

Does hot and dry equal more wildfire? Contrasting short- and long-term climate effects on fire in the Sierra Nevada, CA

MAUREEN C. KENNEDY^{1,†}, RYAN R. BART², CHRISTINA L. TAGUE³, AND JANET S. CHOATE³

¹*School of Interdisciplinary Arts and Sciences, University of Washington (Tacoma), 1900 Commerce Street, Tacoma, Washington 98402 USA*

²*Sierra Nevada Research Institute, University of California, Merced, 5200 Lake Road, Merced, California 95343 USA*

³*Bren School of Environmental Science and Management, University of California, Bren Hall, 2400, Santa Barbara, California 93106 USA*

Citation: Kennedy, M. C., R. R. Bart, C. L. Tague, and J. S. Choate. 2021. Does hot and dry equal more wildfire? Contrasting short- and long-term climate effects on fire in the Sierra Nevada, CA. *Ecosphere* 12(7):e03657. 10.1002/ecs2.3657

Abstract. Climate and wildfire are closely linked. Climate regulates wildfire directly over short timescales through its effect on fuel aridity and indirectly over long timescales through vegetation productivity and the structure and abundance of fuels. Prediction of future wildfire regimes in a changing climate often uses empirical studies that presume current relationships between short-term climate variables and wildfire activity will be stationary in the future. This is problematic because landscape-scale wildfire dynamics exhibit non-stationarity, with both positive and negative feedback loops that operate at different temporal and spatial scales. This requires that such feedbacks are accommodated in a model framework from which wildfire dynamics are emergent rather than pre-specified. We use a new model, RHESys-WMFire, that integrates ecohydrology with fire spread and effects to simulate a 60-yr time series of vegetation, fuel development, and wildfire in a 6572-ha watershed in the Southern Sierra Nevada, USA, with a factorial design of increased temperature and severe drought. All climate scenarios had an initial pulse of elevated area burned associated with high temperature, low precipitation, and high fine fuel loading. There were positive correlations between annual area burned and mean annual maximum temperature and negative correlations with annual precipitation, consistent with understood direct effects of climate on wildfire in this system. Decreased vegetation productivity and increased fine fuel decomposition were predicted with increased temperature, resulting in long-term reduced fine fuels and area burned relative to baseline. Repeated extreme drought increased area burned relative to baseline and over the long-term had substantially reduced overstory biomass. Overstory biomass was resilient to repeat wildfire under baseline climate. The model system predicts that the short-term direct effects of climate on wildfire can differ from long-term indirect effects such that the simple maxim hotter/drier equals more wildfire can be both true and false, depending on scale.

Key words: area burned; climate change; complexity; ecohydrology; feedbacks; fire spread; model; scale; wildfire regimes.

Received 15 September 2020; revised 5 March 2021; accepted 12 March 2021; final version received 13 May 2021. Corresponding Editor: Joel Biederman.

Copyright: © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** mkenn@uw.edu

INTRODUCTION

Fire regimes and climate change

Wildfire is a vegetation disturbance that is distributed throughout the globe (Flannigan et al. 2009), and its prevalence varies along a resource

climate gradient (Krawchuk and Moritz 2011). Trends in wildfire annual area burned and frequency of large fires also vary globally (Riaño et al. 2007), with some regions experiencing increases (Westerling et al. 2006) and others experiencing decreases (Turco et al. 2016). There is

considerable interest in how anthropogenic climate change will modify global wildfire regimes and this can be considered at both relatively short-term (within a year) and long-term (years to decades) timescales.

Climate drives wildfire over relatively short timescales (within a year) by the direct effect on fuel aridity of annual weather variables such as same-year temperature and precipitation (Flannigan et al. 2009). In this short-term, high temperatures and low precipitation tend to be associated with periods of increased fire activity and area burned (Littell et al. 2009, 2018, Parisien and Moritz 2009, Abatzoglou and Williams 2016, Holden et al. 2018). Often precipitation and other moisture-related variables are stronger predictors than temperature alone (Parisien and Moritz 2009, Holden et al. 2018). Direct effects tend to dominate in forested systems (McKenzie and Littell 2017) and the balance of the importance and strength of these differ with the long-term climate and vegetation productivity of a given region, exhibiting varying constraints (Krawchuk and Moritz 2011).

Over longer time frames (years to decades), climate regulates decomposition and vegetation productivity, which drives fuel buildup with effects accumulating over many years. In some systems, particularly arid regions characterized by grasses and shrubs whose productivity is moisture-limited (Littell et al. 2009, 2018, McKenzie and Littell 2017), prior-year precipitation is correlated positively with annual area burned, indicating an indirect facilitative effect of climate on fine fuel abundance and connectivity (Littell et al. 2009, Krawchuk and Moritz 2011). Other ecosystems such as those in the Sierra Nevada, California, exhibit both direct and indirect influences of climate on wildfire area burned (Littell et al. 2009, 2018, McKenzie and Littell 2017) as they exist in the middle of the resource productivity gradient.

While the climate–fire relationships described above tend to be estimated at relatively coarse spatial scales, forest management decisions are made at the landscape scale. Landscape-scale wildfire dynamics are complex (Newman et al. 2019) because they are governed by the interactions of bottom-up or endogenous and top-down or exogenous drivers (Kennedy and McKenzie 2010, Moritz et al. 2011, McKenzie and Kennedy

2012) with both positive and negative feedback loops that may be scale dependent. Landscape-level fire ecological dynamics are also non-stationary, such that models that explain processes driving a given system today may not apply in the future, particularly with climate change (McKenzie and Littell 2017, Newman et al. 2019). Empirical models that rely on correlation or regression analysis require that those relationships are stationary even under novel climates (Harris et al. 2016, McKenzie and Littell 2017). Purely empirical models are unable to accommodate temporal scale dependence of wildfire–climate relationships, where long-term climate effects on forest fuels are uncertain (Flannigan et al. 2009). Nor can they accommodate possible feedback loops among climate, vegetation and fuels, and wildfire, where increased wildfire could possibly represent a negative feedback through self-limitation (Collins et al. 2009) or a positive feedback through change to more flammable vegetation such as grasses and shrubs (Lenihan et al. 2003). Many landscape forest models and dynamic vegetation models are a mixture of mechanistic and empirically derived relationships (Keane et al. 2004, Gustafson 2013, Harris et al. 2016). While included mechanisms may be better able to capture those long-term effects and feedbacks, they also suffer from the limitations of using empirical structures that characterize relationships that may not be stationary in a changing climate.

Ecohydrology and wildfire

Hydrologic influences on vegetation and fuels are likely to be a source of non-stationarity in ecosystem-level climate–fire and vegetation growth feedbacks including post-fire recovery. Increasing temperature directly alters growth (Yeh and Wensel 2000, Aubry-Kientz and Moran 2017, Johnson et al. 2017), but particularly in higher elevation Mediterranean Regions, temperature-driven changes in snowmelt and changes in precipitation patterns can have substantial impacts on biomass accumulation (Aubry-Kientz and Moran 2017). Stand growth and development models such as the U.S. Forest Service Forest Vegetation Simulator (Dixon 2012) that use empirical growth curves or even mechanistic models that do not account for changing water availability with warming will miss these

effects. In contrast, ecohydrological models that combine physical hydrological processes with ecological dynamics are uniquely suited to evaluate both the short and long timescale impacts of climate on both vegetation and wildfire at the watershed scale. Yet, ecohydrological models have not realized this potential because they do not adequately represent disturbances such as wildfire (Hannah et al. 2007).

Recently, the Regional Ecological Simulation System (RHESSys; Tague and Band 2004) has been integrated dynamically with a simple stochastic model of fire spread (WMFire; Kennedy et al. 2017, Kennedy and McKenzie 2017) and fire effects (Bart et al. 2020). This model system is the first of its kind to fully couple hillslope-scale hydrologic processes and ecosystem carbon/nutrient cycling with wildfire. It is designed at an intermediate level of model complexity to project aggregate patterns of fire spread and fire regimes rather than replicating individual wildfire events. It has been shown to robustly replicate emergent fire regime characteristics from contrasting systems without an external specification of those characteristics (Kennedy et al. 2017, Kennedy and McKenzie 2017, Bart et al. 2020). RHESSys-WMFire answers many of the difficulties in predicting wildfire under climate change. It is robust to non-stationary relationships between climate and wildfire because these are not specified internally, rather they emerge from feedbacks between climate, the hydrological cycle, vegetation, fuels, fire spread, and fire effects. Both long-term and short-term effects of climate on wildfire can be evaluated through dynamic simulation of wildfire and vegetation within a watershed over several decades.

Here, we use RHESSys-WMFire to conduct a simulation experiment in a watershed in the Southern Sierra Nevada (California, USA; Fig. 1). Recently, this ecoregion has had positive correlations between current-year temperature and wildfire area burned and negative relationships between current-year precipitation and wildfire area burned (Littell et al. 2009), with evidence for weaker but significant positive relationships between antecedent (prior-year) precipitation and wildfire area burned. This indicates the system is intermediate in the resource productivity gradient, where climate has both a direct effect

and an indirect facilitative effect on wildfire. This provides an exemplar for the complex dynamics of wildfire under climate change and the context under which a system may or may not be moved to a more fuel-limited state in which past climate relationships may no longer pertain.

We simulated a factorial design of increased temperature and drought, both with and without wildfire. This allowed us to disentangle potential effects of increased temperature from those of drought and their combined effects, and to better understand what might drive future changes in vegetation and wildfire. Our ultimate goal was to use the simulations to understand both the individual and combined effects of drought and increased temperature on the short-term direct and long-term indirect effects of climate on wildfire, vegetation, and fuels, and how those effects interact.

