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Tree age estimation across the U.S. using forest inventory and analysis database

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ABSTRACT

Tree age information is crucial for a range of environmental, scientific, and conservation-related purposes. It helps in understanding and managing forest resources effectively and sustainably. This study presents an approach to estimate tree age across diverse U.S. forested ecosystems using field inventory and climate datasets. The age-size relationship modeling framework incorporates species-specific and environmental variables, enabling its application across various regions. Model R^2 values range from 0.51 to 0.87 and relative RMSEs (using the mean as the denominator) ranging from 0.14 to 0.49. These models have higher accuracies and are applicable over larger areas than existing studies. The developed tree age dataset reveals marked differences in tree age distribution between Eastern and Western U.S. forests, attributed to historical land use, disturbance, climatic variations, and forest management practices. In the East, forests exhibit a younger age structure due to historical deforestation and subsequent reforestation, while Western forests show an older age structure, influenced by diverse environmental conditions and less human disturbance. By deriving individual tree ages for all the trees surveyed in the United States Forest Inventory and Analysis Program, the approach increases by more than 20 times the number of tally trees in the FIA database that have age data over what is currently. The curated dataset emerges as a crucial resource for forest management and conservation, enhancing our ability to estimate forest carbon sequestration accurately. The tree age dataset is available at https://zenodo.org/records/14775738.

1. Introduction

The tree age is key information for several scientific and practical reasons. Trees act as natural carbon sinks, absorbing carbon dioxide from the atmosphere. Due to variations in growth rates and biomass accumulation over a tree's life cycle, information on the age of trees improves the estimation of growth rate and the amount of carbon stored in a forest, which is vital for climate change models and carbon management strategies (Köhl et al., 2017; Repo et al., 2021). In a forest setting, understanding the age of trees helps in comprehending stand structural complexity, which is important in resilience to disturbances (Sousa, 1980) and the ability to support biodiversity and habitat diversity (Gilhen-Baker et al., 2022; Tullus et al., 2022), among other factors. Knowing the age of trees is also crucial for sustainable management and harvesting practices. In addition to inferring growth rates, tree age also serves as the basis for estimating stand age, which helps evaluate the productivity of the forest and identify optimal harvesting times (Nakajima et al., 2017; Peng, 2000).

To determine the age of a tree, several methods are currently used, each with its own advantages and limitations. Dendrochronology requires a core sample from the tree, taken with an increment borer, then counting the growth rings from the core (Phipps, 1985). The method was proved to be accurate and the "gold standard" for aging most tree species, but it can be destructive, and only suitable for aging a limited number of tally trees because of the cost. For tree species in tropical areas that do not follow regular tree ring increment growth pattern, bud scars or branch whorls are counted instead. Radiocarbon dating is used for very old trees where dendrochronology might not be feasible but can be expensive due to laboratory analysis. Non-destructive modeling approaches have also been developed to estimate age, which consider the empirical relationship between age and other tree structural attributes that can be more readily and accurately assessed in the field, such as

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diameter and height. The general patterns of such relationships are that in early years, trees usually grow more in height than in diameter (King, 2011; Niklas, 1995). This rapid vertical growth is typically to outcompete other vegetation for sunlight. As trees mature, diameter growth becomes more prominent. Height growth slows down once a tree reaches a certain age, which varies by species. The relationship could be influenced by factors such as tree species, local environmental conditions, climate, and management practices, so compared to tree ring analysis, this modeling approach is less precise. For the purpose of estimating ages for a large number of individual trees, however, modeling is the only feasible method. The existing studies explored the use of linear regression (Diallo et al., 2013; Kalliovirta and Tokola, 2005; Rozas, 2003; Silva et al., 2021), polynomial regression (Baker, 2003; Trotsiuk et al., 2012), and other nonlinear functions (Rohner et al., 2013; Zhang et al., 2022) to fit the empirical age-diameter, age-height, age-growth relations for certain species in individual sites. And because of the scale of these studies, many did not consider the impact of environmental variables (i.e., climate, topography) on tree age-size relationships, therefore the modeled relationships may not be easily transferred to other species and regions.

One of the most comprehensive tree age datasets for the contiguous United States (CONUS) is provided by the Forest Inventory and Analysis (FIA) program of the US Forest Service (Burrill et al., 2023). The FIA program provides crucial data on the nation's forest resources, including tally tree- and plot-level measurements. This dataset provides field-based age estimates for selected tally trees over plot locations distributed across the country that have been traditionally used to age forest stands and as input into estimates of site productivity. The FIA sample is designed is to provide unbiased population estimates of timber volume and other key forest attributes (Smith, 2002) and has been used in hundreds of applications (Tinkham et al., 2018). However, applications that examine how *individual* tree structure/biomass change with age, or that require individual tree age measurements are challenging nationally. Though FIA-based tree-ring datasets have been recently developed (DeRose et al., 2017), only a fraction of all trees measured by the FIA program are surveyed for age and the fraction varies across the nation (Fig. 1).

The purpose of this study is to introduce and evaluate an approach for estimating tree age based on diameter and/or other individual tree-level attributes as measured for forest inventories. This approach considers species and environmental factors in age estimation, and hence may have the generality to be applied to different regions. In this study, the developed approach is used to derive age estimates for all trees in the FIA database (FIADB) that had diameter measurements collected in FIA's annual sampling system since 2001. In the FIADB, more structural measurements (e.g., diameter, height) than age measurements are available for individual trees by an order of 1–2 magnitudes in most ecoregions (Fig. 1). This data gap provides an incentive and opportunity to estimate tree age from the structural measurements. In this study, we take advantage of the plentiful diameter data from FIA and use the developed modeling approach to estimate the age for all trees in the FIADB (with diameter and species measurements) for all measurement years since 2001. We then generate age estimation for the tree population in 2015 and evaluate spatial and temporal patterns at multiple scales.

2. Materials and methods

2.1. FIA tree and plot data

The USFS FIA program, a comprehensive nationwide forest monitoring program implemented across four regions (Pacific Northwest region (PNW), Rocky Mountains (RM), Northern (NR), and Southern (SR)) has collected, analyzed, and reported forest-related data for decades. In the annualized sampling design, permanent plots are revisited periodically (i.e., every 5 years for eastern states and 10 years for western states) to collect data on a wide range of attributes, which allows for tracking changes over time and assessing the health and productivity of forests (Bechtold and Patterson, 2005) An annual non-urban, FIA Nationwide Forest Inventory survey plot consists of four subplots (7.32-m radius) and nested within each is a microplot (2.07 m radius). Within this footprint, all live tally tree species and dead trees are sampled; however, sample protocols vary by attribute (for full protocols please refer to the national FIA field guide version 9.2 https://www.fs.usda.gov/research/understory/nationwide-forest-inventory-field-guide). A tree must meet two criteria to be considered as a tally tree: 1). The species must be on the FIA tree list[1] (i.e., it is a recognized species for measurement); 2) The tree's diameter must meet the size requirements based on the subplot, macroplot, or microplot where it is measured.

It is a FIA program priority to minimize damage to current or prospective tally trees that could be caused by the field inventory itself, so direct measurements of tree age are collected in field for only a subset of trees. Also, when a stand has previous stand age or site tree age available or has not been seriously disturbed since the previous survey no additional age or site tree increment cores are taken. Cores are taken to evaluate initial age measurements. The primary reason and intent of use for age data collected from "site" trees (site index and productivity expressed by the height to age relationship of dominant and codominant trees) and/or "age" trees (stand age) dictate selection criteria and protocols. For example, site trees are often selected off the subplot, which may limit use for structural re-measurements, to prioritize other criteria including that the site tree should have remained a dominant or codominant crown class throughout their lifespan, and they should be at least 12.7 cm (5 in.) in diameter, or at least 20 years old. Where possible, at least one site tree is selected for each forest condition class from a species that is common to the condition class. Age trees are almost always within the radius of the subplot (or for certain species a similar representative is chosen off plot), and tree age estimates usually include the time of tree establishment. While measurement methods are consistent nationally, age tree selection specifics can vary to accommodate local realities. In FIA PNW, for each condition class present on a plot within each crown class, one age tree is sampled for counting tree rings for each species. In FIA RM, a single age tree is sampled for age increment coring for each species and broad diameter class present on a plot. In FIA SR and NR, age is only measured for site trees. In certain situations, cores from site trees can be used for stand age.

