

Aboveground biomass and seedling responses to forest disturbances across the conterminous United States

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ABSTRACT

Increases in the frequency and severity of forest disturbances over recent decades have raised concerns regarding the future health and functioning of forest ecosystems. Previous ground- and remote-sensing-based studies have quantified disturbance impacts and recovery, but we have limited understanding of the immediate impacts and short-term recovery of seedling density and live biomass across broad geographic regions. We quantified short-term impacts and recovery of seedling density and live biomass stocks following different disturbances (fire, harvest, and insect/disease) in forests of the conterminous United States (U.S.) using nationwide forest inventory data and a remote-sensing-based burn-severity product. Harvest and fire were the most common forms of severe (stand-replacing) disturbance in the eastern and western U.S., respectively. Insect/disease disturbances were common in both regions but were rarely stand-replacing. In the West, live tree aboveground biomass (AGB) was substantially lower following severe fire compared to other severe disturbances, although multiple disturbance agents (e.g., drought and insects) may interact to affect fire severity and its impacts. Furthermore, most conifer forests in the West impacted by large, severe fire remained classified as stand age zero with low seedling density (< 400/ha) for at least 10 years post-fire, indicating sparse and delayed regeneration. Our results show that in the western U.S., forests recover slowly from large, severe fire, and the short-term impacts of fire are more severe than other types of episodic disturbance. Given the ongoing intensification of wildfire regimes in the western U.S., these findings imply a threat to forest carbon stocks and other ecosystem services.

1. Introduction

Disturbances play a fundamental role in forest ecosystem dynamics and functioning (Franklin et al., 2002; Trumbore et al., 2015; Turner, 2010). When disturbance regimes and environmental conditions are constant, carbon losses from disturbance and carbon gains from recovery should be balanced at broad spatial and temporal scales (Harmon, 2001; Williams et al., 2016). Terrestrial carbon sinks thus imply broad-scale disequilibria, with forest recovery from previous land use and increasing forest productivity—e.g., due to CO₂ fertilization, nitrogen deposition, and/or other factors—both likely contributing to U.S. and global forest carbon sinks (Caspersen et al., 2000; Hogan et al., 2025; Quinn Thomas et al., 2010; Schimel et al., 2015; Williams et al.,

2016). However, increasing frequency and severity of disturbances in recent years, attributed to climate change and other global change drivers, potentially threaten the regrowth and resiliency of forest ecosystems (Franklin et al., 2002; Seidl et al., 2017; Sommerfeld et al., 2018). Changes in forest disturbance regimes could severely impact forest carbon storage and other ecosystem functions (Anderegg et al., 2022; Anderson-Teixeira et al., 2013; Dugan and Baker, 2015; McDowell et al., 2020; Wu et al., 2023). For example, such changes could shift forest ecosystems from acting as carbon sinks to sources (Baldocchi, 2008; Fu et al., 2017; Le Quéré et al., 2013; Sánchez et al., 2021).

Disturbance impacts and post-disturbance recovery depend, in part, on disturbance type and severity (Fu et al., 2017; Turner, 2010). For example, wildfires are often reported to lead to longer recovery times

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than timber harvesting (Jean et al., 2019; Madoui et al., 2015; White et al., 2022), with impacts of insect and disease outbreaks often being shorter duration than fire or harvest (Zeppenfeld et al., 2015). However, it can be difficult to untangle the potentially complex direct and indirect effects of disturbances. For example, effects of insects and disease on forest ecosystems can be difficult to quantify due to their interaction with other disturbances and their continued effects for multiple years (Anderegg et al., 2015; Hicke et al., 2012; Kasischke et al., 2013). Furthermore, disturbance severity, by definition, largely determines impacts and may also affect recovery times. For example, ecosystem carbon stocks may recover from low-severity fires in less than a decade, whereas it might take decades or centuries to recover from high-severity (stand-replacing) fires (Dore et al., 2008; Hurteau et al., 2014; Hurteau and North, 2010; Kashian et al., 2006; Thornton et al., 2002).

Forest recovery from disturbance further depends on a variety of additional factors, including site characteristics, species traits, climate, biological legacies, and pre-disturbance forest properties, which in turn depend on the history of disturbance and management (Lindenmayer et al., 2019; Sturtevant et al., 2014). Post-disturbance recovery of tropical forests in French Guiana was more associated with pre-disturbance species composition than pre-disturbance forest structure, and forests with a high proportion of pioneer species recovered poorly (Hérault and Piconiot, 2018). Some North American studies found that conifers tend to regenerate more slowly than 'hardwoods' (angiosperms) following stand-replacing fires (Collins and Roller, 2013; Roccaforte et al., 2012; Sturtevant et al., 2014). However, the generality of this pattern across regions and disturbance types is unknown, and a recent synthesis showed diverse post-fire recovery pathways (Smith-Tripp et al., 2026).

Forests of the conterminous U.S. provide valuable opportunities for broad-scale studies due to their substantial contribution to the global forest carbon sink (Pan et al., 2024), the wide range of climate conditions and forest types, and the availability of a standardized nationwide forest inventory (NFI) program spanning multiple decades (Bechtold & Patterson, 2015). Until the late 1990s, forest disturbances in the U.S. were mainly driven by land use and management, but climate change, insects, disease, and fire have become increasingly impactful over recent decades (Cohen et al., 2016; Goetz et al., 2012; Williams et al., 2016). Dominant forest disturbance types in the U.S. vary by region and forest type (Wang et al., 2022). For example, fire, native insect outbreaks, and drought are the most important disturbance types in the western U.S., whereas harvest, fire and non-native insect outbreaks are the dominant disturbance types in the eastern U.S., based on affected area and their impact on carbon stocks (Domke et al., 2018; Williams et al., 2016). Most previous studies of forest disturbance in the U.S. focused on local or landscape scales and single disturbance types (e.g., Bormann et al., 2008; Collins and Roller, 2013; Dodson and Root, 2013; Fu et al., 2017; Hurteau and North, 2010; Kemp et al., 2016; Turner et al., 2019), although some have been conducted at regional to national scales and/or included multiple disturbance types (e.g., Fitts et al., 2022; Healey et al., 2018; Shaw et al., 2017; Williams et al., 2014; Williams et al., 2016). Nevertheless, we still have limited understanding of the factors that determine forest disturbance impacts and recovery across the conterminous U.S. For example, most of the previous national-scale studies relied on satellite data and/or aggregated forest inventory data and thus do not resolve factors affecting stand-scale biomass and seedling dynamics.

In this study, we used NFI data and a remote-sensing-based burn-severity product to study the short-term impacts and early-stage recovery associated with different disturbance types and severities across the conterminous U.S. We focus on episodic disturbances (e.g., > 25% of trees in a stand affected over a ~5–10 year period), rather than chronic disturbances that may be detected as increases in background mortality rates (e.g., van Mantgem et al., 2009). Given the observed increase in fire frequency and severity in the western U.S. (Holden et al., 2018; Parks and Abatzoglou, 2020; Reilly et al., 2017), the expected

continuation of this trend in the future (Abatzoglou et al., 2021; Liu and Wimberly, 2016), and concern over post-fire regeneration failure in this region (Halofsky et al., 2020; Rammer et al., 2021; Stevens-Rumann et al., 2018; Stevens-Rumann et al., 2022; Turner et al., 2019), we placed particular emphasis on exploring the impacts of severe fire in the western U.S. Specifically, across both the eastern and western U.S., we used NFI data to quantify (1) rates of severe (stand-replacing) and mild (non-stand-replacing) disturbance by type (fire, harvest, and insect/disease) and we compared these rates to remote-sensing-derived disturbance rates; (2) initial impacts on live tree aboveground biomass (AGB) and seedling density for both mild and severe disturbances; and (3) for severe disturbances, how post-disturbance AGB and seedling density relate to pre-disturbance forest attributes and topographic factors. Additionally, in the western U.S., we combined NFI and remote-sensing data to quantify (4) early-stage recovery (in terms of AGB and seedling density) of conifer and hardwood forests as a function of time since severe fire. By studying fine-scale data (e.g., seedling density and other stand-level attributes) across a broad geographic region, our study bridges the gap between previous site-level (Collins and Roller, 2013; Dodson and Root, 2013; Fu et al., 2017; Hurteau et al., 2014; Kemp et al., 2016) and broad-scale studies (Fitts et al., 2022; Healey et al., 2018; Stavros et al., 2014; Williams et al., 2014, 2016).

2. Methods

We used NFI data and a remote-sensing-based burn-severity product to quantify disturbance impacts and initial recovery (up to ~10 years post-disturbance) in U.S. forests. Our study area includes the conterminous U.S. (Fig. 1), except for Wyoming where remeasured NFI plots were not available at the time the data were accessed. We analyzed East and West regions separately due to differences in plot remeasurement intervals, forest types, and disturbance regimes (e.g., more severe fires and insect outbreaks in the West; more harvest in the East). We used the ecosystem province boundaries (Bailey, 2016) near the 100°W meridian to split the U.S. into eastern and western regions (Fig. 1).

