



Wildfires correlate with reductions in aboveground tree carbon stocks and sequestration capacity on forest land in the Western United States

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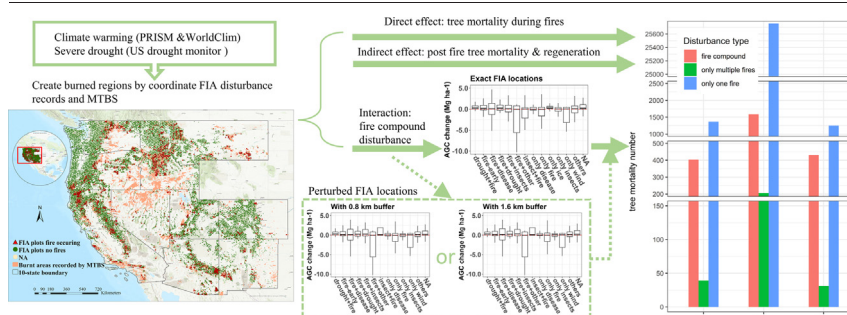
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HIGHLIGHTS

- We use multiple data sources to estimate forest carbon following disturbances.
- Fire effects had a greater reduction in forest carbon density than non-fire areas.
- Biotic factors significantly impacted post-fire aboveground carbon stock change.
- Fire plus other disturbances led to higher aboveground carbon loss and tree death.
- Estimates consistent from actual to perturbed NFI plots at large spatial scales.

GRAPHICAL ABSTRACT



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ABSTRACT

In the United States (US), forest ecosystems are the largest terrestrial carbon sink, offsetting the equivalent of >12 % of economy-wide greenhouse gas (GHG) emissions annually. In the Western US, wildfires have shaped much of the landscape by changing forest structure and composition, increasing tree mortality, impacting forest regeneration, and influencing forest carbon storage and sequestration capacity. Here, we used remeasurements of >25,000 plots from the US Department of Agriculture, Forest Service Forest Inventory and Analysis (FIA) program and auxiliary information (e.g., Monitoring Trends in Burn Severity) to characterize the role of fire along with other natural and anthropogenic drivers on estimates of carbon stocks, stock changes, and sequestration capacity on forest land in the Western US. Several biotic (e.g., tree size, species, and forest structure) and abiotic factors (e.g., warm climate, severe drought, compound disturbances, and anthropogenic interventions) influenced post-fire tree mortality and regeneration and had concomitant impacts on carbon stocks and sequestration capacity. Forest ecosystems in a high severity and low frequency wildfire regime had greater reductions in aboveground biomass carbon stocks and sequestration capacity compared to forests in a low severity and high frequency fire regime. Results from this study can improve our understanding of the role of wildfire along with other biotic and abiotic drivers on carbon dynamics in forest ecosystems in the Western US.

1. Introduction

Forest land is the largest terrestrial carbon sink in the United States (US), offsetting the equivalent of >12 % of economy-wide greenhouse gas

(GHG) emissions annually (US EPA, 2022). Natural disturbances such as windthrow, wildfire, insect and/or disease outbreaks, or anthropogenic activities (e.g., harvesting, prescribed fire, and cutting) in forest stands may cause tree death and/or damage, influencing forest carbon storage and sequestration capacity (defined here as the amount of carbon removed from or emitted into atmosphere) (Pugh et al., 2019; Masek et al., 2013; Raffa et al., 2008; Van Mantgem et al., 2009; Westerling et al., 2006; Table 1).

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In the Western US, the number of fires that burned forest areas > 400 ha has increased substantially over the last three decades with marked interannual variability and increased CO₂ emissions (Balch et al., 2018). Although soil is a larger reservoir of carbon than trees in forestland, understanding how biotic and abiotic factors contribute to changes in aboveground carbon stocks (AGC) before, during, and after disturbances like wildfire is critical to understanding forest carbon cycling in the Western US.

The amount of AGC consumed during wildfire varies across forest ecosystems due to the severity of the fire, stand structural attributes, species composition, geographic location, weather, climate, and interactions between these biotic and abiotic factors (Fettig et al., 2019). Tree death is often the culmination of damage resulting directly or indirectly from fires (Fig. 1). Estimates of tree mortality from wildfires vary among tree species due to bark thickness and percentage of crown scorched (Kane et al., 2017b; Grayson et al., 2017; Hood and Lutes, 2017). Greater variability in forest structure increases resilience by reducing fire-caused tree mortality in dry Western US coniferous forests (Koontz et al., 2020). For interactions between fires and other forest disturbances, their effect on tree mortality ranges from antagonistic to synergistic if time between disturbances is relatively short (Kane et al., 2017a). For example, postfire mortality of ponderosa pine (*Pinus ponderosa* Laws.) in Arizona, Colorado, and Montana increased with bark beetle (*Coleoptera: Scolytinae*) infestation following wildfires (Sieg et al., 2006). In contrast, postfire mortality was stable between sites with low and high bark beetle infestation levels that were widespread following the Wallow Fire in Arizona (Roccaforte et al., 2018). Species and plant competition combined with topography may impact tree regeneration following fire, which contributes to forest carbon loss and reductions in potential sequestration capacity in the future. In the Western US, post-fire regeneration establishes more quickly in low-elevation, dry forest types than in high-elevation forest types (Stevens-Rumann and Morgan, 2019). Furthermore, carbon storage and change induced by wildfires are not only controlled by forest and topographic conditions but are also sensitive to increasing temperature and decreasing precipitation (Forzieri et al., 2022; Frelich et al., 2020; Holden et al., 2018; Ontl et al., 2020).

Forest capacity to sequester carbon in the context of disturbance depends on resistance (defined here as ‘the influence of forest structure and composition on disturbances’) and resilience (defined here as ‘forest capacity to withstand and recover from natural and anthropogenic perturbations’) (DeRose and Long, 2014; Forzieri et al., 2022). In regions where fire is common, forest ecosystems may have developed resistance and/or resilience to the effects of fire. Thus, these ecosystems may lose less carbon directly from combustion of live and dead woody material and maintain the capacity to continue sequestering and storing carbon (Meng et al., 2020;

Müller et al., 2016; Ontl et al., 2020). Warming and changes in precipitation patterns in the Western US have also encouraged longer fire seasons and hotter summers that dry out woody fuels (Abatzoglou and Kolden, 2013; Holden et al., 2018; Westerling et al., 2006; Williams et al., 2016). Overall, both temperature and precipitation increased over the 20th century across the Western US (Fig. 2). However, at the end of the 20th century, coinciding with temperature increases, summer precipitation started decreasing across the Western US, correlating with increased wildfire occurrences (Holden et al., 2018). This decrease in precipitation along with fewer wetting days (i.e., days with >2.54 cm of rainfall) increased burned areas either directly through its regulation effects of the wetting environment or indirectly through feedback to vapor pressure deficit during the fire season (Holden et al., 2018). Increased temperatures and decreased precipitation have intensified Western US droughts, coinciding with higher severity burns covering large forest areas during droughts at the end of the last century (Crockett and Westerling, 2018). As a result, tree mortality has increased while forest post-fire recovery has been impeded (Buotte et al., 2019; Keen et al., 2022). In recent decades, in the Rocky Mountain region of the US, wildfires have been so intense that tree regeneration has decreased, and forest recovery has slowed, due, in part, to increasing temperatures and reduced moisture availability (Kannenberg et al., 2021; Stevens-Rumann and Morgan, 2019).

National forest inventory (NFI) data from the US Department of Agriculture (USDA) Forest Service Forest Inventory and Analysis (FIA; U.S. Department of Agriculture, Forest Service. Forest Inventory and Analysis, 2021) program has long been used to characterize the status and trends of forest resources in the US (Chojnacky and Heath, 2002; Copenhaver-Parry and Bell, 2018; Fettig et al., 2019; Hoover et al., 2022; Huang et al., 2018; Lister et al., 2020; Ma et al., 2020; Prisley et al., 2009; Riemann et al., 2010; Shaw et al., 2005; Wilson et al., 2013). These data are often harmonized with auxiliary information (e.g., land cover/land use products, Monitoring Trends in Burn Severity (MTBS), Moderate Resolution Imaging Spectroradiometer (MODIS) fire products) to produce spatially explicit and spatially continuous predictions of forest attributes (Lister et al., 2020; Riley et al., 2021; Sleeter et al., 2018). To quantify forest carbon stocks and sequestration capacity across space and through time, there have been several methods to leverage remote sensing data and/or field measurements from NFIs (Fitts et al., 2021; Yu et al., 2022). Integrated remote sensing and forest inventory datasets have been used to estimate large-scale carbon turnover capacities for whole ecosystems (Chen et al., 2017; Ma et al., 2020; Zheng et al., 2013).