Species data is recorded for all live tally trees within the radius of the subplots. These are grouped for reporting purposes into 24 softwood species groups and 24 hardwood species groups, each with their own unique code in FIADB (see FIADB user guide for group codes and their associated names). Diameter measurements are recorded for all tally trees within subplots as follows: for timber species, diameter at breast height (d.b.h.), and for woodland species, diameter at the root collar (d.r.c.). Trees with diameters > 12.7 cm are recorded within subplots, while saplings (2.5 cm $\leq$ diameter $<$ 12.7 cm) are recorded only within microplots. FIA seedling data were not used in this study.

For this study, we queried the FIADB to select for live tree records that had nonnull records for age, DBH and species. Additional variables included FIA total height (HT) which the FIA user guide describes as collected for all live and standing dead tally trees $\geq$ 2.54 cm d.b.h./d.r.c.). Height measurement methods vary (i.e., field measured, visually estimated, and modeled) and are described in the height method code (HTCD). For this study, only field measured height was included. Prior to plots collected with protocols in FIA field manual 7.0 (October 2017), sapling height was not a national core variable, meaning FIA regions could opt in or out of the protocol, and minimum heights for measurements were 1.524 m (5 ft) for timber species and 0.3048 m (1 ft) for

[1] See the full master tree species list here: https://usfs-public.app.box.com/v/FIA-TreeSpeciesList

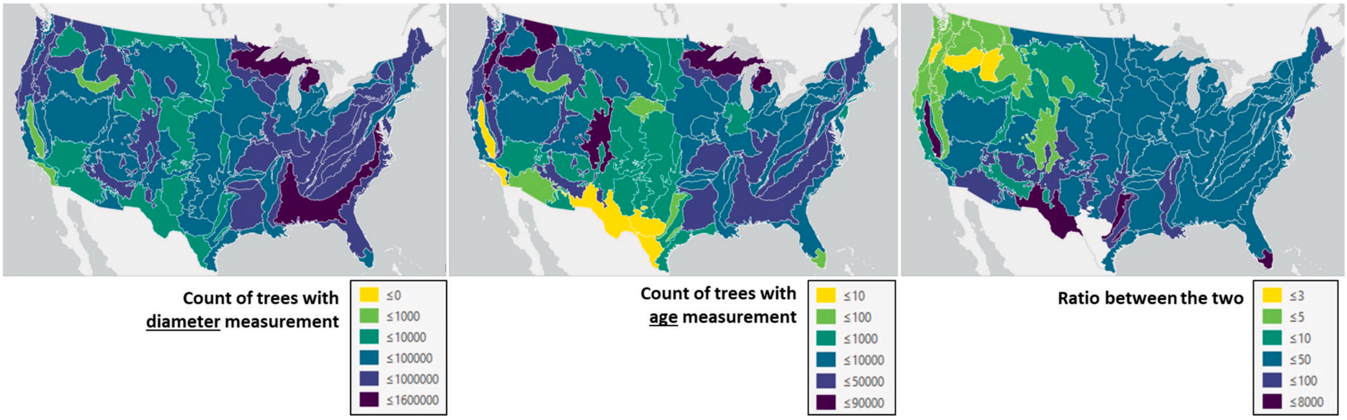

Fig. 1. Count of FIA sampled trees that have diameter measurements (left), age measurements (middle), and the ratio between the two (right) at EPA level 3 ecoregion scale.

woodland species. After our selection query, for tree records with age measurements, the percentage with reported height is 75–100 %. See Fig. 2 for data availability in each mapping zone.

Topographic variables including slope, elevation, and aspect, and geographic variables such as the approximate plot coordinates were also extracted and used. Elevation, slope, and aspect are collected at the subplot level with slope and aspect reported for each condition class on the plot. Values from the dominant condition class (i.e., condition class with highest proportion of the plot) were used in the modeling (done at the plot level). Publicly available plot location coordinates were used (latitudes and longitudes in decimal degrees using NAD83 datum). The publicly available coordinates are within + /- 804.67–1609.34 m (0.5–1 mile) from the actual location, within 804.67 m (0.5 miles) for most plots and up to 1609.34 m (1.0 mile) on a small subset of them, Private plot locations could have additional uncertainties caused by swapping plot coordinates for up to 20 percent of the plots with another similar private plot within the same county, though the only difference will occur when users want to subdivide a county using a polygon. Even then, results will be similar because swapped plots are chosen to be similar based on attributes such as forest type, stand-size class, latitude, and longitude (Burrill et al., 2023).

2.2. *Climate data*

The PRISM (Parameter-elevation Regressions on Independent Slopes Model) climate dataset developed by the PRISM Climate Group at Oregon State University, is designed to provide detailed high-resolution spatial climate data (Daly et al., 2000). PRISM used climatological gradients and patterns in conjunction with geographical and topographical information to interpolate climate data from weather stations to other locations. The 800 m 30-year (1981–2010) normals dataset used in this study describes average annual conditions for seven climate element variables that can affect the tree growth: precipitation (ppt), minimum temperature (tmin), maximum temperature (tmax), mean temperature (tmean), mean dew point (tdmean), minimum vapor pressure deficit (vpdmin), and maximum vapor pressure deficit (vpdmax). The climate variables were extracted at the approximate plot locations to determine the climate conditions.

2.3. *Tree age modeling*

2.3.1. *Modeling framework*

The modeling unit followed the mapping zones partitioned for the

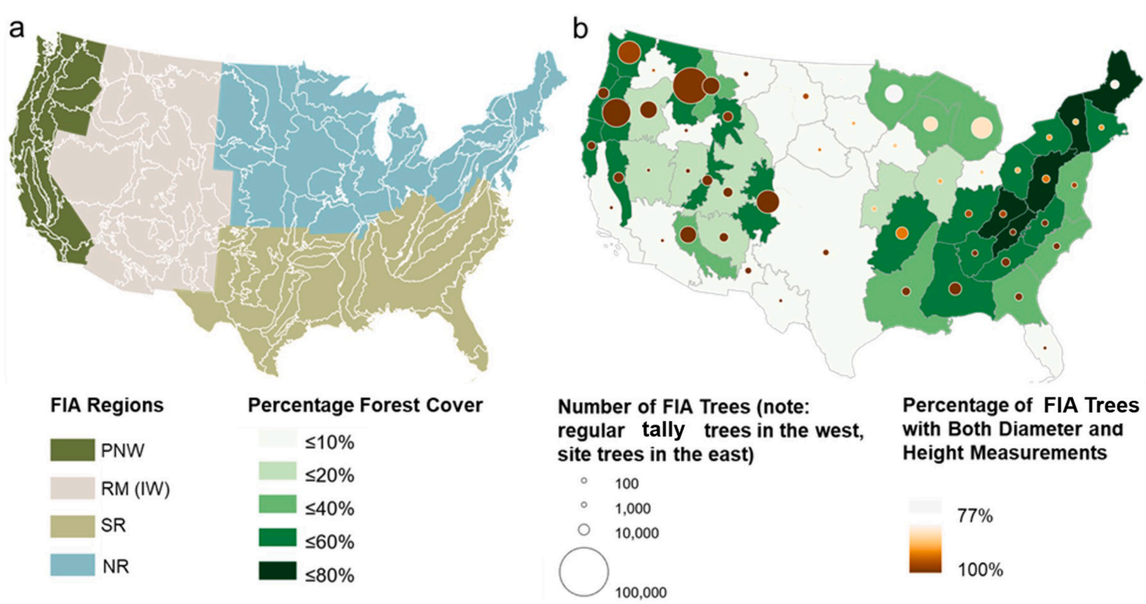

Fig. 2. Map of EPA level 3 ecoregion boundaries (white lines in a), and mapping zones boundaries (gray lines in b). The colors denote the FIA region, forest cover calculated from NLCD, and percentage of trees with both diameter and height measurements. The size of circles maps available FIA tree (regular tally trees in the west, and site trees in the east) data counts in each mapping zone.