METHODS

Study site

The 6572-ha Big Creek watershed in the Southern Sierra Nevada, USA (Fig. 1) encompasses the Soaproot and Providence components of the Southern Sierra Critical Zone Observatory and the Providence component of the Kings River Experimental Watersheds. The mean elevation is 1493 m and is located within the rain–snow transition zone. The mean annual precipitation is 131 cm, and the mean minimum and maximum temperatures are 3.1°C and 14.4°C, respectively. The site is characterized as a mixed-conifer forest with the understory comprised of chaparral shrubland species and young conifers. Historically, the area had a frequent-fire low-severity fire regime with return intervals on the order of 5–9 yr over scales of 3–16 ha (Kilgore and Taylor 1979) that likely maintained low fine fuel accumulations and a mosaic of canopy structures. Nearby fire history reconstructions of the pre-suppression era estimated mean intervals between fires of 1.2 yr, mean fire size ranging from 120 to 300 ha, and fire rotations ranging from 8 to 24 yr with fires seen to be self-limiting (Scholl and Taylor 2010). Recent land and fire management have resulted in a shift to a higher density of smaller diameter size classes (Scholl and Taylor 2010, McIntyre et al. 2015). Further site details are given in Appendix S1.

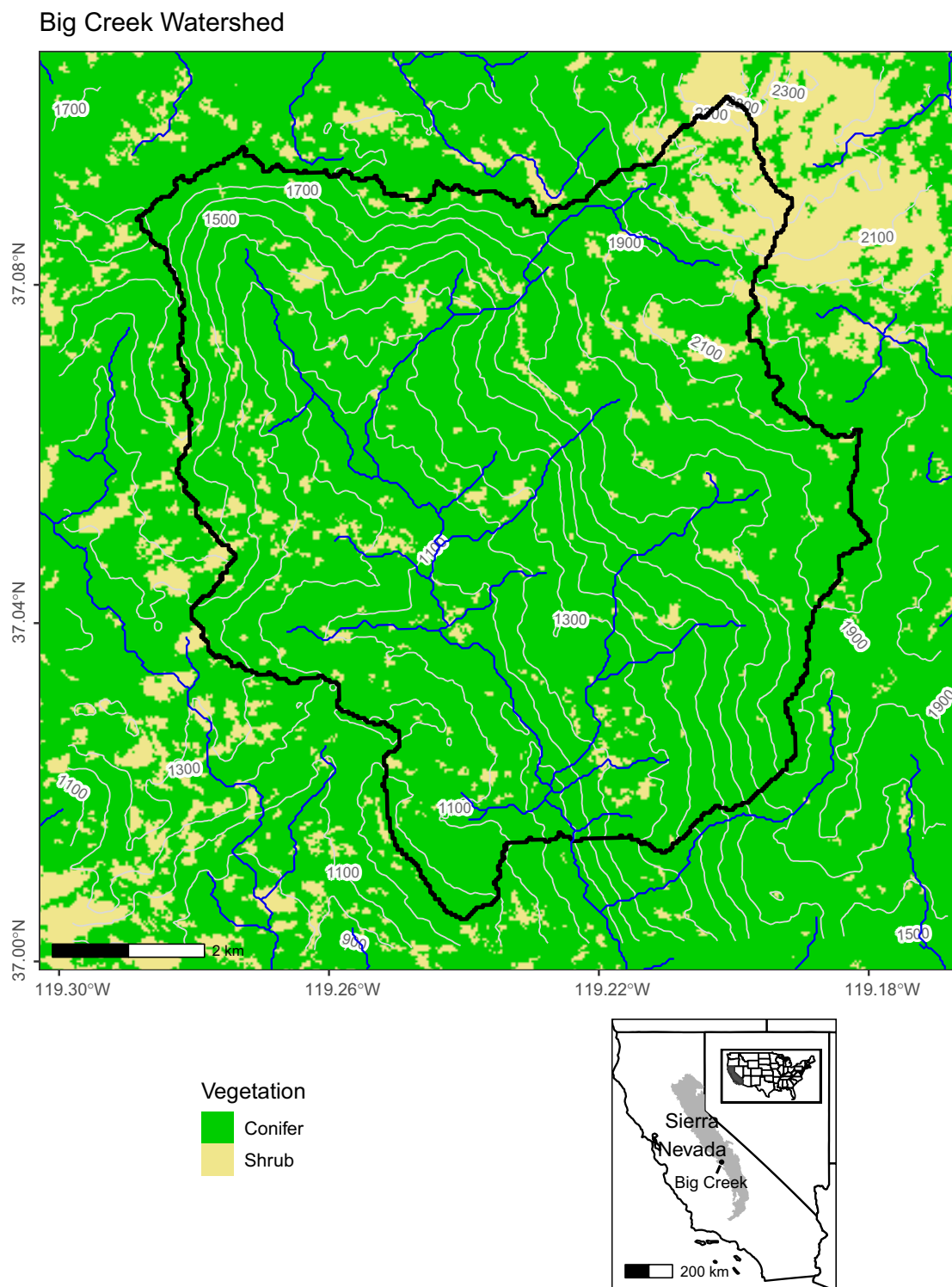


Fig. 1. Map of the study area including topography, land classification, and location in California, USA. Dark blue lines show major streams, and the black lines shows the watershed boundary. Elevation contours are given in meters.

RHESSys ecohydrology and calibration

Regional Ecological Simulation System is a spatially distributed model of fully coupled ecohydrologic processes. For this paper, we used RHESSys version 7.0. RHESSys partitions the landscape into spatial units (typically 30–120 m cells termed patches), that account for spatial variation in meteorologic (temperature and precipitation) forcing and radiative environments. Each spatial unit includes overstory and understory vegetation, litter, and organic soil. Vegetation growth in RHESSys occurs by modeling photosynthesis, respiration, and the allocation of net assimilation to storage (as non-structural carbohydrate), leaves, stems, and roots. Plant components turnover (such as seasonal litterfall) and any vegetation mortality feeds coarse wood debris and litter carbon and nitrogen pools, which decompose to soil organic matter as a function of material quality, moisture, and air temperature. Most eco-physiological processes vary with species-specific parameters. To generate the landscape watershed model, parameter sensitivity analysis, spin-up, and calibration were performed in a multi-step process detailed in Appendix S1.

Additional details on RHESSys estimates of carbon, evapotranspiration (ET), and potential evapotranspiration (PET) can be found in Tague and Band (2004), more recent updates in (Garcia et al. 2013, Tague et al. 2013, Garcia and Tague 2015), on the RHESSys github site (<https://github.com/RHESSys/RHESSys>), and in Appendix S1. RHESSys model skill at estimating plant carbon cycling and growth, and hydrologic processes (including evapotranspiration, snowmelt, and runoff) in semi-arid systems is well documented (in particular, see Tague et al. 2013, Vicente-Serrano et al. 2015, Bart et al. 2016, Garcia et al. 2016, Son and Tague 2019, Tsamir et al. 2019).

RHESSys and WMFire

WMFire is a stochastic model of fire initiation and spread that is described in detail in Kennedy et al. (2017). The model successfully reproduces spatial patterns of fire spread (Kennedy and McKenzie 2017) and aggregate fire regime characteristics (Kennedy et al. 2017) in contrasting fire regimes. Each month RHESSys passes to WMFire variables that are required to simulate fire spread. The monthly mean fine fuel load (kg/m^2) is represented by RHESSys litter carbon

pools that approximate 1–100-h fuel classes. Mean monthly actual and potential evapotranspiration (ET and PET, respectively; $\text{mm}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$; Stephenson 1998) are used by WMFire to calculate relative deficit ($1 - \text{ET}/\text{PET}$; Swann et al. 2012, Kennedy and McKenzie 2017) for both the understory and the overall canopy.

Fire initiation and spread are stochastic in WMFire. The number of ignitions tested each month was drawn from a Poisson distribution with a mean of 2 ignitions per month. Ignition locations were then located randomly within the watershed. Probability of ignition success depended on the fine fuel load and understory relative deficit. With successful ignition, the probability of spread to neighboring cells depended on fine fuel load, overall relative deficit, direction of spread relative to the topographic slope (uphill or downhill), and direction of spread relative to the wind direction.

After fire spread is simulated on the watershed, RHESSys interprets the spread probability as a fire intensity index (FII) that is used to calculate fire effects on vegetation. For all patches that experience fire, RHESSys consumes a proportion of the surface fuels (litter, coarse woody debris) after empirical equations in the Consume model (Prichard et al. 2017). Understory and overstory biomass for the model are defined based on height thresholds. Understory mortality is a function of FII and overstory mortality is a function of the surface and understory biomass consumed. Thus, the RHESSys fire effects model accounts for the role of ladder fuels (understory canopies) in propagating fire into the canopy. RHESSys also differentiates between biomass consumed and biomass lost to vegetation mortality but remains on the landscape and is later added to litter pools and ultimately decomposes. The proportion of understory and overstory mortality that is consumed also varies with FII. Bart et al. (2020) showed the fire effects module to reproduce expected patterns in wildfire effects and recovery for several diverse watersheds, including Big Creek.

