Boisramé *et al. Fire Ecology* (2022) 18:8
https://doi.org/10.1186/s42408-022-00129-4

Fire Ecology

ORIGINAL RESEARCH

Open Access

Trends in western USA fire fuels using historical data and modeling

Gabrielle F. S. Boisramé[1], Timothy J. Brown[2*] and Dominique M. Bachelet[3]

Abstract

Background: Recent increases in wildfire activity in the Western USA are commonly attributed to a confluence of factors including climate change, human activity, and the accumulation of fuels due to fire suppression. However, a shortage of long-term forestry measurements makes it difficult to quantify regional changes in fuel loads over the past century. A better understanding of fuel accumulation is vital for managing forests to increase wildfire resistance and resilience. Numerical models provide one means of estimating changes in fuel loads, but validating these models over long timescales and large geographic extents is made difficult by the scarcity of sufficient data. One such model, MC2, provides estimates of multiple types of fuel loads and simulates fire activity according to fuel and climate conditions. We used the Forest Inventory and Analysis Database (FIADB) observed data to validate MC2 estimates of fuel load change over time where possible.

Results: We found that the MC2 model's accuracy varied geographically, but at a regional scale the distributions of changes in fuel loads were similar to distributions of FIADB values. While FIADB data provided consistent measurement types across a wide geographic area, usable data only spanned approximately 30 years. We therefore supplemented this quantitative validation with a qualitative comparison to data that covered less area, but for much longer time spans: long-term forestry plots outside of the FIA plot network and repeat photography studies. Both model results and long-term studies show increases in fuel loads over the past century across much of the western USA, with exceptions in the Pacific Northwest and other areas. Model results also suggest that not all of the increases are due to fire suppression.

Conclusions: This model validation and aggregation of information from long-term studies not only demonstrate that there have been extensive fuel increases in the western USA but also provide insights into the level of uncertainty regarding fire suppression's impact on fuel loads. A fuller understanding of changing fuel loads and their impact on fire behavior will require an increase in the number of long-term observational forestry studies.

Keywords: FIA, Forest, Fuels, Long-term trends, MC2, Modeling, Western USA

*Correspondence: Tim.Brown@dri.edu

[2] Division of Atmospheric Sciences, Desert Research Institute, Reno, NV 89512, USA
Full list of author information is available at the end of the article

Resumen: Tendencias en los combustibles de fuego en EEUU utilizando datos históricos y modelos.

Antecedentes: Aumentos recientes en la actividad de los incendios en el oeste de los EEUU son comúnmente atribuidos a la confluencia de factores incluyendo el cambio climático, la actividad humana, y la acumulación de combustibles debido a la supresión del fuego. Sin embargo, una carencia de mediciones forestales de largo plazo hace difícil cuantificar cambios regionales en la carga de combustibles en los últimos cien años. Un mejor entendimiento de la acumulación de combustible es vital en el manejo de los bosques para incrementar la resistencia a los incendios y la resiliencia. Modelos numéricos proporcionan una forma de estimar los cambios en las cargas de combustible, pero validar estos modelos a lo largo del tiempo y para extensiones geográficas grandes es difícil por la falta de datos necesarios. Uno de esos modelos, MC2, provee múltiples tipos de estimadores de carga y simula la actividad del fuego de acuerdo al combustible y las condiciones del clima. Nosotros utilizamos los datos observados del Inventario Forestal y Análisis de Datos (FIADB por su siglas en inglés), para validar las estimaciones del cambio en la carga de combustible del MC2 a través del tiempo donde fue posible.

Resultados: Encontramos que la precisión del modelo MC2 varió geográficamente, pero a una escala regional los cambios en las distribuciones en la carga de combustible fueron similares a los valores de las distribuciones de FIADB. Mientras que los datos del FIADB proporcionaron tipos consistentes de mediciones a lo largo de un área geográfica amplia, los datos utilizables solo abarcaron 30 años aproximadamente. Por lo tanto, complementamos esta validación cuantitativa con una comparación cualitativa de datos que abarcó un área menor pero con lapsos de tiempo mucho mayores: parcelas forestales de largo plazo por fuera de la red de parcelas de FIA y repetimos estudios fotográficos. Ambos resultados del modelo y varios estudios de largo plazo muestran incrementos en la carga de combustible en los últimos cien años en gran parte del oeste de los EEUU, con excepciones en el noroeste del Pacífico y otras áreas. Los resultados del modelo también sugieren que no todos los incrementos son debidos a la supresión del fuego.

Conclusiones: La validación de este modelo y el agregado de información de estudios de largo plazo demuestran que han habido grandes aumentos de combustible en el oeste de los EEUU, pero también se puede apreciar el nivel de incertidumbre en el impacto de la supresión de fuegos sobre la carga de combustible. Una comprensión más completa del cambio en las cargas de combustible y su impacto en el comportamiento del fuego requerirá un aumento en el número de observaciones de largo plazo en estudios forestales.

Background

There is general agreement that widespread century-scale fire suppression has caused increases in wildfire fuel loads in low elevation dry forests of the western USA (e.g., Parks et al. 2018; Collins et al. 2011). This is a cause for concern as higher fuel loads can lead to larger, higher severity fires (Steel et al. 2015; North et al. 2015; Parks et al. 2018; Tubbesing et al. 2019) and make it difficult to perform prescribed burning safely. The large and destructive fires occurring in the past couple of decades are resulting from the confluence of climate, fuels, and people. There are numerous studies linking climate to fire (e.g., Flannigan et al. 2009) and clearly human population distribution is a factor for ignitions (e.g., Balch et al. 2017). However, to date, minimal quantitative information has been provided in the literature supporting the general agreement of fuel load increases, which for many places (not all) are largely thought to be due to fire exclusion beginning with early twentieth century fire suppression policy.

Not surprisingly, there is high uncertainty regarding the magnitude and extent of historical changes in fuel loads. Mapping fuels is complicated by fuels' spatial and temporal variability, but fuel maps are vital to predicting fire risk (Keane et al. 2001). Models which simulate vegetation growth and mortality have been used to estimate fuel loads across areas without observations, estimate past changes in fuel loads over time when historical data are unavailable, and/or simulate fuel loads under future climate and management scenarios. Fire models can then use these vegetation model results to determine the impacts of changing fuel loads on fire behavior. However, it is very difficult to validate models' fuel load estimates, especially those that estimate changes in fuel loads over long periods of time and/or large geographic extents. One difficulty is that there are limited observational data available prior to 1950 for validating forest dynamics models (Zhang et al. 2015). Some studies using forestry plot measurements have found that fuel dynamics calculated across intervals of less than 10 years display high variability and can be potentially misleading (Sollins 1982), demonstrating the importance of collecting long-term datasets. Another difficulty is that anthropogenic disturbances as well as unpredictable natural events (such as avalanches or strong windstorms) can cause changes to land cover which are not easily captured by a coarse-scale computer simulation. The large variety of ecosystems present in the western USA also makes it

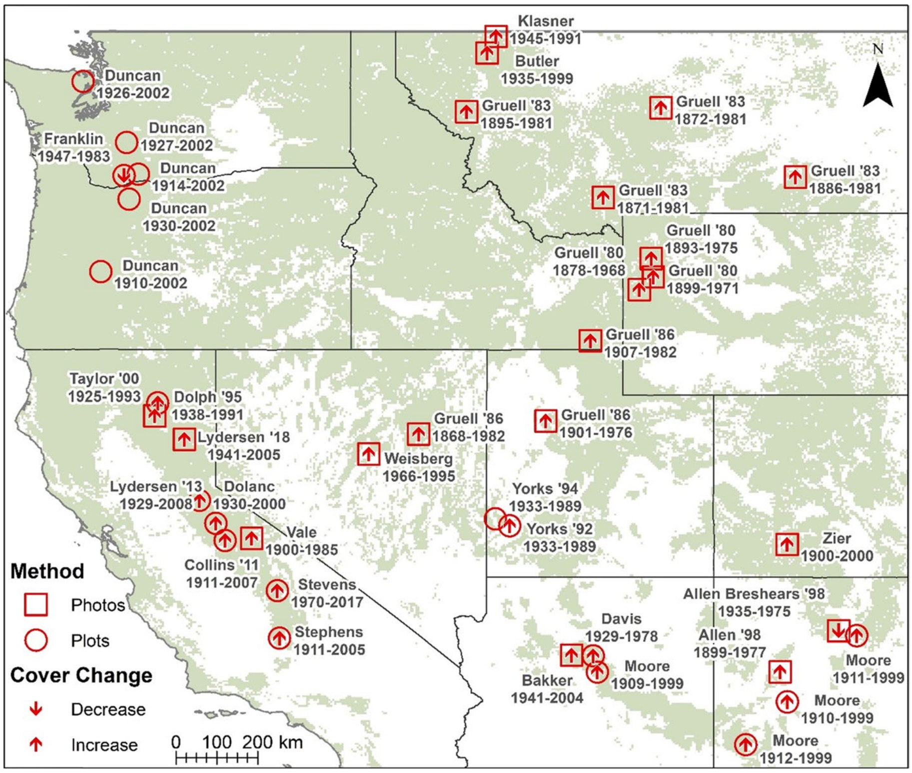

Fig. 1 Approximate locations of vegetation change studies spanning at least 30 years. Circles show forestry plots, while squares show repeat-photography studies. These symbols are meant to show general locations only, and their size on the map is not indicative of the actual surface area studied. Arrows indicate the general trend of forest cover over the years (up or down; no arrow indicates that the study did not show a net trend in either direction). Each location is labeled with the author (and year of publication if needed to differentiate between studies), as well as the years spanned by the study. Green shading denotes areas dominated by forest or shrubland, while white indicates deserts, grasslands, agricultural lands, etc. See Appendix A for details of each study

difficult to extrapolate any observations regarding the impact of fire suppression. The scarcity of field data and difficulty in model validation make it hard to even answer the fundamental question of how fuel loads are changing over time.

Although there are multiple gridded datasets that estimate fuel loads and/or forest characteristics across the entire western US (e.g., National Tree List, Drury and Herynk 2011), these datasets rely on observations from satellites such as Landsat that only go back to the 1970s (NASA n.d.) and thus cannot be used to assess changes over longer time periods. They also cannot be used to predict future fuel loads the way a process-based numerical model can.

Long-term studies using plot measurements and photographic analysis show increased live fuels over much of the western USA in the past century, except in the Pacific Northwest (Fig. 1). These studies are extremely valuable but are limited in spatial coverage.

Non-fire-suppressed reference forests provide some insight into how fire suppression has affected fuel loads. For example, the Sierra de San Pedro Martir (SSPM) forests in northern Mexico did not experience fire suppression until the late 1900s (Stephens and Fulé 2005). Measurements in the SSPM found that it contained less coarse woody debris than did Sierra Nevada forests that had been fire-suppressed but were otherwise similar (Stephens et al. 2007a). On the other hand, canopy cover was similar between SSPM and a fire-suppressed forest in the eastern Sierra Nevada, likely because the dry forests in this region grow very slowly (Stephens et al. 2007a). In the 1970s, some land managers started allowing more wildfires to burn—under conditions that provided safety to life, property, and human health—as a strategy for managing resilient landscapes (Van Wagtendonk 2007; Hessburg et al. 2019). Observations in two California forests that experienced this type of restored fire regime—Illilouette Creek Basin of Yosemite and Sugarloaf Creek Basin of Sequoia and Kings Canyon National Park—have shown that fuel loads were lower than in unburned forests in the same region (Collins et al. 2016). However, reintroduction of fire to suppressed landscapes does not always yield the same results: forested extent decreased by 24% in Illilouette Creek Basin over 40 years of repeated mixed-severity fires (Boisramé et al. 2017), while fires in the drier Sugarloaf Creek Basin reduced forest cover by only 1% over a similar time period due to lower fire severities and lower forest productivity in Sugarloaf Creek Basin (Stevens et al. 2020a). Comparing fire-suppressed forests to reference forests such as the Sierra de San Pedro Martir, Illilouette Creek Basin, and Sugarloaf Creek Basin is an important method for demonstrating fire suppression's impact on fuel loads, but such comparisons are limited in extent, which is unfortunate given the spatial variability in forest structure and fire regimes.

In this study, we work toward answering the questions of how fuel loads have changed in the Western USA over time and how much of that change is due to fire suppression. We approach this question by aggregating observations of western USA fuel loads from a variety of sources. These sources include:

1) The Forest Inventory and Analysis (FIA) Database
2) Repeat forestry measurements in plots not associated with FIA
3) Repeat photography analysis

We use these observations to investigate temporal trends in fuel loads across a range of landscapes. They also allow us to validate the MC2 fuels model, which we can then use to investigate trends in fuel loads across the entire western USA over the past century. Forest Inventory and Analysis (FIA) data compiled by the US Forest Service are commonly used for model validation. For example, a study of the regional ecosystem model LPJ-GUESS found that modeled values of net primary productivity and biomass in New England were within ranges measured by FIA data (Tang et al. 2010). It is important to note that Tang et al. (2010) grouped FIA data by forest type for this comparison, rather than trying to compare model output to specific plots.

Our study focuses on live trees, as they are the most commonly recorded type of fuel across large ranges in space and time, although surface fuels can be very important to determining fire risk (Agee and Skinner 2005). Studies have shown canopy cover to be positively correlated with fine surface fuel loads (Collins et al. 2016), suggesting that tracking changes in live trees over time can also offer insight into the likely fine fuel loads. Our main questions are:

1) What do historical records show in terms of long-term changes in fuel loads throughout the western USA?
2) Can the MC2 model's representation of changing fuel loads be validated by plot data?
3) What spatiotemporal patterns in fuel loads are revealed by the MC2 model?

Methods

Study area

This study covers the western USA (west of 103° longitude), which primarily includes the states of Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming. We focus on this region because of the large role that fire suppression has historically played there. Prior to European settlement, fire frequencies were under 35 years for most forests in California and the Southwest, but fire suppression policies and increased levels of livestock grazing (which reduced fine fuel loads) led to longer fire-free intervals in many areas throughout the twentieth century (Hessburg et al. 2019). In contrast, colder and wetter forests in the northwestern regions or high altitudes had fire return intervals of up to 200 years and therefore would not be greatly affected by a century of fire suppression (Hessburg et al. 2019). We therefore expect to see large spatial variation in fuel load trends throughout the region. We also focus on the western USA because it is the primary region in the US where large high-impact and high-severity fires have been substantially increasing for the past two decades (Parks and Abatzoglou 2020).

Fire and fuels model

The MC2 model simulates vegetation growth, mortality, and decay. It is a combination of the biogeography MAPSS model and the biogeochemical CENTURY model, with a fire module called MCFIRE (Bachelet et al. 2001). This model has been used in multiple studies to project fuel and fire behavior under climate change (Kim et al. 2018; Bachelet et al. 2015). Previous studies validated the MC2 model against National Biomass and Carbon Dataset data as well as national maps of potential vegetation type and fire return intervals (Bachelet et al. 2015). However, the model's ability to accurately represent historical vegetation changes has not been validated at a large scale, though it has been verified to simulate historical carbon loads in California (Lenihan et al. 2003).

This model includes simulations of the impact of fire and post-fire regrowth on the landscape. In the model, fire always occurs (up to one time per year) if thresholds of weather and fuel moisture are met within a given cell (Bachelet et al. 2015; Conklin et al. 2016). The model then uses estimates of fuel loads (live and dead) to determine the extent of fire spread within the cell, as well as whether

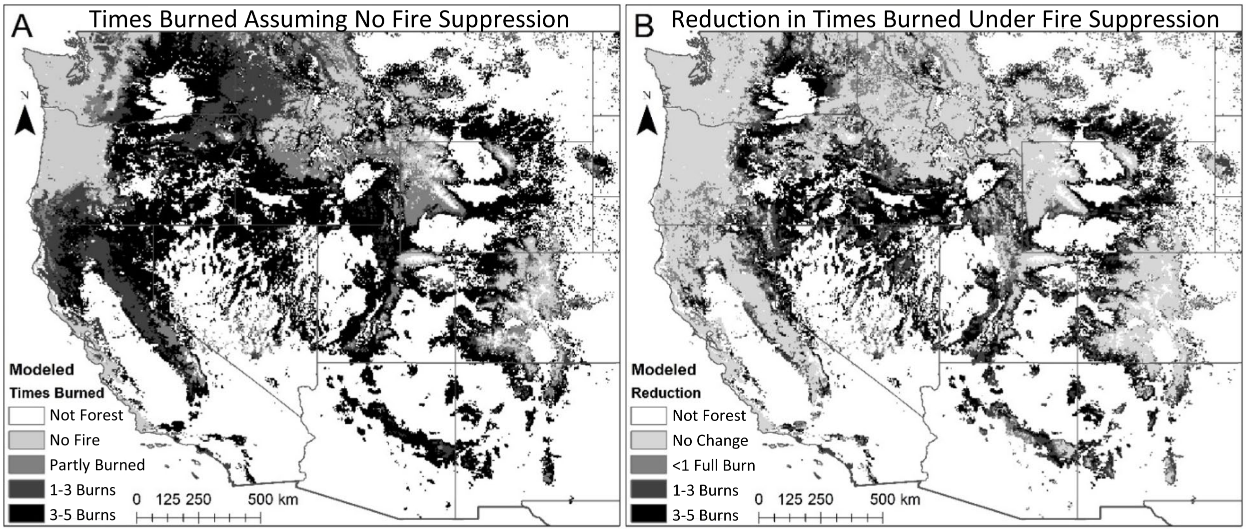

Fig. 2 **A** Cumulative proportion of each model cell that burned during the modeled period of 1895–2010 under the fire-suppressed scenario. **B** Reduction in cumulative burns in the fire-suppressed model scenario. Non-forested areas are shown in white regardless of modeled fire activity

crown mortality occurs (Bachelet et al. 2018; Conklin et al. 2016). Although fire does not spread from one cell to another, areas with similar climate experience similar fire impacts, often creating contiguous burned areas larger than one cell (Fig. 2A). The amount of area burned has been found to match well with observed pre-suppression values at a continental scale (Bachelet and Turner 2015) as well as within California (Lenihan et al. 2003) and South Dakota (King et al. 2015).

