



Continental-scale mapping of forest tree density in North America using remote sensing and deep learning with uncertainty quantification

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ABSTRACT

Accurate, spatially consistent estimates of tree density remain elusive at continental scales, limiting our ability to assess forest structure, carbon stocks, and biodiversity. Existing global assessments have relied on simplified statistical models and sparse, heterogeneous ground data that are insufficient to capture nonlinear ecological interactions and spatial variability. To address these limitations, we integrated more than 600,000 harmonized ground-based forest inventory plots with satellite-derived vegetation indices, climate surfaces, soil properties, and topographic covariates to develop a deep learning framework for high-resolution mapping of tree density across North America. We evaluated four modeling approaches—generalized linear models (GLMs), ridge

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regression (RR), random forest (RF), and a feedforward neural network (FFNN). Among all models tested, the FFNN achieved the highest predictive accuracy (RMSE = 344.8; $R^2 = 39.53\%$), and was used to produce a wall-to-wall tree density map at 3 km resolution for the continent. We estimated that the total number of forest trees with diameter at breast height (DBH) ≥ 10 cm across North America ranges from 339 to 514 billion, substantially lower than the widely cited estimate of 603 billion trees reported by Crowther et al. (2015). When smaller stems were included (no DBH threshold), totals more than doubled, reaching 738 billion to 1.12 trillion trees. We quantified uncertainty using Monte Carlo (MC) Dropout, generating pixel-level error estimates and confidence intervals. Spatial patterns reveal high tree densities in boreal and temperate forests, intermediate densities in mixed broadleaf regions, and relatively low densities in deserts, Mediterranean systems, and tundra. Compared to the global GLM-based benchmark by Crowther et al. (2015), our deep learning framework achieves markedly higher predictive accuracy, aligns more closely with national forest inventory statistics, and provides explicit uncertainty quantification, supporting applications in carbon accounting, biodiversity modeling, and ecosystem monitoring at scales through region specific calibration and validation.

1. Introduction

Accurately estimating tree density is critical for understanding forest health, carbon storage, and biodiversity, as it underpins assessments of forest structure, productivity, and ecological resilience (Crowther et al., 2015; Lausch et al., 2016; Paquette and Messier, 2011). Tree density serves as a fundamental indicator of forest condition and carbon sequestration potential (Bonan, 2008; Potapov et al., 2021) and is increasingly used to model biodiversity patterns and ecosystem function at global scales (Liang et al., 2022; Reichstein et al., 2019). Tree density also serves as a critical input for land use planning, conservation policy, and climate change mitigation strategies (Curtis et al., 2018; Griscom et al., 2017; Lee et al., 2023). Traditionally, field-based forest inventories provide highly reliable estimates of tree density and structure, forming the empirical foundation for forest monitoring and model calibration (Lausch et al., 2016). However, the limited spatial coverage and high logistical costs associated with ground-based measurements pose major constraints for coarse-scale assessments (Potapov et al., 2021; Liang et al., 2022).

Advances in remote sensing and machine learning have substantially improved our capacity to characterize forest structure across broad spatial extents (Dubayah et al., 2022; Reichstein et al., 2019). Although tree density cannot be directly observed from space at continental scales, multisource remote sensing provides complementary constraints on stem abundance through well-established size–density and biomass–structure relationships. Long-term multispectral archives such as Landsat enable detection of canopy dynamics and disturbance histories (Banskota et al., 2014), while Sentinel-2 enhances spatial and temporal resolution for resolving productivity gradients and compositional variability. Synthetic aperture radar (SAR) observations and LiDAR-derived structural metrics provide sensitivity to woody volume, canopy height, and vertical structure, improving inference of forest architecture in high-biomass and cloud-prone regions (Dubayah et al., 2022; Potapov et al., 2021; Shimada et al., 2014). In particular, the Global Ecosystem Dynamics Investigation (GEDI) mission has extended waveform LiDAR measurements of forest height and biomass globally, enabling improved structural characterization across diverse biomes (Dubayah et al., 2022; Potapov et al., 2021).

Translating these diverse structural signals into spatially consistent estimates of tree density requires modeling frameworks capable of linking field observations to high-dimensional environmental predictors. A landmark global assessment by Crowther et al. (2015) integrated forest inventory plots with remotely sensed climatic and edaphic variables using generalized linear models (GLMs) with a negative binomial error structure and log-link function to estimate approximately three trillion trees worldwide. This formulation appropriately accounted for the discrete and over-dispersed nature of tree count data and represented a major advance in global forest quantification. Nevertheless, while the log-link induces nonlinearity on the original scale, the model remains additive and linear in parameters on the logarithmic scale, requiring interactions to be explicitly specified. Ecological theory and

empirical evidence indicate that tree density often exhibits threshold responses and saturation dynamics along hydrothermal gradients, consistent with self-thinning and size–density scaling theory (Reineke, 1933; West et al., 2009; Yoda et al., 1963). In productive systems, additional resource availability frequently manifests as greater individual tree size rather than proportional increases in stem number (Pacala et al., 1996; Searle and Chen, 2017), whereas recruitment in environmentally constrained regions may shift abruptly across moisture or temperature thresholds (Allen et al., 2010; Bonan, 2008). Representing such context-dependent and higher-order interactions across heterogeneous biomes becomes increasingly complex within strictly additive parametric frameworks.

Continental-scale modeling further requires integration of multi-source predictors that are often collinear and interact non-additively. In parametric regression settings, these interactions must be prespecified, and model structure is assumed to be globally consistent across environmental space. Yet ecological responses frequently vary regionally, challenging the assumption of a single stationary functional form at continental scales (Zimmerman and Hoef, 2024).

Building on the global benchmark established by Crowther et al. (2015), subsequent studies have advanced coarse-scale tree-density estimation through spatially explicit modeling and multisource data fusion. At national scales, Barreras et al. (2023) generated wall-to-wall predictions of tree density and height across Mexico by integrating forest inventory plots with Sentinel-2 and climatic covariates using ensemble learning. In dryland ecosystems, Brandt et al. (2020) demonstrated sub-meter individual tree mapping across the West African Sahara and Sahel using high-resolution imagery and deep learning. More recently, biome-scale assessments have modeled boreal forest density patterns across North America using extensive plot compilations (Xu et al., 2025). Collectively, these studies reflect a shift from global empirical extrapolation toward regionally resolved, spatially explicit approaches.

Despite this progress, several limitations constrain continental-scale synthesis. Most existing efforts remain restricted to national or biome-specific domains (Barreras et al., 2023; Brandt et al., 2020; Xu et al., 2025), limiting cross-biome comparability across heterogeneous climatic gradients. Crown-based detection approaches, while effective in open canopies, remain computationally demanding and challenging to operationalize wall-to-wall across structurally diverse landscapes (Brandt et al., 2020; Li et al., 2023). Other large-area efforts rely on heterogeneous inventory networks compiled across countries with differing sampling designs and forest definitions (Crowther et al., 2015; FAO, 2020; Glick et al., 2016). Moreover, relatively few studies quantify pixel-level predictive uncertainty or propagate alternative forest definitions and model-based uncertainty into continental totals (Duncanson et al., 2022; McRoberts et al., 2022; Saarela et al., 2020). Consequently, a pan-continental, uncertainty-aware framework integrating harmonized inventories with multisource remote sensing remains lacking.

Flexible machine learning architectures provide methodological capacity to address these challenges by modeling nonlinear and

interacting environmental controls while integrating high-dimensional optical, SAR, and LiDAR predictors (Belgiu and Drăguț, 2016; Reichstein et al., 2019). Multisensory fusion studies combining GEDI waveform metrics with optical and radar observations have improved large-scale structural attribute estimation (Dubayah et al., 2022; Sothe et al., 2022), yet comparatively few efforts have applied such approaches to harmonized continental forest inventories for tree density estimation with explicit uncertainty quantification.

Here, we develop a continent-wide framework for estimating forest tree density across North America (Canada, the United States, and Mexico). We integrate over 600,000 harmonized forest inventory plots with wall-to-wall environmental covariates derived from Landsat and

Sentinel-2 spectral indices, GEDI waveform metrics, ALOS PALSAR-2 structural signals, and gridded biophysical layers representing productivity, climate, topography, and soils. These predictors are used to train advanced machine learning models and generate 3-km resolution predictions across the continent. Predictions are subsequently scaled using alternative forest-extent datasets to produce continental totals with associated uncertainty bounds. By combining harmonized inventories, multisource data fusion, flexible predictive modeling, and explicit uncertainty propagation, this framework establishes a reproducible benchmark for continental-scale forest monitoring, biodiversity assessment, and carbon accounting.

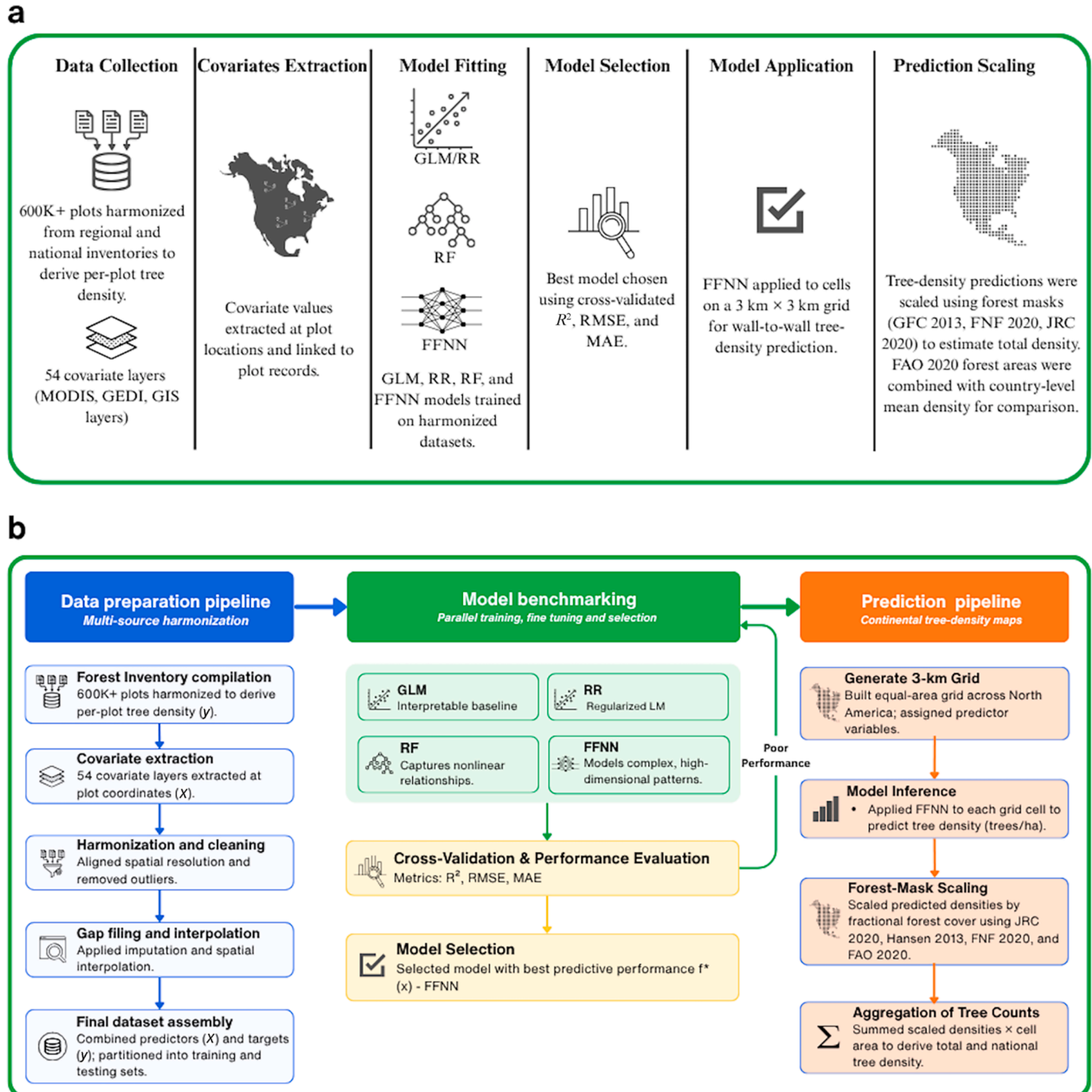


Fig. 1. (a) Methodological workflow for continental-scale tree density estimation. (b) Modular framework of the deep learning and remote sensing pipeline used in this study.

2. Data and methods

2.1. Overview

We implemented a spatial modeling framework that integrates ground-based forest inventories with multi-source remote-sensing and environmental covariates. Plot-level observations were paired with corresponding predictor variables extracted from wall-to-wall spatial layers, producing a harmonized dataset for model training. Multiple statistical and machine-learning algorithms were benchmarked, and the best-performing model was used to generate spatially continuous predictions on a continental grid. These predictions were combined with independent forest-extent datasets to scale local tree-density estimates to regional and national totals, providing a consistent representation of forest structure across North America (Fig. 1).

2.2. Study area

The study area encompasses the entire North America continent, including Canada, the United States, and Mexico, spanning a latitudinal range from approximately 14° N to 83° N and a longitudinal extent from 53° W to 168° W (Fig. 2). This region includes a wide range of forest ecosystems, from tropical dry and moist forests in southern Mexico, to temperate deciduous, coniferous, and mixed forests in the United States, and boreal coniferous forests across Canada and Alaska.

Climatic conditions across the continent vary significantly, encompassing tropical, subtropical, temperate, and subarctic zones. Mean annual temperatures range from below -10°C in northern boreal forests to above 25°C in tropical lowlands, with annual precipitation ranging from less than 400 mm in arid regions to over 2,000 mm in humid coastal zones (Xiao et al., 2024). This broad climatic gradient creates considerable variability in forest structure, productivity, and species composition.

Dominant genera include *Picea*, *Abies*, and *Pinus* in boreal forests, *Quercus*, *Acer*, *Populus*, *Pinus*, and *Pseudotsuga* in temperate regions, and *Bursera*, *Lysiloma*, and *Brosimum* in tropical areas. Biophysical and topographic heterogeneity further contribute to spatial variation in tree density, influencing forest management strategies and carbon dynamics (Seidl et al., 2012).

To delineate areas of active forest cover, we applied the global forest change (GFC) forest mask (Hansen et al., 2013), refined to include only pixels classified as forested in the year 2020. This yielded a continental-scale prediction domain limited to current forested areas, ensuring alignment between ground-based plot data and remote sensing covariates used in modeling.

