

Restoring forest structure and process stabilizes forest carbon in wildfire-prone southwestern ponderosa pine forests

MATTHEW D. HURTEAU,^{1,6} SHUANG LIANG,² KATHERINE L. MARTIN,³ MALCOLM P. NORTH,⁴ GEORGE W. KOCH,⁵ AND BRUCE A. HUNGATE⁵

¹Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA

²Intercollege Graduate Degree Program in Ecology and Department of Ecosystem Science and Management, Pennsylvania State University, University Park, Pennsylvania 16802 USA

³Center for Integrated Forest Science, Southern Research Station, USDA Forest Service, Triangle Park, North Carolina 27709 USA

⁴Pacific Southwest Research Station, USDA Forest Service, Davis, California 95618 USA

⁵Center for Ecosystem Science and Society and Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA

Abstract. Changing climate and a legacy of fire-exclusion have increased the probability of high-severity wildfire, leading to an increased risk of forest carbon loss in ponderosa pine forests in the southwestern USA. Efforts to reduce high-severity fire risk through forest thinning and prescribed burning require both the removal and emission of carbon from these forests, and any potential carbon benefits from treatment may depend on the occurrence of wildfire. We sought to determine how forest treatments alter the effects of stochastic wildfire events on the forest carbon balance. We modeled three treatments (control, thin-only, and thin and burn) with and without the occurrence of wildfire. We evaluated how two different probabilities of wildfire occurrence, 1% and 2% per year, might alter the carbon balance of treatments. In the absence of wildfire, we found that thinning and burning treatments initially reduced total ecosystem carbon (TEC) and increased net ecosystem carbon balance (NECB). In the presence of wildfire, the thin and burn treatment TEC surpassed that of the control in year 40 at 2%/yr wildfire probability, and in year 51 at 1%/yr wildfire probability. NECB in the presence of wildfire showed a similar response to the no-wildfire scenarios: both thin-only and thin and burn treatments increased the C sink. Treatments increased TEC by reducing both mean wildfire severity and its variability. While the carbon balance of treatments may differ in more productive forest types, the carbon balance benefits from restoring forest structure and fire in southwestern ponderosa pine forests are clear.

Key words: climate change mitigation; forest carbon; forest restoration; LANDIS-II; ponderosa pine; wildfire.

INTRODUCTION

Fire is a globally distributed disturbance that can alter carbon (C) source-sink dynamics in forest ecosystems by affecting both the sign and rate of C fluxes (Bowman et al. 2009, Hurteau 2013). Unlike many other disturbances, forest management can influence fire (Hurteau and Brooks 2011). However, management to alter fire behavior is also a form of disturbance that releases C and can affect forest C dynamics. Choosing to mitigate wildfire risk guarantees direct and immediate impacts on the forest C cycle, because thinning and prescribed fire reduce C stocks. The longer-term, indirect effects of management on forest C depend on the stochastic nature of wildfire and the resultant C dynamics from the influence of

management on fire behavior. While fuels treatments have an immediate cost because they reduce forest C storage, there may be future benefits by reducing C loss from high-severity wildfire, particularly as warming climate increases wildfire frequency (Westerling et al. 2011).

The natural frequency of fire in ecosystems varies as a function of climate and productivity (Littell et al. 2009, O'Connor et al. 2014). Infrequent-fire systems are characterized by climatic conditions that preclude regular fires, and when one does occur, a large area burned with high rates of tree mortality is a natural outcome (Schoennagel et al. 2004). In frequent-fire systems, fire is self-limiting, controlled by the availability of biomass for combustion (Collins et al. 2009, Moritz et al. 2011). Fire suppression policy has removed the biomass constraint in many frequent-fire forests, increasing the risk of stand-replacing wildfire, which can affect both short- and long-term C dynamics (Hurteau et al. 2014a, Steel et al. 2015). Restoring historic fire regimes requires human

Manuscript received 22 February 2015; revised 13 May 2015; accepted 26 June 2015. Corresponding Editor: B. P. Wilcox.

⁶E-mail: mhurteau@unm.edu

intervention in the form of biomass removal through thinning or prescribed burning, which also affects C dynamics.

There is considerable debate in the scientific and policy communities regarding the C balance implications of management intervention to restore forest structure and reduce wildfire severity compared to the alternative of not intervening and allowing large, high-severity wildfires to occur. Restoring frequent fire and reducing the risk of high-severity wildfire requires reduction of tree density by forest thinning and reduction of surface biomass through prescribed burning. These actions reduce the C stock and result in the direct emission of C to the atmosphere, the effect of which has been quantified empirically in a number of forest types (Finkral and Evans 2008, North et al. 2009, Stephens et al. 2009, Hurteau et al. 2011). When wildfire does intersect a treated forest stand, the reduction in surface and ladder fuels and canopy density alters fire behavior, leading to reduced tree mortality and C emissions (Agee and Skinner 2005, North and Hurteau 2011). The sources of uncertainty and debate on this topic lie in the stochastic nature of fire, the C removal required to reduce fire severity, and post-fire succession in areas burned by high-severity fire. The probability of wildfire intersecting a treated area during its effective life span is small, and treatments could lead to cumulative carbon losses that exceed those of wildfire alone, because effective wildfire risk reduction often requires treating more forest than will be burned by wildfire (Mitchell et al. 2009, Campbell et al. 2012).

Southwestern ponderosa pine (*Pinus ponderosa*) forests are a historically frequent-fire forest type where fire is generally limited by fuel availability (Littell et al. 2009, Steel et al. 2015). Their structure has been fundamentally altered by a century of fire exclusion and in many places is now characterized by high tree density and a build-up of surface biomass, both of which can alter fire behavior and increase the risk of high-severity wildfire (Fulé et al. 2012). These structural changes have increased the C density of this forest type and the probability that when wildfire does occur, mortality and carbon emissions will be high

(Wiedinmyer and Hurteau 2010, Hurteau et al. 2011). Restoring forest structure and frequent fire requires a substantial (~30–40%) reduction in live tree C (Finkral and Evans 2008, Hurteau et al. 2011b). Thinning also initially reduces stand-level net primary productivity (NPP) because lower leaf area decreases gross primary productivity, but NPP recovers and can surpass unthinned levels within several years (Dore et al. 2012). However, when untreated forests are burned by high-severity wildfire they can remain a source of C to the atmosphere for years to decades (Dore et al. 2012). Because the ecological and economic costs of high-severity wildfire are driving efforts to restore southwestern ponderosa pine forest structure on a large scale (Sitko and Hurteau 2010), understanding how treatments influence C dynamics is important in the context of climate regulation.