The particular MC2 model runs used here simulated vegetation growth, mortality, and decay, as well as fire activity, from 1985 to 2010 using historical PRISM weather data. Vegetation type in the model is determined based on potential vegetation for a given location's soil, landscape, and climate, rather than using contemporary vegetation maps. Details are given in Mote et al. (2014).

The model results include a "fire suppression" and a "no fire suppression" scenario. Under the first scenario, fires are still possible but are suppressed if the calculated fireline intensity, rate of spread, and energy release component are below predefined thresholds (Sheehan et al. 2015). While the areas that experience fire are similar between the two scenarios, the number of times that a given cell experiences fire is much higher in the scenario with no fire suppression (Fig. 2).

By comparing the "fire suppression" and "no fire suppression" scenarios, we can use the model to estimate the impact of fire suppression on fuel loads, as well as identify areas where fuel loads might change even without aggressive fire management.

Table 1 Dates of data available for all states in this study. Each column gives the longest available time span for: FIA plot data available online, longer-term plots found through a literature search, and repeat photography studies found in the literature

State	Longest date range, FIA plots	Longest date range, other plots	Longest date range, repeat photography
Arizona	1980–2017	1909–1999	1941–2004
California	1991–2017	1911–2007	1941–2005
Colorado	1979–2017		1900–2000
Idaho	1981–2018		1907–1982
Montana	1988–2018		1871–1982
Nevada	1978–2018		1868–1982
New Mexico	1985–2018	1910–1999	1899–1977
Oregon	1995–2017	1910–2002	
Utah	1988–2017	1933–1989	1901–1976
Washington	1996–2017	1914–2002	
Wyoming	1983–2018		1892–1975

FIA dataset

The US Forest Service maintains the Forest Inventory and Analysis (FIA) Database, recording standardized forestry plot measurements across the USA (USFS 2019; Gray et al. 2012). Within the western USA, the online FIA Database contains measurements spanning 21–40 years, depending on the state (Table 1). The database includes field measurements such as tree heights and diameters with descriptions of tree species and condition, as well as calculated values such as biomass (Gray et al. 2012). The earliest plot measurements date back to the 1930s, while permanent sample points were established on a national grid beginning in the 1960s, and the current inventory methodology was adopted nationally in 2000 to provide more consistent measurements (Gray et al. 2012). Individual plots are re-measured every 5–10 years (Gray et al. 2012). At each plot, trees are measured on four 7.3 m radius subplots (Gray et al. 2012). Aboveground carbon (excluding foliage) is calculated for all live and standing dead trees of at least 1 inch diameter by assuming that carbon is one half of the tree's biomass which is calculated using a set of species-specific equations and tables. The carbon content of each measured tree is then multiplied by the associated estimated number of trees per acre to obtain carbon biomass per acre (Burrill et al. 2018). The FIA database includes litter depth which is measured 7.3 m from the subplot center along each subplot transect; this depth is then converted to a weighted average based on the proportion of the plot that is in the same condition (i.e., mapped as having the same vegetation cover type) as the location of each measurement (Burrill et al. 2018). An estimate of total litter carbon in each FIA plot is also calculated using equations based on geographic area, forest type, and stand age rather than directly using measurements (Burrill et al. 2018).

Comparing FIA and MC2 data

FIA data should not necessarily be expected to match any gridded model exactly, due to differences in scale (< 700 m^2 measured on each FIA plot, versus approximately 10^7 m^2 within each grid cell of the MC2 output used here). Aggregating FIA plot data within larger areas, as well as examining the cumulative distributions of the two datasets (FIA data and model output), can be a more meaningful comparison (Riemann et al. 2010). Because the MC2 model assumes fires will occur whenever fuel and weather conditions are optimal (no limitation on ignitions), and since it is impossible to exactly predict real fire ignitions, we do not expect the fire history of the model to exactly match reality for any given location. Consequently, we excluded any model cells that had burned between 1980 and 2010 (the period when most FIA data were collected). Because strict adherence to this rule led to a very small number of acceptable plots, we relaxed the standard to allow model cells that had experienced fire on less than 1% of their area cumulatively from 1980 to 2010. The MC2 model also does not simulate logging. Therefore, all comparisons between datasets exclude any FIA plots that had burned or been harvested during the study period, or where over 25% of the plot's trees were damaged or killed due to factors such as disease or insects, which are also not included in the model. For most variables we used only individual plots that included multiple measurements spanning at least 10 years. While aggregating data from all FIA plots within a given region for each year would have given a larger dataset for calculating rates of change, it would have potentially introduced too many errors due to changes in inventory design (Goeking 2015). We made one exception for litter depth: since this variable was only measured starting in 1999, there were very few plots available spanning 10 or more years, and most plots were measured after the inventory design was standardized, so we included all measurements of litter depth from undisturbed plots regardless of whether the individual plot's data spanned 10 years.

We compared FIA and MC2 data at the scale of ecological sections, as well as subregions within those sections. The US Forest Service defines these spatial divisions by dividing the country into groups of related climates, then by land cover type, and finally based on terrain features (Cleland et al. 2007). Ecological sections cover an average of 4 million ha (ranging from $5.5X10^5$–$3.4X10^7$ ha). For the analyses presented here, ecological section-scale values were calculated as the average of all plots fitting our criteria (e.g., no disturbance) that fell within an ecological section, and the average of all MC2 grid cells that both contained a valid plot and fell within the ecological section. Omitting grid cells that did not contain plots helped us to avoid sampling intensity errors that might be caused by averaging over large areas simulated by MC2 that were not covered by forestry plots (Riemann et al. 2010). It should be noted that the FIA plot coordinates provided in the database are up to 1.6 km away from their actual location, in order to protect the privacy of landowners (Gray et al. 2012). While FIA plot data are labeled by subregion and therefore grouping them within ecological sections is not affected by spatial uncertainty, inaccurate locations could affect the selection of model grid cells for comparison. However, since 1.6 km is smaller than the width of grid cells in the MC2 model (approximately 3–4 km, depending on latitude), this should only create a minimal level of error. To include an ecological section in the comparison, we required it to contain at least ten valid FIA plots.

Comparing data at the ecological section level likely provided a more valid assessment than plot-level comparisons, but it limited the amount of data that could be used. The majority of FIA data that fit our criteria (no disturbances, at least a 10-year time span of measurements, and at least ten plots per ecological section) only covered 10–20 years for most plots (Fig. 3) and omitted large portions of the desired study area (Fig. 4).

Our comparisons assessed the ability of MC2 to capture observed changes in fuel loads over time (in terms of mass per year). This change was calculated using a

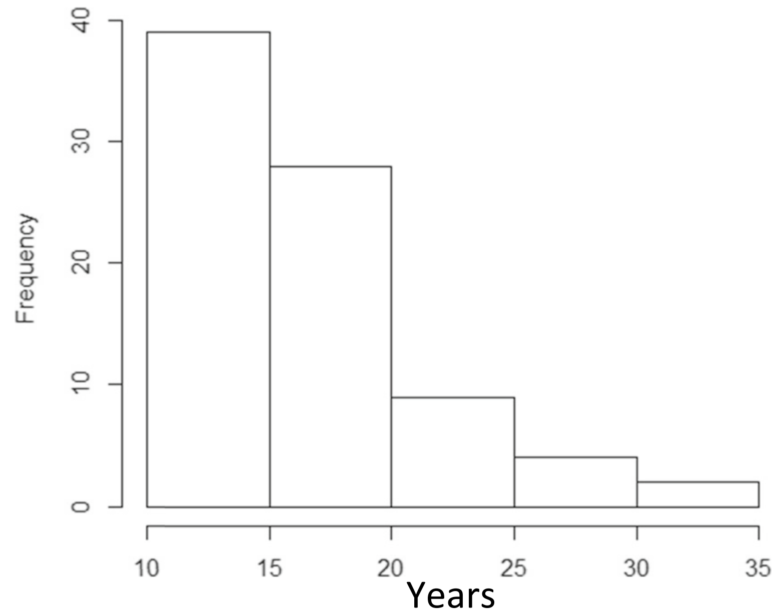

Fig. 3 Histogram of the time spans covered by the FIA analysis at the ecological subregion level

simple linear regression of mass versus year (when only two distinct measurements were available, this is the same as taking total change in mass divided by the number of years between measurements). For each FIA data point, we extracted model data from that location and year (or from 2010, the latest modeled year, for measurements after 2010) from the MC2 fire-suppressed scenario and used these values to calculate modeled rate of change. We limited our calculations to data spans of at least 10 years, since other studies have found shorter periods to be potentially misleading when calculating fuel accumulation rates (Sollins 1982). We also omitted the small number of FIA data points measured later than 2015 in order to avoid long time spans between the latest available model year (2010) and the latest FIA measurements.

Not all variables measured by the FIA surveys had a comparable output from MC2. Therefore, we focused on three variables that were both measured and modeled, with similar definitions: litter carbon, live aboveground carbon, and dead aboveground carbon. In MC2, litter carbon ("wood1" in the model) includes the mass of carbon in the dead fine branch component of the forest system, while in FIA datasets this is provided as litter carbon in the plot condition table—an estimate based on geographic area, forest type, and stand age—where litter is defined as "organic material on the floor of the forest, including fine woody debris, humus, and fine roots… above mineral soil" (Burrill et al. 2018). FIA data also include point measurements of litter depth (Burrill et al. 2018). Since this depth value is not directly comparable to modeled litter carbon, we instead compared percent change in measured litter depth to percent change in modeled litter carbon in order to assess whether both datasets showed similar trends in litter's relative change over time. We used litter depth in order to avoid the uncertainties involved in converting depth to mass. The FIA variable "CARBON_AG" (aboveground carbon) measures the aboveground carbon biomass of live and standing dead trees, excluding foliage. For our comparisons, we separated live and dead trees to compare them to modeled live and dead aboveground carbon, respectively. MC2 defines live aboveground carbon ("aflivc" in the model) as the sum of carbon in all live components of the forest system, minus root carbon. We subtracted modeled leaf carbon (rleavc) from the modeled live aboveground carbon pool to make it more comparable to the FIA data. We selected the dead large wood component of MC2 output (wood2c) as the most appropriate value to compare to standing dead trees from FIA.

We compare modeled and FIA data using the mean and 95% confidence intervals of fuel change rates within each ecological section. For all variables except litter depth, we define the 95% confidence interval as the range of values excluding the highest and lowest 2.5% of values for all plots; this was calculated using the quantile function in R (RDocumentation n.d.). For litter depth change, we used the 95% confidence interval for the slope of the linear fit of depth versus

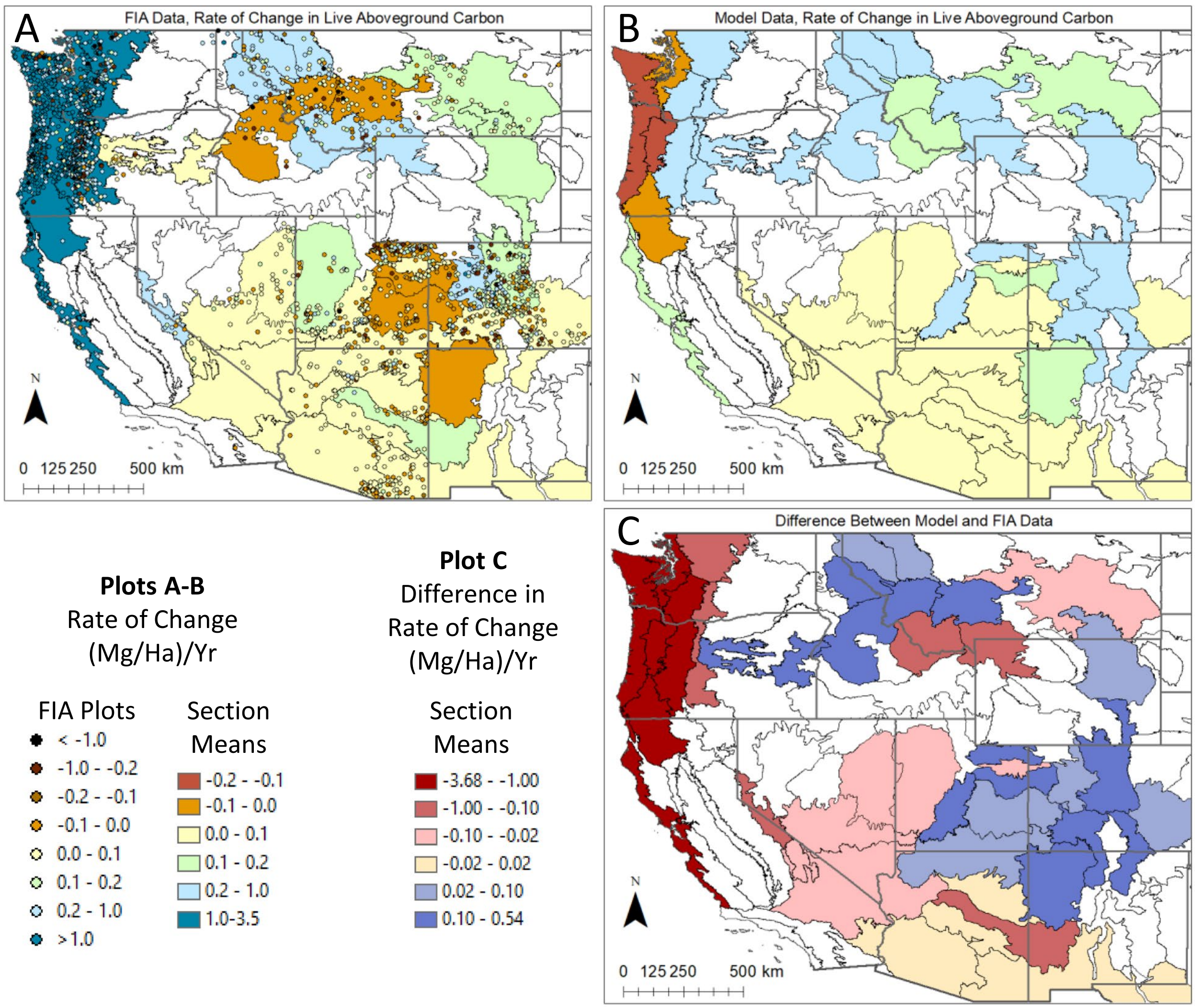

Fig. 4 **A** Change in live aboveground carbon (Mg ha^{-1} year^{-1}) in all FIA plots with no disturbance and at least 10 years between remeasurements. Ecological sections are outlined in black; those containing at least 10 plots are shown in the color corresponding to mean change among all plots. **B** Mean change in live aboveground carbon within each ecological section, calculated from MC2 model output. **C** Difference between the mean rates of change calculated using model (**B**) or FIA (**A**) data; red colors show where the model underestimated the mean according to FIA data, whereas blue shows areas where it overestimated the increase in live fuels. For all plots, white ecological sections did not have enough appropriate FIA plots for analysis. See Appendix C for locations of plots excluded from analyses, as well as breakdown according to smaller ecological subregions

time (calculated using the lm function in R). We test both whether the modeled mean for each section is within the 95% confidence interval for all FIA data and whether it is within one standard error of the FIA data's mean.

Following methods in Riemann et al. (2010), our comparisons include cumulative distribution curves. These curves are created by ranking each region from the smallest change in fuel load (or most negative) to the greatest change, then dividing this rank number by the total number of regions to obtain a value between 0 and 1. The regions are then plotted with the fuel load change on the x-axis and the rank (normalized to be between 0 and 1) on the y-axis. These plots allow us to show how the distribution of change values varies between modeled and FIA data. Kolmogorov-Smirnov tests were performed using R software to determine whether FIA and modeled values were likely drawn from the same continuous distribution or not. Using this type of test allows comparison of two datasets without making any assumptions about the data's underlying distribution (Riemann et al. 2010).

Literature search for long-term observational studies

While the FIA dataset provides a variety of fuel-related information across many geographic locations, it is limited in terms of time span (Fig. 3). Therefore, we chose to supplement the quantitative comparison to FIA data with a qualitative comparison to observations from studies that cover less geographic area but were recorded over longer periods of time (Table 1). A qualitative comparison is necessary due to these additional studies not all having consistent measurement types and since it is not appropriate to compare modeled MC2 data to individual plots rather than to a large collection of plots (see the "Comparing FIA and MC2 data" section). We searched for studies that used either repeat forestry measurements or repeat photography to cover time periods longer than the available FIA database record. Few long-term studies provided direct measurements of fuel loads. Instead, we relied on the following proxies for fuel loads: tree density, forest extent, vegetation percent cover, biomass, and/or woody debris mass.

Results

Comparing FIA data and MC2 model output

When compared to FIA, MC2 tended to overestimate the total amount of live wood carbon, while underestimating the amount of litter carbon. However, the modeled values were within observed ranges at the scale of the full model domain (Results not shown).

For aboveground live carbon, the mean modeled rate of change for each ecological section was within the 95% confidence interval for FIA plots in that same section (Fig. 5), though only 62% of sections had the modeled mean within one standard error of the FIA mean. The model mean rates of change matched the FIA means' cumulative distribution closely for the lower 70% of ecological sections and subregions but underestimated the maximum increases (Fig. 14). The distributions were not significantly different, according to a KS test ($p = 0.29$). The median rate of change was approximately 0.1 Mg ha^{-1} year^{-1} for both datasets, and 40% percent of ecological sections had rates of change modeled within 0.1 Mg ha^{-1} year^{-1} of the mean calculated from FIA data.