2.1. Forest inventory and analysis (FIA) database

The Forest Inventory and Analysis (FIA) program within the U.S. Department of Agriculture Forest Service is a systematic, ongoing NFI which assesses the status and trends of U.S. forests using permanent sample plots across all ownerships (McRoberts et al., 2005). In our filtered FIA dataset (see details below), mean plot remeasurement intervals in the eastern and western U.S. were 5.3 and 9.7 years, respectively. Each FIA plot includes four 7.32-m radius subplots and may also include 17.95-m radius macroplots for very large trees in some western U.S. regions (Fig. S1). Our analysis is based on the publicly available FIA database version 8.0 (Burrill et al., 2018; USDA Forest Service, 2020). Our analysis primarily involves the following FIA data tables: (1) the Plot table includes data that describe a plot's location (e.g., approximate latitude and longitude, elevation), as well as information related to each sampling event at a given plot location, including measurement date and plot sampling design (the current national standardized design vs. older region-specific designs); (2) the Condition table includes data on the conditions within a plot (multiple conditions may be present in a single plot) at the time of each plot measurement, including stand age (see details below), stand-size class (see details below), soil physiographic class, disturbance type and severity, and the fraction of the plot's area assigned to the condition; (3) the Tree table reports, for each plot measurement, the species identity, diameter at breast height (DBH), status (alive, dead, or harvested), and other tree-level attributes for tallied individuals (DBH ≥ 2.54 cm in microplots; DBH ≥ 12.7 cm in subplots; region-specific thresholds for optional macroplots; Fig. S1); (4) the Seedling table reports, for each plot measurement, the number of live seedlings present by species, where 'seedling' is defined by FIA as individuals with DBH < 2.54 cm and height ≥ 15.24 cm for 'softwoods'

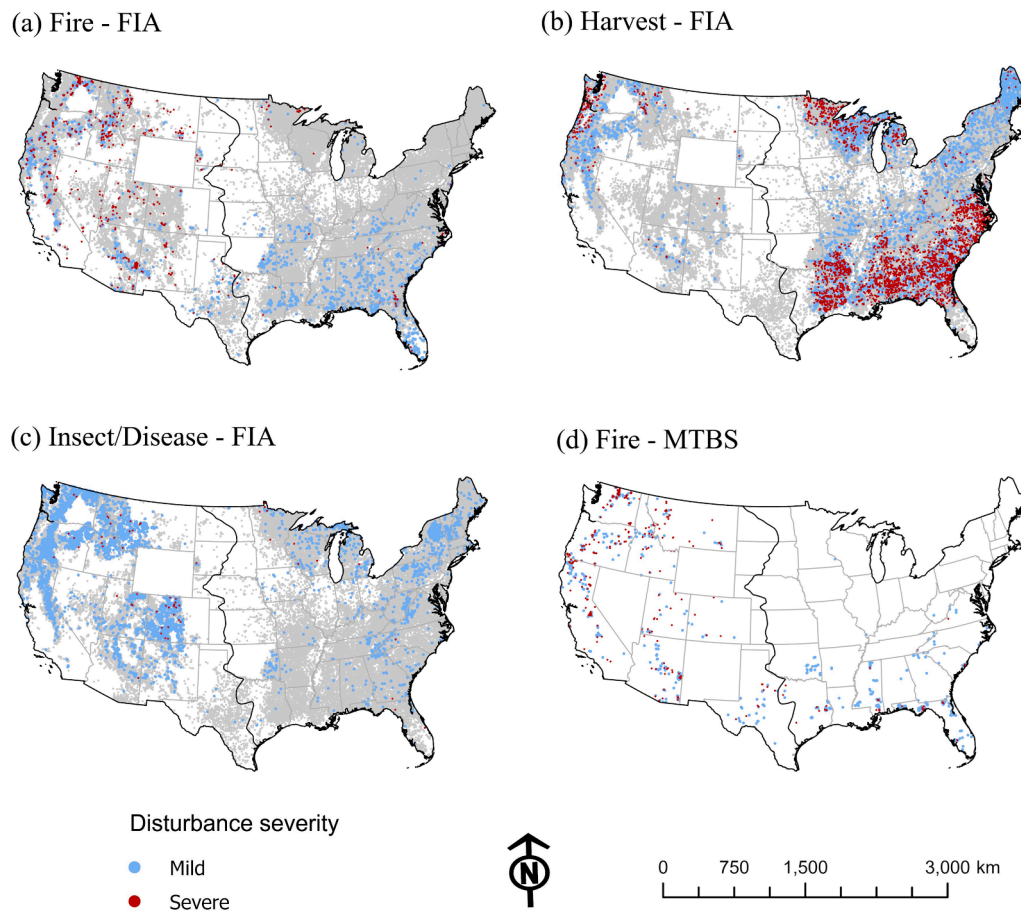


Fig. 1. Locations of mild and severe forest disturbances across the conterminous U.S. from roughly 2000–2020. (a–c) Fire, harvest, and insect/disease disturbances (bold colors) and locations of all FIA plots (light grey). (d) MTBS fires included in our analysis (Table 2), colored according to our MTBS burn-severity classification; these are MTBS fires that included an FIA plot remeasurement in our filtered dataset and where the FIA remeasurement interval included the MTBS fire year (regardless of whether FIA reported a fire). FIA plot locations in (a–d) are from the public FIA database and are restricted to the plots in our filtered FIA dataset (see Supplementary Methods in the Supporting Information). Thick lines show the boundaries of the East and West regions used in our study. State boundaries were obtained from U.S. Census Bureau Cartographic Boundary Files (U.S. Census Bureau, 2023), and maps were created using ArcGIS Pro 3.5.1 (Esri, 2025).

(conifers), or DBH < 2.54 cm and height $\geq$ 30.48 cm for ‘hardwoods’ (angiosperms).

Two important variables in our analysis are stand age and stand-size class. FIA defines stand age (STDAGE in the Condition table) as the mean age of trees in the dominant size class, which is estimated by coring two or three representative trees (USDA Forest Service, 2019). FIA reports a stand-size class code (STDCLCD in the Condition table) based on the predominant diameter class of live trees in a condition: large, medium, or small diameter trees, or nonstocked (< 10% stocking of live trees; Burrill et al., 2018). In cases where there is delayed recovery following severe disturbance, a plot may be classified as nonstocked with a stand age of zero for multiple years. Thus, FIA’s stand age and time-since-disturbance are not equivalent (Stevens et al., 2016).

For each FIA plot measurement, we calculated the plot-level live tree aboveground biomass (AGB; Mg ha⁻¹) by summing the tree-level AGB values (DRYBIO_AG in the FIA Tree table), each weighted by the number of trees per hectare it represents (based on TPA_UNADJ in the FIA Tree table). We calculated plot-level seedling densities from the species-level seedlings per hectare values (based on TPA_UNADJ in the FIA Seedling table).

For consistency, we restricted our analysis to plot locations that were measured at least twice (i.e., at least one remeasurement) using FIA’s national standardized sampling design (Bechtold and Patterson, 2015), which was initiated around the year 2000 in most U.S. states (see details of plot selection in the Supplementary Methods in the Supporting Information). Using older (non-standardized) FIA data is complicated

due to the inconsistent plot designs and identifying codes needed to link recent FIA plot data to those collected prior to implementation of the national design.

We used the disturbance and treatment codes (DSTRBCD and TRTCD) in the FIA Condition table to identify the type(s) of disturbance that occurred at a plot between successive measurements, which we refer to as the pre- and post-disturbance measurements. To focus our analysis on cases where disturbance could potentially have a substantial impact on forest structure, we excluded plot measurements where the pre-disturbance stand age was < 20 years and the pre-disturbance condition was classified as nonstocked (< 10% live tree cover). For simplicity, we restricted our analysis to plot records that were dominated by a single condition (at least 90% of plot area), and we treated the descriptors of this dominant condition (variables reported in the FIA Condition table) as plot-level descriptors. We defined three types of disturbance for analysis: fire, harvest, and insect/disease. Disturbance types that were less commonly reported (e.g., drought and windthrow) were combined into a single ‘other’ category, and we limited our analysis of this category to summarizing disturbance frequency. We classified each reported disturbance as being mild or severe as follows: a disturbance was considered ‘severe’ if the post-disturbance stand age was less than or equal to the interval between successive inventory dates (as indicated by the REMPER field in the FIA Plot table), which implies an age-resetting (stand-replacing) disturbance, and if the post-disturbance AGB was less than 50 Mg/ha; disturbances not classified as ‘severe’ were considered ‘mild’. The 50 Mg/ha AGB threshold is

somewhat arbitrary but helps guard against database errors or anomalous conditions in our severe disturbance category. Combined with our stand age criteria (pre-disturbance stand age ≥ 20 years; post-disturbance stand age $\leq$ REMPER), the 50 Mg/ha AGB filter ensures that all plots included in our severe disturbance category can potentially support trees at least 20 years old, and had a reduction in stand age coinciding with a disturbance documented in the FIA Condition table. This filter resulted in removing 2.5% of severe disturbance plots to the mild disturbance category (Fig. S2). Additional details on plot filtering and disturbance classification are provided in the [Supplementary Methods](#) in the [Supporting Information](#) and in [Table S1](#).

