

Enhancing carbon storage through proactively managing fire-prone coniferous mountain forests

Weichao Guo ^{a, ID}, Mohammad Safeeq ^{a,b,* ID}, Guotao Cui ^{c,a ID}, Philip C. Myint ^{a,d ID},
Panmei Jiang ^{a ID}, Han Guo ^{a ID}, Michael L. Goulden ^{e ID}, Kristen D. Emmett ^{f ID},
Stephen C. Hart ^{a,g ID}, Roger C. Bales ^{a,b ID}

^a Sierra Nevada Research Institute, University of California, Merced, CA, USA

^b Department of Civil and Environmental Engineering, University of California, Merced, CA, USA

^c School of Geography and Planning, Sun Yat-sen University, Guangzhou, Guangdong, China

^d Physics Division, Lawrence Livermore National Laboratory, Livermore, CA, USA

^e Department of Earth System Science, University of California, Irvine, CA, USA

^f USDA Forest Service, Pacific Northwest Research Station, Olympia, WA, USA

^g Department of Life and Environmental Sciences, University of California, Merced, CA, USA

ARTICLE INFO

Keywords:

Climate solutions
Forest management
Sierra Nevada
Wildfire

ABSTRACT

Mountain ecosystems typically serve as carbon (C) sinks. However, studies also suggest that they could be C sources due to climate warming, drought and insect-related mortality, wildfires, and management actions. We applied the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS), a process-based dynamic vegetation-ecosystem model, to investigate the role of ecosystem management in C storage under Mediterranean climate over the 21st century. We modified LPJ-GUESS to include implementing mechanical thinning by vegetation size classes, components, and types along with a new mechanistic fire-occurrence model that accounts for wind speed and lightning ignition. Simulations show that mechanical thinning or prescribed fire performed 5–20 years in advance of a high-severity wildfire reduced direct wildfire C emissions by 38–66 %. Our results also show that long-term management actions repeated every 5–20 years, including thinning relatively small trees (diameters up to 7 inches or ~178 mm), can maintain stable C levels in the forest and lower dead-fuel amounts. We found that, although prescribed fire mitigated wildfire severity, ecosystem C storage from reduced wildfire emissions can be outweighed by the added emissions from the prescribed fire themselves. Thinning plus removing and sequestering the thinned biomass can ensure that forests act as net C sinks through the end of the 21st century. However, addition of prescribed fire is needed to reduce understory and lower the projected extent of high-severity wildfire. Achieving the competing goals of reducing wildfire and making the Sierra Nevada long-term C sink can be advanced through carefully coordinated thinning, sequestration of thinned biomass, and prescribed fire.

1. Introduction

For centuries, the structure and function of most forests in the western United States (US) were maintained by naturally occurring low-to-mid severity fires and proactive management by Native Americans (Hessburg et al., 2019; Stephens et al., 2020). However, selective harvesting of large trees and subsequent long-term fire suppression beginning in the early 20th century disrupted historical fire regimes at low- and mid-elevations, resulting in increased forest density and fuel loads (Marlon et al., 2012; Taylor et al., 2016). These activities led to

increased density of small, shade-tolerant trees that can act as ladder fuels during fires and a concomitant loss of larger, more fire-resistant trees, a condition that is being exacerbated by rising temperatures (Harrison et al., 2018) and drought-driven mortality resulting from climate change (Goulden and Bales, 2019). Consequently, the relatively frequent low-to-mid severity fires have been replaced by more occasional, but extreme-severity fires that have become well ingrained in public memory over the past decade. For example, in the record-setting year of 2020, wildfires in California alone incurred an estimated cost of US\$ 149 billion (equivalent to 1.5 % of the state of California's gross

* Corresponding author.

E-mail address: msafeeq@ucmerced.edu (M. Safeeq).

<https://doi.org/10.1016/j.ecolmodel.2025.111332>

Received 14 April 2025; Received in revised form 24 August 2025; Accepted 29 August 2025

Available online 5 September 2025

0304-3800/© 2025 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

domestic product), including US\$ 28 billion in capital losses, US\$ 32 billion in health costs, and US\$ 89 billion through suppressed economic activity extending beyond California (Wang et al., 2021; Seipp et al., 2023). This irruption in wildfire severity and extent occurred even though more than US\$ 2 billion were spent during that year by the federal government on fire suppression. To reduce economic losses, proactive forest management, which is targeted towards reducing the density of ladder fuels by mechanically thinning small-diameter tree, conducting controlled burns, or both combined, has become a well-accepted set of practices to potentially mitigate the damaging effects of wildfires (Hessburg et al., 2019; Stephens et al., 2020; Hagsmann et al., 2021).

In addition to alleviating the societal and ecological impacts of high-severity wildfires, there is also an open question of whether proactive forest management might promote carbon (C) sequestration by reducing wildfire emissions and enhancing the natural capacity of forests to store C (Campbell et al., 2012; Foster et al., 2020). According to the Forest Inventory and Analysis (FIA) program record, forest management can either reduce or increase forest C sequestration capacity (Jiang et al., 2023). Mechanical thinning of trees in mixed conifer forests of the western US generally removes fuels to reduce the occurrence of stand-replacing wildfires, and it also increases resources for the remaining trees, improving their productivity and reducing the occurrence of stand-replacing wildfire (North et al., 2009; Tubbesing et al., 2019; Stephens et al., 2024). In contrast, excessive thinning and associated loss of stand leaf area may reduce the productive capacity of these forests despite reducing their susceptibility to severe wildfires (Hessburg et al., 2016). Across the US, reforestation and proactive management of forests may have more potential for C sequestration than projects on grasslands, croplands, or wetlands, and forest-based activities are also attractive owing to their relatively low costs (Fargione et al., 2018). Because forests sequester more C than other land cover types, modified or improved forest management is a prominent component of California's climate-mitigation strategy aimed at achieving C neutrality by 2045 (Baker et al., 2020; Coffield et al., 2022). Therefore, a better understanding of the impact of management on C dynamics in forests affected by fires is essential for enhancing nature-based solutions to climate change (Stephens et al., 2021).

How ecosystem management can increase long-term forest production and C sequestration capacity in a changing climate depends on the interactions of disturbance, harvesting, and other factors like changes in species suitability or exposure to nitrogen deposition (Bellassen and Luysaert, 2014; Lindner et al., 2014). Moreover, it can be challenging to separate the impacts of the above individual drivers on wildfire activity due to the simultaneous occurrence of three constraints: the availability of live and dead fuel, whether fire weather conditions are sufficiently dry to desiccate these fuels, and ignition condition and probability of occurrence (Bistinas et al., 2014; Kelley et al., 2019; Abram et al., 2021). These drivers and constraints on fire lead to debate about the causes of major wildfire events and the contributions of bioclimatic and human factors to those events (Chen, and Jin, 2022). Future wildfire activity is projected to increase with climate change (Brown et al., 2023), but non-climatic factors introduce uncertainty because humans can modulate fuel loads and ignitions, and thus in turn, climatic effects on wildfire spread and intensity. How forest thinning and prescribed fires enhance ecosystem resilience, C sequestration, and water conservation, in the face of an increasing number of high-severity wildfires, are areas of ongoing research, especially in semi-arid, fire-prone mountain ecosystems.

There is a long-standing interest and a pressing need for including a detailed representation of forest management in coupled climate-vegetation models for scenario analyses (Schelhaas et al., 2015; Yue et al., 2018). Computational models of global-vegetation dynamics are valuable tools to evaluate forest dynamics, development, and management in a changing climate, and to assess long-term effects on forest C and water cycling (Kirschbaum et al., 2012; Wang et al., 2013).

Model-based assessments of climate scenarios on ecosystem C and water balances are generally based on strong foundational knowledge of plant physiology, but major uncertainties surround the scaling up from trees to ecosystem and landscapes, long-term dynamics, and the interactions between physiology and stand structural changes (De Kauwe et al., 2013; Keenan et al., 2013; Fisher et al., 2017). Vegetation demographic models simulate both stand level dynamics and are computationally efficient enough to simulate large landscapes. While this added complexity increases uncertainty, model calibration and evaluation with data at multiple scales constrain predictions leading to more robust models (Prentice et al., 2015; Fisher et al., 2017; Keane, 2019). One important limitation is that the oversimplified algorithms of fire disturbance in models lack tracking of area burned, fire spread, and flame length, thus hindering realistic simulation of wildfire occurrence (Dickman et al., 2023).

Investigating the impact of ecosystem management on high-severity wildfire disturbance and C sequestration is urgent, especially in the context of a warmer and drier future in California's semi-arid, fire-prone mountain ecosystems. In our previous ecosystem-modeling study using a dynamic vegetation ecosystem model that included simulated wildfire, without management, California's Sierra Nevada was found to be a consistent C sink when climate warming was accompanied by CO₂ fertilization (Guo et al., 2022). However, this previous modeling effort used a model version that represented future wildfire disturbance in these forests poorly; more realistic simulation of future fire occurrence and behavior could shift the findings from a C sink to C source (Liang et al., 2018; Hemes et al., 2023).

Here, we build upon our previous modeling assessment (Guo et al., 2022) of the C budget in Sierra Nevada forests. Our study has three main research objectives. First, we evaluate model performance with an improved fire module that considers detailed fire behavior, including rate of spread, area burned, and scorch height. Second, we quantify the sensitivity of the model to different management actions, such as prescribed fire and mechanical thinning of different size classes of vegetation to varying extents. And third, we estimate the extent to which ecosystem management can prevent or decrease high-severity wildfire disturbance and examine the net effects of management on C emissions and long-term C sequestration in Sierra Nevada forests.

2. Methods

2.1. Overview

Our overarching goal was to explore C cycling and storage in a typical watershed within the northern Sierra Nevada of California using a well-constrained ecosystem-simulation model that had been refined to include realistic wildfire disturbance and plausible management scenarios. These simulations were explored within the context of recent multi-year droughts and frequent high-severity wildfires that have occurred across California's Mediterranean mountain ecosystems. Towards this goal, we use the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS), which was originally developed >20 years ago and has since enjoyed adoption in numerous subsequent ecological studies (Smith et al., 2001, 2014; Lindeskog et al., 2021). LPJ-GUESS is a dynamic, gridded, process-based, regional-to-global vegetation model that is widely applied to examine the climate-C-water nexus (Smith et al., 2001, 2014), including Mediterranean-climate mountain ecosystems (Guo et al., 2022). Our study utilizes the most updated version of the code, LPJ-GUESS-V4 (Lindeskog et al., 2021), to which we added an improved wildfire module and other capabilities, described in subsequent sections below, to enable the exploration of a range of potential ecosystem-management actions (i.e., thinning and prescribed fire at specific intervals) being planned and applied in California's fire-prone mountain ecosystems.

2.2. Study area

We selected the American River Basin in California's Sierra Nevada as the numerical testbed (Fig. 1), an area with a long-term wildfire-disturbance and ecosystem-management history. The basin is located over the hydrogeologic transition, from a drier and granitic south to wetter and volcanic north and thus serves as a more "average" hydrogeological condition of the Sierra Nevada than the northern and southern extremes. The American River Basin study site has an area of 4825 km², with elevations spanning between 140 and 3090 m. Vegetation in the study area goes from grassland and oak savannah at lower elevations, through pine-oak forest, to mixed-conifer forest at intermediate elevations, and to subalpine forests at higher elevations. Broadly classified, its vegetation cover is 47 % tree, 27 % shrub, and 15 % herbaceous. It has a Mediterranean-type climate, dominated by winter precipitation, spring snowmelt, and warm dry summers with frequent wildfire disturbance. The long-term (1979–2021) average monthly temperature ranged between 4 °C (December) and 22 °C (July), while the annual precipitation levels ranged between 440 mm (in 2013) and 2574 mm (in 1983).

