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Quantifying Western US tree carbon stocks and sequestration from fires

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Abstract

Background Forest ecosystems function as the largest terrestrial carbon sink globally. In the Western US, fires play a crucial role in modifying forest carbon storage, sequestration capacity, and the transfer of carbon from live to dead carbon pools. We utilized remeasurements of more than 700,000 trees from 24,000 locations from the US Department of Agriculture Forest Service's Forest Inventory and Analysis program (FIA) and incorporated supplementary information on wildfires from the Monitoring Trends in Burn Severity dataset. These datasets allowed us to develop models that examined the impact of fires, in conjunction with other abiotic and biotic drivers, on estimates of carbon stocks, stock changes, and sequestration capacity in forested areas in the Western US.

Results Wildfires were a primary factor contributing to the reduction of aboveground carbon storage in Western U.S. forests. All models indicated that biotic factors (e.g., tree density, canopy coverage, and tree height) played a more significant role than abiotic factors (e.g., elevation, mean annual temperature and drought severity) in determining fire effects on forest carbon storage and sequestration capacity. Due to a lower occurrence of fires and higher precipitation, forests in the Pacific Northwest-West region with lower-elevation exhibited higher productivity compared to other regions.

Conclusions The findings of this study enhance our understanding of the influence of fires on carbon dynamics in forest ecosystems in the Western US. In particular, the importance of understanding biotic conditions such as forest structure and composition was revealed as a primary determinant of carbon emissions from fire. These insights are valuable for forest carbon estimation beyond FIA sampling plots, extending to inaccessible forest land in future studies. Consequently, they are beneficial for forest managers developing strategies for storing and sequestering carbon in fire-prone forest ecosystems.

Keywords Aboveground carbon, Climate, Combustible fuel, Drought, Fire effects, Linear mixed effects model, Random forest, Standing trees, Western USA

Resumen

Antecedentes Los ecosistemas forestales funcionan como la reserva de carbono terrestre más grande del mundo. En el oeste de los EEUU, los fuegos juegan un rol crucial en la modificación de las reservas de carbono, en la capacidad de secuestro de ese carbono, y en la transferencia de esos almacenes de carbono de plantas vivas a material orgánico muerto. Utilizamos la remedición de más de 700 mil árboles de 24.000 ubicaciones del Inventario Forestal y del programa de análisis (FIA) del Servicio Forestal dependiente del Departamento de Agricultura de los EEUU, e incorporamos información suplementaria sobre incendios tomada de las tendencias de monitoreo y conjunto de datos sobre

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severidad de los incendios. Estos conjuntos de datos nos permitieron desarrollar modelos para examinar el impacto de los incendios, en conjunción con otros conducentes bióticos y abióticos, sobre la estimación del stock de carbono, los cambios en esos stocks, y la capacidad de secuestro de carbono en áreas forestadas del oeste de los EEUU.

Resultados Los incendios forestales fueron el factor primario que contribuyó a la reducción de las reservas de carbono en las partes aéreas de la vegetación en los bosques del oeste de los EEUU. Todos los modelos indicaron que los factores bióticos (i.e. la densidad de árboles, cobertura del dosel, y altura de los árboles) jugaron un rol más significativo que los factores abióticos (i.e. elevación, temperatura y severidad de la sequía), en la determinación de los efectos del fuego en el almacenaje de carbono y en la capacidad de secuestro de ese carbono. Debido a una menor ocurrencia de incendios y una precipitación más alta, los bosques de la región noroeste del Pacífico, con menores elevaciones, exhibieron una productividad más alta que las otras regiones.

Conclusiones Los resultados de este estudio aumentaron nuestro conocimiento sobre la influencia de los incendios en la dinámica del carbono en los ecosistemas forestales del oeste de los EEUU. En particular, la importancia de entender las condiciones bióticas como la estructura forestal y su composición se reveló como la principal determinante de las emisiones de carbono por los incendios. Estas percepciones son muy valiosas para la estimación del carbono más allá de las parcelas de muestreo del inventario forestal (FIA), pudiendo extenderse a los bosques inaccesibles en futuros estudios. Consecuentemente, estas percepciones son beneficiosas para los gestores forestales que desarrollan estrategias para almacenar y secuestrar carbono en ecosistemas forestales propensos al fuego.

Introduction

Forest land serves as the largest terrestrial carbon sink in the United States (US), offsetting over 12 percent of economy-wide greenhouse gas (GHG) emissions annually (EPA 2022). In the Western US, there has been a substantial increase in the number of wildland fires that have burned forest areas larger than 400 ha over the last three decades, accompanied by marked interannual variability of burned areas and heightened CO_2 emissions associated with wildfires (Balch et al. 2018). While some of this carbon was re-sequestered over time through vegetation growth and regeneration, subsequent fires can release it back into the atmosphere, creating a cycle of carbon gain and loss (Pellegrini et al. 2021). However, if sufficient time passed between fires, forests can potentially sequester more carbon than was lost, maintaining their role as carbon sinks rather than shifting to carbon sources.

Fires impact forest carbon storage directly by increasing mortality of trees, and indirectly through subsequent impacts on forest regeneration and fuel availability. Previous studies have shown mixed results for the effect of fire severity and frequency on forest carbon storage change, emphasizing the importance of understanding the factors that lead to different fire effects (Parks & Abatzoglou 2020). Climate (temperature and precipitation) and drought can influence tree growth, mortality, fire severity, and frequency, potentially altering the impact of fire on forest carbon stocks (Wasserman & Mueller 2023). Forests in warm and moist conditions typically experience fewer fires and accumulate less combustible fuels. For example, rainforests in the Pacific Northwest-West experienced fewer fires than Pacific Northwest-East, Pacific Southwest, and Rocky Mountains in the past 300 years (Hoover et al., 2023). In contrast, forests facing warm and prolonged drought seasons may have more fires and higher tree mortality (Westerling et al. 2006; Crockett & Westerling 2018; Holden et al. 2018; Buotte et al. 2019; Keen et al. 2022).

Over the past 30 years, states in the Western US have experienced an increase in the area burned due to climate change. Historical logging efforts in the nineteenth century led to lower carbon storage and tree density, thereby reducing the amount of fuel present (Hagmann et al. 2021). In addition, at the beginning of the twentieth century, western US forests experienced fewer fires because of fire suppression laws, policies and culture (Hagmann et al. 2021). However, since 2000, there has been an increase in the total forest area burned (Van Mantgem et.al., 2009; Wilson et.al., 2013; Williams et al. 2016). This can be attributed to the warmer and less drought-prone twentieth century, which increased forest productivity making forests denser with greater carbon biomass (Littell et al. 2016; Halofsky et al. 2020). In addition, the warming climate has led to more days per year with possible extreme windstorms and a lack of extremely cold temperatures in winters, which contributed to increased insect infestation (Jiang et al. 2023; Seidl et al. 2017). This combination resulted in greater dead fuels accumulation, thereby increasing the risk of high severity fires (Jiang et al. 2023; Seidl et al. 2017).

The structure and composition of the forest canopy can modify the impact of fires on forest carbon storage and sequestration capacity through forest regeneration and tree mortality. This is particularly evident in Western US forests that have diverse forest types and trees with varying life spans. Young trees release larger proportions of stored carbon when burned due to their generally thin bark and high surface area to volume ratio, resulting in high mortality (Brando et al. 2012; Harmon et al. 2022). Tree age also influences post-fire forest regeneration, as seed production generally increases with tree maturity but declines in large old trees during physiological decline (Qiu et al. 2021).

Tree species are another essential factor affecting seed abundance and survival for post-fire forest regeneration. Fir and mixed-conifer forests in the Western US have stronger post-fire seed availability compared to pines due to differences in shade tolerance and competitiveness in the low elevation forests of California (Stewart et al. 2021). Forests dominated by fire-tolerant species, like Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), ponderosa pine (*Pinus ponderosa* Laws.), western larch (*Larix occidentalis* Nutt.), and western white pine (*P. monticola* Douglas ex D. Don) may buffer fire effects due to their thick bark and high crown positions (Jiang et al. 2023). These characteristics make them highly fire-resistant and less susceptible to post-fire mortality (Dunn & Bailey 2016; Hagmann et al. 2022; Hessburg et al. 2022). For fire-intolerant species, tree mortality caused by fires may be lower in forests dominated by older trees with larger diameters (Dunn & Bailey 2016; Stevens et al. 2020; Hessburg et al. 2022). These responses in forest regeneration and tree mortality can have ecoregion-level implications, influencing forest type or land cover change (Kemp et al. 2019; Wang et al. 2020).