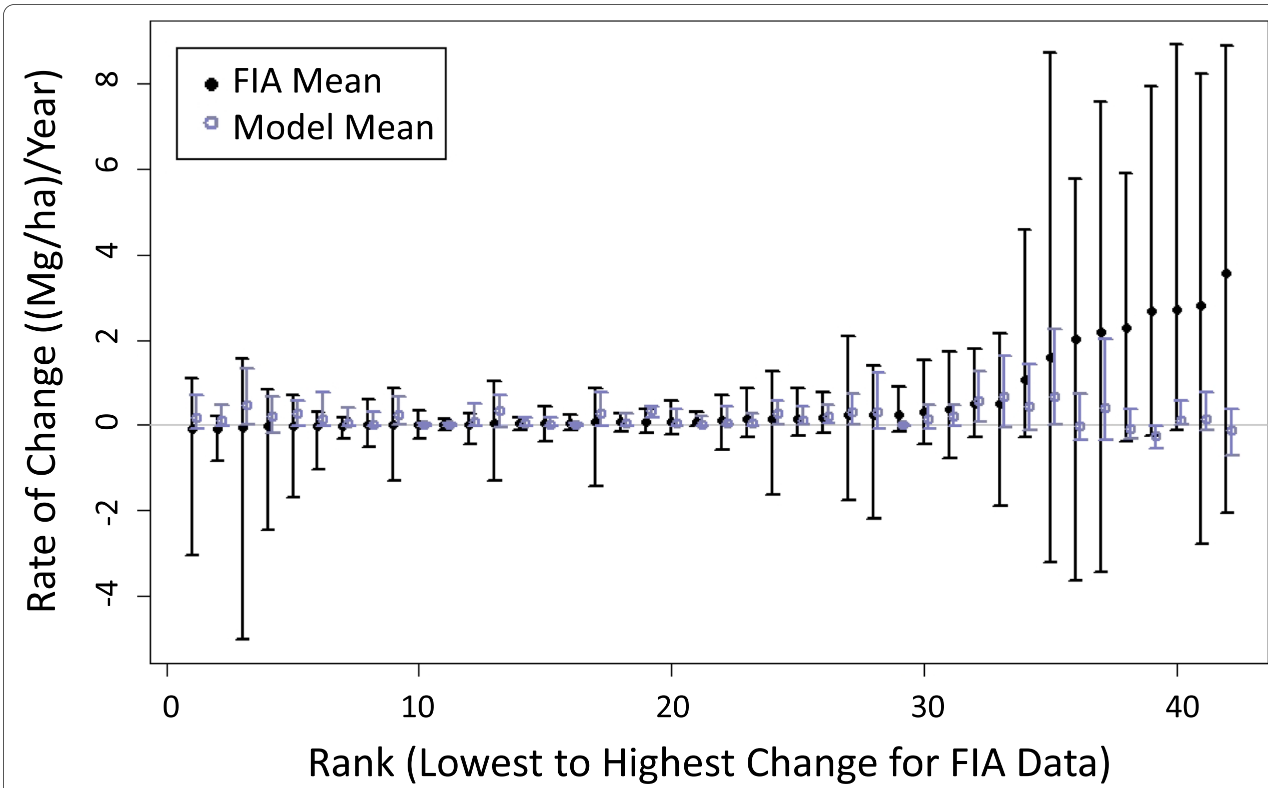

Fig. 5 Rate of change in live aboveground carbon within each ecological region, ordered from lowest to highest according to calculations from FIA data. Mean values for all appropriate FIA plots within each section are shown with black dots, while mean across matching model pixels is shown with open gray circles. Error bars denote the 95% confidence interval. All model means (and most of the model confidence intervals) fall within the FIA confidence interval, but some model means are far below the FIA means

Most ecological subregion and sections that were modeled as having the greatest increases in live aboveground carbon also had the greatest increases according to FIA data (Fig. 14, Fig. 5), but the model also predicted that several sections would have slightly decreasing live fuel loads on average while the FIA data showed increasing values (Figs. 4, 5) and the correlation coefficient between modeled and observed rates was slightly negative (− 0.16). Unfortunately, much of the study region did not contain ecological subregions with enough plots that fit our criteria, so we have very little basis for the model validation in California, Eastern Oregon and Washington, Idaho, New Mexico, or Wyoming (Fig. 4A).

Differences between model and FIA data were not randomly distributed geographically (Fig. 4C). Notably, along the West Coast, the model tended to underpredict sections' live carbon increases or even to predict a decrease in live carbon where FIA data showed an increase (Fig. 4). However, individual FIA plots show that there are areas of the Pacific Northwest which have experienced decreasing stocks of live carbon as is modeled by MC2, even if on average there is an increase (Fig. 4A). In fact, most sections contain plots with a mix of increasing and decreasing fuel loads (Fig. 4A).

For the rates of change of carbon in dead large wood (standing dead trees for the FIA plots), the mean modeled rates for each section were always within the 95% confidence interval for FIA plots within the same ecological section, though FIA and modeled data did not always agree on whether mean change was positive or negative (Fig. 6). The correlation coefficient between modeled and observed rates of change was 0.20. The median rate of change was between 0 and 0.02 Mg ha^{-1} year^{-1} for both datasets. Only 12% of ecological sections had rates of change modeled within 0.02 Mg ha^{-1} year^{-1} of the mean calculated from FIA data, while 83% of sections had modeled mean values falling within the standard error of the FIA-calculated mean. The two cumulative distribution curves have strong overlap for subregions with negative or near-zero changes in dead wood carbon, suggesting that decay rates are modeled well at the scale of the study area (Fig. 15). According to a two-sided KS test, the two datasets are not from significantly different distributions ($p = 0.22$).

Compared to FIA data, the MC2 model showed a narrower range in the rates of change in litter carbon over time, although the modeled values fell within the observed ranges (Figs. 7A, 16). The FIA estimates of litter carbon are themselves derived from a set of equations rather than being based on direct measurements; therefore, we also compared the percent change of the MC2 modeled carbon litter to the percent change in mean litter depth over time in order to compare the model results to an actual plot measurement. This comparison shows the model predicting higher rates

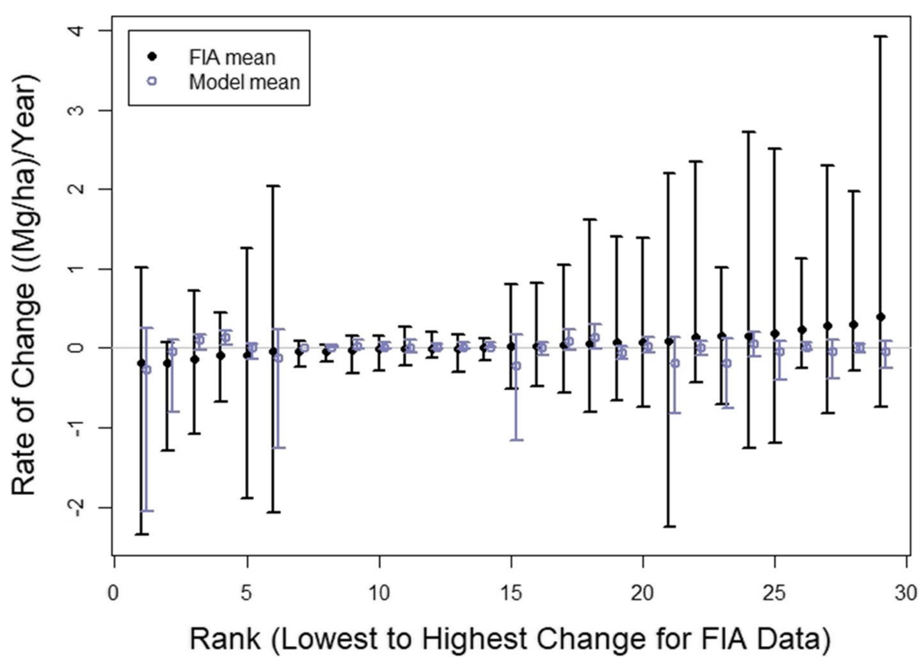

Fig. 6 Change in the carbon of dead trees over time within each ecological section with sufficient FIA data. Mean values for all appropriate FIA plots within each section are shown with black dots, while mean across matching model pixels is shown with gray circles. Error bars show 95% confidence intervals. All model means fall within the FIA confidence interval, but often the signs of the means do not match

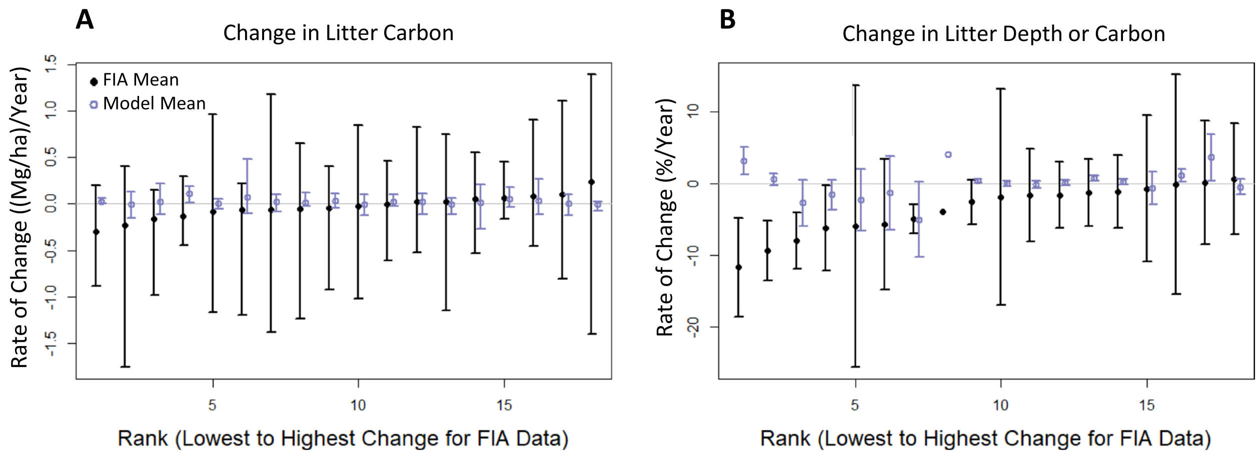

Fig. 7 Change in litter over time within each ecological section with sufficient FIA data. Mean values for all appropriate FIA plots within each section are shown with black dots, while mean values across matching model pixels are shown with gray circles. Error bars show 95% confidence intervals. Results are shown in terms of Mg ha^{-1} year^{-1} (**A**) and as % change per year in litter depth for FIA and litter carbon from the model (**B**)

of change in litter than the FIA data for most sections (Fig. 7B). Litter depth data were only available from 1999 onward, so the propensity for observed litter depth change to be negative may be due to plots entering a period where decomposition exceeds accumulation, since a long time has passed since the most recent disturbance and litter accumulation rates can be highest in earlier years of regrowth (Keifer et al. 2006; Smith and Heath 2002). For some ecological sections, the rate of change in litter carbon was matched fairly closely by the MC2 model, while in others, it was either greatly overestimated or underestimated. For both litter carbon and litter depth, model and FIA section mean values were found to be from significantly different distributions according to KS tests ($p < 0.01$).

Literature search results

Long-term studies of vegetation changes, both repeat measurements of study plots as well as analyses of repeat photography, are available across a range of landscape types in the western USA (Fig. 1). For some regions, FIA provided the longest-spanning dataset (e.g., Eastern Washington, Eastern Oregon). For most states, however, the literature search showed longer records of forestry plot and/or photographic data were available from other sources (Table 1).

Many long-term studies using repeated measurements of forestry plots showed an increase in tree density, canopy cover, and/or basal area (Collins et al. 2011; Lydersen et al. 2013; Moore et al. 2004; Smith and Smith 2005; Bakker 2005). Exceptions included areas with increased tree mortality due to drought stress, insects, and/or pathogens (van Mantgem et al. 2009; Allen and Breshears 1998) as well as some old-growth forests where mortality of older trees was not matched by recruitment (Franklin and DeBell 1988). In some plots in Colorado, increased mortality rates did not prevent an increase in live tree biomass (Chai et al. 2019). Sloan (1998) found that tree basal area nearly doubled from 1850 to 1950 in an undisturbed area of Central Idaho, then decreased slightly from 1950 to 1993 due to increased mortality (although this study used tree rings and estimated year of death for dead trees to reconstruct past forest structure, rather than using repeat measurements). There is high spatiotemporal variability both in standing fuel loads and in rates of fuel accumulation, especially for large fuels (Keane 2016).

Repeat photography studies have shown that forest homogeneity has increased since the 1940s in many areas (Klasner and Fagre 2002; Lydersen and Collins 2018; Feldman and Gruell 2003). Repeat photographs also showed increases in the extent and/or density of many forests (Zier and Baker 2006; Weisberg et al. 2007; Allen et al. 1998; Gruell 1980; Gruell 2001); examples are shown in Figs. 8, 9, and 10. Colder forests show less change over time (Hessburg et al. 2019).

Forest structure shifts over time, as well as total cover and extent. Studies of forestry plots in the Sierra Nevada of California found that large tree density decreased over 70 years while small trees' density increased (Bouldin 1999; Dolanc et al. 2014). Other Sierra Nevada plots also showed large increases (> 3.5 times greater) in the number of small trees (< 61 cm DBH), while the density of large trees (> 91.4 cm DBH) showed little change in the Yosemite area since

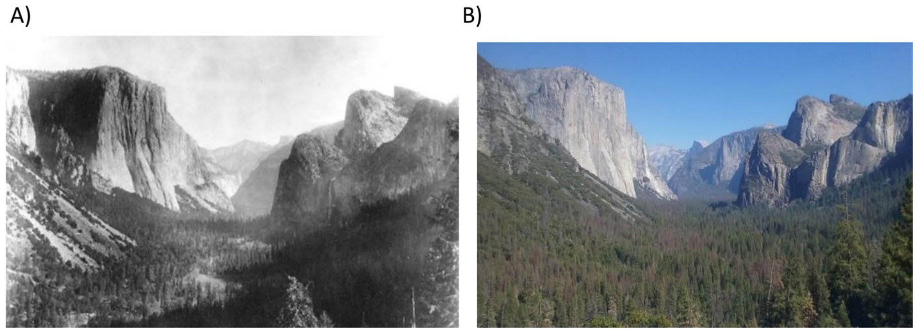

Fig. 8 Photographs of Yosemite Valley in California from 1892 (**A**) and 2011 (**B**) show denser forest and shrub growth. Source for A: https://www.usgs.gov/news/yosemite-science , Photo B by Gabrielle Boisrame

1911 (Collins et al. 2011) and even a decrease in the more southern Sequoia National Forest since 1970 (Stephens et al. 2015). Repeat measurements of old growth, undisturbed forests in Oregon and Washington showed increasing density of shade-tolerant trees in many plots over time, even in stands over 100 years old (Acker et al. 1998), demonstrating how understory forest growth can continue for many years post-disturbance. Studies in California have also shown increased density of small, understory trees in recent decades (Dolph et al. 1995; Collins et al. 2011). Dense growth of understory trees can be especially important to increasing fire risk and fire severity as such fuels can help propagate fires from the forest floor into the canopy (Allen et al. 1998; Schoennagel et al. 2004; Agee and Skinner 2005). Unfortunately, the MC2 model does not strictly simulate overstory versus understory, including only competition for resources in forests between herbaceous vegetation and trees, large and small, but not including actual shrubs.

Fig. 9 Wallowa Mountains in Oregon. Photos from 1936 (top) and 2018 (bottom). Adapted from Hessburg et al. (2019). Original sources: U.S. Forest Service National Archive (1936) and John F Marshall (2018)

A) B)

Fig. 10 Photos taken in Ross' Hole, Montana, in 1895 (**A**) and 1980 (**B**). Photos from Gruell 1983

Changes to fuels are not limited to forested regions. Historical data from the Jornada Experimental Range in New Mexico showed increases in shrub cover between 1898 and 1963 (Grover and Brad Musick 1990), while repeat photography showed juniper expansion in areas of Arizona, Idaho, New Mexico, and Utah (Davis and Turner 1986; Allen et al. 1998; Gruell 1986). Shrubland expansion in the southwest can be attributed to multiple factors, including climate, grazing, changing land use, fertilization effect due to increasing CO_2 concentrations, and fire suppression (Grover and Brad Musick 1990; Samuels and Betancourt 1982).

While most studies we found focused on tree characteristics, some did discuss fuels. Coarse woody debris in Oregon and Washington was found to accumulate at a rate of 1.5–4.5 $\mathrm{Mg\,ha^{-1}\,year^{-1}}$ (Sollins 1982). Assuming that approximately half of total dry fuel mass is carbon (as is done in the FIA dataset), these values are similar to the largest increases in dead fuel types found by the FIA data analyzed here, but larger than estimates from the MC2 model (Figs 6 and 7).

Spatial patterns in fuel changes

The MC2 model shows spatial variation in the increase of live aboveground carbon due to fire suppression (Fig. 11C). The direction of change in live fuels (increase or decrease) generally matches between the model and long-term observational studies (Fig. 11B). Most of the modeled grid cells, and most observational studies, show increased carbon loads over time. Spatial variability of fire behavior (Fig. 2A) contributed to the spatial variability in modeled fuel loads and their change over time. Modeled spatial patterns in litter changes are similar to those in live fuels (Figs. 11 and 12); this is consistent with observations of canopy cover being positively correlated with fine surface fuel loads, likely due to the canopy's role in providing leaves and fine branches to the litter pool (Collins et al. 2016).

Northwest model results versus observations

Long-term forestry plots in Oregon and Washington, mostly located in the Western Cascades region, show long-term decreases or no change in fuel loads. These same locations mostly contain a mix of model grid cells with increasing and decreasing values, although most grid cells show increases (Fig. 11B). The lack of fuel increases due to fire suppression in the Western portions of Oregon and Washington (Fig. 11C) is consistent with the literature stating that these wetter forests are climate-limited rather than fuels-limited when it comes to fire disturbance (Hessburg et al. 2019).

