

Potential wildfire and carbon stability in frequent-fire forests in the Sierra Nevada: trade-offs from a long-term study

DANIEL E. FOSTER,^{1,†} JOHN J. BATTLES,¹ BRANDON M. COLLINS,^{2,3} ROBERT A. YORK,¹ AND SCOTT L. STEPHENS¹

¹*Ecosystem Sciences Division, Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720 USA*

²*Center for Fire Research and Outreach, University of California, Berkeley, California 94720 USA*

³*USDA Forest Service, Pacific Southwest Research Station, Davis, California 95618 USA*

Citation: Foster, D. E., J. J. Battles, B. M. Collins, R. A. York, and S. L. Stephens. 2020. Potential wildfire and carbon stability in frequent-fire forests in the Sierra Nevada: trade-offs from a long-term study. *Ecosphere* 11(8):e03198. 10.1002/ecs2.3198

Abstract. Forests are the largest terrestrial carbon stock, and disturbance regimes can have large effects on the structure and function of forests. Many dry temperate forests in the western United States are adapted to a regime of frequent, low-to-moderate severity fire. The disruption of this disturbance regime over the last century has shifted forest conditions, making them more susceptible to high-severity fire. Fuel treatments have been shown to effectively reduce wildfire hazard, often with co-benefits to ecological values. However, the effects of fuel treatments on forest carbon are complex, often characterized by direct costs (e.g., carbon emissions from prescribed fire) and wildfire-contingent benefits (increased resistance of live tree carbon to wildfire). In this study, we employ risk-sensitive carbon accounting and empirical data from a replicated field experiment to evaluate the stand-scale carbon effects of four management regimes over a 14-yr period in a historically frequent-fire adapted forest. All three active treatment regimes immediately increased stable live tree carbon stocks over no-treatment controls. In most contexts examined, mechanical-only or no-treatment controls will maximize expected total carbon stocks when incorporating wildfire risk and the carbon stability of live biomass, dead biomass, and offsite forest products, although we acknowledge our wildfire modeling may underestimate C losses, particularly in the control stands. Undoubtedly, many other ecosystem and social values besides carbon will be important factors that influence fuel and restoration treatments.

Key words: fire risk; fire surrogate; forest restoration; fuel reduction; fuel treatments.

Received 22 April 2020; **accepted** 28 April 2020; **final version received** 3 June 2020. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2020 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** danfoster@berkeley.edu

INTRODUCTION

Forest ecosystems worldwide represent a major terrestrial pool of carbon and may function as sinks or sources of carbon (Pan et al. 2011). Long-term modeling suggests that intact disturbance regimes have little long-term effect on terrestrial carbon stocks, as biomass losses are replaced by forest recovery (Hurteau and Brooks 2011). In contrast, disruptions to disturbance

regimes can durably alter carbon stocks by driving type conversion of forests to other ecosystems (Kashian et al. 2006, Landry and Matthews 2016). Disruption to the disturbance regime (and the impact of these disruptions on carbon storage) is a pressing issue in the extensive frequent-fire forests of the American west (Fulé et al. 2012, Hessburg et al. 2016). For example, the California mixed conifer forest (MCF) covers more than 32,000 km² and stores approximately 664 TgC

(Christensen et al. 2017). Historically, the structure and function of the MCF were maintained by natural disturbances, most notably frequent low-to-moderate severity fire. In the 20th century, Euro-American patterns of land use (i.e., timber harvesting and fire exclusion) altered this disturbance regime. Consequently, much of the MCF has accumulated a large disturbance debt in the last century, resulting in contemporary forests which are denser, younger, more carbon-rich, and more homogeneous than they were historically (North et al. 2012, Stephens et al. 2015, Levine et al. 2016, Safford and Stevens 2017, Lydersen and Collins 2018).

In addition to these considerable structural changes, forest carbon stored in necromass has increased in long-unburned MCF, as surface fuels and snags have accumulated in California's Mediterranean climate (Cousins et al. 2015, Safford and Stevens 2017). The combined effects of these changes increase susceptibility to uncharacteristic patterns of high-severity wildfire (Taylor et al. 2014) and reduce the stability of forest carbon stocks (Hurteau and Brooks 2011). Wildfires in forests account for a disproportionate share of recent declines in California's carbon stocks and can cause long-term type conversions to other ecosystem types (Stevens et al. 2014, Gonzalez et al. 2015, Hessburg et al. 2016, Stephens et al. 2020a). This trend is expected to continue given projected climatic conditions, threatening forests' carbon stocks and their ability to sequester additional carbon (Westerling et al. 2011, Liang et al. 2017).

Fuel reduction treatments can effectively mitigate fire behavior and effects in both simulated and real-world wildfires at the stand scale (Stephens and Moghaddas 2005, Safford et al. 2009, Stephens et al. 2009a, North and Hurteau 2011, Fulé et al. 2012, Stevens et al. 2014, Kalies and Yocom Kent 2016). However, given the potential for carbon sequestration in forests it is essential to understand the impact of these treatments on carbon stocks, carbon fluxes, and carbon stability in order to inform forest management (Finney 2005, Fahey et al. 2010, Chiono et al. 2017). Some of the carbon-related effects of fuel treatments are inherent in their implementation (direct effects), while others are contingent upon whether stands experience wildfire (indirect effects; Carlson et al. 2012, Stephens et al. 2012). Even if direct effects reduce standing carbon

stocks, fuel treatments may provide net benefits over the long term by protecting forest carbon stocks from future wildfire-related losses and facilitating the return of large fire-resistant trees as key structural features (Hurteau and North 2009, Stephens et al. 2009b). However, it is also possible that the indirect carbon benefits produced will be insufficient to overcome the direct costs of treatment installation and maintenance (Ager et al. 2010, Campbell et al. 2012, Chiono et al. 2017). The key question is whether fuel treatments provide a net carbon benefit (Hurteau et al. 2008, Hurteau and North 2009, Campbell et al. 2012, Liang et al. 2018). The answer is a function of the carbon costs of the treatments (e.g., emissions from prescribed fires, reductions in forest productivity), their carbon benefits (e.g., increased productivity, increased resistance to wildfire), and the probability of a wildfire.

This study advances the current understanding of direct and indirect carbon impacts associated with fuel treatment by using a risk-sensitive carbon accounting of carbon stocks. Previous studies have employed empirical data to describe fuel treatment effects on carbon but estimating wildfire-contingent indirect effects has been done with modeling (e.g., Hurteau and North 2009, Stephens et al. 2009b, 2012, Wiechmann et al. 2015) or post-fire field measurements (e.g., North and Hurteau 2011). While simulations are necessary to incorporate the stochastic nature of wildfire occurrence in the calculation of indirect effects (Ager et al. 2010, Hurteau et al. 2016, Chiono et al. 2017, Liang et al. 2017, 2018, Krofcheck et al. 2018), we minimized the reliance on models by taking advantage of a long-term experiment to quantify disturbance effects on forest carbon dynamics. Such long-term studies not only provide a necessary complement to theoretical models but also offer data-driven insights at scales relevant to management (Lindenmayer et al. 2012).

We used new data from the Fire and Fire Surrogate project (FFS) at Blodgett Forest Research Station to examine the effects of four different treatment regimes on aboveground forest carbon stocks and fluxes fourteen years after the treatments were initially installed. This builds on previous FFS work describing the carbon implications of fuel treatments in the MCF (Stephens et al. 2009b, Dore et al. 2016, Battles et al. 2018) by extending the measurement record,

incorporating previously neglected carbon pools (shrubs and standing dead trees), and incorporating an accounting of wildfire risk in our assessment of carbon stocks. Our specific research questions were as follows:

1. What effects do fuel treatments have on aboveground forest carbon stocks and how do these change over the treatments' effective lifetime?
2. What effects do fuel treatments have on the accumulation of live tree biomass?
3. What effects do fuel treatments have on the stability of live tree carbon stocks?
4. When we incorporate risk and uncertainty into accounting of treatment effects on carbon, do treatments provide a net carbon benefit?

METHODS

Study site

Blodgett Forest Research Station (BFRS) is located near Georgetown, California, USA (38°54'45" N; 120°39'27" W), between 1100 and 1410 m elevation. Soils are well-developed and drained sandy loam Ultic Haploxeralfs (Alfisols), ranging in depth from 85 to 115 cm. Mean slopes are generally <30%. Climate at BFRS is Mediterranean, with a long dry-warm season and cool-wet winters. Average precipitation is approximately 160 cm/yr, falling mostly in the winter and spring. Temperatures range from 0° to 8°C in the winter and from 10° to 29°C in the summer (Hart et al. 1992, Stephens and Collins 2004, Stephens et al. 2009b). The species mixture is typical of MCF, predominantly *Abies concolor*, *Calocedrus decurrens*, *Pinus lambertiana*, *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Quercus kelloggii* (North et al. 2016). BFRS was historically maintained by a regime of frequent low-to-moderate severity fires with fire return intervals from 8 to 15 yr (Stephens and Collins 2004). Intensive logging in the early 20th century and decades of effective fire suppression have resulted in a structure typical of fire-suppressed, young-growth forests throughout the MCF region: moderate to high canopy cover, heavy fuel loads, and high tree densities with more small trees, fewer large trees, and a species composition shifting away from

fire-resistant pines toward less fire-resistant firs (Levine et al. 2016, Safford and Stevens 2017).

Treatments

At BFRS, 12 similar experimental units (stands) were selected for inclusion in the FFS study. Important points on treatment implementation are described below, and more details are available in Stephens and Moghaddas (2005) and Stephens et al. (2009b). The stands ranged in size from 14 to 29 ha for a total of 225 ha. Each of the four treatments (control, mechanical-only, burn-only, and mechanical-burn) was assigned to replications of three randomly selected stands. Pre-treatment baseline measurements confirmed that stands were similar and treatments were installed in late 2001 and 2002 (Stephens and Moghaddas 2005). Treatments were designed to reduce fire severity while using management practices common to northern Sierra Nevada (Agee and Skinner 2005, Schwikl et al. 2009).

Control stands received no management during the study period. Mechanical-only stands were commercially harvested using crown thinning followed by a conventional thin from below to a target basal area (BA). The harvest maximized crown spacing while retaining 28–32 m²/ha BA (pre-treatment mean BA across all stands was 53 m²/ha) and an even species mixture of residual conifers. Activity fuels (tree foliage, limbs, and tops) were left onsite. After the timber harvest, small trees <25 cm diameter at breast height (DBH, breast height = 1.37 m) were masticated across 90% of the stand, with masticated material left onsite and residual small trees distributed throughout the stand in ~0.04-ha clumps.