The primary goal of this study was to assess the impact of fire on forest aboveground carbon (AGC) stocks, and sequestration capacity (change of the AGC standing live carbon pool) in Western US forests. This study aimed to address a knowledge gap regarding the specific effects of fires on carbon dynamics, crucial for informing management strategies and understanding the resilience of forest carbon stocks in the face of climate-driven fire severity. Additionally, the study aimed to investigate how forest biotic factors (such as structure and conditions) and abiotic factors (such as topography, fire in conjunction with other disturbances, climate, and forest management) can modify these effects. To accurately test these effects, potential collinearity between fire and environmental variables under localized conditions must be considered. Random forest and linear mixed effects models were used to examine the effects of biotic and abiotic drivers on relationships between fires and forest AGC change. The focus was on understanding changes in forest AGC stocks and sequestration capacity, as well as carbon transfer from standing live to standing dead carbon pools (hereafter termed TRANSFER), which represent the amount of carbon removed from or emitted into the atmosphere. The specific objectives were to: (1) compare AGC storage and sequestration capacity in fire-affected and unaffected areas from 2000 to 2018, (2) develop models that identified if biotic factors influenced the impacts of fire on forest AGC changes more than abiotic factors, and (3) assess the biotic and abiotic impacts on forest AGC associated with different fire severities and frequencies.

Methods

Study area and sampling design

The forests sampled were located in Arizona, Colorado, Idaho, Montana, Nevada, Oregon, Utah, Washington, New Mexico, and California. The majority of forests are coniferous from the Rocky Mountains to the Pacific Northwest. Within these ten states, the northern Pacific lowlands exhibit a climate favoring wetter and mixed deciduous and coniferous forests. In contrast, the southern regions encompassing the California coastline, Cascade Range, and Plateau areas feature drier conditions conducive to coniferous forests. Across the ten states during the last thirty years (from 1991 to 2020), the mean annual temperature and precipitation were 10.45 °C and 536.53 mm, respectively. In the northwest forests, the Olympic rainforest in Pacific Northwest-West region received the highest precipitation, while the coldest area was in the Rocky Mountain North (Fig. 6; Jiang et al. 2023). In contrast, in the southwest forests, the area near the Sonoran Desert was the driest and hottest (Jiang et al. 2023).

We selected 24,733 remeasurement sample plots from 2000 to 2018, based on Forest Inventory and Analysis (FIA) program plots on forest land that remained as forest land during the remeasurement period in ten States in the Western US (Fig. 1). The FIA sampling frame was designed with approximately 2,428 ha hexagons each containing one randomly located permanent ground plot, utilizing a system where measurements were taken every ten years (Reams et al. 2005; Yu et al. 2022). Each permanent ground plot consisted of four fixed-radius subplots, positioned at the plot center and extending 36.6 m from the plot center at 0°, 120°, and 240° from north (Bechtold & Scott 2005; Woolman et al. 2022; Yu et al. 2022). Each subplot included a two-meter fixed-radius microplot and was surrounded by an 18-m fixed-radius macroplot. Multiple conditions may be mapped within a plot to delineate unique features, such as different ownerships, stand age, forest types, slope and aspect (Bechtold & Scott 2005; Jiang et al. 2023). Consequently, 25,328 remeasurement conditions (2.4% of plots have multiple conditions) were considered in this study. To safeguard the privacy of landowners and maintain the ecological integrity of plots, the actual plot locations were not included in the publicly

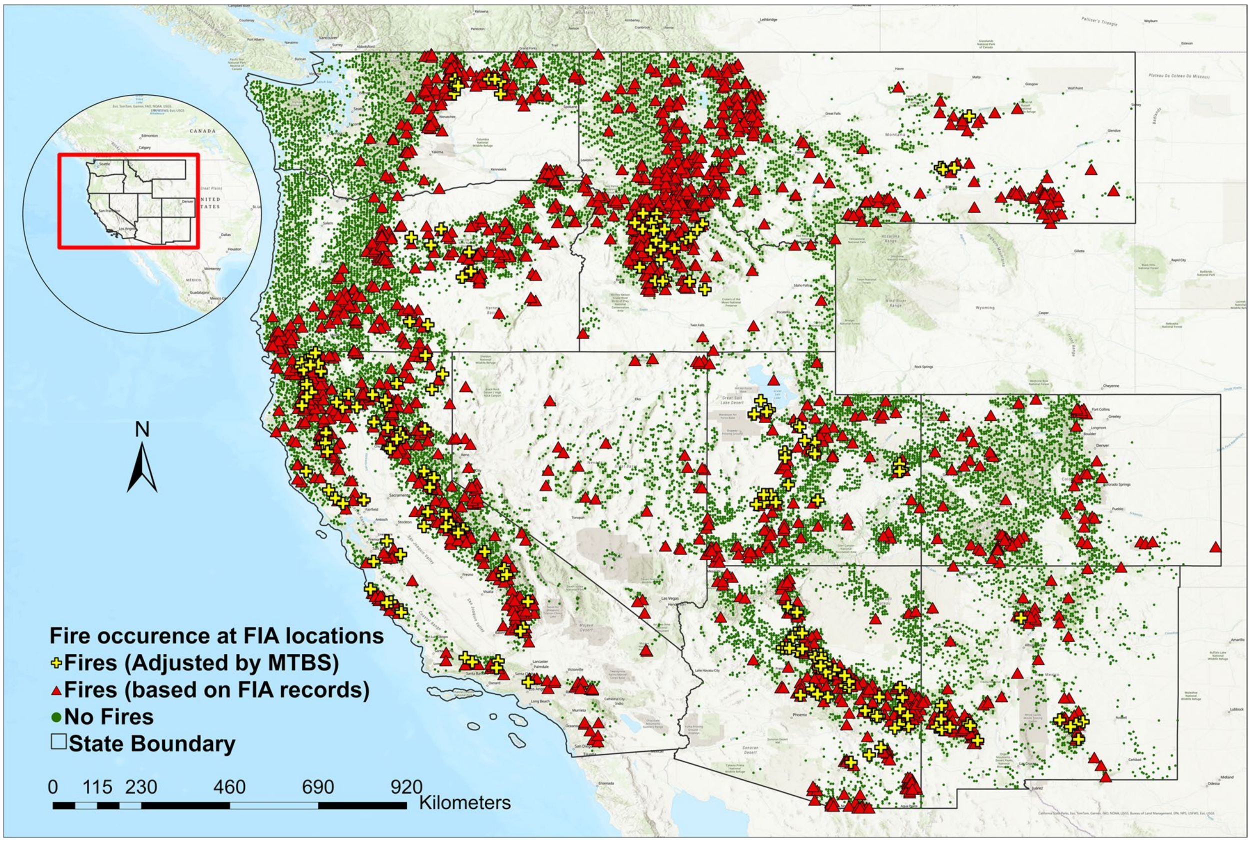

Fig. 1 Fire distribution on forest land in the western United States (10 states). There were 25,328 conditions selected from the public Forest Inventory and Analysis (FIA) data. The FIA locations marked as green dots present conditions without evidence of fire disturbances. The conditions with FIA fire disturbance records were assigned as red triangles. The conditions without FIA fire disturbances records but located within Monitoring Trends in Burn Severity (MTBS) fire boundaries were assigned as yellow crosses

available FIA database (Huang et al. 2018). As a result, the perturbed locations were up to 0.8 km away from the exact locations in a random direction (Bechtold & Scott 2005). So, we generated a circular buffer with 1.6 km diameter around the perturbed FIA plot locations to cover the actual locations. A subset of plot locations were swapped with other plot locations (Prisley et al. 2009). Hence, the perturbed FIA locations were buffered with a radius of 800 m during the process of merging with fire disturbances.