National Land Cover Dataset (NLCD) 2000, which segmented the United States into 66 areas that are relatively homogenous in terms of ecological and climatic characteristics. The mapping zones were initially based on ecoregions defined by (Omernik, 1987), then the boundaries were modified to ensure homogeneity in land cover types, ecological conditions, and climatic features within each zone (e.g., large ecoregions that have wide latitude or longitude ranges were divided into smaller units, small ecoregions with similar land cover types and climatic features were combined into larger units, etc.). For age modeling, the mapping zones that have too few reference data to train an individual model were combined with nearby mapping zones (Fig. 2).

The modeling approach used in this study was built upon the idea that tree age can be estimated using the relationship between tree age its size, species and site characteristics (i.e., topographic, geographic, and climate variables).

$$age = f(size, species, topographic, geographic, climate\ variables) \quad (1)$$

See Table 1 for the complete list of variables included in each group.

To apply the approach in Eq. 1 to national wide data, the model was slightly modified depending on the variations in availability of variables collected by FIA regional units through time (see 2.1). For most mapping zones in the PNW and RM regions, most trees (>99 %) have both diameter and height measurements, only less than 1 % of trees have only diameter but no height recorded from the field. Mapping zones where there are 1–10 % of selected tree records without height measurements are near Columbia Plateau, Northern Rockies, Idaho Batholith, and Middle Rockies. In these PNW and RM zones, for trees with height measurements, Random Forest (RF) models were developed using all the variables in Table 1 as the predictor variables. For trees without height measurements, all variable groups except height were used to build the RF model.

Within each mapping zone that overlaps the FIA SR and NR regions, multiple sets of models were needed for each zone. In these areas, all FIA age measurements come from site tree samples, which are chosen to represent growing conditions, not the variety of ages in the stand. Due to the size guides for site trees, all site trees have age, diameter, and height measurements through time. However, at most, only 75 % of additional trees surveyed in the two regions have height measurements (see changes to FIA core variables described in 2.1). Since RF models are not able to extrapolate beyond the range of training data, we also trained two ordinary least squares (OLS) regression models, one for trees with height, one for trees without height. The OLS models were used to estimate the age of trees with DBH smaller than 12.7 cm through extrapolation. While the predictions derived this way typically had larger uncertainties than OLS predictions within the value range of training data, this extrapolation method provided a viable approach for estimating the age of trees with DBH less than 12.7 cm. A summary of the various models developed for each of the four FIA regions is provided in Table 2.

2.3.2. Accuracy assessment

In assessing the model's performance across various mapping zones, a 10-fold cross-validation approach was employed. This entailed randomly dividing the reference plot samples into ten distinct subsets. Subsequently, ten separate models were constructed, each trained on nine subsets and validated against the one remaining subset. This process ensured that each subset was utilized exactly once as a validation set. The validation outcomes from all ten sets were then aggregated to yield an overall estimate of the model's efficacy. Cross-validation helps in identifying models that may perform well on the training data but poorly on unseen data. By using multiple training and testing sets, it ensures that the model's performance is tested across different subsets of data. Model performance was quantified using the coefficient of determination (R^2, as per Eq. 8) and the Root Mean Square Error (rRMSE, as delineated in Eq. 9). Mean R^2 and mean RMSE were calculated from all 10 folds to provide an overall performance metric for the model. These mean values represent the average explanatory power of the model across different subsets of data. The evaluation was performed for all RF and OLS model sets in Table 2.

In addition to the assessment for the zone-based models, we also assessed the performance of a single set of nationwide models (cross-validated by all available CONUS data), and region-based models (cross-validated results pulled from four FIA regional based models), and mapping zone-based models (cross-validated results pulled from individual zone-based models), to evaluate the efficiency difference of a large generic model and more locally calibrated models in tree age estimation.

Table 1
List of tree and site variables used in age modeling.

Variable Groups	Data Source	Variable (Variable name in FIADB if applicable)
Tree Size	FIA TREE	Diameter at Breast Height (DBH, DIA in FIADB), Height (ACTUALHT)
Tree Species	FIA TREE	Species Group (SPGPCD)
Topographic	FIA PLOT	Elevation, Slope, Aspect
Geographic	FIA PLOT	Latitude (LAT), Longitude (LON)
Climate	PRISM	Precipitation, Minimum/Maximum/Mean Temperature, Mean Dew Point, Minimum/Maximum Vapor Pressure Deficit

Table 2
Tree age modeling framework. In the west, each RF zone model was trained using all sampled tree records (with and w/o height measurements). For the mapping zones in the FIA SR and NR, OLS regression models were developed to extrapolate the age prediction for small trees outside the range of training data.

	With Height		Without Height	
PNW/RM (Regular Tally Trees)	RF age = ***f*** (diameter, <u>height</u>, species group, topographic, geographic, and climatic variables)		RF age = ***f*** (diameter, species group, topographic, geographic, and climatic variables)	
SR/NR (Site Trees)	RF age = ***f*** (diameter, <u>height</u>, species group, topographic, geographic, and climatic variables)	OLS age = ***f*** (diameter, <u>height</u>, species group, topographic, geographic, and climatic variables)	RF age = ***f*** (diameter, species group, topographic, geographic, and climatic variables)	OLS age = ***f*** (diameter, species group, topographic, geographic, and climatic variables)

2.3.3. Bias correction

It is common for RF and OLS models to slightly overestimate the low end and substantially underestimate the high end of predictions. To correct such bias, a median adjustment approach was adopted and updated from (Huang et al., 2014), where the medians of reference ages were binned with 3-year intervals and used to calculate then the medians of the predicted ages within those reference data age bins. If the tree count within a bin was less than 0.1 % of all data, that bin was combined with the bin before. After determining the bin medians of both reference and predicted age, 2nd order polynomial functions were fitted through the medians, then the fitted functions were applied to the original model predictions to get the bias corrected age. Where the corrected age for the low-end small ages was corrected to below zero, these negative values were forced to a minimum age of 1 year. While on the high end, because the tree count is small in the last few bins, they were combined to the younger bins. The actual tree age in the last bin could be much higher than the bins median value. The polynomial increase may bring the corrected values of trees in the older bins extremely high. To mitigate the high values, the corrected value's high end was capped to 85th percentile of the last bin. To keep the distributions of corrected values consistent with the reference ages, the average of prediction and bias corrected value was used as the final corrected value.

The bias of the initial model predictions and averaged estimates were calculated to test the effectiveness of bias correction. The bias was compared separately for the young trees that were overestimated and older trees that were underestimated. To categorize the predictions, a linear regression was fitted to the reference-prediction data, then the intersection of the fitted line and the 1:1 line was used as the threshold. Trees younger than the intersect reference age were grouped into the overestimation trees, and trees older than the intersect age were grouped as the underestimation trees. The bias for each group in all the modeling zones was calculated using the following formula,

$$ME = \frac{1}{n}\sum_{i=1}^{n}(\hat{y}_i - y_i) \tag{2}$$

Where $\hat{y}_i$ are the predicted or averaged values, and y_i are the reference age. A positive value indicates a tendency to overestimate, while a negative value indicates a tendency to underestimate.

2.4. Tree age distribution assessment

2.4.1. Age estimation for "All" trees across CONUS

From the previous steps, we derived individual tree-level age estimates for all live FIA-sampled trees. To calculate year-specific population estimates, we followed procedures modified from FIA's Population Estimation Guide (Westfall et al., 2022). FIA evaluations, which link plot-level data to stratification and population information, were used to select appropriate plots for estimating the number of live trees ($\geq$2.54 cm d.b.h) on forest land for the 2015 inventory year across the 48 CONUS states. After selecting the evaluations and linking the relevant tables, tree-level age estimates were grouped into age classes, multiplied by expansion factors, and aggregated or disaggregated based on population strata. This process provided species-level population estimates by age group. Details on the tables and linkages used are provided in Supplement Table S1.