The burn-only stands were treated with prescribed fires in 2002 and then re-burned in 2009. The stands were burned using strip head fires in October/November, with prescriptions designed to reduce surface and ladder fuel loads, while limiting mortality to ≤10% of trees larger than 46 cm DBH. Burns were completed under similar fire-weather conditions, with relative humidity of 25–40%, 10-h fuel moisture of 6–10%, surface winds from 0 to 10 km/h, and temperatures from 10° to 25°C (Kobziar et al. 2006). Fire behavior in all burns was characterized by flame lengths <2 m and occasional torching of live trees.

The combination mechanical-burn stands were treated in two stages. First, they received the same mechanical treatment as described above for the mechanical-only stands. After the mechanical treatment, activity and natural fuels were broadcast burned using the same prescription as the burn-only stands, except that the mechanical-burn stands were burned only once (during Fall 2002) using backing fire. Surface fuels in the mechanical-burn stands were dominated by masticated chips of woody material which had cured for a single season before the burns; these fuels burned with longer duration than those in the burn-only stands.

Field sampling

Field measurements were conducted in permanent 0.04-ha plots to describe trends in vegetation and fuels in the summers of 2001, 2003, 2009, and 2016 (pre-treatment, 1-, 7-, and 14-yr post-treatment, respectively). In each stand 15–20 circular plots were installed on a regular 60-m grid. Plot locations were restricted to a 10-ha core area in the center of each stand to avoid edge effects. Tree species, DBH, height to crown base, and total height were recorded for all live trees ≥ 11.4 cm DBH on the 0.04-ha plots. Species, DBH, height to crown base, and total height were also recorded for all live trees ≥ 1.0 cm DBH on 0.004-ha subplots in 2001, 2003, and 2009. In 2016, trees ≥ 1.0 cm DBH and < 11.4 cm DBH were tallied by species within binned diameter classes of 0–2.5, 2.5–5.0, 5.0–7.6, 7.6–10.2, and 10.2–11.4 cm. We assigned each tallied small tree a specific DBH within its bin range from a uniform distribution, and assigned height based on observed relationships between DBH and height for small trees in the 2001, 2003, and 2009 data.

DBH and height were recorded for all snags (standing dead trees) ≥ 20.5 cm DBH. In 2016, protocols also included information on snag limb condition, wood hardness, bark coverage, and estimated years since death. These data were used to determine an appropriate live:dead carbon ratio for BFRS snags (see *Observed carbon stocks* below for details).

Surface and ground fuels (coarse woody debris, fine woody debris, litter, and duff) are important necromass carbon stocks, and surface fuels play a major role in fire behavior (Agee and Skinner 2005). Data on fuels were collected using

Brown's line-intercept method (Brown 1974) on two 11.43-m transects per plot. For each transect, litter, and duff depths were measured at two locations and intersections of 1-h (0–0.64 cm), 10-h (0.64–2.54 cm), and 100-h (2.54–7.62 cm) woody fuel particles were tallied along sub-transects of 1.83, 1.83, and 3.05 m length, respectively. Field crews recorded diameter and decay class of any 1000-h fuels (≥ 7.62 cm) along the entire 11.43 m length of each transect. Fuels were measured for all plots in the summers of 2001 (pre-treatment), 2003 (post-1), 2009 (post-7), and 2016 (post-14).

Understory forbs and shrubs were recorded on each 0.04-ha plot as ocular estimates of percent cover by species, binned into classes of $< 5\%$, 5–25%, and 25–100%. The bins were interpreted as central values of 2.5%, 15%, and 63%, respectively, and these percent-cover categories were used to estimate the total area of cover by each species on each plot. This study includes only the understory shrub species common in BFRS understories: *Arctostaphylos* spp., *Ceanothus* spp., *Chamaebatia foliosa*, *Chrysolepis* spp., *Notholithocarpus densiflorus*, *Ribes roezlii*, *Rosa gymnocarpa*, and *Symphoricarpos mollis*. These measurements of shrub occupancy are coarse but they are sufficiently precise to improve our ability to assign fuel models (see *Fire modeling and carbon stability* below). Shrubs are a minor carbon stock in these forests and any error associated with estimating shrub carbon stocks will have little influence on carbon accounting; we still include them in this study for completeness when describing above-ground forest carbon (AFC; see Table 1 for definitions of terms).

Analyses

Observed carbon stocks.—Aboveground live tree biomass was calculated from tree measurements (species, DBH, and height) using regional biomass equations (Forest Inventory and Analysis 2010). These equations predict biomass of the entire tree stem from estimates of cubic volume and species-specific wood density. Separate allometric equations were used to calculate the biomass in bark and branches. Aboveground live tree biomass is the sum of the stem, bark, and branch mass. For western U.S. states, the Pacific Northwest Forest Inventory and Analysis program considers estimates of tree biomass using

Table 1. Definitions used in paper.

Abbreviation	Term	Meaning
AFC	Aboveground forest carbon	Carbon in aboveground live and dead biomass
LTC	Live tree carbon	Carbon in aboveground stem, bark, and branches of live trees
SLTC	Stable live tree carbon	Carbon in trees predicted to survive a wildfire
ELTC	Expected live tree carbon	Mean of LTC and SLTC, weighted by wildfire probability
TAC	Total aboveground carbon	Carbon in aboveground live biomass, dead biomass, and offsite forest products
ETAC	Expected total aboveground carbon	Mean of pre-fire TAC and post-fire TAC, weighted by wildfire probability

the regional equations to be more accurate than the national analysis (PNW 2015). Snag biomass was initially estimated using the equations for live trees described above and then corrected using a live:dead biomass ratio of 0.88. The 0.88 ratio was selected based on the findings of Cousins et al. (2015) for decay class 2, which was the modal and the median decay class for all snags where decay information was available (all snags in 2016).

Plot-level biomass is the sum of the individual tree or snag biomass scaled by plot size and is expressed in Mg/ha. Plot-level biomass estimates were converted to Mg of carbon assuming a ratio of 0.48 Mg C per Mg biomass for live trees (live tree carbon, LTC) and a ratio of 0.5145 Mg C per Mg biomass for all snags (IPCC 2003, Cousins et al. 2015, Dore et al. 2016). Again, the snag carbon concentration was selected by assigning decay class 2 to all snags in our study and using the species-specific carbon density estimates from Cousins et al. (2015).

Shrub carbon stocks for each plot were estimated using our observed percent-cover data and the biomass equations given by McGinnis et al. (2010). We estimated the number of average-sized individuals of each species on each plot using our field data. The estimated number of average-sized individuals was multiplied by the per-individual biomass to estimate the total biomass of each species on each plot. These estimates were summed and scaled by plot size to estimate the Mg biomass per hectare on each plot. The shrub plot biomass per hectare estimates were multiplied by a carbon density ratio of 0.49 to estimate the total shrub Mg carbon per hectare (Mg C/ha; Chojnacky and Milton 2008).

Fuel loads were estimated from transect data using equations and species-specific coefficients

for Sierra Nevada forests (Van Wagtenonk et al. 1996, 1998). The coefficients used for each plot were generated by taking an average of the species-specific coefficients (weighted by species' basal area as a proportion of the plot total), following Stephens (2001). The two transect-level estimates for total fuel load on each plot were averaged to generate a plot-level estimate, which was converted to Mg C per hectare assuming 50% carbon concentration for coarse and fine woody fuels and 37% for litter and duff (IPCC 2003, Stephens et al. 2012). For analysis, we summed the litter and 1–100-h fuel load estimates into a fine fuels load. We also analyzed duff load and 1000-h (coarse woody debris, CWD) loads. Finally, we analyzed treatment effects on AFC, which is the sum of the carbon stored in live trees, snags, shrubs, fine fuels, duff, and coarse woody debris.

Fire modeling and carbon stability.—We modeled potential fire behavior for each inventory plot in each observation year with the Fire and Fuels Extension (FFE) to the Forest Vegetation Simulator (Reinhardt and Crookston 2003). FFE uses established equations to predict fire behavior and crown fire potential based on user-input tree lists and fire weather (Rebain 2010). The fire-weather conditions used were similar to those observed during large spread events in two nearby wildfires, the 2013 American Fire and the 2014 King Fire. By using actual conditions from nearby wildfires that posed substantial fire control problems, we believe predicted fire behavior may better characterize wildfire potential, as opposed to using conditions based on fire-weather percentile thresholds. The vast majority of area burned by wildfires in California is burned by large fires, and it is reasonable to assume that if a treated area does experience a

wildfire, it will likely be under intense weather conditions (Starrs et al. 2018).

We assigned surface fuel models by stand and year, based on average surface fuel loads and shrub cover. To capture the uncertainty associated with surface fuel model assignment and recognizing the influence of these assignments on predicted fire behavior, we assigned low and high fuel models for each combination (Chiono et al. 2017). Low fuel models predict more mild fire behavior (e.g., lower flame lengths and scorch heights) and high models more intense fire behavior. Modeled fire behavior for each plot-time period combination was the average of the low and high surface fuel model runs.

Our analysis focuses on the predicted mortality output (PMORT) from FFE, which is the percent of plot basal area predicted to die within the first three years following a wildfire. PMORT incorporates both immediate and delayed mortality. For each individual tree, FFE estimates the probability that the tree will die within three years of a surface fire using crown length, diameter, tree species, and predicted scorch height. These estimates are based on crown length, diameter, tree species, and predicted scorch height. Mortality estimates rely on empirical relationships (Reinhardt and Ryan 1988) modified by coefficients specific to Western Sierra tree species (Rebain 2010). If FFE predicts passive or active crown fire, PMORT is increased based on the predicted crown fraction burned (Rebain 2010).

To account for potential losses due to wildfire, we defined stable live tree carbon (SLTC) as:

$$\text{SLTC} = \text{LTC} \times (1 - \text{PMORT}). \quad (1)$$

For example, on a plot with 100 Mg/ha of LTC and predicted PMORT equal to 0.30, SLTC equals 70 Mg/ha. Note that SLTC describes the amount of carbon predicted to remain in live trees after a wildfire: the carbon contained in fire-killed snags would not be included in SLTC. A stand experiencing high-severity fire might be expected to retain relatively high total carbon stocks (in the short term) but would have few live trees and low LTC post-fire. By contrast, a treated stand with $\text{SLTC} \approx \text{LTC}$ would experience low severity fire even under the severe fire-weather conditions we modeled, indicating that

the treatment effectively reduced wildfire hazard.