Data and variables

Fire disturbances

First, we determined the presence of fire disturbances based on FIA records or Monitoring Trends In Burn Severity (MTBS). FIA records documented the type of disturbance and the year of occurrence during the remeasurement period for FIA conditions, including recording the reasons for tree death for standing dead trees. MTBS provided not only annual burn boundaries, but also fire severity mosaics that classified fire severity from low to high. Four fire severity classes were selected from MTBS at the FIA plot locations: unburned, low severity, moderate severity, and high severity. In this project, we extracted class one to four to calculate fire severity in the FIA locations. Therefore, we considered an FIA condition to have experienced a fire if there were records of fire disturbance in the FIA condition records, tree death occurred due to fires, or MTBS burn mosaics overlapped with FIA locations. Second, we determined fire severity and frequency by analyzing disturbance records from FIA conditions and MTBS burn severity mosaics. We assumed fires recorded in the same year in the buffered FIA condition records and MTBS mosaics to be the same fires. We calculated fire severity based on the average severity index of fires recorded in MTBS during the remeasurement period for each condition, and classified as 'low', 'moderate' and 'high' severity. We determined fire frequency by counting the number of fires recorded in FIA and MTBS records and then dividing them by length of the remeasurement period (fires per year). Third, we identified FIA conditions recording fire and other disturbances (such as insects, diseases, and drought disturbances; 0.4% of FIA conditions experienced both fire and other disturbances) by merging FIA fire records with MTBS records, and then checking if other disturbances occurred in the same FIA condition during the remeasurement period. If the record of other disturbances occurred earlier than the recorded fire year, we assumed that this disturbance occurred before the fires.

Trees and forests

There were 786,310 standing trees extracted from the FIA database. Between 2000–2010 (T1), 490,633 trees with a dbh ≥ 2.54 cm were measured, and then remeasured between 2011–2018 (T2). Out of these trees, 97,777 trees with a minimum dbh of ≥ 12.70 cm were alive at T1 but were standing dead at T2. Additionally, 90,593 trees with dbh ≥ 12.70 cm were recorded as standing dead at both T1 and T2. Furthermore, 100,251 trees with dbh ≥ 2.54 cm were not recorded at T1 but were recorded at T2, while 7,056 trees with dbh ≥ 2.54 cm were recorded at T2 but were not recorded at T1. We categorized forest type at T1 based on FIA classification, as vegetation composition at each site varied substantially. To provide an overview of the status of trees and forests prior to fire disturbances, we selected average age of trees at breast height, basal area density of live trees, sum of stocking percent values of all live trees, sum of stocking percent values of all growing-stock trees, live canopy coverage (canopy of live trees, saplings, and seedlings), and live plus missing canopy coverage (canopy of live plus dead trees, saplings, and seedlings, including dead portions of live trees) at T1. We used the measurement of the dbh and height of each tree at T1 and T2 to illustrate tree growth during the remeasurement period. Tree density referred to the number of measured trees under FIA conditions at T1. We calculated tree mortality as the percentage of standing live trees at T1 but standing dead trees at T2, as well as new growth trees that died at T2, over the total measured trees under FIA conditions. We calculated the tree mortality caused by fire as the percentage of standing live trees at T1 but standing dead trees at T2, as well as new growth trees that died at T2 due to fires, over the total measured trees under FIA conditions. AGC change per hectare was calculated using these standing trees.

Topography

Nineteen ecological regions encompass the Western US (Burrill, et al., 2018). These 19 ecological regions were grouped into five large areas: Pacific Northwest West, Pacific Northwest East, Pacific Southwest, Rocky Mountain North and Rocky Mountain South (Fig. 6). We collected elevation data at FIA plot locations, covering an elevation range from 0 to 3706 m. We also collected latitude and longitude coordinates at the FIA plot level. The FIA recorded aspect and slope information, at the FIA condition level.

Forest management

To identify forest management, we used recordings of stand treatment type and year at each FIA condition measurement. FIA categorized treatments into: no observed treatment, cutting, site preparation, artificial regeneration, natural regeneration, and other silvicultural treatments. We then grouped the FIA conditions into 30 categories to illustrate the type and frequency of stand treatments before or after fire disturbance (Table S8).

Climate

To calculate climate averages from 1991–2020, we used PRISM which integrates data from 1991 to 2020 using an 800-m resolution raster dataset and spatially extrapolated the values by incorporating latitude and longitude from FIA plots. This time span of climate data overlapped with the duration of FIA remeasurements, enabling the retrieval of recent annual and normal (from 1991 to 2020) climate variables. To calculate climate averages from the twentieth century, we used WorldClim which stores historical data from 1895 to 2010, allowing for the extraction of twentieth century climate variables using counties as coordinate keys with FIA plots. To investigate the associations between climate and AGC stock density change, carbon sequestration capacity, and AGC TRANSFER associated with fires, we chose the following climate variables: 1) Recent (from 1991 to 2020) annual, normal, and 20th-century precipitation, as precipitation plays a significant role in fuel accumulation and fire frequency and severity; 2) Recent annual, normal, and 20th-century maximum, mean, and minimum temperature, which have impacts on biogeochemical processes, and fire frequency and severity (Hagmann et al. 2021). To quantify drought severity, we used the United States Drought Monitor (USDM), which classifies drought severity into five drought categories (abnormally dry, moderate drought, severe drought, extreme drought, and exceptional drought) and records them biweekly in each county. We extracted the USDM drought severity and coverage index from 2000–2018 for each FIA observation. We used the drought severity and coverage index, which is an aggregate of drought over each year, to estimate drought severity. We estimated the length and start month of the seasonal drought in each year based on the duration of drought severity above zero.

Statistical analysis

We examined 67 variables to determine the impact of wildfires on AGC stock change and sequestration capacity on forest land (Table S1). Prior to conducting statistical tests, we removed any variables with insufficient data or high correlations with other variables according to the statistical summary. As a result, we selected 45 variables in the statistical analysis (Table S1). For the variables dbh and height, we created new variables to represent changes from T1 and T2. For example, we created a normalized tree height change variable as follows:

$$Height_c = \frac{HeightatT2 - HeightatT1}{HeightatT2 + HeightatT1}$$

We assumed that the new trees, recorded as standing live or standing dead at T2, had a dbh, height, and AGC measurements of 0 at T1. We assumed these trees as standing live when calculating forest AGC density change, carbon sequestration capacity, and carbon TRANSFER. Therefore, the forest AGC stock density change was:

$$F_{AGC\_change} = \sum_{i=1}^{n} (AGC_{T2} - AGC_{T1})$$

where n was the number of trees in each condition, with $i = 1,2, \ldots,$ n. The carbon sequestration capacity was:

$$F_{carbonsequesterationcapacity} = \sum_{i=1}^{n} \left(AGC_{standingliveatT2} - AGC_{standingliveatT1}\right)$$

where n was the number of always standing live trees (remeasured trees) and new trees that were still standing live at T2 in each condition, with $i = 1,2, \ldots,$ n. The carbon TRANSFER was:

$$F_{carbontransfer} = \sum_{i=1}^{n} (AGC_{standingliveatT1butstandingdeadatT2} + AGC_{newtreesstandingdeadatT2})$$

where n was the number of standing live trees at T1 but standing dead at T2 (remeasured trees) and new trees that were standing dead at T2 in each condition, with $i = 1,2, \ldots,$ n.

We utilized the Random forest machine learning algorithm to determine variables that were used in mixed effect models based on variable importance. The independent variables included AGC stock density change, carbon sequestration capacity, and carbon transfer out of the standing live carbon pool (standing live AGC transfer to standing dead AGC). To improve the accuracy of the Random forest algorithm, we split the data into training and testing sets (70% for training and 30% for testing). The training set was used to establish a Random forest model and the testing set was loaded into the model to compute model accuracy. We set the ntree and mtry parameters for each type of Random forest based on the out-of-bag (OOB) error (Fig. S1 as an example). We used the 'randomForest' package in R to run each Random forest 100 times (Liaw & Wiener 2002).