2.3. Data

The model was forced with gridded (4 km × 4 km) monthly climate data, including monthly maximum and minimum air temperature, precipitation, shortwave solar radiation, and wind speed. We selected two Representative Concentration Pathways (RCPs) for our model runs, RCP4.5 and RCP8.5, which represent additional radiative forcings of 4.5 W/m² and 8.5 W/m², respectively, compared to pre-industrial levels (Van Vuuren et al., 2011). To illustrate a range of possible extremes (Bedsworth et al., 2018) for each RCP scenario, we ran simulations using downscaled climate data from two general circulation models (GCMs): HadGEM2-ES365 (biased toward warmer, drier conditions) and CNRM-CM5 (biased toward cooler, wetter conditions). The downscaled climate data are based on the Coupled Model Intercomparison Project 5 (CMIP5) from Multivariate Adaptive Constructed Analogs (MACA; Abatzoglou and Brown, 2012), which provide data spanning a 150-year period from 1950 to 2099. Likewise, we used atmospheric-CO₂-concentration data for both RCP4.5 and RCP8.5 scenarios during 1950–2099 (Meinshausen et al., 2011). LPJ-GUESS was calibrated and validated using evapotranspiration (ET) data from six eddy-covariance flux towers, extending from 129 to 2700 m in elevation and representing the major forest types, along with using a spatially gridded ET dataset for the Sierra Nevada (Guo et al., 2022). The model was further

refined with both Penman-Monteith-Leuning evapotranspiration V2 data product (PML-v2), plus gross primary productivity (GPP) and ET from a MODIS-based dataset that proved to be similar or noticeably better than the major state-of-the-art products (Zhang et al., 2019). Parameters related to vegetation and soil biomass were calibrated using field observation as described by Guo et al. (2022). Results from Guo et al. (2022) do not show a strong dependence on the choice of RCPs and GCMs for simulating the C pools and ET (Table S1); considering two GCMs (HadGEM2-ES365 and CNRM-CM5) enable us to quantify some of the uncertainties associated with these different projections/scenarios.

2.4. Model setup and parameterization

LPJ-GUESS was set up in cohort model and to use nine local tree species (Sierra lodgepole pine [*Pinus contorta* var. *murrayana* (Grev. & Balf.) Engelm.], Jeffrey pine [*Pinus jeffreyi* Balf.], canyon live oak [*Quercus chrysolepis* Liebm.], red fir [*Abies magnifica* A. Murray bis], white fir [*Abies concolor* (Gord. and Glend.) Lindl. ex Hildebrand], western juniper [*Juniperus occidentalis* Hook.], ponderosa pine [*Pinus Ponderosa* Douglas ex C. Lawson], deciduous woodland oak [*Quercus robur* L.], and California black oak [*Quercus kelloggii* Newberry]). European plant functional types (PFTs; Hickler et al., 2012) were used to simulate understory shrubs and C-3 photosynthetic pathway grass species rather than global PFTs (Smith et al., 2001) to better represent vegetation types in our regional-scale study area (Fig. 1). Default bioclimatic limits were adjusted using gridMET climate (Abatzoglou, 2013) and vegetation data from the USFS CALVEG (<https://data.fs.usda.gov/geodata/edw/datasets.php?xmlKeyword=calveg>). Soil type and associated physical parameters were derived from the Soil Survey STATSGO Geographic Database (NRCS, 2010). In our previous research (Guo et al., 2022), we made refinements to relevant soil parameters in the model to improve the representation of plant-available water in Sierra Nevada forests. Our simulations were initialized to an equilibrium state with a 500-year spin-up phase and used five 1000-m² replicate patches in each stand (i.e., in each 4 km × 4 km grid cell). We used detrended observed historical climate forcing for 1979 to 2021 (Abatzoglou, 2013) along with corresponding CO₂ data (Meinshausen et al., 2011) during the model initialization. Role of management was not considered during the model initialization process.

2.5. Model refinements

2.5.1. Wildfire

We introduced a mechanistic fire module, LMfireCF (Emmett et al.,

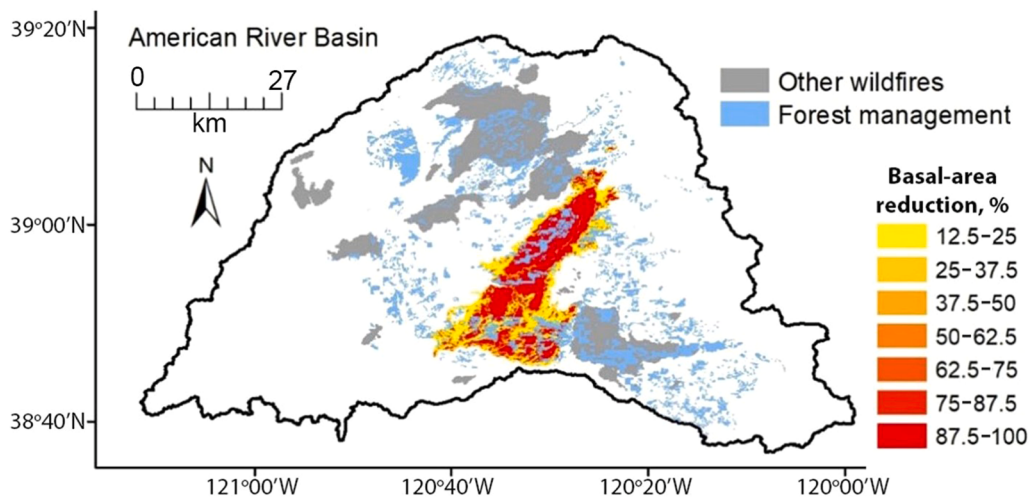


Fig. 1. American River Basin. The gray patches show historical wildfires and blue patches show historical management actions that have been performed in this basin. Yellow-orange-red patches show the 2014 King Fire region, with the basal area reduction indicating the severity of wildfire disturbance.

2021), an updated version of LMfire (Pfeiffer et al., 2013) that includes crown fire, into the LPJ-GUESS model. The inclusion of crown fire allows vertical spread of wildfire and provides dozens of layers for vertical fire spread along the tree stem to the top of the canopy. The LMfireCF module simulates fire occurrence, behavior, and impact by incorporating fire-danger indices with fire-spread modeling (Thonicke et al., 2010; Pfeiffer et al., 2013). This improved wildfire model successfully simulated the 1988 fire across the Greater Yellowstone Ecosystem (Emmett et al., 2021). We implemented the LMfireCF into LPJ-GUESS, replacing the default Glob-FIRM module (Thonicke et al., 2001), to facilitate simulating more-realistic fire disturbance. Modeled fire occurrence depends on fuel load and moisture, with fire effects driven mainly by the fire season duration and the PFT-specific fire resistances (Smith, 2001; Emmett et al., 2021). The Glob-FIRM module failed to match high-severity wildfire occurrence in a warming climate for the California's fire-prone Mediterranean-type ecosystems, especially during recent multi-year droughts (Guo et al., 2022). The LMfireCF module, together with different management regimes (prescribed fire and mechanical thinning at user-specified targets and intervals described in Section 2.5.2), were aimed at providing an improved assessment of the potential treatment scenarios and allowed the evaluation of tradeoffs between reducing wildfire through increasing prescribed fire.

Implementation of the LMfireCF module into LPJ-GUESS-V4 involved the following three steps. First, we addressed the fact that LMfireCF was developed for an earlier version of the code, LPJ-GUESS-V2, that did not incorporate biogeochemical or biogeophysical attributes (e.g., nitrogen, management, and landscape features). We added or revised parameters, variables, and functions, including input, spin-up, vegetation and soil nitrogen dynamics, canopy exchange, plant growth, and soil water to introduce LMfireCF into LPJ-GUESS-V4. We parameterized fire-relevant variables, including PFT-specific ignition efficiency, fuel bulk density, scorch-height-related parameters, emission factors (Tables S2–3), surface-area-to-volume ratios of the fuel (a constant value of $5 \text{ cm}^2 \text{ cm}^{-3}$, Pfeiffer et al., 2013), and mineral damping coefficient (a value of 0.41739 from Pfeiffer et al., 2013), in a similar manner to that reported for comparable geospatial research in Yellowstone National Park (Emmett et al., 2021) and further described in Pfeiffer et al. (2013). Unless specified, we used lightning-based ignition as described in Pfeiffer et al. (2013). Second, to use both horizontal and vertical fire-spread routines in LMfireCF, we added the PFT-specific allometric parameters for estimating crown-length (tree height minus crown base height), and allometric values for trees and shrubs relating bark-thickness to tree diameter and tree diameter to tree height variables developed by Emmett et al. (2021). This enables modeling crown fire as an extension to surface fire. Variable crown-height and bark-thickness parameters were calculated primarily using observation-based robust linear- and quadratic-regression fitting (Emmett et al., 2021). We did not further calibrate the fine fuel accumulation and ignitions to approximate crown fire occurrences. Instead, calibrated parameters were generalized from Emmett et al. (2021). Third, by allowing for a daily timestep, rather than an annual timestep as in the default Glob-FIRM fire module, and including pixel interactions, reburning within a single calendar year was forbidden in LMfireCF. This change allowed us to explore vegetation C-water interactions and the tradeoff between frequent small fires, where fire-driven mortality may disproportionately affect small trees, and high-severity wildfire after prolonged fire exclusion, where drought-driven mortality and wildfire together will affect larger trees (Hurteau et al., 2019).

2.5.2. Management

LPJ-GUESS is one of the few dynamic-global-vegetation models that incorporates a detailed representation of forest ecosystem composition and stand dynamics, making it suitable for the implementation of forest management. LPJ-GUESS-V4 model features a relatively well-developed management module, including two types of silvicultural systems in managed forest stands, clear-cutting and thinning, in addition to non-

managed (i.e., natural) stands (Lindeskog et al., 2021). We did not alter the subroutines for natural disturbance events (e.g., windstorms or landslides) and mortality resulting from self-thinning, reduced growth efficiency, old age, and wildfires.

We revised thinning rules and algorithms in the model by adding size classes based on tree-stem diameter using diameter at breast height (DBH). This allows achieving a target biomass removal from overstocked forests by removing trees up to a given size (called “thinning from below”) rather than the default even-aged thinning for density reduction. This approach is consistent with current stewardship contracts in California (North et al., 2007). Otherwise, the simplified default forest-harvesting stand-age rules in the model result in cutting older stands and avoiding cutting stands younger than 15 years. We also do not allow cutting trees larger than 30 inches (762 mm) DBH, consistent with current limitations on public lands in California (Kane et al., 2023).

We set different dead-fuel removal fractions for alternative management actions. In simulating prescribed fire alone or after thinning, amount of dead fuel, including three yearly litter pools (leaf, sapwood, and heartwood) and four subsequent surface-soil organic-matter pools, remaining can be manually specified in the model. When we introduced prescribed fire, most of the burned C was released to the atmosphere. A small fraction of fuel C (5 %) was returned into soil pools as “ash” (Possell et al., 2015). For dead-fuel removal, we proportionally burned both one-year transient litter pools (leaf, sapwood, and heartwood pools) and long-term surface pools (i.e., metabolic litter and two woody litter pools (fine and woody) as described in Kirschbaum & Paul (2002)). For thinning, we provided the option of adding leaves, small branches, and stems to the litter pools, or removing them from the stand. For shrub removal, we did not introduce a size threshold and applied the default proportional removal based on the density.

2.6. Management actions and scenarios

Actual historical management in the study area on both private and public land involved a range of management actions (Table S4), including the removal of both live and dead fuel, dead-fuel removal only, and live-fuel removal only. We used prescriptions applied on public lands, namely Timber - Medium Intensity (TMI), Fuel Reduction - Prescribed Fire (FRPF), and Fuel Reduction — Mechanical Thinning (FRMT), as a crosswalk table to calibrate the removal intensities or desired targets of live and dead fuels. Two forest management actions were created, mechanical thinning (MT) and prescribed fire (PF) after performing a detailed sensitivity analysis of live and dead fuels to different size classes and severity of dead-fuel removal by prescribed fire (discussed in Section 3.2). In the MT action, all trees < 7 inches (~178 mm) diameter were removed, which corresponds to 80 % live fuel remaining in the residual stand, along with the removal of 80 % of the total shrub biomass. In the PF action, 80 % of the dead fuels were removed along with 80 % of the shrubs. Like the historical management action on public land involving prescribed fire (FRPF, Table S4), our PF action has no effect on live tree biomass and corresponds to 20 % shrub and dead fuel remaining. This contrasts with wildfire, which affects live trees, shrubs, and dead fuel. In this study, we have explored thinning intervals of 5, 10, 15, and 20 years to contrast the management effects of these different strategies on C cycle and net effect on C sequestration.