The objective of this study is to characterize changes in aboveground standing live (hereafter LIVE) tree (≥ 2.54 cm diameter at breast height [dbh]) and standing dead (hereafter DEAD) tree (remeasured tree:

Table 1

Summary of different fire disturbance types impact aboveground Carbon (AGC) based on disturbances records from Forest Inventory and Analysis (FIA) conditions. Negative estimates of storage change and sequestration capacity indicate carbon removal from atmosphere. Positive estimates of storage change and sequestration capacity indicate carbon emission into atmosphere. Positive estimates of transfer from standing live (hereafter LIVE) to standing dead (hereafter DEAD) indicate carbon transfer out of forest LIVE carbon pool. Fire combined with other disturbances are grouped into fire compound. Others include any types of disturbances without fires. T1 presents time one and T2 presents time two. Total presents LIVE AGC plus DEAD AGC.

Disturbance type	Conditions	Annual AGC (Mg ha ⁻¹ yr ⁻¹)			T1 AGC pool (Mg ha ⁻¹)			T2 AGC pool (Mg ha ⁻¹)		
		Storage change	Sequestration capacity	Transfer from LIVE to DEAD	Total	LIVE	DEAD	Total	LIVE	DEAD
No disturbance	21,163	-0.7 (± 8.68E-04)	-0.88 (± 9.18E-04)	0.75 (± 1.10E-03)	47.56 (± 2.07E-02)	43.84 (± 2.15E-02)	3.72 (± 1.27E-02)	55.73 (± 2.16E-02)	52.28 (± 2.25E-02)	3.45 (± 1.17E-02)
Only one fire	1537	0.29 (± 3.59E-03)	0.14 (± 3.44E-03)	0.78 (± 3.60E-03)	55.29 (± 7.37E-02)	48.63 (± 7.67E-02)	6.66 (± 5.36E-02)	44.58 (± 7.85E-02)	28.29 (± 9.98E-02)	16.29 (± 5.05E-02)
Only multiple fires	16	0.47 (± 5.41E-02)	0.46 (± 5.29E-02)	0.85 (± 6.40E-02)	47.32 (± 9.68E-01)	44.44 (± 1.00E+00)	2.88 (± 5.81E-01)	33.76 (± 8.56E-01)	12.87 (± 7.56E-01)	20.89 (± 9.23E-01)
Fire compound	140	0.09 (± 1.22E-02)	-0.24 (± 1.17E-02)	0.95 (± 1.24E-02)	81.93 (± 2.53E-01)	73.85 (± 2.63E-01)	8.09 (± 1.69E-01)	72.69 (± 2.60E-01)	53.04 (± 2.90E-01)	19.65 (± 1.90E-01)
Others	5135	-0.54 (± 1.47E-03)	-0.8 (± 1.57E-03)	0.96 (± 1.38E-03)	64.00 (± 3.58E-02)	57.58 (± 3.72E-02)	6.42 (± 2.48E-02)	68.31 (± 3.70E-02)	57.81 (± 3.98E-02)	10.50 (± 2.36E-02)

Total conditions: 27,991 (25,107 plots).

Mean estimates (± standard error).

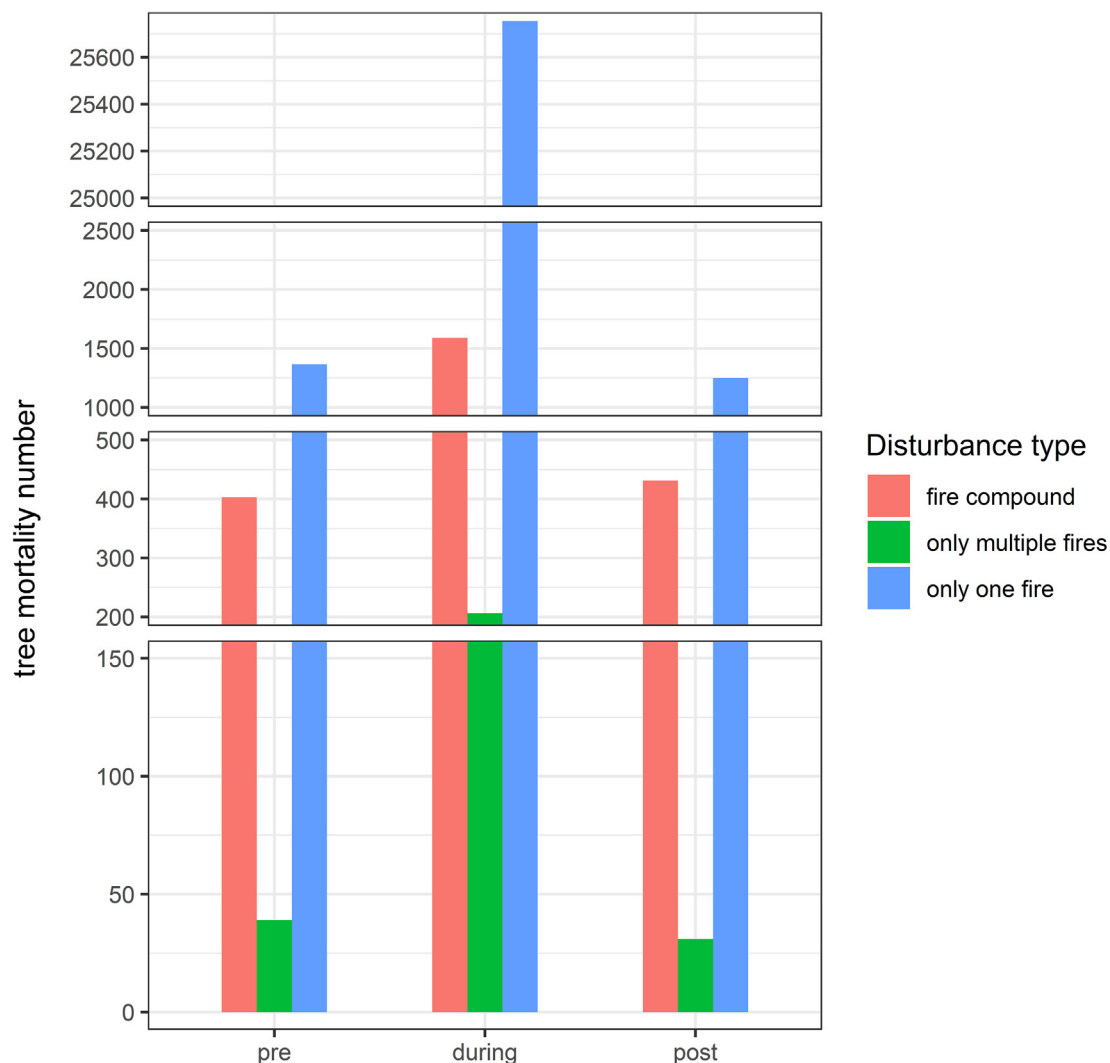


Fig. 1. Tree mortality numbers pre, during and post fire disturbances for forests in the Western United States. The color of bars indicates fire disturbance types occurring during the remeasurement periods. Blue bars show only one fire disturbance; green bars describe multiple fire disturbances; red bars indicate forests suffering both fire and other types of disturbances. 'Pre' column group states that tree mortality before fire disturbance, which shows standing dead trees at time one. 'During' column group presents the number of standing dead trees during fire disturbances. 'Post' column group indicates tree mortality after fires.

≥ 12.7 cm dbh; new trees that grew [hereafter termed in-growth trees] after time one [T1]: ≥ 2.54 cm dbh) carbon stocks and sequestration capacity on forest land in the Western US following natural and anthropogenic disturbances, with particular emphasis on wildfire over the last two decades. Specifically, we will: 1) characterize fire severity and frequency on forest land in the Western US and quantify evidence of recent natural and anthropogenic disturbances, 2) characterize the amount of tree damage and mortality resulting in changes in carbon stocks in LIVE and DEAD trees on remeasured NFI plots in the Western US, 3) estimate carbon sequestration capacity of forest land in the Western US, and 4) attribute changes in carbon stocks and sequestration capacity to particular natural and anthropogenic drivers. The primary hypothesis is that forests which have experienced recent wildfires have experienced greater tree damage and mortality than forests without evidence of recent fires and thus have reduced AGC stocks and capacity to sequester and store carbon. Specifically, we expect that forests with evidence of low severity and high frequency fires in the Western US store more carbon in LIVE and DEAD trees over time than forests with high severity and low frequency fires. We suspect tree mortality will be lower in low-severity-fire regions even if fire return intervals in these regions are shorter. In other words, AGC changes less after low severity and high frequency fires than high severity and low frequency fires.