Given the C losses associated with treatments and the C stability that can be realized when fire does burn through a restored forest, how does the stochastic nature of fire occurrence alter C dynamics between treated and untreated forest? We hypothesized that (1) in the absence of wildfire, treatments would reduce total ecosystem C relative to controls; (2) the C sink-strength of treated forests would be greater than untreated forests regardless of wildfire occurrence; and (3) in the presence of wildfire, the treated landscape would have higher total ecosystem C and remain a larger sink for C than the untreated landscape.

METHODS

Study area

Camp Navajo is a 11610-ha military installation located approximately 20 km west of Flagstaff, Arizona, USA (Fig. 1). The mean elevation of the installation is 2050 m, with a mean annual temperature of 6.9°C and mean winter minimum winter and summer maximum temperatures of −11°C and 27°C, respectively. Mean annual precipitation is 493 mm and has a bimodal distribution with approximately 50% of the precipitation

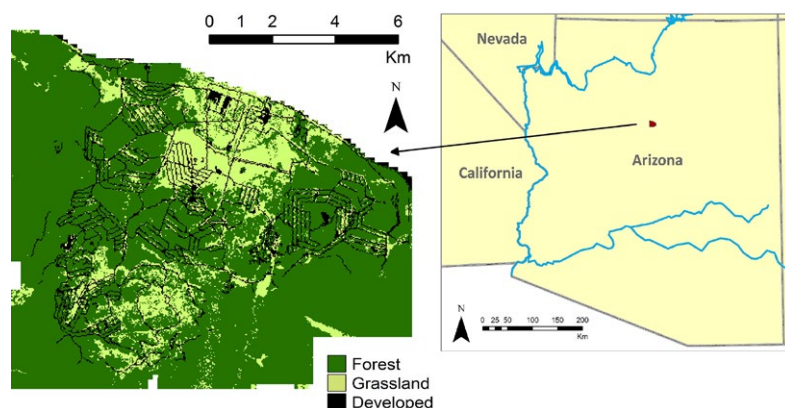


FIG. 1. Map of Camp Navajo, which is located approximately 20 km west of Flagstaff, Arizona, USA. The installation is predominately forested, with *Pinus ponderosa* and *Quercus gambelii* comprising a majority of the forest biomass.

occurring as winter snow and 50% as summer monsoon rains falling between July and August (National Climate Data Center, GHCND USC00020678). Soils are predominantly sandy loams with a substrate of primarily volcanic origin (Fulé et al. 1997). Forest cover is dominated by ponderosa pine, with occasional patches occupied by Gambel oak (*Quercus gambelii*) and Rocky Mountain juniper (*Juniperus scopulorum*). The northern part of the installation is occupied by grassland. Ponderosa pine forests within the region have a historic mean fire return interval ranging from 2 to 20 yr (Swetnam and Baisan 1996). A combination of 19th century logging and grazing, coupled with early 20th century episodic regeneration events and on-going fire suppression have altered the structure from an open-canopy, fire-maintained system to a closed-canopy system across the region (Covington and Moore 1994).

Data

We collected vegetation, soil, and surface fuels data for model parameterization and validation during summer 2011 from 240 plots that were distributed across Camp Navajo. Sampling sites were selected to capture the range of forest conditions across the installation, working within access restrictions resulting from military training schedules. Prior to sampling, we established a 200-m grid to locate plots. We used a 1/5 ha nested circular plot design to measure all trees ≥ 50 cm diameter at breast height (1.37m DBH). Trees ≥ 30 cm DBH were measured in a 1/10-ha subplot and trees ≥ 5 cm DBH were measured in a 1/50-ha subplot. We recorded species, DBH, height, and status (live, dead, decay class for dead) of each tree. We tallied regeneration by height class in a 2 m radius sub-plot at plot center. Surface fuels and coarse woody debris were measured along three 15-m modified Brown's fuel transects originating at plot center within each plot (Brown 1974). Soil samples were collected at 0–15 and 15–30 cm depths from three stands and were analyzed at the Colorado Plateau Stable Isotope Lab, Northern Arizona University, Flagstaff, Arizona, USA. Soils were oven dried and ground. Sub-samples were analyzed by Dumas combustion on an elemental analyzer (ThermoFinnigan Delta Advantage, CE Elantech, Lakewood, New Jersey, USA) to quantify total C.

Landscape model description

To quantify the C tradeoffs associated with fuels treatments and wildfire, we used the LANDIS-II forest succession and disturbance model (Scheller et al. 2007). LANDIS-II uses an age-cohort based approach to simulate forest succession, where species are represented by biomass in age classes. The study area is represented by a grid of interacting cells that are populated with initial communities of age-specific cohorts of species. Growth and succession are dictated by species-specific life history parameters, such as dispersal distance, shade and fire tolerance, among others (Scheller et al. 2007). Cohorts grow,

compete, disperse, and reproduce within and among grid cells and are impacted by disturbances that can affect clusters of grid cells.

We used three extensions to the core LANDIS-II model, the Century succession, leaf biomass harvest, and dynamic fire and fuels extensions. We used the Century succession extension to simulate ecosystem C dynamics (Scheller et al. 2011b), which was developed based on the CENTURY soil model (Metherell et al. 1993, Parton et al. 1993, Parton 1996). Century succession simulates above- and belowground carbon pools and fluxes from photosynthesis and respiration, including C transfer between dead biomass pools and C movement through three soil organic matter pools. Carbon dynamics within the extension are governed by species-specific attributes (e.g., C:N ratios and lignin of component parts), climate, soil properties, and their interaction (Scheller et al. 2011a,b).