Using LPJ-GUESS, we simulated and evaluated the resulting carbon balance, wildfire dynamics, etc. under 10 different MT and PF scenarios, nine of which involve some type of management action and the tenth being the baseline, no-management scenario (Table 1). The scenarios differ in the involvement of MT and PF actions at different intervals, either done separately or together, as well as three different levels of removal of thinned material from the forest (i.e., removal of all thinned material (“all biomass out”), stems only (“stems out”), or none (“all biomass in”). Following cutting trees and shrubs in MT scenarios, we added the material not removed from the study area into dead pools. Also, for scenarios involving removal of thinned material, we did not

Table 1
Management actions^{a,b}.

Frequency	Thinning Removal	Scenario
None (Baseline) ^c	–	–
Intervals of 5-, 10-, 15-, and 20-year	All biomass in	MT
	All biomass in	MT+PF
	All biomass out	MT
	All biomass out	MT+PF
	Stems out	MT
	Stems out	MT+PF
MT once, 1st year of study period (2006), and PF at	All biomass in	MT
Intervals of 5-, 10-, 15-, and 20-year	All biomass in	MT+PF
Intervals of 5-, 10-, 15-, and 20-year	–	PF

^a Mechanical Thinning (MT) involves cutting all trees < 7 inches (~178 mm) in diameter. Prescribed Fire (PF) includes reduction of shrubs and dead fuels by 80 %.

^b For “All biomass in”, all removable live-fuel material from thinned trees (stems, twigs, and leaves) were moved into the dead-fuel pools. For “All biomass out”, all removable live-fuel material from thinned trees were removed from the forest and sequestered in long-lived products. “Stems out” represents only stems (65 % of total biomass from sapwood and heartwood) were removed from the forest and sequestered in long-lived products. No dead fuel removed by MT.

^c No MT or PF introduced in this scenario.

consider the role of decay, material extraction, hauling, and/or development of sustainable wood products on carbon balance.

Across all scenarios, we follow the sign convention where positive values of C fluxes represent C emissions into the atmosphere. Examining the broad range of possible treatments covered by these scenarios enabled us to disentangle the multiple factors that determine the conditions under which the Sierra Nevada forests can become a consistent C sink or source in the 21st century.

3. Results

3.1. Simulating wildfire behavior and effects

Mean C emissions from the new LMfireCF module and default Glob-FIRM fire module were 29 and 43 g C m⁻² yr⁻¹, respectively, across the two RCPs and two GCMs examined in this study (Table 2). This analysis considered both cold/wet and warm/dry climate scenarios in both historic and future periods, and with or without management. Emission estimates using the default wildfire module were consistently about 30 to 50 % higher than those from LMfireCF (Figure S1). This may be driven by the fact that the burn area in the default model is strictly calculated using fire season length, a parameter derived from upper layer soil moisture as a proxy for fuel moisture and litter flammability with no consideration of fuel classes (Smith, 2001; Thonicke et al., 2001). Contrastingly, LMfireCF not only introduces fuel classes but takes a

Table 2
Wildfire carbon emission (g C m⁻² yr⁻¹) over the study area based on the new (LMfireCF) and default (Glob-FIRM) wildfire modules^a.

Climate Model	Scenario	LMfireCF	Glob-FIRM
CNRM-CM5	Historic	29 ± 28	41 ± 34
	RCP4.5	30 ± 32	42 ± 32
	RCP8.5	29 ± 32	36 ± 31
	Historic	32 ± 30	49 ± 37
HadGEM2-ES365	RCP4.5	28 ± 28	53 ± 36
	RCP8.5	25 ± 26	38 ± 31

^a The historic period covers 1950–2005, while RCP 4.5 and RCP 8.5 are two climate change pathways for the simulated study period (2006 to 2099); HadGEM2-ES365 is a warm-dry and CNRM-CM5 a cold-wet climate model. Values shown are means, with ± values reflecting the range of management scenarios simulated.

holistic approach combining fire occurrence, behavior, and ignition for estimating impacts and associated C losses (Pfeiffer et al., 2013). The effect of forest management through FRMT on wildfire was especially notable using LMfireCF, with cumulative C emissions of only 40 to 80 % of emission levels in the control (no treatment) case, depending on the management frequency.

Using the LMfireCF module, wildfire C emissions for our study area are very close to those that we previously reported across the Sierra Nevada based on 1984 to 2017 observed basal-area reduction and LPJ-GUESS aboveground vegetation and litter C densities (Guo et al., 2022). Because of the very-large, high-severity 2014 King Fire in the American River Basin, the emission value for our study area in the historical period was much higher than the Sierra Nevada average. We thus used the Sierra Nevada-wide average wildfire emission as a historical baseline for comparisons with wildfire emissions.

3.2. Simulating ecosystem sensitivity to management intensity

Thinning with a larger tree-diameter cutoff will remove more live aboveground biomass, extending the time required for the forest stand to return to its pre-thinning biomass level. With stewardship treatments in the Sierra Nevada involving the removal of smaller-diameter trees and associated vegetation and leaving larger trees (i.e., so-called “thinning from below”), we first determined the effect of removing live aboveground vegetation up to a certain diameter on total biomass removal amounts over the study period. Removal of vegetation with DBH up to about 4 inches (~102 mm) has little effect on standing live biomass, whereas removal up to 13 inches (~330 mm) results in cutting about 60 % of the live tree biomass (i.e., 40 % remaining; Fig. 2a). Thinning up through 15 inches (381 mm) diameter decreases live biomass by 70 % (data not shown). At higher thinning intensities, as the tree diameter cutoff reaches 10 inches (254 mm) and above, return of the stand to its original pre-thinning biomass requires several decades. The drop at year 39 on Fig. 2a is caused by a modeled wildfire disturbance. Based on these results, we designate cutting trees through about 5–6 inches (~127–152 mm) and 7–8 inches (~178–203 mm) to represent live trees remaining under Timber - Low Intensity (TLI) and Timber - Medium Intensity (TMI) management actions (Table S4), respectively. In addition, thinning more and larger trees creates more resources for the remaining trees, increasing their individual growth rates in water-limited periods (data not shown). Although prescribed fire seems to have a smaller effect on live fuel reduction than the modeled wildfire disturbance at year 39 (Fig. 2b), prescribed fire does decrease the seedling-recruitment rate (data not shown).

Thinning does not change dead-fuel amounts directly but rather decreases the source of dead fuel (Fig. 3a). This is because in these scenarios we do not add thinned materials to the dead-fuel pool but instead remove them from the site. The differences in dead-fuel biomass among the different thinning threshold-diameter scenarios increased initially over time before eventually decreasing. This contrasts with the live-fuel biomass, where the scenarios converge in a roughly monotonic fashion over time (Fig. 2a). Prescribed fire decreased dead fuels directly (Fig. 3b), but this was followed by a period of rapid increase in response to the regrowth and recovery of live biomass after the management action, accompanied by tree mortality and tree-tissue senescence. Again, the dead-fuel level spiked at 39 years because of a wildfire disturbance, but it then gradually decreased over time as the wildfire disturbance reduced the source of the dead fuel. That is, the wildfire disturbance removed some of the live biomass in the study area that would otherwise eventually die and become dead fuel.

In addition to the effects from one-time treatment (either thinning or prescribed fire) portrayed in Figs. 2 and 3, we also examined the effect of repeated thinning at 5- to 20-year intervals up through a given size range as a strategy for maintaining a relatively constant amount of live biomass (Fig. 4). While no single thinning threshold maintained a constant biomass level over the study period, some combination involving

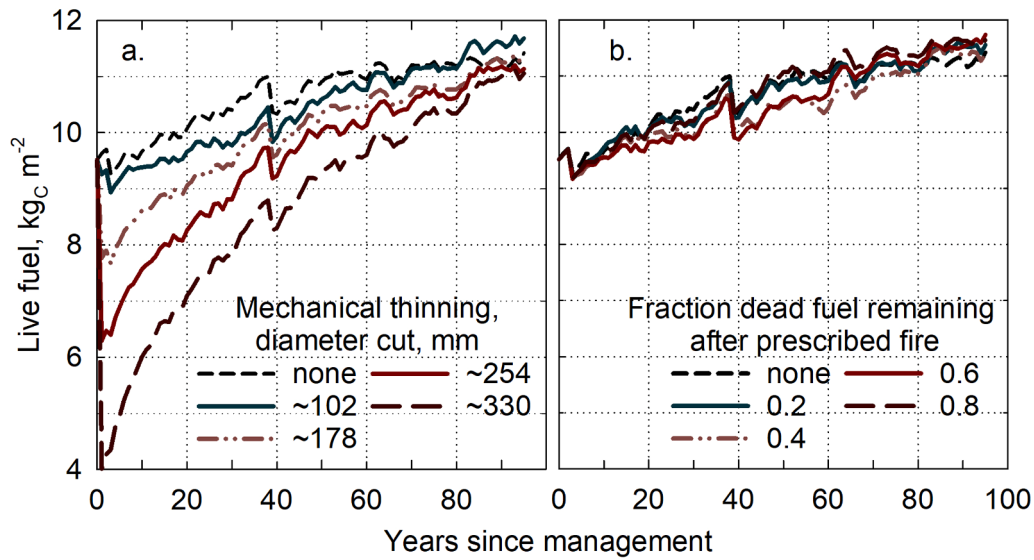


Fig. 2. Sensitivity analysis for live fuel (vegetation) changes after: a) thinning from below (smallest diameter trees removed first) up to a cutoff diameter size from 4 to 13 inches (~ 102 to ~ 330 mm), with the diameter size being mapped to a particular percentage of live fuel remaining in forested regions and b) prescribed fire with removal of the remaining dead fuel to various fractions. Thinning all trees up to the 13 inches (~ 330 mm) cutoff diameter will result in 40 % of the live fuel biomass remaining (i.e., 60 % being cut). We start management in the first year of the future scenario (2006–2099). This figure shows the result for HadGEM2-ES365 (warm-dry) and RCP 8.5. Results are similar for CNRM-CM5 (cool-wet).

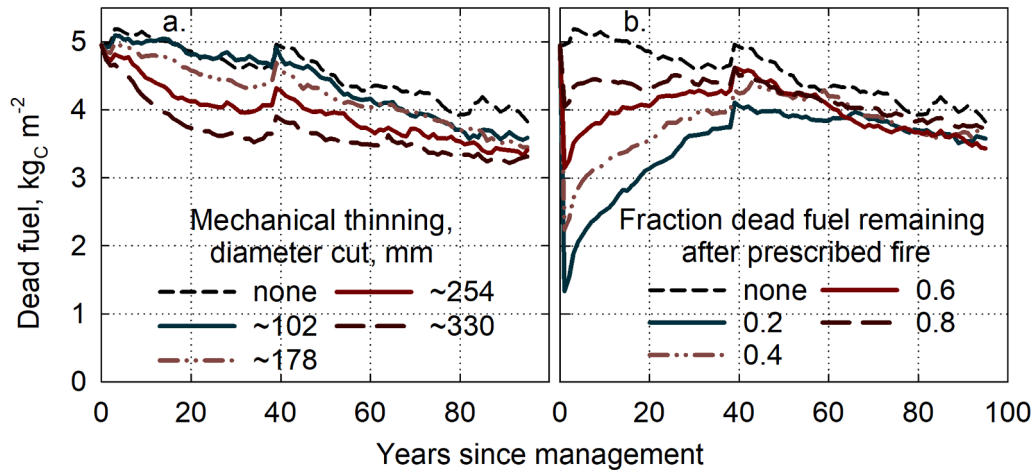


Fig. 3. Sensitivity analysis for above-ground dead fuel after: a) thinning from below (smallest diameter trees removed first) to a cutoff diameter size from 4 to 13 inches (~ 102 to ~ 330 mm). Thinning all trees up to a 13 inches (~ 330 mm) diameter results in 40 % remaining (60 % being cut); and b) changing patterns in dead fuels after prescribed fire that initially removes from 20 to 80 % of the dead fuel carbon (C). We started management in the first year of the future scenario (2006–2099). This figure shows the result for HadGEM2-ES365 (warm-dry) and RCP 8.5. Results were similar for CNRM-CM5 (cool-wet).

thinning in the cutoff diameter range of 6 to 7 inches (~ 152 to 178 mm) at 5- to 20-year intervals provided a relatively stable projected live-biomass level at 80–90 % of the pre-thinning value; this result is consistent with the 80 % levels of live tree fuel remaining that is sustained in historic management actions that have been carried out in California (Table S4). In contrast, thinning through a threshold diameter below 6 inches (~ 152 mm) decreased live fuel by <5 % (i.e., it has little effect, especially considering the rapid subsequent regrowth), while thinning over 8 inches (~ 203 mm) cutoff diameter resulted in continually declining biomass levels that fall well below 80 % if the thinning is performed at relatively frequent (i.e., 5 to 10 year) intervals (Fig. 4c, d).