Expected carbon stocks.—In order to evaluate the relationship between direct treatment effects, wildfire-contingent treatment effects, and the probability of treated stands interacting with wildfire, we applied the concept of expected utility to risk-adjust the plots' carbon stocks (Schoemaker 1982, Finney 2005, Ager et al. 2010). The expected carbon stock is a weighted average, with each possible outcome (observed stocks and predicted post-wildfire stocks) weighted by the probability of its occurrence. For example, consider the expected live tree carbon stock (ELTC) for a plot i in year j :

$$\text{ELTC}_{ij} = [\text{LTC}_{ij} \times (1 - P(\text{burned}|j))] + [\text{SLTC}_{ij} \times P(\text{burned}|j)] \quad (2)$$

where ELTC_{ij} is the expected live tree carbon stock for plot i in year j after accounting for wildfire risk; LTC_{ij} is the observed live tree carbon stock for plot i in year j ; SLTC_{ij} is the stable live tree carbon stock for plot i in year j ; and $P(\text{burned}|j)$ is the cumulative probability that the forest will have been burned in a wildfire by year j .

We assume that the annual wildfire probability P_{annual} remains constant throughout our study period and across stands, and calculate $P(\text{burned}|j)$ for each year j using the equation:

$$P(\text{burned}|j) = 1 - (1 - P_{\text{annual}})^n \quad (3)$$

where n is the number of years between treatment installation (2002) and year j , $0 \leq n \leq 14$. We applied an envelope approach and calculated ELTC for each treatment across a range of possible values for P_{annual} (from 0.01 to 0.011).

We also quantified the expected total aboveground carbon stocks (ETAC) for each treatment type. The process was similar to that used for risk-adjusting the live tree carbon stocks: We applied Eq. 4 to calculate ETAC_{ij} for each observation, fit a linear mixed-effects model (LME; further explanation provided below), and averaged the post-treatment group means to quantify overall effects on for each treatment on ETAC.

$$\text{ETAC}_{ij} = [\text{TAC}_{ij} \times (1 - P(\text{burned}|j))] + [\text{STAC}_{ij} \times P(\text{burned}|j)] \quad (4)$$

where ETAC_{ij} is the expected total aboveground carbon stock for plot i in year j ; TAC_{ij} is the total

aboveground carbon stock for plot i in year j : the sum of the carbon stocks in live trees, snags, shrubs, fine fuels, coarse woody debris, duff, and offsite forest products; and $STAC_{ij}$ is the stable total aboveground carbon stock for plot i in year j : the total amount of carbon we expect to remain sequestered after a wildfire in live trees, snags, shrubs, fine fuels, coarse woody debris, duff, and offsite forest products; and $P(\text{burned}|j)$ is the cumulative probability that the forest will have been burned in a wildfire by year j .

We summed the observed amounts for each stock type to get the no wildfire total aboveground carbon for each observation (TAC_{ij}). Additional assumptions (described below) were necessary to estimate the stable total aboveground carbon stocks for each observation ($STAC_{ij}$) and the amount of carbon sequestered in harvested forest products.

To account for the benefit of sequestering carbon offsite in durable forest products, we included sequestered forest product carbon as a component of TAC and $STAC$. An average of 31.7 Mg C/ha of live tree carbon was moved offsite as sawlogs from stands treated with mechanical-only or mechanical-burn treatments (Stephens et al. 2009b). We assumed that for each mechanical-only or mechanical-burn plot, there were $(31.7 \times SEQ)$ Mg C/ha of carbon sequestered offsite in forest products after treatment installation (where the assumed sequestration efficiency SEQ was 1%, 34%, 67%, or 100%). These products remain sequestered even if the forest experiences wildfire, so we also included the sequestered offsite stocks as a component of $STAC$. $STAC_{ij}$ is the sum of the biomass and necromass stocks for plot i and year j we expect to remain sequestered from the atmosphere if i experienced wildfire sometime before j . $SLTC$ estimates the post-wildfire live tree carbon stock, but to calculate $STAC$ we needed some estimate of the post-wildfire amounts for the other stocks (shrubs, fine fuels, duff, coarse woody debris, pre-fire snags, and trees which were killed by the fire). We assumed that some proportion (1%, 34%, 67%, or 100%) of the carbon in fire-killed trees ($LTC - SLTC$) would be emitted to the atmosphere over the 14-yr study duration, and that the rest would move to the snag pool. For each of the other stock types, we assumed that some proportion (1%, 34%, 67%, or 100%) of the

pre-fire stock would be lost to the atmosphere in the event of a wildfire.

Again, we used an envelope approach and calculated $ETAC$ for each treatment under each unique combination of assumptions. To make our analysis more robust we included a wide range of values for each assumed parameter. With ten levels of wildfire probability and four levels each of sequestration efficiency, proportion of killed tree carbon directly emitted, proportion of duff stocks combusted, proportion of fine fuel stocks combusted, proportion of CWD stocks combusted, proportion of shrub stocks combusted, and proportion of snag stocks combusted, there were 163,840 unique sets of assumed parameters ($10 \times 4^7 = 163,840$). We iterated over the entire set of combinations and calculated $ETAC$ for each treatment under each combination of assumptions.

Linear mixed-effects models.—Treatment effects on carbon stocks were analyzed using a LME for each stock type using the nlme package in R version 3.5.0 (Quinn and Keough 2002, Zuur et al. 2009, Pinheiro et al. 2016, R Core Team 2016). Treatment, year, and treatment-year interactions were the fixed effects. Stand and plot (nested within stand) were the random effects. The response variable was aboveground carbon stock for a given plot, at each time period. LME assumptions were validated by using plots of residuals vs. fitted values, histograms of residuals, and QQ plots. All observed response variables except AFC and LTC were $\log_{10}(x + 1)$ transformed to meet model assumptions.

The analysis used treatment contrasts constraints, with the pre-treatment (2001) control treatment mean as the intercept. The coefficients of interest were the main effects of year (changes in the control group over time) and the treatment-year interactions (difference between treatment group mean and control group mean for a given year, after accounting for pre-treatment differences between groups). A significant treatment-year interaction indicates that the treated stands were significantly different from control stands in that year, after accounting for pre-treatment differences and time-dependent changes in the control treatment. We did not run pairwise comparisons.

The large number of response variables and hypothesis tests analyzed in this study risks

inflating our type I error rate; therefore we used the Bonferroni procedure to adjust significance levels (Quinn and Keough 2002). Conservatively, we treated all fixed-effect hypothesis tests for observed stocks as a single family (144 tests) for the purposes of adjusting the significance level. Results meeting this stringent requirement ($\alpha = 0.000035$) are reported as highly significant. Because this adjustment may be too conservative, we also calculated an adjusted significance level using each response variable as the family (16 tests). We report results meeting this requirement ($\alpha = 0.00312$) as significant. Finally, results meeting an unadjusted significance level of $\alpha = 0.05$ are reported as weakly significant.

Carbon accumulation.—Woody net primary production (WNPP) describes the net rate of carbon accumulation in woody biomass of live trees (growth minus mortality). We analyzed treatments' effects on plot-level WNPP ($\text{Mg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) during two periods (2003–2009 and 2009–2016) using a before–after control–impact (BACI) approach (Stewart-Oaten et al. 2001, Dore et al. 2016). Specifically, we applied an LME to

the plot-level live tree carbon stocks but restricted the analysis to only two levels of year (2003 and 2009 for the first period, 2009 and 2016 for the second). A significant main effect of time indicates that WNPP in the control stands was significantly different from zero. A significant treatment-time interaction indicates that WNPP in the treated stands was significantly different from the control. Fitted means were used to estimate the carbon stock deltas, and the deltas divided by the number of years between measurements to obtain annualized accumulation rates for interpretation.

RESULTS

Observed carbon stocks

LTC increased across the 14-yr period in the control treatment, which had significantly more live tree carbon in 2009 (+30 Mg C/ha) and 2016 (+61 Mg C/ha) than in 2001 (mean 166 Mg C/ha ; Fig. 1; Appendix S1: Table S1). As expected, mechanical-only and mechanical-burn treatment significantly reduced live tree carbon stocks

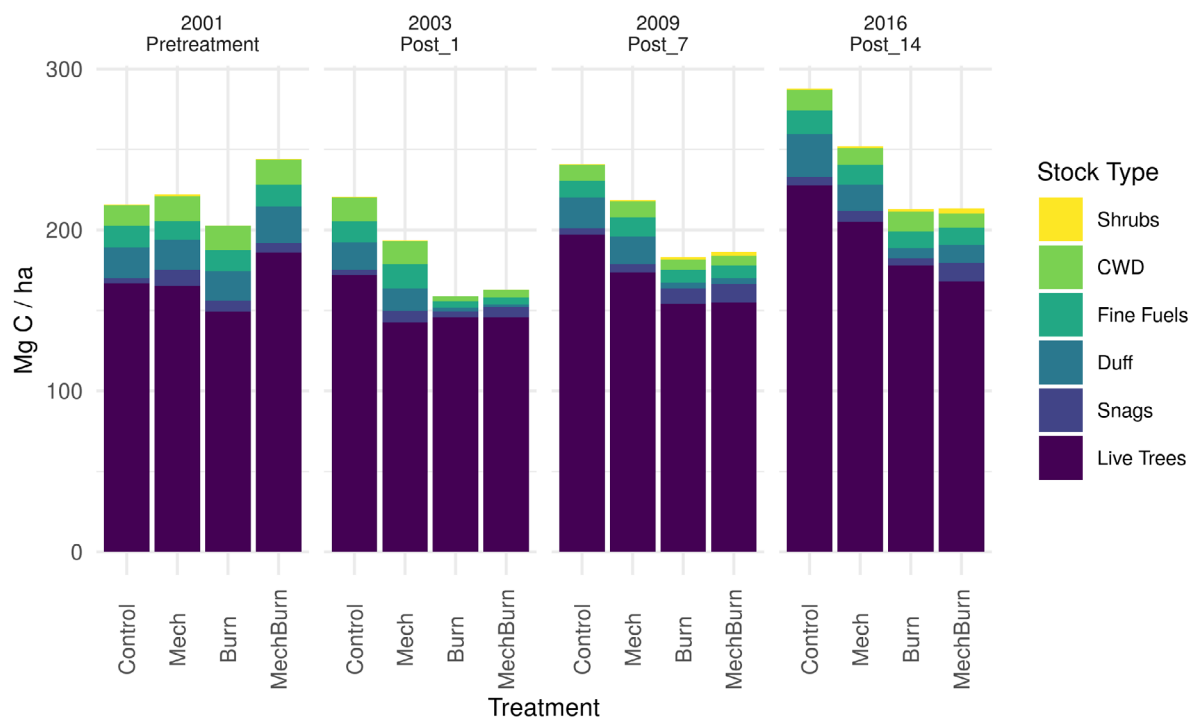


Fig. 1. Mean carbon stocks by treatment, year, and stock type. CWD is coarse woody debris (1000-h fuels), and fine fuels are litter plus 1–100-h fuels. Treatments were installed between 2001 and 2003 measurements, and burn-only stands were burned a second time in fall 2009 after the Post_7 measurements.

immediately following treatment (−28 and −45 Mg C/ha, respectively). Burn-only treatment did not have a significant immediate effect on live tree carbon stocks. Seven years post-treatment, all three treatments had significantly less LTC than control, with the strongest effect on the mechanical-burn treatment (−61 Mg C/ha) and lesser effects on thinned (−22 Mg C/ha) and burned (−26 Mg C/ha) stands. In 2016, all three treatments still had less live tree carbon than control, again with the strongest effect on mechanical-burn treatment (−79 Mg C/ha), followed by burn-only (−32 Mg C/ha) and mechanical-only (−21 Mg C/ha). In both 2009 and 2016, burn-only and mechanical-burn effects were highly significant, and the mech-only effects were significant.

