Remote sensing and geographic analysis of woody vegetation provide means of evaluating the distribution of natural resources, patterns of biodiversity and ecosystem structure, and socio-economic drivers of resource utilization. While these methods bring geographic datasets with global coverage into our day-to-day analytic spheres, many of the studies that rely on these strategies do not capitalize on the extensive collection of existing field data. We present the methods and maps associated with the first spatially-explicit models of global tree density, which relied on over 420,000 forest inventory field plots from around the world. This research is the result of a collaborative effort engaging over 20 scientists and institutions, and capitalizes on an array of analytical strategies. Our spatial data products offer precise estimates of the number of trees at global and biome scales, but should not be used for local-level estimation. At larger scales, these datasets can contribute valuable insight into resource management, ecological modelling efforts, and the quantification of ecosystem services.

Design Type(s) | data integration objective • observation design
--- | ---
Measurement Type(s) | tree density
Technology Type(s) | digital curation
Factor Type(s) | Data Type
Sample Characteristic(s) | Earth • elevation • slope • physiographic feature • soil • surface soil • air temperature • hydrological precipitation process • evapotranspiration • arid • vegetation layer • anthropogenic geographic feature • anthropogenic environmental process • terrestrial biome

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Background & Summary

In this paper we detail the background, methods, and data associated with the first spatially-continuous model of global tree density. This research was motivated by (i) a gap in the publically available forest-based geospatial data products, (ii) a specific request from Plant for the Planet Foundation, and (iii) recently published estimates of tree density in the Amazon basin implying that the previous estimate of the number of trees globally was potentially an order of magnitude too low.

Forests cover approximately one-third of the world’s terrestrial land surface. They are fundamental in dictating ecosystem structure, biogeochemical processes, animal habitat, biomass and carbon sequestration, and anthropogenic demand for building materials, pulp products, and fuelwood. An understanding of the extent of forest resources plays a critical role in sustainable forest management, helping to guide policy and to provide key targets for initiatives like the Convention on Biological Diversity’s Strategic Plan for Biodiversity 2011–2020 (ref. 13), the United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation in Developing Countries (REDD)14, and the landmark 2015 United Nations Conference of Parties Agreement15–17.

A number of recent studies inform our understanding of the distribution and extent of forest resources. However, until recently, global scale models have not focused on estimating forest population parameters such as total tree numbers or tree density. These variables complement existing data (e.g., refs 19,22–24) and lend themselves to modelling biogeochemical processes, nutrient cycling, habitat suitability, forest biodiversity27, and drivers of forest structure and heterogeneity28,29. Furthermore, the number and density of trees are intuitive metrics of interest to public and non-governmental organizations, particularly those focused on tree planting, such as New York City’s MillionTreesNYC32 and the United Nations Environment Programme’s (UNEP) ‘Billion Tree Campaign’33.

To quantify the proportional impact of these reforestation campaigns and to establish meaningful reforestation targets, a baseline understanding of current tree numbers was essential. We initially developed the global tree density analysis to address this uncertainty. Further, we hypothesized that available data would demonstrate the extent to which biophysical and social variables interact to regulate global patterns in tree abundance. The previous estimate for the global number of trees was approximately 400.25 billion—a mere 10 billion more than has been estimated for the Amazon basin during a recent broad-scale inventory—highlighting a critical gap in our understanding of global tree densities.

We emphasize that the modelling approach described herein provides precise estimates of total number of trees and mean tree density at global and biome scales. However, this precision does not necessarily apply to smaller scales and our data products should not be used for local- or regional-scale analysis without further assessment (see Usage Notes).

Methods

Overview

To model global tree density we employed a spatially-explicit approach in which (i) field measurements were first linked to a suite of remote sensing and GIS covariates; (ii) predictive regression models were then developed using model selection criteria; and (iii) these models were then applied in a pixel-level map algebraic framework to develop spatially-explicit predictions of global tree density (Fig. 1).