3.3. Simulating management effects on ecosystem C

3.3.1. C pools and fluxes

Regardless of whether thinned material was removed from the stand

or left remaining as dead fuel, all management scenarios considered in this study (Table 1) resulted in less live biomass in the study area compared to the no-management baseline, accumulated over the 2006–2099 study period (Fig. 5). The effect of management is qualitatively similar for the four different management intervals (5-, 10-, 15-, 20-year), although there are some quantitative differences. More frequent MT resulted in less live biomass (Fig. 5a), while PF after thinning resulted in 40–60 % less fuel available for wildfire and 2–10 percent more live biomass in the study area compared to MT without PF (Fig. 5b). Taking thinned material out of the study area, thereby not increasing dead fuel available for wildfire within the stand, resulted in 2–6 % more live biomass, also owing to less fuel being available for wildfire (Fig. 5b). One-time MT, with or without subsequent PF, had a minor effect on live fuel. Even without being preceded by MT, PF at regular intervals resulted in less dead fuel available for wildfire (Fig. 5b) and a slight increase in live biomass in the study area compared to

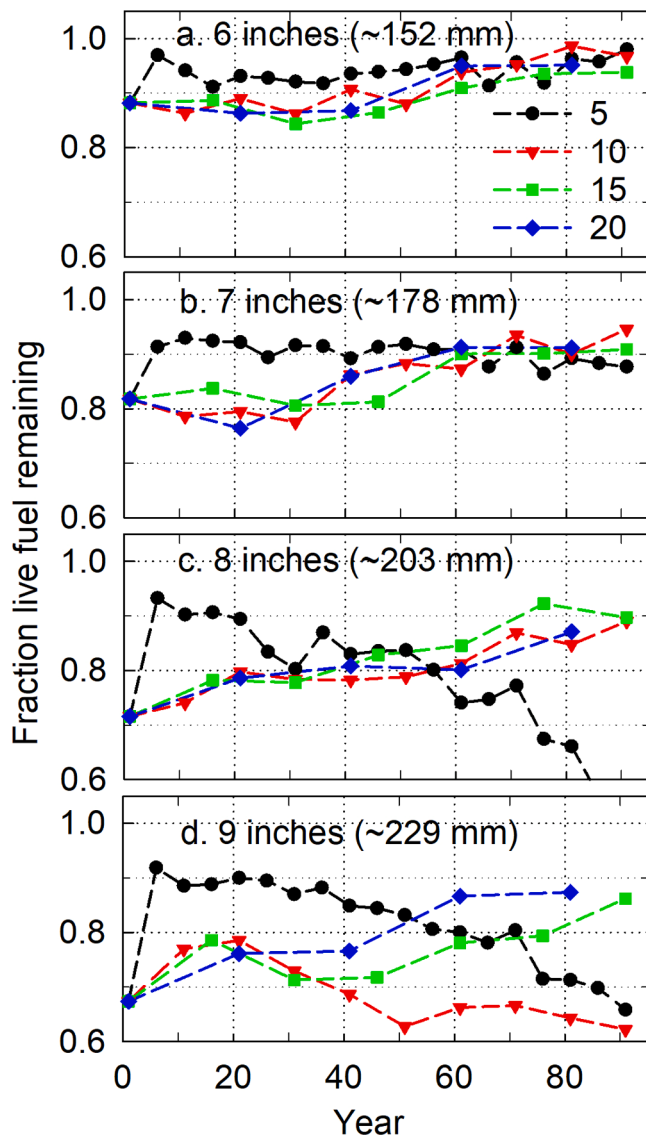


Fig. 4. Fraction of live fuel remaining as a function of time, with year 0 being 2006. Panels a-d provide results for different threshold tree diameters for thinning from below (smallest diameter trees removed first), while the different lines in each panel represent different thinning intervals. This figure shows the result for HadGEM2-ES365 (warm-dry) and RCP 8.5. Results are similar for CNRM-CM5 (cool-wet).

scenarios involving MT.

All PF scenarios resulted in less aboveground dead fuel in the study area (Fig. 5b) because these scenarios involve removing dead fuel, leaving only 20 % remaining. One-time MT had a seemingly negligible effect on the dead-fuel C pool over the study period (2006 - 2099), as indicated by the second-to-last cluster in Fig. 5b (MT once + PF at intervals) being nearly the same as the last cluster (PF without MT).

MT without PF, either with some or no material removed from the study area, resulted in more soil C, but removing all thinned material resulted in lower soil C storage (Fig. 5c). More specifically, our model treats fire as removing 95, 93, 79, and 33 % of the dead fuel C through combustion for 1-hr, 10-hr, 100-hr, and 1000-hr fuel classes, respectively, with the remaining going into soil as “ash.” PF alone had a very slight positive effect on soil C, similar to the result from PF at intervals after one-time MT.

Compared to the baseline, all management scenarios resulted in a reduction in the total amount of C stored in the study area (Fig. 5d). That is, removing biomass from the study area decreased total ecosystem C.

Again, one-time MT had a small effect so that PF alone versus PF with one-time MT resulted in similar total ecosystem C storage (Fig. 5d).

A subset of the 10 management scenarios considered in Fig. 5 and Table 1 to illustrate the main effects of management actions on C fluxes (Fig. 6). Fluxes for the full set of scenarios follow the same qualitative trends (Figure S2). The baseline scenario shows a small positive flux, or net C loss, from the ecosystem to the atmosphere when averaged over the 2006 to 2099 study period (as represented by the net biome productivity (NBP) in Fig. 6d). That is, C loss from the ecosystem by heterotrophic respiration plus wildfire in Fig. 6b is greater than the net primary productivity (NPP) in Fig. 6a, so that NBP is slightly positive.

Scenarios involving MT at intervals with no biomass removed from the stand and no PF resulted in higher NPP (Fig. 6a). However, heterotrophic respiration was also higher in these scenarios (Fig. 6b), resulting in the net ecosystem productivity (NEP) for 10-year management intervals being positive (i.e., net loss of C to the atmosphere at the ecosystem scale), and for 20-year intervals being nearly zero (Fig. 6c). Adding PF to thinning at intervals resulted in lower heterotrophic respiration and negative NEP values. Although NEP is negative with PF, with an accompanying reduction in heterotrophic respiration relative to MT alone, the NBP, which additionally accounts for C fluxes due to fires, is strongly positive (i.e., the result of fires releasing significant amounts of C to the atmosphere via combustion; Fig. 6d). Introducing PF lowers wildfire C emissions by about 50 % relative to MT alone.

Scenarios involving removal of some biomass (stems of cut trees) show lower C fluxes from heterotrophic respiration and PF and thus result in a greater negative NEP than for scenarios with no biomass removed from the study area. In the absence of PF (i.e., MT only at intervals with “stems only” biomass removed), NBP values are also negative. Although the introduction of PF results in positive NBP values, removal of some biomass results in these fluxes being much smaller than the very large positive NBP that occurs when none of the thinned material is removed. Adding harvest (Fig. 6e), which accounts for storage of C in products external to the study area, to NBP can yield negative overall C fluxes (Fig. 6f) even if NBP is positive.

Where MT once had a negligible effect on C pools, all fluxes for the MT-once scenario with no PF turned out to be nearly the same as those of the baseline (i.e., no proactive management) scenario. The scenarios of MT once followed by PF at intervals show qualitatively similar patterns to those for MT at intervals with PF, but the C fluxes were smaller in magnitude owing to lower heterotrophic respiration.

3.3.2. High-severity wildfire

Management actions combining both MT and PF decreased high-severity wildfire C emissions (Fig. 6b). To further demonstrate this, we reconstructed the high-severity 2014 King Fire using a human rather than a lightning ignition in the model to maintain consistent disturbance timing across scenarios. We implemented the historical FRMT for public land, which involves thinning and prescribed fire that leaves 85 % of trees, 10 % of shrubs, and 30 % of dead fuels remaining, at 5- 10-, 15-, and 20-yr in advance of 2014 King fire. Both simulated historical GPP and ET match the MODIS-based product (PLM2) before wildfire in the 2014 King Fire area (Figure S2). After wildfire, ET did not show an obvious decrease, both for baseline (non-managed) and managed scenarios, reflecting a decrease in transpiration and a corresponding increase in evaporation. In contrast, GPP (Figure S2) and transpiration (Figure S3), which are both directly related to leaf area, decreased markedly after high-severity wildfire. Thinning from below (understory thinning) and prescribed fire using historical FRMT scenario, though less severe disturbance than the 2014 King Fire, resulted in similar changes to GPP and ET (Figure S2) for 3 to 5 years following their implementation at 5-, 10-, 15-, and 20-yr in advance of wildfire. However, the effect of FRMT, which involves thinning followed by prescribed fire, on reducing wildfire severity, as indicated by scorch height, lasted for at least 20 years. Forest management performed 15 to 20 years in advance of wildfire outbreak reduced emissions by about 65 % compared to the