We used the Leaf Biomass Harvest extension to simulate both thinning and prescribed burning treatments. This extension is capable of simulating multiple, overlapping harvest prescriptions (Gustafson et al. 2000). We simulated stochastic wildfire events using the Dynamic Fire and Fuels extension. This extension captures changes in fuels, such as those initiated by thinning, and couples fuel conditions with climate and topographic data to simulate wildfire using a methodology based on the Canadian Forest Fire Behavior Prediction System (Van Wagner et al. 1992, Sturtevant et al. 2009). Because the model is spatially explicit, it allows for examining the effects of both biotic and abiotic factors on fire. We used this capability to identify areas of high fire risk as a result of topographic and fuel conditions.

Model parameterization and validation

The LANDIS-II model requires that a user-defined grid be established and that the study area be subdivided into abiotically similar ecoregions. We used a 150-m grid and subdivided the landscape into six ecoregions based on soil properties and topographic variables, since climate is heavily influenced by topography in this region. We developed the initial forest communities layer using field inventory data from the installation and age-size distributions from Fulé et al. (1997) and Mast et al. (1999). We parameterized two species, *Pinus ponderosa* and *Quercus gambelii*, which accounted for greater than 99% of the biomass in our field data, using values from the literature (Appendix S1: Table S1).

To parameterize the Century succession extension, we field collected soil samples and used the SSURGO database (*available online*) to determine soil attributes.⁷ Soil C values were divided into three pools following Metherell et al. (1993). We calibrated soil organic matter decay rates such that soil C values fell within the field-sampled range following model spin-up (Loudermilk et al. 2013, Martin et al. 2015). Soil C values were compared against field data

⁷<http://websoilsurvey.nrcs.usda.gov>

and values from the literature (Grady and Hart 2006, Dore et al. 2008, 2010, 2012) and simulated values fell within the ranges reported by these studies. We used 103 yr of climate data (1909–2012) from the Flagstaff, Arizona, USA, Pulliam Airport weather station (GHCND: USW00003103), obtained from the National Climate Data Center because of its nearby location and temporal depth. Species-specific parameter values were gathered from the literature, U.S. government databases, and the CENTURY user guide (Burns and Honkala 1990, Parton et al. 1993, Simonin 2000, Howard 2003, Dore et al. 2008, 2010, 2012). Parameter values for the Century extension are presented in the supplemental material (Appendix S1: Tables S2–S5). Following model spin-up, our landscape was a C sink with mean net ecosystem productivity (NEP) of $175 \text{ g C m}^{-2} \text{ yr}^{-1}$ (SD = 53). Dore et al. (2012), using eddy covariance, reported a range of NEP from 19 (76) $\text{g C m}^{-2} \text{ yr}^{-1}$ to 174 (57) $\text{g C m}^{-2} \text{ yr}^{-1}$ over a 5-yr period, inclusive of a year with significant drought. We used our inventory data and allometric equations from Jenkins et al. (2003) to calculate individual tree biomass and then scaled these values to a per unit area basis for comparison with simulated aboveground biomass values. Our inventory aboveground biomass values ranged from 1917 to 25645 g m^{-2} , with a mean value of 12106 g m^{-2} . Our simulated aboveground biomass values ranged from 2084 to 14032 g m^{-2} , with a mean value of 11 540 g m^{-2} .

We simulated common forest treatment practices in southwestern ponderosa pine, including understory thinning to reduce fuel continuity between the forest floor and canopy and prescribed burning to reduce surface fuel loads. We used the Leaf Biomass Harvest extension to implement both thinning and prescribed burning treatments following Syphard et al. (2011). We used this approach for prescribed burning to facilitate wildfire simulations using the Dynamic Fire extension because both prescribed fire and wildfire cannot be simulated simultaneously in the Dynamic Fire extension. We simulated understory thinning by preferentially targeting the youngest cohorts of trees following common forest restoration practice based on historical forest reconstructions (Fulé et al. 1997, Finkral and Evans 2008). We excluded treatments from areas with slopes >14% as these areas are operationally difficult to treat and are often nest sites for the federally threatened Mexican spotted owl (*Strix occidentalis lucida*; Prather et al. 2008). We ran a series of wildfire simulations prior to implementing thinning treatments to identify geographic locations with the highest fire risk. We then ranked treatment implementation timing as a function of fire risk (Appendix S1: Fig. S1). We implemented thinning treatments on 12% of the installation per year, minus the excluded areas, until all areas identified for treatment were completed. To simulate prescribed burning with the Leaf Biomass Harvest extension, we implemented a treatment that removed 90% of 1–10-yr-old cohorts, 33% of 11–30-yr-old cohorts, and a small fraction of older cohorts (2–10%) to simulate fire-induced mortality. Following Syphard et al. (2011), fuels were reduced

and crown base height was increased to simulate consumption by fire after each prescribed burn. The prescribed fire treatment used a 10-yr return interval.

We used the Dynamic Fire and Fuels extension to simulate stochastic wildfire events across the installation. We used the Coconino National Forest wildfire database to obtain data to parameterize the fire size distribution, ignition frequency, and seasonality for fires occurring between 1970 and 2013. Following Scheller et al. (2011b), we adjusted parameter values from the Canadian Forest Fire Behavior Prediction System using spread rates in Scott and Burgan (2005). We ran simulations with two different fire occurrence probabilities (2%/yr and 1%/yr). These probabilities represent the lower end of the historic range of regional large wildfire probability estimated by Dickson et al. (2006) and equate to mean fire rotations of 61 (2%/yr) and 121 (1%/yr) years in the absence of treatment. We held all other fire parameters constant between simulations. We used data from the KFAST station for Flagstaff, Arizona, USA, to provide fire weather data and Fire Family Plus (Bradshaw and McCormick 2000) to evaluate seasonality and severity as a function of weather conditions. We used this extension to produce spatial fire severity outputs for each time step. Fire severity is categorical and ranges from one to five, with one being low severity surface fire and five being high severity. At a severity of three, fires begin to torch (burn up into tree canopies) and can initiate a crown fire.