AFC had a pre-treatment mean of 215 Mg C/ha (Fig. 1; Appendix S1: Table S1) for the control with highly significant increases in 2009 (+25 Mg C/ha) and 2016 (+72 Mg C/ha). All three active treatments caused highly significant reductions to AFC in all post-treatment years.

The largest magnitude effect was for mechanical-burn treatment in 2016 (−103 Mg C/ha), and the smallest was for mechanical-only in 2009 (−28 Mg C/ha). For analyses of treatment effects on subsets of AFC (live trees, shrubs, snags, duff, fine fuels, and coarse woody debris) see Fig. 1 and Appendix S1.

Carbon stability

SLTC in the control increased from their 2001 levels (mean 51 Mg C/ha; Fig. 2; Appendix S1: Table S1) in 2009 (+31 Mg C/ha) and 2016 (+31 Mg C/ha). Note that the effect magnitudes are relative to 2001: there was no change in SLTC from 2009 to 2016 in the control. One year post-treatment, burn-only and mechanical-burn treatments had highly significant and positive effects on stable live tree carbon (+58 and +61 Mg C/ha, respectively). The positive effect of the burn-only treatment was durable and remained highly significant prior to the re-burn in 2009 (+51 Mg C/ha) and 2016 (+69 Mg C/ha). Significance of

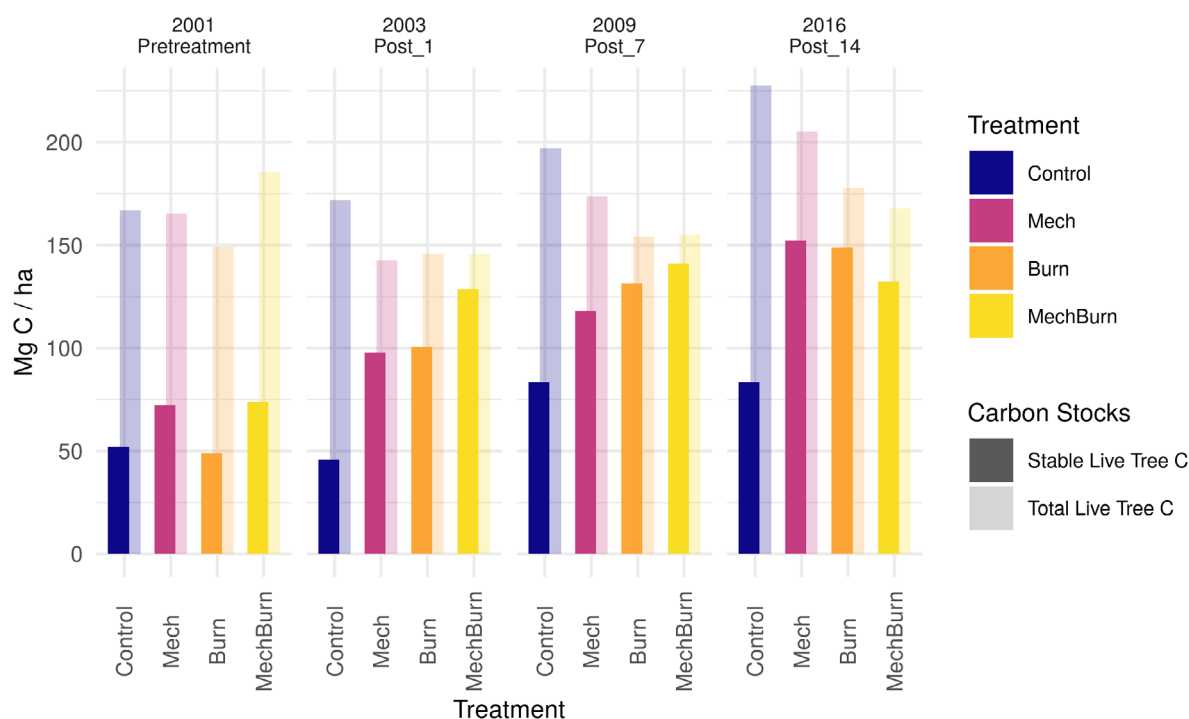


Fig. 2. Stability of live tree carbon stocks. Bar heights are treatment means for a given measurement year. Faded bars indicate observed live tree carbon stocks, while solid bars indicate stable live tree carbon stocks. Stable live tree C is the amount of carbon in live trees which are expected to survive at least three years after a modeled wildfire.

the mechanical-burn effect declined to weak significance in 2009 (+36 Mg C/ha) and 2016 (+27 Mg C/ha). Mechanical-only treatments had a weakly significant positive effect on stable live tree carbon (+32 Mg C/ha) in 2003 and a significant positive effect in 2016 (+49 Mg C/ha).

Expected live tree carbon

If the annual probability of a wildfire (P_{annual}) is less than ~ 0.035 , the control treatment maximized ELTC, followed by the burn-only and mechanical-only treatments (Fig. 3). As P_{annual} increases, ELTC declines steeply in the control indicating high fire risk in the control stands. By contrast, ELTC of the active treatment stands is relatively insensitive to wildfire probability, and as P_{annual} increases, ELTC of the controls falls below ELTC of the active treatments. Burn-only treatment maximizes ELTC if $P_{\text{annual}} > 0.035$, and mechanical-only treatment provides higher ELTC than control if $P_{\text{annual}} > 0.05$. The mechanical-burn treatment had the lowest ELTC for all $P_{\text{annual}} \leq 0.11$, though it was approaching the

effectiveness of controls at the highest levels of wildfire probability used in this analysis.

Expected total aboveground carbon

As with ELTC, when P_{annual} is low the control treatment maximizes ETAC (Fig. 4). At low levels of P_{annual} , the gap between the control and the two fire treatments (burn-only and mechanical-burn) is wider for ETAC than for ELTC, reflecting the low observed necromass stocks in the burned stands (Fig. 1; Appendix S1: Figs. S1, S2). If carbon in harvested trees is efficiently sequestered, then the mechanical-only treatment is competitive with control, even at low levels of wildfire probability (Fig. 4, first and second rows from top). Unlike ELTC, ETAC of the control stands does not decline steeply with increased probability of wildfire: A wildfire in the control stands would cause high tree mortality, but most of the carbon in killed trees would remain (temporarily) sequestered as necromass. When necromass stocks are included in the carbon accounting,

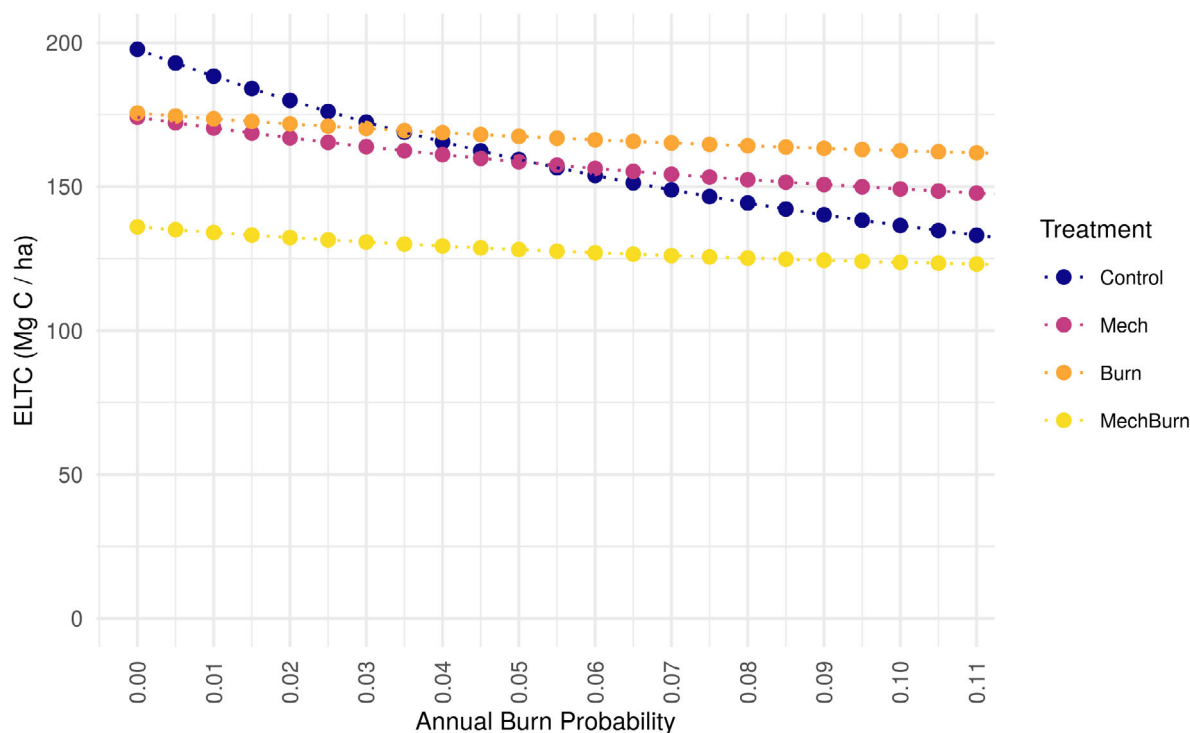


Fig. 3. Expected live carbon stocks (ELTC) for a given treatment type and annual burn probability. ELTC values are averaged across all three post-treatment measurement years for each treatment. See methods for details.