In the dataset we analyzed, FIA reported the year of disturbance (DISTRBYR and TRTYR in the FIA Condition table) in only ~30–80% of cases, depending on disturbance type. In the remaining cases, the year of disturbance was missing or reported as code 9999 to indicate a disturbance that occurs continuously over time. Given the large number of missing or ambiguous cases, we did not attempt to determine disturbance years using FIA data. However, for many fire disturbances reported by FIA, we were able to determine the burn year using a remote-sensing data product (Monitoring Trend of Burn Severity, MTBS), which allowed for a more detailed analysis of forest attributes as a function of time-since-disturbance (see details below).

2.2. Pre- and post-disturbance comparisons using FIA data

We compared pre- and post-disturbance AGB and seedling density across disturbance types (fire, harvest, and insect/disease) and severities (mild and severe). We used ANOVA and pairwise Tukey's test to compare disturbance types with respect to (i) pre-disturbance AGB, (ii) post-disturbance AGB, (iii) pre-disturbance seedling density, and (iv) post-disturbance seedling density. These analyses were performed separately within each region (East and West) and severity category (mild and severe). We do not report comparisons between severe and mild disturbances, as the definition of the two severity classes is somewhat arbitrary.

2.3. Predicting AGB and seedling density following severe disturbances using FIA data

The raw data summaries described above do not control for potentially confounding variables when comparing across disturbance types. To better isolate the effects of disturbance type (controlling for potentially confounding variables, including soil, topography, and pre-disturbance forest attributes) on the early stages of post-disturbance recovery, we used the 'random forest' machine learning algorithm (Ho, 1995) to predict post-disturbance AGB and seedling density as a function of disturbance type and other explanatory variables. Separate models were fit for the East and West. We restricted this analysis to severe (age-resetting) disturbances (as defined above) observed in FIA plot remeasurements (i.e., a pre- and post-disturbance pair of measurements at a given plot location). Explanatory variables included in the random forest model were disturbance type (fire, harvest, or insect/disease), pre-disturbance forest type, pre- and post-disturbance stand age, edaphic and topographic variables, and either pre-disturbance AGB (when modeling post-disturbance AGB) or pre-disturbance seedling density (when modeling post-disturbance seedling density); see [Table S2](#) for a complete list of explanatory variables. In preliminary analyses, we also considered disturbance history (any previous disturbances reported at a given plot location) as an explanatory variable. However, disturbance history added very little explanatory power, likely due to the limited historical data (only back to ~2000) and/or because effects of previous disturbances are captured by other variables we included (e.g., pre-disturbance stand age); therefore,

we do not report the disturbance history results. In addition to models where disturbance type was treated as an explanatory variable, we also fit separate models for each disturbance type (fire, harvest, and insect/disease) to check the stability of the estimated importance of explanatory variables. Finally, we repeated the random-forest model analysis with post-disturbance stand age excluded from the analysis. Since this variable is tightly linked to post-disturbance recovery (e.g., a non-zero stand age indicates establishment of new tree cohorts), excluding it from the list of predictor variables allowed us to evaluate if the estimated importance of other predictors was robust.

Analyses were performed in R (R Core Team, 2022). We implemented the random forest algorithm using the *randomForest* package (Liaw and Wiener, 2002), we used K-fold cross-validation to train and select the best model using the *trainControl* function in the *caret* package (Kuhn, 2008), and we quantified the partial dependence of different explanatory variables using the *pdp* package (Greenwell, 2017).

For each of the above-mentioned models, we split the data for training (80%) and testing (20%). We trained the random forest model using the training dataset by applying the K-fold method (Kuhn, 2008), with K set to five. Alternate models were trained and validated multiple times within the K-fold wrap before providing the best model with a best *mtry* (number of predictors used at each node of the decision tree). While training the model, we tested all possible values of *mtry* from 1 to 11 (maximum number of predictor variables in our analysis) with 1000 classification trees (*ntree*). After identifying the best random forest model with a specific *mtry* based on (wrapped within) K-fold analysis, we evaluated the best model with the test dataset (20% of data, which were not used for training) using standard R^2 and RMSE metrics.

2.4. Comparing fire occurrence and severity reported by FIA and MTBS

We explored the consistency of fire occurrence and severity reporting between FIA and the Landsat satellite-based MTBS dataset (MTBS, 2020; Smith and Hoover, 2024). MTBS uses pre-fire and one-year post-fire differenced normalized burn ratio (dNBR) to map fire perimeters (larger than 202 ha in the eastern U.S. and larger than 405 ha in the western U.S.) and burn severity in Landsat pixels (roughly 30 × 30 m) across the conterminous U.S. annually since 1984 (Eidenshink et al., 2007; Whit- tier and Gray, 2016).

To overlay FIA and MTBS data, we used non-public FIA plot location data, which are accurate to within ~5–10 m of a plot's true location (McRoberts et al., 2018). Our analysis of MTBS data was restricted to MTBS burn perimeters that included at least one remeasured FIA plot that passed our data filters (see [Supplementary Methods](#) in the [Supporting Information](#)) and whose remeasurement period included the MTBS fire year. For each of these FIA plots, we extracted a 3 × 3 grid of MTBS pixels, roughly corresponding to the area sampled by an FIA plot (Fig. S1). The data for each pixel consists of the fire year and a burn severity code: 0 = no data, 1 = underburned to low severity, 2 = low severity, 3 = moderate severity, 4 = high severity, 5 = increased greenness, and 6 = masked area (water bodies, clouds, snow, etc.). We restricted our analysis to pixels with severity codes 1–4, consistent with MTBS burn severity mapping protocols (Picotte et al., 2020). This filter (i.e., excluding pixels with codes 0, 5, or 6) removed, on average, only 0.75 of the nine pixels in the 3 × 3 grid. We then averaged the severity codes across the burned pixels in the 3 × 3 grid to obtain a plot-level MTBS burn severity. We classified MTBS burn severity for each of these FIA plots as either mild (plot-level MTBS burn severity ≤ 2.5) or severe (plot-level MTBS burn severity > 2.5). This threshold (2.5) separates the low (code 2) and moderate (code 3) MTBS burn categories. For the FIA plots included in our analysis, the mean plot-level MTBS burn severities were 1.79 for our mild MTBS burn category in the East ($n = 238$), 2.88 for our severe MTBS burn category in the East ($n = 12$),

1.75 for our mild MTBS burn category in the West ($n = 298$), and 3.45 for our severe MTBS burn category in the West ($n = 212$).

We compared our MTBS-based classification to our FIA-based fire classification during the FIA remeasurement interval that included the MTBS fire year. For this MTBS-FIA comparison, we used the following FIA disturbance categories: (1) the same FIA-based mild and severe fire categories described previously (see also [Supplementary Methods](#) in the [Supporting Information](#)); (2) an additional ‘mixed fire’ category for all other fires reported in the FIA Condition table (i.e., fires not considered mild or severe fire in our classification system because fire was not the primary disturbance); and (3) ‘non-fire disturbance’ (any disturbance reported in the FIA Condition table not included in one of the above categories).

2.5. Chronosequence analysis following severe fire in the western U.S. using FIA and MTBS data

We used a chronosequence approach that combined FIA and MTBS data to study forest dynamics following severe fires in the western U.S. We restricted this analysis to the West because few severe fires were reported by MTBS or FIA in the East (see Results). The chronosequence analysis was restricted to FIA plots in MTBS burn perimeters that met both our FIA- and MTBS-based criteria for severe fire: age-resetting (FIA) and mean burn severity code > 2 (MTBS). Unlike our other analyses that were based only on FIA data (for which the fire year was unknown), the chronosequence analysis included data on time-since-fire (which was determined by comparing the post-fire FIA measurement date to the MTBS burn year) and was restricted to fires larger than the minimum MTBS mapping size in the western U.S. (405 ha).

The chronosequence analysis involved summarizing FIA-derived forest attributes in relation to time-since-fire, including AGB, seedling density, and stand age. As explained above, FIA defines stand age as the mean age of trees in the dominant size class, which may differ from time-since-fire ([Stevens et al., 2016](#)). For example, FIA reports stand age as zero if the plot is classified as nonstocked ($< 10\%$ stocking of live trees) ([Burrill et al., 2018](#)), a condition that may persist for multiple years following severe disturbance. Preliminary analysis revealed different fire responses for western U.S. conifer (‘softwood’) and angiosperm

(‘hardwood’) forest types, and we report separate results for these forest types.

3. Results

3.1. Frequency and severity of forest disturbances reported by FIA

Fire was the most common type of severe (age-resetting) disturbance in the West, whereas harvest was the most common type of severe disturbance in the East ([Table 1](#)). Severe harvest occurred primarily in the Southeast, and to a lesser extent in the Great Lakes region and Pacific Northwest ([Fig. 1](#)). Severe and total (mild + severe) rates of fire and insect/disease disturbance were higher in the West than in the East, whereas harvest rates were higher in the East than in the West ([Table 1](#)). In the West, mild fires were only moderately more frequent than severe fires. For all other disturbance types in both the West and East, mild disturbances were at least twice as common (sometimes more than 10 times as common) as severe disturbances ([Table 1](#)).