Southwest model results versus observations

In Nevada, Arizona, Utah, and New Mexico the MC2 model shows increased fuel loads due to fire suppression in the areas that were covered by long-term studies (Fig. 11C). This is generally consistent with observational studies showing increased tree cover in the mountains of northern Arizona (Bakker 2005; Biondi 1999, 1996), the Great Basin of central Nevada (Weisberg et al. 2007; Gruell 1986), and the Bonneville Basin of Utah (Yorks et al. 1992; Gruell 1986). The increase in fuels within many parts of the southwest is also consistent with observations of woodland areas expanding (Weisberg et al. 2007; Zier and Baker 2006). Another study (Moore et al. 2004) also showed increases in forest density that qualitatively match with the MC2 model in Arizona and New Mexico, but many of the 1909–1913 plots measured in that study had been logged and therefore the increase in stand density is not purely due to fire suppression. Historical studies showing increasing fuel loads in multiple regions within New Mexico agree with model results (Fig. 11B, C), except for one study which found decreasing vegetation cover due to drought (Allen and Breshears 1998), though some model pixels nearby also showed decreasing fuel loads. One study in Utah showed increases in

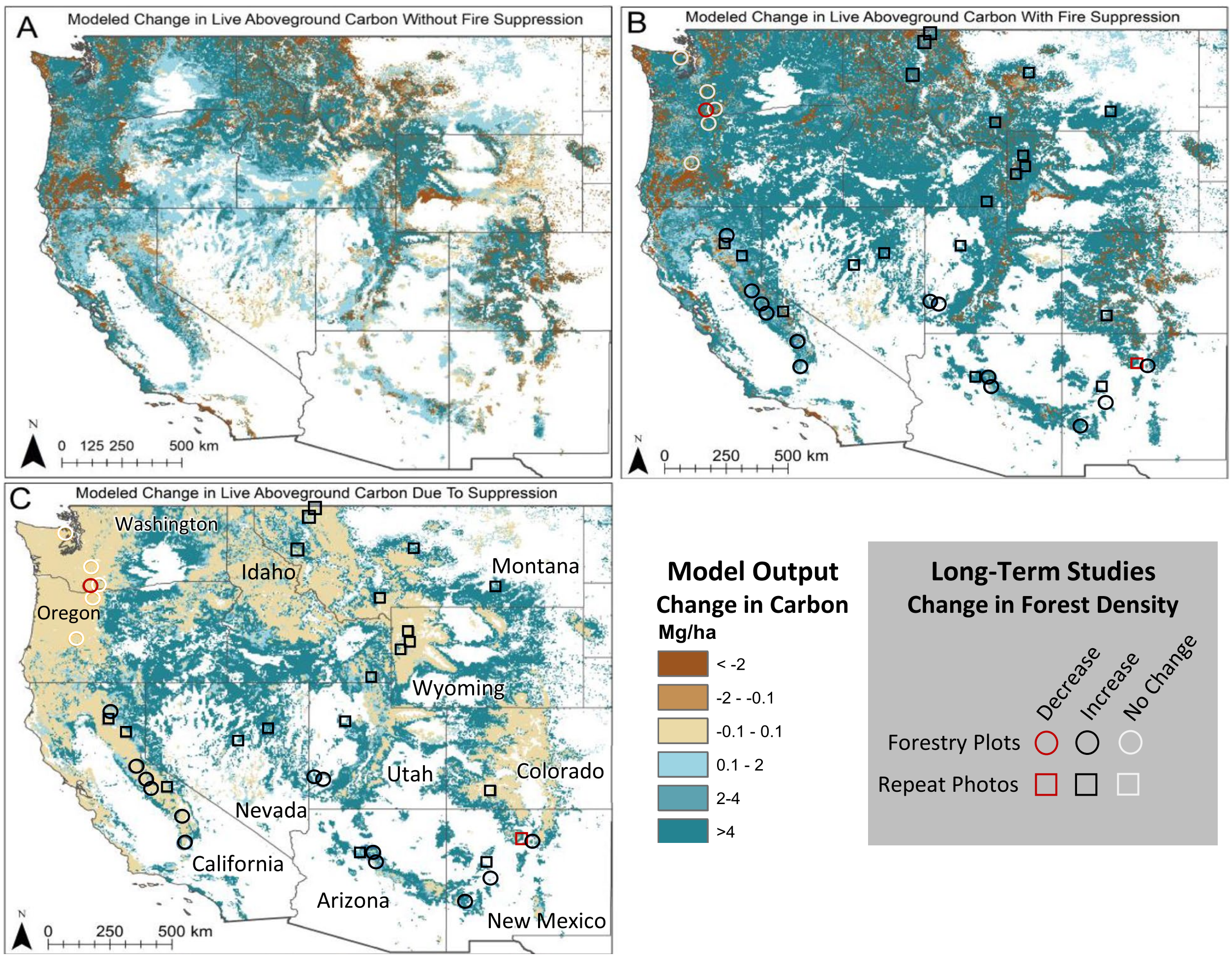

Fig. 11 Modeled change in live aboveground carbon from 1895 to 2010. **A** Model scenario without fire suppression. **B** Model scenario with fire suppression. **C** Change attributed to fire suppression (difference between **A** and **B**). State lines are shown in gray. Studies in the literature search are shown as squares (repeat photography) or circles (forestry plot remeasurements) colored according to observed direction of change in forest density or similar metric

tree density but decreases in total cover, due to a change in the dominant species, making it difficult to determine the direction of change in total fuel load (Yorks et al. 1994). The model gives mixed results on change direction in Colorado, while one repeat photography study in Colorado's San Juan Mountains showed increased extent of forested area (Zier and Baker 2006).

California model results versus observations

MC2 matches observations of increased live forest fuels in the northeast portion of California (Dolph et al. 1995; Lydersen and Collins 2018) and throughout the Sierra Nevada mountain range (Lydersen et al. 2013; Collins et al. 2011; Dolanc et al. 2014; Stephens et al. 2015) (Fig. 11). However, the model shows roughly equal increases in fuels within the montane forests of California under both fire-suppressed and non-suppressed scenarios (Figs. 11 and 12), which does not match with multiple observation-based studies which found that fire suppression was the primary driver of these increases (Collins et al. 2011; Stephens et al. 2015; Taylor 2000).

Idaho, Montana and Wyoming model results versus observations

Montana and Southern Idaho generally exhibit increased fuel loads due to fire suppression in the MC2 model, which matches with observations of denser forest cover from repeat photography (Gruell 1983; Butler and DeChano 2001; Klasner and Fagre 2002; Gruell 1986). Repeat photographs in Western Wyoming show a general increase in forest area and forest density in areas where growth is not restricted by soil type (Gruell 1980). MC2 output also shows a large increase in fuel loads in

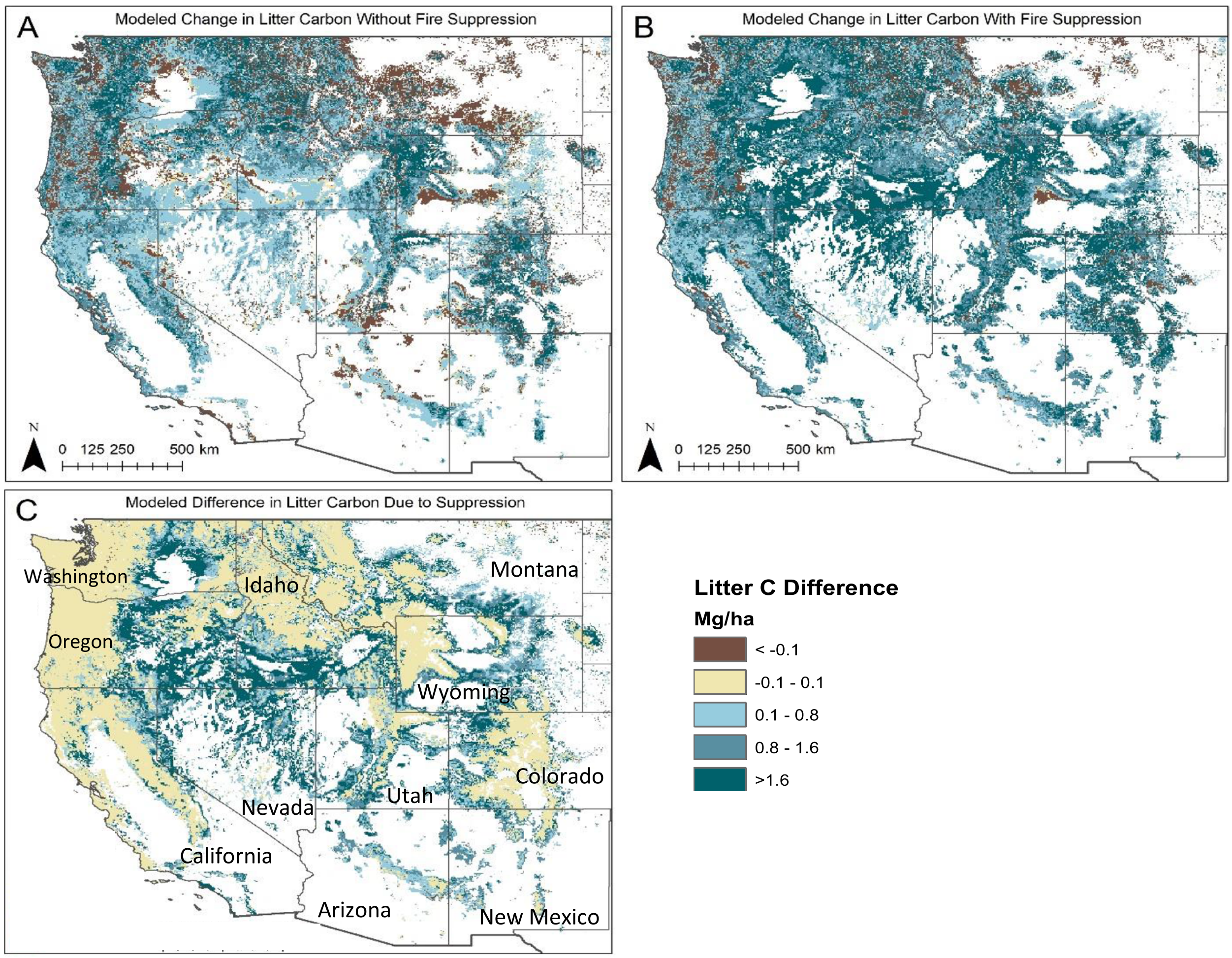

Fig. 12 Modeled changes in the carbon contained in surface litter between 1895 and 2010, in Mg/ha. **A** Model scenario without fire suppression. **B** Model scenario with fire suppression. **C** Change attributed to fire suppression (difference between **A** and **B**). State lines are shown for reference

this region (Figs. 11B and 12B) but does not attribute this increase to fire suppression (Figs. 11C and 12C) since this region was not modeled as experiencing a large amount of fire in either the fire-suppressed or non-fire-suppressed scenarios (Fig. 2).

Temporal patterns in fuel change

Having verified that the MC2 model is capturing large scale trends in fuel behavior over time, we can use the model to explore these large-scale fuel changes at temporal resolutions that are not possible with observed data alone. Time series of the changing fuel load—aggregated across the entire study area—show that not all types of fuel are expected to change in exactly the same way or to change monotonically over time (Fig. 13). In 1950, fire suppression in the model begins to reduce the area consumed by fire (Fig. 13A). The amount of dead wood carbon initially decreases due to fire suppression since fewer trees are killed by fire, but then increases as less dead wood is consumed (Fig. 13B). In response to less fire, litter and live aboveground carbon both begin to increase immediately, but the rate of change plateaus or reverses course in later years (Fig. 13C, D) as the difference in biomass consumed each year approaches zero (Fig. 13A) and potentially because accumulation rates are beginning to equilibrate with mortality/decay rates. This initial increase in modeled litter due to fire suppression, followed by a slowing of the rate of increase, is consistent with observations in Sierra Nevada study plots showing that surface fuel accumulated rapidly in the first decade following fire, but then reached a stable state where accumulation matched decomposition rates within about 40–90 years (Keifer et al. 2006).

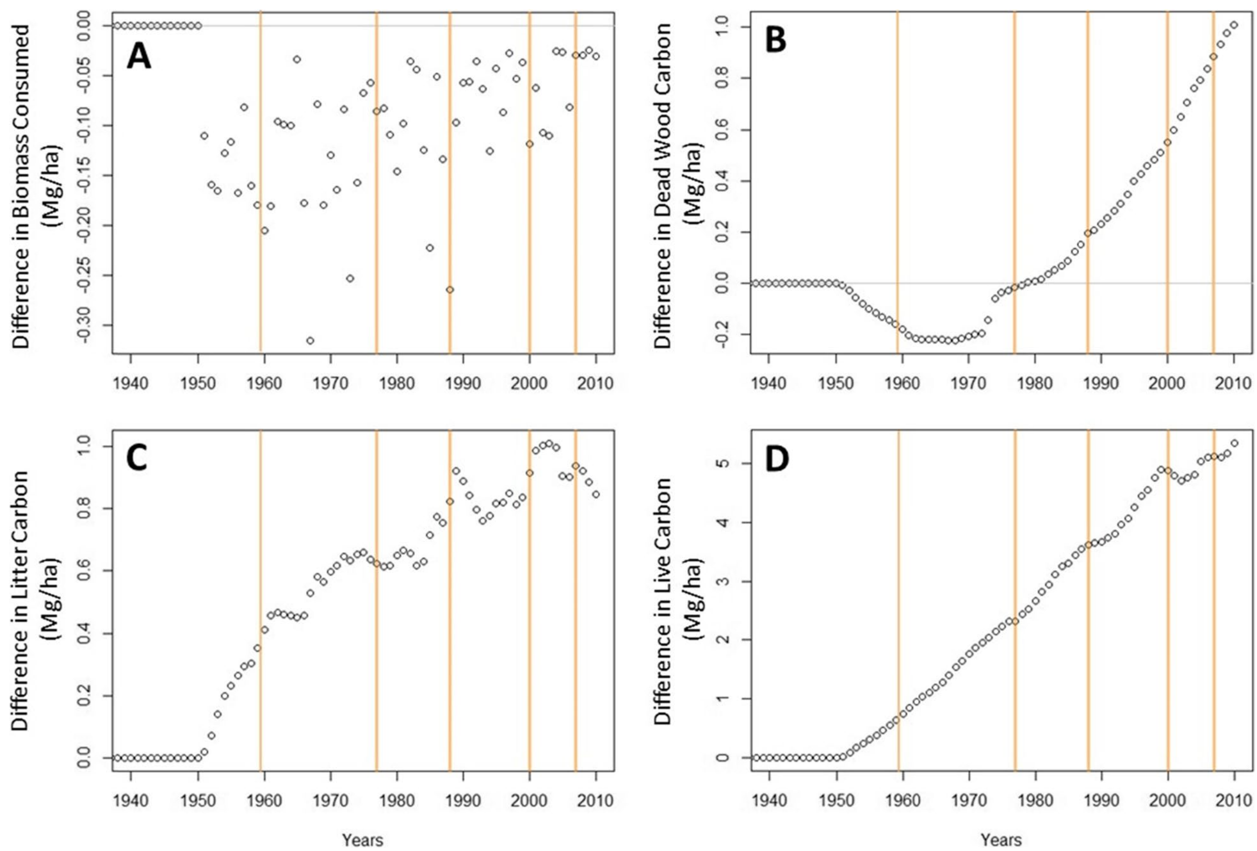

Fig. 13 **A** Difference in biomass consumed by wildfire between the fire suppression and no fire suppression model scenarios. **B**–**D** Differences in fuel loads averaged across all forested grid cells in the study area for each year (based on which grid cells were modeled as tree-dominated in 2010). All differences are calculated as the mean fire-suppressed value minus the mean value with no fire suppression. Vertical orange lines show the beginning years of large droughts which appear to impact the model results. Fuel loads shown are dead wood carbon (**B**), litter carbon (**C**), and live aboveground carbon (**D**)

Droughts beginning approximately in 1959, 1977, 1988, 2000, and 2007 (shown as vertical bars in Fig. 13) affected much of the Western USA, though to varying degrees (NOAA 2020). The MC2 output appears to show that increases in live fuels due to fire suppression are halted or reversed during these droughts (Fig. 13D), with fire suppression's impact on litter loads also reducing slightly during most droughts (Fig. 13C).

Discussion

Validating MC2 model output using FIA plot data

This study gave mixed results in terms of validating MC2 model output. At the scale of the western USA, changes in fuel loads over time were generally within realistic ranges as calculated by FIA data (Figs. 5, 6, and 7). However, spatial patterns of fuel load changes did not always match between MC2 and FIA (e.g., Fig. 4). Specifically, the model tended to predict decreases in live tree mass in the Pacific Northwest region over periods when FIA data showed increases, and throughout the Interior West, there were areas where the model did not capture observed decreases in live biomass (Fig. 4). The Pacific Northwest mismatch could be due to the model overpredicting mortality rates of older trees. Some of the model's overpredictions in live carbon accumulation could be due to the fact that it is not capturing tree mortality events due to causes such as drought stress (embolism is not simulated in MC2) or insect outbreaks (which the model does not incorporate). Plots with insect or disease damage should have been removed from the FIA data used for analysis, but some plots may have remained in the analysis if damage affected less than 25% of trees or if surveyors were not able to distinguish disease/pest mortality from background mortality.

We should not expect the model to exactly match observations, especially since the MC2 model does not incorporate information about actual forest disturbances (fire, disease, etc.), models potential vegetation rather than incorporating actual land use information, and assumes a fire occurs whenever conditions are optimal. Another limitation is that accurate soils data (which have an important impact on MC2 output with regard to plant water availability) and weather observations can be difficult to obtain in montane forested areas. However, we can expect the model outputs to fall within observed ranges, which it did accomplish within ecological sections and at the scale of the western USA. Given that MC2 was designed as a global model, this scale appears appropriate to the model's original intent.