Fire effect calculation

To evaluate the impact of fire on AGC stock density change, carbon sequestration capacity, and TRANSFER, we considered where fire occurred or was absent initially. To accomplish this, the study followed two steps: (1) we created a binary variable to distinguish between conditions with and without evidence of fire using FIA and MTBS records; (2) we analyzed linear regression models with only one prediction (fire occurrence), and mixed effects models using fire occurrence interacted with other variables as fixed effects. The variables selected as predictors in mixed effect models were ordered by importance from the Random forest analysis. Then, we performed model selection. The intercept of the random effects of the mixed effect models included variables related to forest type group, forest type change, ecological region, type of fire combined with other disturbance, and forest management. We tested model significance using F tests and ANOVA. In all cases of mixed effects models, we determined the inclusion of fixed interactions and random effects using Akaike information criterion (AIC), with the lowest AIC indicating the best fit (Brewer et al. 2016; Kirana, et al., 2023; Pellegrini et al. 2021).

Influence of fire frequency and severity

For conditions with evidence of fires, we tested the effects of different fire severity and frequency, on AGC stock density change, carbon sequestration capacity, and TRANSFER associated with different biotic and abiotic factors. We performed the model selection by incorporating covariates related to vegetation, other disturbances, climate, drought, topography, and forest management into mixed effects models to test for pairwise interactions and possible collinearities. We selected a subset of 2,100 observations, which experienced fire disturbances, out of 25,328 for this analysis. We ordered the variables according to their importance in the Random forest analysis. We included the categorical variables unrelated to fire as random effects in the mixed effects models. We selected the best-fitting models based on the lowest AIC. We conducted all statistical analyses in R (R Core Team, 2020).

Results

Impacts of fires on forest carbon

Of the 25,328 observations considered, we have 8.29% (2100) conditions with evidence of fires over the period of 2000–2018 with either MTBS or FIA records (Fig. 1). Among the conditions with evidence of fires, 10.48% (220) conditions were indicated by MTBS records but not FIA records (Fig. 1). Forests that experienced fire released $0.06 \pm 2.73*10^{-2}$ Mg ha^{-1} yr^{-1} of carbon into the atmosphere, while those without evidence of fire sequestered $0.79 \pm 9.45*10^{-3}$ Mg ha^{-1} yr^{-1} of carbon from the atmosphere (Table S9; Fig. 2 & 3). Comparing forests with and without evidence of fires revealed that fires significantly decreased the ability of forests to sequester carbon ($P = 2.36*10^{-56}$). For carbon sequestration, forests without evidence of fires removed $0.92 \pm 9.46*10^{-3}$ Mg ha^{-1} yr^{-1} of carbon from the atmosphere, which was twice as much as those with evidence of fires ($0.42 \pm 1.78*10^{-2}$ Mg ha^{-1} yr^{-1}; Table S9; Fig. 2 & 3). The difference in forest sequestration capacity between forests with and without evidence of fires was due to fires increasing TRANSFER in forests, which was $0.32 \pm 1.67*10^{-2}$ Mg ha^{-1} yr^{-1} with evidence of fires compared to no fire at $0.07 \pm 1.72*10^{-3}$ Mg ha^{-1} yr^{-1}(Table S9; Fig. 2 & 3). When comparing 2,100 FIA conditions that had experienced fires, forests with high fire frequency emitted significantly more carbon into the atmosphere (AGC storage change: coefficient: -14.08 ± 6.67, $P = 0.035$).

Biotic factors: Impacts of forest structure and composition

Fire-driven changes in forest AGC density were more significantly influenced by biotic factors than by abiotic factors according to Random forest importance rank (Fig. 4). The chosen models demonstrated that the forest type played a crucial role in the impact of fires on AGC storage change, sequestration capacity, and TRANSFER (Table S2, S3, and S4). Moreover, older trees increased post-fire AGC storage and sequestration capacity (Table S2 and S3). Additionally, the initial AGC of the forest had a notable effect on AGC storage change, carbon sequestration capacity, and TRANSFER response to fires ($P = 2.39*10^{-48}$, $F_{2,7859} = 111.20$, $P = 3.03*10^{-236}$, $P = 1.12*10^{-316}$, respectively). Among the aforementioned biotic factors, the Random forests assigned greater importance to the initial AGC, average age of tree at breast height, and changes in forest types (Fig. 4).

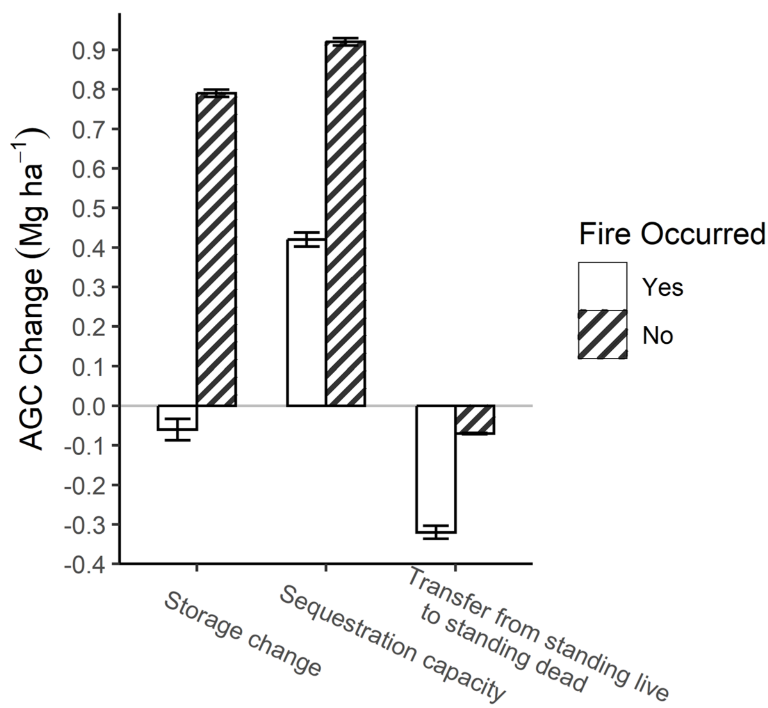

Fig. 2 Changes in aboveground carbon (AGC) in forested land across 25,328 conditions. For carbon storage change, a negative number represented carbon emissions, while a positive number represented carbon uptake by the forest from the atmosphere. The sequestration capacity was shown as a positive value, indicating the amount of carbon removed from the atmosphere. The transfer of carbon from the standing live pool to the standing dead pool was presented as a negative value, illustrating the amount of carbon transferred during the remeasurement period. The error bar represented the 95% confidence interval of AGC change at each category

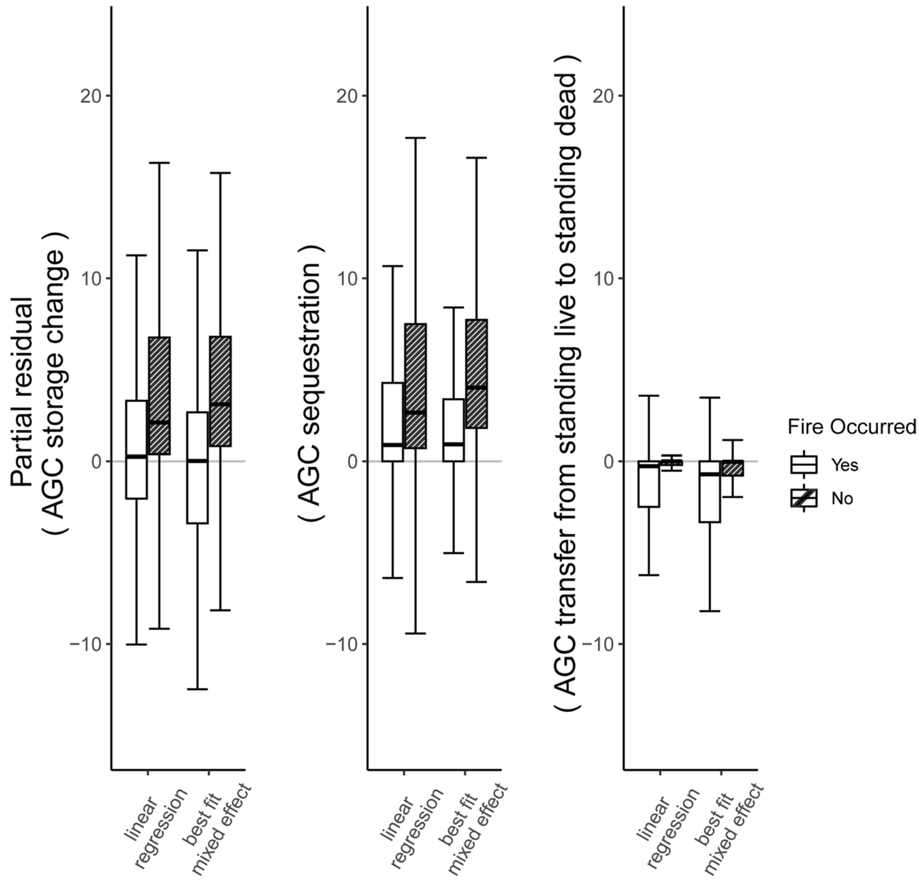

Fig. 3 Partial residuals of linear regressions and best fit mixed effect models. The partial residuals were different between linear regressions (predictor: fire occurred) and best fit mixed effect models (predictors: fire occurred and other factors). This indicated that other factors impact relationships between fire effects and forest aboveground carbon (AGC) storage change, sequestration capacity, and transfer from standing live to standing dead. In addition, the partial residuals were different within same models between fire occurred and fire absent indicating AGC change caused by fires. White solid fill presented partial residuals at conditions with evidence of fires. Hatch lines fill presented partial residuals at conditions without evidence of fires