Simulation study design

We implemented a simple factorial design of temperature and precipitation to represent climate change. A more complex representation of climate change that incorporates downscaled

general circulation model (GCM) predictions would complicate the simple scenarios that we investigated and impede our ability to explore the distinct effects of increased temperature and changes to precipitation on fire regimes in systems like these. For the baseline scenario (no change; Base), we used historical daily weather obtained from the Grant Grove station (NOAA GHCND:USC00043551) over the water years 1942–2000 (hereafter simulation years 1–59). For the temperature scenario, we add +2°C and +4°C (Plus2, Plus4, respectively; Fig. 2) to the daily minimum and maximum temperatures. These values were chosen to be consistent with moderate to high warming. Climate projections of mean annual precipitation generally show minimal change in California (Cayan et al. 2007); however, inter-annual variability of precipitation is expected to increase, with dry years becoming drier and wet years becoming wetter (Swain et al. 2018). By the end of the 21st century, Berg and Hall (2015) have estimated that the frequency of extremely dry years may increase 1.5–2 times in California. To simulate a drought effect, we repeated daily precipitation from a decade (2009–2018) encompassing recent extreme California drought years and repeated it over the historical daily precipitation every 10 yr (simulation years 5–14, 25–34, 45–54; Drought; Fig. 2). This resulted in six total climate scenarios: Base, BasePlus2, BasePlus4, Drought, DroughtPlus2, and DroughtPlus4.

RHESSys is deterministic whereas WMFire is stochastic. For each scenario, we conducted a single run of RHESSys without wildfire (NoFire) to isolate the effects of climate change on vegetation and fuels, which would represent its indirect long-term effect on wildfire. We then simulated 200 Monte Carlo (MC) replicates of the fully coupled model with wildfire spread and effects (Fire). This number of simulations takes an experimental design approach to balance the computational burden of the fully coupled model with the expected variability in model predictions (Kennedy 2019). This resulted in 6 scenarios \times 200 MC replicates for a total of 1200 simulations.

Analysis: fire regime summaries

All fire regime and vegetation variables were summarized as mean values in a water year

(October–September). We evaluated short-term direct climate effects on area burned by calculating correlations for each replicate time series between log of annual area burned for those years with at least one fire and the following climate variables: annual mean maximum temperature, summer mean maximum temperature, and annual precipitation the year of the fire, and annual precipitation the year preceding the fire. The distributions of correlations were compared across scenarios to understand how direct effects of climate were predicted to vary with longer-term climate patterns.

We summarized trajectories of annual area burned across replicates for each scenario to understand common temporal patterns and variability. For each simulation year, we calculated the first quartile, median, and third quartile of annual area burned across all replicates for each scenario. This highlights prominent periods of wildfire activity for a given scenario, though ignoring the potential temporal dependence in area burned for a given time series replicate. Trajectories of area burned over time across all replicates are given in Appendix S1.

Since each simulated time series represents an independent replicate in the simulation study design, we also summarized each by common wildfire regime characteristics: mean annual area burned (AAB; ha), mean fire return interval for all successful ignitions anywhere in the watershed (FRI_0 ; yr^{-1}), mean fire return interval for fires >100 ha anywhere in the watershed (FRI_{100} ; yr^{-1}), and natural fire rotation (NFR; yr; calculated as the ratio of the area of the watershed to mean annual area burned; Heinzelman 1973). We also identified simulation years where more than 50% of model replicates had area burned >400 ha and overlaid these on climate and vegetation time series in order to evaluate climate and vegetation conditions in the proximity of higher wildfire activity for each scenario.

Analysis: vegetation summaries

We focused on trajectories of overstory and understory aboveground biomass and fine fuel loading. Daily data were aggregated to annual mean values for both the Fire and NoFire scenarios to match the resolution of area burned metrics. For each simulation year in the Fire

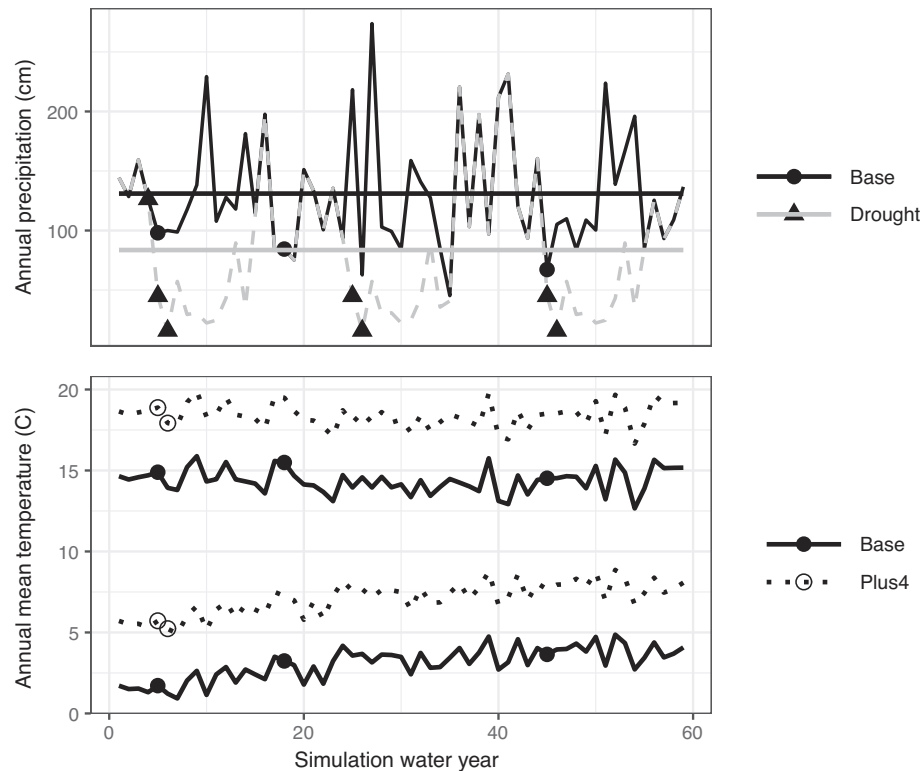


Fig. 2. Time series of annual climate variables for each climate scenario. Total water year precipitation and annual mean maximum and minimum temperatures. Mean precipitation across the simulation time period for each scenario is given as a solid horizontal line. Points represent years where >50% of independent Monte Carlo replicate simulations have >400 ha annual area burned.

scenarios, we calculated the first quartile, median, and third quartile of vegetation biomass across all replicates for each climate scenario, and graphed those across time. Graphs of vegetation biomass across all fire replicates are given in Appendix S1. We used a simple linear trend analysis to understand the trajectory of vegetation and fuels over time, and how that might differ among the scenarios. We calculated linear trends separately for each fire replicate and evaluated the distribution of the slope and intercepts for the fire and compared those with the NoFire run for each scenario. These were calculated after simulation year 10 to understand the trends after the first decade with wildfire.

Model corroboration

While WMFire and RHESSys have been through rigorous peer review and WMFire has been shown to robustly replicate spatial patterns

of fire spread and fire regime characteristics of different watersheds, it is also important to corroborate current results with patterns expected for a new watershed. We compared simulated values for mean annual area burned, fire return interval, and NFR to fire history reconstructions of the area to corroborate the model skill in reproducing fire regime characteristics (Table 1). We expected mean fire size between 120 and 300 ha, fire return interval of 1.2 yr (years between at least one fire across the entire watershed), and fire rotation between 8 and 24 yr. We also compared correlations between climate variables and area burned with those estimated in the region, with expected positive correlation between current-year temperature and area burned, negative correlation between current-year precipitation and area burned, and a weaker positive correlation between prior-year precipitation and area burned.

Table 1. Summary statistics for simulated variables.

Variable†	Fire scenario	Base	BasePlus4	Drought	DroughtPlus4
AAB‡ (120–300)	Fire	299.7 (41.0)	192.4 (34.1)	428.2 (105.7)	202.3 (58.5)
FRI ₁₀₀ §	Fire	4.9 (1.4)	5.5 (1.4)	5.9 (1.4)	6.8 (2.5)
FRI ₁ § (1.2)	Fire	1.05 (0.03)	1.02 (0.02)	1.15 (0.05)	1.15 (0.05)
NFR¶ (8–24)	Fire	22.4 (3.3)	35.4 (7.4)	16.5 (5.0)	37.1 (20.0)
Overstory#	NoFire	7.88	7.41	7.03	6.44
Overstory	Fire	5.5 (0.40)	6.8 (0.15)	4.4 (0.41)	5.6 (0.37)
Understory#	NoFire	0.94	0.95	0.35	0.33
Understory	Fire	0.56 (0.06)	0.59 (0.05)	0.27 (0.03)	0.27 (0.02)
Fine fuels#	NoFire	0.38	0.19	0.2	0.11
Fine fuels§	Fire	0.30 (0.01)	0.18 (0.003)	0.17 (0.008)	0.11 (0.003)

† For each variable with a comparable fire history, the reconstructed value is given in parentheses next to the variable name in the first column.

‡ Mean annual area burned (ha).

§ Fire return interval for fires of 100 ha, or any burned pixel (subscripts of 100 and 1, respectively; years).

¶ Natural fire rotation (years).

Vegetation variables (overstory, understory, and fine fuels) refer to mean biomass amounts (kg/m²).

|| A single value mean is given for the NoFire scenarios with one simulation. For simulations with fire, the mean values are given across replicates, with standard deviation in parentheses.

RESULTS

Short-term climate–fire correlations

Predicted log annual area burned was positively correlated with both annual and summer mean maximum temperature and negatively correlated with current-year annual precipitation (Fig. 3; Plus2 scenario results are given in Appendix S1: Fig. S1). The magnitudes of these correlations differed by scenario. Correlation between predicted log annual area burned and previous year precipitation was positive for the Base and Drought scenarios, was negative for BasePlus4, and centered at zero for the DroughtPlus4 scenario (Fig. 3). The general patterns of these correlations match those expected for the area (positive with current-year temperature, negative with current-year precipitation, and weaker positive with prior-year precipitation), corroborating the ability of the model to replicate short-term fire–climate relationships.