2. Methods

2.1. Study area

Our study domain is broadly characterized as forests in the Western US and these lands have experienced increases in fire activity and tree mortality in recent decades (Van Mantgem et al., 2009; Williams et al., 2016; Wilson et al., 2013). The study region includes the Arizona, Colorado, Idaho, Montana, Nevada, Oregon, Utah, Washington, New Mexico, and California. These states have FIA plot remeasurement data that can be used to compare forest conditions between two points in time over the last few decades (Fig. 2a). Wyoming is not included because it does not contain any FIA plots that were visited at two time points (U.S. Department of Agriculture, Forest Service. Forest Inventory and Analysis, 2021). According to WorldClim (Global climate and weather data; Vose et al., 2014), mean temperature and mean precipitation were 9.84 °C and 43.08 mm, respectively, at the study sites during the 20th century; generally, the northwest forests were colder with greater precipitation, and the southwest forests were hotter and drier. In the northwest forests, the highest precipitation region was in the Olympic rainforest (mean precipitation: 219.13 mm) and the coldest region was in the northern Rocky Mountains (mean temperature: 2.6 °C), while in the southwest forests, the region

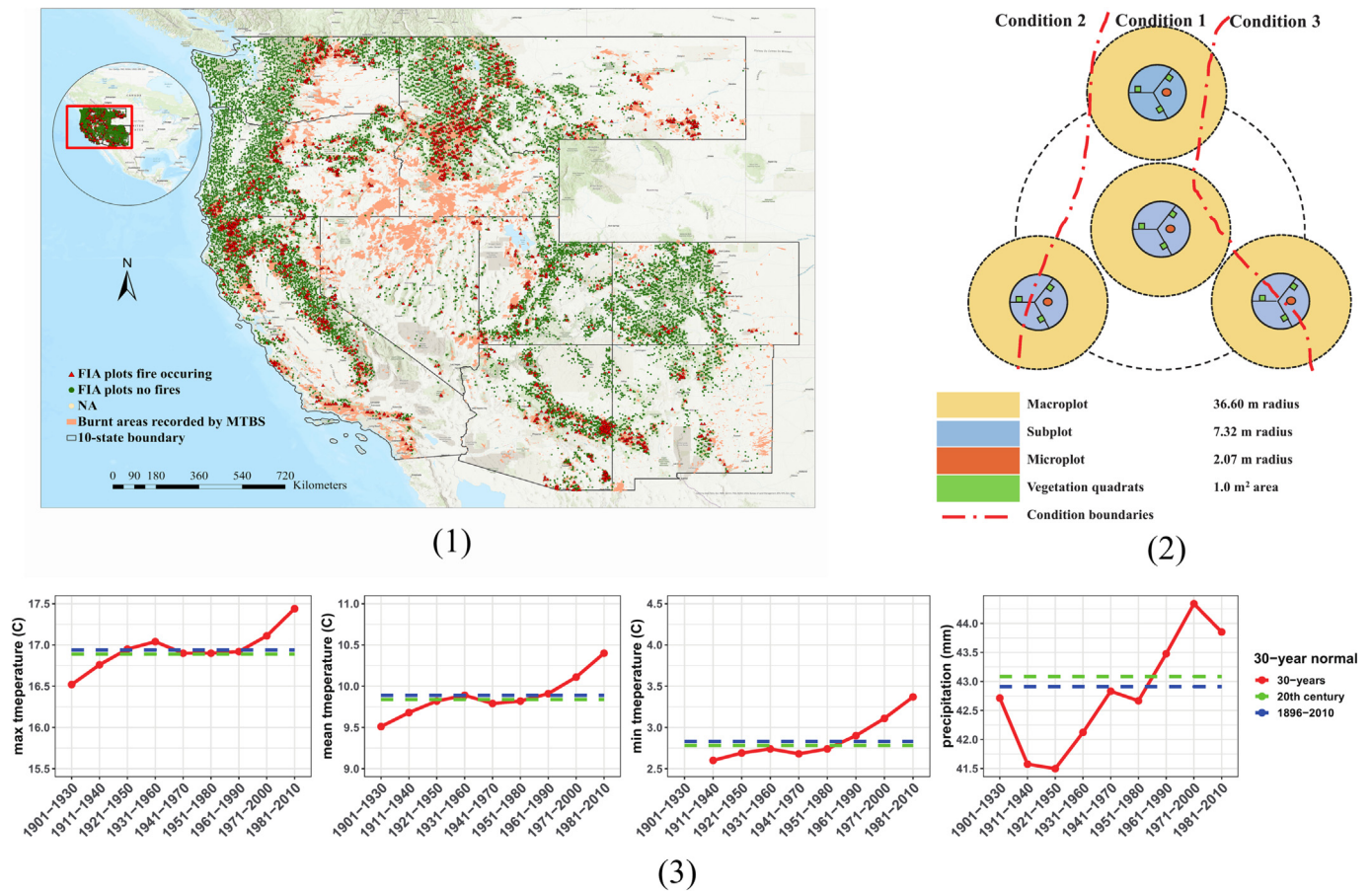


Fig. 2. (a) Distributions of Forest Inventory and Analysis (FIA) remeasurement plots in the ten Western United States from 2000 to 2018 (25,107 plots with 27,991 conditions). Note that plot locations are perturbed. Red triangles show forests had evidence of fires according to FIA records. Green dots present forests without evidence of fires based on FIA records. Orange polygons are burned areas extracted from Monitoring Trends in Burn Severity. (b) FIA mapped plot design and each plot may be divided into two or more conditions (a plot was divided by dash-dotted lines) according to ownerships, stand age, forest types, etc. (c) Historical climate records are from Global climate and weather data at every 30-year normal, 20th century, and from 1890 to 2010 in the studied ten states.

near the Sonoran Desert was the driest (mean precipitation: 9.94 mm) and hottest (mean temperature: 21.6 °C). Most regions within the study area are semiarid; however, precipitation is abundant in some inland mountains and along the Pacific coast due to geographic and landform variation (Liu and Wimberly, 2016).

In the Western US, forest wildfires are a major disturbance causing tree mortality, alongside bark beetle outbreaks and timber harvesting (Oswalt et al., 2019; Williams et al., 2016). According to recent work characterizing disturbances in forests of the US, wildfires were primarily distributed in the Western US conifer or conifer-mixed forests (Williams et al., 2016). Conifer forests are the primary forest type from the Rocky Mountains to the Pacific Northwest (Jang et al., 2015; Liang et al., 2016; Milota and Puettmann, 2017).

2.2. Data

To better understand wildfire impacts on forest carbon stocks, NFI, remote sensing, and drought monitor data were used to extract land types, biomass, vegetation, ecological system types, topography, disturbances, climate, and drought variables. Among remote sensing databases, MTBS (US Geological Survey and USDA Forest Service, 2021) and PRISM (PRISM Climate Group, 2022) were used to obtain fire disturbances and recent climate information. The FIA program (USDA Forest Service, 2020) was used primarily for site and vegetation data. MTBS and PRISM variables were intersected with plot locations as were WorldClim and US Drought Monitor variables (USDM; National Drought Mitigation Center, 2021) by county

(Table S1). Steps performed in raw data selection and compilation are described below.

2.2.1. Forest inventory data

The FIA program has operated a nationally consistent annual forest inventory to characterize forest status and trends since 1999 (Woolman et al., 2022; U.S. Department of Agriculture, Forest Service. Forest Inventory and Analysis, 2021). The FIA program does not include actual plot locations in the publicly available FIA database to protect the privacy of landowners and ecological integrity of plots (Huang et al., 2019). Instead, perturbed FIA plot locations add a random error (up to 1.6 km) to the actual locations and a subset of plot locations are swapped with other plot locations (Prisley et al., 2009). The inventory program is organized into three data collection phases. The first phase relies on remotely sensed imagery to determine land use types at ground plot locations (Reams et al., 2005; U.S. Department of Agriculture, Forest Service. Forest Inventory and Analysis, 2021). The sampling frame is designed as an approximately 2428 ha hexagon for each permanent ground plot with a ten-panel rotation in phase two and three (Reams et al., 2005; Yu et al., 2022). Each permanent ground plot comprises four fixed-radius subplots; one at the plot center and three extending 36.6 m from the plot center at 0°, 120°, and 240° from north (Bechtold and Scott, 2005; Woolman et al., 2022; Yu et al., 2022) (Fig. 2b). Each subplot contains a two-meter fixed-radius microplot and is surrounded by an 18-m fixed radius macroplot. There may be multiple conditions mapped within a plot to delineate unique features (e.g., different ownerships, stand age, forest types; Bechtold and Scott, 2005). Tree- and

site-level attributes, such as topography (latitude, longitude, elevation, aspect, slope), vegetation (forest type, tree age, tree species, tree diameter, tree height, canopy coverage), disturbance (type and year), treatment (type and year), and ecological section were measured at each plot that had at least one forest condition. For tree-level data, rare occurrences, such as large trees and mortality were measured on macroplots. Trees with dbh larger than 12.7 cm were measured on subplots and trees with dbh between 2.54 and 12.7 cm were measured on microplots within each subplot (Bechtold and Scott, 2005). To estimate forest land carbon stocks and stock changes, all forested FIA plots with an approximately 10-year-remeasurement cycle at the initial measurement (T1) and current measurement (time two, hereafter T2) were selected. In this study, 26,026 FIA plots and 33,882 unique forest conditions re-measured from 2000 to 2018 in ten states in the Western US were utilized (Fig. 2a). Estimates of AGC (Mg ha^{-1}) at conditions obtained directly from the FIA observations and adjusted according to tree density, F_{AGC} , were calculated as:

$$F_{\text{carbon_AG } i} = 0.5 \times (W_{\text{BOLE}} + W_{\text{STUMP}} + W_{\text{TOP}} + W_{\text{SAPLING}} + W_{\text{WDL}}) \quad (1)$$

$$F_{\text{AGC}} = \sum_{i=1}^n \frac{F_{\text{carbon_AG } i} \times \text{TPA_UNADJ}_i}{892} \quad (2)$$