Simulation experiment and analysis

To evaluate the effects of forest treatments on C dynamics, we ran three different treatment scenarios: control, thin-only, and thin and burn. Both the thin-only and thin and burn used an understory thin to remove approximately 30% of the live tree C, an approach common for this forest type (Hurteau et al. 2011). The thin and burn treatment included a simulated prescribed fire implemented with a 10 yr return interval, such that 10% of the installation was burned by prescribed fire every year. We ran each of these simulations with three levels of wildfire: no wildfire, ignition probability of 2%/yr, and ignition probability of 1%/yr. We ran 50 replicates of each scenario for 100 yr to capture the stochastic nature of wildfire occurrence. To quantify the effects of forest treatments and wildfire on C stocks and fluxes, we calculated the mean and 95% confidence intervals for total ecosystem carbon (TEC) and net ecosystem carbon balance (NECB). TEC values include above and belowground C, inclusive of soil C. NECB accounts for both C assimilation from net primary productivity and losses due to respiration and disturbance (Chapin and Matson 2011). Our NECB values include net primary productivity, respiration, and C loss from prescribed burning and wildfire. We did not include C removal from understory thinning in our NECB calculations, because the fate of the thinned biomass is variable in this region. Previous work has shown that harvested trees can end up sequestered in wood products, burned for

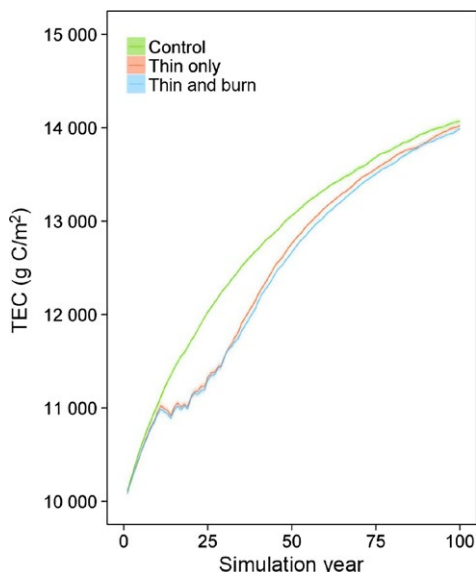


FIG. 2. Total ecosystem carbon (TEC) for the three simulated treatments (control, thin-only, and thin and burn) in the absence of simulated wildfire over the 100-yr simulation period. The dark lines represent mean TEC by treatment for 50 simulation replicates. Shaded areas are the 95% confidence intervals.

home heating, or burned in the forest. Wood products and home heating both require a life-cycle assessment to determine the effects and result in different C outcomes (Finkral and Evans 2008). However, the C loss from thinning is reflected in TEC. To determine the effectiveness of forest treatments on altering fire effects, we calculated the mean and coefficient of variation for fire severity outputs from the Dynamic Fire and Fuels extension for each scenario using all time steps from the 50 replicates for each grid cell in the study area that burned during each simulation year. Analyses of simulation data were conducted in R using the Raster package and figures were produced using the ggplot2 package (Wickham 2009, Hijmans and van Etten 2012, R Core Team 2012).

RESULTS

As we hypothesized, TEC in the absence of wildfire was consistently higher in the control than in either of the treatments (Fig. 2). We had expected a sustained reduction in TEC with both treatments and a larger reduction for the thin and burn treatment. However, thin-only and thin and burn TEC differed little over the majority of the 100-yr simulation. Treatments reduced mean TEC by approximately 100 g C/m² below the control in the absence of wildfire at the end of the 100-yr simulation period (Fig. 2). Thin-only and thin and burn treatments enhanced NECB relative to the control over the first half of the simulation period (Fig. 3). Increased NECB results from the growth release that occurs after thinning, as supported by empirical research in southwestern ponderosa pine (McDowall

et al. 2006, Kerhoulas et al. 2013). In simulations that included wildfire, mean fire sizes were consistent across treatments because fire size parameters were held constant to isolate the effects of treatment on fire behavior and fire rotation varied as a function of treatment (Table 1). The longer fire rotation under the thin and burn was driven by the effects of prescribed burning on fuel availability for wildfires. The change in fuels in the thin and burn treatment reduced both mean fire severity and its coefficient of variation (Figs. 4 and 5). On the western edge of the landscape are areas excluded from thinning because of steep slopes and potential Mexican spotted owl habitat. The effect of slope interacting with fuels on fire severity is evident across all three scenarios, as these steeper areas had higher mean fire severity (Fig. 4). However, mean severity in the thin and burn tended to be lower than other treatments because of the combined effects of thinning and burning on reducing fuel continuity between the forest floor and canopy, resulting in slower fire spread. In the thin and burn treatment, untreated areas exhibited a higher coefficient of variation for fire severity compared to treated areas (Fig. 5C). When the probability of fire occurrence was simulated at 2%/yr, the thin and burn treatment had substantially higher TEC than the control and thin-only by the end of the simulation period (Fig. 6). When the probability of fire occurrence was simulated at 1%/yr, the control had higher TEC for the first half of the simulation period, but was surpassed by the thin and burn during the second half of the simulation period (Fig. 6). When we included wildfire with a probability of occurrence of 2%/yr in the simulations, the thin-only and thin and burn had

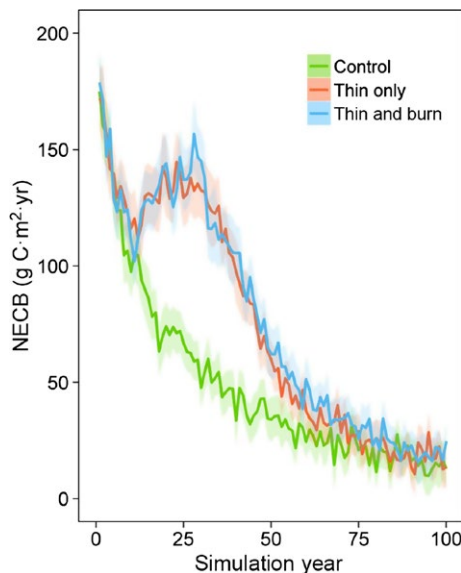


FIG. 3. Net ecosystem carbon balance (NECB) for the three simulated treatments (control, thin-only, and thin and burn) in the absence of simulated wildfire over the 100-yr simulation period. The dark lines represent mean NECB by treatment for 50 simulation replicates. Shaded areas are the 95% confidence intervals.

enhanced NECB, while the control NECB decreased more rapidly with wildfire than in the absence of wildfire (Fig. 7).