3.2. Comparison of fire occurrence and severity reported by FIA and MTBS

In the West, most fires reported by MTBS (minimum MTBS size is 405 ha in West) were also considered fire disturbance in our FIA classification ([Table 2](#)), but the reverse was not true: only 198/662 (30%) of FIA mild fires and only 193/480 (40%) of FIA severe fires were reported by MTBS ([Table 2](#)). Of the 298 mild MTBS fires in the West that overlapped with an FIA plot remeasurement, 57% were also mild fires according to our FIA classification (i.e., the FIA field crew reported fire disturbance, but the disturbance was not age-resetting), and 13% were some other fire types in our FIA classification ([Table 2](#)). Of the 212 severe MTBS fires in the West that overlapped with an FIA plot remeasurement, 77% were also severe fires according to our FIA classification, and 21% were some other fire types in our FIA classification ([Table 2](#)).

The agreement between MTBS and FIA fire reporting was weaker in the East than in the West. As in the West, most fires in the East reported by MTBS (minimum MTBS size is 202 ha in East) were also considered fire disturbance in our FIA classification ([Table 2](#)). However, the fraction

Table 1

Annual disturbance rates by disturbance type, severity, and region based on remeasured FIA plots. Each cell in the table reports the number (n) of FIA plot remeasurement intervals that we classified as a given type/severity of disturbance and the corresponding annual disturbance rate (%/year), calculated as $100 \times n / \sum(\text{REMPER})$, where REMPER is the FIA plot remeasurement interval and the summation is over all plot remeasurements included in our analysis for western ($N = 20,638$) and eastern ($N = 85,451$) regions. Total disturbance rates are calculated as row and column sums. Our methodology is designed to identify the single dominant type of disturbance (if any) during a plot remeasurement interval and thus likely underestimates the true disturbance rates (see Table Notes).

Disturbance type	West			East		
	Mild	Severe	Total (Mild + Severe)	Mild	Severe	Total (Mild + Severe)
Harvest	$n = 624$ 0.31%/yr	$n = 152$ 0.08%/yr	$n = 776$ 0.39%/yr	$n = 5652$ 1.26%/yr	$n = 2245$ 0.50%/yr	$n = 7897$ 1.75%/yr
Fire	$n = 662$ 0.33%/yr	$n = 480$ 0.24%/yr	$n = 1142$ 0.57%/yr	$n = 1735$ 0.39%/yr	$n = 56$ 0.01%/yr	$n = 1791$ 0.40%/yr
Insect/Disease	$n = 3556$ 1.77%/yr	$n = 46$ 0.02%/yr	$n = 3602$ 1.80%/yr	$n = 3868$ 0.86%/yr	$n = 14$ 0.00%/yr	$n = 3882$ 0.86%/yr
Other disturbance	$n = 1395$ 0.70%/yr	$n = 106$ 0.05%/yr	$n = 1501$ 0.75%/yr	$n = 6423$ 1.43%/yr	$n = 344$ 0.08%/yr	$n = 6767$ 1.50%/yr
Total disturbance	$n = 6237$ 3.09%/yr	$n = 784$ 0.39%/yr	$n = 7021$ 3.48%/yr	$n = 17678$ 3.93%/yr	$n = 2659$ 0.59%/yr	$n = 20337$ 4.52%/yr

Table Notes:

In our paper, relative frequencies of different disturbance types are based on the rates in this table. For example, relative to the total rate of severe disturbance (0.39%/yr in the West and 0.59%/yr in the East), the most common severe disturbance in the West is fire (0.24/0.39 = 83% of severe disturbance in the West), and the most common severe disturbance in the East is harvest (0.5/0.59 = 85% of severe disturbance in the East).

Our disturbance classification identifies the single dominant disturbance (if any) on a plot during a remeasurement interval (for details, see [Supplementary Methods](#) in the [Supporting Information](#)). Cases where harvest was reported along with any other disturbance type were classified as ‘Other disturbance’ because we considered the main disturbance type to be ambiguous. Cases with multiple non-harvest disturbances were classified as the main disturbance type indicated by FIA. Thus, we classified each plot measurement interval as having either zero or one disturbance, which results in conservative estimates of disturbance rates. The degree of underestimation increases with the length of the remeasurement interval, because longer intervals are more likely to experience multiple disturbances (which would be classified as a single disturbance in our analysis). Thus, we expect the degree of underestimation to be greater in the West (~10 year intervals) than in the East (~5 year intervals).

Table 2

Comparison between the satellite-based MTBS fire data product and fire disturbances reported by FIA for plots that overlap the MTBS burns in space (FIA plot located within MTBS burn perimeter) and time (plot remeasurement period includes the MTBS fire year). Values are the number of FIA plots and the percent of FIA plots in a table column reported by FIA to have mild fire, severe fire, mixed fire (fire + harvest, or fire not the primary disturbance), non-fire disturbance, or no disturbance within each of three MTBS categories: no data (i.e., no burn detected, or burn area did not exceed minimum area threshold for MTBS mapping), mild burn, or severe burn. Columns sum to 100%. Fires reported by FIA were classified as severe if stand age was reset following fire and classified as mild otherwise. MTBS fire was classified as severe if the mean MTBS burn severity code was greater than 2 and classified as mild otherwise. The analysis includes all MTBS burn perimeters that included at least one overlapping FIA plot remeasurement in our filtered dataset (see [Supplementary Methods](#) in the [Supporting Information](#)).

FIA disturbance category	MTBS fire category							
	West				East			
	Mild fire	Severe fire	No data	Total	Mild fire	Severe fire	No data	Total
Mild fire	171 (57.38%)	27 (12.74%)	464 (2.31%)	662 (3.21%)	139 (58.4%)	7 (58.33%)	1589 (1.87%)	1735 (2.03%)
Severe fire	30 (10.07%)	163 (76.89%)	287 (1.43%)	480 (2.33%)	3 (1.26%)	1 (8.33%)	52 (0.06%)	56 (0.07%)
Mixed fire	8 (2.68%)	17 (8.02%)	87 (0.43%)	112 (0.54%)	10 (4.20%)	0 (0.00%)	509 (0.60%)	519 (0.61%)
Non-fire disturbance	21 (7.05%)	0 (0.00%)	5746 (28.55%)	5767 (27.94%)	17 (7.14%)	1 (8.33%)	18009 (21.14%)	18027 (21.10%)
No disturbance	68 (22.82%)	5 (2.36%)	13544 (67.29%)	13617 (65.98%)	69 (28.99%)	3 (25%)	65042 (76.34%)	65114 (76.2%)
Total	298 (100%)	212 (100%)	20128 (100%)	20638 (100%)	238 (100%)	12 (100%)	85201 (100%)	85451 (100%)

of FIA fires that were reported by MTBS was smaller in the East than in the West: only 146/1735 (8%) of FIA mild fires and only 4/56 (7%) of FIA severe fires in the East were reported by MTBS (Table 2). Of the 238 mild MTBS fires in the East that overlapped with an FIA plot remeasurement, 58% were also mild fires according to our FIA classification, and 5% were some other fire types in our FIA classification (Table 2). Of the 12 severe MTBS fires in the East that overlapped with an FIA plot remeasurement, only 8% (1/12) were also severe fires according to our FIA classification, and 58% (7/12) were mild fires in our FIA classification (Table 2).

3.3. Pre- and post-disturbance comparisons using FIA data

Following severe (age-resetting) disturbance in both the East and West, AGB decreased dramatically, and seedling density either increased or did not significantly change (Fig. 2 and Table S3-S4). In the West, AGB following severe disturbance differed significantly among disturbance types, being lowest following fire and highest following insect/disease (Tables S3-S4). In contrast, in the East, AGB following severe disturbance did not differ significantly among disturbance types. Forest attributes preceding severe disturbance also differed among disturbance types. In both the East and West, pre-disturbance AGB was higher for harvest than for fire and insect/disease; and in the East, pre- and post-