Fire regime characteristics: large fire years and climate

For all scenarios, there was a peak in predicted annual area burned within the first decade of the simulation following the fire-free spin-up period (Fig. 4; Plus2 scenarios and a graph of all model replicates are given in Appendix S1: Figs. S2, S3). In order, this peak

area burned was highest in the Drought scenario, followed by DroughtPlus2, DroughtPlus4, Base, BasePlus2, and BasePlus4.

After the initial decade of wildfire activity, all scenarios showed cycles of large fire years. The height of the peaks of wildfire area burned declined over time (Fig. 4). Years in the Base scenario with more than 50% of simulation replicates having predicted area burned >400 ha occurred in years with high to moderate mean temperatures and those of low annual precipitation that followed higher annual precipitation (Fig. 2), and had high to moderate fine fuel loading (Fig. 5). Regardless of Base or Drought precipitation, scenarios with higher mean temperature (Plus2, Plus4) had lower area burned with similar temporal patterns of occurrence (Fig. 4; Appendix S1: Figs. S2–S4). This indicated that the indirect long-term effect of increased mean temperature reducing productivity and increasing decomposition of fine fuels (Fig. 5) is stronger than the direct effect on wildfire of a mean increase in temperature of 4°C. Over the entire simulation period, DroughtPlus4 had less predicted mean annual area burned than Base (Table 1; Appendix S1: Fig. S4), associated with a reduction in biomass due to a larger initial pulse in wildfire (Fig. 4) followed by decreased productivity and increased decomposition of fine fuels (Fig. 5).

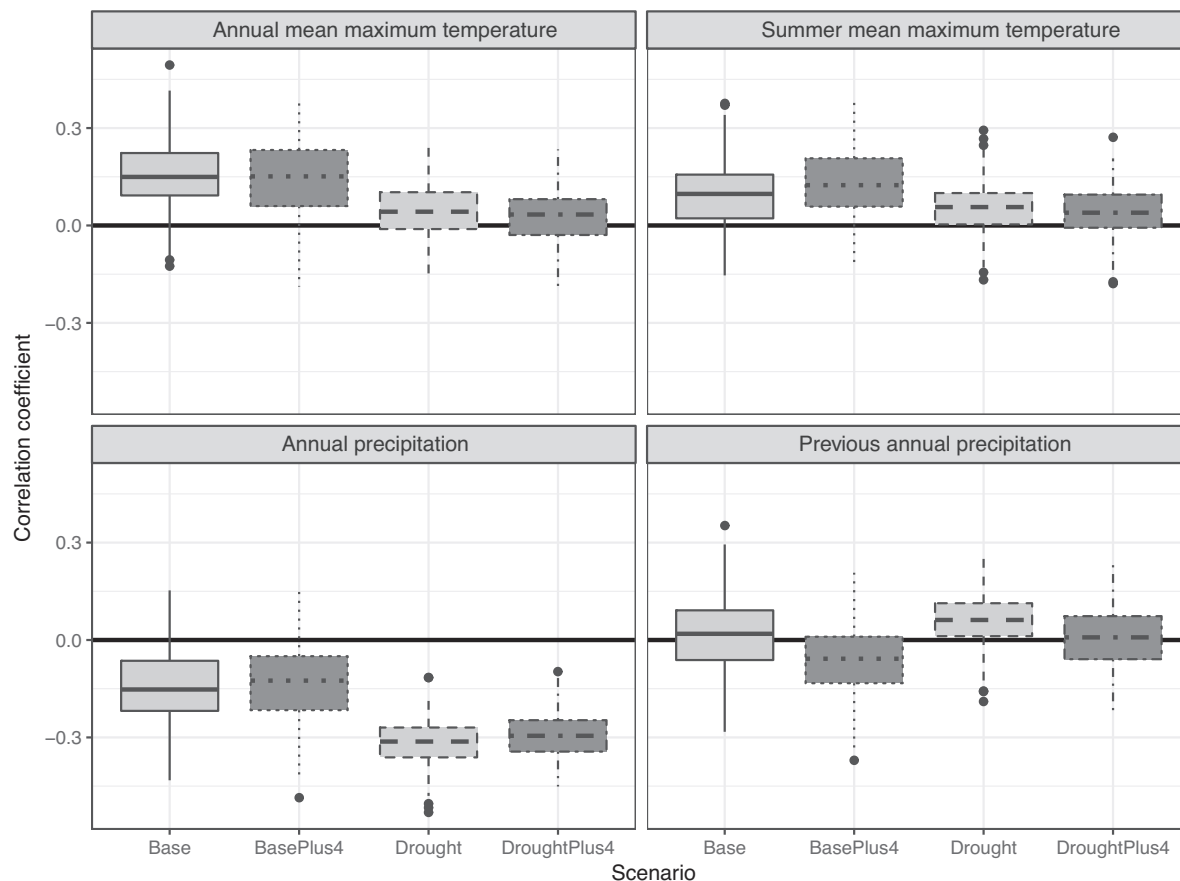


Fig. 3. Distribution of Pearson's correlation coefficients between annual area burned for years with a wildfire and climate variables. Distributions represent variability across 200 independent Monte Carlo replicates for each scenario.

Fire regime characteristics: fire return interval

The return interval for fire starts (any successful ignition that burns at least 1 pixel across the entire watershed) was shorter with an increase in mean temperature relative to baseline and was longer for drought relative to baseline (Table 1; Appendix S1: Fig. S4). The return interval for the occurrence of fire >100 ha across the entire watershed was similar among all scenarios, with larger variability for DroughtPlus4 (Table 1). The return interval was shortest for Base and longer for Drought, reflecting the synchrony of fire occurrence with simulated drought periods and longer fire-free intervals between droughts (Fig. 4). Generally, these fire regime statistics were similar to reconstructions in the study region (Kilgore and Taylor 1979, Scholl and Taylor 2010), corroborating the robustness of the

model system to reflect expected fire regime patterns.

Climate impact on vegetation and fine fuels without wildfire

Under baseline climate (Base) without wildfire (NoFire), both overstory and understory aboveground biomass were predicted to have an increasing trend (Fig. 5; Appendix S1: Fig. S10). Both overstory and understory aboveground biomass were reduced with drought relative to baseline (Table 1), with cycles of decline and recovery corresponding to the simulated drought periods (Figs. 2, 5). Proportional declines in biomass with drought were greater for understory vegetation than for overstory vegetation. Predicted overstory biomass was lower with increased temperature, indicating decreased

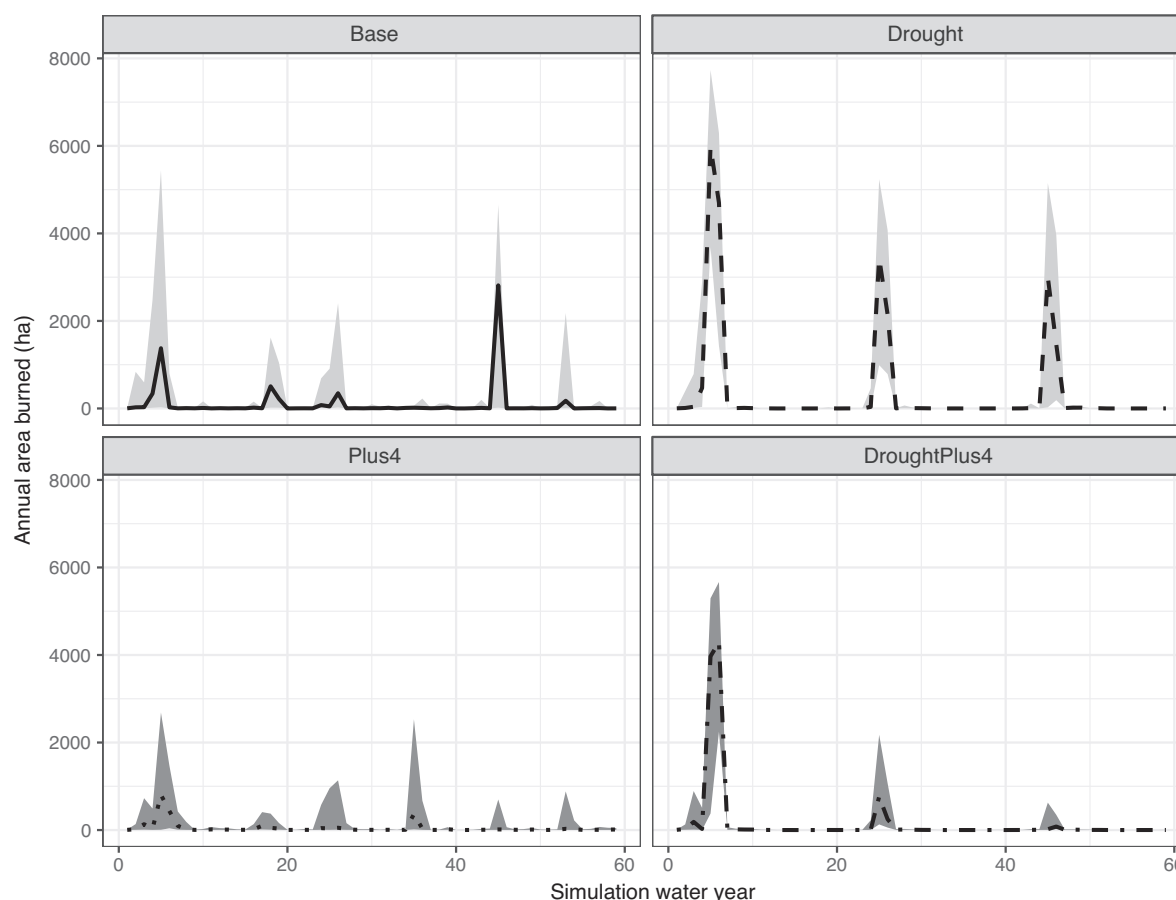


Fig. 4. Annual area burned (AAB; ha) with simulation water year for each climate scenario. The line represents median AAB across independent Monte Carlo replicate simulations for a given year, and the ribbon encompasses the first and third quartiles across all replicates.

productivity (Table 1). Temperature had a negligible effect on understory aboveground biomass.