In the analysis conducted using Random forest, features related to initial density exhibited relatively higher importance ranks (Fig. 4). Forests characterized by higher initial tree density demonstrated the most pronounced changes in fire-induced effects on forest carbon density compared to fire-free forests (AGC storage: $P=7.70*10^{-22}$; sequestration capacity: $P=1.32*10^{-28}$; TRANSFER:$P=5.34*10^{-3}$; Fig. 5). Among the initially existing standing live trees, both the initial basal area per hectare of live trees and the initial sum of stocking percent values of all live trees significantly influenced AGC storage change in forests without evidence of fires (Table S2). Particularly in forests without evidence of fires, the initial sum of stocking percent of all live trees had a notable impact on forest capacity to sequester carbon from the atmosphere (Table S3). Moreover, the initial sum of stocking percent values of all growing-stock trees significantly affected forest AGC sequestration in both fire-present and fire-free forests, while it only exhibited a significant influence on AGC storage change in forests with evidence of fires (Table S2 and S3).

The pre-fire forest canopy coverage demonstrated a substantial impact on altering the effects of fire. The initial proportion of live canopy coverage had a significant influence on AGC storage, sequestration capacity, and TRANSFER in response to fire, especially in forests with higher initial live canopy coverage (canopy: $P=1.10*10^{-64}$, $P=9.91*10^{-55}$, $P=2.77*10^{-6}$, respectively; Fig. S7). Additionally, the initial proportion of live plus missing canopy coverage significantly affected the change in AGC storage in both forests with and without evidence of fires, while it only impacted AGC sequestration capacity in fire-free forests (Table S2 and S3). In the Random forest models, percentage of live canopy coverage was ranked higher than percentage of live plus missing canopy coverage concerning AGC storage change and sequestration

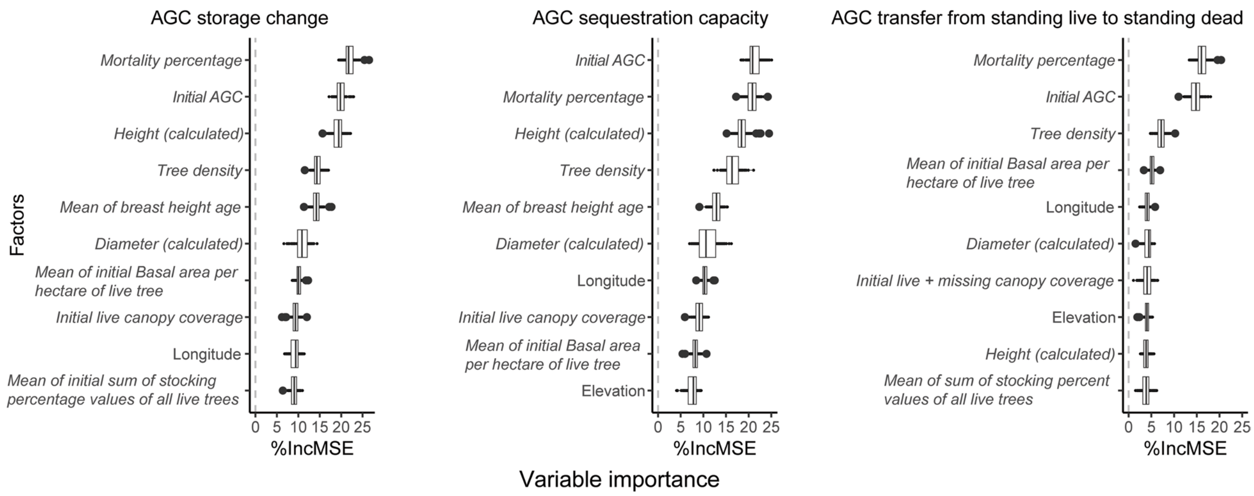

Fig. 4 Top 10 important factors ranked by random forests with aboveground carbon (AGC) storage change, sequestration capacity, and transfer from standing live to standing dead carbon pools as the response variable. The random forests were repeated 100 times. Variable importance was calculated as a percentage increase in mean squared error (%IncMSE). The biotic factors were highlighted in italics. The full lists of variable importance rank were at table S8

capacity, whereas the Random forest model of TRANSFER exhibited the opposite ranking (Fig. 4).

Furthermore, forest regenerative potential determined the effects of fires on forest AGC change and biotic factors ranked higher in the Random forests (Fig. 4). Tree mortality significantly affected AGC storage change, sequestration capacity, and TRANSFER in sites with or without fire disturbance (Table S2, S3 and S4). In forests without fire evidence, changes in tree dbh significantly affected AGC storage change, sequestration capacity, and TRANSFER (tree height: $P<0.001$, $P<0.001$, $P=0.001$, respectively), while changes in dbh only influenced fire effects on carbon TRANSFER (Table S2, S3, and S4). Changes in tree height was significantly impacted by fire effects on forest carbon sequestration (Table S3). Taken together, fire effects on forest AGC change were varied based on available combustible fuels and the growth ability of forests.

Abiotic factors: Impacts of geography, climate and drought

While fires generally affected forest AGC density change, the impact of fire on forest AGC density change was mediated by regional ecology, disturbance, and climate (Table 1, S2, S3, and S4; Fig. 3). Forest management, such as pre- or post-fire cutting, increased AGC sequestration capacity and reduced on TRANSFER, rather than AGC storage change (Table S2, S3, and S4). When comparing forests with fires to those without, the forests exhibited a notably greater reduction in AGC storage change and sequestration capacity, particularly in western longitudes and at lower elevations (storage: [longitude: $P=4.42{*}10^{-15}$; elevation: $P=3.53{*}10^{-4}$]; sequestration: [longitude: $P=2.62{*}10^{-17}$; elevation: $P=6.39{*}10^{-12}$]; Fig. S3). Latitude exerted a negative impact on AGC storage change and sequestration in forests without evidence of fires, while demonstrating a significant positive impact on TRANSFER in forests with or without fire evidence (Table S2, S3, and S4). Forests with steeper slopes had greater reduction of AGC storage and TRANSFER post-fire (Table S2 and S4). However, slopes presented a significant negative impact only on forest carbon sequestration at sites without evidence of fires (Table S3).