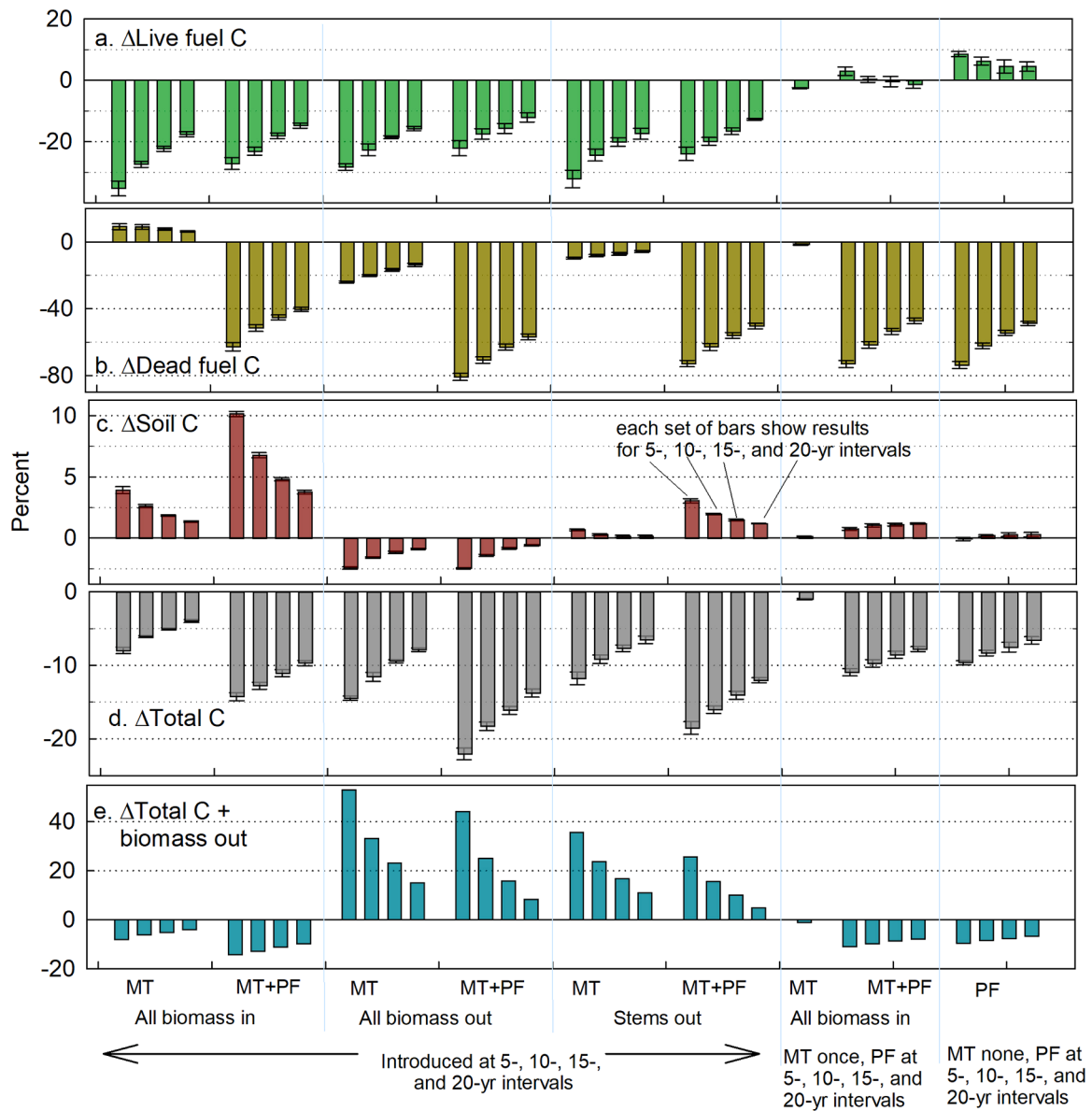


Fig. 5. Carbon (C) pool comparisons for the nine different management scenarios outlined in Table 1. MT refers to mechanical thinning and PF refers to prescribed fire. Here, Δ indicates the difference in the C pools compared to the baseline (i.e., no-management) scenario. The sum of a) Δ Live-fuel C, b) Δ Dead-fuel C, and c) Δ Soil C is d) total C. Panel e) is Total C + the sum of harvested material removed. The four bars in each cluster show study-area average values for 5-, 10-, 15-, and 20-year management intervals (i.e., the frequency of management decreases from left to right in each cluster; legend on panel c). For the MT once scenarios, the thinning action is performed in 2006, which is the first year of the study period. The error bars indicate the standard deviation across warm-dry (HadGEM2-ES365) and cool-wet (CNRM-CM5) climate models, and RCPs (4.5 and 8.5).

baseline, non-managed scenario, while ecosystem management performed 5 and 10 years in advance of wildfire was somewhat less effective, with reduced emissions of 38 % and 53 %, respectively. The high-severity wildfire killed most of the live biomass and resulted in rapid and large increases in dead-fuel C (Figure S3).

4. Discussion

4.1. Linking fire behavior and fire effects in ecosystem simulations

Recent research highlights the need for modeling with improved interaction between fire behavior and fire effects to capture realistic climate-fire-vegetation feedbacks (Hood et al., 2018). As atmospheric aridity continues to increase with warming, altering vegetation-water interactions, live fuels become increasingly important in determining fire behavior and their water cycle and ecological feedbacks (Grossiord

et al., 2020). By directly linking live and dead fuel combustion with vegetation dynamics, and the fire-induced vegetation-mortality process within ecosystem models in a regionally explicit way, our improved LPJ-GUESS model offers at least two advantages in simulating fire behavior and fire effects in fire-prone mountain ecosystems.

First, the new LMfireCF module improved fire-disturbance simulations even in the absence of proactive management. Our previous work has shown that overestimating wildfire disturbance in a fire-prone mountain ecosystem such as the Sierra Nevada has the effect of making it a larger net C source to the atmosphere (Guo et al., 2022). This is the risk introduced by the default GlobFIRM fire module in LPJ-GUESS, which models fire disturbance based on simple, empirical equations over the duration of the fire season. The greater implied fire spread and flame length in such simple models are also associated with overestimating fire effects (vegetation mortality and regrowth) in regional ecosystem simulations (Dickman et al., 2023). Compared to GlobFIRM,

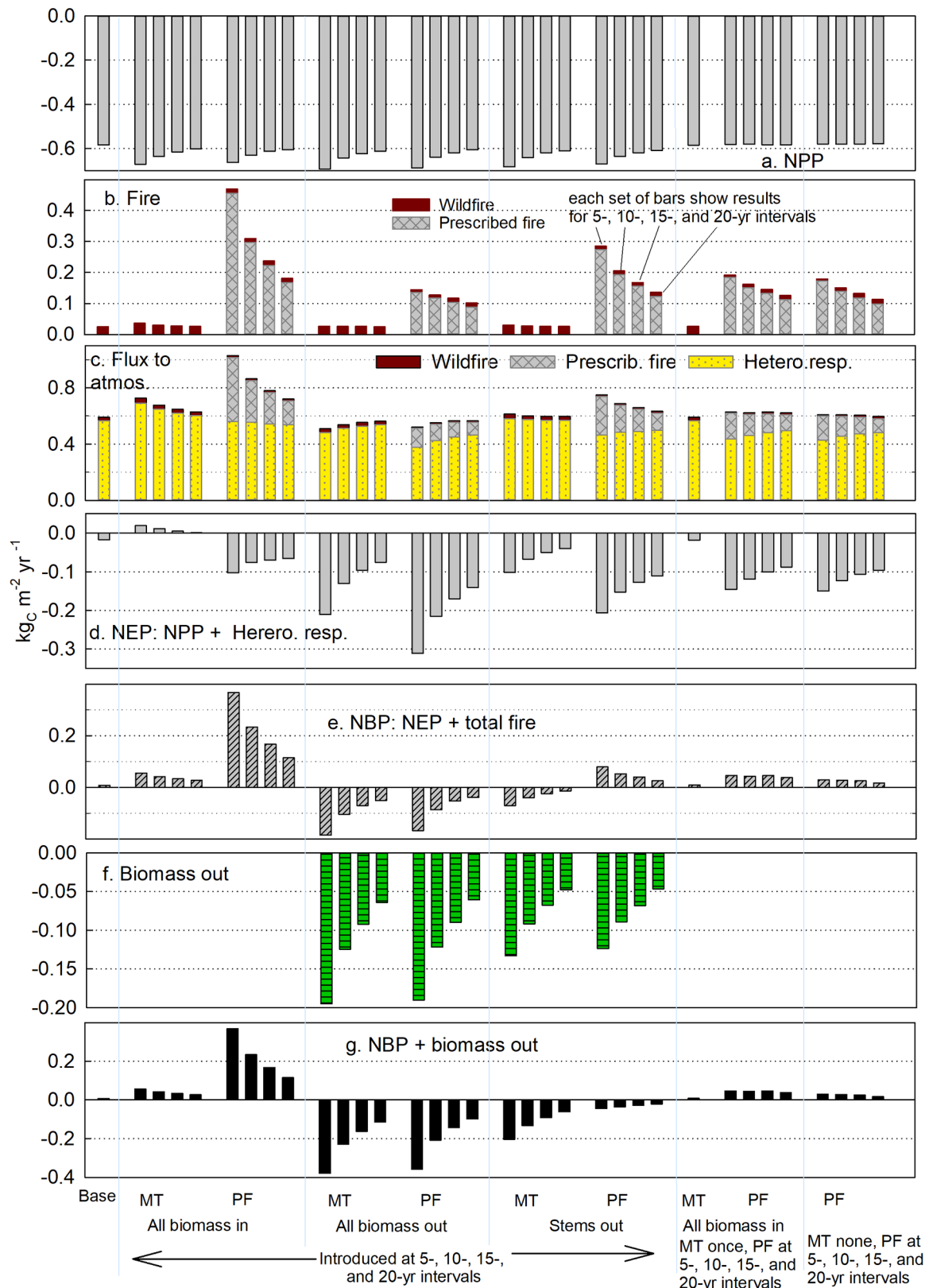


Fig. 6. Carbon (C) fluxes for selected management scenarios (Table 1): a) net primary productivity (NPP); b) fluxes to the atmosphere from heterotrophic respiration, wildfire, and prescribed fire; c) net ecosystem productivity (NEP), which is defined as the sum of NPP and heterotrophic respiration; d) net biome productivity (NBP), which is the sum of NEP plus fluxes from fires, e) harvest (material removed from forest); and f) NBP plus harvest. Base refers to no proactive management, MT refers to mechanical thinning, PF refers to prescribed fire, Stems out refers to all tree stems removed from forest. Negative and positive values indicate C sink and source, respectively. Data are for HadGEM2-ES365 and RCP 8.5. Results for the other climate scenarios (i.e., HadGEM2-ES365 and RCP 4.5 and CNRM-CM5 with RCP 4.5 or 8.5) were similar.

the new mechanistic fire module (i.e., LMfireCF) we implemented in LPJ-GUESS, predicted significantly lower historic and future wildfire disturbance, which better aligns with fire-driven C-loss estimates based on observed basal-area reduction (Guo et al., 2022).

Second, the new fire module also improved simulations of proactive-management scenarios, with more realistic results regarding the observed burned area and ecosystem effects. The default GlobFIRM module showed relatively high vegetation mortality due to fire disturbance. In contrast, fire disturbance in LMfireCF exhibited more gradual consumption of dead fuel, small trees, and shrubs, with spread to medium and large trees also modulated. Consequently, the thinning from below and prescribed fire management actions that we have examined in this study decrease the number, area, and severity of fire disturbances in a multi-faceted way. The benefits of management performed in advance of high-severity wildfire can be mainly attributed to a reduction in the scorch height and thus limits on fire spreading through the canopy. Unlike the dramatic drop in scorch height, the horizontal rate of spread undergoes only a slight change in our simulations incorporating LMfireCF, as understory thinning hinders vertical spread of wildfire yet may leave sufficient vegetation for horizontal fire spread. ET is less sensitive to management than GPP (Figure S2), apparently associated with higher evaporation offsetting a decline in transpiration (Figure S3). These changes in ET observed during the wildfire are consistent across all the scenarios of MT and PF implemented throughout the study area, with a modest reduction in ET by as much as 6.5 % when management action involving thinning is repeated every 5 years (Figure S4). The result of this transpiration-evaporation feedback aligns with our measured ET in the Sierra Nevada (Bales et al., 2018; Guo et al., 2022).

4.2. Projecting ecosystem feedbacks to management of C pools

Based on our modeling results, it is unlikely that in-forest management actions will yield a net increase in C sequestration – compared to the baseline, no-management case – in these fire-prone mountain forests of the Sierra Nevada. This is attributable to C losses from thinning or prescribed fire followed by the subsequent decay of dead biomass, and it is in line with the many earlier studies that have reported declines in forest C from proactive management (e.g. Campbell et al., 2012; Krofcheck et al., 2018; Wang et al., 2022). While previous research has suggested that even in projects incentivized to promote aboveground C storage, there have been marked declines in vegetation coverage (thus leaf area) over the past decade with ongoing climatic warming and aridification (Coffield et al., 2022; Herbert et al., 2022). However, although proactive management does not yield a *relative* increase in C storage compared to the baseline, this does not necessarily mean that, in absolute terms, forests such as those present in the Sierra Nevada lose their ability to sequester C and function as a net C sink.