DISCUSSION

The desire to counteract increasing wildfire risk resulting from a legacy of past forest management is running headlong into the significant role of forests in sequestering C from the atmosphere. Fire-exclusion in historically fire-maintained forests has increased the frequency of severe

wildfires (Miller et al. 2009), a phenomenon that is compounded by climate-driven increases in large wildfire frequency (Westerling et al. 2006). In the southwestern USA, fire is regionally synchronized with La Niña events (Swetnam and Brown 2011), which are projected to increase in frequency with changing climate (Cai et al. 2015). Projected changes in climate and the influence on large wildfire frequency and area burned present an additional challenge to fire management across the region, especially given the role of forests in the global C cycle (Westerling et al. 2011, Hurteau et al. 2014a,b).

TABLE 1. Mean fire size (standard deviation) and fire rotation (standard deviation) for the control, thin-only, and thin and burn treatments with two different wildfire probabilities (2%/yr and 1%/yr).

	Control		Thin-only		Thin and burn	
Wildfire probability	1%	2%	1%	2%	1%	2%
Fire size (ha)	143 (332)	135 (322)	134 (313)	141 (345)	147 (356)	140 (335)
Fire rotation (yr)	121 (44)	61 (14)	127 (48)	65 (13)	334 (231)	155 (62)

Notes: Mean fire size was calculated using all fire occurrences from all 50 replicates. Mean fire rotation was calculated using the fire rotation of each of the 50 replicate simulations of each treatment.

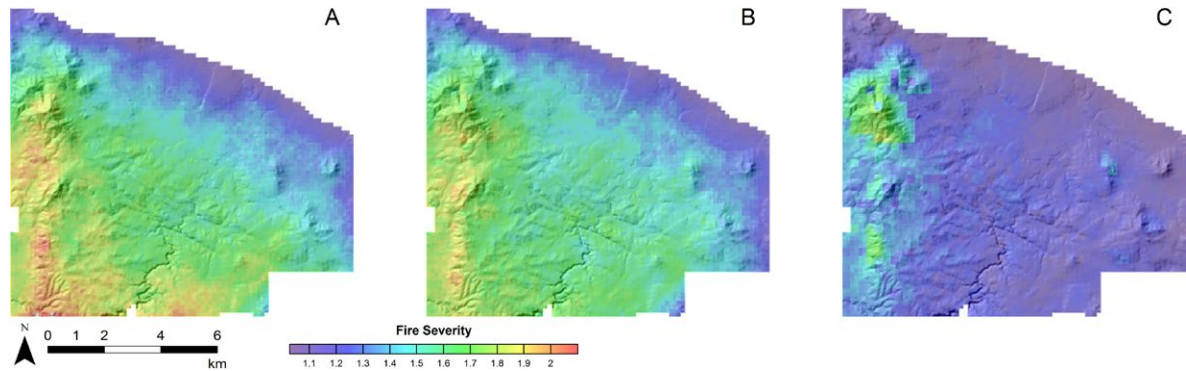


FIG. 4. Mean fire severity calculated from the 50 simulation replicates at Camp Navajo, Arizona, USA, for the (A) control, (B) thin-only, and (C) thin and burn using a probability of fire occurrence equivalent to 0.02. Fire severity is an index ranging from one to five, with one being the least severe and five being the most severe.

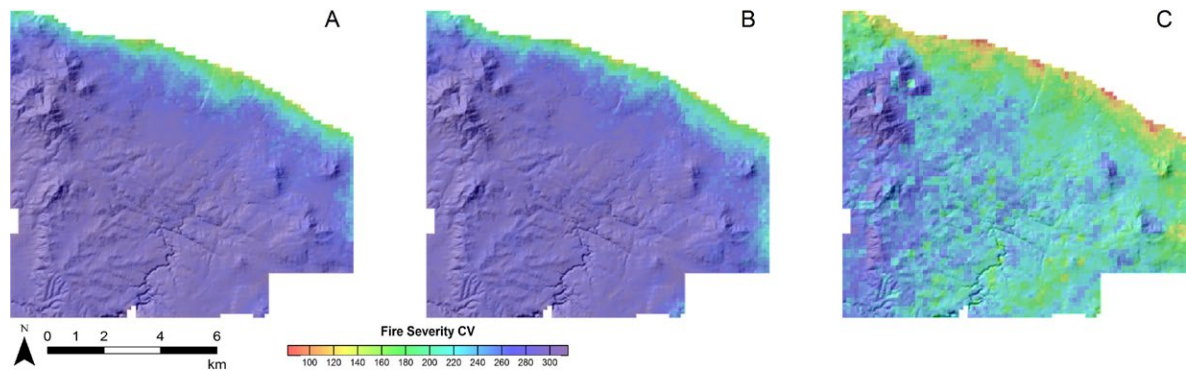


FIG. 5. Coefficient of variation (CV) of fire severity across Camp Navajo, Arizona, USA, for the (A) control, (B) thin-only, and (C) thin and burn using a probability of fire occurrence equivalent to 0.02. CV of fire severity was calculated using spatial severity maps for each of 100 simulation years from all 50 replicate simulations for each treatment.