2.3. Ground-sourced tree density data

The calibration and validation of our model were based on a collection of standardized forest inventory data compiled from regional

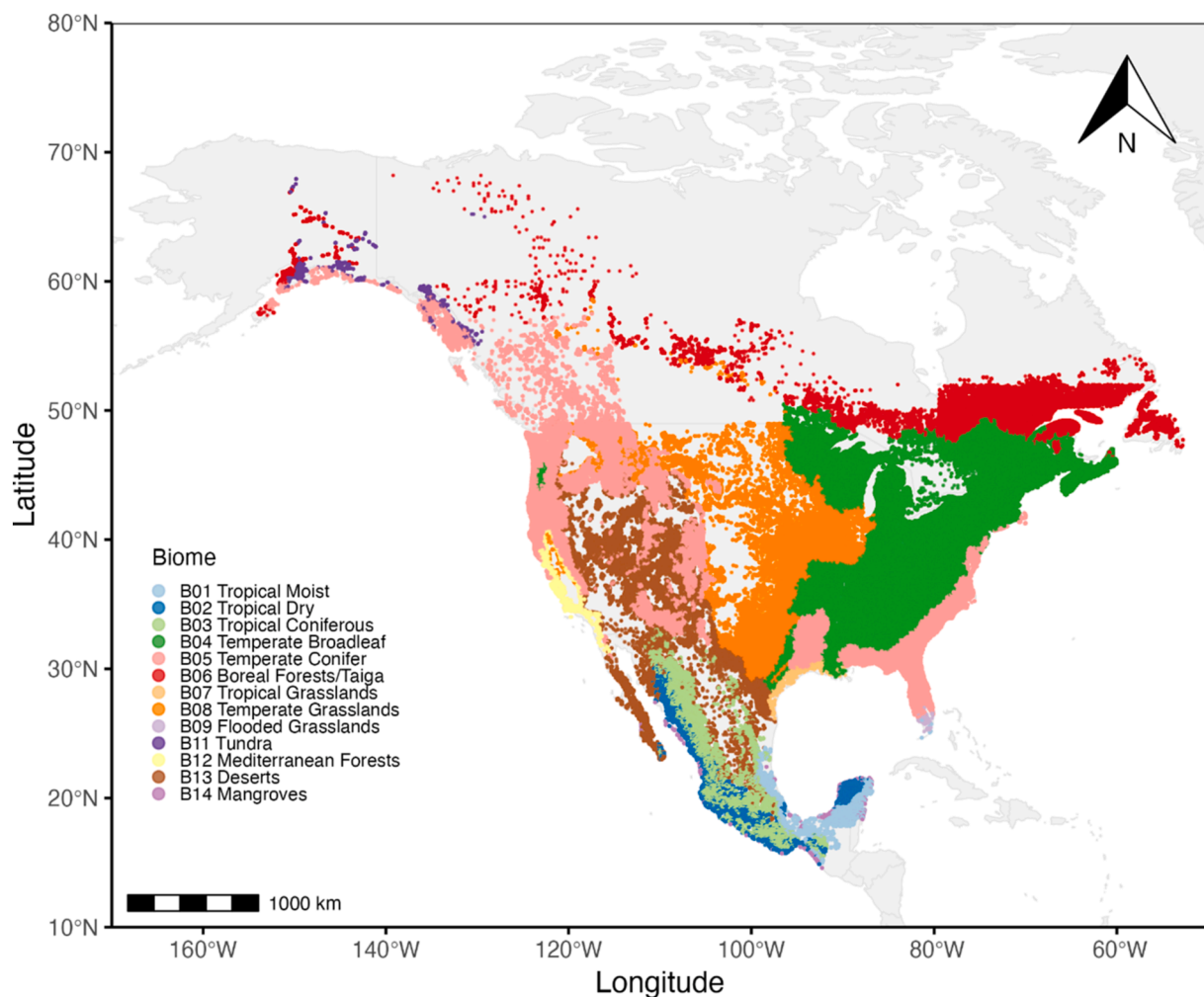


Fig. 2. Geographic distribution of permanent forest inventory plots used for model calibration and validation across North America, classified by biome. Each point represents an individual plot. In regions of high sampling intensity (notably the contiguous USA and southern Canada), multiple plots may appear as a single symbol due to overplotting at this map scale. Apparent clustering reflects true spatial concentration of sampling effort rather than plot footprints or intentional aggregation.

and national sources across the United States, Canada, and Mexico (Table 1). From an initial dataset of 1,262,283 georeferenced permanent sample plots, we retained 616,410 plots for model development (Fig. 2), removing over 50% of the available records to ensure temporal consistency and ecological relevance. Specifically, we removed plots with missing values in either of the covariates and restricted our analysis to inventories collected after the year 2000 to reflect contemporary forest conditions and align with the temporal span of our predictor variables (e.g., remote sensing and climatic variables). The retained plots span a wide range of ecoregions across North America and capture a full spectrum of environmental conditions and tree density patterns for continental-scale modeling.

From each permanent sample plot, tree-level data were aggregated to compute the number of trees per plot. To ensure consistency across plots of varying size and sampling design, observed tree counts were scaled to a per-hectare basis. In line with the widely used ≥ 10 cm diameter at breast height (DBH) threshold, all primary analyses were based on a standardized cutoff across datasets. To assess the impact of this choice, we also implemented the feedforward neural network (FFNN) using each dataset's native DBH threshold. For each of these trees, we integrated plot-level information, such as geographic location and measurement year, with tree-level attributes, including species and DBH. These standardized records were used to quantify forest structure and assess tree density.

To reduce potential measurement error, we excluded plots with implausible total basal area values, which are commonly indicative of data-entry or measurement errors, following criteria established in previous harmonization efforts (Liang et al., 2022). Outlier identification was conducted at the regional inventory level during data compilation, rather than separately by biome. Thresholds were defined within each inventory or region based on local sampling design and ecological context, thereby accounting for differences in forest structure without imposing a uniform biome-wide cutoff. In addition, plots lacking essential attributes (e.g., coordinates, species identification, tree diameter, or measurement date) were removed prior to harmonization. The resulting dataset exhibited a right-skewed distribution of tree density (Fig. 3), with most plots ranging from 1 to 1,500 trees·ha⁻¹ and a smaller subset representing densely stocked stands (1,500 to 10,000 trees·ha⁻¹).

2.4. Remote sensing and environmental data

In addition to field measurements, the modeling framework relied on 54 wall-to-wall covariates spanning vegetative, climatic, edaphic, topographic, biophysical, and anthropogenic domains. Remote sensing-derived predictors were central for capturing forest structure, productivity, and landscape heterogeneity. Vegetation indices, including NDVI, EVI, and fPAR, were obtained from MODIS products (Didan et al., 2015; Myneni et al., 2021) and aggregated to annual composites to represent

canopy greenness and photosynthetic activity. Additional vegetation structure metrics such as leaf area index (LAI) were also derived from MODIS (Myneni et al., 2021) to capture differences in canopy density and vertical layering (Table 2).

To characterize canopy structure, we incorporated GEDI-derived metrics, including RH100 canopy height and aboveground biomass density from the L2A and L4A data products (Dubayah et al., 2022). These LiDAR-based observations provide three-dimensional structural information critical for constraining forest density estimates (Table 2).

Climatic gradients were represented by 19 bioclimatic variables from WorldClim v2 (Fick and Hijmans, 2017), including mean annual temperature, temperature seasonality, and annual precipitation, complemented by evapotranspiration and aridity indices (Running et al., 2021; Zomer et al., 2022). These variables collectively describe thermal and moisture regimes influencing forest growth and distribution (Table 2).

Soil properties were extracted from SoilGrids (Batjes, 2016) and included bulk density, pH, nitrogen, organic carbon, electrical conductivity, and texture fractions, each averaged across 1 km grid cells. Topographic predictors derived from the Global Multi-resolution Terrain Elevation Data (Amatulli et al., 2018) encompassed elevation, slope, terrain ruggedness, curvature, and topographic position index, representing physiographic constraints on vegetation structure (Table 2). Anthropogenic influence was represented using the human footprint index (Venter et al., 2017) and livestock density (Gilbert et al., 2018), both reflecting gradients of human disturbance and land-use intensity across the continent (Table 2).

All environmental layers were projected to the WGS84 geographic coordinate system and resampled to a 0.027° (~3 km) spatial resolution using bilinear interpolation for continuous variables and nearest-neighbor interpolation for categorical variables. Although many covariates were originally available at native resolutions of 500 m to 1 km, final predictions were generated at 3 km resolution to reflect the effective spatial support of forest inventory plots. Positional accuracy of plot coordinates varies among national forest inventories, with some datasets applying spatial masking or perturbation to protect confidentiality (e.g., FIA plot “fuzzing”) (McRoberts et al., 2005). In addition, plot size, sampling design, and reporting protocols differ among national inventories (Tomppo et al., 2010). Aggregating predictors to 3 km therefore provide a harmonized spatial support that reduces the influence of coordinate uncertainty and improves consistency when integrating heterogeneous inventory datasets with remotely sensed covariates (Saarela et al., 2016; Wulder et al., 2008). Covariate values were then extracted at each inventory plot location using R and Python geospatial libraries, forming a spatially standardized dataset for model development and prediction.

2.5. Modeling approach

To estimate tree density across North America, we implemented and compared four modeling approaches: a parametric baseline (GLM), penalized linear regression (ridge regression (RR)), and two non-parametric models (random forest (RF) and FFNN). All models were trained using a single continental-scale framework, with biome classification included as a categorical predictor to represent coarse-scale ecological heterogeneity. This design preserves sample size while allowing models to learn across the full range of environmental conditions represented in the training data. Because biome boundaries often represent transition zones (ecotones) rather than sharp discontinuities, a unified modeling framework also avoids enforcing abrupt step-changes at biome edges and permits continuous transitions across ecoclines where environmental gradients shift gradually (Hufkens et al., 2009). In the non-linear models (RF and FFNN), interactions between biome context and other predictors can be represented without explicitly specifying interaction terms, because tree-based ensembles and neural networks are designed to capture non-linear and interactive structure in

Table 1
Sources of forest inventory data used in this study.

Dataset	Country	Sample size (plots)	Reference
PR	Puerto Rico	634	O'Connell et al. (2014)
CAFI	Alaska-US	2,013	Malone and Liang (2022)
FIA	US	591,851	O'Connell et al. (2014)
CA i	Canada	979	Gillis et al. (2005)
CA ii	Canada	338,823	Paquette and Messier (2011)
MX	Mexico	675	Bongers et al. (1988)
CA	Canada	9,085	Chen and Luo (2015)
GentryNA		40	Phillips et al. (2002)
NA2_US	US	62	Unpublished
NA2_MX	Mexico	9,955	Barreras et al. (2022)
NA2_CA	Canada	131,358	Searle and Chen (2017)
NA2_MXi	Mexico	1,269	Unpublished
NA2_MXii	Mexico	172,758	Unpublished
NA2_USii	US	2	Unpublished
MX i	Mexico	2,808	Corral-Rivas et al. (2016)

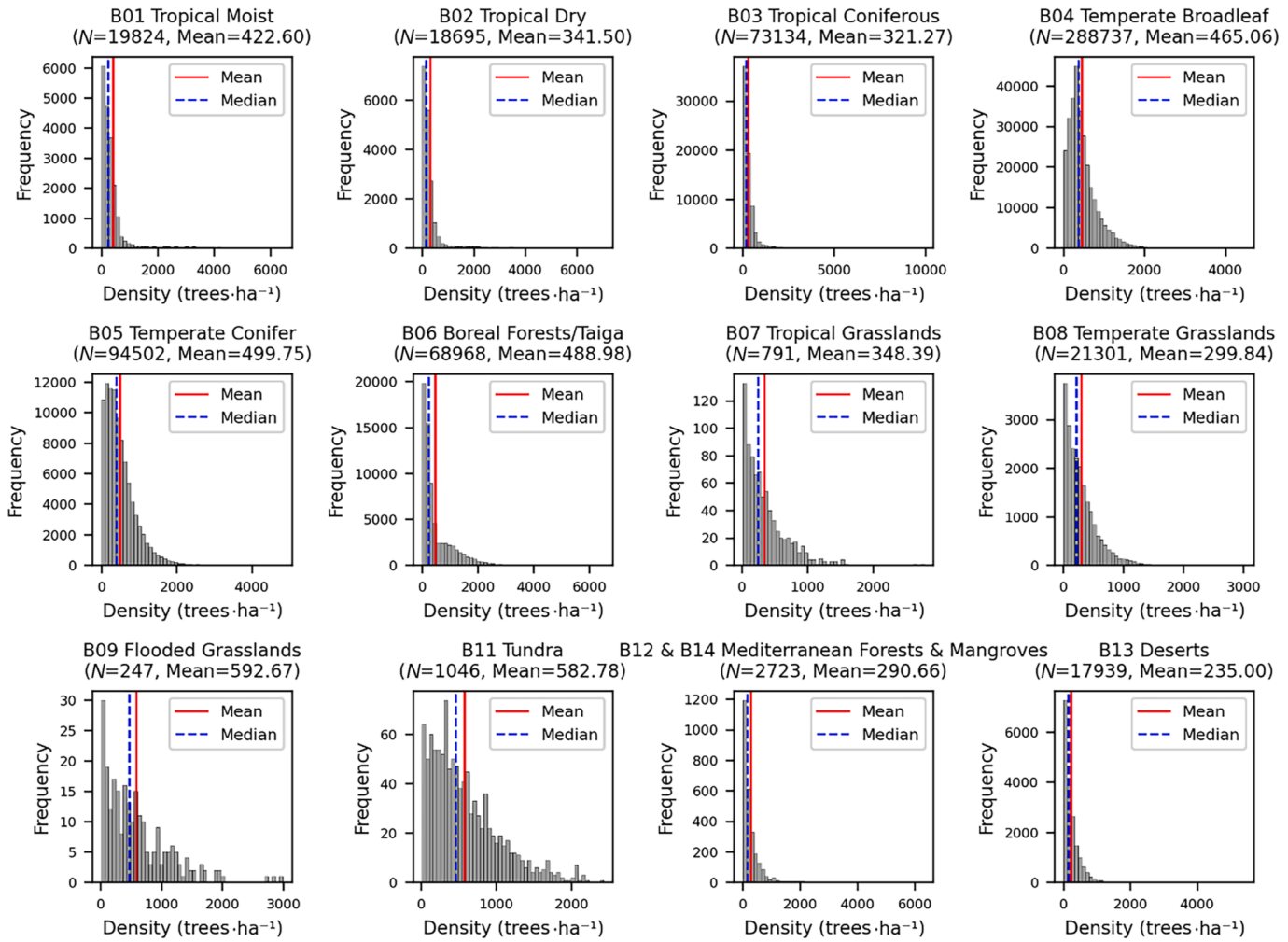


Fig. 3. Observed tree density (trees·ha⁻¹) in the permanent sample plots by biome in North America.

high-dimensional predictor space (Breiman, 2001; Reichstein et al., 2019). However, we note that the interpretation of “biome effects” in such models remains algorithm-dependent and should be treated as predictive context rather than direct causal attribution (Olden and Jackson, 2002).

Spatial uncertainty in forest inventory plot coordinates, arising from anonymization or fuzzy georeferencing, likely reduced pixel-level fidelity of predictions. However, at the 3-km prediction resolution used here, and given that environmental covariates were aggregated at ≥ 1 -km resolution, sub-kilometer positional error is expected to exert limited influence on large-scale patterns. Consistent with previous findings (McRoberts et al., 2022; Zimmerman and Hoef, 2024), coordinate imprecision at resolutions coarser than plot-location uncertainty primarily increases local variance rather than introducing systematic bias in continental-scale forest models. In our results, residual spatial imprecision appears as localized dispersion in predicted values, particularly in environmentally heterogeneous and data-sparse regions. These effects are reflected in elevated epistemic uncertainty estimated via Monte Carlo (MC) Dropout (Section 2.8) (García-Soria et al., 2024; Saarela et al., 2020), while broad biome-level and continental patterns remain coherent.

The full plot dataset was first randomly partitioned into two independent subsets, with 90% used for model training and 10% reserved for final testing. Model development was carried out exclusively on the training subset. We selected the best-performing model using cross-validated accuracy on the training data and subsequently evaluated

this final model on the held-out 10% test data using the coefficient of determination (R^2), root mean squared error (RMSE), and mean absolute error (MAE). The final model was then applied to wall-to-wall gridded covariates to produce 3-km tree-density maps across North America.

2.5.1. General linear model (GLM)

The GLM was implemented as a baseline to quantify the explanatory power of a linear approach for predicting tree density. As a classical parametric method, GLM assumes a linear relationship between covariates and the response variable, offering transparency, computational efficiency, and interpretability. Model coefficients were estimated by minimizing the residual sum of squares (Eq. 1):

$$\hat{y}_{\text{GLM}} = X\beta \quad (1)$$

where X is the predictor matrix and β is the coefficient vector. Despite their transparency, GLMs are limited in their ability to model nonlinear relationships and are sensitive to multicollinearity among predictors.

We implemented the GLM using the statsmodels library in Python, specifying a Gaussian distribution with an identity link function. Continuous predictors were standardized, and categorical variables were one-hot encoded (excluding the reference level). To mitigate multicollinearity among correlated environmental covariates, we applied principal component analysis (PCA) and retained components explaining 95% of the total variance.

Table 2

List of covariates used in this study.