While the FIA dataset is impressive and unique in terms of its large number of plots covering the entire USA, only a relatively small fraction of those sites could be used for our analysis of changing fuel loads over time (Fig. 4). Although the FIA program began in 1929, standardized data that could be used in this analysis were only available beginning in 1978, and some measurements (such as litter depth) were not standardized until 1999 (Burrill et al. 2018). A 20–30-year observational record cannot capture the full extent of fire suppression's impact on forest fuels over the past century. While we could not validate the full time period of fire suppression, this dataset did allow us to verify that modeled rates of change in various fuel types are within realistic ranges, at least for the past 30 years and within sections that contained enough undisturbed plots.

Comparing fire and fuel trends in MC2 output to historical observations

In Central Oregon, Utah, and the Southern Cascades mountain range of California, the MC2 model qualitatively matches reductions in fire frequency over the past century (Fig. 2B) that have been shown by fire scars in dendrochronological records (Taylor 2000; Voelker et al. 2019; Wadleigh and Jenkins n.d.). The low levels of fuels changes in Sequoia-Kings Canyon National Park in the southern Sierra Nevada, found by Stevens et al. (2020a; see Fig. 1), suggest low productivity, which matches with MC2 showing little fire activity in this study's area (Fig. 2A) as well as minimal changes in live forest carbon over time (Fig. 11). The model also appears to agree with fire scar reconstructions in the Colorado Front Range showing that fire suppression has only reduced fire frequency in the lower elevations of that region, while most of the area had infrequent fires even prior to active suppression (Fig. 2) (Sherriff and Veblen 2007).

While multiple studies have shown increased tree density in Sierra Nevada forests due to fire suppression (Hessburg et al. 2019; Keifer et al. 2006; Collins et al. 2011; Lydersen et al. 2013; Dolanc et al. 2014), the MC2 model shows relatively little increase in fuel loads directly attributable to fire suppression (Figs. 11 and 12). This could be due to how fire suppression was modeled: the model shows little difference in fire activity between the suppressed and non-suppressed scenarios in the Sierra Nevada (Fig. 2B). This suggests the model may under-predict the efficacy of fire suppression in the Sierra Nevada, especially given tree ring evidence showing reductions in fire occurrence over the last century (Stephens et al. 2007b). Some of this error may be due to the relatively poor quality of interpolated soil and weather data in mountain regions, which can cause inaccuracies in fire behavior modeling by misrepresenting water availability. In other areas, such as high elevation mountains in Colorado, the model results showing minimal impact of fire suppression on fuels (Figs. 12C and 13C) are consistent with observations (Sherriff and Veblen 2007).

Repeat photography in Colorado showed increased extent of forested area (Zier and Baker 2006), while MC2 shows a mix of increase and decrease in live fuels for that same location (Fig. 12B). This could be partly due to the observations showing regrowth following disturbances (including logging and pine beetle outbreaks) that were not modeled by MC2.

Areas where MC2 shows increases in carbon load even without fire suppression could reflect increases in forest density that are due to warmer temperatures rather than (or in addition to) fire suppression, especially in higher-elevation areas (Hessburg et al. 2019; Butler and DeChano 2001). One plot measurement study found that forest density increased from the 1930s to the 2000s even in high elevation forests (> 2500 m) that have had minimal fire suppression activity, suggesting that changing climatic conditions may be partially responsible for increased forest densities (Dolanc et al. 2014). Repeat photography studies have also shown increases in forest density at the tree line in both California (Vale 1987) and Montana (Klasner and Fagre 2002; Butler and DeChano 2001) over the past 50–80 years, which could be due to the influence of climate change.

Areas such as subalpine forests have climate-limited fire regimes, rather than fuel-limited, and thus fuel loads have relatively little impact on fire behavior in such areas (Schoennagel et al. 2004; Steel et al. 2015;

Hanan et al. 2021). The western USA contains a variety of climatic ecological subregions that cover a spectrum from climate-limited (mainly in northern areas) to fuel-limited (Hessburg et al. 2019). The importance of changing fuel loads to fire danger will therefore vary greatly depending on location. There can also be high spatial variability in fuel rates of change even within relatively small areas, as shown both by the many areas with intermixed pixels of positive and negative change from the MC2 model (Fig. 11) and from some studies showing mixes of plots with increases, decreases, and/or no change within the same study area (e.g., Taylor 2000). While this analysis focuses on the landscape scale, for many applications, it is important not to forget about finer-grained heterogeneity that can be caused by variations in topography, vegetation type, and disturbances.

The MC2 model showed a range of increasing and decreasing fuel loads in Oregon and Washington, with fire suppression causing higher fuel loads in the Eastern halves of both of these states (Figs. 11 and 12). Unfortunately, none of the long-term studies found in our literature search covered the Eastern portions of Oregon or Washington (Fig. 1). A study of old growth forests in Western Washington found slight declines in tree density over time (Franklin and DeBell 1988), which matches the MC2 model's finding that some areas of Western Washington forest decreased in live tree carbon even with fire suppression (Fig. 11B). Other long-term plots showed that biomass accumulation could continue even 80 years past the most recent disturbance but that it leveled out over longer periods (Duncan 2004). The MC2 model included almost no fire in western Oregon and Washington for the 116-year modeling period (Fig. 2), and thus, it is realistic that these forests may have reached their peak biomass under these undisturbed conditions, represented by a combination of increases and decreases in MC2 live biomass (Fig. 11B).

Both MC2 and observations showed large-scale responses of live fuel loads to drought. Figure 13 shows that increases in live fuels and litter due to suppression are partially reversed during widespread droughts, which matches observations of reductions in forest cover during droughts (van Mantgem et al. 2009; Allen and Breshears 1998). However, these droughts do not appear to slow the accumulation of dead wood (Fig. 13B), and high numbers of dead trees following droughts can potentially lead to higher severity fires (Stephens et al. 2018).

The observations (from FIA and other studies) do not directly show the causation for any increases or decreases in fuel loading, since they are not generally part of controlled experiments; observed fuel loads could vary for a variety of reasons related to fire, disease, climate, grazing, or other factors. However, some studies have compared nearby burned and unburned plots to show that increases in density are likely due to fire suppression (Collins et al. 2011). In comparing the model scenarios, any differences in fuels must be due to fire suppression since that is the only difference between the model scenarios. In many areas, studies of historical observations attributed increased fuel loads to fire suppression while the MC2 model suggested these increases were due to other factors. This discrepancy illustrates that although multiple lines of evidence agree that fuel loads in the western USA are generally increasing, it can be difficult to attribute this increase to a specific cause. At specific sites, local field studies are more reliable than a global scale model, but large scale models are still helpful in putting those site-specific studies into the context of larger patterns and for filling the gaps where observations are not available.

Benefits and limitations of this study's methods

The methods used in this study aimed to validate model results using the most direct observations available of changing fuel loads over time. Other potential sources of information regarding past fuel loads include studies that use space-for-time substitutions (measuring multiple plots that have had different amounts of time since the last disturbance and using these data to determine the relationship between fuel load and time since disturbance) or dendrochronology (using tree rings to infer the number and size of trees in a plot at various times in the past). Space-for-time substitutions can be valuable for understanding growth and decay rates but may not reflect actual historical trajectories due to changes in climate. While dendrochronology is a valuable tool for studying past forest structure, any interpretation of such datasets rely on multiple assumptions that are often not verifiable (Swetnam et al. 1999). Using repeat measurements (or photographs) rather than reconstructions from dendrochronology or from space-for-time substitutions ensures that we are only measuring actual changes, not inferring the change from another source of evidence.

Due to the types of data available, the analyses presented here contain some important limitations. For example, restricting our comparisons between FIA and MC2 data to areas without disturbance means that our analysis was spatially biased toward areas that are less likely to burn. Our strict requirements for both the FIA data comparison and literature search come at the expense of having a larger dataset. Also, variables were not always defined exactly the same in the FIA dataset and MC2 model.

Some mismatches between MC2 output and observations are due to necessary simplifications in the model's representation of the landscape. For example, MC2 does not capture changes in land management (such as altered grazing practices; Strickler 1961), invasive species that may modify the fire regime (Balch et al. 2013), non-lethal pest outbreaks, or the fact that fire suppression can lead to colonization by fire-intolerant tree species in areas that historically burned frequently (Stevens et al. 2020b).

The long-term studies available were valuable for their insights but did not provide consistent data that could be quantitatively compared to model output. Biomass data were not always available, so we were required to use stand density, percent cover, or forest extent as proxies for fuel load increases for many of the studies from the literature search. We could have used allometric equations to estimate biomass from the measurements available in some cases, but this would have resulted in very few data points for comparison. Few long-term studies included measures of surface fuels, although surface fuels can be very important for initiating a potential crown fire (Stephens et al. 2012, 2009). The results from our literature search are also not necessarily a comprehensive list of available historical measurements of fuel loads; there could be other information that was missed.

Repeat photography is valuable because it is often the only objective record available to show how a given landscape has changed over long time periods (Webb et al. 2010), but of course it can only provide qualitative information. Also, historical photos must often be chosen opportunistically, rather than photos being chosen based on randomized selection criteria that would avoid bias.

Fire suppression and the resulting tree density can make forests more susceptible to drought stress, diseases, and pests (Voelker et al. 2019). While increased drought stress can be captured by the MC2 model, it does not capture causes of mortality such as pest and insect outbreaks. Many FIA plots removed from our analysis showed large decreases in live tree biomass due to disturbances other than fire (including disease and insect damage) and corresponding increases in dead wood mass much larger than those predicted by the model (results not shown). Changing fuel loads and fuel types due to widespread disease/insect mortality is an important factor in forest management that cannot be captured by this type of model (Stephens et al. 2018).

Conclusions

The motivation for this analysis was to validate the common claim that century-scale fuel load increases have been occurring in the western USA. Such increases—along with climate change and human population factors—combine to create the potential for large and destructive wildfires. A major difficulty in validating models of fuel loads lies in the fact that very little data exist extending back more than three decades. However, combining information from the FIA database and other long term forestry studies allowed us to compare observations to MC2 modeled fuel loads over a range of landscapes and time periods.

The MC2 model appears to match the distribution of changing mass of live and dead trees fairly well at a large scale. However, the model's changes in fuel loads are generally difficult to validate due to a scarcity of observations over long time scales. In those areas and time periods where MC2 outputs of fuel trends *can* be validated, there is generally a positive correlation between the model and observations (except for live aboveground carbon). While some ecological sections were modeled closely, others showed opposite trends in fuel loads between the model and plot data. The model tends to underestimate the maximum rates of increase in fuel loads, except for litter. It appears that the MC2 model can be used to capture general, large-scale trends (which was the original intent of the model) especially for carbon loads in live and standing dead trees, but should not be expected to match observations at specific point locations.

Both the MC2 model and historical observations demonstrate that there has been a widespread increase in fuels over the past century. This increase is not completely ubiquitous across all of the western USA; areas with climate-limited fire regimes such as Western Oregon and Western Washington show the least increase (and sometimes even decreases) in fuel loads over the past century. While the model generally appears to match trends in fire behavior, it appears to not be capturing the extent of fire suppression in some areas (especially the northern Sierra Nevada of California, where multiple studies demonstrate the impact of fire suppression on forest density) and therefore may be underestimating the impact of fire suppression on vegetation in those locations. Some of the fuel increases in the western USA may be due to changing climate, increased atmospheric CO_2 concentrations, or simply natural succession, but a substantial amount of these increases can be attributed to reduced fire frequencies.

Appendix A

Table 2

Table 2 The following table gives a summary of all long-term studies we found that quantified changing fuel loads and/or forest cover over time. Some of these studies are not included in Fig. 1 if there were other studies in the same location that provided the same information or covered a longer period of time

Title	Author and year published	Region	Veg type	Years of study	Disturbance during study	Summary	URL
Landscape Changes in the Southwestern United States: Techniques, Long-term Data Sets, and Trends	Allen et al. 1998	Southwest USA	Multiple	1899–1977	?	Juniper expansion can be observed from repeat photos	https://www.researchgate.net/profile/Thomas_Sisk/publication/235079223_Perspectives_on_the_Land_Use_History_of_North_America_A_Context_for_Understanding_Our_Changing_Environment/links/5886bd5daca272b7b44cd66b/Perspectives-on-the-Land-Use-History-of-North-America
Long Term Vegetation Dynamics of Ponderosa Pine Forests	Bakker 2005 (Dissertation)	Northern AZ	Ponderosa Pine	1941–2004	Grazing on some plots	Overstory cover increased while understory decreased.	https://www.mendeley.com/viewer/?fileId=1326931b-fd88-5527-15f3-a7354491dd5b&documentId=9aa57f69-b3a1-3aa5-9730-a8087b28cfda
Periodic Remeasurement of the Gus Pearson Natural Area	Fule et al., 2001 (Report)	Gus Pearson, AZ	Ponderosa pine	1920–2000	No harvesting	General trend toward declining growth. Increased mortality since 1945.	https://openknowledge.nau.edu/2539/
Comparing Tree-Ring Chronologies and Repeated Timber Inventories as Forest Monitoring Tools	Biondi 1999	Gus Pearson, AZ	Ponderosa pine	1920–1990	No harvesting	Decreased growth rates and higher stand density	https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/1051-0761(1999)009%5B0216:CTRCAR%5D2.0.CO%3B2
Twentieth-century changes in forests of the Sierra Nevada	Bouldin 1999	Northern Sierra Nevada, CA	Conifer forests	1935–1992	Fire, drought mortality	Used a large number of forestry plots to show that density of small trees has increased greatly, with decreases in large tree density. Standing dead tree densities are higher than before.	https://www.proquest.com/openview/aac2fa595d16ac697787c3d81b2d330f/1?pq-origsite=gscholar&cbl=18750&diss=y

Table 2 (continued)

Title	Author and year published	Region	Veg type	Years of study	Disturbance during study	Summary	URL
Stand dynamics and topographic setting influence changes in live tree biomass over a 34-year permanent plot record in a subalpine forest in the Colorado Front Range	Chai et al. 2019	CO	Subalpine forest	1982–2016	insects and pathogens	Despite increased mortality rates over time, there was also a trend of increasing biomass in live trees.	https://doi.org/10.1139/cjfr-2019-0023
Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests	Collins et al. 2011	Sierra Nevada, CA	Conifer trees, forb and shrub cover	1911–2007	Fire on some plots	Re-sampled a 1911 timber inventory. Areas with no fire or low severity fire had higher tree density and canopy cover relative to 1911.	esajournals.onlinelibrary.wiley.com/doi/full/10.1890/ES11-00026.1%4010.1002/%28ISSN%292150-8925%28CAT%29VirtualIssue%28VI%29ECS2
Changing forest structure across the landscape of the Sierra Nevada, CA, USA, since the 1930s	Dolanc et al. 2014	Central-Northern Sierra Nevada, CA	Conifer forests	1930s–2000s	Fire in some areas	Used plot data from VTM and FIA to look at changes in forest structure over time (used averages w/in similar regions, not remeasurements of identical plots). Found similar results as Bouldin (above)	https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/ES14-00103.1
Climate, environment, and disturbance history govern resilience of western North American Forests	Hessburg et al. 2019	Western USA	Multiple	1925–2008 (and other time ranges)	multiple	Review of forest structure change across western USA, including repeat photography.	https://kopernio.com/viewer?doi=10.3389/fevo.2019.00239&route=6
Spatiotemporal Variability of Wildland Fuels in US Northern Rocky Mountain Forests	Keane 2016	Rocky Mountains (MT, ID)	All types of fuels	1993–2004	no disturbance	There is high spatiotemporal variability in fuel accumulation, especially for larger fuels.	http://www.mdpi.com/1999-4907/7/7/129
Long-term surface fuel accumulation in burned and unburned mixed-conifer forests of the Central and Southern Sierra Nevada	Keifer et al. 2006	Sierra Nevada, CA	Fuel loads	1971–2003	Fire on some plots	Fuel load increased over time in unburned plots. In burned plots, 31 years post-fire fuel loads were higher than pre-fire.	http://fireecologyjournal.org/journal/abstract/?abstract=11

Table 2 (continued)

Title	Author and year published	Region	Veg type	Years of study	Disturbance during study	Summary	URL
A Half Century of Change in Alpine Treeline Patterns at Glacier National Park, Montana, U.S.A.	Klasner and Fagre 2002	MT	High-altitude forests (near treeline)	1945–1991 (some photos from 1927 to 1997)	Road/trail construction/maintenance	Forest homogeneity increased due to greater area with trees and greater tree density within existing patches.	https://doi.org/10.1080/15230430.2002.12003468
Change in Vegetation Patterns Over a Large Forested Landscape Based on Historical and Contemporary Aerial Photography	Lydersen and Collins 2018	Sierra Nevada, CA	Conifer Forest (via aerial photos)	1941–2005	Fire in some areas	The amount of area with dense forest cover increased, and continuous patches of dense forest grew larger.	http://link.springer.com/10.1007/s10021-018-0225-5
Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Reference conditions and long-term changes following fire suppression and logging	Lydersen et al. 2013	Sierra Nevada, CA	Conifer trees	1929–2008	Logging, all plots	1929 (pre-logging) was treated as a reference condition, with 2007/8 showing regrowth ~80 years after logging. Canopy cover was higher in 2007/8 compared to 1929.	www.sciencedirect.com/science/article/pii/S0378112713003228
Forest vegetation change and surface hydrology following 47 years of managed wildfire	Stevens et al., 2020a	Sierra Nevada, CA	Conifer trees, shrubs	1970–2017	Fire on some plots	Slight increase in total tree density; decrease in density of large trees. Increase in the number of plots with shrub presence.	https://doi.org/10.1007/s10021-020-00489-5
Southern Cascades Bioregion. Ch. 12 of "Fire in California's Ecosystems"	Skinner and Taylor, 2018	So. Cascades, CA	Conifer forests	1925–1993	None	Shows increasing tree density, high levels of recruitment, and some mortality of large trees, as well as increased litter cover, using repeat photography.	https://www.degruyter.com/view/books/9780520961913/9780520961913-015/9780520961913-015.xml
Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, U.S.A.	Taylor 2000	So. Cascades, CA	Conifer forests	1925–1993	None	Repeat photography and tree ring records show increased density in Jeffrey Pine and White Fir forests, but little change in red fir forests. Photos also show increased litter cover.	**https://doi.org/10.1046/j.1365-2699.2000.00353.x**