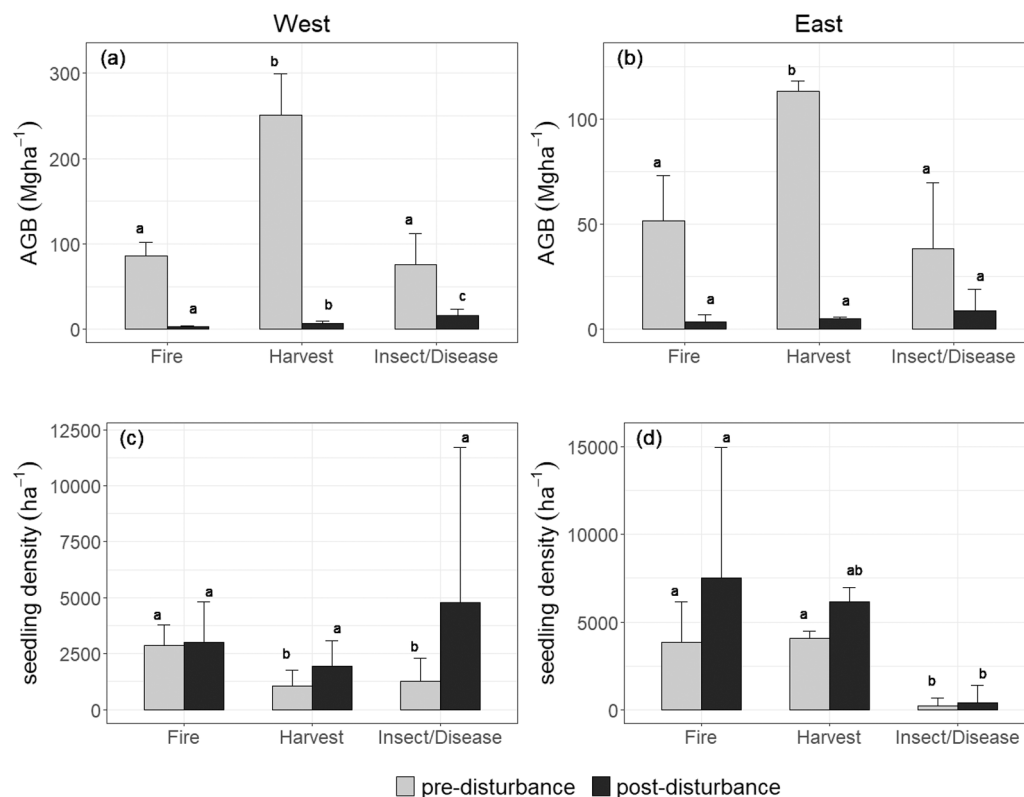


Fig. 2. Mean pre- (gray) and post-disturbance (black) live AGB (Mg ha^{-1}) and seedling density (ha^{-1}) for severe disturbances, based on FIA data. Error bars represent ± 2 SE of the mean. Letters indicate significant differences among fire, harvest, and insect/disease disturbance types (see [Tables S3-S4](#) for sample sizes and other details). No statistical comparisons were made between pre- and post-disturbance conditions. The analysis is based on remeasured FIA plots dominated by a single condition (at least 90% of plot area), with severe disturbance defined as follows: pre-disturbance stand age ≥ 20 years, post-disturbance stand age $\leq$ remeasurement interval, and post-disturbance AGB $< 50 \text{ Mg ha}^{-1}$. Corresponding results for mild disturbances are shown in [Fig. S2](#). We have low confidence in the anomalously low seedling densities in insect/disease-disturbed plots in the East due to small sample size ($n = 14$; [Table S3](#)).

disturbance seedling density was lower for severe insect/disease than for severe fire and harvest (Fig. 2; Tables S3–S4). Pair-wise differences in AGB and seedling density following mild disturbances were significant in some cases, although the differences were small compared to differences among severe disturbance types (Fig. S3 and Table S4).

3.4. Association of forest and topographic attributes with AGB and seedling recovery following severe disturbances

The fraction of variation explained by machine-learning models (training and validation R^2) ranged from 0.02 to 0.38 and tended to be higher for seedling density than for AGB, especially in the East (Table 3). In both the East and West, pre-disturbance AGB and post-disturbance stand age were among the four top predictors of AGB following severe disturbance (Fig. 3a–b and Fig. 4a–b), and pre-disturbance seedling density was among the two top predictors of seedling density following severe disturbance (Fig. 3c–d and Fig. S4c–d). Disturbance type was an important predictor of AGB in the West (Fig. 3a), with AGB being highest following severe insect/disease disturbance and lowest following severe fire (Fig. 4a). Disturbance type was a weak predictor in the other three cases (Fig. 3b–d). AGB and seedling density increased with post-disturbance stand age in most cases (Fig. 4), except for post-fire AGB in the East (Fig. 4b; this may reflect the small range and/or errors in reported stand age). The effects of increasing stand age were often not realized in the West, because a large fraction of post-severe-fire plots had a stand age of zero (Fig. 4a, c).

Excluding post-disturbance stand age from the list of predictor variables resulted in lower R^2 (compare Tables 3 and S5) but led to similar inferences about the relative importance of other predictor variables (compare Figs. 3 and S5).

Table 3

Summary statistics for machine learning (random forests) models of post-disturbance live tree aboveground biomass (AGB) and seedling density following severe (age-resetting) disturbances in the eastern and western U.S. The number of observations (n), number of predictors used at each node of the decision tree (best $mtry$), R^2 and RMSE are presented for training and validation of each model. The number of observations (n) used for some of the models is less than shown in Table 1 because we excluded observations with missing data for any independent variable. Each observation is a remeasured forest inventory plot. ‘AGB all’ and ‘Seedling all’ models included data from fire, harvest, and (in the western U.S.) insect/disease disturbances and included disturbance type as an explanatory variable; other models only included data for one disturbance type. The insect/disease model was not fit for the eastern U.S. due to insufficient sample size ($n = 14$; see Table 1).

Models	Training				Validation			
	best $mtry$	n	R^2	RMSE	n	R^2	RMSE	
West								
AGB all	2	542	0.19	8.5	136	0.16	8.5	
AGB fire	1	384	0.05	7.3	96	0.01	7.0	
AGB harvest	1	121	0.20	10.0	31	0.08	9.3	
AGB insect/disease	1	36	0.22	10.2	10	0.02	15.8	
Seedling all	3	542	0.19	8894.8	136	0.24	3615.9	
Seedling fire	2	384	0.16	8853.3	96	0.32	7262.9	
Seedling harvest	1	121	0.18	3085.8	31	0.06	2652.2	
Seedling insect/disease	1	36	0.19	10959.3	10	0.01	5310.5	
East								
AGB all	1	1838	0.07	8.7	460	0.28	7.3	
AGB fire	1	44	0.19	6.1	12	0.06	4.8	
AGB harvest	1	1782	0.08	9.1	446	0.05	8.0	
Seedling all	2	1838	0.34	8103.1	460	0.38	5968.2	
Seedling fire	1	44	0.24	12359.2	12	0.33	9503.0	
Seedling harvest	2	1782	0.36	7318.8	446	0.4	8084.0	

3.5. Chronosequence analysis following severe fire in the western U.S.

Chronosequence analysis following severe fire in western U.S. forests suggested that the large fraction of post-fire age-zero plots in the larger FIA dataset (Fig. 4a, c) resulted from persistent age-zero conditions in western conifer forests (in this section of Results, conifer and hardwood forest types refer to the pre-fire forest type reported by FIA, regardless of the post-fire species composition). This chronosequence analysis focused on relatively large fires (minimum MTBS mapping size in the western U.S. is 405 ha) that we classified as severe in both FIA and MTBS data (see details in Methods). The mean MTBS burn severity code in these 162 FIA plots was 3.65 out of a maximum possible of 4 (compared to a mean of 3.45 across all 212 severe MTBS fires in Table 2). Seventy-one percent of conifer plots in the chronosequence dataset (0–10 years post-fire) had an FIA-assigned stand age of zero (Fig. 5a), compared to only 24% of hardwood plots (Fig. 5b). In all conifer forest types in the western U.S. with more than two FIA plots in the chronosequence dataset, > 50% of FIA plots had a post-fire stand age of zero (Table S6). At 8–10 years post-fire, > 50% of conifer plots still had an FIA-assigned stand age of zero (Fig. 5c). The fraction of age-zero hardwood plots increased with time-since-fire (Fig. 5d), but this may largely reflect sampling error given the very small sample sizes for hardwood plots in the chronosequence dataset.

Post-fire stand age was roughly consistent with the FIA classification of plots as stocked ($\geq 10\%$ stocking of live trees) vs. nonstocked ($< 10\%$ stocking of live trees). Most non-zero-age plots were classified as stocked, whereas most zero-age plots (including 88% of zero-age conifer plots) were classified as nonstocked (Table S7).

Post-fire AGB was much lower than pre-fire AGB, but AGB did not differ consistently between non-zero and zero-age plots during the 10-year post-fire period (Fig. 5d–e; Tables S8–S9). In conifer plots, most post-fire AGB was comprised by conifer species (Fig. 5d). In hardwood plots, most post-fire AGB was comprised by hardwood species (Fig. 5e).

Seedling densities in conifer plots were relatively high ($> 3000/\text{ha}$) in non-zero-age plots both before and after fire, intermediate in pre-fire zero-age plots ($\sim 2300/\text{ha}$), and low in post-fire zero-age plots ($< 400/\text{ha}$; Fig. 5g and Table S10). Seedling species composition in conifer plots was dominated by hardwoods 0–4 years post-fire and by conifer seedlings 4–10 years post-fire (Fig. 5g). Seedling densities in hardwood plots were relatively high ($> 1300/\text{ha}$) in non-zero-age plots both before and after fire, low in pre-fire zero-age plots ($\sim 400/\text{ha}$), and had zero density (no seedlings tallied) in post-fire zero-age plots (but with very small size; Fig. 5h and Table S11). Seedling species composition in hardwood plots was dominated by hardwood species (Fig. 5h).