2.4.2. Quantification of tree age distribution

Based on the tree age data derived above, tree age distribution is quantified in three ways. First, tree age histograms are analyzed at the national, sub-national (i.e., eastern vs western US), and ecoregion levels. The level 3 ecoregions are used in this study because the number of ecoregions and the size of the individual ecoregions are deemed more suitable for this analysis than higher or lower-level ecoregions. At the ecoregion level, median tree ages are calculated as the aggregate statistic to reduce effects of outliers. Finally, the oldest trees in each ecoregion are examined to evaluate how their ages differ by species and ecoregion. Ecoregions with low median tree ages are dominated by young trees that have not reached their peak carbon sequestration potential yet, whereas regions having more old stands should have higher median tree ages. In eastern US where much of the original forests were cleared for agricultural uses in the past, the age of the oldest trees is likely to be more determined by past land use history. In the western US where intensive land use has a smaller footprint, the age of the oldest trees may serve as an indicator of the resilience of some species to climatic variations, natural disturbance regimes and the longevity of those trees (Lindenmayer and Laurance, 2017; Piovesan and Biondi, 2021).

3. Results

3.1. Performance of the tree age model approach

3.1.1. Improvements from the zone-based modeling framework

The mapping zones provided a robust framework for modeling relationships between tree age and the predictor variables. Although the RF is capable of modeling complex, nonlinear relationships, age values predicted by a set of models where each model was developed for an individual zone or zone group were substantially more accurate than those predicted by models developed over larger areas (Fig. 3). At the CONUS level, predictions by the zone-based models had an R^2 of 0.75 and an RMSE of 26.99, while predictions by the FIA region-based models had slightly poorer performance with a smaller R^2 of 0.72 and higher RMSE of 29.00. Predictions by a single model developed for CONUS had the lowest R^2 of 0.57 and highest RMSE of 36.05. Given these demonstrated advantages of the zone-based modeling framework, all results presented in the remaining sections of this chapter were produced using this modeling framework.

3.1.2. Complementarity of different age models

The modeling approach consisted of RF models developed with and without using height as predictor variables in order to produce robust age estimates for all trees above 2.54 cm d.b.h, accounting for the fact that sapling height was not always measured populated consistently across all FIA regions (Table 2). While the models that included height as a predictor variable performed slightly better than those that did not use height as a predictor variable (see Supplement Fig S1, Fig S2, Fig S3, and Fig S4) in many zones, the two groups of models had essentially the same accuracies as indicated by their R^2 and RMSE values in other zones. This indicates that together, the RF models could produce robust age estimates regardless of whether the reference tree data had height measurements or not. As expected, the OLS models developed for the zones located in eastern US were less accurate than the RF models. However, the OLS models were only applied to saplings (trees with DBH less than 12.7 cm). The age of trees with DBH greater than 12.7 cm were predicted using the RF models.

3.1.3. Effectiveness of Bias correction through median adjustment

Models generated with different spatial subsets of reference data all show similar tends of biases - slight overestimation on the low end and substantial underestimation for the trees older than 200 years. Consequently, bias correction was necessary to improve the precision of the age estimates. Fig. 4 shows examples of the median adjustment approach and results in two zones. Polynomial functions were able to capture some of the relationships between the predicted and reference age (Fig. 4 second column). After applying these functions, the bias was eliminated in the corrected values (Fig. 4 third column), where the fitted line between corrected values and reference values overlapped with the 1:1 line. After the correction, although a slight increase was seen in RMSE, the overall model performance (evaluated by RMSE in conjunction with R^2) was not largely influenced. However, directly using polynomial functions may lead to different tree age distribution from the reference dataset, because the polynomial functions produces negative values, which were forced to 1 in the correction, and also because the polynomial increasing brought the corrected values of high-end values to extremely high levels, which were capped to 85 percentile of ages in the last bin, (see the side histograms in Fig. 4 third column of zone 1 for an example of such alterations in distribution). To ameliorate these impacts on the tails of the predictions, the average of prediction and bias corrected value was used as the final corrected value (Fig. 4 fourth column). With this solution, the effectiveness of bias correction was not as evident as the original corrections from the polynomial functions, but the distributions of corrected values were kept consistent with the reference ages.

From the comparison between biases before and after the averaging correction (Fig. 5), we can see for most zones, the bias after correction is closer to 0 than the initial model predictions. Tests proved the method was effective in reducing the bias in both directions (i.e., underestimation and overestimation).

3.1.4. Accuracies of the age estimates after Bias correction

We produced Maps of R^2 and relative RMSE for the age models (Fig. 6) to show the accuracy of final age estimation in each zone. For

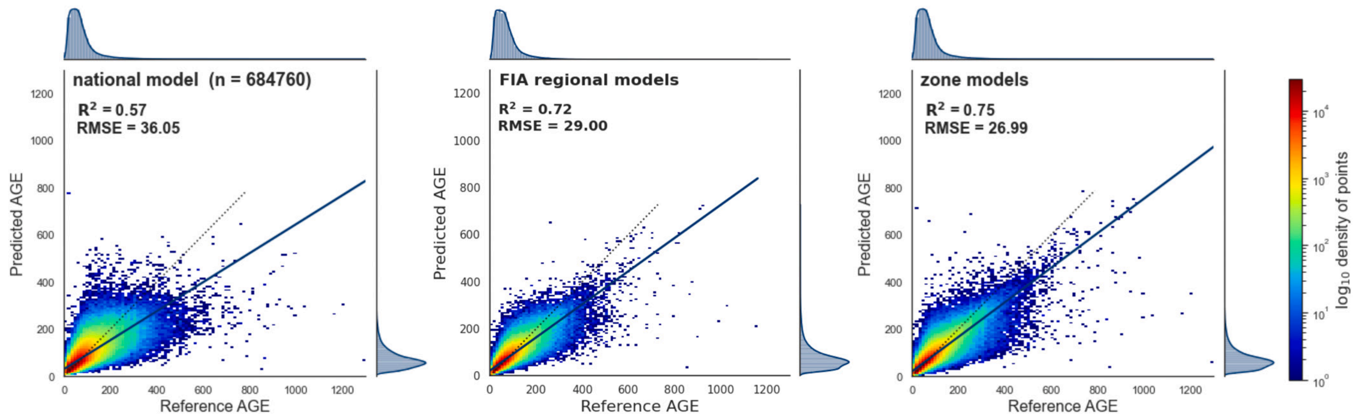

Fig. 3. Comparison of the validation results of a single national model, individual FIA regional, and zone-based models. Left: cross validation of the single national model using set aside reference plots not used in model calibration; middle: scatterplot of cross validation results pulled from FIA regional models; right: scatterplot of cross validation results pulled from zone-based models. The dashed lines are the 1:1 line. The blue solid line is the fitted line between reference and predicted values.