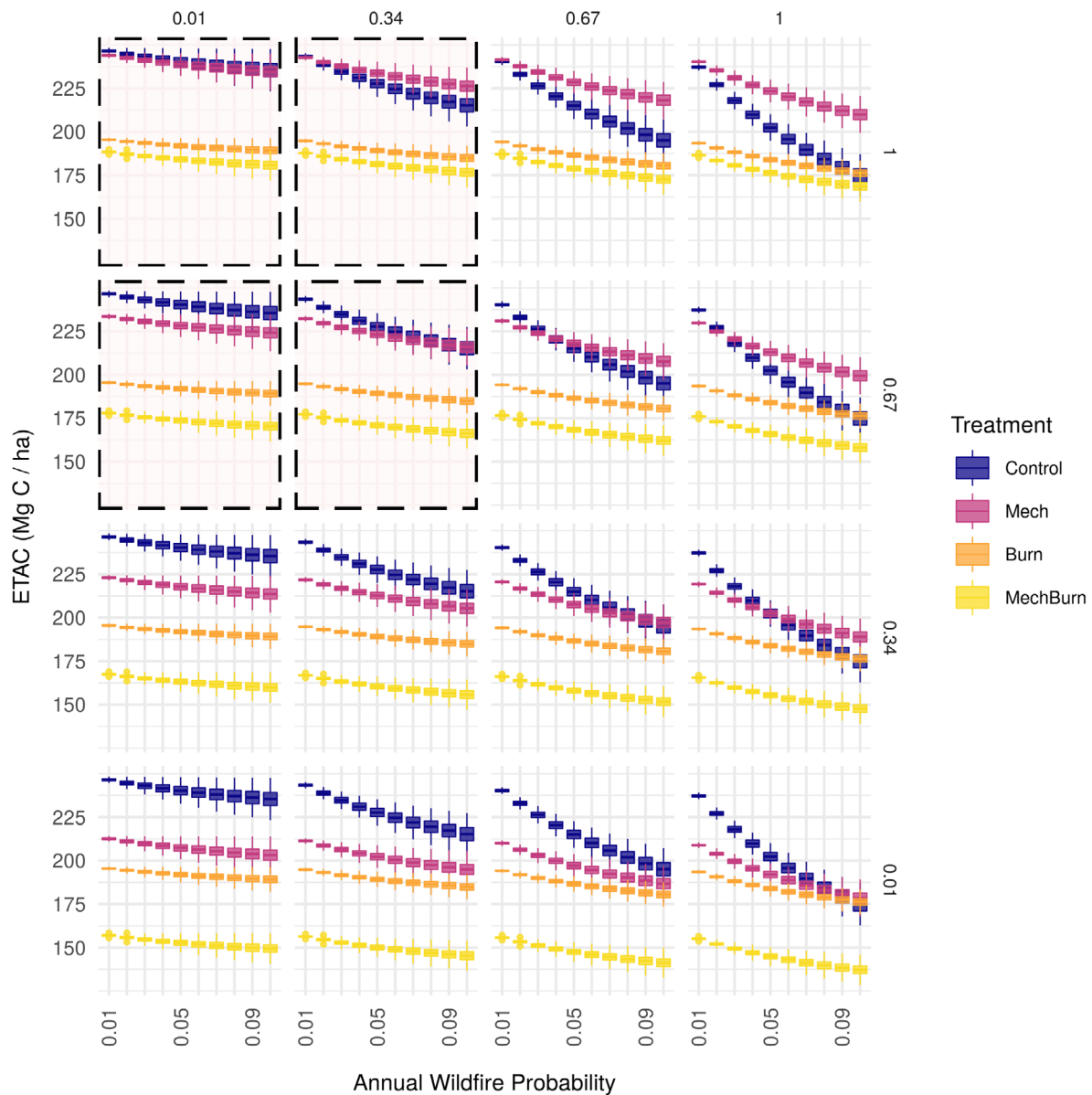


Fig. 4. Expected total aboveground carbon (ETAC) for a given treatment type and annual burn probability. Panel rows divide results by the (assumed) proportion of harvested carbon stocks sequestered for at least 14 yr. Columns divide results by the (assumed) proportion of carbon which is transferred to the atmosphere (rather than to the snag pool) when trees are killed by wildfire. The panels corresponding with the most realistic set of assumptions are highlighted with dashed lines.

burn-only and mechanical-burn treatments fail to offer higher ETAC than the control even at high levels of wildfire probability, unless all of the carbon in fire-killed trees is assumed to emit to the atmosphere over the 14-yr study duration (Fig. 4, rightmost column).

Carbon accumulation

There was highly significant growth in live tree carbon stocks (woody net primary production, WNPP) in control stands between 2003 and 2009 ($4.2 \text{ Mg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$; Table 2). Mechanical-only stands accumulated LTC at a comparable

Table 2. Terms from the two-way ANOVA used for the BACI analysis.

Time period	Treatment	BACI parameter	Effect†		P	WNPP†	
			Mean	SE		Total	Annual
2003–2009	Control	Post_7	25.09	2.94	<0.01	25.09	4.18
	Mech	Mech:Post_7	5.78	4.2	0.17	30.87	5.15
	Burn	Burn:Post_7	–16.82	4.09	<0.01	8.28	1.38
	MechBurn	MechBurn:Post_7	–15.9	4.12	<0.01	9.2	1.53
2009–2016	Control	Post_14	30.4	4.88	<0.01	30.44	4.35
	Mech	Mech:Post_14	1.13	6.96	0.87	31.57	4.51
	Burn	Burn:Post_14	–6.84	6.78	0.31	23.60	3.37
	MechBurn	MechBurn:Post_14	–17.45	6.83	0.01	12.99	1.86

Notes: Post_7 and Post_14 are the mean change in the control stands from 2003 to 2009 and from 2009 to 2016, respectively. WNPP is woody net primary production of live tree carbon.

† Mg C/ha.

rate of 5.2 Mg C·ha^{–1}·yr^{–1} (no significant difference with control). LTC did increase on both burn treatments (1.4 and 1.5 Mg C·ha^{–1}·yr^{–1}, respectively) but the reductions in WNPP relative to controls were highly significant.

In the second period (2009–2016), WNPP remained relatively high in control and mechanical-only stands (4.4 and 4.5 Mg C·ha^{–1}·yr^{–1}, respectively) again with no significant differences between the two (Table 2). WNPP on burn-only stands increased in this period to 3.4 Mg C·ha^{–1}·yr^{–1}, which was not significantly lower than WNPP of the control despite a 2nd-entry burn in the fall of 2009. Mechanical-burn treatment had a weakly significant negative effect on WNPP, which remained low at 1.9 Mg C·ha^{–1}·yr^{–1}.

DISCUSSION

The stability of live tree carbon stocks is particularly important to carbon management goals because the live tree carbon stock is the largest aboveground stock in most forests (North et al. 2009, Fahey et al. 2010). Furthermore, photosynthetic sink strength of forest ecosystems is strongly linked to the size of live tree carbon stocks (Ryan et al. 1997, Stephenson et al. 2014). However, capturing offsite carbon stocks is also critical for a more complete understanding of forest dynamics. For example, ELTC does not account for carbon sequestered in forest products and therefore underestimates the carbon benefits of mechanical-only and mechanical-burn treatments. More than 65% of the wood in sawlogs

can be sequestered in wood products, with additional benefits from using much of the remaining wood for energy production (Stewart and Nakamura 2012).

Forest necromass stocks (carbon stored in duff, fine fuels, coarse woody debris, and snags) must also be considered when describing forest carbon dynamics. ELTC does not incorporate the direct emissions associated with combustion of surface fuels in the prescribed burns, which are a direct carbon cost of prescribed fire. In control or mechanical-only stands, these stocks may be sequestered for long periods of time in the absence of wildfire, or largely lost if a wildfire does occur (Campbell et al. 2007, Eskelson et al. 2016). By including treatment effects on live shrubs, offsite carbon stocks, and forest necromass carbon stocks, ETAC may provide a more complete accounting of forest carbon dynamics. However, ETAC treats live and dead biomass as equally valuable, which obfuscates the effects of treatments and wildfire probability on expected live tree carbon. Neither ELTC nor ETAC fully capture carbon dynamics in fire-prone forests individually, but together they provide valuable insight for decision making.

For both ELTC and ETAC, treatment efficacy relative to controls increases with wildfire probability (Figs. 3, 4). All active treatments incur upfront carbon costs, which can only have realized benefits if a wildfire occurs during the treatments' effective lifespan.

Managers cannot be certain that a wildfire will occur within the expected lifespan of a fuel treatment, so the probability of a wildfire occurring is

an important factor to consider when attempting to predict the net carbon impact of fuel treatments (Finney 2005, Hurteau et al. 2009, Campbell et al. 2012, Krofcheck et al. 2018). Starrs et al. (2018) found annual wildfire probabilities in California forests ranging from 0.005 to 0.025 during the years 2000–2015. However, the probability of treatment–wildfire interactions is likely to increase as large wildfires become more frequent as climate is expected to be more conducive for wildfire spread (Westerling et al. 2011, Collins 2014).

An annual fire probability of 0.035 is an important threshold in this study for determining whether active management can maximize ELTC. At and above this threshold the burn-only treatment outperforms all other treatments (Fig. 3). This study found that as wildfire probabilities exceed 0.05 the mechanical-only treatment will also provide a net benefit to ELTC over the control. Mechanical-only treatment boosted the growth of individual trees in this experiment (Dore et al. 2016) likely by increasing available growing space for the residual trees (Smith et al. 1997). Because some trees were removed, stand-level WNPP in mechanical-only stands was not significantly higher than controls, despite this increased growth of individual trees (Table 2). The negative effect of burn-only treatment on WNPP was temporary, even though the burn-only treatment included an initial-entry burn in 2002 and a second-entry burn in 2009. The live tree carbon stocks in mechanical-burn stands were affected by both the immediate reduction associated with timber harvest and the reduced accumulation rate associated with the prescribed fire, imposing large costs to observed live tree carbon stocks (Fig. 1; Appendix S1: Table S1).

Other studies have found that treatments may increase WNPP by reducing competitive stress for resources or decrease WNPP by increasing stress from injuries or vulnerability to pests (Collins et al. 2014, Hood et al. 2015). It is beyond the scope of this work to fully investigate whether negative effects of prescribed fire on WNPP were due to increased mortality, slower growth by surviving trees due to fire-caused injuries, and/or reduced ingrowth of trees. Dore et al. (2016) cored trees in the same plots used for this study to investigate treatment effects on individual tree growth (up to 2009) and found a significant

negative effect of burn-only, a significant positive effect of mechanical-only, and no significant effect of mechanical-burn treatments for the period 2003–2009. However, Collins et al. (2014) report increased mortality rates in burn-only and mechanical-burn stands for the years 2003–2009. An exploratory analysis on our data suggests that trees in burn-only stands experienced high mortality rates between 2003 and 2009 (as a proportion of live stems and as the number of deaths). Mechanical-burn and control stands had similar proportional mortality rates in 2003–2009 and 2009–2016, but the mechanical-burn trees were much larger on average than trees in the control stands. As a result, the impact of individual tree mortality on stand-level carbon stocks is much greater in the mechanical-burn stands than in the control stands.