Where $F_{\text{carbon_AG } i}$ is carbon in the aboveground portion (LIVE and DEAD tree) in the i^{th} tree. W is the oven-dry biomass (pounds) of merchantable bole, tree stump, top and limbs of tree, sapling, and woodland tree species collected from the sampling frame. n is the number of remeasured trees in each condition with $i = 1, 2, \dots, n$. The variable TPA_UNADJ_i is the tree density per acre collected at the subplot (U.S. Department of Agriculture, Forest Service. Forest Inventory and Analysis, 2021). And dividing 892 was to transfer unites from pounds per acre to Mg ha^{-1} .

Across the 33,882 remeasured conditions, a total of 1,000,514 trees were involved. Among these trees, those with DEAD status at T1 and LIVE status at T2, and those without dbh and height records at both T1 and T2, were removed. The threshold for remeasured trees was LIVE trees with a dbh of ≥ 2.54 cm and DEAD trees with a dbh of ≥ 12.7 cm at T1 (Table 2). In-growth trees were defined as LIVE trees with a dbh of ≥ 2.54 cm and DEAD trees with a dbh of ≥ 2.54 cm at T2 (Table 2). Therefore, a total of 884,499 remeasured trees and 148,513 in-growth trees were selected in this study. Consequently, the number of conditions was reduced to 27,991 (25,107 plots). Tree status change was grouped into five categories (Table 2). They were 'always live', 'always standing dead', 'dead during remeasurement', 'in-growth trees after T1 and alive at T2', and 'in-growth trees after T1 but standing dead at T2' (Table 2). The LIVE AGC density was estimated based on LIVE trees with dbh ≥ 2.54 cm on each condition. For the DEAD AGC density, their estimation used trees with dbh ≥ 12.7 cm at T1 and dbh ≥ 2.54 cm at T2. In this way, the amount of carbon of live trees with dbh between 2.54 cm and 12.7 cm at T1 transferred out live

carbon pool could involve in the dead carbon pool. T1 carbon, average change of diameter and height, and average age of trees at each condition were calculated during measurement period. Tree mortality caused by the same disturbance was grouped by condition using cause of death agent code (AGENTCD) to account for small-scale fires that affected areas < 0.4 ha in size or $< 25\%$ of trees in the condition (Fitts et al., 2022). Tree mortality rate caused by fires was estimated through dividing the number of trees killed by fires by the number of recorded trees on the conditions at T2.

2.2.2. Time series of burned area and severity data from MTBS

Revisited FIA plots may not be processed immediately after a wildfire to record fire severity. In addition, if multiple fires occurred during remeasurement periods, it was difficult to detect fire frequency. Therefore, FIA data were harmonized with MTBS datasets to characterize fire severity and frequency (Table 3; Table 4). The MTBS dataset contains forest fire burn severity data from 1984 to near present and includes all fires approximately 400 ha in size or larger in the Western US. The burn severity mosaics design includes six burn severity classes based on changes in the normalized burn ratio (NBR) before and after fire. NBR is the normalized difference in reflectance between near-infrared (NIR) and short-wave infrared (SWIR) wavelengths. MTBS uses Landsat imagery to calculate changes in NBR every year. Burn severity classes one to four (one is unburned to low; two is low; three is moderate; four is high) were extracted at FIA plot locations from 2000 to 2018 to detect multiple fire occurrences during the FIA remeasurement periods. Classes five (increased greenness post fire) and six (masks that affected the severity classification) were not used because they do not represent fire severity directly. The MTBS burn severity classes extracted at FIA conditions annually. When actual FIA plot locations were applied, fire severity classes were the same as MTBS burn severity. Therefore, class one and two at MTBS were assigned as low severity, class three was assigned as moderate severity, and class four was assigned as high severity. When MTBS burn severity mosaics were intersected with perturbed FIA plot locations, a mean burn severity was calculated based on perturbed locations' buffer areas to set the fire severity classes (Table S2). Hence, fire severity was assigned as low when mean burn severity was < 2.5 , moderate when mean burn severity was between 2.5 and 3.5, high when mean burn severity was > 3.5 . Fire frequencies were first counted from yearly MTBS burn severity mosaics across each FIA plot remeasurement period and then adjusted with FIA recorded fire disturbances that year. If the fire year recorded by FIA had the same fire occurrence year in MTBS, the fire frequency was the same number from the MTBS records; if not, this project assumed that there was evidence that one more fire occurred during FIA remeasurement periods. According to the fire frequency distribution, one fire occurrence was assigned as low frequency, two fire occurrences were assigned as moderate frequency, and equal or more than three fire occurrences were assigned as high frequency.

Table 2

Summary of tree status from time one (T1) to time two (T2). In the group of 'standing live tree at T1 that were standing dead trees at T2' and 'standing dead trees at T1 that were still standing at T2', dbh and height are assumed as zero at T2 if their recording are missing. In the group of 'in-growth tree after T1 that were alive at T2' and 'in-growth trees after T1 that were standing dead at T2', dbh and height are assumed as zero at T1. The 'in-growth trees' referred to new trees that grew after T1.

Tree status	Selected tree dbh threshold (cm)	Tree number	dbh (cm)		Height (m)	
			T1	T2	T1	T2
Standing live tree at T1 that were still alive at T2	≥ 2.54 At T1&T2	613,881	28.34 ($\pm 2.86\text{E-}02$)	30.55 ($\pm 2.92\text{E-}02$)	14.31 ($\pm 1.37\text{E-}02$)	15.62 ($\pm 1.42\text{E-}02$)
Standing live tree at T1 that were standing dead trees at T2	≥ 2.54 At T1&T2	121,023	22.61 ($\pm 5.19\text{E-}02$)	15.53 ($\pm 5.29\text{E-}02$)	13.31 ($\pm 2.51\text{E-}02$)	9.31 ($\pm 2.48\text{E-}02$)
Standing dead trees at T1 that were still standing at T2	≥ 12.70 At T1&T2	109,595	32.43 ($\pm 8.22\text{E-}02$)	19.97 ($\pm 9.32\text{E-}02$)	17.05 ($\pm 3.33\text{E-}02$)	10.22 ($\pm 4.02\text{E-}02$)
In-growth trees after T1 that were alive at T2	≥ 2.54 At T2	139,227	0 NA	17.98 ($\pm 4.71\text{E-}02$)	0 NA	10.73 ($\pm 2.31\text{E-}02$)
In-growth trees after T1 that were standing dead at T2	≥ 2.54 At T2	9286	0 NA	25.85 ($\pm 3.40\text{E-}01$)	0 NA	13.37 ($\pm 1.46\text{E-}01$)
Total number of trees		993,012				

Mean estimates ($\pm$ standard error) and NA suggests no record.

Table 3

Comparison of condition numbers of fires base on Forestry Inventory and Analysis (FIA) database only and FIA merges with Monitoring Trends in Burn Severity (MTBS). Fire combined with other disturbances are grouped into fire compound. Others include any types of disturbances without fires.