Climate and drought played significant roles in explaining the changes observed in the forest carbon sink and AGC density caused by fire (Table S2, S3, and S4). The areas that experienced higher rainfall in the twentieth century and recent normal periods, but less rainfall in recent decades, showed most of the larger differences in AGC storage change resulting from fires (twentieth century precipitation: $P=7.58{*}10^{-6}$; recent normal precipitation: $P=8.75{*}10^{-3}$; recent decade precipitation: $P=3.68{*}10^{-4}$; Fig. S4a-f). The effects of fire on the ability of forests to sequester AGC were greatest in areas with higher rainfall in the twentieth century and recent normal periods (twentieth century precipitation: $P=7.99{*}10^{-10}$; recent normal precipitation: $P=1.62{*}10^{-3}$; Fig. S5a-d). Moreover, the differences in TRANSFER resulting from fires were most significant in forests that experienced reduced rainfall in recent decades and higher recent normal minimum and mean temperatures (recent decades precipitation: $P=6.09{*}10^{-4}$; recent normal mean temperature: $P=2.15{*}10^{-3}$; recent normal minimum temperature: $\mathrm{P}=3.59{*}10^{-3}$; Fig. S6). The start time and duration of the drought season had a significant impact

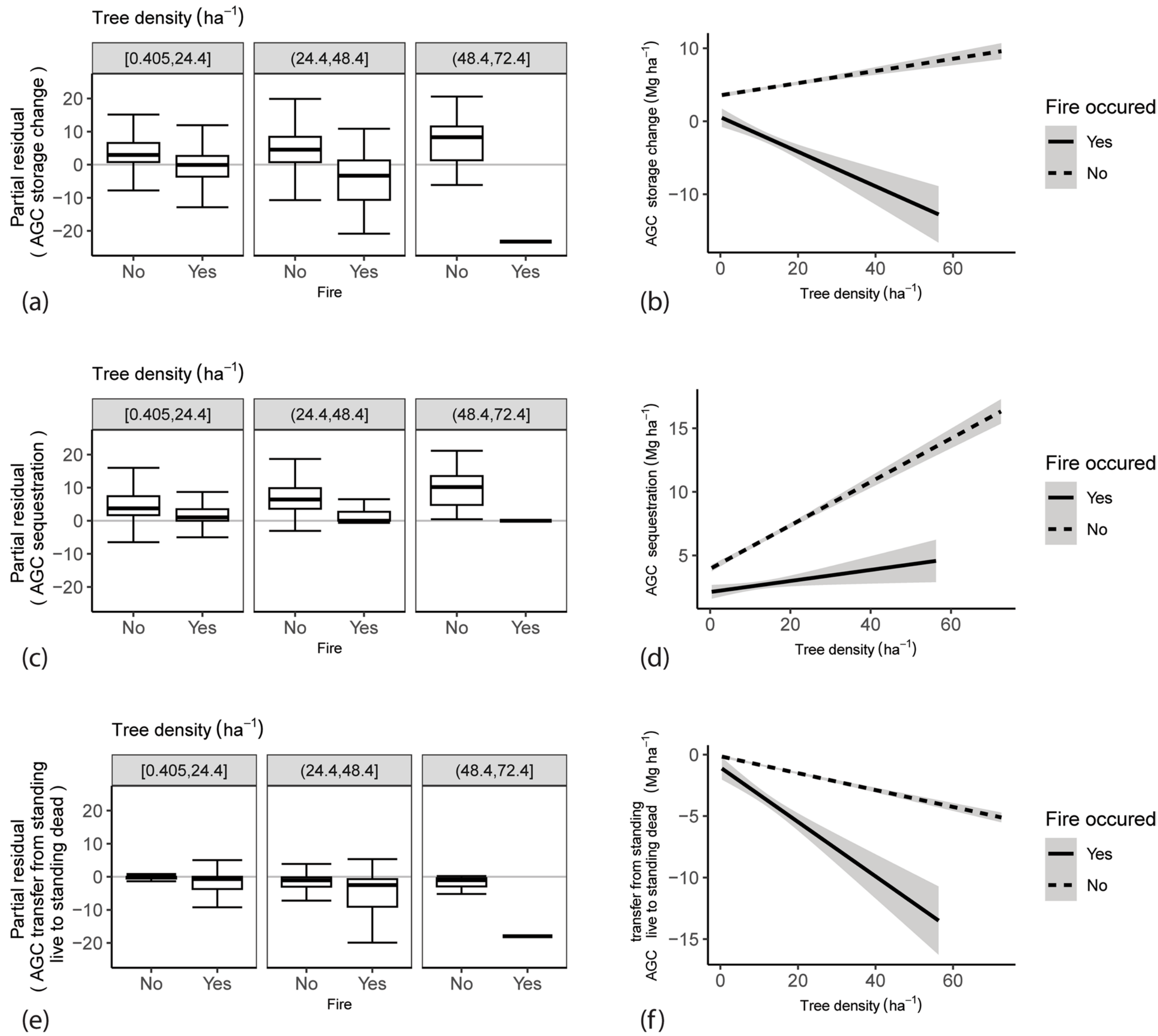

Fig. 5 Forest initial tree density influenced fire effects on forest aboveground carbon (AGC) storage change, sequestration capacity and transfer from standing live to standing dead (TRANSFER) carbon pools. Forests with a higher initial density of trees exhibited the most significant changes in the impact of fire on AGC storage change and the ability of sequestering carbon and TRANSFER in the forest, in comparison to forests unaffected by fire. (a, c & e) Partial residuals of the best fit linear mixed effects models were shown. The box presented the partial residuals for interactions between tree density and burned conditions, with or without fire. (b, d & f) AGC storage change, sequestration capacity and TRANSFER by tree density in conditions where fire did and did not occur

on the effects of fire on forest AGC storage, sequestration capacity, and TRANSFER (Table S2, S3, and S4). Sites with shorter drought seasons exhibited the greatest differences in AGC storage and sequestration capacity across forests with and without evidence of fires (Fig. S4g-h and 6e-f).

Impacts of fire severity and frequency

The influence of fire severity and frequency on changes in forest AGC density varied across different environmental conditions (Fig. S2; Table 2). However, fire effects on changes of AGC stocks associated with different fire characteristics had no significant differences across ecoregions, human management activities, and fire combined with other disturbances (Table S5, S6, and S7). Slope positively affected the impact of fire frequency on AGC storage change and sequestration capacity (Table S5 and S6). Longitude positively influenced the response of AGC storage and sequestration capacity to fire frequency (Table S5 and S6). Fire effects on AGC storage change at

Table 1 Summary of models fit on the aboveground carbon (AGC) of forest conditions in the Western United States. Simple linear regression model only had 'fire_occured' as predictor. Linear mixed effect models had 'fire_occured' and its covariate with biotic and abiotic features. The response values were AGC storage change, sequestration capacity, and transfer from standing live to standing dead

Model	Simple linear regression using all conditions	Simple linear regression using conditions with complete records	Best fit linear mixed effect	Linear mixed effect
AGC storage change				
Observations	25,328	7920	7920	7920
Marginal R^2/Conditional R^2	0.026 / 0.026	0.068 / 0.068	0.421 / 0.447	0.434 / NA
AGC sequestration capacity				
Observations	25,328	7920	7920	7920
Marginal R^2/Conditional R^2	0.010 / 0.010	0.027 / 0.027	0.504 / 0.603	0.497 / 0.609
AGC transfer from standing live to standing dead carbon pools				
Observations	25,328	7920	7920	7920
Marginal R^2/Conditional R^2	0.041 / 0.041	0.049 / 0.049	0.334 / 0.370	0.337 / 0.372

Table 2 Summary of models fit on the aboveground carbon (AGC) of forest conditions in the Western United States. Simple linear regression model only had fire frequency and fire severity as predictors. Linear mixed effect models had fire frequency and fire severity and their covariates with biotic and abiotic features. The response values were AGC storage change, sequestration capacity, and transfer from standing live to standing dead

Model	Simple linear regression using all conditions	Simple linear regression using conditions with complete records	Best fit linear mixed effect	Linear mixed effect
AGC storage change				
Observations	2099	860	860	860
Marginal R^2/Conditional R^2	0.006 / 0.005	0.010 / 0.007	0.362 / 0.395	0.391 / NA
AGC sequestration capacity				
Observations	2099	860	860	860
Marginal R^2/Conditional R^2	0.002 / 0.001	0.005 / 0.002	0.396 / 0.399	0.398 / NA
AGC transfer from standing live to standing dead carbon pools				
Observations	2099	860	860	860
Marginal R^2/Conditional R^2	0.006 / 0.005	0.007 / 0.004	0.335 / 0.359	0.388 / NA

the burned areas with evidence of low severity and frequent fires showed significant differences at different elevations (Table S5). Forests that have recently experienced lower precipitation generally showed a positive effect on altering the impact of fire frequency on AGC storage changes, sequestration capacity, and TRANSFER (Table S5, S6, and S7). Similarly, forests with recent higher temperatures positively influenced changes in AGC storage and sequestration capacity in response to fire frequency (Table S5 and S6). Additionally, recent normal mean temperatures only impacted AGC sequestration capacity response to fire frequency (Table S6).