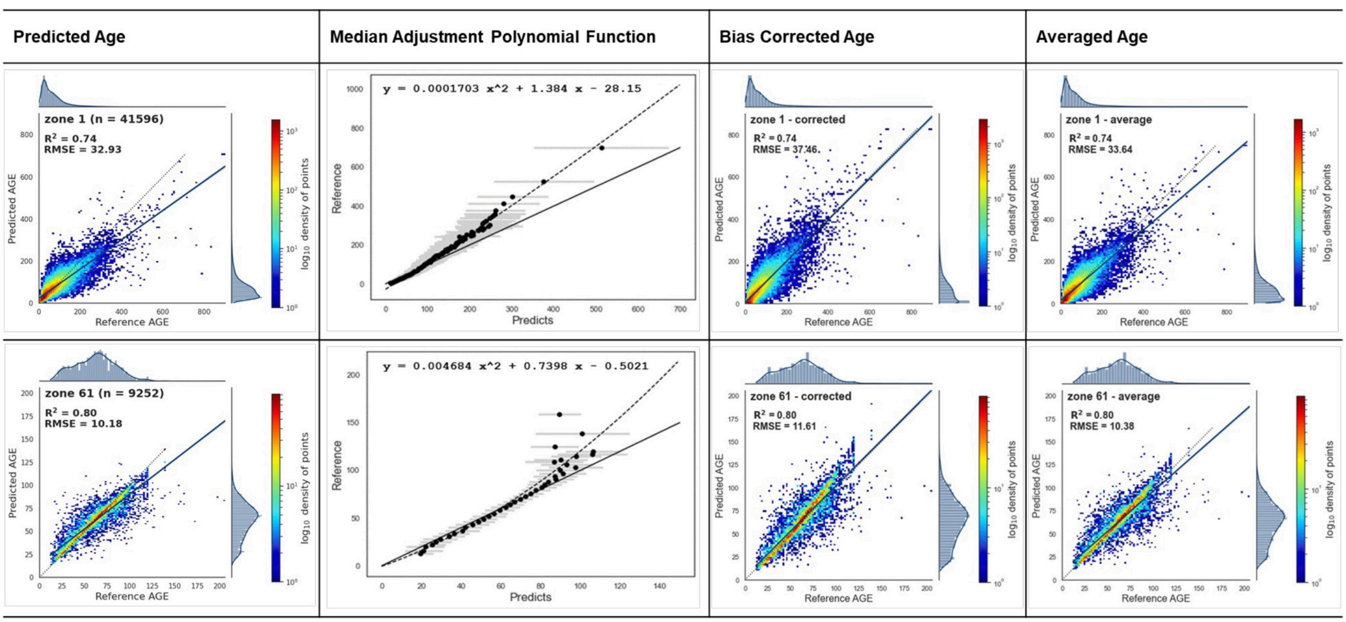

Fig. 4. Examples of using the median adjustment polynomial functions to correct model prediction bias in mapping zone 1 and 61. First column: original model predictions; second column: the fitted median adjustment polynomial function and curve. The curve was fitted through the medians of 3-year bins; third column: corrected age after applying fitted function to the original predictions. The correction's high end was capped to 85th percentile of the last bin, the negative values on the low end, if any, was forced to 1 year old; fourth column: the average between prediction and corrected age.

trees with both diameter and height measurements, the R^2 ranged from 0.51 to 0.87 (Fig. 6 A-1), and the relative RMSE ranged from 0.14 to 0.49 (Fig. 6 A-2). The mapping zones in the middle of the country had the lowest R^2s and relatively high rRMSEs. Most of these zones had low forest cover, for example, zone 26 is located near Chihuahuan Deserts, which has less than 1 % forest cover; zone 29 and 30, located near the central areas of Northwestern Greater Plain, has roughly 6 % forest cover. Models over the coast zones also show higher rRMSE possible due to the wide range of tree ages in those areas. The rRMSE of older age trees can be particularly high since the mean was used as the denominator in calculations. Highest R^2 and lowest rRMSE were seen in the eastern zone models. Fig. 6 B-1 and B-2 are the R^2 and rRMSE maps for tree ages estimated with diameter measurements only. The accuracy of these models was overall similar to models including height as a predictor in the western zones. In eastern zones such as zones 39, and 59, the R^2s of these models were lower than models including height as a predictor, and the rRMSEs were higher. The zone model's performances show that the modeling method can be applied to the whole country and the accuracies were higher or at least comparable to methods in published studies focusing on smaller sites (1).

3.2. Tree age distribution assessment

3.2.1. Tree age distributions at the national scales

At the national scale, the age of trees (DBH > 12.7 cm) roughly follows a log-normal distribution, with the age group 54–70 having the highest percentage of trees (Fig. 7). The tree percentage decreases slightly faster along the right tail than along the left tail. This slight asymmetry is likely due to a more obvious asymmetry in the age histogram of trees in eastern US, which also peaks at the 54–70 age group. To the left side of the peak, the percentages of trees in age groups between 25 and 54 years are also high, but the slope of percentages in older age bins decrease sharply after the peak. In the modeled eastern tree age distributions, there are few trees older than 148 years. The Western US modeled tree age histogram exhibits a more typical log-normal distribution, with nearly 60 % of trees falling in the age bins from 54 to 148.

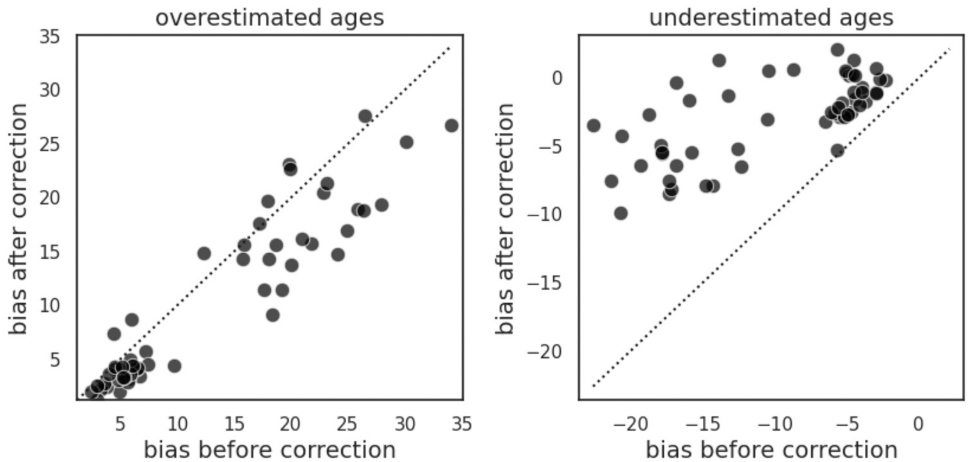

Fig. 5. Comparison of bias before and after the median adjustment and average process. Each dot represents the bias of one modeling zone. Left: bias comparison for tree ages that were overestimated in the initial model prediction. Right: bias comparison for tree ages that were underestimated in the initial model prediction.

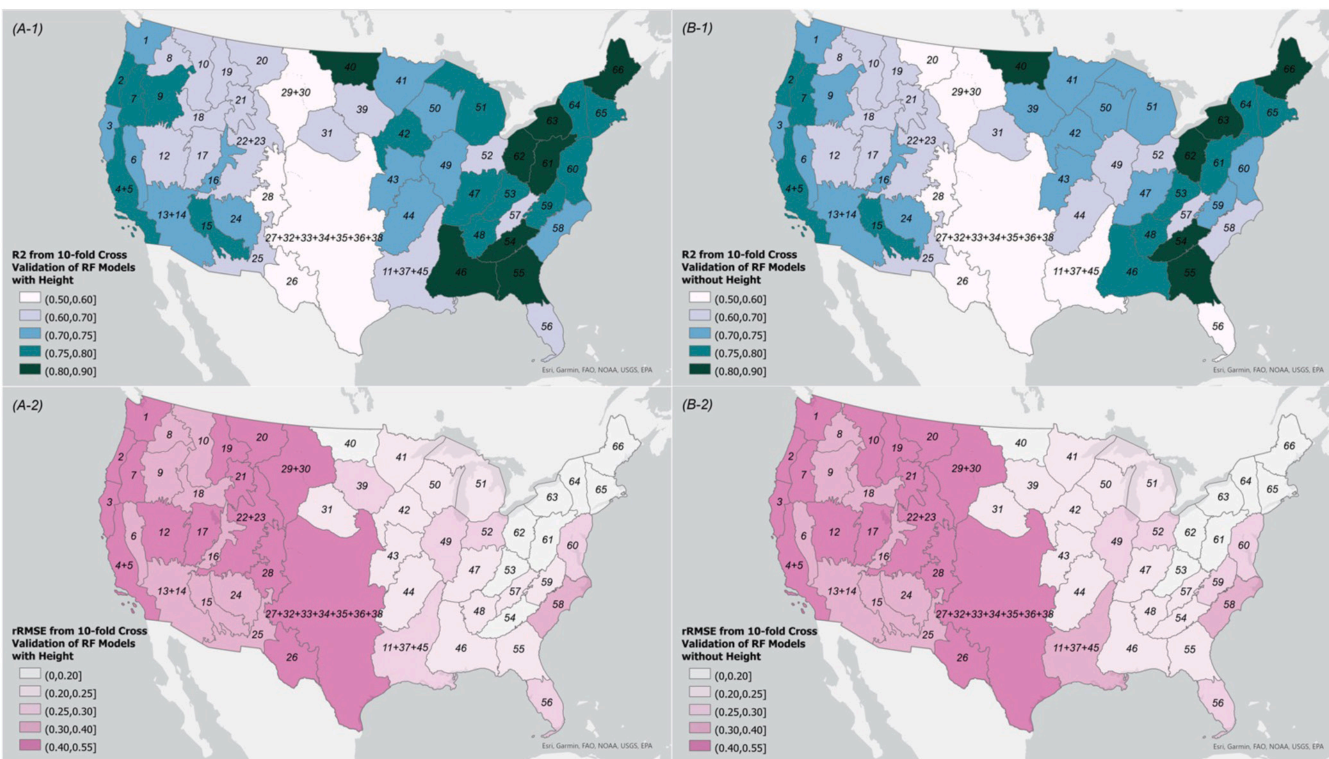

Fig. 6. Maps of R^2 and relative RMSE for the age models including (A-1, A-2) and not including (B-1, B-2) height as a predictor variable.