Four assumptions are especially important drivers of the expected total aboveground carbon (ETAC) for each treatment regime. First, the fate of carbon in harvested trees, or harvest sequestration efficiency SEQ (Fig. 4), is the proportion of harvested LTC sequestered for the 14-year treatment lifespan. With ~70% of sawlog carbon sequestered for longer than 14 years (North et al. 2009, Stephens et al. 2009b), $SEQ = 0.67$ (Fig. 4, 2nd row from top) is a plausible assumption. However, this is likely a conservative estimate (Stewart and Nakamura 2012), hence it makes sense to consider higher efficiency values (Fig. 4). The second key assumption is the probability that a treatment will encounter wildfire within the study period, which was discussed previously. The third key assumption is that the PMORT values from FVS capture actual wildfire hazard. The fire behavior predictions in FVS and other operational fire behavior models fail to capture extreme fire behavior observed in large wildfires (Coen et al. 2018) and as a result underrepresent actual proportions of high-severity effects (Collins et al. 2013). Given the number of empirical studies demonstrating reductions in fire severity in fuel treatments (e.g., Safford et al. 2009, North and Hurteau 2011, Lydersen et al. 2017), this likely underprediction in fire behavior (hence PMORT) is more pronounced for the untreated control. This means that our ETAC values for the control probably overestimate the actual aboveground carbon. The proportion of killed tree carbon released to the atmosphere

during and after a wildfire is the fourth key assumption. When trees are killed by high-severity wildfire, little of the carbon stored in them is immediately emitted to the atmosphere. Rather, much of the carbon remains temporarily sequestered in snags, and then surface fuels as the snags decay. These pools can persist for over a decade in dry climates (Roccaforte et al. 2012, Dunn and Bailey 2015, Eskelson and Monleon 2018). If not salvage harvested as the years pass after a wildfire, carbon in fire-killed snags will move to surface fuels and eventually to the atmosphere as wood breaks down and decomposes, effectively increasing the consumption of killed tree carbon (Dunn and Bailey 2015, Eskelson et al. 2016). The likelihood of another wildfire occurring shortly after the first fire (i.e., re-burn potential), which would result in rapid dead tree carbon release to the atmosphere, is another consideration (Coppoletta et al. 2016, Lydersen et al. 2019). Variation in other assumed parameters (the consumed portion of carbon stored in snags, duff, fine fuels, coarse woody debris, or shrub biomass directly emitted by wildfire) drives relatively small changes in the risk-adjusted total carbon stocks within each facet and level of wildfire probability (individual boxplots within Fig. 4 facets).

Taken together, these points indicate that the most plausible scenarios for the expected total aboveground carbon comparison are those in the left two columns and the top two rows of Fig. 4 (1–34% of killed tree carbon emitted over the study duration and 67–100% of harvested carbon sequestered for at least 14 yr). Under these assumptions, the mechanical-only and control stands have the largest expected total aboveground carbon stocks, while the burn-only and mechanical-burn stands lag behind. The most optimistic (for treatment efficacy) assumptions are 100% sequestration of sawlog carbon (which maximizes the benefits of sequestered forest products) and 100% immediate consumption of killed tree carbon (which maximizes the benefit of reducing fire severity). Even for these highly implausible assumptions (the top-right facet), the carbon costs of prescribed fire outweigh the benefits even if the annual wildfire probability is as high as 0.09 (indicating that the probability of a wildfire entering the stand within 14 yr of treatment installation is <0.73).

The low carbon cost of mechanical-only treatments has important implications for forest management. If harvested tree carbon is efficiently sequestered (or efficiently offsets emissions from other sources such as fossil fuels or cement production), mechanical-only treatments become highly competitive, with greater ETAC than control stands for a wide range of wildfire probabilities. By harvesting live tree carbon and sequestering it offsite, the mechanical-only treatments provide increased stability of carbon stocks, and they provide this benefit without reducing sink strength or pre-emptively emitting carbon from surface fuel necromass. Recall that control stands were harvested with railroad logging ~100 yr ago and, as confirmed with our results, are still increasing in standing volume. As stand-level growth in untreated stands declines, mechanical treatments are likely to become even more favorable. The mechanical treatments also provided more revenue than the other treatments, enhancing the scalability of the mechanical-only regime (Hartsough et al. 2008). In this project, masticated biomass was left onsite and the conventional harvest left tops and limbs to decompose. The carbon balance of mechanical-only treatment could be improved further by incorporating biomass utilization and whole tree yarding, which would allow some of the masticated necromass carbon present in these stands to be used to offset fossil fuels and would further reduce mechanical-only stands' vulnerability to wildfire.

This study does not include direct emissions associated with mechanical treatments, but emissions associated with running mechanical harvest equipment and transporting harvested material offsite are extremely small in magnitude relative to the effects of fuel treatments (Stephens et al. 2009b). We also do not address effects of fuel treatments on soil carbon, a large and important forest carbon stock (Boerner et al. 2008). However, others have found little to no immediate effect of treatments on soil carbon stocks (Boerner et al. 2008, North et al. 2009, Dore et al. 2016) including at this study site where no initial treatment effects were detected (Moghaddas and Stephens 2007).

We assumed that fuel treatments would only affect wildfire severity (the proportion of live tree carbon expected to survive a wildfire). We did

include a range of assumptions about wildfire effects on other forest carbon stocks (e.g., the consumption of coarse woody debris carbon), but we held these effects constant across treatments. There is mixed evidence on whether fuel treatments significantly alter wildfire effects on necromass stocks (Campbell et al. 2007, North and Hurteau 2011, Carlson et al. 2012, Maestrini et al. 2017).

Summary and management implications

Our empirical data describe the effects of stand-level management on carbon stocks, and we assume that the probability of a stand experiencing wildfire is independent of treatment type. There is potential for strategically placed networks of fuel treatments to alter wildfire at the landscape scale, reducing fire probability and/or fire effects in both treated and untreated stands (Finney 2001, Collins et al. 2013, Dow et al. 2016). Campbell et al. (2012) argue that because wildfires are rare and treatments require ongoing maintenance to be effective, the carbon costs incurred by maintaining a landscape-scale network are likely to exceed the benefits of reduced wildfire sizes. There is mixed evidence on this question (Ager et al. 2010, Chiono et al. 2017, Krofcheck et al. 2018), but our envelope approach to assessing treatment effects on ELTC and ETAC is relatively robust.

It is worth noting that our empirical approach does not account for the potential post-wildfire carbon trajectories of these stands. The amount of carbon stored in an untreated stand's fire-killed snags may initially be similar to that stored in a treated stand's surviving trees (North and Hurteau 2011, Eskelson et al. 2016), but unless they are harvested snags will become carbon sources while live trees remain carbon sinks (Dore et al. 2008, Carlson et al. 2012). Furthermore, we do not explicitly account for the potential for a long-term deforested condition due to the lack of tree regeneration following large severe wildfires (e.g., Collins and Roller 2013, Stephens et al. 2020a). Attempting to account for these long-term benefits of fuel treatments was beyond the scope of this study. Several studies suggest that reductions in fire severity can significantly improve post-wildfire carbon stock trajectories (Carlson et al. 2012, Yocom Kent et al. 2015). Recently, Liang et al. (2018) projected

forest carbon stocks over 90 yr across the Sierra Nevada, and incorporated vegetation growth, necromass decay, thinning, prescribed fires, and wildfires. Their results suggest that carbon accounting on a long-time horizon may provide a more favorable view of fuel treatments.

It is also important to note that the control stands in this study are young-growth stands which, like many Sierra Nevada MCF, are still accumulating biomass as they recover from intensive logging approximately 100 yr ago (Safford and Stevens 2017). The relatively high rates of live tree carbon accumulation we observed in control stands are unlikely to persist (Ryan et al. 1997). More importantly, the apparent efficacy of the disturbance-exclusion regime practiced on our control stands highlights a larger issue: A myopic focus on maximizing in-forest carbon stocks risks creating perverse incentives for management of frequent-fire forests.

Our findings provide empirically based information about treatments' effects on carbon stocks and fluxes but clearly carbon is not the only goal of forest management. For example, treatments can facilitate several aspects of wildfire containment and/or suppression, helping to protect lives and property from wildfire (Moghaddas and Craggs 2007, Safford et al. 2009, Moghaddas et al. 2010, Murphy et al. 2010). By promoting beneficial wildfire behavior (Stevens et al. 2014), treatments may facilitate the use of managed wildfire to restore an important ecosystem process at large scales (Collins et al. 2009, North 2012). Timber harvests can directly alter forest structure, potentially restoring important attributes such as horizontal heterogeneity (Churchill et al. 2013) and producing revenue (Hartsough et al. 2008). Restoration of frequent mixed-severity fire across watersheds can increase the amount of water delivered downstream (Boisramé et al. 2016, 2019), and by reducing competitive stress on residual trees, fuel treatments may increase forests' ability to resist drought-related mortality (Young et al. 2017). In many contexts, the host of ecological and social benefits of fuel treatments (Stephens et al. 2020b) could outweigh narrow carbon accounting.

ACKNOWLEDGMENTS

This work was supported by the California Fourth Climate Change Assessment, the McIntire-Stennis

project CA-B-ECO-0144-MS, and the California Greenhouse Gas Reduction Fund (GGRF). Previous support from the US Joint Fire Sciences Program created the FFS experiment and BFRS and GGRF has maintained it. Support also came from UC Office of the President's UC Laboratory Fees Research Program, Smart Practices and Architecture for Prescribed Fires in California (SPARx-Cal). Mr. Klaus Scott from the California Air Resources Board provided valuable advice and technical assistance throughout this project, and we appreciated his help. We especially thank all of the Blodgett Forest managers (Bob Heald, Rob York, Ariel Rough-ton) for their support of this project.