The relationships between fire characteristics and forest AGC were also impacted by forest biotic factors. In forests with evidence of fire disturbance, their initial AGC stocks significantly affected AGC storage change, sequestration capacity, and transfer response to different fire severities ($P=3.90*10^{-27}$, $P=2.48*10^{-9}$, $P=1.41*10^{-61}$, respectively). The initial live canopy coverage significantly impacted AGC storage change in forests with evidence of frequent fires (Table S5), and sequestration capacity in forests with evidence of high severity fires (Table S6). Tree mortality significantly impacted forest carbon effects regardless of fire severity (storage: $P=1.19*10^{-20}$; sequestration: $P=1.75*10^{-13}$; TRANSFER: $P=5.84*10^{-14}$). Tree height positively influenced fire effects on AGC sequestration capacity in forests with evidence of high severity fires (Table S6).

Discussion

We found that fire reduced AGC storage in Western US forests, which was consistent with research from Hudiburg et al.(2019), Buotte et al.(2020), and Higuera & Abatzoglou (2021). Although fires were ranked of lower importance in the Random Forest model due to the small proportion of FIA conditions with evidence of fire,

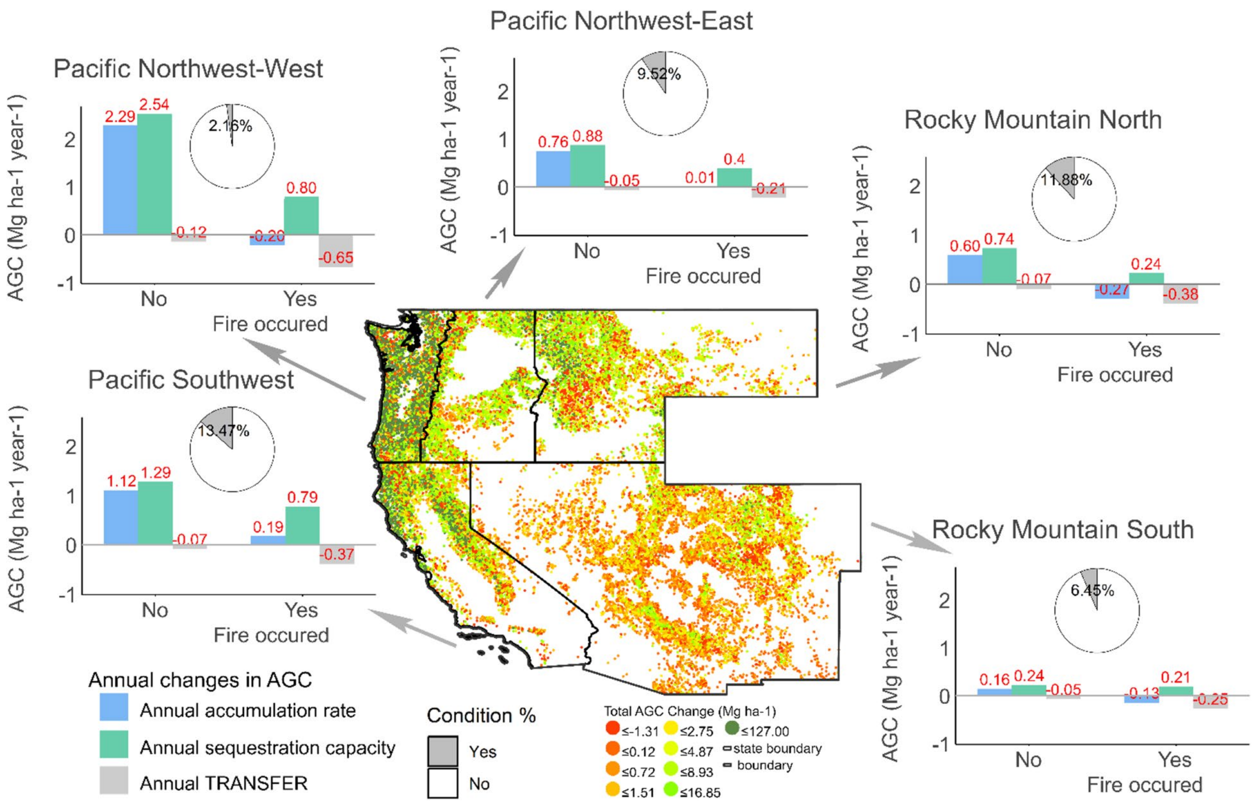

Fig. 6 Variations in aboveground carbon (AGC) across different fire regions in the western United States. The study area comprised 19 ecological regions, which were grouped into five regions: Pacific Northwest-West, Pacific Northeast-East, Pacific Southwest, Rocky Mountain North, and Rocky Mountain South. The map illustrate changes in AGC storage between two time points, based on Forest Inventory and Analysis (FIA) conditions. The bar plots represent the annual changes in AGC for forests with and without evidence of fires. The pie charts display the percentage of forests with and without fire evidence out of the total sampled conditions in each region

forests undergo a transformation, shifting from their role as carbon sinks to becoming a source of carbon emissions when affected by fires (Table 1; Fig. S8; Gonzalez et al. 2015; Haight et al. 2020; Case et al. 2021). When compared to the average AGC uptake of 0.5 Mg ha^{-1} yr^{-1} across the entire US (Domke et al., 2019), forests in the Western US with evidence of fires sequestered less AGC (0.42 Mg ha^{-1} yr^{-1}), while those without fire evidence sequestered more AGC (0.92 Mg ha^{-1} yr^{-1}) than the average (Table S9). This indicates that immediately following fires, the ability of forests to sequester carbon was diminished. However, in forests without fire evidence, the rate of AGC accumulation was nearly twice the overall level observed in the US. This discrepancy can be attributed to high productivity of forests in the western side of the Pacific Northwest (Table S9; Fig. 6; Domke et al., 2019; Hoover et al., 2023). Additionally, the reduced sequestration capacity in fire-affected forests resulted from a higher TRANSFER (Table S9; Fig. 6), which was directly correlated with tree mortality and indirectly related to the short-term recovery of forests after a fire (Buotte et al. 2020; Case et al. 2021). These patterns caused by fire effects varied across different regions. Therefore, it was necessary to explore other features to explain the variations in AGC storage and sequestration capacity response to fires across forest land.

Forest structure and composition had more important fire effects on carbon dynamics than abiotic factors across ecozones. The extent of canopy coverage, the type of forest, and the age of trees played crucial roles in determining the ratio of immediate carbon emissions to the overall carbon storage during fires. The presence of a denser canopy had a direct impact on fire intensity, resulting in increased tree damage and mortality, and heightened fire severity (Koontz et al. 2020). Tree mortality varied across different forest types because dominant tree species exhibited varying levels of fire tolerance (Kane et al. 2017). This was because some tree species, such as ponderosa pine, western larch, and western white pine, exhibited a higher tolerance to fires due to their thick bark, which contributed to their survival during such events (Dunn & Bailey 2016; Stevens et al. 2020; Hessburg et al. 2022; Jiang et al. 2023). However, the effects of forest type on AGC storage could be modified in old-growth and mature forests, as older trees occupied a greater proportion of forest AGC storage, and their demise resulted in a substantial release of carbon or its transfer from live AGC pools (Fairman et al. 2016; Jiang et al. 2023). Moreover, forest type played a significant role in the response to fire, as the response of seeds or cones from different tree species to fire effects varied, by leaving material legacies that influenced forest regeneration following fires (Johnstone et al. 2016). Aside from biotic factors, abiotic factors can also help explain the variability in carbon storage across the Western US.