Abbreviation	Descriptive name	Covariate Group	Resolution (km)	Units	References
livestock	Number of livestock per unit area	Anthropogenic	10	Count·10 km ⁻²	Gilbert et al. (2018)
rh100	Canopy height	Biophysical	1	m	Dubayah et al. (2022)
GEDIBiomass	Mean above-ground biomass density	Biophysical	1	mg·ha ⁻¹	Dubayah et al. (2022)
Aridity	Indexed annual aridity	Climatic	1	Unitless	Zomer et al. (2022)
Evapot	Evapotranspiration rates	Climatic	1	mm·month ⁻¹	Zomer et al. (2022)
HumanFP	Human footprint index	Anthropogenic	1	Unitless	Venter et al. (2017)
corr_annual_precip	Corrected annual precipitation	Climatic	1	mm·year ⁻¹	Beck et al. (2020)
rmf	Root mass fraction	Edaphic	1	Unitless	H. Ma et al. (2021)
bio1	Mean annual air temperature	Climatic	1	°C	Fick and Hijmans (2017)
bio2	Mean diurnal air temperature range	Climatic	1	°C	Fick and Hijmans (2017)
bio3	Isothermality (ratio)	Climatic	1	°C	Fick and Hijmans (2017)
bio4	Temperature seasonality	Climatic	1	°C	Fick and Hijmans (2017)
bio5	Mean daily maximum air temperature of the warmest month	Climatic	1	°C	Fick and Hijmans (2017)
bio6	Mean daily minimum air temperature of the coldest month	Climatic	1	°C	Fick and Hijmans (2017)
bio7	Annual range of air temperature	Climatic	1	°C	Fick and Hijmans (2017)
bio8	Mean daily mean air temperatures of the wettest quarter	Climatic	1	°C	Fick and Hijmans (2017)
bio9	Mean daily mean air temperatures of the driest quarter	Climatic	1	°C	Fick and Hijmans (2017)
bio10	Mean daily mean air temperatures of the warmest quarter	Climatic	1	°C	Fick and Hijmans (2017)
bio11	Mean daily mean air temperatures of the coldest quarter	Climatic	1	°C	Fick and Hijmans (2017)
bio13	Precipitation amount of the wettest month	Climatic	1	kg·m ⁻²	Fick and Hijmans (2017)
bio14	Precipitation amount of the driest month	Climatic	1	kg·m ⁻²	Fick and Hijmans (2017)
bio15	Precipitation seasonality (coefficient of variation)	Climatic	1	kg·m ⁻²	Fick and Hijmans (2017)
bio16	Mean monthly precipitation amount of the wettest quarter	Climatic	1	kg·m ⁻²	Fick and Hijmans (2017)
bio17	Mean monthly precipitation amount of the driest quarter	Climatic	1	kg·m ⁻²	Fick and Hijmans (2017)
bio18	Mean monthly precipitation amount of the warmest quarter	Climatic	1	kg·m ⁻²	Fick and Hijmans (2017)
bio19	Mean monthly precipitation amount of the coldest quarter	Climatic	1	kg·m ⁻²	Fick and Hijmans (2017)
maxEVI	Enhanced vegetation index	Vegetative	1	Unitless	Didan et al. (2015)
maxLAI	Leaf area index	Vegetative	1	Unitless	Myneni et al. (2021)
meanFpar	Fraction of photosynthetically active radiation absorbed by vegetation.	Vegetative	1	Unitless	Myneni et al. (2021)
meanLST_day	Mean land surface temperature during the day.	Climatic	1	°C	Wan and others (2013)
maxNDVI	Normalized difference vegetation index	Vegetative	1	unitless	Didan et al. (2015)
sumET	Evapotranspiration	Climatic	1	mm·year ⁻¹	Running et al. (2021)
sumPET	Potential evapotranspiration	Climatic	1	mm·year ⁻¹	Running et al. (2021)
BD	Bulk density	Soil	1	g·cm ⁻³	Batjes (2016)
Nit	Soil nitrogen	Soil	1	g·kg ⁻¹	Batjes (2016)
CN	Soil organic C:N ratio	Soil	1	Unitless	Batjes (2016)
pH	Soil pH level	Soil	1	Unitless	Batjes (2016)
EC	Electrical conductivity of soil	Soil	1	dS·m ⁻¹	Batjes (2016)
Clay	Percentage clay	Soil	1	%	Batjes (2016)
OCC	Organic carbon content	Soil	1	g·kg ⁻¹	Batjes (2016)
aspectcosine	Aspect cosine	Topographic	1	Unitless	Amatulli et al. (2018)
aspectsine	Aspect sine	Topographic	1	Unitless	Amatulli et al. (2018)
dx	First-order partial derivative (E-W slope)	Topographic	1	Unitless	Amatulli et al. (2018)
dxx	Second-order partial derivative (E-W slope)	Topographic	1	Unitless	Amatulli et al. (2018)
dy	First-order partial derivative (N-S slope)	Topographic	1	Unitless	Amatulli et al. (2018)
dyy	Second-order partial derivative (N-S slope)	Topographic	1	Unitless	Amatulli et al. (2018)
pcurv	Profile curvature	Topographic	1	Unitless	Amatulli et al. (2018)
roughness	Surface roughness index	Topographic	1	Unitless	Amatulli et al. (2018)
slope	Steepness of the terrain	Topographic	1	Degree	Amatulli et al. (2018)
tcurv	Tangential curvature	Topographic	1	Unitless	Amatulli et al. (2018)
tpi	Topographic position index	Topographic	1	Unitless	Amatulli et al. (2018)
tri	Terrain ruggedness index	Topographic	1	Unitless	Amatulli et al. (2018)
elevation	Elevation	Topographic	1	m	Amatulli et al. (2018)

2.5.2. Ridge regression (RR)

RR was implemented to evaluate the effect of l_2 regularization on predictive performance in the presence of multicollinear ecological predictors. RR extends the GLM by adding a penalty on the magnitude of coefficients, shrinking them toward zero to reduce variance and improve generalizability, which is particularly helpful in modeling geographically and remotely sensed environmental data (Roosbeeh et al., 2018). Coefficients were estimated by minimizing the penalized residual sum of squares:

$$\hat{\beta}_{RR} = \operatorname{argmin}_{\beta} \|Y - X\beta\|_2^2 + \lambda \|\beta\|_2^2 \quad (2)$$

where λ controls the extent of shrinkage. By balancing bias and variance, RR retains interpretability while offering increased robustness in high-dimensional modeling scenarios.

We implemented RR using the Ridge estimator from scikit-learn (Pedregosa et al., 2011). Continuous predictors were standardized, and categorical variables were one-hot encoded (excluding the reference level) to prevent multicollinearity among dummy variables. The model employed an l_2 regularization term with $\lambda = 1.0$, determined through prior experimentation. RR inherently mitigates multicollinearity among correlated predictors by shrinking coefficient magnitudes, thereby enhancing numerical stability and generalization performance.

2.5.3. Random forest (RF)

RF was employed to model tree density due to its capacity to capture complex, non-linear interactions among covariates without assuming a functional form. As a non-parametric ensemble method, RF builds multiple decision trees using bootstrap samples and random subsets of

predictors, enhancing robustness to overfitting and multicollinearity. While correlated predictors can obscure individual feature importance, RF remains well-suited for ecological modeling due to its high predictive accuracy and tolerance to outliers.

The model was implemented using RandomForestRegressor from scikit-learn (Pedregosa et al., 2011), with standardized continuous predictors and one-hot encoded categorical features (excluding the reference level).

We used 500 trees, a maximum depth of 20, a minimum of 10 samples per split, and 5 samples per leaf. Hyperparameters were optimized via grid search with five-fold cross-validation. The prediction for any given pixel $\hat{y}_{RF}$ was the average of the predictions from all individual trees $\hat{y}_t$:

$$\hat{y}_{RF} = \frac{1}{T} \sum_{t=1}^T \hat{y}_t(\mathbf{x}) \quad (3)$$

where $\hat{y}_t$ denotes the prediction from the t -th tree, and $\mathbf{x}$ represents the covariate vector at the pixel location.

2.5.4. Feed forward neural network (FFNN)

The FFNN was implemented to model complex, nonlinear relationships between environmental covariates and tree density. Unlike ensemble methods such as RF, FFNN learns hierarchical data representations across stacked layers, enabling it to capture deep interactions among features.

We constructed the FFNN in PyTorch (Paszke et al., 2019), using seven fully connected hidden layers with 1,024, 1,024, 512, 512, 256, 256, and 128 neurons, each followed by rectified linear unit (ReLU) activation and dropout ($p = 0.1$) for regularization. The final output layer employed a linear activation to predict continuous tree density values. The transformation at each layer is defined as Eq. 4:

$$x_i = f(W_{i-1}x_{i-1} + b_{i-1}) \quad (4)$$

where x_{i-1} is the input from the previous layer, W_{i-1} is the weight matrix, b_{i-1} is the bias, and f is the activation function (ReLU). The complete transformation from input covariates to predicted tree density can be described as Eq. 5:

$$\hat{y}_{FFNN} = f(W_L x_L + b_L) \quad (5)$$

Categorical inputs were processed using embedding layers, while continuous features were standardized. The combined input was passed through the network for training using the Adam optimizer ($\beta_1 = 0.9$, $\beta_2 = 0.999$) with a batch size of 512 and mean squared error (MSE) loss. Training was conducted for 100 epochs with early stopping based on validation loss to prevent overfitting.

2.6. Model selection and validation

To evaluate predictive performance, we adopted validation strategies tailored to each model type. For the classical regression models (GLM and RR), we trained each model on 90% of the data and assessed accuracy using a withheld 10% test set, providing a consistent benchmark for these interpretable baselines. For the machine-learning models (RF and FFNN), we implemented 5-fold cross-validation within the training subset to assess robustness and reduce overfitting. The training data were divided into five equally sized folds; models were iteratively trained on four folds and validated on the fifth, ensuring that each fold served once as the validation set. Predictions across all folds were aggregated to examine residual structure and spatial consistency.

In all cases, an independent 10% of the full dataset, held out before model development, was used exclusively for final out-of-sample evaluation. Three standard regression metrics were used to quantify model accuracy (Eqs. 6–8):

$$MAE = \frac{1}{n} \sum_{i=1}^n |y_i - \hat{y}_i| \quad (6)$$

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2} \quad (7)$$

$$R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (8)$$

where y_i , $\hat{y}_i$, and $\bar{y}$ represent the observed value, predicted value, and mean observed tree density, respectively. We selected the model with the best predictive performance and generalizability to produce wall-to-wall tree density maps.

To assess the impact of spatial scale mismatch between plot-level observations and gridded predictors, model performance was evaluated across multiple spatial supports. In addition to plot-level comparisons, observations were aggregated to the 3-km prediction grid and to coarser spatial resolutions (e.g., 5 km). Furthermore, within-cell variability was quantified using the standard deviation of observed tree density within each grid cell, and its relationship with model residuals was evaluated.

2.7. Model interpretability

To interpret model predictions, we applied SHapley Additive Planations (SHAP) to the FFNN and extracted feature importance scores from the RF model. These two models were selected for interpretation based on their comparable predictive performance ($R^2 = 0.39$ and 0.39 , respectively), whereas GLM and RR were excluded due to substantially lower accuracy.

SHAP values are derived from cooperative game theory and quantify the marginal contribution of each feature to the prediction, satisfying axioms such as efficiency and symmetry (Lundberg et al., 2020). The SHAP value for a feature j is defined as Eq. 9:

$$\phi_j(f) = \sum_{S \subseteq N \setminus \{j\}} \frac{|S|!(|N| - |S| - 1)!}{|N|!} (f(S \cup \{j\}) - f(S)) \quad (9)$$

where f is the prediction function, N is the set of all features, and S is any subset excluding j . This expression evaluates how the inclusion of feature j alters predictions across all possible feature subsets.

In contrast, RF computes feature importance based on the mean decrease in impurity, reflecting the contribution of each variable to reducing prediction uncertainty across the ensemble (Cao et al., 2011). Permutation importance further estimates this by measuring the increase in prediction error when feature values are randomly shuffled.

Both SHAP and RF analyses revealed overlapping patterns in feature influence, identifying a common set of key predictors. While RF feature importance provided a global view of feature relevance, SHAP feature importance offered observation-level explanations that revealed context-dependent effects, particularly relevant for spatial and ecological applications.

2.8. Spatial modeling and uncertainty quantification

To generate wall-to-wall predictions of tree density across North America, FFNN was applied to predictor variables at each 3 km grid cell. Prediction domains were restricted to forested areas using spatial masks derived from JRC2020 (Bourgoin et al., 2024), FNF2020 (Shimada et al., 2014), and GFC2013 (Hansen et al., 2013), thereby defining an ecologically consistent prediction domain. Each forest mask was applied

independently to the same continuous tree density surface to evaluate the sensitivity of aggregated tree totals to alternative forest definitions. This framework separates uncertainty arising from forest classification schemes and canopy-cover thresholds from uncertainty attributable to the predictive model, enabling forest-definition effects to be quantified independently of model performance.

To maintain consistency with the training pipeline, all covariates underwent the same preprocessing steps: numerical features were standardized using a pre-fitted StandardScaler, and categorical features were encoded into numerical indices using label encoders fitted during training (Pedregosa et al., 2011). The processed feature vectors were then passed through the trained FFNN, implemented in PyTorch (Paszke et al., 2019), to generate continuous predictions of tree density, expressed as trees per hectare, for each grid cell.

There are several approaches described for generating model-based uncertainty estimates in forest monitoring (McRoberts et al., 2022). To quantify model uncertainty, a component of population estimate uncertainty, we implemented Monte Carlo (MC) Dropout (Gal and Ghahramani, 2016), a Bayesian approximation technique that allows for stochastic inference by enabling dropout during prediction. Unlike standard dropout, which is applied only during training to prevent overfitting, MC Dropout enables random omission of neurons at inference time, simulating a distribution over the model's output.

For each input, we performed 100 stochastic forward passes through the trained neural network, each with different dropout realizations. This yielded a sample of predictions approximating draws from the model's posterior predictive distribution.

Mathematically, if $f(x)$ is the output of the neural network for input x , then the sample predictions $f(x)^{(i)}$ for $i = 1, \dots, n$, allow estimation of the predictive mean μ and mean variance σ^2 :

$$\mu = \frac{1}{n} \sum_{i=1}^n f(x)^{(i)} \quad (10)$$

$$\sigma^2 = \frac{1}{n} \sum_{i=1}^n (f(x)^{(i)} - \mu)^2 \quad (11)$$

From the calculated variance, a confidence interval can then be derived around the mean prediction. For example, a 95% confidence interval can be constructed using the mean prediction and the estimated standard deviation:

$$CI_{95\%} = [\mu - 1.96\sigma, \mu + 1.96\sigma] \quad (12)$$

To visualize the spatial pattern of uncertainty, we generated a standard error (SE) map by computing the per-pixel standard deviation of the 100 MC Dropout predictions for each 3 km grid cell. These standard deviations, reflecting model-based epistemic uncertainty, were reported as SE values, providing a spatially explicit depiction of prediction confidence.

2.9. Estimation of the total number of forest trees

To estimate total tree density across North America, predicted tree densities (trees·ha⁻¹) were scaled onto a 3 km × 3 km grid, where each cell represented 900 ha. These densities were scaled by the fraction of forest cover in each cell, such that total trees = density × 900 ha × forest fraction. Grid cells with no forest cover contributed zero trees, while partially forested pixels contributed proportionally to their forested area. This approach restricted estimates to the forested landscape, aligning with the scope of global forest assessments.

Forest cover fractions were derived from the same three spatially explicit datasets described in the Introduction: JRC2020, GFC2013, and FNF2020. Each dataset was resampled to match the 3 km prediction grid by averaging the proportion of forested area within each pixel. For GFC2013, forested pixels were identified using a ≥10% canopy over

threshold from the 2020 layer, in line with international forest definitions (FAO, 2020). These masks were applied post hoc to constrain total tree count estimates by excluding predictions outside forested areas, without influencing model training or covariate selection. The full estimation pipeline using FFNN was executed independently for each spatial forest extent dataset—JRC2020, GFC2013, and FNF2020—yielding three separate estimates of total tree density.

To quantify predictive uncertainty, we applied MC Dropout during inference, generating 100 stochastic forward passes for each 3 km forested grid cell. For each realization, predicted tree density (trees·ha⁻¹) was converted to total tree count by multiplying density by pixel area and the proportion of forest cover within the cell. Pixel-level epistemic uncertainty was estimated as the standard deviation of the 100 stochastic predictions, while the mean was retained as the expected value.

Regional and continental totals were obtained by summing pixel-level tree counts within each spatial unit. Aggregated uncertainty was computed by summing pixel-level variances under an assumption of independence among prediction errors. This approach does not explicitly model spatial covariance; consequently, confidence intervals for regional and continental totals might be conservative with respect to spatially correlated errors among neighboring pixels.

To estimate total tree density, predicted counts were summed across all forested pixels within each country of Canada, the United States, and Mexico as well as across the entire continent. This produced a distribution of total tree counts for each region based on the 100 MC samples. From these distributions, we calculated 95% confidence intervals as the 2.5th and 97.5th percentiles. This approach allowed us to quantify how local uncertainty accumulates at national and continental scales.

To provide an independent benchmark, we incorporated national forest area statistics from the FAO Global Forest Resources Assessment to assess the alignment of our results with other estimates of country-level tree density. For each country, we calculated the mean tree density across all forested pixels from 100 MC realizations and multiplied these values by the corresponding FAO-reported forest area. This yielded a distribution of total tree counts per country, from which 95% confidence intervals were derived. While this approach does not preserve spatial detail, it offers a harmonized reference point for evaluating the plausibility and internal consistency of national and continental-scale tree density estimates.