4. Discussion

Our analysis of the national standardized FIA dataset indicates that the most common form of severe (age-resetting) disturbance in eastern U.S. forests is harvest (85% of age-resetting disturbances in the East, primarily in the Southeast; Table 1 and Fig. 1), and the most common form of severe disturbance in western U.S. forests is fire (62% of age-resetting disturbances in the West; Table 1). Insect/disease (a single combined category in our analysis) was the most common disturbance type in western U.S. forests (57% of mild disturbances and 51% of all disturbances in the West; Table 1) but rarely caused age-resetting disturbances in the West or East. There was no single dominant type of mild disturbance in the East (Table 1).

The FIA-based rates of mild and severe disturbance for eastern and western U.S. forests reported here (Table 1) provide a regional perspective that complements previous U.S.-wide studies. A literature review identified timber harvest as having the largest impact on conterminous U.S. forest biomass, followed by fire and cyclones (Williams et al., 2016). Similarly, an analysis of condition- and tree-level FIA data identified silviculture as the most severe form of disturbance (median of $\sim 50\%$ trees killed) followed by fire (median of $\sim 30\%$ of trees

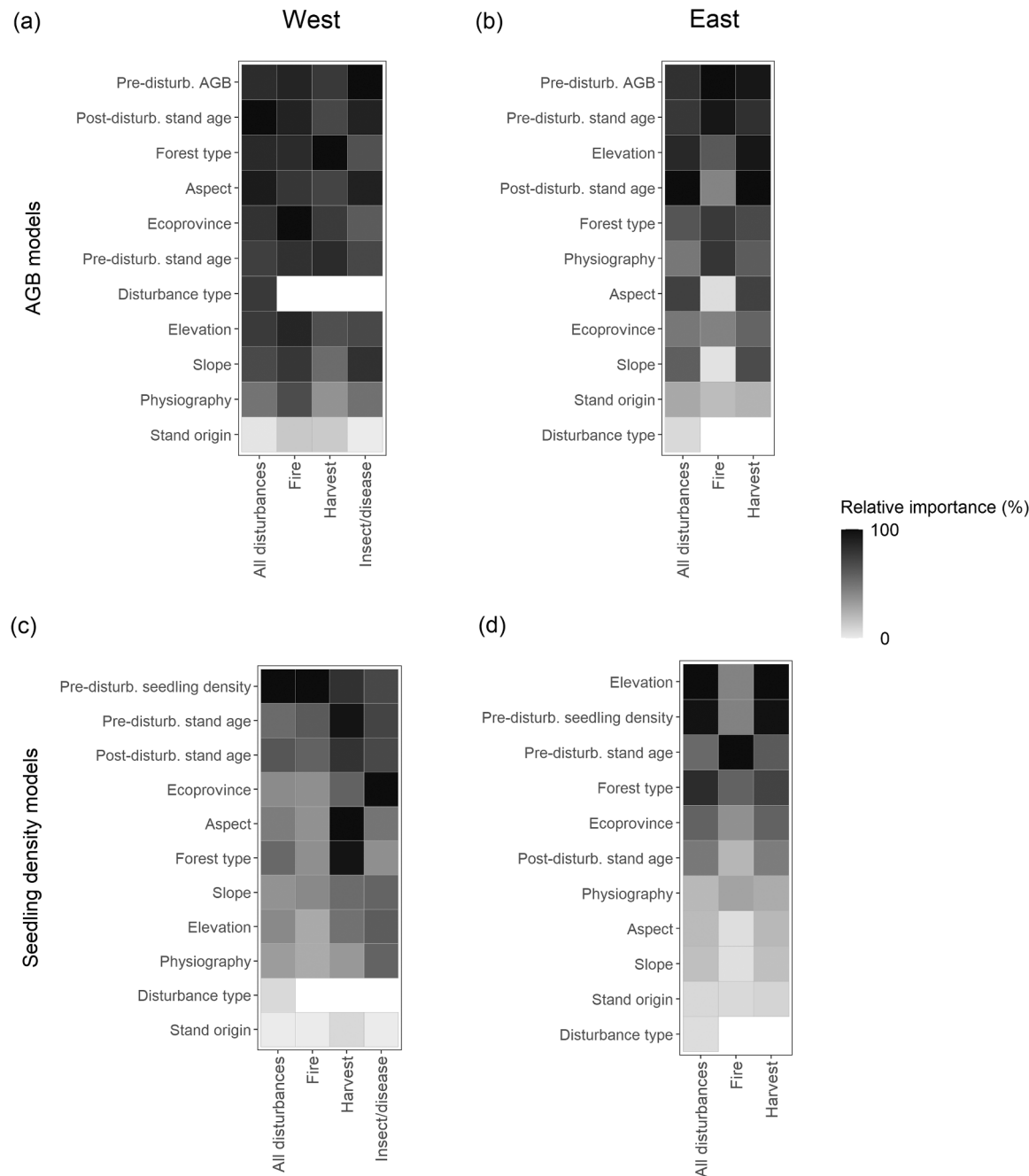


Fig. 3. Importance values (relative to the most important variable for each model) for predictor variables in machine-learning models of live tree aboveground biomass (AGB) and seedling density following severe (age-resetting) disturbance. Darker shading indicates greater importance. Models were fit separately for East and West regions. The ‘disturbance type’ predictor variable is only relevant for the ‘All disturbances’ models; its variable importance is shaded white (NA) for the other models. Variables are ordered from top to bottom in terms of their average importance across all four (West) or three (East) models. Sample sizes, fit statistics, and other details are given in Table 3. Variables are defined in Table S3.

killed (Fitts et al., 2022). The only disturbances in conterminous U.S. forests that routinely cause plot-level mortality rates approaching 100% are silviculture and fire (Fitts et al., 2022). The disturbance rates we report (Table 1) should be interpreted with caution for several reasons. First, we identified disturbances based on FIA disturbance and treatment codes, which are reported if at least 25% of trees are affected during a plot remeasurement interval (Burrill et al., 2018); thus our study may not detect chronic disturbances that affect background mortality rates (van Mantgem et al., 2009) or mild disturbances affecting < 25% of trees in a stand (Fitts et al., 2022). Second, our reported rates of severe disturbance depend on our filtering criteria (e.g., minimum

pre-disturbance stand age of 20 years) and our definition of severe disturbance (age-resetting, with post-disturbance AGB less than 50 Mg/ha). Finally, the total disturbance rates in Table 1 are underestimates, because our analysis does not account for multiple disturbances during a remeasurement interval; the degree of underreporting likely increases with the length of remeasurement intervals, which in FIA data tend to be longer in the western than in the eastern U.S. Despite these limitations, our conclusion that harvest and fire are the most common forms of severe disturbance in forests of the conterminous U.S. is likely robust and is consistent with previous studies (Fitts et al., 2022; Wang et al., 2022; Williams et al., 2016). In terms of