Disturbance type	Only FIA	FIA + MTBS		
		Actual	0.8 km buffer perturbed	1.6 km buffer perturbed
No disturbances	21,163	20,660	20,884	20,953
Only fire	1553	2056	1832	1763
Fire compound	140	140	140	140
Others	5135	5135	5135	5135

2.2.3. Climate data from PRISM, WorldClim and drought data from USDM

The climate data sources used in the study were PRISM climate produced by the Northwest Alliance for computational science and engineering, WorldClim produced by the National Oceanic and Atmospheric Administration (NOAA), and USDM produced jointly by the National Drought Mitigation Center at the University of Nebraska-Lincoln, NOAA, and the USDA (Lotfata, 2022). PRISM developed an 800-m resolution raster dataset for precipitation, mean temperature, maximum temperature, and minimum temperature in the last 30-years (from 1991 to 2020) to collect 30-year mean (here after normal) and annual data in recent decades. Thus, latitude and longitude of FIA plots were used directly on PRISM raster images to extract recent 30-year (from 1991 to 2020) normal climate data and calculate mean temperature and precipitation between the current ten years (from 2010 to 2020) and previous ten years (from 2000 to 2010). In contrast to PRISM offering recent climate data, WorldClim archives historical 30-year normal climate data for the entire 20th century and from 1895 to 2010. Although WorldClim provides the Palmer Drought Severity Index, it is recorded only at the state level; therefore, USDM was included to obtain drought-related estimates from 2000 to 2018. USDM collects data biweekly and defines five drought classes: abnormally dry, moderate drought, severe drought, extreme drought, and exceptional drought. The drought severity and coverage index was aggregated over time and was used to estimate annual drought severity, seasonal drought length and seasonal drought start month.

Table 4

Comparison of fire occurrence (on condition levels) is conducted using only Forestry Inventory and Analysis (FIA) database, actual FIA database coordinates with Monitoring Trends in Burn Severity (MTBS), and perturbed (0.8 km buffer and 1.6 km buffer) FIA database coordinates with MTBS.

Year	FIA only	FIA + MTBS		
		Actual	0.8 km buffer perturbed	1.6 km buffer perturbed
1999	NA	106	77	122
2000	NA	223	87	100
2001	NA	99	48	70
2002	23	348	150	99
2003	18	189	62	61
2004	17	75	56	48
2005	26	116	42	32
2006	53	231	92	131
2007	67	309	144	173
2008	124	197	131	238
2009	58	90	55	71
2010	49	33	15	17
2011	68	181	69	44
2012	121	342	153	208
2013	64	157	84	129
2014	93	186	136	192
2015	115	321	111	155
2016	41	133	80	95
2017	47	384	143	193
2018	17	378	221	343

2.3. Data analysis

In general, AGC stocks include LIVE and DEAD trees, leaf litter, and fall down trees, however, in this study, AGC stocks are defined as total carbon in LIVE and DEAD trees. Annual change of AGC storage (total carbon storage), LIVE carbon sequestration capacity, and transfer from LIVE to DEAD carbon pools were summarized for remeasured FIA conditions in the Western US. The carbon change was computed based on carbon at T1 minus carbon at T2. Negative estimates of carbon storage change and carbon sequestration capacity indicated carbon removal from the atmosphere. Positive estimates of transfer from LIVE to DEAD indicated carbon transfer out of LIVE carbon pool. The amount of total, LIVE and DEAD AGC were summed at T1 and T2 separately to further compare carbon pool change at two time points. For categorical drivers, fire interactions with other disturbances and their effects on carbon change and tree mortality were compared to test fire impacts on tree damage and mortality and thus carbon stocks and sequestration capacity. The carbon change between plots with evidence of fires and fire absence were compared among different forest types, ecological sections and pre- or post-fire treatments to characterize AGC storage change associated with natural and anthropogenic drivers. The numeric drivers (defined here as discrete and continuous variables) impact on carbon change were tested by several regression models by setting fire occurrence or absence as a dummy variable to examine relationships between these numeric drivers and carbon change. These drivers were topographic (latitude, longitude, elevation, aspect, slope), tree conditions (ages, growth diameters, and tree height change), forest conditions (T1 forest carbon storage, tree density, and canopy coverage), recent and historical climate conditions (temperature and precipitation), drought severity, seasonal drought length and seasonal drought start month. After harmonizing fire events between FIA and MTBS, the FIA conditions were grouped into six fire types (no fires, high severity and low frequency, low severity and high frequency, low severity and high frequency, high severity and high frequency, and other fires) based on fire severity and frequency adjusted by MTBS (Table S2). Pairwise *t*-tests were applied to test the primary hypothesis that variation of AGC storage change, sequestration capacity and transfer from LIVE to DEAD across different fire groups. Resulting *P*-values were adjusted by the Benjamini Hochberg method. All results were expressed as the means $\pm$ standard error.

2.4. Use of actual and perturbed FIA plot locations to create data layers

Auxiliary geospatial datasets were harmonized with perturbed FIA plots by creating 0.8 km (hereafter perturbed_0.8) or 1.6 km (hereafter perturbed_1.6) buffer areas around the FIA perturbed locations (Copenhaver-Parry and Bell, 2018; Westfall et al., 2021). Since temperature and drought conditions were expected to be consistent within 1.6 km, the perturbed locations could be used to extract the same information as the actual FIA locations. By contrast, a fire or a precipitation event may be missed when using a perturbed FIA plot location to merge a MTBS burn area or a precipitation region. Thus, data were extracted from the perturbed FIA plot locations' buffer areas, which increased the probability of overlapping burned area and reduced risks of missing fire or precipitation events. All data extracted from perturbed FIA plots and their buffer areas were processed with the same statistical analysis as data from actual FIA plot locations to compare the results.

3. Results

3.1. AGC increased in the forest land without evidence of fires

Forest land without evidence of fire disturbances stored 0.70 ($\pm 8.68 \times 10^{-4}$) Mg ha⁻¹ carbon annually. In conditions without evidence of fires, forests removed 0.88 ($\pm 9.18 \times 10^{-4}$) Mg ha⁻¹ carbon from atmosphere and transferred 0.75 ($\pm 1.10 \times 10^{-3}$) Mg ha⁻¹ carbon from LIVE to DEAD carbon pools annually. During the FIA remeasurement period, the LIVE carbon pools increased from 43.84 (± 0.02) Mg ha⁻¹ to 52.28

(± 0.02) Mg ha^{-1} in the conditions without evidence of fires while the DEAD carbon pools maintained at similar status (T1: $3.72 \pm 0.01 \text{ Mg ha}^{-1}$, T2: $3.45 \pm 0.01 \text{ Mg ha}^{-1}$). Therefore, forests without evidence of fires increased AGC in the Western US.

3.2. Wildfire reduced forest land AGC storage and sequestration capacity

In the Western US, 6.05 % of the forest (around 21,100 ha) had evidence of fire disturbances in recent decades, based on remeasured FIA plots (1693 unique conditions). The forests in which fires occurred generally had higher T1 AGC compared to forests with no disturbances and transferred more carbon from the LIVE to DEAD carbon pools over the remeasurement period (Table 1). FIA plots with one fire disturbance ($0.78 \pm 3.60 \times 10^{-3} \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and multiple fire disturbances ($0.85 \pm 0.06 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) caused large AGC transfers from LIVE to DEAD carbon stocks compared to forests with no evidence of disturbances ($0.75 \pm 1.10 \times 10^{-3} \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Forested conditions with evidence of one fire ($28.29 \pm 0.10 \text{ Mg ha}^{-1}$) had more than twice the amount of LIVE AGC compared to forests with evidence of multiple fires ($12.87 \pm 0.76 \text{ Mg ha}^{-1}$) at the end of FIA remeasurement periods, showing that lower frequency fire areas lost less AGC than higher frequency fire areas (AGC reduction: $0.14 \pm 3.44 \times 10^{-3} \text{ Mg ha}^{-1} \text{ yr}^{-1}$, $0.46 \pm 0.06 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, respectively). The amount of carbon transferred from the forest AGC pool to other carbon pools (any carbon pools except for the forest AGC pool, such as atmosphere carbon pool) was generally higher in forests with fire disturbances than in forests without evidence of fire disturbances across different ecological sections (Fig. S1c). Forests with evidence of fire disturbances in the Southern California Coast had the largest carbon stocks emissions into the atmosphere ($4.50 \pm 0.66 \text{ Mg ha}^{-1}$) (Fig. S1c). This was 30 times higher than the highest carbon emission into the atmosphere in forests where fire disturbances were absent ($0.11 \pm 0.04 \text{ Mg ha}^{-1}$). Merging FIA and MTBS fire events together, there were 2284 conditions with evidence of at least one fire disturbance, indicating 8.16 % of remeasured FIA forest land had evidence of fire in the last two decades (Table S11). According to FIA records, most tree mortality occurred during fire disturbances (Fig. 1). For annual AGC change, more carbon was emitted instead of transferred from LIVE to DEAD trees in conditions with evidence of fires than in conditions without evidence of fires (Table S11).