3. Results

3.1. Estimation accuracy

The four modeling approaches—GLM, RR, RF, and FFNN—showed distinct differences in predictive performance (Table 3). Across all metrics, the FFNN achieved the best results, with the lowest RMSE (344.80), lowest MAE (227.07), and highest explained variance ($R^2 = 0.39$). The RF model performed comparably (RMSE = 347.8; $R^2 = 0.39$) (Fig. S1) but slightly below the FFNN, while GLM and RR explained less than 19% of the variance and produced substantially higher errors.

Model performance exhibited clear scale dependence. At the plot level, FFNN predictions captured much of the observed variability, with residuals distributed around the 1:1 line and no evident systematic bias (Fig. 4a), although dispersion increased at higher densities (>2000

Table 3
Comparison of model performance metrics of traditional and ML models.

Algorithm	MAE	RMSE	R-squared (%)
GLM	270.49	393.72	16.31
RR	266.26	388.81	18.38
RF	228.89	347.76	39.12
FFNN	227.07	344.80	39.53

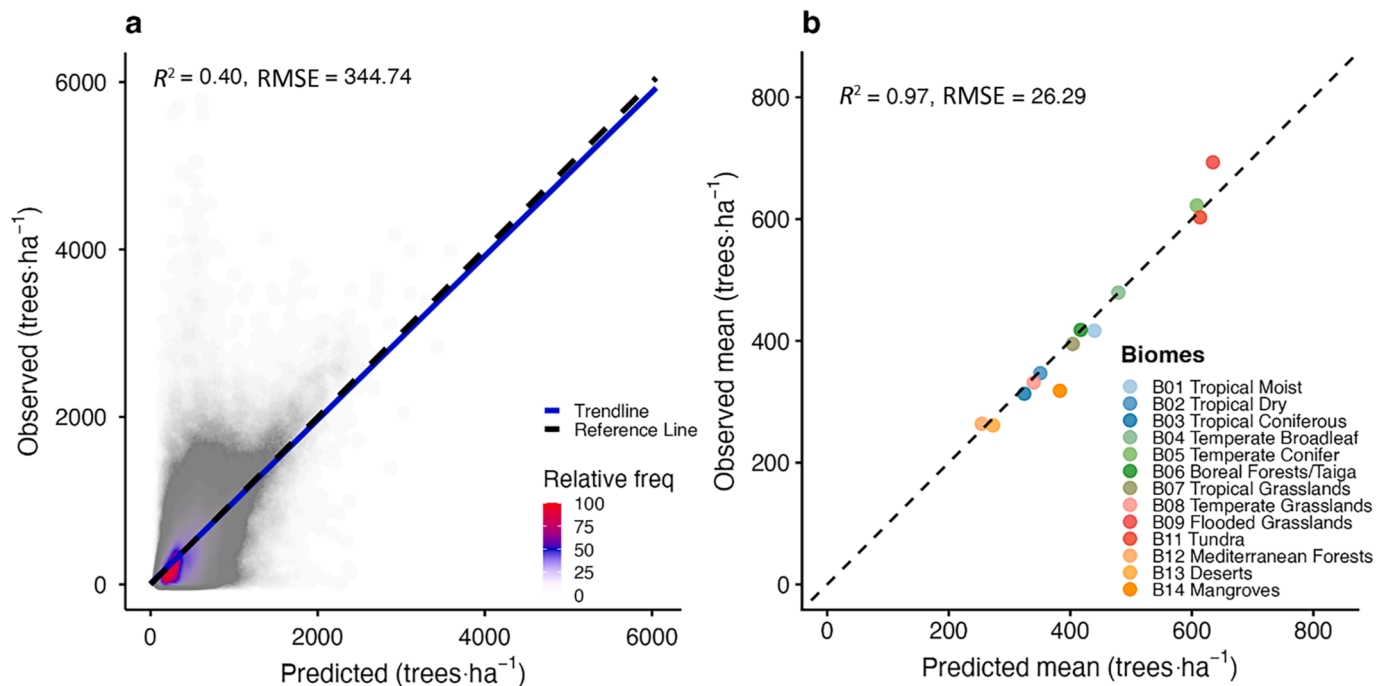


Fig. 4. Cross-validation of the Feedforward Neural Network (FFNN) model. (a) Observed vs. predicted tree density at the plot level. (b) Observed vs. predicted mean tree density at the biome level across North America.

trees·ha⁻¹). Agreement at the plot level was moderate ($R^2 \approx 0.40$). When observations were aggregated to the 3-km grid corresponding to the prediction resolution, agreement improved ($R^2 \approx 0.52$) and increased further at coarser spatial supports (e.g., 5 km) (Fig. S2 and S4).

Residual magnitude increased with within-cell variability, as measured by the standard deviation of observed tree density within grid cells (Fig. S3). At broader ecological scales, aggregation reduced variability and predicted and observed mean values were closely aligned at the biome level ($R^2 = 0.97$; Fig. 4b).

Biome-specific comparisons (Fig. 5) further revealed consistent model performance across major forest types. Dense biomes such as tropical moist (B01) and temperate coniferous (B05) forests showed strong agreement between predicted and observed values along the 1:1 line, whereas open-canopy systems including grasslands (B08) and savannas (B09) displayed wider scatter and localized overestimation in sparsely vegetated pixels. Intermediate accuracy in Mediterranean and mixed forests reflects transitional canopy structure and variable disturbance regimes.

3.2. Spatial modelling and uncertainty

Spatially continuous predictions from the FFNN produced continent-wide maps of tree density at 3 km resolution (Fig. 6a). Predicted values ranged from near zero in non-forested areas to more than 6,000 trees·ha⁻¹ in dense forest regions. High densities were concentrated along the Pacific coast, western Canada, and the northeastern United States, while intermediate values occurred across the Great Lakes and Appalachian regions. Lower densities dominated the interior plains, southwestern United States, and northern Mexico, consistent with climatic constraints on forest structure.

At the biome scale, predicted density distributions (Fig. 7) reproduced broad contrasts observed in the inventory record. Boreal and temperate conifer forests (B06, B05) exhibited among the highest mean densities, while Mediterranean and desert systems (B12–B14, B13) showed substantially lower values. Flooded grasslands (B09) and tundra (B11) also displayed relatively high mean densities in both observations and predictions, reflecting dense localized stands within heterogeneous

landscapes. Compared with the inventory distributions, predicted histograms were smoother and exhibited attenuated high-density tails, particularly in boreal and temperate conifer biomes. This compression of extremes likely reflects the spatial support of ≥ 1 km environmental covariates and the 3 km prediction grid, which cannot fully resolve sub-kilometer structural heterogeneity. In contrast, several open or sparsely forested systems, including temperate grasslands (B08) and deserts (B13), showed moderately higher predicted means than observed, indicating potential overprediction in low-density environments.

Uncertainty derived from 100 MC Dropout realizations exhibited coherent spatial structure (Fig. 6b). SE were generally below 20 trees·ha⁻¹ across much of the USA and southern Canada, and increased toward northern boreal, arid, and mountainous regions. The highest SE occurred in portions of the northern boreal forest and along the western cordillera, where environmental heterogeneity and relative sparsity in representative training conditions likely reduced predictive constraint.

3.3. Total forested tree density

We estimate approximately 430–435 billion trees (DBH ≥ 10 cm) across North America. This value represents the central tendency of continental totals derived by applying four alternative forest-extent products (GFC2013, JRC2020, FNF2020, and FAO2020) to a single FFNN-predicted tree-density surface. For each mask, tree density (trees·ha⁻¹) was predicted for every 3-km grid cell, multiplied by pixel area (900 ha) and the pixel-level forest fraction, and then summed continent-wide. This produced totals of 339.32, 421.36, 451.12, and 513.79 billion trees, respectively. The mean (431.4 billion) and median (436.2 billion) of these values define the 430–435 billion central estimate, while the full range (339–514 billion) represents a sensitivity envelope reflecting definitional differences in forest extent rather than uncertainty in the density model itself.

Despite variation in magnitude, country-level rankings were consistent across all forest masks (Fig. 8b). Canada consistently showed the highest tree abundance, followed by the United States and Mexico. Under JRC2020, totals were 296.10 billion for Canada, 198.64 billion for the United States, and 19.05 billion for Mexico. Using FAO,

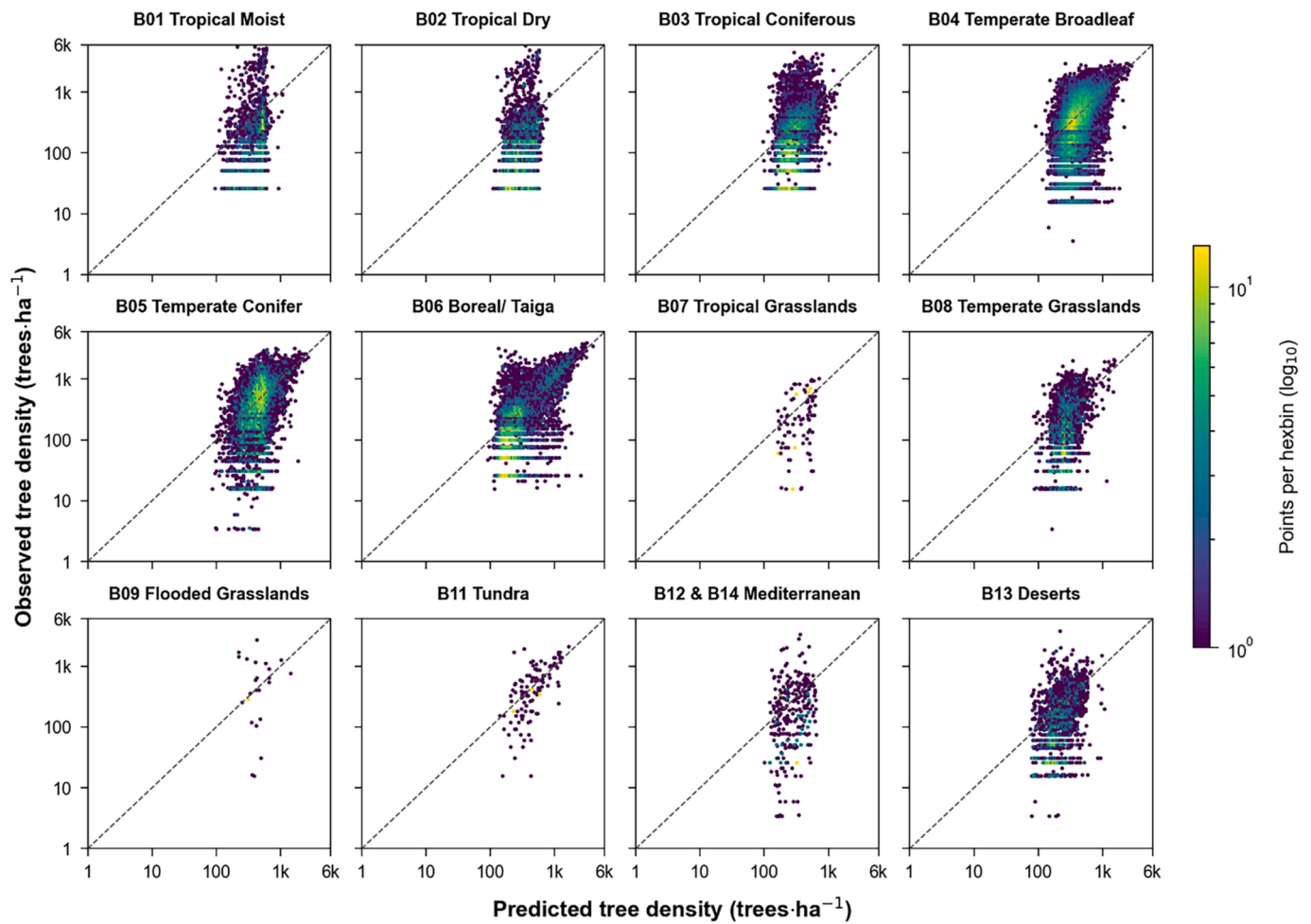


Fig. 5. Comparison of Feedforward Neural Network (FFNN) predictions and observed tree density (trees·ha⁻¹) across 13 biomes in North America. Point colors denote relative frequency; the dashed line represents the 1:1 relationship between observed and predicted values.

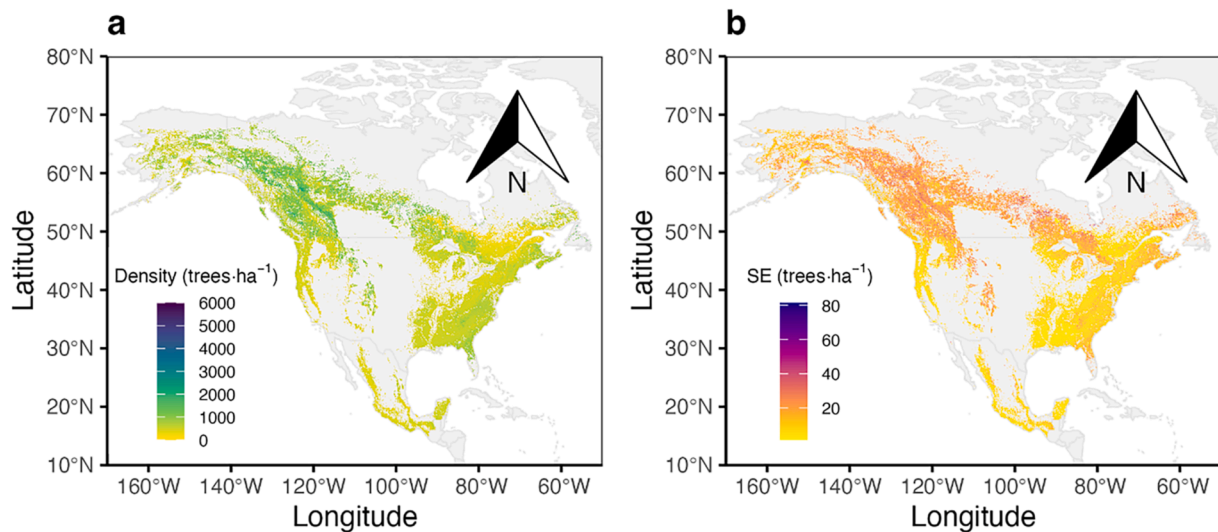


Fig. 6. (a) Mean tree density (trees·ha⁻¹) from Feedforward Neural Network. (b) Standard error showing epistemic uncertainty from 100 Monte Carlo Dropout realizations. Both panels depict per-pixel predictions at 0.027° (~3 km) resolution in geographic coordinates (WGS 84).

corresponding estimates were 259.74, 164.63, and 26.75 billion, respectively. FNF2020 yielded 249.91 (Canada), 153.77 (USA), and

17.68 billion (Mexico), while GFC2013 produced the lowest country totals: 200.35 (Canada), 126.91 (USA), and 12.06 billion (Mexico).