The modeled age data show western zones having substantially more old trees than the eastern zones. More than 20 percent of the trees are older than 148 years.

3.2.2. *Tree age structure patterns at ecoregion scales*

At sub-national scales, tree age distribution exhibited substantial regional variations. To reveal the regional patterns of tree age structure, the number of trees binned at a 5-year interval was plotted for each of the level 3 ecoregions in (see supplement Fig. S5). Fig. 8 shows a few representative age structures of selected ecoregions. The difference in tree age structure is the result of a combination of factors, including climatic conditions, elevation and topography, soil types and quality, disturbance regimes, species adaptations and diversity, etc.

Many ecoregions in the west have an overall tree age structure similar to that of Cascades or Eastern Cascades Slopes and Foothills, where the age of highest peak in tree age frequencies is after 50 years old, then the tree count gradually decreases as age increases. Due to variations in species, disturbance history, and other factors, the distributions of ages per ecosystem could be different. In most ecoregions in the east, the tree age structure is similar to the pattern observed in Blue Ridge and Southwestern Appalachians, where there is consistent frequence of trees from 20 to 80 years old, then a steep drop in the frequency of trees between the ages of 80–120 years.

3.2.3. *Age of the average trees*

As with the tree age distributions, the age of average trees also exhibited substantial variations among the ecoregions. Fig. 9 shows that ecoregions with higher median tree ages occur in predominantly arid to

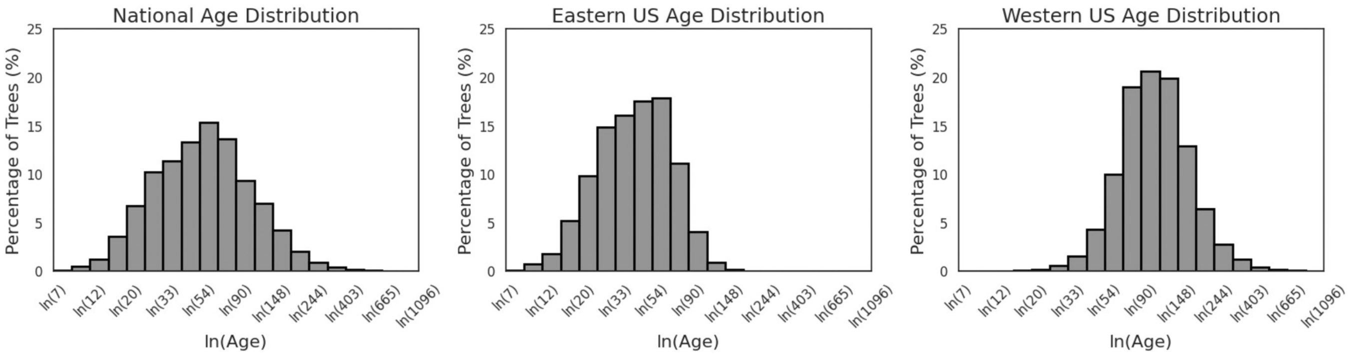

Fig. 7. Tree age distribution of national, eastern and western forests in 2015. x-axis: natural logarithm of tree age (range: 2–7), labeled by the actual age: 7–1096. y-axis: percentage of tree population in each age group in 2015. Note: seedlings and saplings were not included.

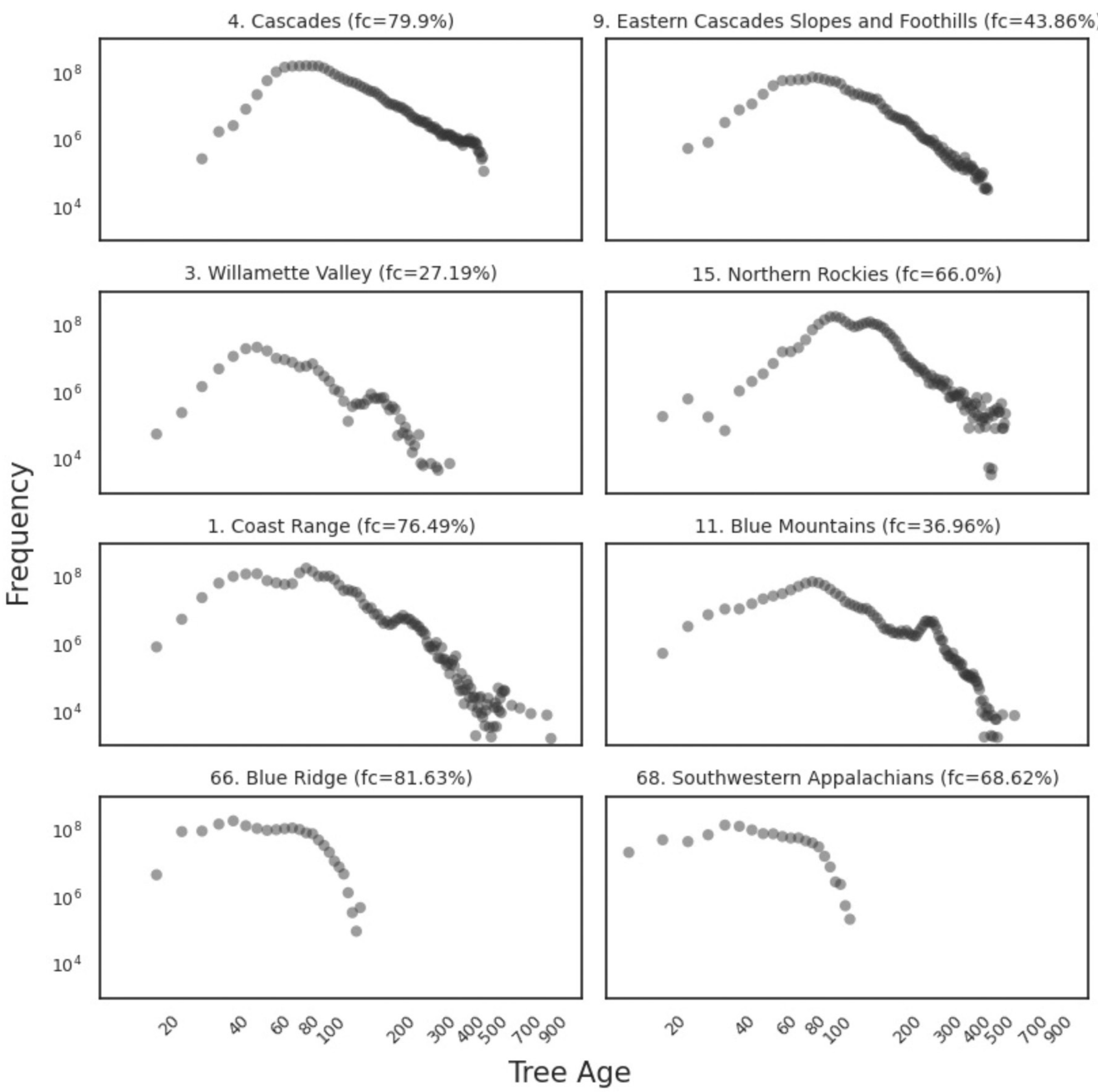

Fig. 8. Tree age distribution in selected US level 3 ecoregions showing different patterns. Both axes are on logarithm base 10 scale. The title of each plot is showing the ecoregion code, ecoregion name, and the percentage forest cover in that ecoregion calculated from NLCD dataset (Note: seedlings and saplings were not included).