Among area burned, forests with evidence of high severity and low frequency fires transferred $1.35 \pm 8.70 \times 10^{-3} \text{ Mg ha}^{-1} \text{ yr}^{-1}$ carbon from LIVE to DEAD; forests with evidence of low severity and high frequency fires transferred $1.87 \pm 0.07 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ carbon from LIVE to DEAD (Table S3). These amounts were two to three times greater than the average amount observed in forests with evidence of fires. In contrast, forests with evidence of low severity and low frequency fires transferred less carbon from the LIVE to DEAD pool than the average amount in forests with evidence of fires ($0.67 \pm 4.84 \times 10^{-3} \text{ Mg ha}^{-1} \text{ yr}^{-1}$), and therefore, their AGC storage and sequestration capacity had the potential of more annual carbon removal from the atmosphere ($0.13 \pm 4.47 \times 10^{-3} \text{ Mg ha}^{-1} \text{ yr}^{-1}$ and $0.28 \pm 4.32 \times 10^{-3} \text{ Mg ha}^{-1} \text{ yr}^{-1}$, respectively) (Table S3). Although both low severity and high frequency fires and high severity and low frequency fires reduced AGC, conditions with evidence of low severity and high frequency fires had lower reductions in AGC stocks and sequestration capacity compared to high severity and low frequency fires (AGC stocks reduction: $0.67 \pm 0.05 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ and $0.91 \pm 9.04 \times 10^{-3} \text{ Mg ha}^{-1} \text{ yr}^{-1}$, respectively; AGC sequestration capacity reduction: $0.37 \pm 0.04 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ and $0.62 \pm 8.39 \times 10^{-3} \text{ Mg ha}^{-1} \text{ yr}^{-1}$, respectively) (P -value < 0.05) (Table S3; Table S4; Table S5; Table S6). The conditions with evidence of low severity and high frequency fires had less ($7.14 \pm 1.88 \text{ Mg ha}^{-1}$) DEAD carbon change during FIA remeasurement periods than conditions with evidence of high severity and low frequency fires. As a result, forests with evidence of low severity and high frequency fires stored more AGC ($0.24 \pm 0.06 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) than forests with evidence of high severity and low frequency fires, which suggested that the high severity and low frequency fires emitted more forest carbon into the atmosphere. However, the amount of carbon transferred from LIVE to DEAD tree carbon pools in

burned forests may either increase or decrease depending on biotic and abiotic factors.

3.3. Biotic factors

The AGC change on forest land with evidence of a recent fire was influenced by the following forest biotic factors: AGC, forest type, tree dbh, tree age, tree density at T1, and changes in height, canopy coverage, and diameter. Factors significantly impacting forest AGC change included forest T1 AGC (P -value < 0.001), T1 tree density (P -value < 0.001), diameter growth (P -value < 0.001), tree height change (P -value < 0.001), and T1 age (P -value < 0.001) (Table S7). The forests with higher density (coefficient of tree density: $(2.35 \pm 0.36) \times 10^{-4}$), larger diameter growth (coefficient of dbh change: 0.41 ± 0.03), larger tree height growth (coefficient of tree height change: 0.64 ± 0.04), larger T1 AGC (coefficient of AGC at T1: $0.12 \pm 3.50 \times 10^{-3}$), and younger forest age (coefficient of tree age: $(-3.06 \pm 0.62) \times 10^{-3}$) stored more AGC (Table S7). All forest types had reduced AGC with evidence of fire, except for ponderosa pine forests, which had a small increase in AGC post-fire (Fig. S1a). When these forests had no evidence of fires, their AGC increased (Fig. S1a).

3.4. Abiotic factors

The ecological regions, and topography were considered as abiotic factors. For topography, only slope (P -value < 0.05) significantly impacted forest AGC change, indicating that flat regions (coefficient of slope degree: $(-2.46 \pm 1.21) \times 10^{-3}$) contributed to greater AGC storage (Table S7). The AGC had a greater reduction in lower elevations (coefficient of elevation: $(1.68 \pm 1.73) \times 10^{-5}$), however, the elevation did not show a significant impact. Across the 19 ecological regions, the Alpine Meadow province, which comprised southern Rocky Mountains steppe, open woodland, and coniferous forests, lost the most AGC due to fires in the past decades (Fig. S1b).

3.5. Compound disturbances

In forests of the Western US, carbon stock transfer from LIVE trees to DEAD trees was highest in conditions with evidence of compound disturbances, which included evidence of fires (Table 1). In the Western US, fire plus insect, disease, and drought were the most common compound disturbances. The compound disturbances and their effects on AGC and tree mortality varied due to different disturbance orders. Among these compound disturbances, fire combined with insects caused the largest forest AGC loss and tree mortality. AGC sequestration capacity was reduced in forests where both fire and insect damage occurred compared to forests only experiencing fires. In this combination, fires that occurred in insect-disturbed forests caused slightly more tree mortality (48.70 ± 2.65 % of total trees) than insect disturbances in post-fire forests (46.80 ± 1.70 % of total trees), but there were no significant differences (Fig. 3). When a fire occurred in insect-disturbed forests ($1.83 \pm 1.12 \text{ Mg ha}^{-1}$), the amount of carbon transfer from LIVE to DEAD carbon was similar to when the insect disturbance happened post fire ($1.87 \pm 0.42 \text{ Mg ha}^{-1}$). Forest LIVE carbon emission post disturbances was slightly higher when a fire occurred in an insect disturbed forest (insect + fire: $3.18 \pm 1.62 \text{ Mg ha}^{-1}$; fire + insect: $2.72 \pm 0.58 \text{ Mg ha}^{-1}$) but there were still no significant differences (Fig. 3). Consequently, even though forests with insect disturbances before fires (carbon emission of insect + fire: $1.35 \pm 0.75 \text{ Mg ha}^{-1}$) had lower total AGC stocks than fire disturbances before insects (carbon emission of fire + insect: $0.85 \pm 0.37 \text{ Mg ha}^{-1}$), there was no significant differences whether a fire occurred before insects or not (Fig. 3). The AGC reduction was lower at sites with evidence of fire plus drought ($0.51 \pm 1.09 \text{ Mg ha}^{-1}$) than at sites with evidence of fires and less drought-prone ($1.52 \pm 0.07 \text{ Mg ha}^{-1}$) but there was not significant difference (Fig. 3). When the post-fire forests suffered drought (46.10 ± 6.50 % of total trees), tree mortality became higher than forests in drought areas suffering fire disturbances (15.20 ± 0.00 % of total trees) (Fig. 3). In FIA