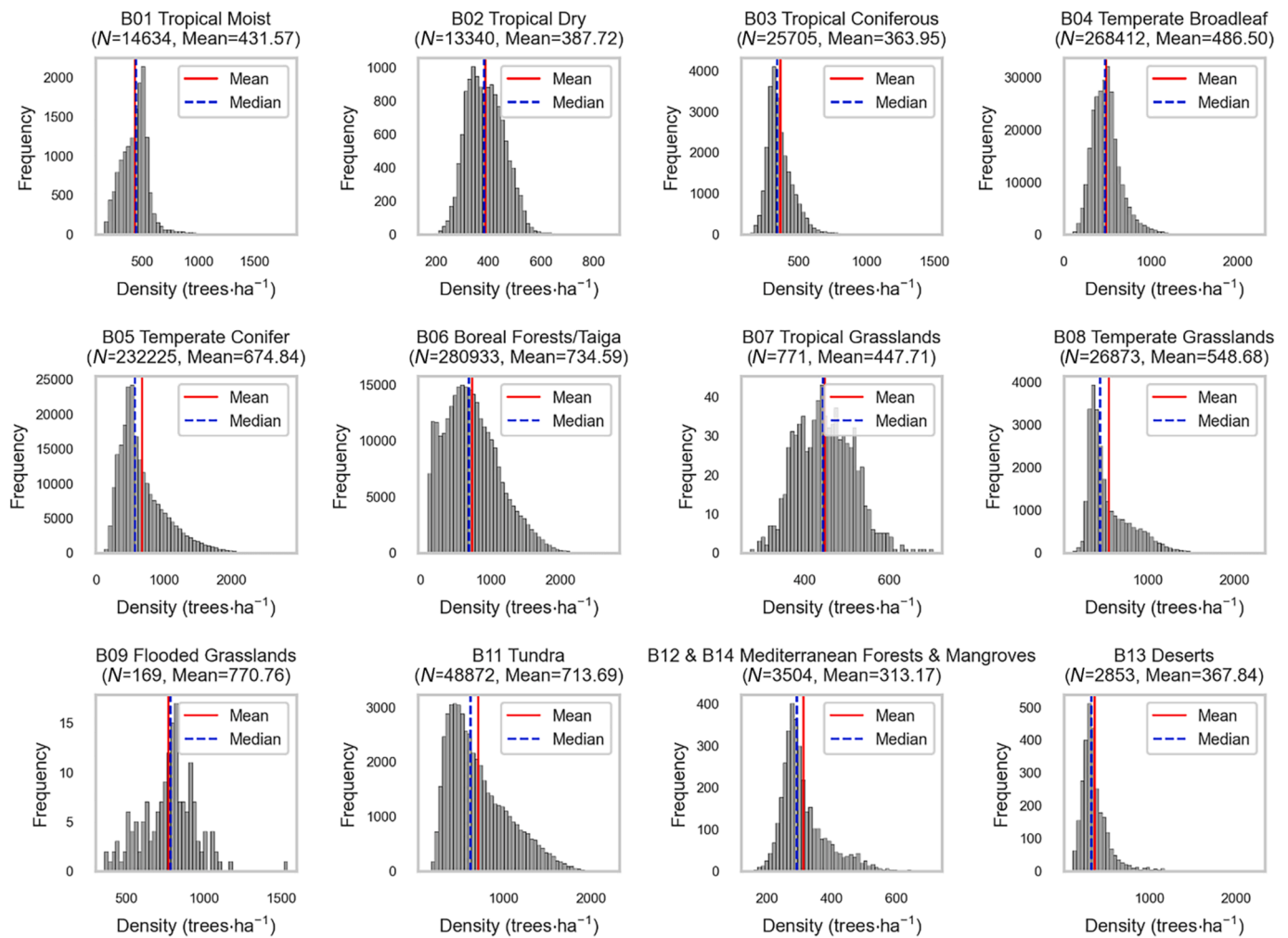


Fig. 7. Histogram of FFNN-predicted tree density (trees-ha⁻¹) by biome.

Uncertainty estimates, derived from MC Dropout, reflect epistemic uncertainty in pixel-level predictions aggregated to national and continental scales. At the continental scale, relative uncertainty ranged from $\pm 5.6\%$ (GFC2013: 339.32, 95% CI: 320.49–347.78 billion trees) to $\pm 10.0\%$ (FAO: 451.12, 95% CI: 406.01–496.23 billion trees), with JRC2020 showing $\pm 5.7\%$ (513.79, 95% CI: 484.67–526.16 billion) and FNF2020 showing $\pm 5.6\%$ (421.36, 95% CI: 397.87–431.92 billion). At the country level, Canada exhibited relative uncertainties of $\pm 5.4\%$ (JRC2020), $\pm 5.3\%$ (GFC2013), $\pm 5.3\%$ (FNF2020), and $\pm 10.0\%$ (FAO). The United States showed uncertainties of $\pm 6.0\%$ (JRC2020), $\pm 5.9\%$ (GFC2013), $\pm 6.0\%$ (FNF2020), and $\pm 10.0\%$ (FAO). Mexico displayed relative uncertainties of $\pm 6.0\%$ (JRC2020), $\pm 6.1\%$ (GFC2013), $\pm 6.3\%$ (FNF2020), and $\pm 9.9\%$ (FAO). The FAO forest mask consistently produced the widest confidence intervals ($\pm 10\%$) across all spatial scales, while JRC2020, GFC2013, and FNF2020 showed narrower and more consistent relative uncertainties of approximately $\pm (5\%–6\%)$.

3.4. Spatial patterns

The FFNN-derived tree density map captured clear ecological gradients across North America (Fig. 7). High tree densities (>700 trees-ha⁻¹) were concentrated in the boreal (B06) and temperate conifer (B05) zones of Canada, Alaska, and the Pacific Northwest. These areas, dominated by spruce, fir, and pine, are shaped by cold climates, infrequent disturbance, and short growing seasons. Both B06 and B05 had the highest mean densities among all biomes (553.6 and 519.1 trees-ha⁻¹, respectively).

Intermediate densities (300–500 trees-ha⁻¹) characterized broadleaf forests of the eastern and southeastern United States (B04) and mixed forest-grassland systems (B07, B08) in the central United States and Mexico. Low densities (<300 trees-ha⁻¹) occurred mainly in deserts (B13), Mediterranean woodlands and mangroves (B12/B14), and tropical conifer forests (B03) across the southwestern United States, coastal Mexico, and Central America. High-density outliers (>1000 trees-ha⁻¹) were rare and confined to riparian corridors or sheltered mountain valleys.

Uncertainty estimated from 100 MC Dropout realizations (Fig. 6b) showed distinct spatial patterns. SE was the highest in the Pacific Northwest and northeastern United States, where complex forest structures, steep terrain, and diverse species assemblages increase variability. In contrast, deserts, tundra, and drylands of northern Mexico exhibited low SE, indicating higher model confidence in these simpler ecosystems. The Yucatán Peninsula showed high predicted density but low SE, while transitional regions such as the Appalachian Mountains and Sierra Madre Oriental exhibited moderate uncertainty.

3.5. Influence of remote sensing and environmental predictors

SHAP analysis for the FFNN indicated that Aridity was the most influential predictor of tree density, followed by fraction of photosynthetically active radiation absorbed by vegetation (meanFpar) and bio10 (Fig. 9). Other high-ranking predictors included Evapotranspiration (Evapot), bio4, and bio3, together emphasizing the strong role of energy–water balance in shaping large-scale forest structure. Spectral metrics such as maxEVI and

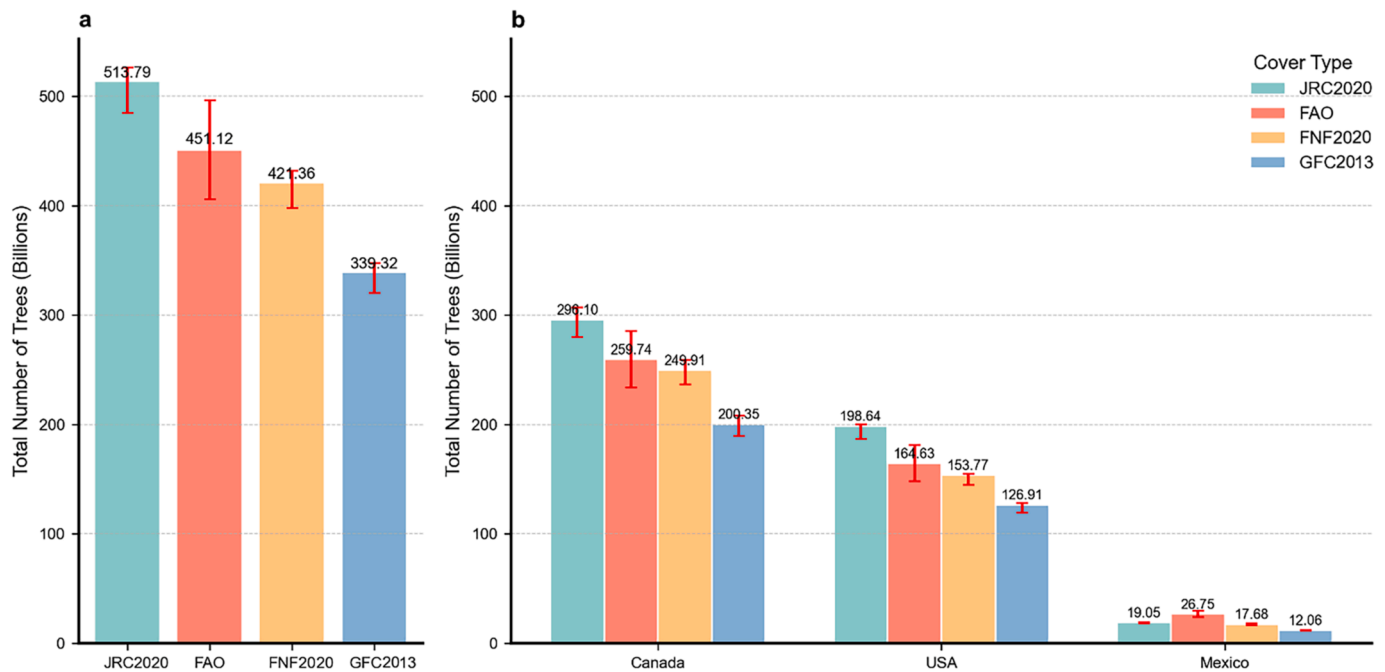


Fig. 8. (a) Estimated total number of trees (in billions) across North America as per forest cover JRC2020, GFC2013, FNF2020, and FAO. (b) Country-level estimates for Canada, the United States (USA), and Mexico using the same datasets. Error bars represent 95% confidence intervals of the estimates.

maxNDVI also ranked prominently, confirming the importance of canopy greenness and photosynthetic activity. In contrast, anthropogenic and edaphic variables—including livestock density, HumanFP, and soil pH—contributed minimally to FFNN predictions.

The RF model revealed a distinct pattern of feature importance. While aridity and meanFpar remained influential, RF assigned substantially greater weight to soil pH, livestock density, and precipitation seasonality (bio15), reflecting the model's sensitivity to edaphic constraints, human disturbance, and climatic variability. Remote-sensing predictors such as maxNDVI and meanFpar ranked next, whereas temperature-related variables (including bio1 and bio6) played a comparatively minor role.

4. Discussion

4.1. Model performance

RF and FFNN achieved comparable predictive accuracy at the plot level (Table 3), indicating that both nonlinear approaches capture the dominant large-scale relationships between environmental predictors and tree density. Linear models (GLM and RR), constrained by additive structures, are less suited to representing threshold responses and higher-order interactions that characterize ecological systems (Dormann et al., 2013; Elith and Leathwick, 2009). Although RF accommodates nonlinearity through recursive partitioning (Breiman, 2001), its piecewise structure can yield discontinuous response surfaces and may be less effective in approximating smooth environmental gradients (James et al., 2013). In contrast, the FFNN provides a continuous functional representation of predictor space, enabling flexible modeling of interacting biotic, climatic, edaphic, and topographic controls (Reichstein et al., 2019; Zhu et al., 2017).

At regional and biome scales, the close agreement between predicted and observed means ($R^2 \approx 0.98$) indicates that the FFNN effectively captures coarse-scale spatial patterns despite local plot-level variability. Such scale-consistent performance is particularly relevant for continental assessments, where aggregated trends rather than site-level deviations inform forest monitoring and carbon accounting (McRoberts et al., 2015; Olofsson et al., 2014).

Model selection for continental mapping was therefore guided not by marginal differences in point-based metrics, but by structural and practical considerations. The FFNN supports pixel-level epistemic uncertainty estimation via MC Dropout, which provides a tractable approximation to Bayesian predictive uncertainty (Gal and Ghahramani, 2016), produces spatially coherent prediction surfaces, and integrates heterogeneous predictors within a unified framework. These properties are critical for large-area inference and uncertainty-aware aggregation.

Remaining unexplained variance likely reflects fine-scale stand dynamics, disturbance history, and species composition not resolved at 3 km resolution. Future improvements may arise from incorporating multi-temporal disturbance metrics, expanded high-resolution LiDAR coverage, and heteroscedastic neural network architectures that jointly model predictive mean and variance.

4.2. Sensitivity to forest-cover definitions and inventory thresholds

Tree-density totals were strongly influenced by the forest-extent dataset used to constrain model predictions. Applying four widely used forest masks, JRC2020 (Bourgoin et al., 2024), FAO2020 (FAO, 2020), FNF2020 (Shimada et al., 2014), and GFC2013 (Hansen et al., 2013), yielded continental estimates ranging from 339 to 514 billion trees. These differences reflect variation in canopy-cover thresholds, spatial resolution, and treatment of sparse or fragmented forests across products rather than differences in the underlying tree-density model.

The JRC2020 dataset produced the highest total, consistent with its finer spatial resolution and greater inclusion of heterogeneous and open-canopy forest patches. In contrast, GFC2013 yielded the lowest total, consistent with its more conservative canopy-cover threshold. FNF2020 and FAO2020 generated intermediate estimates despite differing in data sources and classification approaches. Similar sensitivities to forest-definition choice have been reported in large-scale biomass and canopy-height mapping studies (Duncanson et al., 2022; Potapov et al., 2021), underscoring the extent to which structural metrics depend on the spatial delineation of forest area.

The objective of applying multiple forest masks was not to identify a single definitive estimate, but to quantify the sensitivity of continental tree abundance to forest-definition criteria. We therefore interpret the

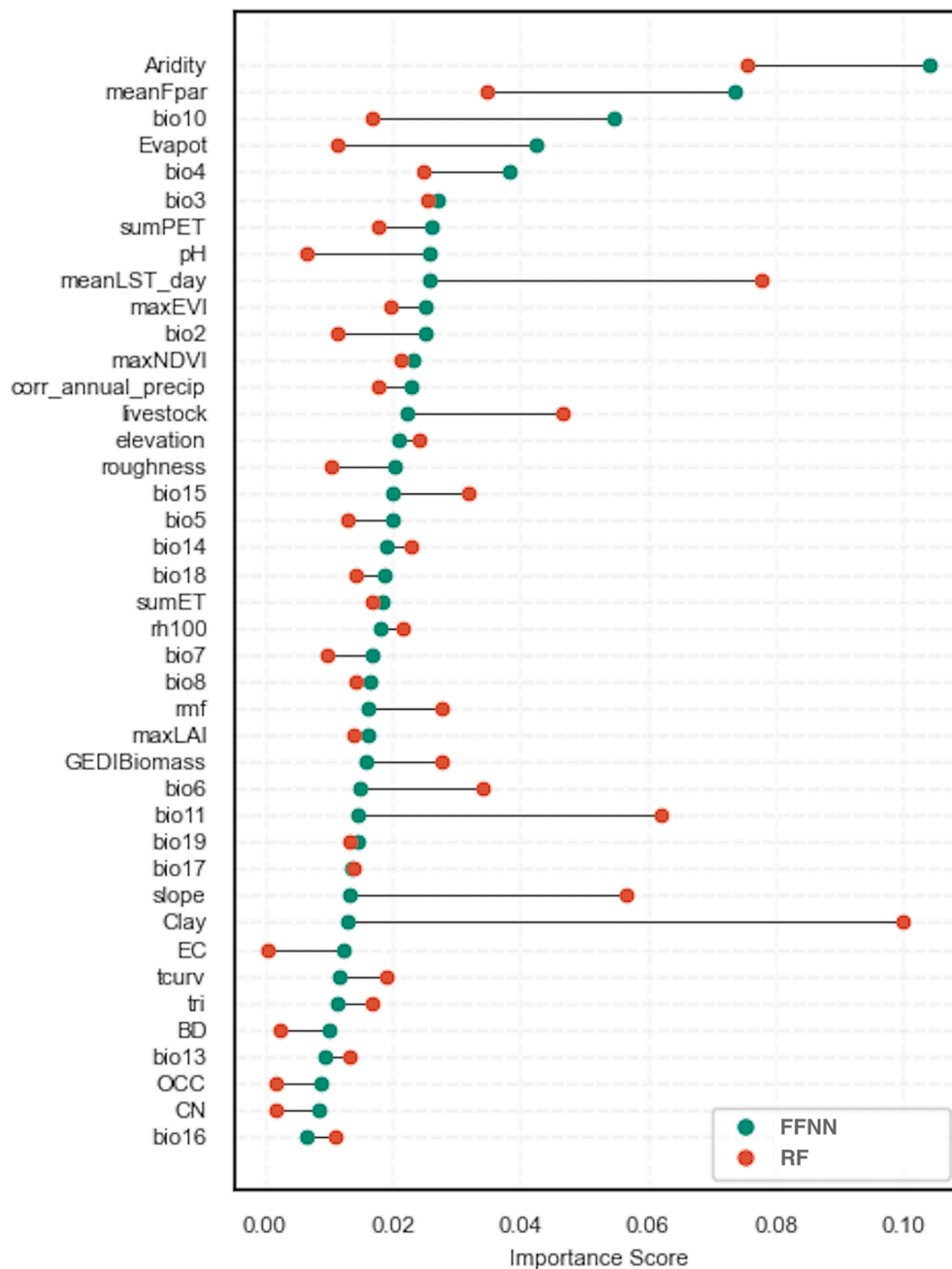


Fig. 9. Feature importance derived from SHAP values (FFNN) and impurity-based scores (RF). Higher score indicates greater influence on model prediction.