A closer look at the various contributing fluxes reveals that the nature and frequency of management actions can play a significant role in shaping the extent to which fire-prone mountain forests can act as C sinks. Our results show that the rate of C addition to these ecosystems (i.e., NPP) was greater after management, with the average long-term rate being generally higher for more-frequent management interventions. This was because these management practices reduced wildfire severity in forests, decreasing the risk of soil nitrogen loss through combustion, soil erosion, surface runoff, and leaching to the streams after wildfires (Gustine et al., 2022). Trees can better maintain their capacity for C sequestration (greater negative NPP) with lower combustion-related nitrogen losses (Fenn et al., 2003). Previous research supports our finding that understory thinning helps bolster vegetation C accumulation and helps make the ecosystem a more-stable C-sequestration sink (Hurteau et al., 2024). Our thinning (i.e., MT) and prescribed fire (i.e., PF) treatments were designed to remove a greater proportion of the youngest tree cohorts and shift the age distribution toward older cohorts, which should reduce the projected wildfire severity when wildfire does occur (Davis et al., 2024). However, a potential drawback of

thinning is that it may increase heterotrophic respiration while reducing stand leaf area (and hence NPP), so that NEP (sum of NPP and heterotrophic respiration) may be positive, indicating that forests are transitioning from being a C sink to a C source after thinning. Stephens et al. (2024) reported lowering wildfire risk when thinning is combined with mastication, albeit not at the same level as when thinning is combined with prescribed fire. In the absence of mastication, we found that thinning alone does not lead to a noticeable reduction in wildfire C emissions. However, prescribed fire or removal of dead fuel following thinning can ameliorate C emissions by reducing heterotrophic respiration along with a reduction in wildfire emissions by altering their occurrence, burned area, and severity. An important drawback with prescribed fires is that the C emissions they introduce can be larger than C reductions in heterotrophic respiration and wildfire emissions, which can result in a positive NBP (sum of NEP and total fire) even in scenarios where NEP is negative. In our scenarios, introducing prescribed fire lowers wildfire C emissions by about 50 %, but the added emissions from the prescribed fires themselves were up to 20 times the wildfire fluxes. However, this finding comes with a caveat that our prescribed fire scenario involves removing the shrubs and dead fuel across the watershed by 80 %, and 95 % of the burned C is returned to atmosphere. While these numbers were derived from historical actions, we acknowledge the spatial and temporal variability in the effectiveness of prescribed fire and inherent uncertainties. Reduction in fuel loads after prescribed fire is highly variable (Stephens et al., 2024), and will likely depend on fuel conditions, local weather, and implementation methods. Also, prescribed fires are strategically placed to manage vegetation, reduce wildfire risk, and restore ecosystem health. Introducing prescribed fire uniformly across the landscape is highly unlikely, so, these simulated prescribed fire driven C emissions number may reflect the upper envelope. Increasing the threshold of remaining shrub and dead fuel or lowering the spatial extent will lower the flux to atmosphere from prescribed fire but will likely increase the C fluxes associated with wildfire and heterotrophic respiration. It would be interesting to further investigate how different intensities of management and their implementation, e.g., uniformly vs strategic breaks, impact C pools and fluxes in these ecosystems.

A potential key to balancing these competing effects is removal of biomass from the forest and storing this material in long-lived wood products. Our results suggest cutoff diameter limits of 6 to 7 inches (~152 to ~178 mm) may be the “sweet spot” for sustainable management if thinning is executed at 5-to-20-year intervals. We found NBP to be negative (i.e., there is net C sequestration) for scenarios where some or all the small-diameter thinned biomass is removed and sequestered, particularly in the absence of prescribed fire. Sequestering some or all the thinned biomass by harvesting it for lumber or other wood products can significantly increase the C-storage benefit of management and can potentially result in a net-negative C flux (i.e., NBP plus biomass out scenarios). However, at present much of the thinned tree biomass is contained in small trees that do not provide timber revenue (Stephens et al., 2021). Hence, a grand challenge of the forest wood-products industry is to continue to develop products that can utilize these small-diameter tree materials and convert them into long-lived wood products (Cabiyo et al., 2021).

There are some limitations to our modeling approach. First, as we stated earlier that we have not investigated strategically placed landscape treatments of fuels (i.e., SPLATS; Finney, 2001) versus treating the whole forest over the defined time interval. Previous research has found that SPLATS over areas with the greatest likelihood of high-severity wildfire should result in lower C emissions and provide ecosystem resistance and resilience to disturbance (Krofcheck et al., 2018). Second, in our scenarios with prescribed fire, we introduced fire over the whole basin, whereas in practice it would also be strategically placed. Still, with nearly three-fourths of the basin in tree and shrub cover, the area needing periodic treatment is still extensive. Third, we note that a C flux of $0.1 \text{ kg m}^{-2} \text{ yr}^{-1}$, which is in the range of sequestered harvest for our

~5000 km² study area, translates to an annual flux of about 0.5 million metric tonnes of CO₂ equivalent, which is only about 0.13 % of California's annual C emission level of 370 million metric tonnes (California Air Resources Board, <https://ww2.arb.ca.gov/ghg-inventory-data>). Fourth, our analysis did not account for C losses from post-fire soil erosion that can account for as much as 10–13 % of the C emissions produced by wildfires (Pierson et al., 2019; Girona-García et al., 2024). Erosion can also remove critical nutrients like nitrogen (Pierson et al., 2019), further constraining the CO₂ fertilization effect (Norby et al., 2010; Terrer et al., 2019). Future studies should scale up this work to include all fire-prone forests of the Sierra Nevada to evaluate the potential for Sierran forest ecosystems to help fulfill their potentially enormous promise for C sequestration within California and in other fire-prone forests of the western US (Griscom et al., 2017; Fargione et al., 2018).

4.3. Managing tradeoffs between C storage and wildfire protection

The large increase in C emissions involving widespread use of repeated prescribed fire over the whole forest is a striking feature of the modeling results. This burning does reduce wildfire severity and thus wildfire emissions but also reduces the residence time of dead biomass in the forest. Reducing dead fuel and wildfire severity offers additional benefits unrelated to C sequestration through lower expected wildfire risk to built-infrastructure, water quality, public health, wildlife habitat quality, recreation, and other ecosystem services (Ericksson et al., 2023). However, the tradeoff is lowering C storage more quickly through prescribed fire versus over a longer period through heterotrophic respiration. This tradeoff has also been addressed in other studies in mountain forest ecosystems experiencing a Mediterranean-type climate. In a modeling study involving limited thinning and wildfire over the 21st century, management scenarios showed greater C emissions compared to the unmanaged control in early decades, but lower C emissions and enhanced net C storage toward the end of the century (Liang et al., 2018). In contrast, an earlier modeling study suggested that larger area treatments were needed to reduce burned areas and thus wildfire C emissions; however, the avoided C emissions were less than the C removed through fuels treatments, resulting in less net C stored within the ecosystem (Campbell et al., 2012). That is, more-frequent management means greater burning or decay of the resulting dead biomass and commensurate increases in net C fluxes to the atmosphere

(Hurteau et al., 2017, 2024). In our baseline, no-management scenario, heterotrophic respiration plus wildfire was greater than NPP, so that NBP was slightly positive. Hence, based on our modeling results, the ecosystem will act as a small net C source to the atmosphere over the course of the 21st century if no management action is taken.

The net effect on these two competing objectives, reducing wildfire damage with associated release of C to the atmosphere versus storing C, requires carefully coordinated thinning and prescribed fire, plus offsite sequestration of thinned biomass. This can be seen more clearly by narrowing our focus to the C fluxes associated with wildfire, NBP, and harvest using a smaller set of the scenarios shown in Section 3.3 (Fig. 7). Thinning plus removal of stems without prescribed fire is sufficient for achieving net C storage (i.e., yields a negative NBP). Further, this option is even more favorable if we consider sequestration of C in the removed biomass. However, this option results in only a small reduction in wildfire extent and severity, and thus C emissions. Alternatively, prescribed fire significantly mitigates wildfire C emissions (about a 50 % reduction), but the emissions that this treatment produces result in a positive NBP. The far-right scenario in Fig. 7, which involves both thinning and prescribed fire plus removal of *all* thinned biomass, offers a reasonable compromise in achieving both competing objectives. Crucial to this scenario is accounting for the C sequestered in the removed biomass in wood products. Other studies have also considered harvest of removed biomass in their analysis (North et al., 2009; Wiechmann et al., 2015), and a recent study (Stephens et al., 2024) has put forth thinning plus prescribed fire with revenues from harvested biomass as a financially sustainable approach for wildfire treatment.

5. Conclusions

Three main conclusions emerge from this work. First, replacing the default GlobFIRM fire module in LPJ-GUESS with the LMfireCF module, which linked fire behavior and fire effects, improved fire-disturbance simulations, providing fire occurrence, extent, and vegetation mortality more in line with observations. Second, through our modeling, we found that thinning alone (no prescribed fire) does not lead to a significant reduction in wildfire C emissions. In our scenarios, introducing prescribed fire lowers wildfire C emissions by about 50 %, but the added emissions from the prescribed fires themselves far outweigh the C benefits from reduction in C fluxes due to wildfire. This can result in a positive Net Biome Productivity (NBP, which is the sum of C in Net

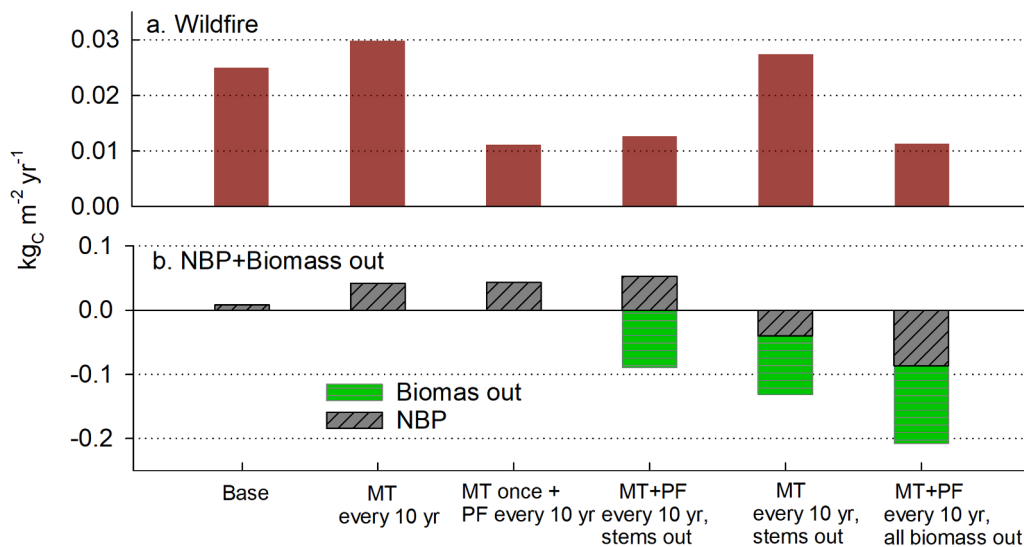


Fig. 7. Mean annual carbon (C) fluxes for a) wildfire, and b) net biome productivity (NBP) and biomass removed from the forest as a result of proactive management performed using mechanical thinning (MT) and prescribed fire (PF) at intervals over the 2006 to 2099 period. This figure provides an expanded view of selected scenarios from Fig. 6. Negative and positive values indicate C sink and source, respectively.

Ecosystem Productivity and total fire C emissions) even in scenarios where Net Ecosystem Productivity (NEP, sum of C fluxes due to Net Primary Productivity and heterotrophic respiration) is negative. Biomass removal scenarios where tree stems or all thinned biomass is removed offsite and sequestered in long-term products can offset positive NBP and result in a net negative C balance (i.e., a net C sink for the ecosystem). Third, thinning small-diameter trees plus sequestering thinned material and introducing prescribed fire to further reduce understory offers both lower wildfire risk and more sequestered C. Thinning small-diameter trees and sequestering thinned material provides an overall negative C balance (NBP plus sequestered C), but without prescribed fire does not reduce high-severity wildfire. While prescribed fire without thinning and sequestration can lower high-severity wildfire extent, it does not provide a near-zero NBP. That is, the combination of understory thinning, prescribed fire, and biomass removal/sequestration can mitigate wildfire severity and emissions, while also contributing to California's 2045 C-neutrality goal and end-of-century C sequestration.