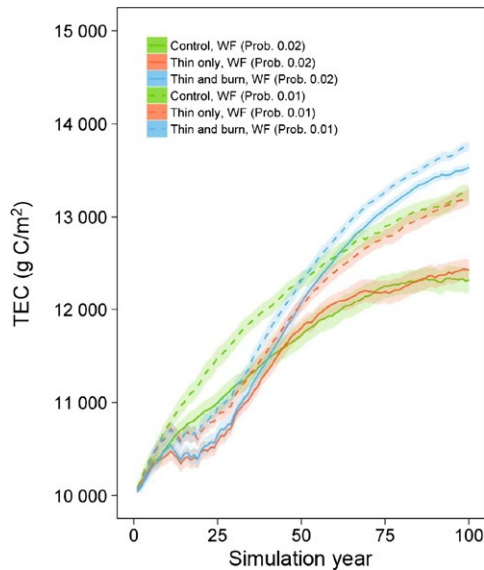


FIG. 6. Total ecosystem carbon (TEC) for the three simulated treatments (control, thin-only, and thin and burn) with the probability of wildfire occurrence simulated at 2%/yr and 1%/yr over the 100-yr simulation period. The dark lines represent mean TEC by treatment for 50 simulation replicates. Shaded areas are the 95% confidence intervals. WF is wildfire.

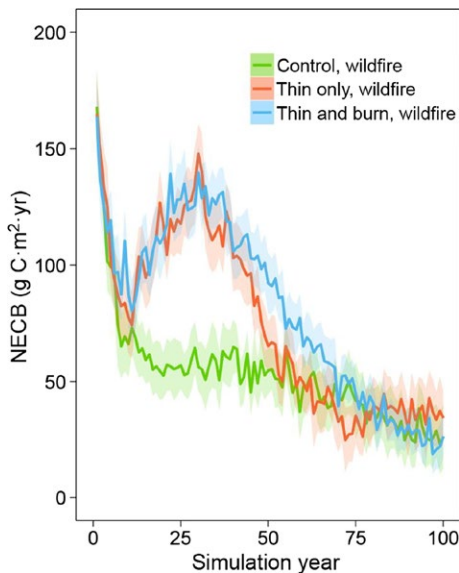


FIG. 7. Net ecosystem carbon balance (NECB) for the three simulated treatments (control, thin-only, and thin and burn) with the probability of wildfire occurrence simulated at 2%/yr over the 100-yr simulation period. The dark lines represent mean NECB by treatment for 50 simulation replicates. Shaded areas are the 95% confidence intervals.

The stochastic nature of wildfire has fueled considerable debate in the literature on the C balance of forest restoration treatments. Hurteau et al. (2008) hypothesized that the change in fire severity resulting from treatments and

the resultant decrease in wildfire emissions could yield increased C stocks. Hurteau and North (2009) found higher C stocks with thinning and burning treatments in the presence of wildfire in the Sierra Nevada. Simulation studies in both moist and dry forests in the Pacific Northwest USA found significant C stock reductions when reducing fire risk in moist forests and a potential slight C stock increase in drier forests (Mitchell et al. 2009, Campbell et al. 2012, Hudiburg et al. 2013). In drier forest types, subsequent simulation research has found that the potential range of C stocks is lower in treated compared to untreated forests and that the C stability is considerably higher following thinning and burning treatments (Earles et al. 2014).

Our results demonstrate, as others have (e.g., Hurteau et al. 2011, Campbell et al. 2012), that in the absence of wildfire, treatments do reduce C stocks (Fig. 2). However, when treating wildfire as a stochastic process, the C losses caused by thinning and burning treatments are outweighed by the C gains from decreased tree mortality rates and increased sequestration (Figs. 6 and 7). The transition to increased C stocks from thinning and burning treatments is not immediate because of the initial C losses from treatment. However, the thin and burn mean TEC surpasses the control in year 40 for the 2%/yr wildfire probability and in year 51 for 1%/yr wildfire probability (Fig. 6). These C stock increases are realized because prescribed burning reduces surface fuel loads and thinning reduces connectivity between the forest floor and canopy, resulting in both decreased mean and variability in fire severity (Figs. 4 and 5). The addition of prescribed fire to treat surface fuels is important for maintaining treatment effectiveness. As our thin-only simulations demonstrate, neglecting surface fuels increases fire severity and yields TEC results similar to the control (Figs. 4 and 6). Our total ecosystem C results with two different probabilities of fire occurrence also demonstrate that C benefits of treatment are realized even under the lower end of the range of current wildfire probability for the region (Dickson et al. 2006). Given our results with two low probabilities of fire occurrence, we would expect that increasing fire probability would cause the thinned and burned TEC to surpass the control earlier in the simulation period.

There are three primary caveats salient to our findings. First, our results are specific to southwestern ponderosa pine forests. Eddy covariance studies in Arizona ponderosa pine found high-severity wildfire transitions the forest from C sink to source and that thinning reduces NEP in the short-term relative to unthinned stands, but not during periods of high water stress. Moreover, within 5 years, NEP of thinned stands does not differ from unthinned stands (Dore et al. 2010, 2012). Second, in water limited southwestern forests, increasing water demand resulting from projected increases in temperature and vapor pressure deficit have the potential to increase climate-driven mortality rates beyond those we used for this study (Williams et al. 2010). Widespread, climate-induced regional tree mortality could alter the C balance of these

forests. However, evaluation of post-thinning tree growth has found that large ponderosa pine trees are less impacted by drought following moderate and heavy thinning than are smaller individuals (Kerhoulas et al. 2013), an important finding given that C accumulation rates are higher in larger trees (Stephenson et al. 2014). Both the effects of climate on southwestern forests and the potential for management actions such as thinning to mitigate increasing water stress require additional investigation to isolate the effects of projected changes in climate. Third, by using the Leaf Biomass Harvest extension to simulate prescribed burning and reflecting the effects of burning by changing the fuel type, we have treated each 2.25-ha grid cell uniformly and treated 100% of the C in cohorts removed as an emission. In reality, prescribed fire burns less than 100% of the treated area (Knapp et al. 2005) and little of the C in tree boles is combusted (Campbell et al. 2007). For these reasons, the contribution of prescribed fire emissions to NECB is likely overstated. The complete burning of each grid cell by prescribed burning also makes treated grid cells unavailable to burn by wildfire in the same year because of a lack of fuels. This had the effect of increasing fire rotation for the thin and burn treatments (Table 1).