339–514 billion range as a defensible uncertainty envelope associated with classification variability.

Tree-number estimates were also affected by inventory design, particularly minimum diameter thresholds. Using the ≥ 10 cm DBH, the model predicted 339 to 514 billion trees. Removing this threshold more than doubled totals to over 1.12 trillion individuals under the broadest forest mask, driven by inclusion of small-stemmed trees prevalent in boreal, tundra, and grassland ecosystems (Fig. 10 and Table 4). Canada and the United States showed increases exceeding 100%, reflecting the exclusion of small stems in their harmonized datasets, whereas Mexico, with an inventory that records stems ≥ 7.5 cm DBH (Barreras et al., 2023), exhibited minimal change. Including sub 10 cm trees also raised densities in open and transitional biomes such as grasslands, deserts, and Mediterranean woodlands, ecosystems often omitted from global forest assessments due to low canopy cover or biomass.

Together, these findings show that both forest-cover definitions and DBH thresholds strongly influence uncertainty in results for this type of mapping study. Harmonizing these criteria and reporting them transparently are essential for reproducibility and comparability.

4.3. Spatial patterns and uncertainty

The spatial distribution of predicted tree density follows established ecological gradients across North America (Fig. 6a). High densities occur in boreal and temperate coniferous regions of Canada, Alaska, and the Pacific Northwest, where closed-canopy forests with high biomass dominate (Bonan, 2008; Pan et al., 2011). In contrast, arid and semi-arid regions exhibit low predicted densities, consistent with climatic constraints on tree establishment, particularly moisture limitation (Allen et al., 2010). Intermediate densities across the eastern and central United States correspond to mixed forest systems shaped by moderate

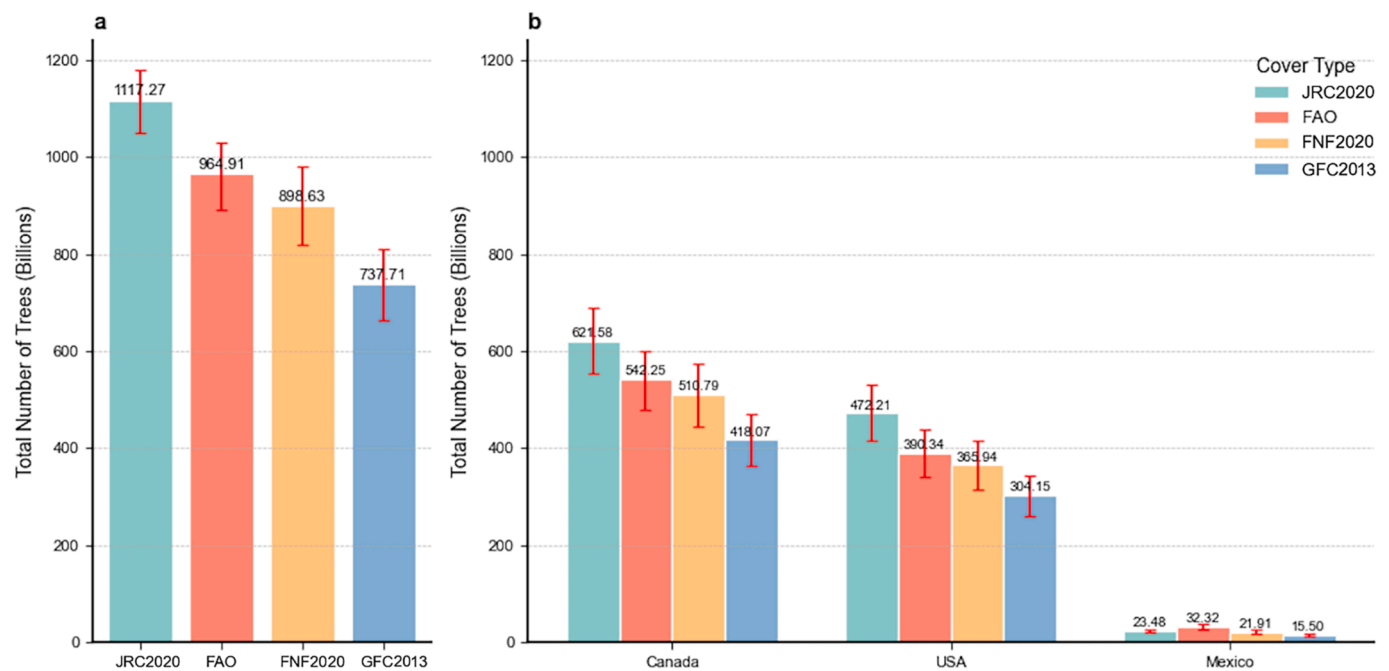


Fig. 10. Estimated total number of trees (in billions) across North America (without DBH threshold) as per forest cover JRC2020, GFC2013, FNF2020, and FAO. (b) Country-level estimates for Canada, the United States (USA), and Mexico using the same datasets. Error bars represent 95% confidence intervals of the estimates.

Table 4
Total estimated number of trees (in billions) in Canada, Mexico, and USA, based on FFNN predictions constrained by three spatial forest extent datasets—GFC2013, JRC2020, and FNF2020—and national statistics from FAO. Estimates are compared against Crowther et al. (2015).

		Current model (FFNN, DBH ≥10 cm)				Current model (FFNN, no DBH threshold)			
Country	Crowther et al. (2015)	JRC2020	GFC2013	FNF2020	FAO	JRC2020	GFC2013	FNF2020	FAO
Canada	318.18	281.23	190.31	239.48	245.48	621.58	418.07	510.79	542.25
Mexico	56.78	21.87	13.33	20.24	30.14	23.48	15.50	21.91	32.32
USA	228.29	193.00	124.39	150.72	160.46	510.79	304.15	365.94	390.34

productivity, land-use legacies, and disturbance regimes (Curtis et al., 2018; Hansen et al., 2013).

At the biome scale (Fig. 7), mean tree density varies substantially. Boreal and temperate coniferous forests exhibit the highest averages (664–682 trees·ha^{−1}), whereas tropical dry, Mediterranean, and desert systems show markedly lower values. Across biomes, density distributions are right-skewed, indicating that moderate densities dominate most landscapes, while very dense stands occupy a smaller proportion of total area, consistent with size–density and self-thinning dynamics (Reineke, 1933; Yoda et al., 1963). Even within deserts and tundra, localized riparian corridors and favorable microclimates support scattered tree presence, illustrating structural continuity across transitional ecosystems.

Spatial patterns of predictive uncertainty exhibit coherent continental organization (Fig. 6b). SE are generally low across much of the United States and southern Canada and increase toward northern boreal, mountainous, and environmentally heterogeneous regions. Elevated uncertainty is particularly evident in the Pacific Northwest, north-eastern forests, and portions of the western cordillera. These regions are characterized by strong environmental gradients, complex canopy structures, and mixed disturbance regimes that increase variability in spectral and structural predictors (Saarela et al., 2020; Turner, 2010). However, predictive uncertainty does not arise from ecological complexity alone.

Under MC Dropout, uncertainty represents epistemic variability associated with model parameter estimation (Gal and Ghahramani,

2016). Regions with dense and representative plot coverage constrain model weights and yield stable predictions across stochastic forward passes. Conversely, areas that lie near the margins of the training feature space or exhibit environmental heterogeneity that is unevenly sampled require greater extrapolation, increasing predictive dispersion (Meyer et al., 2021). Thus, elevated uncertainty in regions such as the Pacific Northwest and northeastern United States likely reflects a combination of ecological variability, feature-space sparsity, and sampling representativeness rather than ecological complexity alone.

In contrast, deserts and tundra exhibit comparatively lower uncertainty, consistent with narrower ranges of predictor variability and more constrained response surfaces. Because structural predictors such as GEDI canopy height were included in the model (Dubayah et al., 2022; Potapov et al., 2021), residual uncertainty is unlikely to result solely from missing structural information, but instead reflects the interaction between environmental heterogeneity, sampling density, and model extrapolation at 3-km resolution.

Comparisons between predicted tree density and biome classifications further indicate that structural vegetation patterns do not always align with categorical boundaries. Regions mapped as grassland or desert may still contain measurable tree cover, reflecting woodland remnants, riparian corridors, or transitional ecotones. This divergence underscores the value of structure-based monitoring derived from remote sensing, which captures canopy gradients continuously rather than relying solely on discrete land-cover classes (Hansen et al., 2013; Bonan, 2008).

4.4. Implication of remote sensing and environmental covariates

A notable result is that the FFNN and RF models achieved comparable predictive performance ($R^2 \approx 0.39$) while producing markedly different feature-importance rankings. The FFNN emphasized integrative climatic variables—aridity, canopy productivity (meanFpar), and temperature—suggesting strong sensitivity to broad hydroclimatic gradients. In contrast, the RF elevated precipitation seasonality (bio15), soil properties (clay content, pH), thermal extremes, and livestock density, highlighting edaphic constraints, climatic variability, and localized disturbance signals.

This divergence likely reflects structural differences in how the algorithms partition predictor space. Neural networks distribute weights across continuous gradients and nonlinear interactions, favoring predictors that explain smooth variation across environmental space (Reichstein et al., 2019; Olden and Jackson, 2002). Random Forests, by contrast, rely on recursive partitioning, which can accentuate threshold responses and may bias importance toward variables that produce strong splits (Strobl et al., 2007). Importantly, variable-importance measures in machine-learning models reflect algorithm structure and predictor correlation patterns rather than direct causal influence (Olden and Jackson, 2002).

One ecological interpretation is that tree density may be governed by hierarchical controls: Large-scale hydroclimatic gradients define broad constraints on forest structure, while soil properties, disturbance regimes, and climatic extremes modulate local expression within those limits. Broad climatic regulation of forest structure at continental scales is well documented (Bonan, 2008; Pan et al., 2011). However, an alternative explanation is equifinality—multiple correlated predictor sets yielding similar predictive performance without uniquely identifying dominant causal drivers (Beven, 2006).

Distinguishing between hierarchical control and equifinality requires scale-explicit analysis and potentially comparison with process-based ecosystem models that explicitly represent growth limitations and resource constraints. At present, the comparable predictive performance combined with divergent importance rankings suggests that both broad climatic gradients and local constraints contribute to continental forest structure, but their relative importance may vary across spatial scales and environmental contexts.

4.5. Methodological contributions and advances

This study introduces a modular and scalable framework for continental-scale estimation of tree density and total tree density across North America. By integrating harmonized forest inventory data with satellite-derived and environmental predictors, the framework bridges the gap between ground-based observations and wall-to-wall mapping. Its architecture, which comprises modules for data harmonization, forest masking, model training, spatial prediction, and uncertainty estimation—enables each component to evolve as new datasets or algorithms become available. This modularity enhances adaptability across regions and forest definitions while maintaining transparency and reproducibility.

In this study, the confidence-weighted, data-driven predictions arise specifically from the FFNN implementation. The neural network learns tree density directly from harmonized inventory and environmental data without imposing predefined functional forms, allowing complex nonlinear and interacting controls to emerge from the data. Importantly, the use of MC Dropout enables estimation of pixel level epistemic uncertainty alongside the predicted mean. Each 3 km prediction therefore includes both an expected tree density and an associated measure of reliability.

Pixel-level tree density predictions were generated at 3 km resolution and aggregated using four major forest-extent products (JRC2020; FAO2020, FNF2020; and GFC2013) to estimate total tree density. The resulting continental totals (339–514 billion trees) demonstrate both the

scalability of the approach and the sensitivity of large-area estimates to canopy-cover definitions. This integration of predictive modeling with multiple forest masks provides a practical means to reconcile divergent forest definitions, a long-standing challenge in global forest monitoring.

Epistemic uncertainty was quantified using MC Dropout, which samples multiple stochastic model realizations to approximate Bayesian inference (Gal and Ghahramani, 2016). This approach provides spatially explicit estimates of model confidence, enabling uncertainty-aware interpretation of predicted tree density and identification of regions where additional data collection or model refinement may be most beneficial.

The modular design readily accommodates emerging remote sensing data streams such as GEDI canopy structure (Dubayah et al., 2022), Sentinel-1 SAR backscatter, and multi-temporal Landsat or Sentinel-2 composites to improve temporal and vertical sensitivity. Comparable adaptive architectures underpin recent global biomass and canopy-height mapping efforts (Duncanson et al., 2022; Potapov et al., 2021), yet this framework advances the field by uniting harmonized inventories, interpretable deep learning, and spatially explicit uncertainty quantification within a reproducible, transferable pipeline for coarse-scale forest mapping.

4.6. Limitations and future directions

Despite broad spatial coverage and improved predictive accuracy, some opportunities for improvement in our approach remain. The spatial anonymization of plot coordinates introduces location uncertainty, which can reduce local precision in heterogeneous landscapes. Because our covariates are used at coarse resolution (≥ 1 km), that effect is partly mitigated, though edge conditions and ecotones may still impact results. Prediction accuracy also depends on data density: under-sampled regions such as tundra margins, arid zones, and parts of the boreal interior tend to carry higher epistemic uncertainty due to sparse ground observations (García-Soria et al., 2024).

A further source of uncertainty arises from the mismatch between fine-scale field measurements and coarser-resolution predictor variables. Differences in spatial support are known to increase variability and attenuate statistical relationships when point observations are compared with spatial averages (Atkinson and Tate, 2000; Heuvelink and Pebesma, 1999). In our case, this mismatch contributes to increased dispersion at the plot level. The observed increase in residual variability with within-cell heterogeneity, together with improved model agreement under spatial aggregation, suggests that sub-grid variability is a major contributor to this dispersion.

Our model produces a temporally static snapshot of tree density; it does not account for disturbance, succession, or land-use change, so it reflects current structure rather than temporal dynamics. While MC Dropout quantifies epistemic uncertainty (i.e., uncertainty in model weights) (Gal and Ghahramani, 2016), it does not capture aleatoric uncertainty arising from measurement noise, observer variation, or inherent environmental variability, uncertainties that heteroscedastic neural networks are designed to handle (Immer et al., 2023). Although harmonizing plot inventories improves consistency, residual regional bias may persist due to differences in sampling design, plot size, or DBH thresholds. Overcoming these limitations will require updated forest inventories and increased harmonization of ground datasets.

Future extensions should increase temporal and ecological sensitivity, potentially by combining multi-temporal optical or radar time series (e.g., Landsat, Sentinel) that could detect structural change and capture disturbance regimes (Amitrano et al., 2021). Incorporating intermediate-resolution datasets (e.g., Landsat) within multi-resolution or hierarchical modeling frameworks could also help reduce scale mismatch between field observations and coarse predictors. Including historical land-use, fire, logging records, or other data that reflects change and change agents could potentially inform model and feature selection, as well as data filtering. Moreover, employing heteroscedastic

models that jointly predict mean and variance can capture input-dependent aleatoric uncertainty, producing more complete confidence quantification (Gawlikowski et al., 2023). When combined with ensemble or probabilistic frameworks, such models could support scenario-based forecasting under climatic or ecological uncertainty (Koutsoyiannis et al., 2007). Although we did not adopt heteroscedastic models here due to computational and tuning demands, such approaches may become viable as computing power and data volumes increase.

5. Conclusion

We present a continent-scale, uncertainty-aware framework for mapping forest tree density at 3 km resolution across North America. By integrating more than 600,000 harmonized forest inventory plots with satellite-derived and environmental predictors, this approach fills spatial gaps in ground-based surveys and enables consistent, wall-to-wall characterization of forest structure across diverse biomes.

Applying this framework yields an estimated 339–514 billion forest trees (DBH ≥ 10 cm) across North America. The wide range highlights that forest-definition uncertainty, driven by differences among forest-extent products, can rival or exceed model-based uncertainty in large-area tree abundance estimates. This finding underscores the importance of explicitly accounting for definitional choices when reporting continental or global forest metrics.

Beyond tree density, the framework provides a modular and transferable pipeline for large-scale forest monitoring. Its combination of harmonized inventories, open-access remote sensing inputs, and explicit uncertainty quantification supports transparent, reproducible estimation of forest structural attributes and can be adapted to other regions with appropriate calibration. As such, this work contributes a practical foundation for uncertainty-aware forest monitoring and reporting at continental scales.