CRedit authorship contribution statement

Weichao Guo: Writing – original draft, Validation, Software, Methodology, Formal analysis, Conceptualization. **Mohammad Safeeq:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Guotao Cui:** Writing – review & editing, Validation, Software, Methodology. **Philip C. Myint:** Writing – review & editing, Validation, Methodology, Software, Formal analysis. **Panmei Jiang:** Writing – review & editing, Visualization, Formal analysis. **Han Guo:** Writing – review & editing, Visualization, Formal analysis. **Michael L. Goulden:** Writing – review & editing, Validation. **Kristen D. Emmett:** Writing – review & editing, Validation, Software, Methodology. **Stephen C. Hart:** Writing – review & editing, Visualization, Formal analysis. **Roger C. Bales:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

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

Acknowledgements

This research was supported by the California Wildlife Conservation Board (WC-1732BC), NSF Southern Sierra Critical Zone Observatory (EAR-0725097, 1239521, and 1331939), NSF ECO-CBET (EAR-2318717), California Climate Investments program through the Strategic Growth Council (CCR20021), the National Natural Science Foundation of China (42301012), Fundamental Research Funds for the Central Universities, Sun Yat-sen University (24qnp020), and under the auspices of the U.S. Department of Energy (DOE) by Lawrence Livermore National Laboratory (LLNL) under Contract No DE-AC52-07NA27344, with the support of LLNL's Professional Research or Teaching Leave program. This research was also supported in part by an appointment to the United States Forest Service (USFS) Research Participation Program administered by the Oak Ridge Institute for Science and Education (ORISE) through an interagency agreement between the U.S. Department of Energy (DOE) and the U.S. Department of Agriculture (USDA). ORISE is managed by ORAU under DOE contract number DE-SC0014664. All opinions expressed in this paper are the authors' and do not necessarily reflect the policies and views of USDA, DOE, or ORAU/ORISE. Simulations with LPJ-GUESS were conducted using the MERCED (NSF-MRI 1429783) and Pinnacles (NSF MRI 2019144) computer clusters at the Cyberinfrastructure and Research

Technologies (CIRT) at University of California, Merced.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2025.111332.

Data availability

The source code of LPJ-GUESS is open access and available for users under MPL2.0 license and can be found: <https://web.nateko.lu.se/lpj-guess>. The revised source code along with the calibrated model parameters for the new coupled LPJ-GUESS- LMfireCF can be requested through our GitHub page: <https://github.com/msafeeq/LPJ-GUESS>. The gridMET and MACA climate data are from <http://www.climatologylab.org/gridmet.html> and <http://www.climatologylab.org/mac.html>, respectively. Soil data are from the Soil Survey Geographic Database (<https://www.nrcs.usda.gov/resources/data-and-reports/soil-survey-geographic-database-ssurgo>).

References

- Abatzoglou, J.T., Brown, T.J., 2012. A comparison of statistical downscaling methods suited for wildfire applications. *Int. J. Climatol.* 32, 772–780. <https://doi.org/10.1002/joc.2312>.
- Abatzoglou, J.T., 2013. Development of gridded surface meteorological data for ecological applications and modelling. *Int. J. Climatol.* 33 (1), 121–131. <https://doi.org/10.1002/joc.3413>.
- Abram, N.J., Henley, B.J., Sen Gupta, A., Lippmann, T.J., Clarke, H., Dowdy, A.J., et al., 2021. Connections of climate change and variability to large and extreme forest fires in southeast Australia. *Commun. Earth Environ.* 2 (1), 1–17.
- Baker, S.E., Stolaroff, J.K., Peridas, G., Pang, S.H., Goldstein, H.M., Lucci, F.R., et al., 2020. Getting to neutral: options for negative carbon emissions in California (No. LLNL-TR-796100). https://www-gs.llnl.gov/content/assets/docs/energy/Getting_to_Neutral.pdf.
- Bales, R.C., Goulden, M.L., Hunsaker, C.T., Conklin, M.H., Hartsough, P.C., O'Geen, A.T., et al., 2018. Mechanisms controlling the impact of multi-year drought on mountain hydrology. *Sci. Rep.* 8 (1), 690.
- Bedsworth, L., Cayan, D., Franco, G., Fisher, L., & Ziaja, S. (2018). Statewide summary report California's fourth climate change assessment. Publication number: SUMCCCA4-2018-013.
- Bellassen, V., Luyssaert, S., 2014. Carbon sequestration: managing forests in uncertain times. *Nature* 506, 153–155. <https://doi.org/10.1038/506153a>.
- Bistinas, I., Harrison, S.P., Prentice, I.C., Pereira, J.M.C., 2014. Causal relationships versus emergent patterns in the global controls of fire frequency. *Biogeosciences* 11 (18), 5087–5101.
- Brown, P.T., Hanley, H., Mahesh, A., Reed, C., Strenfel, S.J., Davis, S.J., et al., 2023. Climate warming increases extreme daily wildfire growth risk in California. *Nature* 621 (7980), 760–766. <https://doi.org/10.1038/s41586-023-06444-3>.
- Cabiyo, B., Fried, J.S., Collins, B.M., Stewart, W., Wong, J., Sanchez, D.L., 2021. Innovative wood use can enable carbon-beneficial forest management in California. *Proc. Natl. Acad. Sci.* 118 (49), e2019073118.
- Campbell, J.L., Harmon, M.E., Mitchell, S.R., 2012. Can fuel-reduction treatments really increase forest carbon storage in the western US by reducing future fire emissions? *Front. Ecol. Environ.* 10 (2), 83–90. <https://doi.org/10.1890/110057>.
- Chen, B., Jin, Y., 2022. Spatial patterns and drivers for wildfire ignitions in California. *Environ. Res. Lett.* 17 (5), 055004. <https://doi.org/10.1088/1748-9326/ac60da>.
- Coffield, S.R., Vo, C.D., Wang, J.A., Badgley, G., Goulden, M.L., Cullenward, D., et al., 2022. Using remote sensing to quantify the additional climate benefits of California forest carbon offset projects. *Glob. Change Biol.* 28 (22), 6789–6806. <https://doi.org/10.1111/gcb.16380>.
- Davis, K.T., Peeler, J., Fargione, J., Haugo, R.D., Metlen, K.L., Robles, M.D., Woolley, T., 2024. Tamm review: a meta-analysis of thinning, prescribed fire, and wildfire effects on subsequent wildfire severity in conifer dominated forests of the Western US. *For. Ecol. Manag.* 561, 121885.
- De Kauwe, M., Medlyn, B., Zaehle, S., Walker, A.P., Dietze, M.C., Hickler, T., et al., 2013. Forest water use efficiency at elevated CO₂: a modeldata intercomparison at two contrasting temperature forest FACE sites. *Glob. Change Biol.* 19, 1759–1779. <https://doi.org/10.1111/gcb.12164>.
- Dickman, L.T., Jonko, A.K., Linn, R.R., Altintas, I., Atchley, A.L., Bär, A., et al., 2023. Integrating plant physiology into simulation of fire behavior and effects. *New Phytol.* <https://doi.org/10.1111/nph.18770>.
- Emmett, K.D., Renwick, K.M., Poulter, B., 2021. Adapting a dynamic vegetation model for regional biomass, plant biogeography, and fire modeling in the Greater Yellowstone ecosystem: evaluating LPJ-GUESS-LMfireCF. *Ecol. Model.* 440, 109417. <https://doi.org/10.1016/j.ecolmodel.2020.109417>.
- Eriksson, M., Safeeq, M., Pathak, T., Egoh, B.N., Bales, R., 2023. Using stakeholder-based fuzzy cognitive mapping to assess benefits of restoration in wildfire-vulnerable forests. *Restor. Ecol.* 31 (4), e13766.