Because of the potential of high-severity wildfire to cause vegetation type conversion, thinning and prescribed burning in these forests should be viewed from the perspective of avoiding C emissions (Hurteau et al. 2011). Lowering the risk of high-severity wildfire in southwestern ponderosa pine forests can result in both larger C stocks and increased C sequestration when we account for stochastic wildfire events. When considering the increased probability of large wildfires (Westerling et al. 2006), the potential for further climate-driven increases in the area burned by wildfire (Westerling et al. 2011), the C cycle and human health impacts of fire emissions (Hurteau et al. 2014a,b), and the costs associated with wildfire (Wu et al. 2011), it is clear that there are ecological, economic, and ecosystem service benefits to restoring forest structure and fire as a natural process in dry forest systems.

ACKNOWLEDGMENTS

Funding for this research was provided by the U.S. Department of Defense's Strategic Environmental Research and Development Program (SERDP, Project RC-2118). We thank the Camp Navajo field crew for assistance with data collection and Bruce Buttrey and Hannah Telle for providing data and facilitating access to the field site. We thank two anonymous reviewers for helpful feedback.

LITERATURE CITED

- Agee, J. K., and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. *Forest Ecology and Management* 211:83–96.
- Bowman, D. M. J. S., et al. 2009. Fire in the earth system. *Science* 324:481–484.
- Bradshaw, L., and E. McCormick. 2000. FireFamily Plus user's guide. Version 2.0. Technical Report RMRS-GTR-67WWW.
- U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.
- Brown, J. K. 1974. Handbook for inventorying downed woody material. Technical Report INT-16. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Burns, R. M., and B. H. Honkala, editors. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture handbook 654. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.
- Cai, W., et al. 2015. Increased frequency of extreme La Niña events under greenhouse warming. *Nature Climate Change* 5:132–137.
- 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* 112:G04014.
- 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.
- Chapin, F. S., and P. P. A. Matson. 2011. *Principles of terrestrial ecosystem ecology*. Springer, New York, New York, USA.
- Coconino National Forest GIS Data <http://www.fs.usda.gov/detail/r3/landmanagement/gis/cid=stelprdb5209303>
- 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.
- Covington, W. W., and M. M. Moore. 1994. Southwestern ponderosa forest structure and resource conditions: changes since Euro-American settlement. *Journal of Forestry* 92:39–47.
- Dickson, B. G., J. W. Prather, Y. Xu, H. M. Hampton, E. N. Aumack, and T. D. Sisk. 2006. Mapping the probability of large fire occurrence in northern Arizona, USA. *Landscape Ecology* 21:747–761.
- Dore, S., 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.
- Dore, S., et al. 2010. Carbon and water fluxes from ponderosa pine forests disturbed by wildfire and thinning. *Ecological Applications* 20:663–683.
- Dore, S., M. Montes-Helu, S. C. Hart, B. A. Hungate, G. W. Koch, J. B. Moon, A. J. Finkral, and T. E. Kolb. 2012. Recovery of ponderosa pine ecosystem carbon and water fluxes from thinning and stand-replacing fire. *Global Change Biology* 18:3171–3185.
- Earles, J. M., M. P. North, and M. D. Hurteau. 2014. Wildfire and drought dynamics destabilize carbon stores of fire-suppressed forests. *Ecological Applications* 24:732–740.
- Finkral, A. J., and A. M. Evans. 2008. The effects of a thinning treatment on carbon stocks in a northern Arizona ponderosa pine forest. *Forest Ecology and Management* 255:2743–2750.
- Fule, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications* 7:895–908.
- 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.
- Grady, K. C., and S. C. Hart. 2006. Influences of thinning, prescribed burning, and wildfire on soil processes and properties in southwestern ponderosa pine forests: a retrospective study. *Forest Ecology and Management* 234:123–135.