CRediT authorship contribution statement

Mustak Ahmad: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Formal analysis, Data curation, Conceptualization. **Yun Tang:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Andrew J. Lister:** Writing – review & editing, Writing – original draft, Methodology. **Javier G.P. Gamarra:** Writing – review & editing, Writing – original draft. **William G. Powell:** Writing – review & editing. **Nathan R. Beane:** Writing – review & editing. **Wook Jin Choi:** Writing – review & editing, Data curation. **Ankita Mitra:** Writing – review & editing, Data curation. **Amit Kumar:** Writing – review & editing, Data curation. **Anibal Cuchiatti:** Writing – review & editing, Data curation. **Alain Paquette:** Writing – review & editing, Data curation. **Eric Searle:** Writing – review & editing, Data curation. **Jiaxin Chen:** Writing – review & editing, Data curation. **Han Y.H. Chen:** Writing – review & editing, Data curation. **Frans Bongers:** Writing – review & editing, Data curation. **Jorge A. Meave:** Writing – review & editing, Data curation. **Mario Guevara:** Writing – review & editing, Data curation. **Aylin Barreras:** Writing – review & editing, Data curation. **José Armando Alanís de la Rosa:** Writing – review & editing, Data curation. **Rafael Mayorga Saucedo:** Writing – review & editing, Data curation. **Rubi Angélica Cuenca Lara:** Writing – review & editing, Data curation. **César Moreno García:** Writing – review & editing, Data curation. **Carlos Isaiás Godínez Valdivia:** Writing – review & editing, Data curation. **Carina Edith Delgado Caballero:** Writing – review & editing, Data curation. **Maria de los Ángeles Soriano Luna:** Writing – review & editing, Data curation. **Metzli Ileana Aldrete Leal:** Writing – review & editing, Data curation. **Sandra Liliana Medina Casillas:** Writing – review & editing, Data curation. **Johnny Romero Correa:** Writing – review & editing, Data curation. **Sergio Armando Villela Gaytán:** Writing – review & editing, Data curation. **J. Javier Corral Rivas:** Writing –

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Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the author(s) used ChatGPT (OpenAI, GPT-5) to assist in language editing and improving clarity. After using this tool, the author(s) carefully reviewed and edited the content to ensure accuracy and originality and take full responsibility for the final content of the published article.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2026.100466>.

Data availability

Data will be made available on request.

References

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* 259, 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>.
- Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J., Jetz, W., 2018. A suite of global, cross-scale topographic variables for environmental

- and biodiversity modeling. *Sci. Data* 5, 180040. <https://doi.org/10.1038/sdata.2018.40>.
- Amirano, D., Di Martino, G., Guida, R., Iervolino, P., Iodice, A., Papa, M.N., Riccio, D., Ruello, G., 2021. Earth environmental monitoring using multi-temporal synthetic aperture radar: a critical review of selected applications. *Remote Sens.* 13, 604. <https://doi.org/10.3390/rs13040604>.
- Atkinson, P.M., Tate, N.J., 2000. Spatial scale problems and geostatistical solutions: a review. *Prof. Geogr.* 52, 607–623. <https://doi.org/10.1111/0033-0124.00250>.
- Banskota, A., Kayastha, N., Falkowski, M.J., Wulder, M.A., Froese, R.E., White, J.C., 2014. Forest monitoring using landsat time series data: a review. *Can. J. Remote Sens.* 40, 362–384. <https://doi.org/10.1080/07038992.2014.987376>.
- [data set] Barreras, A., Alanís De La Rosa, J.A., Cuenca Lara, R.A., Moreno García, C., Godínez Valdivia, C.I., Delgado Caballero, C.E., Soriano Luna, M.D.L.A., George, S. P., Aldrete Leal, M.I., Medina Casillas, S.L., Romero Correa, J., Villela Gaytán, S.A., Guevara, M., 2022. National Forest and Soils Inventory of Mexico 2009–2014, Environmental Data Initiative. <https://doi.org/10.6073/PASTA/4620375AE631AB6A09C8573C7BF8AFF>.
- Barreras, A., Alanís de la Rosa, J.A., Mayorga, R., Cuenca, R., Moreno-G, C., Godínez, C., Delgado, C., Soriano-Luna, M. de los A., George, S., Aldrete-Leal, M.I., Medina, S., Romero, J., Villela, S., Lister, A., Sheridan, R., Flores, R., Crowther, T.W., Guevara, M., 2023. Spatial predictions of tree density and tree height across Mexico forests using ensemble learning and forest inventory data. *Ecol. Evol.* 13, e10090. <https://doi.org/10.1002/ece3.10090>.
- Batjes, N.H., 2016. Harmonized soil property values for broad-scale modelling (WISE30sec) with estimates of global soil carbon stocks. *Geoderma* 269, 61–68. <https://doi.org/10.1016/j.geoderma.2016.01.034>.
- Beck, H.E., Wood, E.F., McVicar, T.R., Zambrano-Bigiarini, M., Alvarez-Garretón, C., Baez-Villanueva, O.M., Sheffield, J., Karger, D.N., 2020. Bias correction of global high-resolution precipitation climatologies using streamflow observations from 9372 catchments. *J. Clim.* 33, 1299–1315.
- Belgiu, M., Dragut, L., 2016. Random forest in remote sensing: a review of applications and future directions. *ISPRS J. Photogramm. Remote Sens.* 114, 24–31.
- Beven, K., 2006. A manifesto for the equifinality thesis. *J. Hydrol.* 320, 18–36. <https://doi.org/10.1016/j.jhydrol.2005.07.007>.
- Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444–1449. <https://doi.org/10.1126/science.1155121>.
- Bongers, F., Popma, J., del Castillo, J.M., Carabias, J., 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* 74, 55–80. <https://doi.org/10.1007/BF00045614>.
- Bourgoin, C., Amezttoy, L., Verhegghen, A., Desclée, B., Carboni, S., Bastin, J.-F., Beuchle, R., Brink, A., Defourny, P., Delhez, B., Fritz, S., Gond, V., Herold, M., Lamarche, C., Mansuy, N., Mollicone, D., Oom, D., Peedell, S., San-Miguel, J., Colditz, R., Achard, F., 2024. Mapping Global Forest Cover of the Year 2020 to Support the EU Regulation on Deforestation-free Supply Chains, JRC136960. European Commission. <https://doi.org/10.2760/262532>.
- Brandt, M., Tucker, C.J., Kariyaa, A., Rasmussen, K., Abel, C., Small, J., Chave, J., Rasmussen, L.V., Hiernaux, P., Diouf, A.A., 2020. An unexpectedly large count of trees in the West African Sahara and Sahel. *Nature* 587, 78–82. <https://doi.org/10.1038/s41586-020-2824-5>.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45, 5–32. <https://doi.org/10.1023/A:1010933404324>.
- Cao, D.-S., Liang, Y.-Z., Xu, Q.-S., Zhang, L.-X., Hu, Q.-N., Li, H.-D., 2011. Feature importance sampling-based adaptive random forest as a useful tool to screen underlying lead compounds. *J. Chemom.* 25, 201–207.
- Chen, H.Y.H., Luo, Y., 2015. Net aboveground biomass declines of four major forest types with forest ageing and climate change in western Canada's boreal forests. *Glob. Change Biol.* 21, 3675–3684. <https://doi.org/10.1111/gcb.12994>.
- Corral-Rivas, J.J., Torres-Rojo, J.M., Luján-Soto, J.E., Nava-Miranda, M.G., Aguirre-Calderón, O.A., 2016. Density and production in the natural forests of Durango/Mexico. *Allg. Forst Jgdtzgt.* 187, 93–103.
- Crowther, T.W., Glick, H.B., Covey, K.R., Bettigole, C., Maynard, D.S., Thomas, S.M., Smith, J.R., Hintler, G., Duguid, M.C., Amatulli, G., Tuanmu, M.-N., Jetz, W., Salas, C., Stam, C., Piotto, D., Tavani, R., Green, S., Bruce, G., Williams, S.J., Wiser, S.K., Huber, M.O., Hengeveld, G.M., Nabuurs, G.-J., Tikhonova, E., Borchardt, P., Li, C.-F., Powrie, L.W., Fischer, M., Hemp, A., Homeier, J., Cho, P., Vibrans, A.C., Umunay, P.M., Piao, S.L., Rowe, C.W., Ashton, M.S., Crane, P.R., Bradford, M.A., 2015. Mapping tree density at a global scale. *Nature* 525, 201–205. <https://doi.org/10.1038/nature14967>.
- Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. *Science* 361, 1108–1111. <https://doi.org/10.1126/science.aau3445>.
- Didan, K., Munoz, A.B., Solano, R., Huete, A., 2015. MODIS vegetation index user's guide (MOD13 series), Version 3.00. In: *Vegetation Index and Phenology Lab*, vol. 35. The University of Arizona, pp. 2–33.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- Dubayah, R., Blair, J.B., Goetz, S., Fatoyinbo, L., Hansen, M., Healey, S., Hofton, M., Hurr, G., Kellner, J., Luthcke, S., Armston, J., Tang, H., Duncanson, L., Hancock, S., Jantz, P., Marselis, S., Patterson, P.L., Qi, W., Silva, C., 2022. The global ecosystem dynamics investigation: high-resolution laser ranging of the Earth's forests and topography. *Sci. Remote Sens.* 1, 100002. <https://doi.org/10.1016/j.srs.2020.100002>.
- Duncanson, L., Kellner, J.R., Armston, J., Dubayah, R., Minor, D.M., Hancock, S., Healey, S.P., Patterson, P.L., Saarela, S., Marselis, S., Silva, C.E., Bruneing, J., Goetz, S.J., Tang, H., Hofton, M., Blair, B., Luthcke, S., Fatoyinbo, L., Abernethy, K., Alonso, A., Andersen, H.-E., Applin, P., Baker, T.R., Barbier, N., Bastin, J.F., Biber, P., Boeckx, P., Bogaert, J., Boschetti, L., Boucher, P.B., Boyd, D.S., Burslem, D.F.R.P., Calvo-Rodriguez, S., Chave, J., Chazdon, R.L., Clark, D.B., Clark, D.A., Cohen, W.B., Coomes, D.A., Corona, P., Cushman, K.C., Cutler, M.E.J., Dalling, J.W., Dalponte, M., Dash, J., de-Miguel, S., Deng, S., Ellis, P.W., Erasmus, B., Fekety, P.A., Fernandez-Landa, A., Ferraz, A., Fischer, R., Fisher, A.G., García-Abril, A., Gobakken, T., Hacker, J.M., Heinrich, M., Hill, R.A., Hopkinson, C., Huang, H., Hubbell, S.P., Hudak, A.T., Huth, A., Imbach, B., Jeffery, K.J., Katoh, M., Kearsley, E., Kenfack, D., Kljun, N., Knapp, N., Král, K., Krüček, M., Labrière, N., Lewis, S.L., Longo, M., Lucas, R.M., Main, R., Manzanera, J.A., Martínez, R.V., Mathieu, R., Memiaghe, H., Meyer, V., Mendoza, A.M., Moneris, A., Montesano, P., Morsdorf, F., Næsset, E., Naidoo, L., Nilus, R., O'Brien, M., Orwig, D.A., Papathanassiou, K., Parker, G., Philipson, C., Phillips, O.L., Pisek, J., Poulsen, J.R., Pretzsch, H., Rüdiger, C., Saatchi, S., Sanchez-Azofeifa, A., Sanchez-Lopez, N., Scholes, R., Silva, C.A., Simard, M., Skidmore, A., Stereńczak, K., Tanase, M., Torresan, C., Valbuena, R., Verbeeck, H., Vrska, T., Wessels, K., White, J.C., White, L.J.T., Zahabu, E., Zraggen, C., 2022. Aboveground biomass density models for NASA's Global Ecosystem Dynamics Investigation (GED) lidar mission. *Remote Sens. Environ.* 270, 112845. <https://doi.org/10.1016/j.rse.2021.112845>.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Syst.* 40, 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>.
- FAO, 2020. Global forest resources assessment 2020: main report. Food Agri. Organiz. United Nations. <https://www.fao.org/interactive/forest-resources-assessment/2020/en/>. (Accessed 14 November 2025).
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315. <https://doi.org/10.1002/joc.5086>.
- Gal, Y., Ghahramani, Z., 2016. Dropout as a bayesian approximation: representing model uncertainty in deep learning. In: *Proceedings of the 33rd International Conference on Machine Learning*. Presented at the International Conference on Machine Learning, PMLR, pp. 1050–1059.
- García-Soria, J.L., Morata, M., Berger, K., Pascual-Venteo, A.B., Rivera-Caicedo, J.P., Verrelst, J., 2024. Evaluating epistemic uncertainty estimation strategies in vegetation trait retrieval using hybrid models and imaging spectroscopy data. *Remote Sens. Environ.* 310, 114228. <https://doi.org/10.1016/j.rse.2024.114228>.
- Gawlikowski, J., Tassi, C.R.N., Ali, M., Lee, J., Humt, M., Feng, J., Kruspe, A., Triebel, R., Jung, P., Roscher, R., Shahzad, M., Yang, W., Bamler, R., Zhu, X.X., 2023. A survey of uncertainty in deep neural networks. *Artif. Intell. Rev.* 56, 1513–1589. <https://doi.org/10.1007/s10462-023-10562-9>.
- Gilbert, M., Nicolas, G., Cinardi, G., Van Boeckel, T.P., Vanwambeke, S.O., Wint, G., Robinson, T.P., 2018. Global distribution data for cattle, buffaloes, horses, sheep, goats, pigs, chickens and ducks in 2010. *Sci. Data* 5, 1–11.
- Gillis, M.D., Omule, A.Y., Brierley, T., 2005. Monitoring Canada's forests: the national forest inventory. *For. Chron.* 81, 214–221. <https://doi.org/10.5558/frc81214-2>.
- Glick, H.B., Bettigole, C., Maynard, D.S., Covey, K.R., Smith, J.R., Crowther, T.W., 2016. Spatially-explicit models of global tree density. *Sci. Data* 3, 160069. <https://doi.org/10.1038/sdata.2016.69>.
- Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A., Schlesinger, W.H., Shoch, D., Siikamäki, J.V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R.T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M.R., Herrero, M., Kiesecker, J., Landis, E., Laestadius, L., Leavitt, S.M., Minnemeyer, S., Polasky, S., Potapov, P., Putz, F.E., Sanderman, J., Silvius, M., Wollenberg, E., Fargione, J., 2017. Natural climate solutions. *Proc. Natl. Acad. Sci.* 114, 11645–11650. <https://doi.org/10.1073/pnas.1710465114>.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-Century forest cover change. *Science* 342, 850–853. <https://doi.org/10.1126/science.1244693>.
- Heuvelink, G.B.M., Pebesma, E.J., 1999. Spatial aggregation and soil process modelling. *Geoderma* 89, 47–65. [https://doi.org/10.1016/S0016-7061\(98\)00077-9](https://doi.org/10.1016/S0016-7061(98)00077-9).
- Hufkens, K., Scheunders, P., Ceulemans, R., 2009. Ecotones in vegetation ecology: methodologies and definitions revisited. *Ecol. Res.* 24, 977–986. <https://doi.org/10.1007/s11284-009-0584-7>.
- Immer, A., Palumbo, E., Marx, A., Vogt, J., 2023. Effective bayesian heteroscedastic regression with deep neural networks. In: Oh, A., Naumann, T., Globerson, A., Saenko, K., Hardt, M., Levine, S. (Eds.), *Advances in Neural Information Processing Systems*. Curran Associates, Inc., pp. 53996–54019.
- James, G., Witten, D., Hastie, T., Tibshirani, R., 2013. *An Introduction to Statistical Learning: with Applications in R*. Springer, New York. <https://doi.org/10.1007/978-1-0716-1418-1>.
- Koutsoyiannis, D., Efstratiadis, A., Georgakakos, K.P., 2007. Uncertainty assessment of future hydroclimatic predictions: a comparison of probabilistic and scenario-based approaches. *J. Hydrometeorol.* 8 (3), 261–281. <https://doi.org/10.1175/JHM576.1>.
- Lausch, A., Erasmí, S., King, D.J., Magdon, P., Heurich, M., 2016. Understanding forest health with remote sensing -Part I—A review of spectral traits, processes and remote-sensing characteristics. *Remote Sens.* 8, 1029. <https://doi.org/10.3390/rs8121029>.
- Lee, H., Pugh, T.A.M., Patacca, M., Seo, B., Winkler, K., Rounsevell, M., 2023. Three billion new trees in the EU's biodiversity strategy: low ambition, but better