Table 2 (continued)

Title	Author and year published	Region	Veg type	Years of study	Disturbance during study	Summary	URL
Long-term response of old-growth stands to varying levels of partial cutting in the Eastside Pine Type	Dolph et al. 1995	East side of Cascades, CA	Conifer forests	1938–1991	None	Repeat measurements show increased density of small trees, but 6% reduction in "saw-timber component", leading to an overall 13-32% increase in volume of trees over 3.6" DBH.	https://doi.org/10.1093/wjaf/10.3.101
Twenty-year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, USA	Smith and Smith 2005	CO	Aspen and conifers	1979–2003	None?	Aspen density remained stable or decreased, while conifer basal area increased over the 20 year study period.	https://doi.org/10.1016/j.foreco.2005.03.018
Vegetation Change and Park Purposes in the High Elevations of Yosemite National Park, California	Vale 1987	Yosemite, CA	High-altitude forests (near treeline)	1900–1985		Forests at the upper forest line have increased in density, meadows have been encroached by trees	https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1467-8306.1987.tb00141.x
Widespread Increase of Tree Mortality Rates in the Western United States	van Mantgem et al. 2009	Western USA (CA, OR, WA, ID, CO, AZ)	Forests > 200 years old	~ 1981–2004 (first measurement dates ranged from 1955 to 1994)	Undisturbed	Mortality increased across size classes and elevation ranges. Mean tree density and basal area in the study plots declined slightly during the study period.	https://science.sciencemag.org/content/323/5913/521
Comparison of Historical and Contemporary Forest Structure and Composition on Permanent Plots in Southwestern Ponderosa Pine forests	Moore et al., 2004	AZ and NM	Ponderosa pine	1909–1999	Logging, all plots	Stand density increased greatly; tree diameters shifted toward smaller size classes.	https://academic.oup.com/forestscience/article/50/2/162/4617546
Drought-induced shift of a forest–woodland ecotone: Rapid landscape response to climate variation	Allen and Breshears 1998	New Mexico	Ponderosa pine	1935–1975	drought	ponderosa pine forest receded quickly during a drought	https://www.pnas.org/content/95/25/14839.short

Table 2 (continued)

Title	Author and year published	Region	Veg type	Years of study	Disturbance during study	Summary	URL
Spatial Patterns of Pinyon–Juniper Woodland Expansion in Central Nevada	Weisberg et al. 2007	Central NV	Pinyon-juniper woodlands	1966–1995	?	Analysis of aerial photos showed an 11% increase in woodland area.	https://doi.org/10.2111/05-224R2.1
Post-1900 Mule Deer Irruptions in the Intermountain West: Principle Causes and Influences	Gruell 1986	Inter-mountain West (ID, MT, NV, UT, WY)	Various woody plants	1868–1982	Grazing and Fire Suppression	Widespread succession from grass dominance to trees and shrubs due to grazing (Reducing competing grass cover) and fire suppression.	https://www.fs.fed.us/rm/pubs_int/int_gtr206.pdf
Vegetation differences in desert shrublands of western Utah's Pine Valley between 1933 and 1989	Yorks et al. 1992	Western UT	Desert shrubland	1933–1989	Grazing	Canopy cover of grasses greatly increased, with some increase in shrub cover. Density of shrubs decreased (shrubs/m2)	https://journals.uair.arizona.edu/index.php/jrm/article/view/8785
Changes in pinyon-juniper woodlands in western Utah's Pine Valley between 1933-1989	Yorks et al. 1994	Western UT	Pinyon-juniper woodlands	1933–1989	Grazing	Tree % cover decreased while density increased, due to shift in tree cover from juniper to pinyon (narrower crown). Shrub and grass % cover increased. Shrub density increased.	https://repository.arizona.edu/bitstream/handle/10150/644369/8955-8836-1-PB.pdf?sequence=1
A century of vegetation change in the San Juan Mountains, Colorado: An analysis using repeat photography	Zier and Baker 2006	CO	Conifer and aspen forests, grasslands	~1900–~2000	Varying disturbances	Both conifers and deciduous trees increased in extent, partially as recovery from disturbances. There was some encroachment of trees into grass/shrublands.	https://doi.org/10.1016/j.foreco.2006.02.049
Fire and vegetative trends in the Northern Rockies: interpretations from 1871-1982 photographs	Gruell 1983	Northern Rockies, MT	Forest	1871–1982		Woody vegetation increased due to suppressed wildfire	https://www.fs.usda.gov/treesearch/pubs/32994

Table 2 (continued)

Title	Author and year published	Region	Veg type	Years of study	Disturbance during study	Summary	URL
ENVIRONMENTAL CHANGE IN GLACIER NATIONAL PARK, MONTANA: AN ASSESSMENT THROUGH REPEAT PHOTOGRAPHY FROM FIRE LOOKOUTS	Butler and DeChano 2001	MT	Montane forest	1935–1990s	Avalanches, glacial recession, anthropogenic developments	Increased forest density and extent likely due to a combination of fire suppression and climate change (including receding glaciers)	https://doi.org/10.1080/02723646.2001.10642744
Fire's Influence on Wildlife Habitat on the Bridger-Teton National Forest, Wyoming - Volume I: Photographic Record and Analysis	Gruell 1980	WY	Multiple tree and shrub types	1872–1975	Some fires, mostly prior to 1941	Increases in conifers and sagebrush	https://digitalcommons.usu.edu/barkbeetles/95/
100,000 Trees Can't Be Wrong: Permanent Study Plots and the Value of Time	Duncan 2004 (FS publication for managers)	Pacific NW (OR, WA)	Multiple forest types	1910–2002	Varying disturbances	There is a network of long term forestry plots in OR and WA, managed by the PNW region of the USFS. Biomass accumulation can continue even after 80 years post-disturbance.	https://www.fs.usda.gov/treesearch/pubs/6956
Thirty-six years of tree population change in an old-growth Pseudotsuga- Tsuga forest	Franklin and DeBell 1988	Cascade Range, WA	Conifers	1947–1983	Undisturbed	Old growth forest showed slight decline in tree density. The diameter distribution shifted upward, and 22% of the original stems died during the study period (though this was almost matched by recruitment)	https://doi.org/10.1139/x88-093
Carbon stocks and accumulation rates in Pacific Northwest forests: role of stand age, plant community, and productivity	Gray et al., 2016	Pacific NW (OR, WA, CA, ID)	Live and dead trees, many types	1993–2007	disturbance on some plots	Older trees accumulate C slower, but forests still have net C increase until ~400 years old when high mortality outweighs growth	http://doi.wiley.com/10.1002/ecs2.1224

Table 2 (continued)

Title	Author and year published	Region	Veg type	Years of study	Disturbance during study	Summary	URL
Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington	Sollins 1982	Pacific NW (OR,WA)	Coarse woody debris	16–46 year span	Undisturbed	Tree mortality resulted in dry-matter transfer of 1.5–4.5 Mg•ha − 1•year− 1 of boles and branches to the forest floor and 0.3–1.3 Mg•ha − 1•year− 1 of large-diameter roots directly to the mineral soil. , with decay rates slower than accumulation.	http://www.nrcresearchpress.com/doi/10.1139/x82-003
Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada	Stephens et al. 2015	Southern Sierra Nevadas, CA	Ponderosa pine and mixed conifer forest	1911–2005	Very little disturbance	Compared tree density and canopy cover measured by 1911 surveys and modern FIA inventories in same area, though not the same exact plot locations. Found increases in tree density, fir dominance, and canopy cover.	https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/ES14-00379.1
Vegetation and Soil Condition Changes on a Subalpine Grassland in Eastern Oregon	Strickler 1961	Wallowa Mountains, OR	Grasslands/shrubs	1938–1956	Grazing	Total biomass and veg. cover increased over the 20 years due to improved range management.	https://www.fs.fed.us/pnw/pubs/pnw_os_rp-40.pdf

Appendix B

In order to provide a more detailed comparison of the distributions of FIA and modeled data, we used cumulative distribution curves as suggested in Riemann et al. (2010). These curves are created by calculating the mean rate of change within each region, ranking these mean values from the smallest change in fuel load (or most negative) to the greatest change, then dividing this rank number by the total number of regions to obtain a value between 0 and 1. Values are then plotted with the fuel load change on the x-axis, and the rank (normalized to be between 0 and 1) on the y-axis. These plots allow us to show how the distribution of change values varies between the modeled and FIA data. We show results using two scales: ecological sections and ecological subregions contained within those sections.

Figure 14

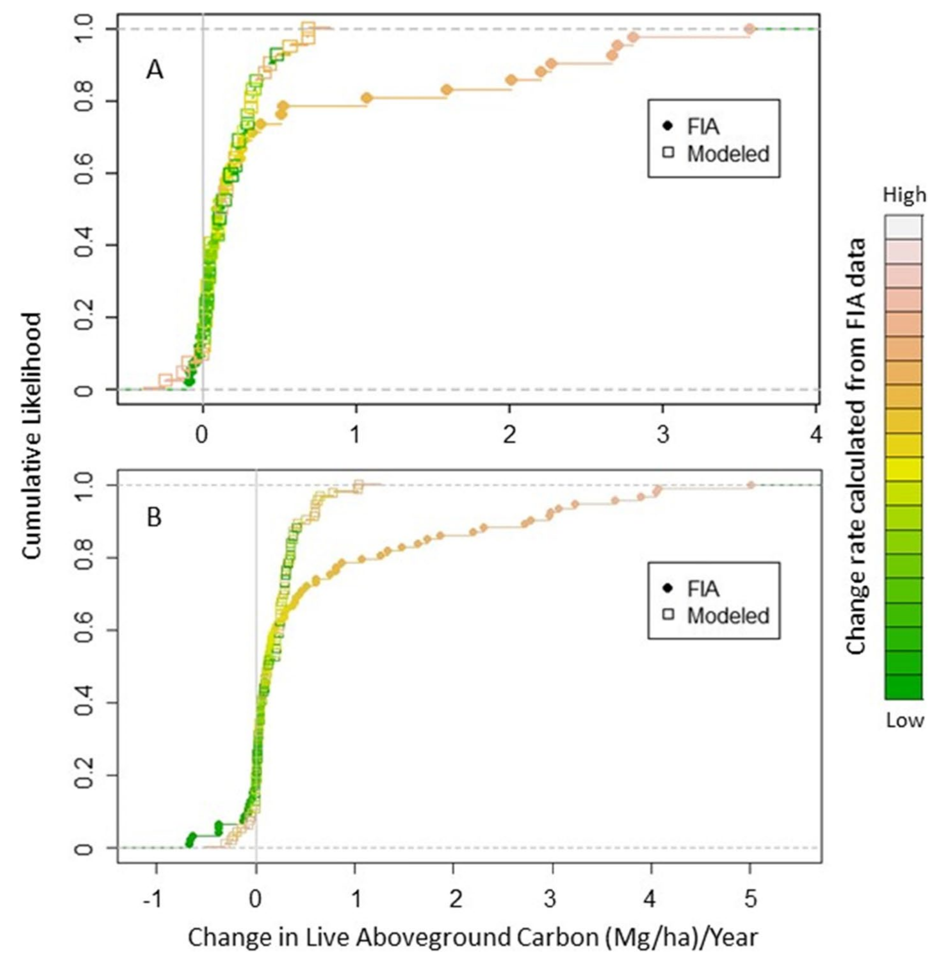

Fig. 14 Cumulative distribution of modeled (squares) versus measured (circles) rates of change in live aboveground carbon. Each point on the curve represents the mean within an ecological section (**A**) or subregion (**B**). Points are colored according to the ranking of the FIA data from most negative to most positive rate of change, such that if regions' rates of change were ranked exactly the same in each dataset the color pattern would be the same for both curves. The largest positive rates of change are shown in pink for both curves, showing that both datasets agree as to the group of subregions with the fastest increases in carbon mass over time, but the color mismatch at the left end of each curve shows that those subregions that the FIA data shows to be losing the most live carbon are not captured by the model

Figure 15

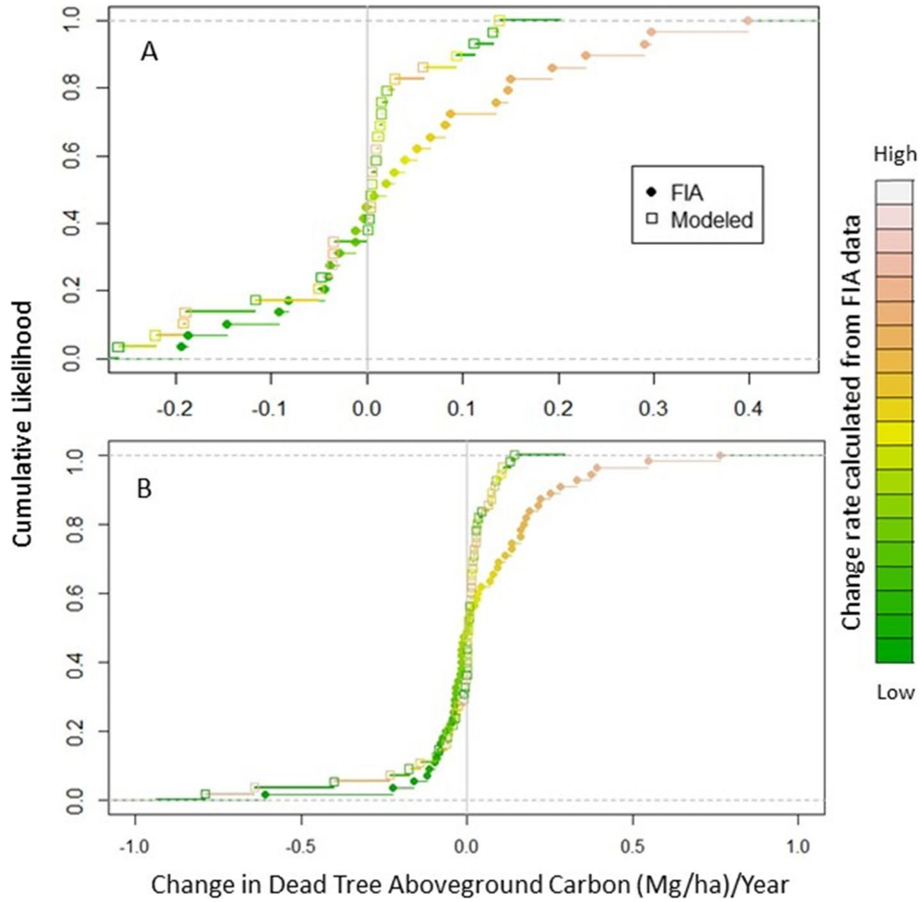

Fig. 15 Cumulative distributions of modeled (squares) versus measured (circles) rates of change in the carbon of dead trees. Each point on the curve represents the mean within an ecological section (**A**) or subregion (**B**); points are colored based on that subregion's rate of change according to the FIA dataset

Figure 16

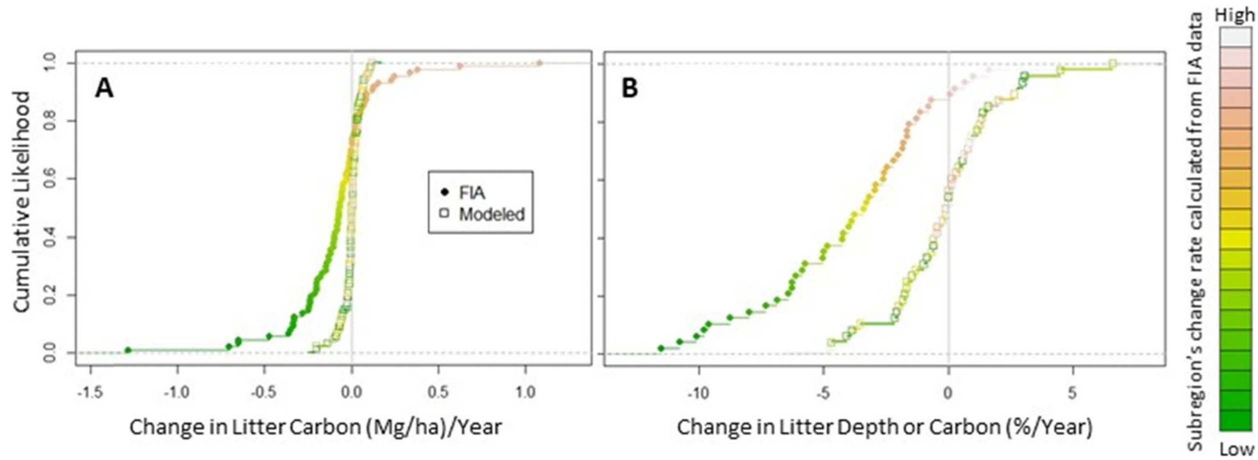

Fig. 16 Cumulative distributions of the rate of change in litter carbon at the ecological subregion scale. Model results are shown as squares, and plot measurements as circles. Results are shown in terms of Mg ha^{-1} $year^{-1}$ (**A**) and as % change per year in litter depth for FIA and litter carbon for the model (**B**). Each point in the cumulative distribution is colored by ecological subregion such that if the order of ecological subregions from most negative to most positive change was the same in both datasets, the colors would match for each y value. The fact that most points with negative changes are in green for both datasets in (**A**) shows that most (but not all) of the ecological subregion's changes have the same direction of change for both datasets

Appendix C

The maps in this appendix show the results of doing analyses at the ecological subregion level rather than larger ecological sections.