semi-arid climate, featuring a relatively dry climate with limited precipitation, such as Colorado Plateau and Arizona/New Mexico Plateau. Such environments tend to support slower-growing tree species that are adapted to dry conditions. Idaho Batholith also has high median tree age, partly due to the granitic soils common to see in this area which can affect the tree growth rates, and also due to mountainous terrain. The

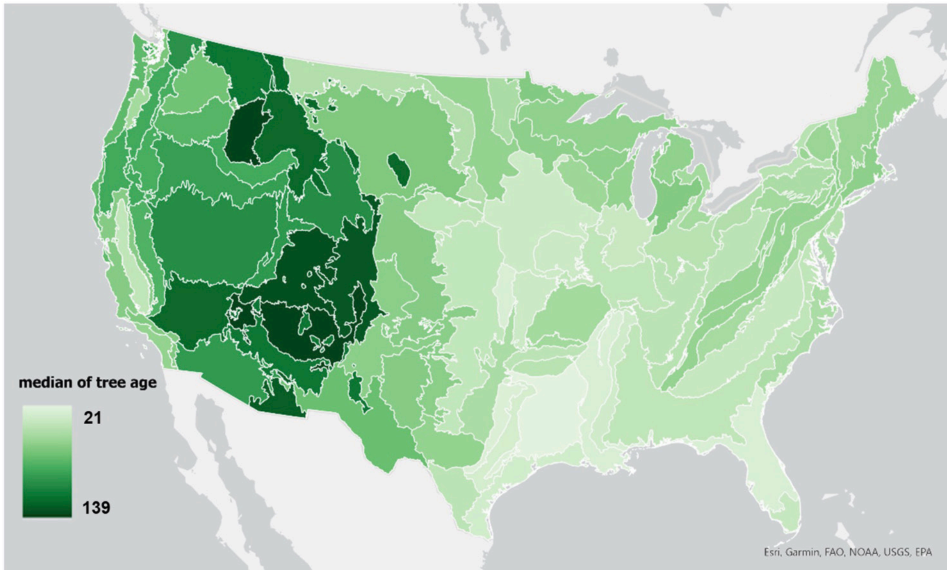

Fig. 9. Map of median tree age in US level 3 ecoregions. Overall, western forests have higher median ages than eastern forests. High median values are in arid/semi-arid areas, such as Colorado Plateau and Arizona/New Mexico Plateau, and mountainous areas such as Idaho Batholith and Southern Rockies (Please see Table S2 for the median tree age values of each ecoregion.).

higher elevations create a range of microclimates including lower temperatures, which contribute to slow growth rate. The mountainous terrain and climate (limited access) can also likely contribute to the reason for high median tree age in the Southern Rockies. In the eastern ecoregions, the median tree ages are mostly 30–40 years. The younger aggregate tree age in the Southern ecoregions, the "wood basket" of the nation (Oswalt et al., 2019), is clearly affected by agriculture, forestry, and other land uses (AFOLU) as many southeast ecoregions are dominated by conifers and conifers species generally have higher longevity (Biondi et al., 2023). The history of AFOLU has, in aggregate, had a clear impact on the younger age of eastern forests. Disturbance regimes also impact tree ages, but less so at these aggregated spatial scales, since disturbance is by nature usually highly localized in space and time. Please see Table S2 for the median tree age values of each ecoregion.

3.2.4. *The age of the oldest trees*

Older trees play a particularly significant role in forest ecosystems. They provide a wide range of ecological functions, many of which could not be provided by younger trees (Lindenmayer and Laurance, 2017). While the term "old trees" suggests a definition based on age, practically

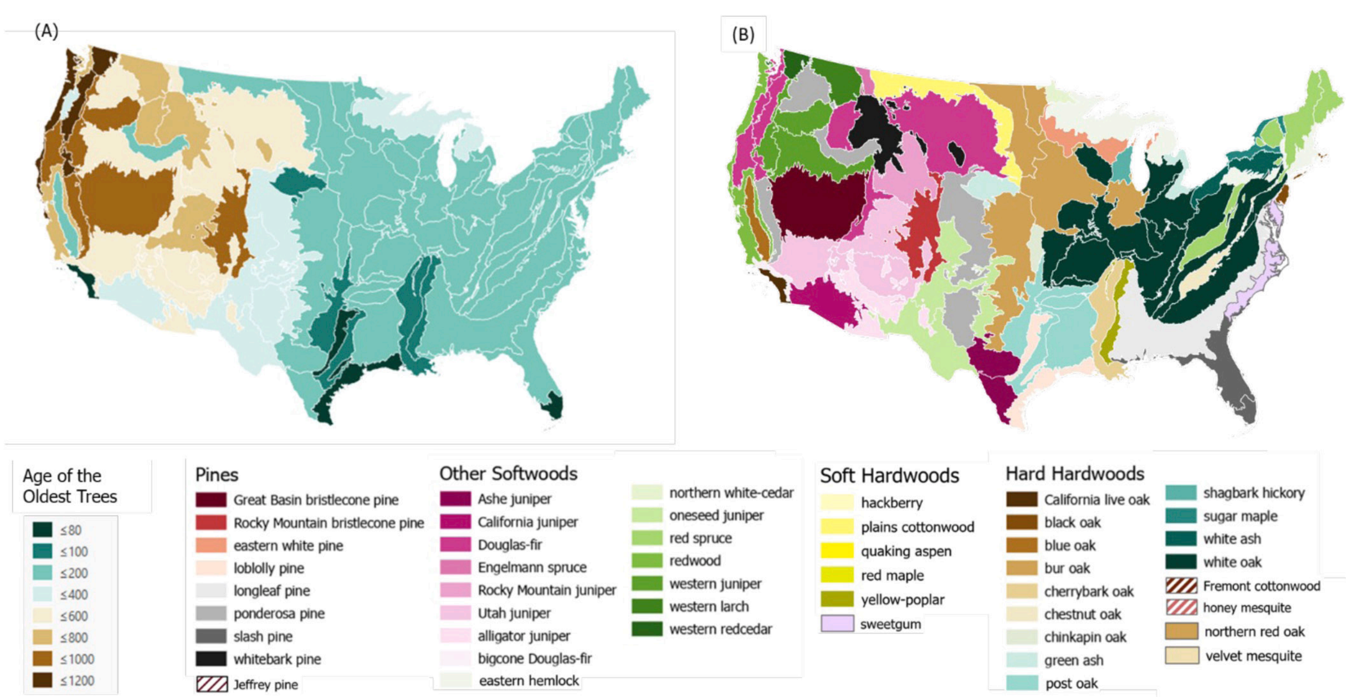

Fig. 10. Age of the oldest living trees (A) and the species of the oldest living trees (B) in each ecoregion. We conservatively define the age of the oldest tree within a study domain as the median of the 9 oldest trees in that domain. Please see Table S2 for the detailed listing of oldest tree age values of each ecoregion, and their species information.

speaking this is challenging to prove because individual tree age data is very difficult to acquire (Gray et al., 2023). The age data modeled through this study provides an opportunity to explore predictions of the old trees across the US. This section focuses on the age of the oldest tree predictions, which may still be shaped by past disturbance and/or land use history. But can offer a window into the questions of species longevity (Piovesan and Biondi, 2021). The specific questions posed of the predictions in this section include: How old are the oldest trees across the country? What are the species types of those oldest trees? And to what extent does the age of the oldest trees of the same species vary across the landscape?