LITERATURE CITED

- Agee, J. K., and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. *Forest Ecology and Management* 211:83–96.
- Ager, A. A., M. A. Finney, A. McMahan, and J. Cathcart. 2010. Measuring the effect of fuel treatments on forest carbon using landscape risk analysis. *Natural Hazards and Earth System Science* 10:2515–2526.
- Battles, J. J., D. M. Bell, R. E. Kennedy, D. S. Saah, B. M. Collins, R. A. York, J. E. Sanders, and F. Lopez-Ornelas. 2018. Innovations in measuring and managing forest carbon stocks in California. California's Fourth Climate Change Assessment, California's Natural Resources Agency, Sacramento, California, USA.
- Boerner, R. E. J., J. Huang, and S. C. Hart. 2008. Fire, thinning, and the carbon economy: effects of fire and fire surrogate treatments on estimated carbon storage and sequestration rate. *Forest Ecology and Management* 255:3081–3097.
- Boisramé, G., S. Thompson, B. Collins, and S. Stephens. 2016. Managed wildfire effects on forest resilience and water in the Sierra Nevada. *Ecosystems* 20:717–732.
- Boisramé, G., S. Thompson, C. Tague, and S. Stephens. 2019. Restoring a natural fire regime alters the water balance of a Sierra Nevada catchment. *Water Resource Research* 55:5751–5769.
- Brown, J. K. 1974. Handbook for Inventorying Downed Woody Material. INT-GTR-16. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. *Journal of Geophysical Research: Biogeosciences* 112:1–11.
- Campbell, J. L., M. E. Harmon, and S. R. Mitchell. 2012. Can fuel-reduction treatments really increase forest carbon storage in the western US by reducing future fire emissions? *Frontiers in Ecology and the Environment* 10:83–90.
- Carlson, C. H., S. Z. Dobrowski, and H. D. Safford. 2012. Variation in tree mortality and regeneration affect forest carbon recovery following fuel treatments and wildfire in the Lake Tahoe Basin, California, USA. *Carbon Balance and Management* 7:1–17.
- Chiono, L. A., D. L. Fry, B. M. Collins, A. H. Chatfield, and S. L. Stephens. 2017. Landscape-scale fuel treatment and wildfire impacts on carbon stocks and fire hazard in California spotted owl habitat. *Ecosphere* 8:e01648.
- Chojnacki, D., and M. Milton. 2008. Measuring Carbon in Shrubs. Pages 45–72 in C. Hoover, editor. *Field measurements for forest carbon monitoring: a landscape-scale approach*. Springer, New York, New York, USA.
- Christensen, G. A., A. N. Gray, O. Kuegler, N. A. Tase, and M. Rosenberg. 2017. AB 1504 California Forest Ecosystem and Harvested Wood Product Carbon Inventory: 2006 - 2015. Final Report. California Department of Forestry and Fire Protection agreement no. 7CA02025. California Department of Forestry and Fire Protection and California Board of Forestry and Fire Protection, Sacramento, California, USA.
- Churchill, D. J., A. J. Larson, M. C. Dahlgreen, J. F. Franklin, P. F. Hessburg, and J. A. Lutz. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. *Forest Ecology and Management* 291:442–457.
- Coen, J. L., E. N. Stavros, and J. A. Fites-Kaufman. 2018. Deconstructing the King megafire. *Ecological Applications* 28:1565–1580.
- Collins, B. M. 2014. Fire weather and large fire potential in the northern Sierra Nevada. *Agricultural and Forest Meteorology* 189:30–35.
- Collins, B. M., A. J. Das, J. J. Battles, D. L. Fry, K. D. Krasnow, and S. L. Stephens. 2014. Beyond reducing fire hazard: Fuel treatment impacts on overstory tree survival. *Ecological Applications* 24:1879–1886.
- Collins, B. M., H. A. Kramer, K. Menning, C. Dillingham, D. Saah, P. A. Stine, and S. L. Stephens. 2013. Modeling hazardous fire potential within a completed fuel treatment network in the northern Sierra Nevada. *Forest Ecology and Management* 310:156–166.
- Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. Van Wagendonk, and S. L. Stephens. 2009. Interactions among wildland fires in a long-established Sierra Nevada natural fire area. *Ecosystems* 12:114–128.
- Collins, B. M., and G. B. Roller. 2013. Early forest dynamics in stand-replacing fire patches in the

- northern Sierra Nevada, California, USA. *Landscape Ecology* 28:1801–1813.
- Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. *Ecological Applications* 26:686–699.
- Cousins, S. J. M., J. J. Battles, J. E. Sanders, and R. A. York. 2015. Decay patterns and carbon density of standing dead trees in California mixed conifer forests. *Forest Ecology and Management* 353:136–147.
- Dore, S., D. L. Fry, B. M. Collins, R. Vargas, R. A. York, and S. L. Stephens. 2016. Management impacts on carbon dynamics in a Sierra Nevada mixed conifer forest. *PLOS ONE* 11:1–22.
- Dore, S., T. E. Kolb, M. Montes-Helu, B. W. Sullivan, W. D. Winslow, S. C. Hart, J. P. Kaye, G. W. Koch, and B. A. Hungate. 2008. Long-term impact of a stand-replacing fire on ecosystem CO₂ exchange of a ponderosa pine forest. *Global Change Biology* 14:1801–1820.
- Dow, C. B., B. M. Collins, and S. L. Stephens. 2016. Incorporating resource protection constraints in an analysis of landscape fuel-treatment effectiveness in the Northern Sierra Nevada, CA, USA. *Environmental Management* 57:516–530.
- Dunn, C. J., and J. D. Bailey. 2015. Temporal fuel dynamics following high-severity fire in dry mixed conifer forests of the eastern Cascades, Oregon, USA. *International Journal of Wildland Fire* 24:470–483.
- Eskelson, B. N., and V. J. Monleon. 2018. Post-fire surface fuel dynamics in California forests across three burn severity classes. *International Journal of Wildland Fire* 27:114–124.
- Eskelson, B. N., V. J. Monleon, and J. S. Fried. 2016. A 6 year longitudinal study of post-fire woody carbon dynamics in California's forests. *Canadian Journal of Forest Research* 46:610–620.
- Fahey, T. J., P. B. Woodbury, J. J. Battles, C. L. Goodale, S. P. Hamburg, S. V. Ollinger, and C. W. Woodall. 2010. Forest carbon storage: ecology, management, and policy. *Frontiers in Ecology and the Environment* 8:245–252.
- Finney, M. A. 2001. Design of regular landscape fuel treatment patterns for modifying fire growth and behavior. *Forest Science* 47:219–228.
- Finney, M. A. 2005. The challenge of quantitative risk analysis for wildland fire. *Forest Ecology and Management* 211:97–108.
- Forest Inventory and Analysis. 2010. Regional biomass equations used by the Forest Inventory and Analysis program to estimate bole, bark, and branches (updated 13-Jan-2010), USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA. https://www3.arb.ca.gov/cc/capandtrade/protocols/usforest/2014/biomass_equations.pdf
- Fulé, P. Z., J. E. Crouse, J. P. Roccaforte, and E. L. Kalies. 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management* 269:68–81.
- Gonzalez, P., J. J. Battles, B. M. Collins, T. Robards, and D. S. Saah. 2015. Aboveground live carbon stock changes of California wildland ecosystems, 2001–2010. *Forest Ecology and Management* 348:68–77.
- Hart, S., M. Firestone, and E. Paul. 1992. Decomposition and nutrient dynamics of ponderosa pine needles in a Mediterranean-type climate. *Canadian Journal of Forest Research* 22:306–314.
- Hartsough, B. R., S. Abrams, R. J. Barbour, E. S. Drews, J. D. McIver, J. J. Moghaddas, D. W. Schwillk, and S. L. Stephens. 2008. The economics of alternative fuel reduction treatments in western United States dry forests: financial and policy implications from the National Fire and Fire Surrogate Study. *Forest Policy and Economics* 10:344–354.
- Hessburg, P. F., et al. 2016. Tamm Review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. *Forest Ecology and Management* 366:221–250.
- Hood, S., A. Sala, E. K. Heyerdahl, M. Boutin, and K. F. Raffa. 2015. Low-severity fire increases tree defense against bark beetle attacks. *Ecology* 96:1846–1855.
- Hurteau, M. D., and M. L. Brooks. 2011. Short- and Long-term effects of fire on carbon in US dry temperate forest systems. *BioScience* 61:139–146.
- Hurteau, M. D., B. A. Hungate, and G. W. Koch. 2009. Accounting for risk in valuing forest carbon offsets. *Carbon Balance and Management* 4:1–5.
- Hurteau, M. D., G. W. Koch, and B. A. Hungate. 2008. Carbon protection and fire risk reduction: toward a full accounting of forest carbon offsets. *Frontiers in Ecology and the Environment* 6:493–498.
- Hurteau, M. D., S. Liang, K. L. Martin, M. P. North, G. W. Koch, and B. A. Hungate. 2016. Restoring forest structure and process stabilizes forest carbon in wildfire-prone southwestern ponderosa pine forests. *Ecological Applications* 26:382–391.
- Hurteau, M., and M. North. 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. *Frontiers in Ecology and the Environment* 7:409–414.
- IPCC. 2003. Good practice guidance for land use, land use change and forestry. Page 617 in J. Penman, M. Gytarsky, T. Hiraishi, T. Krug, D. Kruger, R. Pipatti, L. Buendia, K. Miwa, T. Ngara, K. Tanabe, and F. Wagner, Editors. IPCC, Kanagawa, Japan.