Figure 17

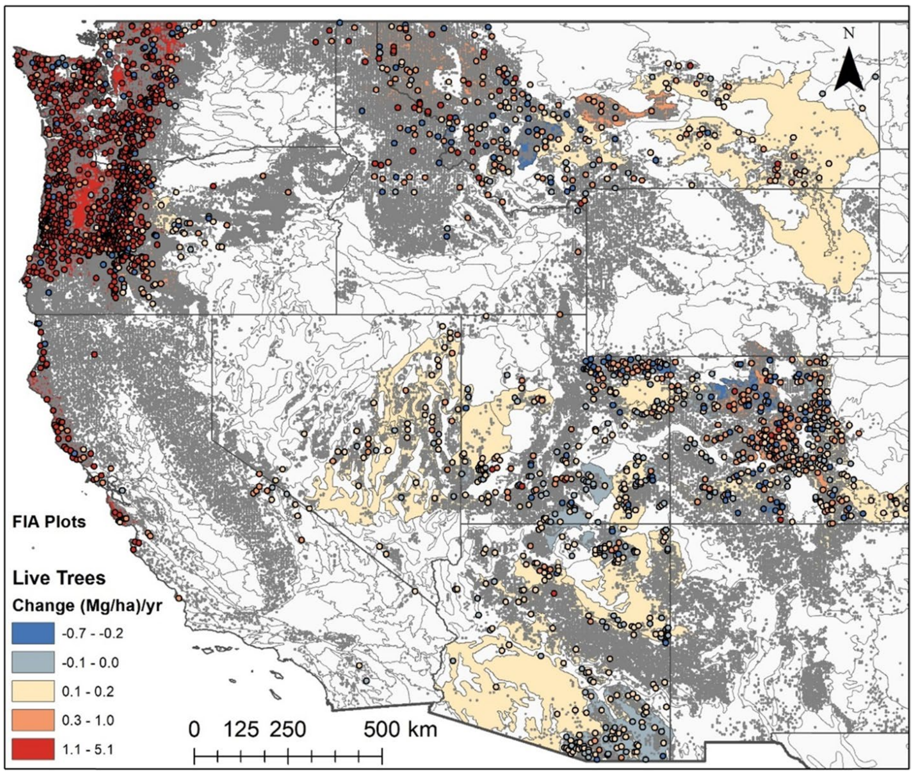

Fig. 17 Change in live aboveground carbon (Mg ha^{-1} year^{-1}) in all FIA plots with no disturbance and at least 10 years between remeasurements. Ecological subregion is outlined in gray; those containing at least 6 plots are shown in the color corresponding to mean change among all plots. Small gray dots show the locations of other FIA plots that did not have disturbance-free data spanning at least 10 years

Figure 18

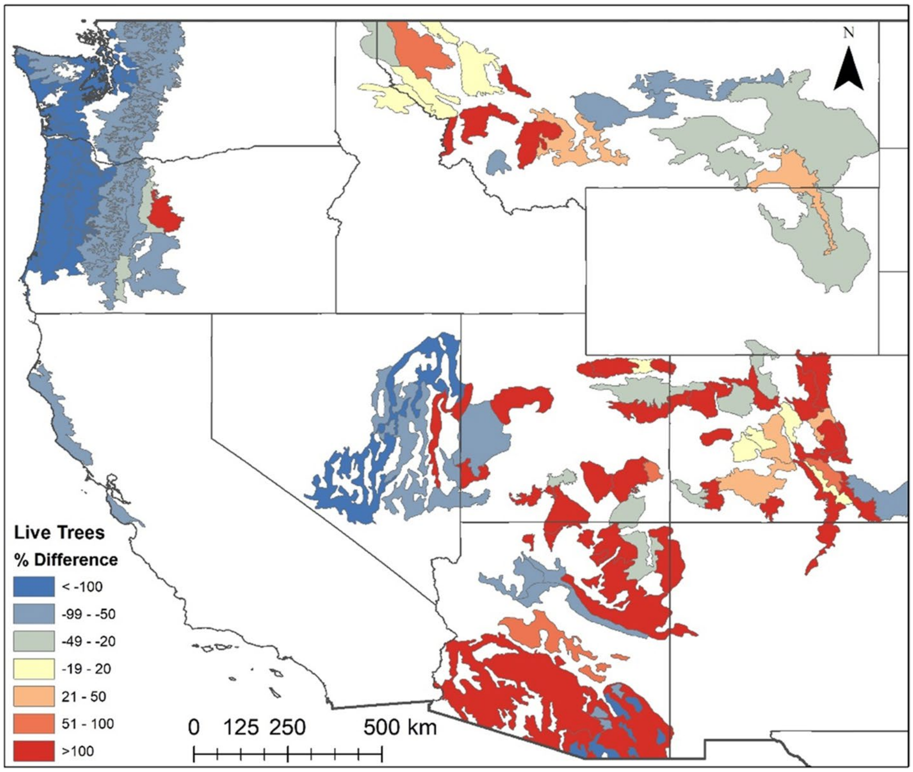

Fig. 18 Percent difference between modeled and FIA estimates of the rate of change in live aboveground tree carbon, at the ecological subregion scale. Blue: The model estimated slower increases (or greater decreases) over time than the FIA data. Yellow: The modeled slope of C/year was within 20% of the FIA estimate. Red: The model estimated a greater increase (or less of a decrease) in carbon than shown by the FIA data

Abbreviations
FIA: Forest Inventory and Analysis; FIADB: Forest Inventory and Analysis Database; DBH: Diameter at Breast Height.

Acknowledgements
We thank Dr. R. Keane, Emeritus Research Ecologist US Forest Service, for numerous conversations inspiring this project.

Authors' contributions
G. Boisrame performed the majority of data analysis and literature searches for this manuscript and contributed to writing in all sections. T. Brown provided the original idea for this manuscript, provided datasets, and contributed to writing in multiple sections of the manuscript. D. Bachelet provided datasets, made substantial contributions to interpretation of data, and contributed to writing in multiple sections of the manuscript. All authors were involved in final editing. The authors read and approved the final manuscript.

Funding
This work was undertaken via US Forest Service Supplemental Agreement 19-CS-11132543-079.

Availability of data and materials
- The FIA data used here is available from https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html.
- MC2 model data is available from https://climate.northwestknowledge.net/IntegratedScenarios/data_portal.php by selecting "Vegetation: MC2" under "PRODUCTS."

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Division of Hydrologic Sciences, Desert Research Institute, Las Vegas, NV 89119, USA. [2]Division of Atmospheric Sciences, Desert Research Institute, Reno, NV 89512, USA. [3]Department of Biological and Ecological Engineering, Oregon State University, Corvallis, OR 97331, USA.

Received: 5 December 2021 Accepted: 14 March 2022
Published online: 10 June 2022

References
Acker, S.A., T.E. Sabin, L.M. Ganio, and W.A. McKee. 1998. Development of Old-Growth Structure and Timber Volume Growth Trends in Maturing Douglas-Fir Stands. *Forest Ecology and Management* 104 (1–3): 265–280. https://doi.org/10.1016/S0378-1127(97)00249-1.

Agee, James K., and Carl N. Skinner. 2005. Basic Principles of Forest Fuel Reduction Treatments. *Forest Ecology and Management* 211: 83–96. https://doi.org/10.1016/j.foreco.2005.01.034.

Allen, Craig D., Julio L. Betancourt, and Thomas W. Swetnam. 1998. Landscape Changes in the Southwestern United States: Techniques, Long-Term Data Sets, and Trends. In *Perspectives on the Land Use History OfNorth America: A Context for Understanding Our Changing Environment*, ed. Thomas D. Sisk, 3rd ed. USGS https://www.researchgate.net/profile/Thomas_Sisk/publication/235079223_Perspectives_on_the_Land_Use_History_of_North_America_A_Context_for_Understanding_Our_Changing_Environment/links/5886bd5daca272b7b44cd66b/Perspectives-on-the-Land-Use-History-of-North-.

Allen, Craig D., and David D. Breshears. 1998. Drought-Induced Shift of a Forest–Woodland Ecotone: Rapid Landscape Response to Climate Variation. *Proceedings of the National Academy of Sciences* 95 (25).

Bachelet, Dominique, Ken Ferschweiler, Timothy J. Sheehan, Benjamin M. Sleeter, and Zhiliang Zhu. 2015. Projected Carbon Stocks in the Conterminous USA with Land Use and Variable Fire Regimes. *Global Change Biology* 21 (12): 4548–4560. https://doi.org/10.1111/gcb.13048.

Bachelet, Dominique, Kenneth Ferschweiler, Timothy J. Sheehan, Benjamin M. Sleeter, and Zhiliang Zhu. 2018. Translating MC2 DGVM Results into Ecosystem Services for Climate Change Mitigation and Adaptation. *Climate* 6 (1): 1. https://doi.org/10.3390/CLI6010001.

Bachelet, Dominique, James M. Lenihan, Christopher Daly, Ronald P. Neilson, Dennis S. Ojima, and William J. Parton. 2001. MC1: A Dynamic Vegetation Model for Estimating the Distribution of Vegetation and Associated Ecosystem Fluxes of Carbon, Nutrients, and Water. *Pacific Northwest Research Station*. https://www.fs.fed.us/pnw/pubs/pnw_gtr508.pdf.

Bachelet, Dominique, and David Turner, eds. 2015. *Global Vegetation Dynamics. Geophysical Monograph Series*. Hoboken: Wiley https://doi.org/10.1002/9781119011705.

Bakker, J.D. 2005. "Long-Term Vegetation Dynamics of Ponderosa Pine Forests." https://openknowledge.nau.edu/2807/.

Balch, Jennifer K., Bethany A. Bradley, John T. Abatzoglou, R. Chelsea Nagy, Emily J. Fusco, and Adam L. Mahood. 2017. Human-Started Wildfires Expand the Fire Niche across the United States. *Proceedings of the National Academy of Sciences of the United States of America* 114 (11): 2946–2951. https://doi.org/10.1073/PNAS.1617394114.

Balch, Jennifer K., Bethany A. Bradley, Carla M. D'Antonio, and José Gómez-Dans. 2013. Introduced Annual Grass Increases Regional Fire Activity across the Arid Western USA (1980–2009). *Global Change Biology* 19 (1): 173–183. https://doi.org/10.1111/GCB.12046.

Biondi, Franco. 1996. Decadal-Scale Dynamics at the Gus Pearson Natural Area: Evidence for Inverse (a)Symmetric Competition? *Canadian Journal of Forest Research* 26 (8): 1397–1406. https://doi.org/10.1139/x26-156.

Biondi, Franco. 1999. Comparing Tree-Ring Chronologies and Repeated Timber Inventories as Forest Monitoring Tools. *Ecological Applications* 9 (1): 216–227. https://doi.org/10.1890/1051-0761(1999)009[0216:CTRCAR]2.0.CO;2.

Boisramé, Gabrielle F.S., S.E. Thompson, M. Kelly, J. Cavalli, K.M. Wilkin, and S.L. Stephens. 2017. Vegetation Change during 40 Years of Repeated Managed Wildfires in the Sierra Nevada, California. *Forest Ecology and Management* 402. https://doi.org/10.1016/j.foreco.2017.07.034.

Bouldin, Jim. 1999. *Twentieth-Century Changes in Forests of the Sierra Nevada, California*. University of California at Davis https://search.library.ucdavis.edu/primo-explore/fulldisplay?docid=01UCD_ALMA51269170670003126&context=L&vid=01UCD_V1&lang=en_US&search_scope=everything_scope&adaptor=Local%2520Search%2520Engine&isFrbr=true&tab=default_tab&query=any,contains,Bouldin%2520Sierra%25.

Burrill, Elizabeth A., Andrea M. Wilson, Jeffery A. Turner, Scott A. Pugh, James Menlove, Glenn Christensen, Barbara L. Conkling, and Winnie David. 2018. "The Forest Inventory and Analysis Database: Database Description and User Guide Version 8.0 for Phase 2." http://www.fia.fs.fed.us/library/database-documentation.

Butler, David R., and Lisa M. DeChano. 2001. ENVIRONMENTAL CHANGE IN GLACIER NATIONAL PARK, MONTANA: AN ASSESSMENT THROUGH REPEAT PHOTOGRAPHY FROM FIRE LOOKOUTS. *Physical Geography* 22 (4): 291–304. https://doi.org/10.1080/02723646.2001.10642744.

Chai, Rachel K., Robert A. Andrus, Kyle Rodman, Brian J. Harvey, and Thomas T. Veblen. 2019. *Stand Dynamics and Topographic Setting Influence Changes in Live Tree Biomass over a 34-Year Permanent Plot Record in a Subalpine Forest in the Colorado Front Range*, 1256–1264. Canadian Journal of Forest Research https://doi.org/10.1139/cjfr-2019-0023.

Cleland, D.T., J.A. Freeouf, J.E. Keys, G.J. Nowacki, C.A. Carpenter, and W.H. McNab. 2007. Ecological Subregions: Sections and Subsections for the Conterminous United States. *General Technical Report WO-76D.* 76D. https://doi.org/10.2737/WO-GTR-76D.

Collins, Brandon M., Richard G. Everett, and Scott L. Stephens. 2011. Impacts of Fire Exclusion and Recent Managed Fire on Forest Structure in Old Growth Sierra Nevada Mixed-conifer Forests. *Ecosphere* 2 (4): 1–14. https://doi.org/10.1890/ES11-00026.1@10.1002/(ISSN)2150-8925(CAT)VIRTUALISSUE(VI)ECS2.

Collins, Brandon M., Jamie M. Lydersen, Danny L. Fry, Katherine Wilkin, Tadashi Moody, and Scott L. Stephens. 2016. Variability in Vegetation and Surface Fuels across Mixed-Conifer-Dominated Landscapes with over 40 Years of Natural Fire. *Forest Ecology and Management* 381 (December): 74–83. https://doi.org/10.1016/J.FORECO.2016.09.010.

Conklin, David R., James M. Lenihan, Dominique Bachelet, Ronald P. Neilson, and John B. Kim. 2016. MCFire Model Technical Description. *Pacific Northwest Research Station*. https://www.fs.fed.us/pnw/pubs/pnw_gtr926.pdf.

Davis, Owen K., and Raymond M. Turner. 1986. Palynological Evidence for the Historic Expansion of Juniper and Desert Shrubs in Arizona, U.S.A. *Review of Palaeobotany and Palynology* 49 (3–4): 177–193. https://doi.org/10.1016/0034-6667(86)90026-6.

Dolanc, Christopher R., Hugh D. Safford, James H. Thorne, and Solomon Z. Dobrowski. 2014. Changing Forest Structure across the Landscape of the Sierra Nevada, CA, USA, since the 1930s. *Ecosphere* 5 (8): art101. https://doi.org/10.1890/ES14-00103.1.

Dolph, K. Leroy, Sylvia R. Mori, and William W. Oliver. 1995. Long-Term Response of Old-Growth Stands to Varying Levels of Partial Cutting in the Eastside Pine Type. *Western Journal of Applied Forestry* 10 (3): 101–108. https://doi.org/10.1093/wjaf/10.3.101.

Drury, Stacy A., and Jason M. Herynk. 2011. *The National Tree-List Layer. Gen. Tech. Rep. RMRS-GTR-254*. Fort Collins https://doi.org/10.2737/RMRS-GTR-254.

Duncan, Sally. 2004. 100,000 Trees Can't Be Wrong: Permanent Study Plots and the Value of Time. In *Science Findings 64. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station*, vol. 5, 64 https://www.fs.usda.gov/treesearch/pubs/6956.

Feldman, James, and George E. Gruell. 2003. Fire in Sierra Nevada Forests: A Photographic Interpretation of Ecological Change since 1849. *Environmental History* 8 (1): 151. https://doi.org/10.2307/3985988.

Flannigan, Mike D., Meg A. Krawchuk, William J. de Groot, B. Mike Wotton, and Lynn M. Gowman. 2009. "Implications of Changing Climate for Global Wildland Fire." International Journal of Wildland Fire 18 (5): 483–507. https://doi.org/10.1071/WF08187.

Franklin, Jerry F., and Dean S. DeBell. 1988. Thirty-Six Years of Tree Population Change in an Old-Growth Pseudotsuga – Tsuga Forest. *Canadian Journal of Forest Research* 18 (5): 633–639. https://doi.org/10.1139/x88-093.

Fule, Peter Z. Waskiewicz, Justin D. and Avery, Charles C. 2001. Periodic remeasurement of the Gus Pearson Natural Area. Technical Report. NAU Ecological Restoration Institute, Flagstaff, United States.

Goeking, Sara A. 2015. Disentangling Forest Change from Forest Inventory Change: A Case Study from the US Interior West. *Journal of Forestry* 113 (5): 475–483. https://doi.org/10.5849/JOF.14-088.

Gray, Andrew, Thomas Brandeis, John Shaw, William McWilliams, and Patrick Miles. 2012. Forest Inventory and Analysis Database of the United States of America (FIA). *Biodiversity & Ecology* 4 (September): 225–231. https://doi.org/10.7809/b-e.00079.

Gray, Andrew N., Thomas R. Whittier, and Mark E. Harmon. 2016. Carbon stocks and accumulation rates in Pacific Northwest forests: role of stand age plant community and productivity. Ecosphere 7(1):10.1002/ecs2.1224

Grover, Herbert D., and H. Brad Musick. 1990. Shrubland Encroachment in Southern New Mexico, U.S.A.: An Analysis of Desertification Processes in the American Southwest. *Climatic Change* 17 (2–3): 305–330. https://doi.org/10.1007/BF00138373.