Under baseline climate (Base) without wildfire (NoFire), fine fuels were predicted to have a slowly decreasing trend (Fig. 5; Appendix S1: Fig. S10). Drought substantially reduced fine fuel loading relative to baseline, likely due to reduced accumulation associated with lower aboveground biomass. For a given precipitation scenario, fine fuel loading decreased with increased mean temperature (Table 1).

Climate impact on vegetation with wildfire

With the return of fire to the system, there was a substantial reduction in predicted overstory biomass for all climate scenarios over the entire time series (Table 1). After the initial decline in overstory biomass associated with the first pulse

of wildfire, baseline precipitation scenarios had a stable and slightly increasing trajectory of overstory biomass (Fig. 5; Appendix S1: Fig. S10). This implies that with baseline precipitation there is recovery to a state that is resilient to subsequent wildfire after the initial wildfire pulse. The drought scenarios had a gradual decline in overstory biomass after the initial pulse of wildfire (Appendix S1: Fig. S10) with wide swings that had lower nadirs and lower peaks of overstory biomass than without wildfire. The lower overstory productivity in drought scenarios was exacerbated by the occurrence of wildfire during the drought period. The scenarios with increased mean temperature had more overstory biomass for a given precipitation scenario, associated with the reduced fire activity with increased mean temperature.

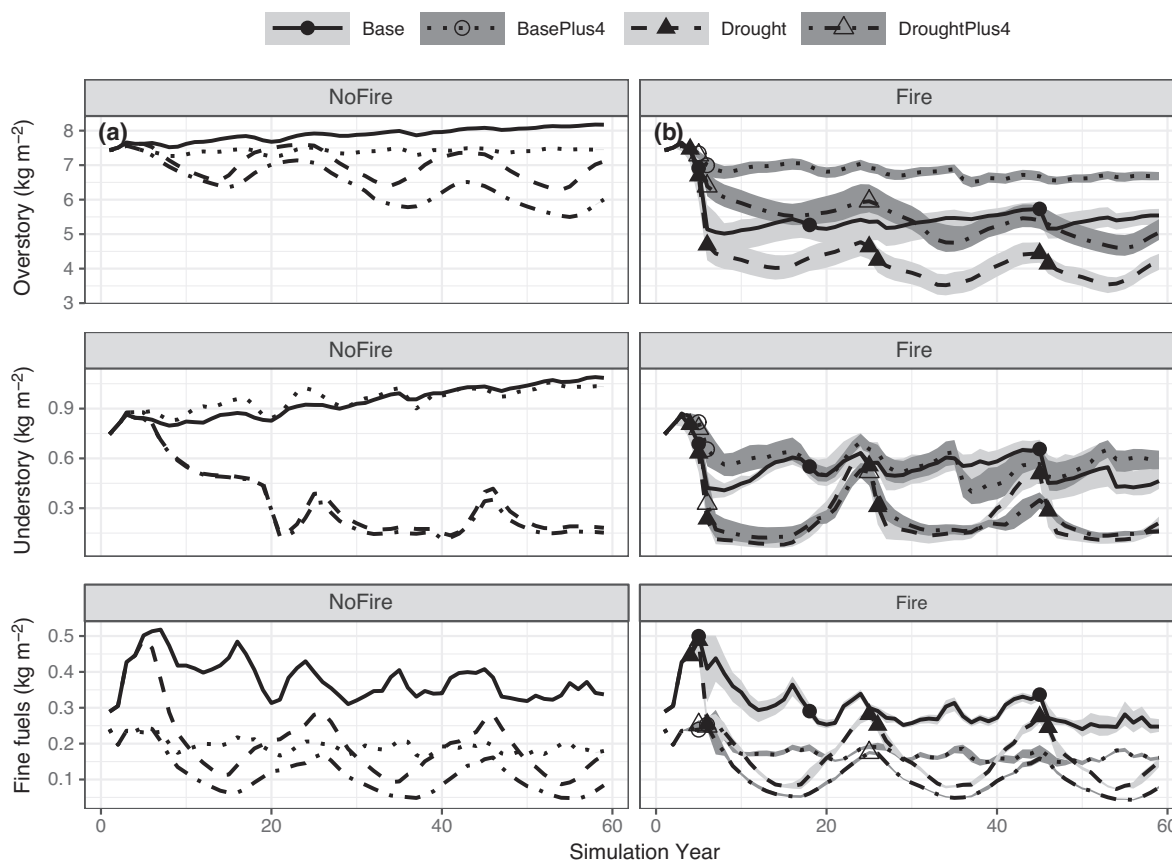


Fig. 5. Vegetation variables with simulation water year for each climate scenario. For NoFire simulations, a single time series of vegetation is given for each scenario. For Fire simulations, the lines represent median values across independent Monte Carlo (MC) replicate simulations for a given year for each scenario and the ribbon encompasses the first and third quartiles across all replicates for a given scenario. Points represent years where >50% of independent MC replicate simulations have >400 ha annual area burned for the scenario. Line types differentiate the scenarios and match those in other figures.

Predicted understory biomass was also less for baseline scenarios with fire than for NoFire (Fig. 5, Table 1). After the initial reduction associated with the first fire period, understory biomass under baseline scenarios (regardless of temperature) showed a stable trajectory indicating a steady-state condition, with periods of reduction and recovery associated with times of substantial wildfire events (Fig. 5). Understory biomass and litter in the drought scenarios had pronounced cycles of biomass loss and recovery corresponding to the effects of wildfire and the simulated drought periods. The initial reduction associated with the first fire period reduced understory biomass well below that in the NoFire scenario. Peak biomass in those periods

of recovery exceeded peak biomass in the NoFire scenario, possibly enabled by reduced overstory biomass. There was little difference in understory biomass associated with increased temperature for both Base and Drought (Fig. 5, Table 1).

Predicted fine fuel loading was less for the baseline scenarios with Fire relative to NoFire (Fig. 5, Table 1). There was an initial steep reduction following the first fire period, then a steady and slow decline in fine fuel loading for the remainder of the simulation. With drought, the cycle of litter reduction and recovery followed a similar trajectory to the NoFire scenario, with lower nadirs and higher peaks (Fig. 5). Regardless of Base or Drought, higher temperature was

associated with lower fine fuel loading across the simulation period (Table 1).

DISCUSSION

The bidirectional coupling of wildfire with ecohydrology accomplished by RHESys-WMFire has illuminated feedbacks between climate and wildfire on landscape-level patterns of vegetation structure and fuels. The model results presented here have a particular context worthy of highlighting. The simulations began with a fire-free spin-up to allow dynamics to stabilize, representing the condition of the forest without recent wildfire and acting as a surrogate for fire exclusion in the watershed. Then, fires were tested for start and spread without suppression. This simulation context is akin to a management strategy of allowing wildland fires to burn (Parsons et al. 1986) with no further fuel management. The simulations occurred within a single watershed, such that wildfires interacted with each other in a relatively limited area. This is in contrast to a regional empirical evaluation of climate–fire relationships where individual wildfires may not interact and fire size is not inhibited by watershed boundaries. Ignition sources were not assumed to be limiting, with an average of two ignition locations tested every month for fire start.

Given this simulation context, all climate scenarios predicted an initial pulse of area burned within a decade of the start of the simulation, consistently the highest area burned across all scenarios except Base (Fig. 4). This period of high AAB was associated with the highest level of fine fuel loading (Fig. 5) that developed over a fire-free spin-up, the lowest precipitation amounts in the first decade, and above-average mean maximum temperature (Fig. 2). This pulse of area burned was higher in the DroughtPlus4 scenario compared with Base and even higher with the Drought scenario. These patterns are consistent with recent trends of increased area burned in the Western United States that correlate with temperature and precipitation (Holden et al. 2018) and provides an example of the role of weather on fire intensity at short timescales (same year) when fuels are readily available.

We will interpret these results in the energy-regulation-scale framework proposed by McKenzie

et al. (2011, see also Newman et al. 2019) that considers transfers between potential and kinetic energy, their distribution across scales, and how those are regulated in the context of wildfire and fire regimes (Fig. 6). In this framework, vegetation and fuel biomass represent potential energy for a wildfire. There is a separation of timescales associated with energy transfers in wildfire regimes (Drossel and Schwabl 1992), where energy is released in a conversion from potential to kinetic energy over short time frames through the process of combustion. Potential energy subsequently builds over longer timescales through vegetation succession and productivity. Climate regulates both of these conversions at a similar separation of timescales. Here, we consider each of these timescales in turn.

Short timescales (same year) and the direct effect of climate

Our modeling results corroborate the empirical evidence for the regulation by climate of the short-term conversion of potential to kinetic energy. Across the entire simulation period for a given climate scenario, predicted annual area burned was positively correlated with same-year mean maximum temperature, negatively correlated with same-year precipitation, and, depending on scenario, weakly positively correlated with previous year precipitation (Fig. 3). The magnitudes of these correlations varied among the climate scenarios. These patterns in the correlations predicted by the simulation system are consistent with empirical studies of this area and with the observation that the direct effect of climate on wildfire depends on the long-term climate context that drives fuel and vegetation dynamics (Littell et al. 2009, 2018, Parisien and Moritz 2009, Krawchuk and Moritz 2011, McKenzie and Littell 2017). The direct effect of temperature was less in the drought scenarios, where the direct effect of climate was more driven by the same-year precipitation (Fig. 3) and the onset of the simulated drought period.