Given that the age estimate derived through this study for each individual tree may have unknowable uncertainties arising from the modeling approach as well as the uncertainties in the input data sources, in this analysis we define the age of the oldest tree within a study domain as the median of the 9 oldest trees in that domain. Here a study domain could include all trees or just the trees of a particular species or species group within an ecoregion. Fig. 10 shows the age of the oldest study domain trees varies substantially across the ecoregions (Fig. 10A). In ecoregions in the northwest, such as Coast Range, Cascades and North Cascades, the oldest study domain trees were predicted to be more than 1000 years old in inventory year 2015. The species of the oldest trees (Fig. 10B) in these three ecoregions are redwood, Douglas fir, and western redcedar. Predictions of very old trees (>800 years) can also be found in arid/semi-arid regions, the study domain species of great basin bristlecone pine, ponderosa pine, and rocky mountain bristlecone pine. These species tend to grow slowly, exhibit high longevity, and grow in areas with (generally) less intensive logging and agricultural land use compared to more fertile and accessible regions, potentially allowing many forest areas to mature without significant human-induced disruption. In the east, the oldest trees in most ecoregions were between 100 and 200 years old. The most common species of these eastern old study domain trees include white oak, bur oak, post oak, red spruce, and longleaf pine. Please see Table S2 for the detailed listing of oldest tree age values of each ecoregion, and their species information.

4. Discussion

Tree age information at the individual tree, stand and population levels is a critical component in various fields, from ecology and climate science to forestry management and urban planning. Tree longevity offers insights into the health, dynamics, and history of both individual trees and forest ecosystems at large. Compared to classic dendrochronology methods, modeling based on the tree age-size relationship can reduce data collection costs, stress on trees, and can be applicable to larger scales.

The tree age dataset presented in this study was derived from models that use individual FIA measurements (tree diameter, height, and species) along with additional topographic, climate and other environmental variables as predictors. Zone based models have higher accuracies than models constructed at the regional and national scales, which could indicate the relevance of local conditions to tree growth and the importance of tailoring predictive models to these unique factors. While broad models can also capture the general trends, they might miss complex interplay of factors influencing tree growth at a fine scale, which are crucial for accurate predictions. The approach exhibits higher accuracy in its age predictions than existing studies in many areas and can be applied over large areas. However, there are limitations with the derived dataset. The data is no more precise than the sum of input data uncertainties and those uncertainties may vary across the landscape. The higher availability of tree age samples in FIA data in the west allows for lower uncertainties in the predicted age in those regions. In the eastern states, uncertainties in model results are higher, where age samples are limited to site trees that help determine timber productivity of a location, skewing available age measurements towards larger older timber species, and there is less reference data for saplings (< 12.7 cm d.b.h) for tree sampled before 2017. More sufficient samples that cover more species types and tree sizes will help improve the age estimations.

The observed spatial variations of tree age distribution across the U. S. could be attributed to local growing conditions, climatic variations, disturbance regimes, and/or anthropogenic factors (forest management practices and additional land uses). For example, in the western forests, compared to Cascades, the Willamette Valley has more young trees and less old trees (Fig. 8). One possible reason is that the Willamette Valley has seen more intensive land use changes due to agriculture and urban development, which can lead to younger forest ages or more homogeneous age structures. In ecoregions like Willamette Valley, Northern Rockies, Coast Range and Blue Mountains, there are substantial variations to the number of trees between sequential age groups (small peaks and valleys in the dot series), which could be the results of intensive historical disturbance events. For example, in the Northern Rockies, there is an obvious smaller number of trees at around 110 years old, compared to neighboring age groups. A plausible cause was the Great Fire of 1910, which occurred on August 20–21 in 1910 in North Idaho and Western Montana. It burned an area of 12,100 km^2, equivalent to the size of Connecticut. In the east, the tree age distribution patterns show evidence of historical events such as the European settlement and agricultural abandonment. The impact of European settlement on forest age structure in what is now the United States became more pronounced during the 17th, 18th, and particularly in the 19th centuries, as the population grew (Hessburg and Agee, 2003). One of the primary impacts was widespread deforestation to clear land for agriculture and settlements, which resulted in the loss of large areas of old-growth forest and reduced the overall age, complexity and size of forested areas. In our study results there are few eastern trees ages older than 120 years. In the late 19th century and continuing into the early 20th century, the first major wave of agricultural abandonment, when land previously used for agricultural purposes is left to revert to its natural state, was documented in the Eastern U.S. due to industrialization and westward expansion (Williams, 1982, 1992). The history of agricultural abandonment leading to a significant increase in newly forested areas, which could explain the sudden increase of trees from older than 120 years to between 80 and 100 years in the tree age distribution in ecoregions such as Blue Ridge and Southwestern Appalachians (Fig. 8).

The quantification of tree age distributions not only sheds light on the history of disturbances and land use, the similarities of conditions that are needed for trees to achieve their greatest longevity, the functioning and growth vigor of forest ecosystems and related management questions. Regions dominated by young and middle-aged tree stands have higher future carbon sequestration *potential* than those dominated by mature and old trees. Mature forests and the older trees within them may represent the accumulation and long-term storage of more atmospheric carbon and contribute significantly to biodiversity conservation and water regulation. The endangered spotted owl, for example, prefers old-growth trees as its habitat (North et al., 2017). Old-growth forests often require protection due to the unique roles they play in terrestrial ecosystems. Identifying ancient or old-growth trees and knowing their age can also provide insights into past climatic conditions, disturbance history, and the possibility of revisiting and updating classic ecological theories (Piovesan and Biondi, 2021). It should be noted that current classifications of young, mature, and old-growth stages are mostly applied to stands or forests rather than individual trees, and species specific longevity is certainly a factor (Gray et al., 2023; Pelz et al., 2023; Woodall et al., 2023). The novel scale and large quantities of tree age data derived in this study could be useful in these types of quantitative classifications, including ones that are regional and species specific. Additionally, these tree age data can be combined with tree growth to investigate tree growth patterns at different ages and potentially through time, such as growth rates. These modeled tree ages could also help augment the FIA sample when characterizing stand age in mixed age forest stands, which are notoriously hard to characterize when only a few trees are sampled in a forest stand (Stevens et al., 2016)

5. Conclusion

In this study, a modeling framework was developed to estimate tree age which leverages nationwide USFS FIA data and environmental variables. Results indicate that local models are more accurate than national and regional models for tree age predictions, which underlines the importance of localized data in the modeling of forest variables. The study built 55 zone-based models and assessed their performance with robust cross validation which indicates higher accuracy of these models over existing methods. The modeling framework is transferable to different regions, and with the developed models, age was quantified for every live tree greater than 2.54 cm d.b.h/d.r.c. in the FIADB (over 10 million trees) across the US, which was previously unavailable. This increases the amount of tree age data at the individual tree level almost 22 times compared to what is data available in FIA's database. From individual tree age, the population distributions of tree age were estimated for 2015. The tree age distribution was different from western to eastern US, and across ecoregions. The legacy of historical land use and forest management practices is visible in the eastern forests younger age structures. The older age structures of western forests document a longer history of diverse environmental conditions and less intensive human disturbance. The developed tree age dataset is not only a valuable tool for forest management and conservation efforts but also has potential to enhance our capacity to accurately estimate carbon sequestration in forests. By providing a clearer picture of tree dynamics, the research can support more informed natural resource decision-making, regarding harvesting schedules, reforestation efforts, and overall forest health maintenance.

Contributions

Chengquan Huang and Jiaming Lu conceived the work. Supervised by Chengquan Huang, Jiaming Lu designed and conducted the research, and developed the initial draft of the manuscript. Karen Schleeweis provided improved understanding of FIA field measurements and edited/enhanced the manuscript. All authors contributed to the investigation, reviewed the text, and provided feedback.

CRediT authorship contribution statement

Schleeweis Karen: Writing – review & editing, Investigation. **Zou Zhenhua:** Writing – review & editing, Investigation. **Gong Weishu:** Writing – review & editing, Investigation. **Lu Jiaming:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Huang Chengquan:** Writing – review & editing, Supervision, Investigation, Funding acquisition, 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.2025.122603.

Data availability

The produced tree age dataset is are available at https://zenodo.org/records/14775738

Tree Age Estimation Across the U.S. Using Forest Inventory and Analysis Database (FIADB) (Zenodo)

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