- Gustafson, E. J., S. R. Shifley, D. J. Mladenoff, K. K. Nimerfro, and H. S. He. 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. *Canadian Journal of Forest Research* 30:32–43.
- Hijmans, R. J., and van Etten J. 2012. Raster: geographic analysis and modeling with raster data. R package version 2.0-12. <http://CRAN.R-project.org/package=raster>
- Howard, J. L. 2003. *Pinus ponderosa* var. *arizonica*. Fire Effects Information System, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, Montana, USA. <http://www.fs.fed.us/database/feis/>
- Hudiburg, T. W., S. Luysaert, P. E. Thornton, and B. E. Law. 2013. Interactive effects of environmental change and management strategies on regional forest carbon emissions. *Environmental Science and Technology* 47:13132–13140.
- Hurteau, M. D. 2013. Effects of wildland fire management on forest carbon stores. Pages 359–380 in D. G. Brown, D. T. Robinson, N. H. F. French, and B. C. Reed, editors. *Land use and the carbon cycle: advances in integrated science, management, and policy*. Cambridge University Press, New York, New York, USA.
- 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., 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.
- 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., M. T. Stoddard, and P. Z. Fulé. 2011. The carbon costs of mitigating high-severity wildfire in southwestern ponderosa pine. *Global Change Biology* 17:1516–1521.
- Hurteau, M. D., J. B. Bradford, P. Z. Fulé, A. H. Taylor, and K. L. Martin. 2014a. Climate change, fire management, and ecological services in the southwestern US. *Forest Ecology and Management* 327:280–289.
- Hurteau, M. D., A. L. Westerling, C. Wiedinmyer, and B. P. Bryant. 2014b. Projected effects of climate and development on California wildfire emissions through 2100. *Environmental Science and Technology* 48:2298–2304.
- Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49:12–35.
- Kerhoulas, L. P., T. E. Kolb, M. D. Hurteau, and G. W. Koch. 2013. Managing climate change adaptation in forests: a case study from the U.S. southwest. *Journal of Applied Ecology* 50:1311–1320.
- Knapp, E. E., J. E. Keeley, E. A. Ballenger, and T. J. Brennan. 2005. Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fire in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* 208:383–397.
- Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. Climate and wildfire area burned in western U.S. ecoregions, 1916–2003. *Ecological Applications* 19:1003–1021.
- Loudermilk, E. L., R. M. Scheller, P. J. Weisberg, J. Yang, T. E. Dilts, S. L. Karam, and C. Skinner. 2013. Carbon dynamics in the future forest: the importance of long-term successional legacy and climate-fire interactions. *Global Change Biology* 19:3502–3515.
- Martin, K. L., M. D. Hurteau, B. A. Hungate, G. W. Koch, and M. P. North. 2015. Carbon tradeoffs of restoration and provision of endangered species habitat in a fire-maintained forest. *Ecosystems* 18:76–88.
- Mast, J. N., P. Z. Fulé, M. M. Moore, W. W. Covington, and A. E. M. Waltz. 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecological Applications* 9:228–239.
- McDowell, N. G., H. D. Adams, J. D. Bailey, M. Hess, and T. E. Kolb. 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications* 16:1164–1182.
- Metherell, A. K., L. A. Harding, C. V. Cole, and W. J. Parton. 1993. CENTURY soil organic matter model environment technical documentation. Agroecosystem Version 4.0. USDA Agricultural Research Service, Fort Collins, Colorado, USA.
- Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12:16–32.
- Mitchell, S. R., M. E. Harmon, and K. E. B. O'Connell. 2009. Forest fuel reduction alters fire severity and long-term carbon storage in three Pacific Northwest ecosystems. *Ecological Applications* 19:643–655.
- Moritz, M. A., P. F. Hessburg, and N. A. Povak. 2011. Native fire regimes and landscape resilience. Pages 51–86 in D. McKenzie, C. Miller, and D. A. Falk, editors. *The landscape ecology of fire*. Springer, New York, New York, USA.
- 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.
- O'Connor, C. D., D. A. Falk, A. M. Lynch, and T. W. Swetnam. 2014. Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleno Mountains, Arizona, USA. *Forest Ecology and Management* 329:264–278.
- Parton, W. J. 1996. The CENTURY model. Pages 283–291 in D. Powelson, P. Smith, and J. Smith, editors. *Evaluation of soil organic matter models*. Springer, Berlin, Germany.
- Parton, W. J., et al. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles* 7:785–809.
- Prather, J. W., R. F. Noss, and T. D. Sisk. 2008. Real versus perceived conflicts between restoration of ponderosa pine forests and conservation of the Mexican spotted owl. *Forest Policy and Economics* 10:140–150.
- R Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Scheller, R. M., J. B. Domingo, B. R. Sturtevant, J. S. Williams, A. Rudy, E. J. Gustafson, and D. J. Mladenoff. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling* 201:409–419.
- Scheller, R. M., D. Hua, P. V. Bolstad, R. A. Birdsey, and D. J. Mladenoff. 2011a. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States mesic forests. *Ecological Modelling* 222:144–153.
- Scheller, R. M., S. Van Tuyl, K. L. Clark, J. Hom, and I. La Puma. 2011b. Carbon sequestration in the New Jersey

- pine barrens under different scenarios of fire management. *Ecosystems* 14:987–1004.
- Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience* 54:661–676.
- Scott, J. H., and R. E. Burgan. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. Technical Report RMRS-GTR-153. USDA, Forest Service, Rocky Mountain Research Station, Missoula, Montana, USA.
- Simonin, K. A. 2000. *Quercus gambelii*. Fire Effects Information System, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, Montana, USA. <http://www.feis-crs.org/beta/>
- Sitko, S., and S. Hurteau. 2010. Evaluating the impacts of forest treatments: the first five years of the White Mountain stewardship project. Nature Conservancy, Phoenix, Arizona, USA.
- Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere* 6:8.
- Stevens, S. L., J. J. Moghaddas, B. R. Hartsough, E. E. Y. Moghaddas, and N. E. Clinton. 2009. 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.
- Sturtevant, B. R., R. M. Scheller, B. R. Mirand, D. Shinneman, and A. Syphard. 2009. Simulating dynamic and mixed-severity fire regimes: a process-based fire extension for LANDIS-II. *Ecological Modelling* 220:3308–3393.
- Swetnam, T. W., and C. H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. Pages 6–17 in C. D. Allen, editor. *Proceedings of the Second La Mesa Fire Symposium*, 29–30 March 1994, Los Alamos, New Mexico.
- Swetnam, T. W., and P. M. Brown. 2011. Climatic inferences from dendroecological reconstructions. Pages 263–295 in M. K. Hughes, T. W. Swetnam, and H. F. Diaz, editors. *Dendroclimatology: progress and prospects*. Springer, New York, New York, USA.
- Syphard, A. D., R. M. Scheller, B. C. Ward, W. D. Spencer, and J. R. Strittholt. 2011. Simulating landscape-scale effects of fuels treatments in the Sierra Nevada, California, USA. *International Journal of Wildland Fire* 20:364–383.
- Van Wagner, C. E., B. J. Stocks, B. D. Lawson, M. E. Alexander, T. J. Lynham, and R. S. McAlpine. 1992. Development and structure of the Canadian forest fire behavior prediction system. Fire Dange Group, Forestry Canada, Ottawa, Ontario, Canada.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–943.
- 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(S1):S445–S463.
- Wickham, H. 2009. *ggplot2: elegant graphics for data analysis*. Springer, New York, New York, USA.
- Wiedinmyer, C., and M. D. Hurteau. 2010. Prescribed fire as a means of reducing forest carbon emissions in the western United States. *Environmental Science and Technology* 44:1926–1932.
- Williams, A. P., C. D. Allen, C. I. Millar, T. W. Swetnam, J. Michaelsen, C. J. Still, and S. W. Leavitt. 2010. Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences USA* 107:21289–21294.
- Wu, T., Y.-S. Kim, and M. D. Hurteau. 2011. Investing in natural capital: using economic incentives to overcome barriers to forest restoration. *Restoration Ecology* 19:441–445.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1890/15-03371.1/supinfo>