Our results indicate that increased drought and temperature will increase area burned relative to baseline for a location not burned previously. Both Drought and DroughtPlus4 showed larger area burned in the first decade of the simulation than Base (Fig. 4). Increasing frequency and severity of drought will increase area burned

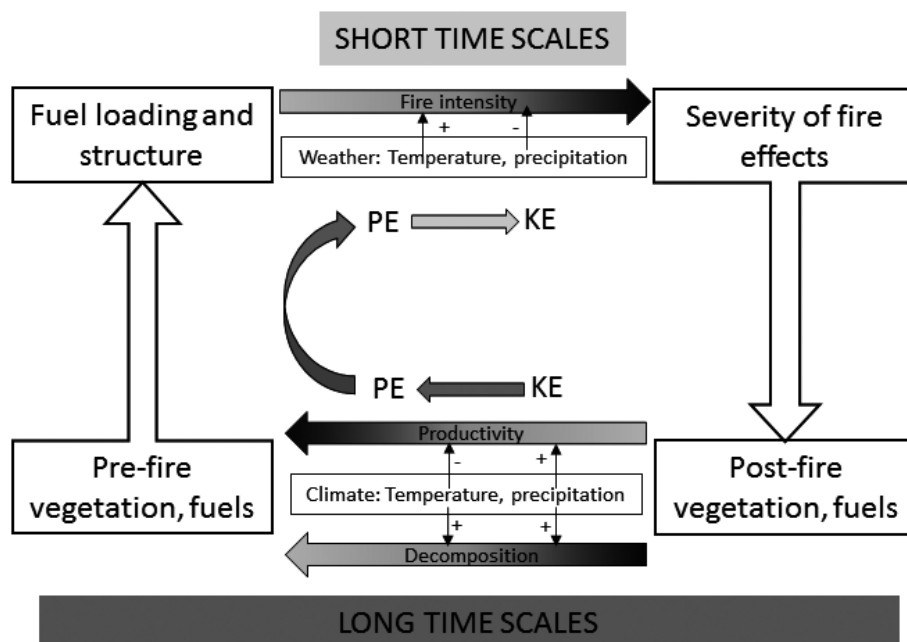


Fig. 6. Landscape fire cycle adapted from McKenzie et al. (2011: Fig. 1.3). Climate regulates the conversion of kinetic to potential energy through development of vegetation and fuels over longer timescales. Over these scales in watersheds of the Sierra Nevada in California, increased temperature decreases productivity and increases decomposition. Increased precipitation both increases productivity and potentially increases decomposition. Increased productivity increases biomass and potential energy, whereas increased decomposition decreases biomass and potential energy. Weather regulates the conversion of potential energy to kinetic energy for a given fuel loading and structure, thereby regulating fire behavior and the severity of fire effects. Over shorter timescales, increased temperature increases fire intensity and increased precipitation decreases it. Dimensions of climate and weather can have counteracting effects on wildfire and fire regimes when considered both over long and short timescales.

and fire hazard. Over regional scales of large area, this indicates elevated fire hazard associated with climate change relative to baseline.

These results also illuminate a limitation of using empirical studies to project long-term climate effects on future wildfire regimes. The distributions of correlations between same-year climate variables and annual area burned for the Base and BasePlus4 climate scenarios were almost indistinguishable (Fig. 3), both supporting the simple maxim hotter and drier = more fire. If the correlations for the base scenario were used to project future wildfire under a simple climate warming scenario with no change in precipitation, increased area burned would be predicted. Yet, the coupled simulation system predicted lower area burned over the entire simulation for the BasePlus4 scenario than Base.

While over the first decade the DroughtPlus4 scenario had a larger pulse of annual area burned (Fig. 4), over the entire simulation period it had a lower mean annual area burned than Base (Table 1). Within a watershed, the longer timescale regulation by climate of the conversion of kinetic to potential energy via vegetation and fuel development (Fig. 6) gives context to the short-term regulation of fire activity by climate and the effects can be confounding.

Long timescales (years to decades) and the indirect effect of climate

At first glance, the lower predicted mean AAB associated with increased temperature for a given precipitation scenario (Table 1; Appendix S1: Fig. S4) seems contradictory to the current understanding of wildfire–climate relationships

in this region. What it demonstrates, however, is the interaction of long-term indirect effects of climate through the accumulation of potential energy with short-term direct effects on regulating the spread of wildfire. The study area has been described to be in the middle of a gradient between where same-year climate effects dominate (forests) and where antecedent climate effects on fine fuel development dominate (deserts, grasslands, and shrublands; McKenzie and Littell 2017). Net fuel loading is a balance of increases through litterfall and mortality and decreases through combustion and decomposition (Peterson et al. 2015). Previous work has shown that forests in this region below around 2200 m in elevation tend to be water-limited and have a negative relationship between net primary productivity and temperature (Tague et al. 2009, Trujillo et al. 2012). Decomposition rate of fine fuels increases with temperature (Moore 1986, Gholz et al. 2000), and the temperature effect on decomposition is independent of moisture (Qi and Xu 2001). Absent wildfire, the model predicted lower overstory productivity and fine fuel loading with long-term increased mean temperature (Fig. 5, Table 1). With warming, the input to fine fuels decreases while the loss of fine fuels to decomposition increases (Fig. 6). This shifts the watershed further to one that is resource constrained (Krawchuk and Moritz 2011), reducing the potential energy available for the wildfire and weakening the direct effects of climate on wildfire.

The proposition that long-term effects of climate on fuel loading may overwhelm short-term correlations between climate and wildfire activity is not new. In Spain, long-term past climate warming may already be associated with a moderation in area burned, potentially due to the effect of warming on fine fuel accumulation (Turco et al. 2014). Batllori et al. (2013) found that warmer-drier scenarios tended to lower fire probability across much of the Mediterranean-type biome, which they attributed to exacerbated fuel limitation. In a modeling study in a eucalypt forest, Matthews et al. (2012) found a decrease in predicted fine fuel loading with climate warming that reduced predicted rate of spread. When fuels were not varied (a common feature of climate–fire studies), predicted rate of spread increased with climate warming. These feedbacks between

climate and fuel development and how those confound climate–fire relationships are not well understood (Flannigan et al. 2009) and the representation of such biological processes in models varies and is often inadequate (Harris et al. 2016). Predicted woody fuel accumulations can be sensitive to decomposition rate (Kennedy et al. 2021), representing a source of uncertainty that is particularly important if a simulation system is used to predict future woody fuels and fire hazard.

Another important link between the direct role of climate to regulate the conversion of potential energy to kinetic energy over short timescales and its role in regulating the long-term accumulation of potential energy is the wildfire itself. Wildfire can be self-limiting, with prior fires constraining the spread and severity of later fires (Collins et al. 2009, Stevens-Rumann et al. 2016). Historically, dry forests in this region experienced frequent low-severity fire (Kilgore and Taylor 1979), which maintained stand structures resilient to subsequent wildfire (Scholl and Taylor 2010). There is evidence that, compared with historical patterns and despite recent increases, area burned in many parts of the Western United States is still in deficit (Parks et al. 2015). An era of fire suppression modified these forest structures from ones in which fuel might be limiting and discontinuous to ones of abundant fuel with connectivity both horizontally and vertically (Covington and Moore 1994, Hessburg et al. 2005), providing ample potential energy for wildfire. Recent observations of fire–climate relationships are often in the context of unusually abundant fuels where resources are no longer constraining wildfire, and in this context direct effects of climate tend to dominate (Krawchuk and Moritz 2011). The initial pulses of wildfire we observed in all simulations reflect this, where they coincided with the first occurrence of below-average precipitation (Fig. 2). Some have indicated that fuels may ultimately be more important than the direct impact of climate in some areas (Lenihan et al. 2003, Honig and Fulé 2012, Parks et al. 2018) and that the relative effects of climate and previous fire suppression on fire regimes depend on whether the area was historically fuel or flammability limited (Hanan et al. 2021).

Within a watershed, the self-limiting property of wildfire is more important than might be

observed at larger scales, having implications for local-scale wildfire and fuel management. There was substantial variability in trajectories of fire and vegetation across individual MC replicates (Appendix S1: Figs. S3, S6–S8), yet this self-limiting property is evident in the general trends across replicate Fire simulations. In the Base scenario after the first period of wildfire, the overstory time series tended to stabilize to a near steady-state behavior that, on average, paralleled the NoFire simulations except with lower magnitude biomass (Fig. 5; Appendix S1: Fig. S10). The understory time series tended to have a more negative trajectory with Fire than in the NoFire simulations, indicating that frequent wildfire reduced ladder fuels in this system and prevented wildfire from entering the overstory. Once wildfire was introduced back into the system, the watershed seemed to settle into a state that may indicate resilience to subsequent wildfires (Peterson 2002, Scholl and Taylor 2010, Moritz et al. 2011). In the Drought scenarios, the self-limiting property of wildfire was evident by the lower peak in area burned for each subsequent drought (Fig. 4). In the Drought scenarios, the overstory vegetation also paralleled that of the NoFire scenarios with lower overall magnitude evidenced by a lower intercept in the trend analysis (Appendix S1: Fig. S9).