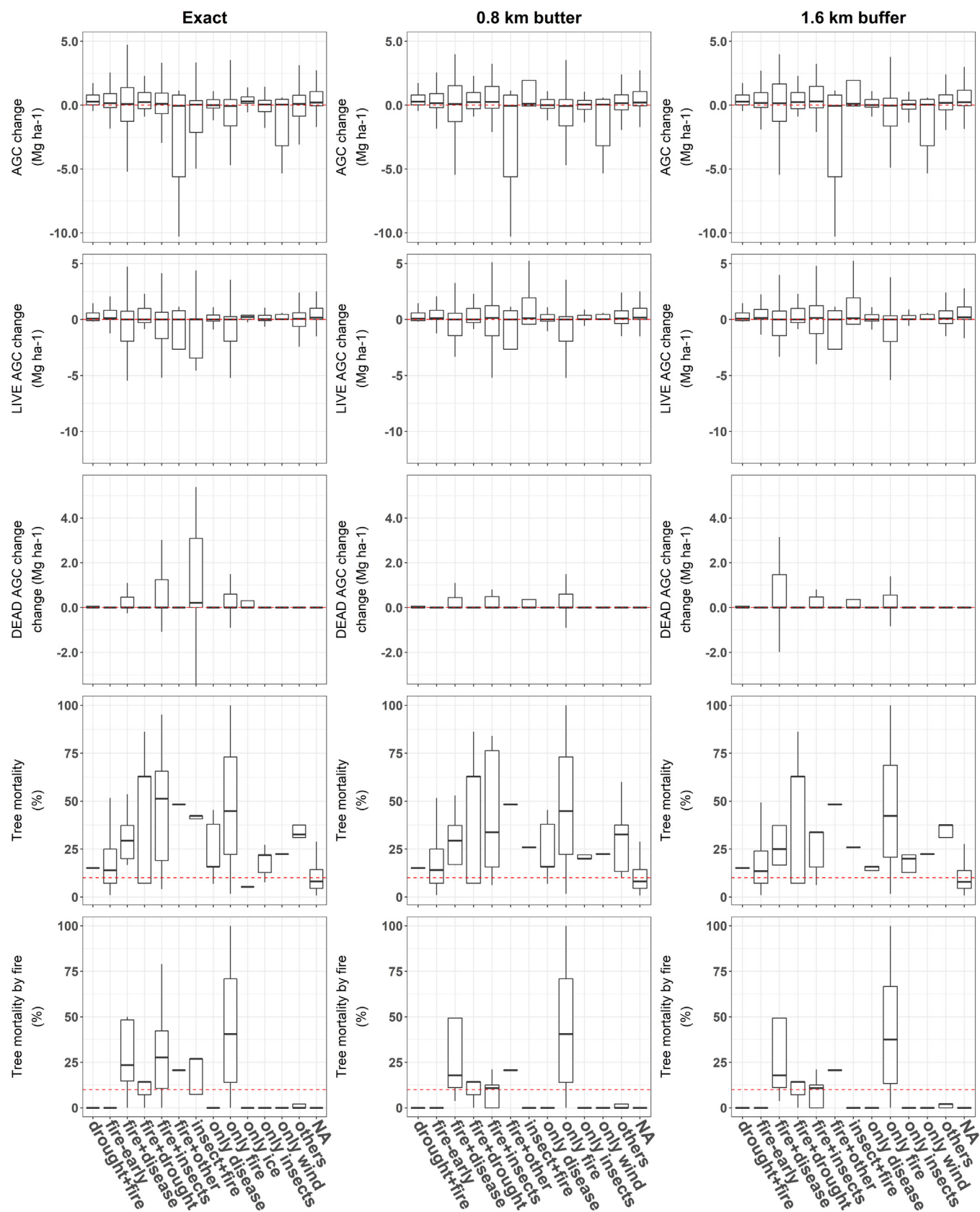


Fig. 3. Impacts of fire plus other disturbances on carbon change and mortality for forests in the Western United States comparing actual and perturbed methods. Negative estimates indicate carbon removals in the forest. The x-axis lists disturbance types. When fire and other disturbances occurred at the same condition, '+' was used to represent compound disturbance types. The disturbance before '+' comes first and after '+' happens later. For example, 'drought + fire' indicates that a fire occurs in a forest which also suffers drought.

plots, there were no records of disease existing before in a region suffering from fire disturbances. The AGC storage could either increase or decrease in fire + disease disturbed forests (Fig. 3). Disease occurring in post-fire forests (change of DEAD pool: $1.48 \pm 0.66 \text{ Mg ha}^{-1}$) reduced carbon transfer from LIVE to DEAD pools compared to fire plus drought (change of DEAD pool: $1.87 \pm 0.42 \text{ Mg ha}^{-1}$) and fire plus insects (change of DEAD pool: $2.11 \pm 0.50 \text{ Mg ha}^{-1}$) compound disturbances. After 2000, two FIA plots had records of extreme winds blowing after a fire ignited, consuming more forest fuel (Cannon et al., 2014). However, prior to 2000, this disturbance combination had never appeared within FIA remeasurement records.

3.6. Climatic warming, reduced precipitation, and severe drought

In recent decades, there was evidence that changes in temperature and precipitation contributed to changes in fire frequency (all P -value < 0.001) (Table S8). Maximum, mean, and minimum temperatures during normal climate period from 1991 to 2020 and the 20th century had effects on fire severity (all P -value < 0.05) (Table S9). The fire frequency was influenced by the 1991–2020 normals for precipitation and temperature, and the 20th century precipitation (P -value < 0.05) (Table S8). Alternatively, changing drought conditions affected fire frequency and severity directly. Annual drought severity and seasonal drought length affected both fire severity and frequency (all P -value < 0.05) (Table S10). The start month of drought impacted fire frequency (P -value < 0.001) but not fire severity (Table S10).

3.7. Anthropogenic interventions

Compared to the burned area without treatments, a cutting treatment before a fire benefited AGC stock increase ($0.78 \pm 0.58 \text{ Mg ha}^{-1}$), while two cutting treatments before a fire led to AGC stock decrease ($-2.31 \pm 1.75 \text{ Mg ha}^{-1}$). Artificial regeneration treatments and other silvicultural treatments before fires increased AGC stocks by $1.46 (\pm 7.00) \text{ Mg ha}^{-1}$ and $1.23 (\pm 2.21) \text{ Mg ha}^{-1}$, respectively. For treatments executed after fires, AGC stocks were reduced by $7.34 \times 10^{-3} (\pm 0.30) \text{ Mg ha}^{-1}$ with a cutting treatment, increased by $1.24 (\pm 1.75) \text{ Mg ha}^{-1}$ with a site preparation treatment, and increased by $0.70 (\pm 0.94) \text{ Mg ha}^{-1}$ with other silvicultural treatments. If a cutting treatment was applied pre-fire and was followed by a post-fire site preparation treatment ($2.43 \pm 3.49 \text{ Mg ha}^{-1}$) or an artificial regeneration plus cutting treatment ($2.46 \pm 3.49 \text{ Mg ha}^{-1}$), AGC increased.

3.8. Comparing actual and perturbed FIA plots

When MTBS was harmonized with the perturbed FIA locations, results were consistent with those from the actual FIA locations, according to the diameter of buffer area. Nevertheless, some results were still inconsistent when comparing the perturbed and actual FIA locations. The distributions developed from the actual and perturbed locations did not overlap in terms of fire severity (Fig. S2). After merging with MTBS, the buffer methods exhibited varying numbers of FIA plots that showed evidence of fire disturbances (Table 3; Table 4). Compared to the low severity and high frequency burned areas, the AGC stock estimates for both buffer methods had lower reductions in areas with high severity and low frequency of burn. This finding contrasted with the results obtained using actual FIA locations (Table S4; Table S5; Table S6). This inferred an opposite conclusion that low severity and high frequency fires released more forest carbon emissions. Contrary to the results obtained using the actual FIA locations, both buffer methods showed that recent precipitation had a significant impact on fire severity. However, the normal maximum, mean, and minimum temperatures from 1991 to 2020 using buffer methods did not affect fire severity. In the perturbed_0.8 buffer, the maximum, mean, and minimum temperatures at the 20th century influenced fire frequency which differed from the results obtained with the actual FIA locations. Regarding drought-related factors, in contrast to the relationships observed at the actual FIA, the drought start season did not exhibit an impact on fire frequency at perturbed_1.6 but showed a significant impact on fire severity with both buffer methods.

4. Discussion

Forests with evidence of fires have a profound impact on reducing standing carbon stocks and sequestration capacity, and transferring carbon from LIVE to DEAD, compared to forests without evidence of fires in the Western US. Without fires, the DEAD carbon pool remained stable, while it was more than doubled in areas that experienced fire disturbances. Because of less tree growth and more carbon transfer from LIVE to DEAD, the amount of LIVE carbon was reduced in areas with evidence of fires but increased in areas without evidence of fires. Therefore, total carbon storage was reduced in areas with evidence of fires. In the study area, reduction in AGC storage in forested areas with evidence of wildfires was greater in areas experiencing high severity and low frequency fires compared to low severity and high frequency fires. However, the estimation of carbon transfer from LIVE to DEAD ecosystem pools was higher on average under conditions with evidence of low severity and high frequency fires than under conditions with evidence of high severity and low frequency fires, because DEAD trees may fall down within the FIA remeasurement period (ca. 10 years) (Stenzel et al., 2019). Estimates of LIVE AGC storage in forests with evidence of low severity and high frequency fires were, on average, around twice as large as in forests with evidence of high severity and low frequency fires at T2, even though they had similar initial LIVE AGC storage. This indicated that high severity fires were correlated with high tree mortality, especially in young forests, as young trees had thin bark, and a relatively large proportion of stored carbon was released if combustion occurred (Brando et al., 2012; Harmon et al., 2022). For example, the largest carbon loss forest, which was a relatively young forest in the Middle Rocky Mountains, experienced a high-severity fire followed by 95.24 % tree mortality, resulting in a carbon reduction of $255.219 \text{ Mg ha}^{-1}$ (81.89 %). However, an extreme forest AGC change may be caused by a low severity fire in an old forest because bigger trees were killed after low severity but shorter interval fires. According to FIA records, a 515-year-old redwood forest on the coast of California with $153.59 \text{ Mg ha}^{-1}$ pre-fire forest AGC lost all AGC after two low-severity fires occurred in less than ten years. However, there was uncertainty regarding the accounting of different fire events as one fire when merging FIA and MTBS records because FIA estimated fires on an annual level.

To best compare GHG emissions from forest land caused by wildfires, IPCC (2006) Tier 1 was selected because it was most similar to the FIA data type, which did not aggregate data relying on prescribed burning or wildfires in forest land. For boreal forests in wildfire disturbances scenarios, the default combustion factor value (proportion of prefire fuel biomass consumed) by IPCC (2006) is 0.40 (SD = 0.06). However, in FIA conditions with evidence of fires, the combustion factor value was found to be 0.15 (SD = 0.07). Additionally, the combustion factor values were 0.30 (SD = 0.04) and 0.20 (SD = 0.10) when the FIA conditions indicated evidence of high severity and low frequency fires, and low severity and high frequency fires, respectively. The differences in estimates may be attributed to the simplified approach used by IPCC Tier 1, which takes into account both aboveground and belowground carbon to calculate forest carbon stock change. Furthermore, forest biotic factors (such as forest type, dbh, height, etc.) and abiotic factors (such as climate, management activities, topographies, etc.) may also affect the forest carbon stock change and the combustion factor.