Data collection and standardization

To model tree density across large geographic extents we collected field-based forest inventory plot records from around the globe. Plot-level data was obtained through three channels: (i) major forestry databases, (ii) peer-reviewed studies, and (iii) correspondence with individual scientists. We used both national and international forestry databases, including National Forest Inventory (NFI) analyses from 21 countries, the Global Index of Vegetation-Plot Database (GIVD http://www.givd.info), the Smithsonian Tropical Research Institute’s in-house database (http://www.stri.si.edu), and ICP-Level-I plot data for most of Europe (http://www.icp-forests.org). These sources provided the vast majority of our data, but were supplemented with inventory data reported through peer-reviewed publications during the last 10 years. Small, unpublished collections of field data were obtained through several contacts where we lacked broad-scale inventory data (P. Umunay, DRC; R. Tavani, European NFI).

Although we defined trees as those larger than 10 cm diameter at breast height (DBH; i.e., to separate established trees from seedlings and saplings), the minimum-diameter thresholds for what constitutes a tree vary by country and inventory purpose. In the U.S. NFI—the Forest Inventory and Analysis National Program (FIA)—a tree is defined as a plant with a woody stem and DBH equal to or greater than 12.7 cm (i.e., 5 in). However, the 10 cm DBH threshold is used across most international forest inventory analyses, and the U.S. FIA was easily adapted to this level. After threshold identification, plot data was cleaned and collated using R (v. 3.1.x, Core R Development Team 2015), providing a total of 429,775 independent records for which we had, at a minimum: (i) latitude, (ii) longitude, and (iii) tree density (trees per hectare). Density measurements were derived through a number of proven field methods, including both fixed and variable radius plot sampling.
Figure 1. A conceptual model of our analytical process. (a) We amassed over 420,000 forest inventory plot records from every continent except Antarctica. (b) We acquired and unified an initial pool of four-dozen spatial covariates to use in model development. (c) We selected a subset of spatial covariates, extracted their values at field plot locations, and bound these values to the plot records. (d) For each of 14 biomes we subjected the enhanced plot records to hierarchical (agglomerative) clustering to identify the least collinear collection of covariates. (e) Generalized linear models were fit to every possible combination of clustered covariates. (f) A top ranking predictive model was selected or created through model averaging. (g) Each biome’s top ranking model was applied in a pixel-level map algebraic framework. (h) We scaled a penultimate spatial model of tree density using land cover data to arrive at our final predictions.
In the U.S., FIA data had been subjected to ‘jiggering’ or ‘fuzzing’, and ‘swapping’, in which plot locations had been spatially relocated by the US Forest Service to prohibit direct knowledge of plot locations36,37. A jiggered plot is generally less than 0.5 mi, but up to 1 mi, from the original plot location, and is to be placed in a stand that shares comparable structural attributes (i.e., the density of a jiggered plot must match the density of its true plot). McRoberts et al.36 suggest that plot jiggering should not introduce extensive bias in regression modelling when working with large pixel sizes (here ~1 km²), large sample sizes, and across broad spatial extents (see Acquisition and pre-processing of spatial data). Swapping describes the swapping of up to 20% of private plot coordinates between comparable plots within the same county, making local-level estimate impossible. Neither jiggering nor swapping should have affected our results given the spatial extents of our models.

Acquisition and pre-processing of spatial data
To generate spatially-explicit estimates of global tree density, we first acquired or developed 48 map-based covariates to consider during model development (Table 1 (available online only)). These datasets were pre-processed using R’s ‘raster’ package38, ArcMap 10.1 (ESRI, Redlands, CA), and conventional spatial data management strategies, including, as necessary: mosaicking raster tiles and unifying projections, ensuring precise pixel-level spatial coincidence using environmental processing controls and nearest neighbor resampling, using map algebraic operators and ArcGIS geoprocessing tools to create derivatives, performing spatial extractions (masking) to ensure a common spatial extent across datasets, and performing spatial joins to extract covariate values (Table 2). Each of the 48 datasets was obtained and initially managed using the World Geodetic System 1984 (WGS84) at a spatial resolution of 30-arc seconds (0.008333 degrees). Covariate pixel values were bound to spatially coincident field plot locations stored in a vector point file, ultimately producing a single tabular dataset from which to generate statistical models. During preliminary data exploration we discarded 28 less useful covariates based on (i) multicollinearity and (ii) mismatches between spatial resolution and scale. The remaining 20 covariates captured a range of topographic, climatic, vegetative, and anthropogenic factors (Table 1 (available online only)). We present the full complement of covariates and their primary sources, including those omitted in final analyses, to provide a clear sense of the data considered throughout model development.