- environmental outcomes? *Environ. Res. Lett.* 18, 034020. <https://doi.org/10.1088/1748-9326/acb95c>.
- Li, S., Brandt, M., Fensholt, R., Kariryaa, A., Igel, C., Gieseke, F., Nord-Larsen, T., Oehmcke, S., Carlsen, A.H., Junttila, S., Tong, X., d'Aspremont, A., Ciaia, P., 2023. Deep learning enables image-based tree counting, crown segmentation, and height prediction at national scale. *PNAS Nexus* 2. <https://doi.org/10.1093/pnasnexus/pgad076>.
- Liang, J., Gamarra, J.G.P., Picard, N., Zhou, M., Pijanowski, B., Jacobs, D.F., Reich, P.B., Crowther, T.W., Nabuurs, G.-J., de-Miguel, S., Fang, J., Woodall, C.W., Svenning, J.-C., Jucker, T., Bastin, J.-F., Wiser, S.K., Slik, F., Hérault, B., Alberti, G., Keppel, G., Hengeveld, G.M., Ibsch, P.L., Silva, C.A., ter Steege, H., Peri, P.L., Coomes, D.A., Searle, E.B., von Gadow, K., Jaroszewicz, B., Abbasi, A.O., Abegg, M., Yao, Y.C.A., Aguirre-Gutiérrez, J., Zambrano, A.M.A., Altman, J., Alvarez-Dávila, E., Álvarez-González, J.G., Alves, L.F., Amani, B.H.K., Amani, C.A., Ammer, C., Ilondea, B.A., Antón-Fernández, C., Avitabile, V., Aymard, G.A., Azihou, A.F., Baard, J.A., Baker, T.R., Balazy, R., Bastian, M., Batumike, R., Bauters, M., Beeckman, H., Benu, N.M.H., Bitariho, R., Boeckx, P., Bogaert, J., Bongers, F., Bouriaud, O., Brancalion, P.H.S., Brandt, S., Brearley, F.Q., Briseno-Reyes, J., Broadbent, E.N., Bruielheide, H., Bulte, E., Catlin, A.C., Cazzolla Gatti, R., César, R.G., Chen, H.Y.H., Chisholm, C., Cienciala, E., Colletta, G.D., Corral-Rivas, J.J., Cuchietti, A., Cuni-Sanchez, A., Dar, J.A., Dayanandan, S., de Haulleville, T., Decuyper, M., Delabye, S., Derroire, G., DeVries, B., Diisi, J., Do, T.V., Dolezal, J., Dourdain, A., Durrheim, G.P., Obiang, N.L.E., Ewango, C.E.N., Eyre, T.J., Fayle, T.M., Feunang, L.F.N., Finér, L., Fischer, M., Fridman, J., Frizzera, L., de Gaspar, A.L., Gianelle, D., Glick, H.B., Gonzalez-Ezido, M.S., Gorenstein, L., Habonay, R., Hardy, O.J., Harris, D.J., Hector, A., Hemp, A., Herold, M., Hillers, A., Hubau, W., Ibanez, T., Imai, N., Imani, G., Jagodzinski, A.M., Janeczek, S., Johannsen, V.K., Joly, C.A., Jumbam, B., Kabelong, B.L.P.R., Kahsay, G.A., Karminov, V., Kartawinata, K., Kassi, J.N., Kearsley, E., Kennard, D.K., Kepfer-Rojas, S., Khan, M.L., Kigomo, J.N., Kim, H.S., Klauberg, C., Klomberg, Y., Korjus, H., Kothandaraman, S., Kraxner, F., Kumar, A., Kuswandi, R., Lang, M., Lawes, M.J., Leite, R.V., Lentner, G., Lewis, S.L., Libalah, M.B., Lisingo, J., López-Serrano, P.M., Lu, H., Lukina, N.V., Lykke, A.M., Maicher, V., Maitrey, B.S., Marcon, E., Marshall, A.R., Martin, E.H., Martynenko, O., Mbayu, F.M., Mbui, M.T.E., Meave, J.A., Merow, C., Mischicki, S., Moreno, V.S., Morera, A., Mukul, S.A., Müller, J.C., Murdjoko, A., Nava-Miranda, M.G., Ndiye, L.E., Neldner, V.J., Nenovic, R.V., Nforbelie, L.N., Ngho, M.L., N'Guessan, A.E., Ngugi, M.R., Ngute, A.S.K., Njila, E.N.N., Nyako, M.C., Ochudo, T.O., Oleksyn, J., Paquette, A., Parfenova, E.I., Park, M., Parren, M., Parthasarathy, N., Pfautsch, S., Phillips, O.L., Piedade, M.T.F., Pionto, D., Pollastrini, M., Poorter, L., Poulsen, J.R., Poulsen, A.D., Pretzsch, H., Rodeghiero, M., Rolim, S.G., Rovero, F., Rutishauser, E., Sagheb-Talebi, K., Saikia, P., Sainge, M.N., Salas-Eljatib, C., Salis, A., Schall, P., Schepaschenko, D., Scherer-Lorenzen, M., Schmid, B., Schöngart, J., Šebek, V., Sellan, G., Selvi, F., Serra-Diaz, J.M., Sheil, D., Shvidenko, A.Z., Sist, P., Souza, A.F., Stereńczak, K.J., Sullivan, M.J.P., Sundarapandian, S., Svoboda, M., Swaine, M.D., Targhetta, N., Tchekakova, N., Trethowan, L.A., Tropek, R., Mukendi, J.T., Ullman, P.M., Usoltsev, V.A., Vaglio Laurin, G., Valentini, R., Valladares, F., van der Plas, F., Vega-Nieva, D.J., Verbeeck, H., Viana, H., Vibrans, A.C., Vieira, S.A., Vlemminckx, J., Waite, C.E., Wang, H.-F., Wasingya, E.K., Wekesa, C., Westerlund, B., Wittmann, F., Wortel, V., Zawila-Niedzwiecki, T., Zhang, C., Zhao, X., Zhu, J., Zhu, X., Zhu, Z.-X., Zo-Bi, C., Hui, C., 2022. Co-limitation towards lower latitudes shapes global forest diversity gradients. *Nat. Ecol. Evol.* 6, 1423–1437. <https://doi.org/10.1038/s41559-022-01831-x>.
- Lundberg, S.M., Erion, G., Chen, H., DeGrave, A., Prutkin, J.M., Nair, B., Katz, R., Himmelfarb, J., Bansal, N., Lee, S.-I., 2020. From local explanations to global understanding with explainable AI for trees. *Nat. Mach. Intell.* 2, 56–67. <https://doi.org/10.1038/s42256-019-0138-9>.
- Ma, H., Mo, L., Crowther, T.W., Maynard, D.S., van den Hoogen, J., Stocker, B.D., Terrer, C., Zohner, C.M., 2021. The global distribution and environmental drivers of aboveground versus belowground plant biomass. *Nat. Ecol. Evol.* 5, 1110–1122. <https://doi.org/10.1038/s41559-021-01485-1>.
- Malone, T., Liang, J., Packee, E.C., 2022. Cooperative Alaska Forest Inventory, Gen Tech Rep PNW-GTR-785. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland. <https://doi.org/10.2737/PNW-GTR-785>.
- McRoberts, R.E., Bechtold, W.A., Patterson, P.L., Scott, C.T., Reams, G.A., 2005. The enhanced forest inventory and analysis program of the USDA forest service: historical perspective and announcement of statistical documentation. *J. For.* 103, 304–308. <https://doi.org/10.1093/jof/103.6.304>.
- McRoberts, R.E., Næsset, E., Gobakken, T., 2015. The effects of temporal differences between map and ground data on map-assisted estimates of forest area and biomass. *Ann. For. Sci.* 73, 839–847. <https://doi.org/10.1007/s13595-015-0485-6>.
- McRoberts, R.E., Næsset, E., Saatchi, S., Quegan, S., 2022. Statistically rigorous, model-based inferences from maps. *Remote Sens. Environ.* 279, 113028.
- Meyer, M., Wiederkehr, I., Koldewey, C., Dumitrescu, R., 2021. Understanding usage data-driven product planning: a systematic literature review. *Proc. Des. Soc.* 1, 3289–3298. <https://doi.org/10.1017/pds.2021.590>.
- [data set] Myneni, R., Knyazikhin, Y., Park, T., 2021. MODIS/Terra+ aqua leaf area Index/FPAR 4-day L4 global 500m SIN grid V061. NASA land processes distributed active archive center. <https://doi.org/10.5067/MODIS/MCD15A3H.061>.
- O'Connell, B.M., LaPoint, E.B., Turner, J.A., Ridley, T., Pugh, S.A., 2014. The Forest Inventory and Analysis Database: Database Description and User's Manual Version 6.0.1 for Phase 2. U.S. Department of Agriculture, Forest Service, Washington, DC.
- Olden, J.D., Jackson, D.A., 2002. Illuminating the “black box”: a randomization approach for understanding variable contributions in artificial neural networks. *Ecol. Model.* 154, 135–150. [https://doi.org/10.1016/S0304-3800\(02\)00064-9](https://doi.org/10.1016/S0304-3800(02)00064-9).
- Olofsson, P., Foody, G.M., Herold, M., Stehman, S.V., Woodcock, C.E., Wulder, M.A., 2014. Good practices for estimating area and assessing accuracy of land change. *Remote Sens. Environ.* 148, 42–57. <https://doi.org/10.1016/j.rse.2014.02.015>.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander Jr., J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1–43. <https://doi.org/10.2307/2963479>.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciaia, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 333, 988–993. <https://doi.org/10.1126/science.1201609>.
- Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Glob. Ecol. Biogeogr.* 20, 170–180. <https://doi.org/10.1111/j.1466-8238.2010.00592.x>.
- Paszke, A., Gross, S., Massa, F., Lerer, A., Bradbury, J., Chanan, G., Killeen, T., Lin, Z., Gimelshein, N., Antiga, L., Desmaison, A., Kopf, A., Yang, E., DeVito, Z., Raison, M., Tejani, A., Chilamkurthy, S., Steiner, B., Fang, L., Bai, J., Chintala, S., 2019. PyTorch: an imperative style, high-performance deep learning library. *Advances in Neural Information Processing Systems*. Curran Associates, Inc.
- Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., Blondel, M., Prettenhofer, P., Weiss, R., Dubourg, V., Vanderplas, J., Passos, A., Cournapeau, D., 2011. Scikit-learn: machine learning in python. *J. Mach. Learn. Res.* 12, 2825–2830.
- Phillips, O., Phillips, O., Miller, J.S., Garden, M.B., 2002. *Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Data Set*. Missouri Botanical Garden Press, St. Louis, Missouri, U.S.A.
- Potapov, P., Li, X., Hernandez-Serna, A., Tyukavina, A., Hansen, M.C., Kommareddy, A., Pickens, A., Turubanova, S., Tang, H., Silva, C.E., Armstrong, J., Dubayah, R., Blair, J. B., Hofton, M., 2021. Mapping global forest canopy height through integration of GEDI and landsat data. *Remote Sens. Environ.* 253, 112165. <https://doi.org/10.1016/j.rse.2020.112165>.
- Reichstein, M., Camps-Valls, G., Stevens, B., Jung, M., Denzler, J., Carvalhais, N., Prabhat, 2019. Deep learning and process understanding for data-driven Earth system science. *Nature* 566, 195–204.
- Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forest. *J. Agric. Res.* 46, 627–638.
- Roosbeh, M., Babaie-Kafaki, S., Naeimi Sadigh, A., 2018. A heuristic approach to combat multicollinearity in least trimmed squares regression analysis. *Appl. Math. Model.* 57, 105–120. <https://doi.org/10.1016/j.apm.2017.11.011>.
- [data set] Running, S., Mu, Q., Zhao, M., 2021. MODIS/terra Net Evapotranspiration 8-day L4 Global 500m SIN Grid V061. NASA Land Processes Distributed Active Archive Center. <https://doi.org/10.5067/MODIS/MOD16A2.061>.
- Saarela, S., Holm, S., Grafström, A., Schnell, S., Næsset, E., Gregoire, T.G., Nelson, R.F., Ståhl, G., 2016. Hierarchical model-based inference for forest inventory utilizing three sources of information. *Ann. For. Sci.* 73, 895–910. <https://doi.org/10.1007/s13595-016-0590-1>.
- Saarela, S., Wästlund, A., Holmström, E., Mensah, A.A., Holm, S., Nilsson, M., Fridman, J., Ståhl, G., 2020. Mapping aboveground biomass and its prediction uncertainty using LiDAR and field data, accounting for tree-level allometric and LiDAR model errors. *For. Ecosyst.* 7, 43. <https://doi.org/10.1186/s40663-020-00245-0>.
- Searle, E.B., Chen, H.Y.H., 2017. Tree size thresholds produce biased estimates of forest biomass dynamics. *For. Ecol. Manag.* 400, 468–474. <https://doi.org/10.1016/j.foreco.2017.06.042>.
- Seidl, R., Spies, T.A., Rammer, W., Steel, E.A., Pabst, R.J., Olsen, K., 2012. Multi-scale drivers of spatial variation in old-growth forest carbon density disentangled with Lidar and an individual-based landscape model. *Ecosystems* 15, 1321–1335.
- Shimada, M., Itoh, T., Motooka, T., Watanabe, M., Shiraishi, T., Thapa, R., Lucas, R., 2014. New global forest/non-forest maps from ALOS PALSAR data (2007–2010). *Remote Sens. Environ.* 155, 13–31. <https://doi.org/10.1016/j.rse.2014.04.014>.
- Sothe, C., Gonsamo, A., Lourenço, R.B., Kurz, W.A., Snider, J., 2022. Spatially continuous mapping of forest canopy height in Canada by combining GEDI and ICESat-2 with PALSAR and sentinel. *Remote Sens.* 14, 5158. <https://doi.org/10.3390/rs14205158>.
- Strobl, C., Boulesteix, A.-L., Zeileis, A., Hothorn, T., 2007. Bias in random forest variable importance measures: illustrations, sources and a solution. *BMC Bioinf.* 8, 25. <https://doi.org/10.1186/1471-2105-8-25>.
- Tomppo, E., Gschwanter, T., Lawrence, M., McRoberts, R.E., 2010. *National Forest Inventories: Pathways for Common Reporting*. Springer, Netherlands, Dordrecht. <https://doi.org/10.1007/978-90-481-3233-1>.
- Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849. <https://doi.org/10.1890/10.0097.1>.
- Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Pekete, B.M., Levy, M.A., Watson, J.E.M., 2017. Data from: global terrestrial human footprint maps for 1993 and 2009. <https://doi.org/10.5061/DRYAD.052Q5>.
- Wan, Z., 2013. MODIS Land Surface Temperature Products Users' Guide. University of California, Santa Barbara CA USA. https://lpdaac.usgs.gov/documents/118/MOD11_User_Guide_V6.pdf. (Accessed 14 November 2025).
- West, G.B., Enquist, B.J., Brown, J.H., 2009. A general quantitative theory of forest structure and dynamics. *Proc. Natl. Acad. Sci.* 106, 7040–7045. <https://doi.org/10.1073/pnas.0812294106>.
- Wulder, M.A., White, J.C., Fournier, R.A., Luther, J.E., Magnussen, S., 2008. Spatially explicit large area biomass estimation: three approaches using forest inventory and remotely sensed imagery in a GIS. *Sensors* 8, 529–560.
- Xiao, J., Sun, G., Potter, K.M., Boggs, J., Zhang, Q., McNulty, S.G., 2024. Do experimental forests and ranges of the southeastern United States represent the climate, ecosystem

- structure, and ecosystem functions of the region? *J. For.* 122, 431–449. <https://doi.org/10.1093/jofore/fvae020>.
- Xu, K., Li, J., Zhang, J., Xing, D., He, F., 2025. How many trees are there in the North American boreal forest? *Ecography* 2025, e07677. <https://doi.org/10.1002/ecog.07677>.
- Yoda, K., Kira, T., Ogawa, H., Hozumi, K., 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *J. Biol.* 14, 107–129.
- Zhu, X.X., Tuia, D., Mou, L., Xia, G.-S., Zhang, L., Xu, F., Fraundorfer, F., 2017. Deep learning in remote sensing: a comprehensive review and list of resources. *IEEE Geosci. Remote Sens. Mag.* 5, 8–36. <https://doi.org/10.1109/MGRS.2017.2762307>.
- Zimmerman, D.L., Hoef, J.M.V., 2024. *Spatial Linear Models for Environmental Data*. Chapman and Hall/CRC, New York. <https://doi.org/10.1201/9780429060878>.
- Zomer, R.J., Xu, J., Trabucco, A., 2022. Version 3 of the global aridity index and potential evapotranspiration database. *Sci. Data* 9, 409.