Reduction of AGC on forest land was directly associated with post-fire tree mortality. The mortality varied across different forest types because different tree species and sizes (dbh) had different fire tolerances. The Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), ponderosa pine, western larch (*Larix occidentalis* Nutt.) and western white pine (*Pinus monticola* Douglas ex D. Don) groups showed low tree mortality ratios caused by fires (1.22 ± 0.11 %, 1.75 ± 0.16 %, 1.44 ± 0.53 %, and 0, respectively) because the dominant tree species of these forest groups were fire-tolerant species which had thick bark and crowns high above the forest floor and have a high fire resistance. However, forests dominated by fire-intolerant species may have low mortality ratios if these trees had larger diameters, for example, mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), and

hemlock and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) species groups, had large dbh (26.87 ± 0.35 cm, 34.98 ± 1.14 cm, respectively) leading to low mortality (1.10 ± 0.13 %, 0.29 ± 0.16 %, respectively) (Fig. S3; Dunn and Bailey, 2016; Hessburg et al., 2022; Stevens et al., 2020). The forest damage and tree mortality future influenced carbon sequestration capacity through regeneration. For example, in western ponderosa pine and California mixed conifer forests, AGC increased post-fire because cones and seeds of conifer tree species survived fires and fires opened understory space, promoting light for these seeds to germinate (Johnstone et al., 2016). In addition, a high severity fire (313 conditions) may change forest types (219 conditions), and consequently affected forest land AGC sequestration capacity (Haffey et al., 2018). For instance, 40 FIA conditions suggested that a conifer forest transformed into a deciduous forest (such as quaking aspen [*Populus tremuloides* Michx.] and canyon live oak [*Quercus chrysolepis* Liebm.]) after a high severity fire, because fires removed seed sources needed for conifer forest to recover. Since the growth rate of deciduous species was slower than conifer species, the LIVE AGC pool post-fire was reduced (Johnstone et al., 2016). Generally, the wildfires increased tree mortality and decreased Carbon stocks. However, the effect of a fire may be beneficial or detrimental based on other abiotic factors such as climate and drought.

Wildfire frequency and severity have been higher in recent decades than the previous century due to climate change and severe drought (Hagmann et al., 2021). In the late 19th century, wildfire frequency started to decrease because expansion of European colonization kept combustion fuel lower in most areas by logging (Hagmann et al., 2021). In the 20th century, area burned in the Western US continued declining because less available combustion fuel left from the 19th century and increased precipitation (Fig. 2c: increased 1.016 mm compared with historical records at the end of the 20th) created more wet periods (Hagmann et al., 2021). Although the fire suppression was executed in the 20th century, it impacted AGC accumulation later in the 20th century (Hagmann et al., 2021). In the last 30 years, area burned has increased due to the climate oscillations associated with El Niño or La Niña, altered climate change because of the mountain ecosystems, more available combustible fuels, increased insect infestation due to the lack of extremely cold temperatures in the winters (DeMeo et al., 2018; Lange et al., 2020; Loehman et al., 2018; Mason et al., 2017; Reed et al., 2018; Seidl et al., 2017; Shepherd et al., 2018). Combined with a warming climate, the longer and warmer summers also increased drought stress, thereby affecting fire characteristics (Halofsky et al., 2020; Littell et al., 2016; van Mantgem et al., 2013). In low frequency and severity fire conditions, fire frequency increased with increased drought severity and longer seasonal drought. In low frequency and moderate severity fire conditions, fire frequency decreased when drought severity decreased, and the seasonal drought was shorter. Therefore, in recent decades, with the occurrence of warm seasonal droughts, igniting fires in forests has become easier and more combustible fuel would be available if other disturbances occurred in areas that subsequently burned.

In the forests with evidence of fire plus other disturbances, AGC change depended on not only fire severity and frequency, but also the types and sequence of other disturbances. This study found that fire combined with insects, fire combined with disease, and fire combined with drought were three common fire compound disturbances in the Western US. First, this study indicated that insect-infected trees had less resistance to fire damage, and dead trees killed by insects were combustible fuels (Urbanski, 2013; Woodall et al., 2021). This was explained by another study that the outbreak of insects can constrain the ecosystem's response to a subsequent fire by altering forest composition and fuel structure (Johnstone et al., 2016). However, another study found that this pattern varied depending on fire severity: in ponderosa pine forests of Western North America, low severity fires induced resin duct production which increased tree defense against bark beetle attacks that may increase tree survival after subsequent herbivory (Hood et al., 2015). Second, this study and other published research showed that the fire-disease interactions impacted long-term populations by reducing resprouting trees, consequently, reducing stand density and AGC stocks (Simler et al., 2018). However, another study

found that this combination could also generate a growth benefit or release for surviving trees because fires may reduce disease pressure (Simler et al., 2018). Third, this study claimed that drought disturbance may not enhance fire damage on forest land. However, this conclusion may be challenging given that AGC prior to fire was higher in forests with evidence of only fires than in forests with evidence of fire plus drought. While compound disturbances might result in more combustible fuel and higher tree mortality, stand treatments may reduce forest damage from wildfires through removal of combustible fuel and increased tree growth.

Cuttings, artificial regenerations, site preparations, and other silvicultural treatments were applied throughout the forests inventoried by FIA to improve forest carbon sequestration capacity. Among these treatments, the frequency and time of cutting were essential factors that impacted post-fire forest recovery (Kleinman et al., 2019; Marcolin et al., 2019). Across the FIA conditions, performing one pre-fire cutting treatment increased post-fire forest regeneration. This was because cutting treatments removed available combustion fuels, which in turn reduced fire frequency and severity, and subsequent tree mortality (Tubbesing et al., 2019). Forest treatments suggested that appropriate human interventions either before or after fires have potential to increase tree survival rate during disturbances and to increase germination rate after disturbances. In contrast, if multiple cuttings were executed pre-fire, forests would be at a low pre-fire AGC storage level prior to a disturbance and less AGC change would follow after disturbances. When a cutting was applied post-fire, FIA conditions showed AGC reduction. This reduction remained in cases where cutting followed artificial regeneration. The reason for this detrimental feedback was that a post-fire cutting altered forest microclimatic conditions by increasing soil temperature and reducing soil moisture, which affected tree establishment and regeneration (Marcolin et al., 2019; Niemeyer et al., 2020).

Buffer methods applied around the perturbed FIA locations influenced accuracy of results compared to actual FIA locations. The influences from the perturbed plot locations presented less impact as ancillary data derived from a coarse resolution with a large sample size (Prisley et al., 2009). Since burned areas covered small landscape scales, the buffer areas around perturbed locations may not exactly overlap burned areas at the exact locations. Thus, fire severity was diluted at low and high severity due to buffer areas including sections where fire was absent or less severe. Therefore, the impact of recent (1991 to 2020) annual precipitation, which affects the fine-scale geographic landscape, on fire severity did not remain consistent between the actual and perturbed FIA locations. However, when sample size were big enough, the impacts of compound disturbances on AGC stock change, LIVE and DEAD carbon change, tree mortality, and tree mortality with evidence of causation by fires showed consistent characteristics from actual to perturbed FIA conditions (Huang et al., 2018). A similar pattern was also found for the relationships of fires and seasonal drought. The relationships between fire severity or frequency, and drought severity or seasonal drought length were consistent from perturbed to actual FIA conditions. Hence, perturbed FIA locations were effective to draw conclusions in this landscape-level study with large sample size.

5. Conclusions

Four conclusions were drawn from this study. First, fires had a profound effect on forest AGC stocks and sequestration capacity. The low severity and high frequency fires had lower reductions in forest AGC stocks and sequestration capacity reduction compared to high severity and low frequency fires in the Western US after 2000. Our estimates of combustion factor value were lower than the default combustion factor used by IPCC (2006). Second, biotic factors impacted tree mortality caused by fires which affected the AGC change both directly and indirectly. The AGC change was impacted directly by tree species, size, and forest structure, which was related to post-fire tree mortality. Third, forest AGC from different ecological regions and forest types responded to wildfires differently in relationships to varying abiotic factors, such as climate change, severe seasonal drought, compound disturbances and anthropogenic interventions. Generally, low severity fires encouraged forest regeneration, as these fires

benefited forest AGC sequestration capacity. Fourth, although the conclusions from the perturbed FIA plots may be different from using the actual FIA locations, their overall major conclusions were consistent at the landscape level. Hence, it may not be necessary to know the exact locations of FIA plots when conducting landscape-level studies.

CRedit authorship contribution statement

Panmei Jiang: Conceptualization, Methodology, Software, Writing – original draft, Visualization. **Matthew B. Russell:** Review & editing. **Lee Frelich:** Review & editing. **Chad Babcock:** Review & editing. **James E. Smith:** Part data & review.

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Data availability

The data sources have been stated in the article's method section.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent any official U.S. Department of Agriculture or U.S. Government determination or policy.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.164832>.

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