stands without wildfire is likely due to the combined effects of reduced canopy cover and surface fuel reduction implemented as part of the treatment. Soil moisture was consistently lower in treated stands than in untreated stands after wildfire but consistently higher in treated stands than in untreated stands without wildfire, suggesting that transpiration by live trees is driving the treatment effects on soil moisture (Wayman and North 2007).

The density of live trees also influenced wildfire-contingent differences in regeneration between treated and untreated stands. Untreated forest that burns at high severity creates high light conditions that, along with the scarifying effects of high-intensity fire on the seeds of fire-stimulated species (e.g., the *Ceanothus* and *Arctostaphylos* species that dominate the shrub layer in most of our plots), promote shrub germination and rapid growth (Franklin 2010). Treatments that reduce fire severity should, therefore, also reduce shrub recruitment after wildfire (Shive et al. 2013). Our data support this prediction, with untreated stands containing more shrub seedlings than treated stands (Fig. 4*b*) and with shrub cover already returning to pre-fire levels only 2–5 years after fire (Fig. 4*c*). Differences in live-tree density across treatment boundaries affected tree regeneration due, in part, to proximity to seed sources. For the five species that had detectably more seedlings in treated stands than in untreated stands after wildfire, each also had a shorter distance to live adult trees in treated stands, suggesting that distance to potential seed sources is an important predictor of the amount of post-fire conifer regeneration (Shive et al. 2013).

We demonstrate that forest structural conditions associated with prolonged fire suppression in the seasonally dry forests of eastern California have dramatically weakened their resilience to first-entry wildfires. In the forests that we studied, human management and the nearly complete lack of fire over the last century have profoundly homogenized forest structure and process, and contemporary forests are marked by novel ecological conditions that bear little resemblance to historical forest conditions (Sugihara et al. 2006; North et al. 2009*b*). Our data show that when these homogenous, unmanaged, fire-suppressed stands burn in wildfire, their ecological characteristics change dramatically, with post-fire stands characterized by dramatically lower live-tree cover, lower tree recruitment, higher shrub cover, and dramatically higher shrub recruitment and bare ground cover (Fig. 6). This suggests that the more severely burned areas in untreated forest may tend to remain in an altered, early seral state for a prolonged period. Although these early seral conditions are important components of a heterogeneous forest mosaic (North et al. 2009*b*; Swanson et al. 2011), if these conditions occur across a high proportion of the landscape and in unusually large patches, this would depart from the historical forest structure promoted by frequent low- and mixed-severity fires (Sudworth 1900; Scholl and Taylor 2010). Conversely, previously treated stands experience a much lower magnitude of ecological change, on average, while maintaining a high degree of structural heterogeneity following wildfire (Fig. 6), indicating that treated stands are much more resilient to first-entry wildfires. Because many of these structural changes are related to the density of live trees, the reduction in wildfire severity due to the reduction of pre-wildfire live-tree density is the driving force behind this resilience (Safford et al. 2012). Importantly, the resilience conferred by fuel treatments applies to forests across a strong precipitation gradient (Fig. 6), suggesting that fuel treatments in less productive forests in this region can still confer resilience to first-entry wildfires.

In addition to the demonstrated resilience of treated stands to first-entry wildfires, we suggest that these stands also have increased resilience to recurring wildfires. With wildfire frequency expected to increase in the western US, the likelihood of stands burning multiple times is increasing (Westerling et al. 2006). Differences in fuel structure and vegetation between treated and untreated stands in our study suggest that treated stands would likely remain forests in the event of a second-entry wildfire. The surviving trees were larger (greater basal area per tree; Fig. 1), litter cover was greater, and shrub regeneration was lower than in untreated stands after wildfire, suggesting that subsequent wildfires would likely be low- to mixed-severity fires. However, second-entry burns in high-severity stands often continue to burn at high severity due to the continuous fuel bed of shrubs and re-sprouting trees, which can lead to continued dominance by these growth forms (Donato et al. 2009; Thompson and Spies 2010). Therefore, untreated stands that re-burn at high severity may exhibit delayed succession to coniferous forests under increasing fire frequency.

We highlight two important considerations for management of seasonally dry coniferous forests. First, although fuel treatments are often implemented as surrogates for wildfire, our data show that they are not true fire surrogates. Additional structural change occurred when treated stands subsequently burned in wildfire, including reductions in tree density and canopy closure, decreases in litter depth and cover, and increases in tree and shrub regeneration. Although treatments move forests towards those characteristics associated with fire, the position of the treated–burned centroid in the NMS ordination (Fig. 6) suggests that any wildfire, even the more moderate fire intensities characteristic of treated areas, causes more ecological change in forests than the act of treatment alone. Thus, in forests such as seasonally dry, mixed-conifer stands of California, which historically burned at short return intervals (Stephens et al. 2007; Van de Water and Safford 2011), implementing fuel treatments alone may not be sufficient to restore conditions found under frequent fires, but rather, subsequent introduction of managed wildfire is likely necessary to further restore these conditions (North et al. 2012).

Second, under conditions of increasing wildfire frequency, fuel treatments can help maintain valuable ecosystem services in these forests. The need for these treatments is particularly strong because current suppression policy generally allows wildfire to escape to burn large areas only when fire weather is at high to extreme levels, when effects on historically suppressed forests are most severe. One criticism of fuel treatments is that they induce changes to forest structure and process that may be detrimental to potentially competing ecosystem services such as provision of wildlife habitat or carbon storage (Lee and Irwin 2005; Pilliod et al. 2006; Campbell et al. 2012). However, Stephens et al. (2012), in a recent synthesis of the ecological effects of fuel treatments in seasonally dry forests, found that direct treatment effects on many ecosystem components, including understory diversity, soil erosion and compaction, wildlife habitat, and bark beetle damage, are relatively minor and short-lived. Similarly, our data show that the extent of forest change that is attributable to fuel treatments alone is considerably less than the extent of change attributable to wildfire without fuel treatments (Fig. 6). This scenario of wildfire contingency is therefore a potential win–win for managers, provided that fuel treatments are viewed as a tool to restore fire into a system, so that fire can continue to maintain conditions that fuel treatments restored, rather than as an alternative to restoration of a natural fire regime, which would achieve more limited and short-term benefits (North et al. 2012). When properly applied, fuel treatments may reduce the chance of hysteresis caused by a century of fire suppression and facilitate restoration of functional disturbance regimes in treated stands.

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