Gruell, G.E. 2001. *Fire in Sierra Nevada Forests: A Photographic Interpretation of Ecological Change since 1849*. Mountain Press.
Gruell, George. 1980. Fire's Influence on Wildlife Habitat on the Bridger-Teton National Forest, Wyoming - Volume I: Photographic Record and Analysis. *The Bark Beetles, Fuels, and Fire Bibliography* 1 (January) https://digitalcommons.usu.edu/barkbeetles/95.
Gruell, George E. 1983. Fire and Vegetative Trends in the Northern Rockies: Interpretations from 1871-1982 Photographs. In *Gen. Tech. Rep. INT-158. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station*, vol. 158, 117 https://doi.org/10.2737/INT-GTR-158.
Gruell, George E. 1986. "Post-1900 Mule Deer Irruptions In The Intermountain West: Principle Cause and Influences." https://www.fs.fed.us/rm/pubs_int/int_gtr206.pdf.
Hanan, Erin J., Jianning Ren, Christina L. Tague, Crystal A. Kolden, John T. Abatzoglou, Ryan R. Bart, Maureen C. Kennedy, Mingliang Liu, and Jennifer Adam. 2021. How Climate Change and Fire Exclusion Drive Wildfire Regimes at Actionable Scales. *Environmental Research Letters* 16 (2): 24051. https://doi.org/10.1088/1748-9326/abd78e.
Hessburg, Paul F., Carol L. Miller, Sean A. Parks, Nicholas A. Povak, Alan H. Taylor, Philip E. Higuera, Susan J. Prichard, et al. 2019. Climate, Environment, and Disturbance History Govern Resilience of Western North American Forests. *Frontiers in Ecology and Evolution* 7 (July): 239. https://doi.org/10.3389/fevo.2019.00239.
Keane, Robert. 2016. Spatiotemporal Variability of Wildland Fuels in US Northern Rocky Mountain Forests. *Forests* 7 (12): 129. https://doi.org/10.3390/f7070129.
Keane, Robert E., Robert Burgan, and Jan van Wagtendonk. 2001. Mapping Wildland Fuels for Fire Management across Multiple Scales: Integrating Remote Sensing, GIS, and Biophysical Modeling. *International Journal of Wildland Fire* 10 (4): 301. https://doi.org/10.1071/WF01028.
Keifer, MaryBeth, Jan W. van Wagtendonk, and Monica Buhler. 2006. Long-Term Surface Fuel Accumulation in Burned and Unburned Mixed-Conifer Forests of the Central and Southern Sierra Nevada, CA USA. *Fire Ecology* 2 (1): 53–72. https://doi.org/10.4996/fireecology.0201053.
Kim, John B., Becky K. Kerns, Raymond J. Drapek, G. Stephen Pitts, and Jessica E. Halofsky. 2018. Simulating Vegetation Response to Climate Change in the Blue Mountains with MC2 Dynamic Global Vegetation Model. *Climate Services* 10 (April): 20–32. https://doi.org/10.1016/J.CLISER.2018.04.001.
King, David A., Dominique Bachelet, and Amy J. Symstad. 2015. Application of MC1 to Wind Cave National Park: Lessons from a Small-Scale Study. In *Global Vegetation Dynamics: Concepts and Applications in the MC1 Model*, ed. D. Bachelet and D. Turner, 115–134. Wiley Blackwell. https://doi.org/10.1002/9781119011705.CH8.
Klasner, Frederick L., and Daniel B. Fagre. 2002. A Half Century of Change in Alpine Treeline Patterns at Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research* 34 (1): 49–56. https://doi.org/10.1080/15230430.2002.12003468.
Lenihan, James M., Raymond Drapek, Dominique Bachelet, and Ronald P. Neilson. 2003. Climate Change Effects on Vegetation Distribution, Carbon, and Fire in California. *Ecological Applications* 13 (6): 1667–1681. https://doi.org/10.1890/025295.
Lydersen, Jamie M., and Brandon M. Collins. 2018. Change in Vegetation Patterns Over a Large Forested Landscape Based on Historical and Contemporary Aerial Photography. *Ecosystems* 21 (7): 1348–1363. https://doi.org/10.1007/s10021-018-0225-5.
Lydersen, Jamie M., Malcolm P. North, Eric E. Knapp, and Brandon M. Collins. 2013. Quantifying Spatial Patterns of Tree Groups and Gaps in Mixed-Conifer Forests: Reference Conditions and Long-Term Changes Following Fire Suppression and Logging. *Forest Ecology and Management* 304 (September): 370–382. https://doi.org/10.1016/J.FORECO.2013.05.023.
Moore, Margaret M., David W. Huffman, Peter Z. Fulé, W. Wallace Covington, and Joseph E. Crouse. 2004. Comparison of Historical and Contemporary Forest Structure and Composition on Permanent Plots in Southwestern Ponderosa Pine Forests. *Forest Science* 50 (2): 162–176. https://doi.org/10.1093/forestscience/50.2.162.
Mote, Philip, David Turner, Dennis Lettenmaier, Dominique Bachelet, and John T. Abatzoglou. 2014. "Integrated Scenarios of Climate, Hydrology, and Vegetation for the Northwest." https://climate.northwestknowledge.net/IntegratedScenarios/pages/publicationsreports/IntegratedScenariosFinalReport2014-10-07.pdf.
NASA. n.d. "Landsat Science: About." https://landsat.gsfc.nasa.gov/about/. Accessed 18 Mar 2020.
NOAA. 2020. "National Centers for Environmental Information, Climate at a Glance." March 2020. https://www.ncdc.noaa.gov/cag.
North, M.P., S.L. Stephens, B.M. Collins, J.K. Agee, G. Aplet, J.F. Franklin, and P.Z. Fulé. 2015. Reform Forest Fire Management. *Science* 349 (6254): 1280–1281. https://doi.org/10.1126/science.aab2356.
Parks, Sean A., and John T. Abatzoglou. 2020. Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests From 1985 to 2017. *Geophysical Research Letters* 47 (22): e2020GL089858. https://doi.org/10.1029/2020GL089858.
Parks, Sean A., Lisa M. Holsinger, Matthew H. Panunto, W. Matt Jolly, Solomon Z. Dobrowski, and Gregory K. Dillon. 2018. High-Severity Fire: Evaluating Its Key Drivers and Mapping Its Probability across Western US Forests. *Environmental Research Letters* 13 (4). https://doi.org/10.1088/1748-9326/aab791.
RDocumentation. n.d. "Home - RDocumentation." https://www.rdocumentation.org/. Accessed 3 Mar 2022.
Riemann, Rachel, Barry Tyler Wilson, Andrew Lister, and Sarah Parks. 2010. An Effective Assessment Protocol for Continuous Geospatial Datasets of Forest Characteristics Using USFS Forest Inventory and Analysis (FIA) Data. *Remote Sensing of Environment* 114 (10): 2337–2352. https://doi.org/10.1016/j.rse.2010.05.010.
Samuels, Michael L., and Julio L. Betancourt. 1982. Modeling the Long-Term Effects of Fuelwood Harvests on Pinyon-Juniper Woodlands. *Environmental Management* 6 (6): 505–515. https://doi.org/10.1007/BF01868379.
Schoennagel, Tania, Thomas T. Veblen, and William H. Romme. 2004. The Interaction of Fire, Fuels, and Climate across Rocky Mountain Forests. *BioScience* 54 (7): 661–676. https://doi.org/10.1641/0006-3568(2004)054[0661:tioffa]2.0.co;2.
Sheehan, T., D. Bachelet, and K. Ferschweiler. 2015. Projected Major Fire and Vegetation Changes in the Pacific Northwest of the Conterminous United States under Selected CMIP5 Climate Futures. *Ecological Modelling* 317 (December): 16–29. https://doi.org/10.1016/J.ECOLMODEL.2015.08.023.
Sherriff, Rosemary L., and Thomas T. Veblen. 2007. A Spatially-Explicit Reconstruction of Historical Fire Occurrence in the Ponderosa Pine Zone of the Colorado Front Range. *Ecosystems* 10 (2): 311–323. https://doi.org/10.1007/S10021-007-9022-2.
Skinner, Carl N. and Taylor, Alan H. 2018. "Chapter Twelve. Southern Cascades Bioregion". Fire in California's Ecosystems, edited by Jan W. van Wagtendonk, Berkeley: University of California Press, pp. 195–218. https://doi.org/10.1525/9780520961913-015
Sloan, John P. 1998. Historical Density and Stand Structure of an Old-Growth Forest in the Boise Basin of Central Idaho. In *Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription. Tall Timbers Fire Ecology Conference Proceedings, No. 20*, ed. Teresa L. Pruden and Leonard A. Brennan.
Smith, Amy E., and Frederick W. Smith. 2005. Twenty-Year Change in Aspen Dominance in Pure Aspen and Mixed Aspen/Conifer Stands on the Uncompahgre Plateau, Colorado, USA. *Forest Ecology and Management* 213 (1–3): 338–348. https://doi.org/10.1016/J.FORECO.2005.03.018.
Smith, James E., and Linda S. Heath. 2002. A Model of Forest Floor Carbon Mass for United States Forest Types. In *Res. Pap. NE-722. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station*, vol. 722, 37 https://doi.org/10.2737/NE-RP-722.
Sollins, Phillip. 1982. Input and Decay of Coarse Woody Debris in Coniferous Stands in Western Oregon and Washington. *Canadian Journal of Forest Research* 12 (1): 18–28. https://doi.org/10.1139/x82-003.
Steel, Zachary L., Hugh D. Safford, and Joshua H. Viers. 2015. The Fire Frequency-Severity Relationship and the Legacy of Fire Suppression in California Forests. *Ecosphere* 6 (1): art8. https://doi.org/10.1890/ES14-00224.1.
Stephens, Scott L., Brandon M. Collins, Christopher J. Fettig, Mark A. Finney, Chad M. Hoffman, Eric E. Knapp, Malcolm P. North, Hugh Safford, and Rebecca B. Wayman. 2018. Drought, Tree Mortality, and Wildfire in Forests Adapted to Frequent Fire. *BioScience* 68 (2): 77–88. https://doi.org/10.1093/biosci/bix146.
Stephens, Scott L., Danny L. Fry, Ernesto Franco-Vizcaíno, Brandon M. Collins, and Jason M. Moghaddas. 2007a. Coarse Woody Debris and Canopy Cover in an Old-Growth Jeffrey Pine-Mixed Conifer Forest from the Sierra San Pedro Martir, Mexico. *Forest Ecology and Management* 240 (1–3): 87–95. https://doi.org/10.1016/j.foreco.2006.12.012.

Stephens, Scott L., and Peter Z. Fulé. 2005. Western Pine Forests with Continuing Frequent Fire Regimes: Possible Reference Sites for Management. *Journal of Forestry* 103 (7): 357–362. https://doi.org/10.1093/jof/103.7.357.
Stephens, Scott L., Jamie M. Lydersen, Brandon M. Collins, Danny L. Fry, and Marc D. Meyer. 2015. Historical and Current Landscape-Scale Ponderosa Pine and Mixed Conifer Forest Structure in the Southern Sierra Nevada. *Ecosphere* 6 (5): art79. https://doi.org/10.1890/ES14-00379.1.
Stephens, Scott L., Robert E. Martin, and Nicholas E. Clinton. 2007b. Prehistoric Fire Area and Emissions from California's Forests, Woodlands, Shrublands, and Grasslands. *Forest Ecology and Management* 251 (3): 205–216. https://doi.org/10.1016/j.foreco.2007.06.005.
Stephens, Scott L., James D. McIver, Ralph E.J. Boerner, Christopher J. Fettig, Joseph B. Fontaine, Bruce R. Hartsough, Patricia L. Kennedy, and Dylan W. Schwilk. 2012. The Effects of Forest Fuel-Reduction Treatments in the United States. *BioScience* 62 (6): 549–560. https://doi.org/10.1525/bio.2012.62.6.6.
Stephens, Scott L., Jason J. Moghaddas, Carl Edminster, Carl E. Fiedler, Sally Haase, Michael Harrington, Jon E. Keeley, et al. 2009. Fire Treatment Effects on Vegetation Structure, Fuels, and Potential Fire Severity in Western U.S. Forests. *Ecological Applications* 19 (2): 305–320. https://doi.org/10.1890/07-1755.1.
Stevens, Jens T., Gabrielle F.S. Boisramé, Ekaterina Rakhmatulina, Sally E. Thompson, Brandon M. Collins, and Scott L. Stephens. 2020a. Forest Vegetation Change and Its Impacts on Soil Water Following 47 Years of Managed Wildfire. *Ecosystems*: 1–19. https://doi.org/10.1007/s10021-020-00489-5.
Stevens, Jens T., Matthew M. Kling, Dylan W. Schwilk, J. Morgan Varner, and Jeffrey M. Kane. 2020b. "Biogeography of Fire Regimes in Western U.S. Conifer Forests: A Trait-based Approach." Edited by Thomas Gillespie. *Global Ecology and Biogeography* 29 (5): 944–955. https://doi.org/10.1111/geb.13079.
Strickler, Gerald S. 1961. *Vegetation and soil condition changes on a subalpine grassland in Eastern Oregon*.
Swetnam, Thomas W., Craig D. Allen, and Julio L. Betancourt. 1999. Applied Historical Ecology: Using the Past to Manage for the Future. *Ecological Applications* 9 (4): 1189–1206. https://doi.org/10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2.
Tang, Guoping, Brian Beckage, Benjamin Smith, and Paul A. Miller. 2010. Estimating Potential Forest NPP, Biomass and Their Climatic Sensitivity in New England Using a Dynamic Ecosystem Model. *Ecosphere* 1 (6): art18. https://doi.org/10.1890/ES10-00087.1.
Taylor, A.H. 2000. Fire Regimes and Forest Changes in Mid and Upper Montane Forests of the Southern Cascades, Lassen Volcanic National Park, California, U.S.A. *Journal of Biogeography* 27 (1): 87–104. https://doi.org/10.1046/j.1365-2699.2000.00353.x.
Tubbesing, Carmen L., Danny L. Fry, Gary B. Roller, Brandon M. Collins, Varvara A. Fedorova, Scott L. Stephens, and John J. Battles. 2019. Strategically Placed Landscape Fuel Treatments Decrease Fire Severity and Promote Recovery in the Northern Sierra Nevada. *Forest Ecology and Management* 436 (March): 45–55. https://doi.org/10.1016/j.foreco.2019.01.010.
USFS. 2019. Forest Inventory and Analysis. *USDA Forest Service.* 2019 https://www.fia.fs.fed.us/.
Vale, Thomas R. 1987. Vegetation Change and Park Purposes in the High Elevations of Yosemite National Park, California. *Annals of the Association of American Geographers* 77 (1): 1–18. https://doi.org/10.1111/j.1467-8306.1987.tb00141.x.
van Mantgem, Phillip J., Nathan L. Stephenson, John C. Byrne, Lori D. Daniels, Jerry F. Franklin, Peter Z. Fulé, Mark E. Harmon, et al. 2009. Widespread Increase of Tree Mortality Rates in the Western United States. *Science* 323 (5913). https://doi.org/10.1126/science.1165000.
Van Wagtendonk, Jan W. 2007. The History and Evolution of Wildland Fire Use. *Fire Ecology Special Issue* 3 (2): 3–17 http://faculty.fortlewis.edu/KORB_J/global/fire/wildland_fire_use.pdf.
Voelker, Steven L., Andrew G. Merschel, Frederick C. Meinzer, Danielle E.M. Ulrich, Thomas A. Spies, and Christopher J. Still. 2019. Fire Deficits Have Increased Drought Sensitivity in Dry Conifer Forests: Fire Frequency and Tree-Ring Carbon Isotope Evidence from Central Oregon. *Global Change Biology* 25 (4): 1247–1262. https://doi.org/10.1111/gcb.14543.
Wadleigh, Linda, and Michael J. Jenkins. n.d., 2019. Fire frequency and the vegetative mosaic of a spruce-fir forest in Northern Utah. In *The Great Basin Naturalist. Monte L*. Bean Life Science Museum, Brigham Young University. Accessed 15 Oct https://doi.org/10.2307/41712923.
Webb, Robert H., Diane E. Boyer, and Raymond M. Turner. 2010. *Repeat Photography: Methods and Applications in the Natural Sciences*. Island Press https://books.google.com/books?id=tvb6h6Dkb64C&pg=PR14&lpg=PR14&dq=Flynn+and+Hager+spring,+Ruby+Valley+NV&source=bl&ots=9g5wgYSIOB&sig=ACfU3U0MVtDKNtKpCZAvB1rSONaXAI29fw&hl=en&sa=X&ved=2ahUKEwjx_uza67XIAhU0KX0KHbJ9D_gQ6AEwAHoECAsQAQ#v=onepage&q=Flynn.and.
Weisberg, Peter J., Emanuele Lingua, and Rekha B. Pillai. 2007. Spatial Patterns of Pinyon–Juniper Woodland Expansion in Central Nevada. *Rangeland Ecology & Management* 60 (2): 115–124. https://doi.org/10.2111/05-224R2.1.
Yorks, T.P., N.E. West, and K.M. Capels. 1994. Changes in Pinyon-Juniper Woodlands in Western Utah's Pine Valley between 1933-1989. *Rangeland Ecology & Management/Journal of Range Management Archives* 47 (5): 359–364 https://journals.uair.arizona.edu/index.php/jrm/article/view/8955.
Yorks, Terence P., Neil E. West, and Kathleen M. Capels. 1992. Vegetation Differences in Desert Shrublands of Western Utah's Pine Valley between 1933 and 1989. *Rangeland Ecology & Management* 45 (6): 278–284. https://journals.uair.arizona.edu/index.php/jrm/article/view/8785.
Zhang, Fangmin, Jing M. Chen, Yude Pan, Richard A. Birdsey, Shuanghe Shen, Ju Weimin, and Alexa J. Dugan. 2015. Impacts of Inadequate Historical Disturbance Data in the Early Twentieth Century on Modeling Recent Carbon Dynamics (1951-2010) in Conterminous U.S. Forests. *Journal of Geophysical Research: Biogeosciences* 120 (3): 549–569. https://doi.org/10.1002/2014JG002798.
Zier, James L., and William L. Baker. 2006. A Century of Vegetation Change in the San Juan Mountains, Colorado: An Analysis Using Repeat Photography. *Forest Ecology and Management* 228 (1–3): 251–262 https://doi.org/10.1016/J.FORECO.2006.02.049.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.