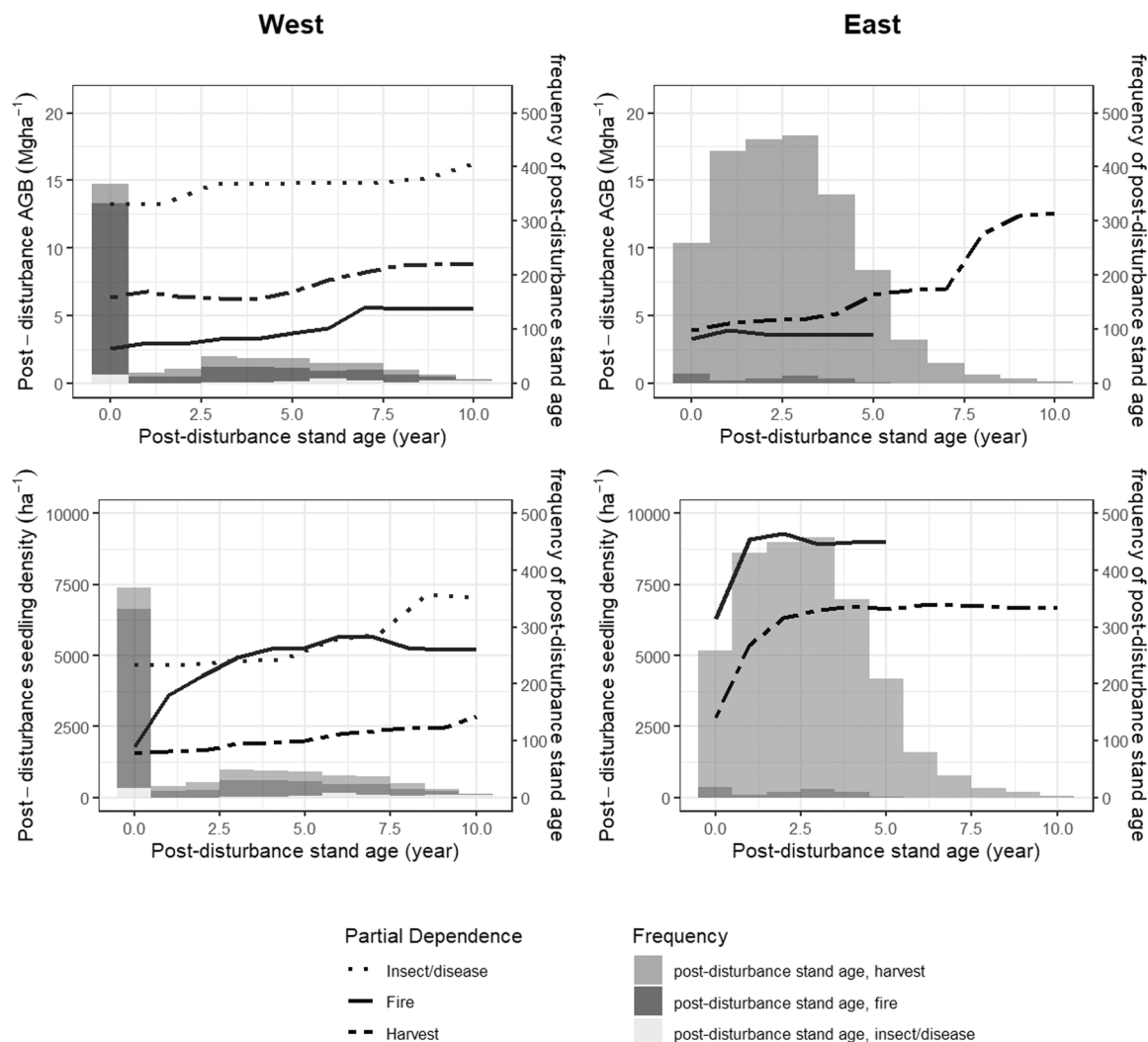


Fig. 4. Dependence of post-disturbance live tree aboveground biomass (AGB; top) and seedling density (bottom) on post-disturbance stand age following severe (age-resetting) disturbances in the western and eastern U.S. Stand age, as reported by FIA, is the mean age of trees in the dominant size class. FIA reports stand age as zero if live tree stocking density is below 10%, a condition which frequently persists in the western U.S. for a decade or more following severe fire (Fig. 5). The curves are partial dependence plots (left vertical axis), derived from machine-learning models, and illustrate the effect of a single predictor variable while holding other predictor variables constant. Histograms show the frequency distribution (number of plot records in our filtered FIA dataset) of post-disturbance stand age (right vertical axis). No insect/disease model was fit for the East due to insufficient sample size.

the proximate causes of biomass mortality, the cumulative impact of less severe but more common disturbances, such as insects or disease outbreaks (Hicke et al., 2012), is likely less than that of harvest or fire (Williams et al., 2016). However, the ultimate causes of biomass loss are difficult to disentangle due to the interacting effects of disturbance agents, such as drought, insects, and fire (Anderegg et al., 2015; Halofsky et al., 2020; but see Hart et al., 2015).

Our analysis suggests that the impacts of severe fire in western U.S. forests are particularly strong. Aboveground biomass (AGB) following age-resetting fire was lower than AGB following other types of age-resetting disturbance in the West in raw FIA data (Fig. 2) and in machine-learning models that controlled for pre-disturbance forest properties and abiotic variables (Figs. 3 and 4). Results showing the impact of age-resetting fire on AGB in the West are in agreement with the findings about the aboveground biomass carbon in the region (Jiang et al., 2023). Seedling densities following age-resetting fire were not unusually low in general (Figs. 2 and 4) but were relatively low in post-fire FIA plots with a reported stand age of zero (Figs. 4 and 5). Chronosequence analysis of western U.S. FIA plots located within MTBS severe fire perimeters revealed that the FIA-assigned stand age of zero

often persisted for at least 8–10 years post-fire and was usually associated with conifer forest types (based on the pre-fire forest type classification), near-zero post-fire AGB, low post-fire seedling density (< 400/ha), and a nonstocked condition classification (< 10% stocking of live trees). For comparison, Turner et al. (2019) considered < 1000 trees/ha to be 'sparse' regeneration in subalpine *Pinus contorta* stands in the western U.S. state of Wyoming. These results suggest sparse and delayed regeneration of western U.S. conifer forests following fires that are relatively severe and large enough to be mapped by MTBS (> 405 ha in the West). In contrast, angiosperm ('hardwood') forests in the West recovered more quickly from severe fire, perhaps because many hardwood species resprout (Pausas and Keeley, 2014), whereas most conifers do not (Stevens et al., 2020).

Although post-fire regeneration failure has been reported in previous studies of western North American forests (Stevens-Rumann and Morgan, 2019; Stevens-Rumann et al., 2022), ours is the first study, to our knowledge, that documents the likely widespread occurrence of this phenomenon using systematically sampled NFI data. Because our study design requires remeasured forest plots, and because few western U.S. FIA plots have been measured more than twice using the current FIA

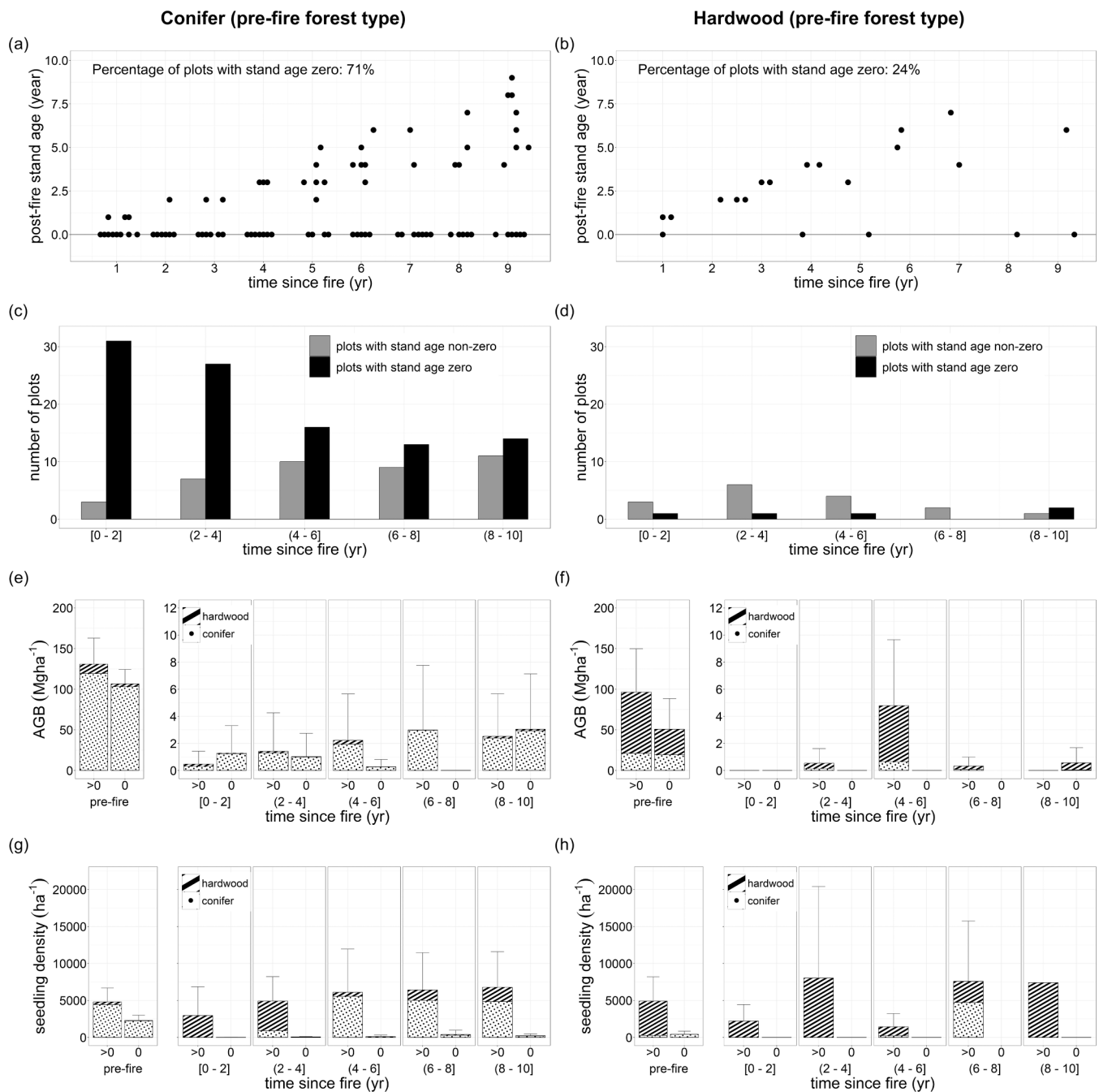


Fig. 5. Chronosequence analysis of conifer (softwood) and angiosperm (hardwood) forests in western U.S. FIA plots that experienced severe fire according to both FIA and MTBS data. Time-since-fire (x-axis) was determined by comparing the FIA plot measurement date to the fire year reported by MTBS. All other data are from FIA. The analysis was restricted to FIA plots with pre-fire live tree stocking of > 10% and pre-fire stand age > 20 years (see [Supporting Information](#) for details of plot filtering). Classification of plots as conifer or hardwood was based on the pre-fire FIA forest type code ([Table S2](#)). Panels (a-b) show the relationship between stand age (from FIA) and time-since-fire; the percent of all FIA plots in the figure with a post-fire stand of zero is given. Panels (c-d) show the data from panels (a-b) in terms of the number of plots with a zero vs. non-zero post-fire stand age (see [Table S6](#) for individual forest types). Most stand-age zero cases were conifer stands classified by FIA as nonstocked (< 10% live tree stocking; [Table S7](#)). Panels (e-h) show mean AGB and seedling density relative to time-since-fire for FIA plots assigned a post-fire stand age greater than zero ('>0' x-axis label) or zero ('0' x-axis label; error bars are 2 SE; see [Tables S8-S11](#) for sample sizes and details; missing error bars indicate n = 1). Each bar in (e-h) is separated into contributions from conifer vs. hardwood species to evaluate how the post-fire species composition compares to the pre-fire forest type. We do not report separate error bars for the two species components.