The apparent stabilization of vegetation patterns in the Drought scenarios does not mean, however, that the future state of the vegetation would necessarily meet management objectives under climate change. Wildfire and drought combined strongly reduced overstory biomass (Fig. 5, Table 1), implying a change in the structure of the forest under their combined effects. Reduction in overstory biomass could correspond to a shift to more grasses and shrubs, which might increase future fire, as predicted by Lenihan et al. (2003). Vegetation management that supports development of the overstory canopy in times of water stress might help counter these effects.

The modeling context and limitations

The results presented in this paper are limited, as are all model-based predictions of future conditions, in that models do not project what the future will be, but rather what the future might be given the assumptions and structures

underlying the model structure and data inputs. As with all modeling studies, the projections should not be considered absent in this model uncertainty context.

The long-term temperature effects of climate change might be over-represented in these simulations. Climate change is not expected to increase mean temperature as high as 4°C immediately in a step function, but rather show an increasing trend in temperature that results in an eventual mean as high as 4°C above current (Cayan et al. 2007). The temperature effects may not be uniform but rather vary seasonally. The immediate effects on productivity and fuel accumulation predicted by our simulations may not manifest in such a dramatic fashion, but rather impact fuels more gradually as mean temperature increases. Long-term past climate warming in some regions, however, may already be associated with a moderation in area burned due to its effect on fine fuel accumulation (Turco et al. 2014). We also see smaller but similar effects with a uniform 2°C warming (Appendix S1).

Wildfire requires not only that the fuel and weather conditions are suitable for burning, but also an ignition source to start the fire. In these simulations, the coincidence of fire activity immediately with the initial period of reduced precipitation may be an artifact of our assumption that ignition sources are not limiting. In reality, ignitions are highly stochastic and difficult to predict. For a given watershed, there may be multiple years of climate-suitable conditions without an ignition source. These simulations should be interpreted then as representing the time when an ignition does coincide with climate conditions suitable for wildfire.

Models are particularly useful when they inspire new hypotheses and directions for empirical research. These model predictions demonstrate that the short- and long-term effects of climate change on wildfire may differ, and we require new empirical analyses that assess these predictions in real-world settings. For example, global analyses have found variable patterns of increased and decreased area burned in different regions (Riaño et al. 2007). An empirical analysis could test whether long-term climate predicts these differences in the changes in area burned (Turco et al. 2014). Furthermore, these results demonstrate that landscape memory (Peterson

2002) is important to explain wildfire regimes at intermediate scales. Statistically, this means that wildfire is autocorrelated because it is a function of both current and past conditions. Standard empirical models treat observations as independent of each other, but recent studies have started to include the spatial autocorrelation structure in explaining burn severity patterns in individual wildfires (Wimberly et al. 2009, Prichard and Kennedy 2014, Stevens-Rumann et al. 2016, Prichard et al. 2020) and have found that the spatial autocorrelation itself explains much of the variability in burn severity (Prichard et al. 2020). It would also be worthwhile to explore temporal autocorrelation structures or some other quantitative measure of landscape memory in climate–wildfire relationships.

The climate scenarios in this study are not meant to represent climate futures predicted by emissions pathways and GCMs. Rather, they decompose potential climate futures in a factorial design intended to explore separate and combined effects of climate warming with changes to precipitation in the form of increased prolonged drought. The simplicity of these climate scenarios allowed us to track the long-term regulation by climate of the conversion of kinetic to potential energy and improve our understanding of feedbacks in the climate/vegetation/fuels/wildfire system. The fire regimes predicted here represent those relationships. For forest management planning and applications, future work will incorporate climate projections from ensembles of GCMs and emissions scenarios with simulations of fuels management.

Management implications

These results support the conclusion that in the near-term we can continue to expect increased area burned, particularly in times of reduced precipitation. If drought is more frequent and severe with climate change, then these periods of increased area burned may also become more frequent over regional scales. Returning some landscapes to a resource-constrained condition through mechanical fuel treatments and prescribed burning may ameliorate some of these effects and help to maintain fire-resilient landscapes. Over the long-term, planning should account for the effects of future climate not only on fire weather but also on the

regulation of biomass and fuel accumulation that provide potential energy for wildfire. The pattern of reduced fuels we predicted for the study watershed would not necessarily be expected everywhere in this region. For example, at higher elevations, increased temperature is predicted to increase productivity (Tague et al. 2009) and the effects on fuels will probably differ from those found in this study. Hanan et al. (2021) propose long-term average soil moisture as a simple metric to discern whether an area is expected to be fuel or flammability-limited. Good planning requires understanding the separation of time-scales that drive wildfire, both the short-term and long-term impacts of climate on vegetation and wildfire and the feedbacks among them. The maxim that hotter and drier = more fire can be both true and false depending on scale, and for land management we need a better understanding of where, how, and why.

ACKNOWLEDGMENTS

The research was funded by the National Science Foundation Science (EAR-1520847), Engineering and Education for Sustainability Award Number 1520847, and the U.S. Forest Service Pacific Northwest Research Station. Kevin Pranoto generated the precipitation drought scenario and Don McKenzie provided valuable feedback on an earlier draft. This manuscript was further improved by comments from two anonymous reviewers.

LITERATURE CITED

- Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences of the United States of America* 113:11770–11775.
- Aubry-Kientz, M., and E. V. Moran. 2017. Climate impacts on tree growth in the Sierra Nevada. *Forests* 8:30–33.
- Bart, R. R., M. C. Kennedy, C. L. Tague, and D. McKenzie. 2020. Integrating fire effects on vegetation carbon cycling within an ecohydrologic model. *Ecological Modelling* 416:108880.
- Bart, R. R., C. L. Tague, and M. A. Moritz. 2016. Effect of tree-to-shrub type conversion in lower montane forests of the Sierra Nevada (USA) on streamflow. *PLOS ONE* 11:1–19.
- Battilori, E., M. A. Parisien, M. A. Krawchuk, and M. A. Moritz. 2013. Climate change-induced shifts in fire

- for Mediterranean ecosystems. *Global Ecology and Biogeography* 22:1118–1129.
- Berg, N., and A. Hall. 2015. Increased interannual precipitation extremes over California under climate change. *Journal of Climate* 28:6324–6334.
- Cayan, D. R., E. P. Maurer, M. D. Dettinger, M. Tyree, and K. Hayhoe. 2007. Climate change scenarios for the California region. *Climatic Change* 87(Suppl 1): S21–S42.
- Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. Wagtendonk, 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: changes since Euro-American settlement. *Journal of Forestry* 92:39–47.
- Dixon, G. E. 2012. Essential FVS: a user's guide to the Forest Vegetation Simulator. Internal Report. Pages 226. USDA Forest Service, Forest Management Service Center, Ft Collins, Colorado, USA.
- Drossel, B., and F. Schwabl. 1992. Self-organized critical forest-fire model. *Physical Review Letters* 69:1629–1632.
- Flannigan, M. D., M. A. Krawchuk, W. J. de Groot, M. B. Wotton, and L. M. Gowman. 2009. Implications of changing climate for global wildland fire. *International Journal of Wildland Fire* 18:483–507.
- Garcia, E. S., and C. L. Tague. 2015. Subsurface storage capacity influences climate – evapotranspiration interactions in three western United States catchments. *Hydrology and Earth System Sciences* 19:4845–4858.
- Garcia, E. S., C. L. Tague, and J. S. Choate. 2013. Influence of spatial temperature estimation method in ecohydrologic modeling in the Western Oregon Cascades. *Water Resources Research* 49:1611–1624.
- Garcia, E. S., C. L. Tague, and J. S. Choate. 2016. Uncertainty in carbon allocation strategy and ecophysiological parameterization influences on carbon and streamflow estimates for two western US forested watersheds. *Ecological Modelling* 342:19–33.
- Gholz, H. L., D. A. Wedin, S. M. Smitherman, M. E. Harmon, and W. J. Parton. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology* 6:751–765.
- Gustafson, E. J. 2013. When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. *Landscape Ecology* 28:1429–1437.
- Hanan, E. J., J. Ren, C. L. Tague, C. A. Kolden, J. T. Abatzoglou, R. R. Bart, M. C. Kennedy, M. Liu, and J. C. Adam. 2021. How climate change and fire exclusion drive wildfire regimes at actionable scales. *Environmental Research Letters* 16, 024051.
- Hannah, D. M., J. P. Sadler, and P. J. Wood. 2007. Hydroecology and ecohydrology: challenges and future prospects. Pages 421–429 in P. Wood, D. M. Hannah, and J. P. Sadler, editors. *Hydroecology and ecohydrology: Past, present, and future*. John Wiley and Sons, West Sussex, UK.
- Harris, R. M. B., T. A. Remenyi, G. J. Williamson, N. L. Bindoff, and D. M. J. S. Bowman. 2016. Climate–vegetation–fire interactions and feedbacks: trivial detail or major barrier to projecting the future of the Earth system? *Wiley Interdisciplinary Reviews: Climate Change* 7:910–931.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3:329–382.
- Hessburg, P., J. Agee, and J. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. *Forest Ecology and Management* 211:117–139.
- Holden, Z. A., A. Swanson, C. H. Luce, W. M. Jolly, M. Maneta, J. W. Oyster, D. A. Warren, R. Parsons, and D. Affleck. 2018. Decreasing fire season precipitation increased recent western US forest wildfire activity. *Proceedings of the National Academy of Sciences of the United States of America* 115: E8349–E8357.
- Honig, K. A., and P. Z. Fulé. 2012. Simulating effects of climate change and ecological restoration on fire behaviour in a south-western USA ponderosa pine forest. *International Journal of Wildland Fire* 21:731–742.
- Johnson, C., S. Chhin, and J. Zhang. 2017. Effects of climate on competitive dynamics in mixed conifer forests of the Sierra Nevada. *Forest Ecology and Management* 394:1–12.
- Keane, R. E., G. J. Cary, I. D. Davies, M. D. Flannigan, R. H. Gardner, S. Lavorel, J. M. Lenihan, C. Li, and T. S. Rupp. 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. *Ecological Modelling* 179:3–27.
- Kennedy, M. C. 2019. Experimental design principles to choose the number of Monte Carlo replicates for stochastic ecological models. *Ecological Modelling* 394:11–17.
- Kennedy, M. C., M. C. Johnson, and S. Harrison. 2021. Model predictions of post-wildfire woody fuel succession and fire behavior are sensitive to fuel dynamics parameters. *Forest Science* 67:30–42.
- Kennedy, M. C., and D. McKenzie. 2010. Using a stochastic model and cross-scale analysis to