Forests with higher historical rainfall, less recent rainfall coinciding with longer and more severe drought seasons, higher temperatures, a western orientation, lower elevation, and forest management, exhibited greater variance in changes in AGC storage, sequestration capacity, and TRANSFER between areas with and without evidence of fires. These abiotic drivers have helped to explain the difference between the Pacific regions and the Rocky Mountains in their response to fires (Fig. 6). In general, the increased burned areas in the overall forest land of the Western US were attributed to higher historical rainfall, which contributed to the accumulation of combustible fuel, as well as recent higher temperatures, reduced precipitation, and increased drought severity, all of which provided more opportunities for ignition (Loehman et al. 2018; Lange et al. 2020; Hagmann et al. 2021; Jiang et al. 2023; Wasserman & Mueller 2023). The lower average accumulation of AGC storage in the Rocky Mountain areas demonstrated how warm climates and drought environments played an essential role in increasing fire occurrence, consequently reducing AGC storage (Fig. 1 and 6; Bailey et al. 2021). The productive rainforests in the Pacific Northwest-West served as another example that indicated how increased moisture from rainfall or less severe drought seasons helped reduce the current fire effects on forest AGC storage, sequestration capacity, and TRANSFER (Fig. S4; DeMeo et al. 2018; Lange et al. 2020). Forests with a western orientation, mainly in the Olympic Range, northern California Coast Range, and western side of the Cascade Range and the Sierra Nevada, exhibited higher AGC storage increases due to their regional climate influenced by moist air from the Pacific Ocean, as well as their lower elevation (Fig. 6; Korb et al. 2019; Buotte et al. 2020; Chen et al. 2021; North et al. 2021; Marcos-Martinez et al., 2022). Therefore, forests from different ecological regions had varying abilities to sequester carbon, resulting in different levels of carbon storage.

Forest carbon storage was lower in the Rocky Mountain region but higher in the Pacific West region (Fig. 6; Buotte et al. 2020; Marcos-Martinez et al., 2022). Within the Pacific Northwest-West forests, only 2.16% of the FIA observed forested areas were affected by fires, and forests without evidence of fire sequestered more carbon than burned region in the Western US forest land (2.54 Mg ha^{-1} yr^{-1}; Fig. 1; Fig. 6). This indicates that the forests in the Pacific Northwest are more productive than the other forests in the western U.S. Our findings corroborated those of Hoover and Smith (2023), that high AGC accumulation rates occur in live trees in Pacific Northwest-West. However, these highly productive forests in the Pacific Northwest-West experienced a reduction in carbon storage (-0.20 Mg ha^{-1} yr^{-1}) when affected by fire disturbances, due to the large transfer of live carbon to dead carbon (-0.65 Mg ha^{-1} yr^{-1}) (Fig. 6; Hall et al. 2024). Compared to the burned forests of the Pacific Northwest, the remaining burned forests in the Pacific West region continued to increase their carbon storage (Fig. 6; Hall et al. 2024). The annual AGC accumulation rate was lower in the Rocky Mountains compared to the Pacific regions, as indicated by the smaller AGC live tree pools in the Rocky Mountain region (Fig. 6; Buotte et al. 2020). In the Rocky Mountain region, the Rocky Mountain North exhibited a higher rate of carbon accumulation compared to the Rocky Mountain South, despite experiencing more fire events, indicating that fire had a greater impact on the Rocky Mountain South (Fig. 6). Given that the Rocky Mountain South contained the least productive forests in the Western US, a fire was likely to release a larger proportion of carbon stock into the atmosphere (Fig. 6). Furthermore, the variation in forest carbon storage across different ecological regions reflected patterns of forest regrowth after fires.

After fires, the AGC storage and sequestration capacity of the forests may be reduced, influencing forest regeneration. Forest types had the potential to undergo changes in their composition after fires, as more seeds or cones from non-dominant species could germinate, altering the forest's capacity to sequester carbon from the atmosphere. (Johnstone et al. 2016; Haffey et al. 2018; Jiang et al. 2023). Furthermore, if fires of high severity and frequency occurred, it could lead to reduced survival of seeds and cones, as well as increased tree mortality, ultimately resulting in the conversion of forest land to non-forest land (Jiang et al. 2023). The changes in dbh and tree height observed during the subsequent measurement periods not only indicated significant damage to the forests during the fires but also showcased their ability to regenerate and sequester carbon afterward. In highly productive forests, such as those found in the Pacific Northwest-West region, the forests with evidence of fires were able to sequester a greater amount of carbon compared to other forests in the Western US affected by fires from 2000 to 2018 (Fig. 1 and 6; Marcos-Martinez et al., 2022). To enhance forest regeneration after fires, appropriate forest management before and after fires can improve forest health.

Forest management plays a crucial role in mitigating the impacts of fires. Pre-fire treatments, such as fuel reduction measures by cutting, can lower fire severity. Post-fire treatments may open more canopy and understory forest space to support forest regrowth and lower tree mortality, enhancing carbon sequestration capabilities (Chen et al. 2021; Hessburg et al. 2021). However, the results of models also showed that biotic drivers, which were part of complex ecosystems, played a more important role than abiotic drivers in the mechanism of forest AGC accumulation rates associated with fires. These treatments, aimed at reducing tree density and canopy cover, can help foresters manage fire risk. In high fire-risk forests, selective cutting practices, such as thinning, reduced available fuel and helped restore the structure and composition seen in the 19th and early twentieth centuries, when lower tree densities and a more balanced distribution of conifer species contributed to fewer fires (Hagmann et al. 2021).

Several uncertainties need to be acknowledged in our analysis of the effects of fire on forest AGC storage change, sequestration capacity, and TRANSFER. First, the perturbed FIA plot locations may not have been situated within the MTBS burned mosaics if they were in close proximity to the burn area's edge. Second, there was a potential uncertainty in distinguishing fire records from MTBS and FIA as distinct fire events when they were actually the same, or as the same fire events when they were actually different. Third, the relatively small number of observed forest conditions with evidence of fire disturbances compared to the overall conditions studied (2,100 out of 25,328 conditions) introduced potential imprecision when assessing the effects of fire severity and frequency on changes in forest carbon density. This limitation is raised because the FIA perturbed locations may not yield consistent results as compared to exact locations, unless within a larger landscape scale and sample size, as emphasized by previous studies (Prisley et al. 2009; Huang et al. 2018; Jiang et al. 2023). Lastly, the core FIA program measures standing trees, while the down dead trees are measured in a different component of the program. Some trees may be dead and down prior to fires, while others may have been standing dead prior to the fire or may have been killed by fire and subsequently fell. Therefore it becomes challenging to know the proportion of dead and down trees when forests are remeasured post fire. Acknowledging these uncertainties provides a better understanding of the potential limitations and implications associated with the analysis of fire effects on forest carbon dynamics.

The findings presented in this study carry important implications for forest managers tasked with devising strategies for carbon storage and sequestration in forests. Particularly focused on the carbon dynamics associated with fires in Western US forests, this research reveals the importance of forest structure and composition and how they influence carbon emissions in fire-prone landscapes. Considering potential extensions of this work, the findings from this study could help identify which biotic and abiotic factors are valuable as predictors in carbon estimation models. These models could then enable carbon estimation beyond FIA plots, including in inaccessible forest areas. Given that biotic factors play a more significant role than abiotic factors and that gathering forest structure and composition data outside of FIA plots is challenging, remote sensing data could be used to assist in obtaining vegetation-related information. Armed with knowledge of forest carbon change across different ecoregions under global warming, forest managers can tailor strategies to enhance carbon storage, promote resiliency, and sustain or increase the health of ecosystems. This study serves as a crucial resource in informing future forest management and natural climate solutions, providing quantitative information that can inform policies and practices that balance ecological resilience with carbon mitigation goals.

Conclusion

Fires played a significant role in diminishing the storage and sequestration of AGC in Western US forests during recent decades. The models developed here placed greater emphasis on biotic drivers such as forest pre-fire biomass, forest type, tree density, tree age, canopy coverage, and changes in tree dbh and height. These biotic drivers played a role in the accumulation of combustible fuel before fires, tree mortality and immediate carbon emissions during fires, and post-fire forest regeneration and the capacity for carbon sequestration. In addition, as the seasons grew longer, warmer, and more prone to drought, the impact of fires on carbon released into the atmosphere intensified. However, this effect was dampened in the moisture-rich forests along the Pacific Coast, while exacerbated in the drought-stricken areas of the Rocky Mountains. Notably, forest management potentially contributed to an augmentation in forest carbon storage by reducing fuel and fostering forest regeneration.

Supplementary Information

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Supplementary Material 1

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Authors' contributions
Panmei Jiang: Conceptualization, Methodology, Software, Writing –original draft, Visualization. Matthew B. Russell: Review & editing. Chad Babcock: Review & editing. Lee Frelich: Review & editing.

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

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.
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