sampling design, our chronosequence analysis ([Fig. 5](#)) was limited to 10 years post-fire. It is possible that some of the apparent cases of regeneration failure we observed (i.e., stand age of zero, near-zero AGB, and low seedling density up to 10 years post-fire) simply reflect FIA's minimum height thresholds for counting seedlings (15 cm for conifers) combined with the slow regeneration dynamics in some western U.S.

forest types ([Stevens-Rumann and Morgan, 2019](#)). However, given that these patterns were common across all western U.S. conifer forest types that were well-represented in our chronosequence dataset ([Table S6](#)), we suggest that sparse and delayed regeneration following large (> 405 ha) and severe fire is widespread in western U.S. conifer forests. Given that fires larger than 400 ha account for ~75% of western U.S.

burn area (Westerling, 2016) and 163/520 (31%) of the western U.S. MTBS fires in our analysis were classified as severe fires in both MTBS and FIA data (Table 2), our chronosequence analysis should apply to ~23% of western U.S. burned area, with sparse and delayed regeneration in over 50% of this area (Fig. 5).

Given the rarity of resprouting among conifers (Stevens et al., 2020), post-fire conifer seedling recovery depends on seed sources. Because our chronosequence analysis was restricted to MTBS burns with a high mean and low range of pixel-level burn severity codes within the burn perimeter, surviving seed trees may have been rare. Among the well-represented western U.S. conifer forest types in our dataset, lodgepole pine (*Pinus contorta*), which is serotinous, had a relatively low proportion of plots assigned a stand age of zero (10/19 FIA plots, compared to 91/122 for other conifer forest types; Table S6). Nevertheless, even serotinous species may experience seed limitation if cones are damaged by fire and/or if fire returns before regenerating trees reach reproductive maturity (Johnstone et al., 2016; Turner et al., 2019). Explicitly accounting for the distribution of seed sources in the landscape could allow for more direct tests of the seed-limitation hypothesis (Haffey et al., 2018; Peeler and Smithwick, 2020; Tautenhahn et al., 2016; Turner et al., 1998), although this would be challenging with FIA data because the plot locations in the public FIA database are approximate due to privacy concerns (Lister et al., 2005).

In addition to seed availability, post-disturbance recovery is affected by pre-disturbance legacies and multiple factors affecting seedling establishment, including edaphic-topographic factors and weather (Harvey et al., 2016; Johnstone et al., 2016; Stevens-Rumann et al., 2022; Tautenhahn et al., 2016). Although our machine learning analysis of post-disturbance recovery identified some important topographic effects, the strongest effects were related to legacies (pre-disturbance AGB, seedling density, and stand age) (Fig. 3). The correlation between pre- and post-disturbance AGB likely reflects individual tree survivors. The correlation between pre- and post-disturbance seedling density may reflect individual survivors—which cannot be assessed directly with FIA data because individuals are not tracked at the seedling stage—and/or edaphic or landscape conditions that similarly affect both pre- and post-disturbance seed rain and establishment. Post-disturbance stand age was also an important predictor of post-disturbance recovery, despite being an imprecise measure of time-since-disturbance (we did not include disturbance year as a predictor, as it was reported by FIA in only ~30–80% of cases, depending on disturbance type; see Methods). Thus, in our machine learning analysis, stand age may reflect both recovery over time as well as distinguishing plots that are recovering vs. those that are not (and thus have a persistent FIA-reported stand age of zero). Given that FIA data do not include detailed information on seedbed conditions and the omission of weather variables from our analysis, it is possible that our analysis underestimates the importance of establishment conditions, which previous studies suggest are important for post-disturbance seedling densities (Davis et al., 2018; Petrie et al., 2016; Stevens-Rumann and Morgan, 2019; Welch et al., 2016).

Our analysis also provides information on the reliability of stand age and disturbance data in the FIA and MTBS datasets. FIA defines stand age as the mean age of trees in the dominant size class (USDA Forest Service, 2019), which lags behind time since the last severe disturbance if regeneration is delayed (Fig. 5). Beyond the mismatch caused by delayed regeneration, many forest stands in the U.S. are multi-aged, so the interpretation of stand age is sometimes ambiguous (Canham et al., 2013; Giebink et al., 2025; Stevens et al., 2016). Nevertheless, FIA stand age provides useful information during the early stages of forest recovery following severe fire; e.g., FIA plots with a stand age of zero (up to 10 years post-fire) had much lower seedling density than plots whose stand age tracked time-since-fire (Fig. 5). We suggest as forests recover from stand-replacing disturbance, FIA stand age provides a useful measure of ‘time since establishment’ of the dominant tree cohorts Table 3.

Our comparison of FIA and MTBS reporting indicated that most fires reported by MTBS were also captured in FIA data (if the MTBS burn

perimeter included an FIA plot remeasurement), but most fires reported by FIA were absent from the MTBS dataset. A likely factor contributing to this disparity is the minimum fire size for inclusion in MTBS: 202 ha in the eastern U.S. and 405 ha in the western U.S. (Kolden et al., 2015). We speculate that many of the fires reported by FIA were too small to be included in MTBS. Beyond mismatches in fire detection, only 1/12 MTBS burns in the eastern U.S. that we classified as severe also met our definition of a severe (age-resetting) FIA disturbance. This discrepancy may partly reflect our classification system, which (for simplicity) combined MTBS moderate and severe burn codes into a single ‘severe fire’ category. Another factor likely contributing to this discrepancy is the fire regime in pine (*Pinus* spp.) forests of the southeastern U.S., which accounted for 11/12 of the eastern U.S. MTBS severe fires in our dataset. Canopy trees often survive fires in southeastern U.S. pine forests, and the fires in this region that appear relatively severe from the MTBS satellite-based perspective may primarily consume grass and other fine fuels in open savanna-like forests (Mitchell et al., 2009; Platt et al., 1988; Reinhart and Menges, 2004). NFI datasets such as FIA and remote-sensing-based datasets—including MTBS and other spectral and lidar remote-sensing data—each have strengths and limitations (Cohen et al., 2017; Coulston et al., 2020; Kolden et al., 2015; Randolph et al., 2021; Smith-Tripp et al., 2026). Combining these different types of data can enhance our capacity to quantify disturbance regimes, their impacts, and different recovery pathways (Shaw et al., 2017; Smith-Tripp et al., 2026; Williams et al., 2016).

5. Conclusion

The two dominant forms of stand-replacing (age-resetting) forest disturbance in the conterminous U.S. are harvest in the East and fire in the West. Insects and disease (considered together in this study) are the most common forest disturbance agents in the conterminous U.S., but these disturbances are rarely stand-replacing. Our study did not consider the effects of compound or repeat disturbances (Turner et al., 2019), but these could be explored in future research using the national standardized FIA dataset as more years of data become available. Chronosequence analysis that combined FIA data with the MTBS satellite-based fire dataset revealed that sparse and delayed seedling recruitment is widespread in western U.S. conifer forests recovering from large (> 405 ha) and severe fires. Given the modest sample of FIA plots currently available for this chronosequence analysis, we did not attempt to quantify if such cases of sparse and delayed regeneration are becoming more frequent over time. As longer time-series of FIA plot remeasurements and remote-sensing data become available, it should be possible to quantify temporal trends in forest recovery and regeneration failure, and how these trends relate to changing disturbance regimes.

CRedit authorship contribution statement

Grant M. Domke: Writing – review & editing, Methodology, Data curation, Conceptualization. **Jeremy W. Lichstein:** Writing – review & editing, Visualization, Methodology, Conceptualization. **Daniel J. Johnson:** Writing – review & editing, Methodology, Conceptualization. **James E. Smith:** Writing – review & editing, Data curation, Methodology, Conceptualization. **Karun Pandit:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Data analysis, Data curation, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2026.123928](https://doi.org/10.1016/j.foreco.2026.123928).

Data availability

Data used in the analysis is publicly available at USDA FIA webpage

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