- evaluate controls on historical low-severity fire regimes. *Landscape Ecology* 25:1561–1573.
- Kennedy, M. C., and D. McKenzie. 2017. Uncertainty and complexity tradeoffs when integrating fire spread with hydroecological projections. Pages 231–244 in K. Riley, P. Webley, and M. Thompson, editors. *Natural hazard uncertainty assessment: Modeling and decision support*. Geophysica. John Wiley and Sons, West Sussex, UK.
- Kennedy, M. C., D. McKenzie, C. Tague, and A. L. Dugger. 2017. Balancing uncertainty and complexity to incorporate fire spread in an eco-hydrological model. *International Journal of Wildland Fire* 26:706–718.
- Kilgore, B. M., and D. Taylor. 1979. Fire history of a sequoia-mixed conifer forest. *Ecology* 60:129–142.
- Krawchuk, M. A., and M. A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 92:121–132.
- Lenihan, J. M., R. Drapek, D. Bachelet, and R. P. Neilson. 2003. Climate change effects on vegetation distribution, carbon, and fire in California. *Ecological Applications* 13:1667–1681.
- 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.
- Littell, J. S., D. McKenzie, H. Y. Wan, and S. A. Cushman. 2018. Climate change and future wildfire in the Western United States: an ecological approach to nonstationarity. *Earth's Future* 6:1097–1111.
- Matthews, S., A. L. Sullivan, P. Watson, and R. J. Williams. 2012. Climate change, fuel and fire behaviour in a eucalypt forest. *Global Change Biology* 18:3212–3223.
- McIntyre, P. J., J. H. Thorne, C. R. Dolanc, A. L. Flint, L. E. Flint, M. Kelly, and D. D. Ackerly. 2015. Twentieth-century shifts in forest structure in California: denser forests, smaller trees, and increased dominance of oaks. *Proceedings of the National Academy of Sciences of the United States of America* 112:1458–1463.
- McKenzie, D., and M. Kennedy. 2012. Power laws reveal phase transitions in landscape controls of fire regimes. *Nature Communications* 3:726. <https://doi.org/10.1038/ncomms1731>
- McKenzie, D., and J. S. Littell. 2017. Climate change and the eco-hydrology of fire: Will area burned increase in a warming western USA. *Ecological Applications* 27:26–36.
- McKenzie, D., C. Miller, and D. Falk. 2011. Toward a theory of landscape fire. Pages 3–25 in D. McKenzie, C. Miller, and D. Falk, editors. *The landscape ecology of fire*. Ecological studies volume 213, Analysis and synthesis. Springer, New York, New York, USA.
- Moore, A. M. 1986. Temperature and moisture dependence of decomposition rates of hardwood and coniferous leaf litter. *Soil Biology and Biochemistry* 18:427–435.
- Moritz, M. A., P. F. Hessburg, and N. A. Povak. 2011. Chapter 3 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.
- Newman, E. A., M. C. Kennedy, D. A. Falk, and D. McKenzie. 2019. Scaling and complexity in landscape ecology. *Frontiers in Ecology and Evolution* 7:1–16.
- Parisien, M.-A., and M. A. Moritz. 2009. Environmental controls on the distribution of wildfire at multiple spatial scales. *Ecological Monographs* 79:127–154.
- Parks, S., S. Dobrowski, and M. Panunto. 2018. What drives low-severity fire in the southwestern USA? *Forests* 9:165.
- Parks, S. A., C. Miller, M. A. Parisien, L. M. Holsinger, S. Z. Dobrowski, and J. Abatzoglou. 2015. Wildland fire deficit and surplus in the western United States, 1984–2012. *Ecosphere* 6:1–13.
- Parsons, D. J., D. M. Graber, J. K. Agee, and J. W. Van Wagendonk. 1986. Natural fire management in National Parks. *Environmental Management* 10:21–24.
- Peterson, G. D. 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems* 5:329–338.
- Peterson, D. W., E. K. Dodson, and R. J. Harrod. 2015. Post-fire logging reduces surface woody fuels up to four decades following wildfire. *Forest Ecology and Management* 338:84–91.
- Prichard, S. J., and M. C. Kennedy. 2014. Fuel treatments and landform modify landscape patterns of burn severity in an extreme fire event. *Ecological Applications* 24:571–590.
- Prichard, S. J., M. C. Kennedy, C. S. Wright, J. B. Cronan, and R. D. Ottmar. 2017. Predicting forest floor and woody fuel consumption from prescribed burns in southern and western pine ecosystems of the United States. *Forest Ecology and Management* 405:328–338.
- Prichard, S. J., N. A. Povak, M. C. Kennedy, and D. W. Peterson. 2020. Fuel treatment effectiveness in the context of landform, vegetation, and large, wind-driven wildfires. *Ecological Applications* 30:1–22.
- Qi, Y., and M. Xu. 2001. Separating the effects of moisture and temperature on soil CO₂ efflux in a

- coniferous forest in the Sierra Nevada mountains. *Plant and Soil* 237:15–23.
- Riaño, D., J. A. Moreno Ruiz, D. Isidoro, and S. L. Ustin. 2007. Global spatial patterns and temporal trends of burned area between 1981 and 2000 using NOAA-NASA Pathfinder. *Global Change Biology* 13:40–50.
- Scholl, A. E., and A. H. Taylor. 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. *Ecological Applications* 20:362–380.
- Son, K., and C. Tague. 2019. A top–down soil moisture and sap flux sampling design of a rain–snow transition mountain watershed. *Hydrological Processes* 33:1553–1568.
- Stephenson, N. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* 25:855–870.
- Stevens-Rumann, C. S., S. J. Prichard, E. K. Strand, and P. Morgan. 2016. Prior wildfires influence burn severity of subsequent large fires. *Canadian Journal of Forest Research* 46:1375–1385.
- Swann, A. L., I. Y. Fung, and J. C. Chiang. 2012. Mid-latitude afforestation shifts general circulation and tropical precipitation. *Proceedings of the National Academy of Sciences USA* 109:712–716.
- Swain, D. L., B. Langenbrunner, J. D. Neelin, and A. Hall. 2018. Increasing precipitation volatility in twenty-first-century California. *Nature Climate Change* 8:427–433.
- Tague, C., and L. Band. 2004. RHESys: regional hydro-ecologic simulation system—An object-oriented approach to spatially distributed modeling of carbon, water, and nutrient cycling. *Earth Interactions* 8:1–42.
- Tague, C. L., J. S. Choate, and G. Grant. 2013. Parameterizing sub-surface drainage with geology to improve modeling streamflow responses to climate in data limited environments. *Hydrology and Earth System Sciences* 17:341–354.
- Tague, C., K. Heyn, and L. Christensen. 2009. Topographic controls on spatial patterns of conifer transpiration and net primary productivity under climate warming in mountain ecosystems. *Ecohydrology* 2:541–554.
- Trujillo, E., N. P. Molotch, M. L. Goulden, A. E. Kelly, and R. C. Bales. 2012. Elevation-dependent influence of snow accumulation on forest greening. *Nature Geoscience* 5:705–709.
- Tsamir, M., S. Gottlieb, Y. Preisler, E. Rotenberg, F. Tatarinov, D. Yakir, C. Tague, and T. Klein. 2019. Stand density effects on carbon and water fluxes in a semi-arid forest, from leaf to stand-scale. *Forest Ecology and Management* 453:117573.
- Turco, M., J. Bedia, F. Di Liberto, P. Fiorucci, J. Von Hardenberg, N. Koutsias, M. C. Llasat, F. Xystakis, and A. Provenzale. 2016. Decreasing fires in Mediterranean Europe. *PLOS ONE* 11:e0150663.
- Turco, M., M. C. Llasat, J. von Hardenberg, and A. Provenzale. 2014. Climate change impacts on wildfires in a Mediterranean environment. *Climatic Change* 125:369–380.
- Vicente-Serrano, S. M., J. J. Camarero, J. Zabalza, G. Sangüesa-Barreda, J. I. López-Moreno, and C. L. Tague. 2015. Evapotranspiration deficit controls net primary production and growth of silver fir: implications for Circum-Mediterranean forests under forecasted warmer and drier conditions. *Agricultural and Forest Meteorology* 206:45–54.
- 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.
- Wimberly, M. C., M. A. Cochrane, A. D. Baer, and K. Pabst. 2009. Assessing fuel treatment effectiveness using satellite imagery and spatial statistics. *Ecological Applications* 19:1377–1384.
- Yeh, H.-Y., and L. C. Wensel. 2000. The relationship between tree diameter growth and climate for coniferous species in northern California. *Canadian Journal of Forest Research* 30:1463–1471.

DATA AVAILABILITY

Data resulting from model simulations are available on Figshare: <https://doi.org/10.6084/m9.figshare.12915368>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3657/full>