- Fargione, J.E., Bassett, S., Boucher, T., Bridgman, S.D., Conant, R.T., Cook-Patton, S.C., et al., 2018. Natural climate solutions for the United States. *Sci. Adv.* 4 (11), eaat1869. <https://doi.org/10.1126/sciadv.aat1869>.
- Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., et al., 2003. Ecological effects of nitrogen deposition in the western United States. *BioScience* 53 (4), 404–420. [https://doi.org/10.1641/0006-3568\(2003\)053\[0404:EEONDI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0404:EEONDI]2.0.CO;2).
- Finney, M.A., 2001. Design of regular landscape fuel treatment patterns for modifying fire growth and behavior. *For. Sci.* 47 (2), 219–228.
- Fisher, R.A., Koven, C.D., Anderegg, W.L.R., Christoffersen, B.O., Dietze, M.C., Farrior, C.E., et al., 2017. Vegetation demographics in earth system models: a review of progress and priorities. *Glob. Change Biol.* 24 (1), 35–54. <https://doi.org/10.1111/gcb.13910>.
- Foster, D.E., Battles, J.J., Collins, B.M., York, R.A., Stephens, S.L., 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.
- Girona-García, A., Vieira, D., Doerr, S., Panagos, P., Santín, C., 2024. Into the unknown: The role of post-fire soil erosion in the carbon cycle. *Global Change. Biology* 30 (6), e17354. <https://doi.org/10.1111/gcb.17354>.
- Goulden, M.L., Bales, R.C., 2019. California forest die-off linked to multi-year deep soil drying in 2012–2015 drought. *Nat. Geosci.* 12 (8), 632–637. <https://doi.org/10.1038/s41561-019-0388-5>.
- Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A., et al., 2017. Natural climate solutions. *Proc. Natl. Acad. Sci.* 114 (44), 11645–11650. <https://doi.org/10.1073/pnas.1710465114>.
- Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T., et al., 2020. Plant responses to rising vapor pressure deficit. *New Phytol.* 226 (6), 1550–1566. <https://doi.org/10.1111/nph.16485>.
- Guo, W., Safeeq, M., Liu, H., Wu, X., Cui, G., Ma, Q., et al., 2022. Mechanisms controlling carbon sinks in semi-arid mountain ecosystems. *Glob. Biogeochem. Cycles* 36 (3). <https://doi.org/10.1029/2021GB007186> e2021GB007186.
- Gustine, R.N., Hanan, E.J., Robichaud, P.R., Elliot, W.J., 2022. From burned slopes to streams: how wildfire affects nitrogen cycling and retention in forests and fire-prone watersheds. *Biogeochemistry* 157 (1), 51–68. <https://doi.org/10.1007/s10533-021-00861-0>.
- Hagmann, R., Hessburg, P., Prichard, S., Povak, N., Brown, P., Fulé, P., et al., 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecol. Appl.* 31 (8), e02431. <https://doi.org/10.1002/eap.2431>.
- Harrison, S.P., Bartlein, P.J., Brovkin, V., Houweling, S., Kloster, S., Prentice, I.C., 2018. The biomass burning contribution to climate–carbon-cycle feedback. *Earth Syst. Dyn.* 9 (2), 663–677. <https://doi.org/10.5194/esd-9-663-2018>.
- Hemes, K.S., Norlen, C.A., Wang, J.A., Goulden, M.L., Field, C.B., 2023. The magnitude and pace of photosynthetic recovery after wildfire in California ecosystems. *Proc. Natl. Acad. Sci.* 120 (15), e2201954120. <https://doi.org/10.1073/pnas.2201954120>.
- Herbert, C., Haya, B.K., Stephens, S.L., Butsic, V., 2022. Managing nature-based solutions in fire-prone ecosystems: competing management objectives in California forests evaluated at a land-scale scale. *Front. For. Glob. Change*. <https://doi.org/10.3389/ffgc.2022.957189>, 5-957189.
- Hessburg, P.F., Miller, C.L., Parks, S.A., Povak, N.A., Taylor, A.H., Higuera, P.E., et al., 2019. Climate, environment, and disturbance history govern resilience of western North American forests. *Front. Ecol. Evol.* 7 (239). <https://doi.org/10.3389/fevo.2019.00239>.
- Hessburg, P.F., Spies, T.A., Perry, D.A., Skinner, C.N., Taylor, A.H., Brown, P.M., et al., 2016. Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. *For. Ecol. Manag.* 366, 221–250. <https://doi.org/10.1016/j.foreco.2016.01.034>.
- Hickler, T., Vohland, K., Feehan, J., Miller, P.A., Smith, B., Costa, L., Sykes, M.T., 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. *Glob. Ecol. Biogeogr.* 21 (1), 50–63. <https://doi.org/10.1111/j.1466-8238.2010.00613.x>.
- Hood, S.M., Varner, J.M., Van Mantgem, P., Cansler, C.A., 2018. Fire and tree death: understanding and improving modeling of fire-induced tree mortality. *Environ. Res. Lett.* 13 (11), 113004. <https://doi.org/10.1088/1748-9326/aae934>.
- Hurteau, M.D., 2017. Quantifying the carbon balance of forest restoration and wildfire under projected climate in the fire-prone southwestern US. *PLoS One* 12, e0169275. <https://doi.org/10.1371/journal.pone.0169275>.
- Hurteau, M.D., Goodwin, M.J., Marsh, C., Zald, H.S., Collins, B., Meyer, M., North, M.P., 2024. Managing fire-prone forests in a time of decreasing carbon carrying capacity. *Front. Ecol. Environ.* e2801. <https://doi.org/10.1002/fee.2801>.
- Hurteau, M.D., North, M.P., Koch, G.W., Hungate, B.A., 2019. Managing for disturbance stabilizes forest carbon. *Proc. Natl. Acad. Sci.* 116 (21), 10193–10195.
- Jiang, P., Russell, M.B., Frelich, L., Babcock, C., Smith, J.E., 2023. Wildfires correlate with reductions in aboveground tree carbon stocks and sequestration capacity on forest land in the Western United States. *Sci. Total Environ.* 893, 164832. <https://doi.org/10.1016/j.scitotenv.2023.164832>.
- Kane, V.R., Bartl-Geller, B.N., Cova, G.R., Chamberlain, C.P., van Wagtenonk, L., North, M.P., 2023. Where are the large trees? A census of Sierra Nevada large trees to determine their frequency and spatial distribution across three large landscapes. *For. Ecol. Manag.* 546, 121351.
- Keane, R.E., 2019. Applying Ecosystem and Landscape Models in Natural Resource Management. CRC Press, p. 236. <https://doi.org/10.1201/9780429324024>. Pages. ISBN 9780367779290.
- Keenan, T., Hollinger, D., Bohrer, G., Dragoni, D., William Munger, J., Schmid, H.P., et al., 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentration rise. *Nature* 499 (7458), 324–327. <https://doi.org/10.1038/nature12291>.
- Kelley, D.I., Bistinas, I., Whitley, R., Burton, C., Marthews, T.R., Dong, N., 2019. How contemporary bioclimatic and human controls change global fire regimes. *Nat. Clim. Change* 9 (9), 690–696.
- Kirschbaum, M.U., Paul, K.I., 2002. Modelling C and N dynamics in forest soils with a modified version of the CENTURY model. *Soil Biol. Biochem.* 34 (3), 341–354.
- Kirschbaum, M., Watt, M., Tait, A., Ausseil, A.-G.E., 2012. Future wood productivity of *Pinus radiata* in New Zealand under expected climatic changes. *Glob. Change Biol.* 18, 1342–1356. <https://doi.org/10.1111/j.1365-2486.2011.02625.x>.
- Krofcheck, D.J., Hurteau, M.D., Scheller, R.M., Loudermilk, E.L., 2018. Prioritizing forest fuels treatments based on the probability of high-severity fire restores adaptive capacity in Sierran forests. *Glob. Change Biol.* 24, 729–737. <https://doi.org/10.1111/gcb.13913>.
- Liang, S., Hurteau, M.D., Westerling, A.L., 2018. Large-scale restoration increases carbon stability under projected climate and wildfire regimes. *Front. Ecol. Environ.* 16 (4), 207–212. <https://doi.org/10.1002/fee.1791>.
- Lindeskog, M., Smith, B., Lagergren, F., Sycheva, E., Ficko, A., Pretzsch, H., Rammig, A., 2021. Accounting for forest management in the estimation of forest carbon balance using the dynamic vegetation model LPJ-GUESS (v4.0, r9710): implementation and evaluation of simulations for Europe. *Geosci. Model Dev.* 14 (10), 6071–6112. <https://doi.org/10.5194/gmd-14-6071-2021>.
- Lindner, M., Fitzgerald, J., Zimmermann, N., Reyser, C., Delzon, S., van der Maaten, E., et al., 2014. Climate change and European forests: what do we know, what are the uncertainties, and what are the implications for forest management? *J. Environ. Manag.* 146, 69–83. <https://doi.org/10.1016/j.jenvman.2014.07.030>.
- Marlon, J.R., Bartlein, P.J., Gavin, D.G., Long, C.J., Anderson, R.S., Briles, C.E., et al., 2012. Long-term perspective on wildfires in the western USA. *Proc. Natl. Acad. Sci.* 109 (9), E535–E543. <https://doi.org/10.1073/pnas.1112839109>.
- Meinshausen, M., Smith, S.J., Calvin, K., Daniel, J.S., Kainuma, M.L., Lamarque, J.F., Matsumoto, K., Montzka, S.A., Raper, S.C., Riahi, K., Thomson, A., Velders, G.J.M., van Vuuren, D.P., 2011. The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Clim. Change* 109 (1–2), 213–241. <https://doi.org/10.1007/s10584-011-0156-z>.
- Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E., McMurtrie, R.E., 2010. CO₂ enhancement of forest productivity constrained by limited nitrogen availability. *Proc. Natl. Acad. Sci.* 107 (45), 19368–19373.
- North, M.P., Hurteau, M.D., Innes, J., 2009. Fire suppression and fuels treatment effects on mixed-conifer carbon stocks and emissions. *Ecol. Appl.* 19, 1385–1396. <https://doi.org/10.1890/08-1173.1>.
- North, M., Innes, J., Zald, H., 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. *Can. J. For. Res.* 37 (2), 331–342.
- NRCS, 2010. Soil Survey Staff, Natural Resources Conservation Service Soil Survey Geographic (SSURGO) Database for Northeast Tennessee. United States Department of Agriculture.
- Pfeiffer, M., Spessa, A., Kaplan, J.O., 2013. A model for global biomass burning in preindustrial time: IPJ-LMfire (v1.0). *Geosci. Model Dev.* 6 (3), 643–685. <https://doi.org/10.5194/gmd-6-643-2013>.
- Pierson, D.N., Robichaud, P.R., Rhoades, C.C., Brown, R.E., 2019. Soil carbon and nitrogen eroded after severe wildfire and erosion mitigation treatments. *Int. J. Wildland Fire* 28 (10), 814–821.
- Possell, M., Jenkins, M., Bell, T.L., Adams, M.A., 2015. Emissions from prescribed fires in temperate forest in south-east Australia: implications for carbon accounting. *Biogeosciences* 12 (1), 257–268. <https://doi.org/10.5194/bg-12-257-2015>.
- Prentice, I.C., Liang, X., Medlyn, B.E., Wang, Y.P., 2015. Reliable, robust and realistic: the three R's of next-generation land-surface modelling. *Atmos. Chem. Phys.* 15 (10), 5987–6005.
- Schellhaas, M.-J., Nabuurs, G.-J., Hengenveld, G., Reyser, C., Hanewinkel, M., Zimmermann, N.E., et al., 2015. Alternative forest management strategies to account for climate change-induced productivity and species suitability changes in Europe. *Reg. Environ. Change* 15 (8), 1581–1594. <https://doi.org/10.1007/s10113-015-0788-z>.
- Seipp, K.Q., Maurer, T., Elias, M., Saksa, P., Keske, C., Oleson, K., et al., 2023. A multi-benefit framework for funding forest management in fire-driven ecosystems across the western U.S. *J. Environ. Manag.* 344–118720. <https://doi.org/10.1016/j.jenvman.2023.118720>.
- Smith, B. (2001). LPJ-GUESS—an ecosystem modelling framework. Department of Physical Geography and Ecosystems Analysis, INES, Sölvegatan, 12(22), 362. <https://web.nateko.lu.se/lpj-guess/guess.pdf>.
- Smith, B., Prentice, I.C., Sykes, M.T., 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Glob. Ecol. Biogeogr.* 10 (6), 621–637. <https://doi.org/10.1046/j.1466-822X.2001.t01-1-00256.x>.
- Smith, B., Wärlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., Zaehle, S., 2014. Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences* 11 (7), 2027–2054.
- Stephens, S.L., Battaglia, M.A., Churchill, D.J., Collins, B.M., Coppletoletta, M., Hoffman, C.M., Stevens, J.T., 2021. Forest restoration and fuels reduction: convergent or divergent? *Bioscience* 71 (1), 85–101.
- Stephens, S.L., Foster, D.E., Battles, J.J., Bernal, A.A., Collins, B.M., Hedges, R., et al., 2024. Forest restoration and fuels reduction work: different pathways for achieving success in the Sierra Nevada. *Ecol. Appl.* 34 (2), e2932. <https://doi.org/10.1002/eap.2932>.

- Stephens, S.L., Westerling, A.L., Hurteau, M.D., Peery, M.Z., Schultz, C.A., Thompson, S., 2020. Fire and climate change: conserving seasonally dry forests is still possible. *Front. Ecol. Environ.* 18 (6), 354–360. <https://doi.org/10.1002/fee.2218>.
- Taylor, A.H., Trouet, V., Skinner, C.N., Stephens, S., 2016. Socioecological transitions trigger fire regime shifts and modulate fire-climate interactions in the Sierra Nevada, USA, 1600–2015 CE. *Proc. Natl. Acad. Sci. USA* 113 (48), 13684–13689. <https://doi.org/10.1073/pnas.1609775113>.
- Terrer, C., Jackson, R.B., Prentice, I.C., Keenan, T.F., Kaiser, C., Vicca, S., et al., 2019. Nitrogen and phosphorus constrain the CO₂ fertilization of global plant biomass. *Nat. Clim. Change* 9 (9), 684–689.
- Thonicke, K., Spessa, A., Prentice, I.C., Harrison, S.P., Dong, L., Carmona-Moreno, C., et al., 2010. The influence of vegetation, fire spread and fire behaviour on biomass burning and trace gas emissions: results from a process-based model. *Biogeosciences* 7 (6), 1991–2011. <https://doi.org/10.5194/bg-7-1991-2010>.
- Thonicke, K., Venevsky, S., Sitch, S., Cramer, W., 2001. The role of fire disturbance for global vegetation dynamics: coupling fire into a dynamic global vegetation model. *Glob. Ecol. Biogeogr.* 10 (6), 661–677. <https://doi.org/10.1046/j.1466-822X.2001.00175.x>.
- Tubbesing, C.L., Fry, D.L., Roller, G.B., Collins, B.M., Fedorova, V.A., Stephens, S.L., Battles, J.J., 2019. Strategically placed landscape fuel treatments decrease fire severity and promote recovery in the northern Sierra Nevada. *For. Ecol. Manag.* 436, 45–55. <https://doi.org/10.1016/j.foreco.2019.01.010>.
- Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., et al., 2011. The representative concentration pathways: an overview. *Clim. Change* 109 (5), 5–31. <https://doi.org/10.1007/s10584-011-0148-z>.
- Wang, D., Guan, D., Zhu, S., Kinnon, M.M., Geng, G., Zhang, Q., et al., 2021. Economic footprint of California wildfires in 2018. *Nat. Sustain.* 4 (3), 252–260. <https://doi.org/10.1038/s41893-020-00646-7>.
- Wang, J.A., Randerson, J.T., Goulden, M.L., Knight, C.A., Battles, J.J., 2022. Losses of tree cover in California driven by increasing fire disturbance and climate stress. *AGU Adv.* 3 (4). <https://doi.org/10.1029/2021AV000654> e2021AV000654.
- Wang, W., Pend, C., Kneeshaw, D., Larocque, G.R., Lei, X., Zhu, Q., et al., 2013. Modelling the effects of varied forest management regimes on carbon dynamics in jack pine stands under climate change. *Can. J. For. Res.* 43 (5), 469–479. <https://doi.org/10.1139/cjfr-2012-0320>.
- Wiechmann, M.L., Hurteau, M.D., North, M.P., Koch, G.W., Jerabkova, L., 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. *Clim. Change* 132, 709–719.
- Yue, C., Ciais, P., Luyssaert, S., Li, W., McGrath, M.J., Chang, J., Peng, S., 2018. Representing anthropogenic gross land use change, wood harvest, and forest age dynamics in a global vegetation model ORCHIDEE-MICT v8.4.2. *Geosci. Model Dev.* 11, 409–428. <https://doi.org/10.5194/gmd-11-409-2018>.
- Zhang, Y., Kong, D., Gan, R., Chiew, F.H.S., McVicar, T.R., Zhang, Q., Yang, Y., 2019. Coupled estimation of 500m and 8-day resolution global evapotranspiration and gross primary production in 2002–2017. *Remote Sens. Env.* 222, 165–182. <https://doi.org/10.1016/j.rse.2018.12.031>.