- Kalies, E. L., and L. L. Yocom Kent. 2016. Tamm Review: Are fuel treatments effective at achieving ecological and social objectives? A systematic review. *Forest Ecology and Management* 375:84–95.
- Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2006. Carbon storage on landscapes with stand-replacing fires. *BioScience* 56:598–606.
- Kobziar, L., J. Moghaddas, and S. L. Stephens. 2006. Tree mortality patterns following prescribed fires in a mixed conifer forest. *Canadian Journal of Forest Research* 36:3222–3238.
- Krofcheck, D. J., M. D. Hurteau, R. M. Scheller, and E. L. Loudermilk. 2018. Prioritizing forest fuels treatments based on the probability of high-severity fire restores adaptive capacity in Sierran forests. *Global Change Biology* 24:729–737.
- Landry, J. S., and H. D. Matthews. 2016. Non-deforestation fire vs. fossil fuel combustion: The source of CO₂ emissions affects the global carbon cycle and climate responses. *Biogeosciences* 13:2137–2149.
- Levine, C. R., F. Krivak-Tetley, N. S. van Doorn, J. A. S. Ansley, and J. J. Battles. 2016. Long-term demographic trends in a fire-suppressed mixed-conifer forest. *Canadian Journal of Forest Research* 46:745–752.
- Liang, S., M. D. Hurteau, and A. L. R. Westerling. 2017. Response of Sierra Nevada forests to projected climate–wildfire interactions. *Global Change Biology* 23:2016–2030.
- Liang, S., M. D. Hurteau, and A. L. Westerling. 2018. Large-scale restoration increases carbon stability under projected climate and wildfire regimes. *Frontiers Ecology and the Environment* 16:207–212.
- Lindenmayer, D. B., W. Blanchard, L. McBurney, D. Blair, S. Banks, G. E. Likens, J. F. Franklin, W. F. Laurence, J. A. Stein, and P. Gibbons. 2012. Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. *PLOS ONE* 7: e41864.
- Lydersen, J. M., and B. M. Collins. 2018. Change in vegetation patterns over a large forested landscape based on historical and contemporary aerial photography. *Ecosystems* 21:1348–1363.
- Lydersen, J. M., B. M. Collins, M. L. Brooks, J. R. Matchett, K. L. Shive, N. A. Povak, V. R. Kane, and D. F. Smith. 2017. Evidence of fuels management and fire weather influencing fire severity in an extreme fire event. *Ecological Applications* 27:2013–2030.
- Lydersen, J. M., B. M. Collins, M. Coppoletta, M. R. Jaffe, H. Northrop, and S. L. Stephens. 2019. Fuel dynamics and reburn severity following high severity fire in a Sierra Nevada mixed-conifer forest. *Fire Ecology* 15:43.
- Maestrini, B., E. C. Alvey, M. D. Hurteau, H. Safford, and J. R. Miesel. 2017. Fire severity alters the distribution of pyrogenic carbon stocks across ecosystem pools in a Californian mixed-conifer forest. *Journal of Geophysical Research: Biogeosciences* 122:2338–2355.
- McGinnis, T. W., C. D. Shook, and J. E. Keeley. 2010. Estimating aboveground biomass for broadleaf woody plants and young conifers in Sierra Nevada, California, forests. *Western Journal of Applied Forestry* 25:203–209.
- Moghaddas, E. E. Y., and S. L. Stephens. 2007. Thinning, burning, and thin-burn fuel treatment effects on soil properties in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management* 250:156–166.
- Moghaddas, J. J., B. M. Collins, K. Menning, E. E. Moghaddas, and S. L. Stephens. 2010. Fuel treatment effects on modeled landscape-level fire behavior in the northern Sierra Nevada. *Canadian Journal of Forest Research* 40:1751–1765.
- Moghaddas, J. J., and L. Craggs. 2007. A fuel treatment reduces fire severity and increases suppression efficiency in a mixed conifer forest. *International Journal of Wildland Fire* 16:673–678.
- Murphy, K., P. Duncan, and C. Dillingham. 2010. A summary of fuel treatment effectiveness in the Herger-Feinstein Quincy Library Group Pilot Project Area. Pages 1–21. R5-TP-031. USDA Forest Service, Pacific Southwest Region, Vallejo, California, USA.
- North, M. 2012. Managing Sierra Nevada forests. PSW-GTR-237. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- North, M. P., B. M. Collins, H. D. Safford, and N. L. Stephenson. 2016. Montane forests. Pages 553–578 in H. A. Mooney and E. Zavaleta, editors. *Ecosystems of California*. University of California Press, Oakland, California, USA.
- North, M., B. M. Collins, and S. Stephens. 2012. Using fire to increase the scale, benefits, and future maintenance of fuels treatments. *Journal of Forestry* 110:392–401.
- North, M. P., and M. D. Hurteau. 2011. High-severity wildfire effects on carbon stocks and emissions in fuels treated and untreated forest. *Forest Ecology and Management* 261:1115–1120.
- North, M., M. Hurteau, and J. Innes. 2009. Fire suppression and fuels treatment effects on mixed-conifer carbon stocks and emissions. *Ecological Applications* 19:1385–1396.
- Pan, Y., et al. 2011. Supporting online material for a large and persistent carbon sink in the world's forests. *Science* 333:988–993.

- Pinhiero, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2016. nlme: linear and Nonlinear Mixed Effects Models. <https://CRAN.R-project.org/package=nlme>
- PNW. 2015. A Data Dictionary and User Guide for the PNW-FIADB database. USDA Forest Service Forest Inventory and Analysis Program, Pacific Northwest Research Station, Portland, Oregon, USA.
- Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rebain, S. A. 2010. The fire and fuels extension to the forest vegetation simulator: updated Documentation. Internal report. USDA Forest Service, Forest Management Service Center, Fort Collins, Colorado, USA.
- Reinhardt, E. D., and N. L. Crookston (Technical Editors). 2003. The Fire and Fuels Extension to the Forest Vegetation Simulator. RMRS-GTR-116. USDA Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.
- Reinhardt, E., and K. Ryan. 1988. Predicting postfire mortality of seven western conifers. *Canadian Journal of Forest Research* 18:1291–11297.
- Roccaforte, J. P., P. Z. Fulé, W. W. Chancellor, and D. C. Laughlin. 2012. Woody debris and tree regeneration dynamics following severe wildfires in Arizona ponderosa pine forests. *Canadian Journal of Forest Research* 42:593–604.
- Ryan, M. G., D. Binkley, and J. H. Fownes. 1997. Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research* 27:213–262.
- Safford, H. D., D. A. Schmidt, and C. H. Carlson. 2009. Effects of fuel treatments on fire severity in an area of wildland-urban interface, Angora Fire, Lake Tahoe Basin, California. *Forest Ecology and Management* 258:773–787.
- Safford, H. D., and J. T. Stevens. 2017. Natural range of variation (NRV) for yellow pine and mixed conifer forests in the bioregional assessment area, including the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests. PSW-GTR-256. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Schoemaker, P. 1982. The expected utility model: its variants, purposes, evidence and limitations. *Journal of Economic Literature* 20:529–563.
- Schwilk, D. W., et al. 2009. The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. *Ecological Applications* 19:285–304.
- Smith, D. M., B. C. Larson, M. J. Kelty, and P. M. S. Ashton. 1997. The practice of silviculture: applied forest ecology. Ninth edition. John Wiley & Sons, Hoboken, New Jersey, USA.
- Starrs, C. F., V. Butsic, C. Stephens, and W. Stewart. 2018. The impact of land ownership, firefighting, and reserve status on fire probability in California. *Environmental Research Letters* 13(),
- Stephens, C. W., B. M. Collins, and J. Rogan. 2020a. Land ownership impacts post-wildfire forest regeneration in Sierra Nevada mixed-conifer forests. *Forest Ecology and Management* 468:118161.
- Stephens, S. L. 2001. Fire history of adjacent Jeffrey pine and upper montane forests in the eastern Sierra Nevada. *International Journal of Wildland Fire* 10:161–176.
- Stephens, S. L., et al. 2012. Fuel treatment impacts on estimated wildfire carbon loss from forests in Montana, Oregon, California, and Arizona. *Ecosphere* 3:38.
- Stephens, S. L., and B. M. Collins. 2004. Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. *Northwest Science* 78:12–23.
- Stephens, S. L., J. M. Lydersen, B. M. Collins, D. L. Fry, and M. D. Meyer. 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. *Ecosphere* 6:63.
- Stephens, S. L., and J. J. Moghaddas. 2005. Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. *Forest Ecology and Management* 215:21–36.
- Stephens, S. L., J. J. Moghaddas, C. Edminster, C. E. Fiedler, S. Haase, M. Harrington, J. E. Keeley, E. E. Knapp, J. D. McIver, K. Metlen, C. Skinner, and A. Youngblood. 2009a. Fire treatment effects on vegetation structure, fuels, and potential fire severity in Western U.S. forests. *Ecological Applications* 19:305–320.
- Stephens, S. L., A. L. Westerling, M. D. Hurteau, M. Z. Peery, C. A. Schultz, and S. Thompson. 2020b. Fire and climate change: Conserving seasonally dry forests is still possible. *Frontiers in Ecology and the Environment* (in press). <http://dx.doi.org/10.1002/fee.2218>
- Stephens, S. L., J. J. Moghaddas, B. R. Hartsough, E. E. Moghaddas, and N. E. Clinton. 2009b. Fuel treatment effects on stand-level carbon pools, treatment-related emissions, and fire risk in a Sierra Nevada mixed-conifer forest. *Canadian Journal of Forest Research* 39:1538–1547.
- Stephenson, N. L., et al. 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507:90–93.

- Stevens, J. T., H. D. Safford, and A. M. Latimer. 2014. Wildfire-contingent effects of fuel treatments can promote ecological resilience in seasonally dry conifer forests. *Canadian Journal of Forest Research* 44:843–854.
- Stewart, W. C., and G. M. Nakamura. 2012. Documenting the full climate benefits of harvested wood products in Northern California: linking harvests to the US greenhouse gas inventory. *Forest Products Journal* 62:340–353.
- Stewart-Oaten, A., J. Bence, A. L. S. T. Aten, J. A. R. B. Ence, and T. A. Continued. 2001. Temporal and spatial variation in environmental impact assessment. *Ecological Monographs* 71:305–339.
- Taylor, A. H., A. M. Vandervlugt, R. S. Maxwell, R. M. Beaty, C. Airey, and C. Skinner. 2014. Changes in forest structure, fuels and potential fire behaviour since 1873 in the Lake Tahoe Basin, USA. *Applied Vegetation Science* 17:17–31.
- van Wagtendonk, J. W., J. M. Benedict, and W. M. Sydoriak. 1996. Physical properties of woody fuel particles of Sierra Nevada conifers. *International Journal of Wildland Fire* 6:117–123.
- van Wagtendonk, J. W., J. M. Benedict, and W. M. Sydoriak. 1998. Fuel bed characteristics of Sierra Nevada conifers. *Western Journal of Applied Forestry* 13:73–84.
- Westerling, A. L., B. P. Bryant, H. K. Preisler, T. P. Holmes, H. G. Hidalgo, T. Das, and S. R. Shrestha. 2011. Climate change and growth scenarios for California wildfire. *Climatic Change* 109:445–463.
- Wiechmann, M. L., M. D. Hurteau, M. P. North, G. W. Koch, and L. Jerabkova. 2015. The carbon balance of reducing wildfire risk and restoring process: an analysis of 10-year post-treatment carbon dynamics in a mixed-conifer forest. *Climatic Change* 132:709–719.
- Yocom Kent, L. L., K. L. Shive, B. A. Strom, C. H. Sieg, M. E. Hunter, C. S. Stevens-Rumann, and P. Z. Fulé. 2015. Interactions of fuel treatments, wildfire severity, and carbon dynamics in dry conifer forests. *Forest Ecology and Management* 349:66–72.
- Young, D. J. N., J. T. Stevens, J. M. Earles, J. Moore, A. Ellis, A. L. Jirka, and A. M. Latimer. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecology Letters* 20:78–86.
- Zuur, A. F., E. N. Leno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer US, New York, New York, USA.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3198/full>