Given the inherent variability of plot-based tree density estimates, we developed spatial models for large geographic extents ensuring a high degree of confidence in mean tree density estimates. We relied on two maps of ecologically unique regions delineated by The Nature Conservancy (TNC): Biomes and Ecoregions (Terrestrial Ecoregions map - http://maps.tnc.org/gis_data.html). Biomes are large geographic areas (i.e., continental scale) linked through similarities in biodiversity and associated drivers, originally developed by the World Wildlife Fund (WWF; www.worldwildlife.org/biomes) as the Terrestrial Ecoregions component of their Global Ecoregions dataset. TNC’s Terrestrial Ecoregions are smaller, more localized regions that share a similar habitat type. Individual predictive models were developed for each of the 14 unique terrestrial biomes and 806 unique ecoregions that possibly contained forested land. These two models—hereafter biome-level and ecoregion-level—were used to create two estimates of global forest density corresponding to two different spatial scales of inquiry.

Statistical modelling
Using the above-mentioned tabular data, we produced statistical models through a multi-step process: (i) hierarchical clustering; (ii) model selection; (iii) model pairing. Given the interactive nature of many biophysical factors, we suspected strong interactions and/or multicollinearity among the selected set of 20 variables (Table 1 (available online only)). To account for this we used ascendant (agglomerative) hierarchical clustering for each biome-level model. Hierarchical clustering is an unsupervised learning

<table>
<thead>
<tr>
<th>Spatial data pre-processing method</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Environmental Controls</td>
<td>Used in conjunction with other operations to control geospatial products.</td>
</tr>
<tr>
<td>Processing extent</td>
<td>Used to process all datasets at a common extent to eliminate unexpected data loss around land mass peripheries prior to controlled masking.</td>
</tr>
<tr>
<td>Snap raster</td>
<td>Used to ensure all datasets of a common resolution had precise pixel-level spatial coincidence.</td>
</tr>
<tr>
<td>Projection</td>
<td>Used to ensure all datasets held a common coordinate system for processing (WGS84) and area-dependent tabulation (Interrupted Goode Homolosine).</td>
</tr>
<tr>
<td>Mosaicking</td>
<td>Used to spatially mosaic datasets delivered in tiled format.</td>
</tr>
<tr>
<td>Nearest neighbor resampling</td>
<td>Used to unify raster cell size across datasets without introducing new data values.</td>
</tr>
<tr>
<td>Map algebra and geoprocessing tools</td>
<td>Used to produce derivative covariates (e.g., slope, aspect, etc.).</td>
</tr>
<tr>
<td>Spatial extraction/masking</td>
<td>Used to reduce all datasets to the smallest common extent prior to model fitting.</td>
</tr>
<tr>
<td>Spatial joining</td>
<td>Used to bind covariate values to coincident plot locations.</td>
</tr>
</tbody>
</table>

Table 2. Basic methods used to manage and pre-process spatial datasets.
algorithm in which groups of values are iteratively split and merged, ultimately dividing them into clusters whose inter-group distance or within-group homogeneity is maximized. In this way, the strategy is similar to other iterative clustering algorithms such as ISODATA or k-means. The product of clustering is a series of discrete groups (clusters) that contain values from one or more covariates that are better correlated with one another than with covariates in another cluster.

We employed ascendant hierarchical clustering using the `hclustvar` function in the `ClustOfVar` R package. Homogeneity of clusters was defined as the sum of the squared correlation between the variables in a cluster and their respective cluster center (here a synthetic quantitative variable equivalent to the first principal component of a PCA mix analysis). To maximize predictive model strength and reduce collinearity, we selected a single best ‘indicator’ variable from each cluster based on the squared loading values. This process produced, for each set of field plot records associated with a given biome or ecoregion, a single set of top-ranking covariates to consider during model development.

To estimate tree density in each biome we used the reduced set of covariates to construct generalized linear regression models with a negative binomial error structure (to accommodate count data that cannot extend below zero). To optimize model strength we used `dredge`, a multi-model dredging function in R’s MuMln package. This function evaluates and ranks all possible candidate models from a set of predictors in a global model according to Akaike Information Criterion (AICc) and AIC likelihood weights (AICw). Where no single covariate was overwhelmingly influential, there were, in most cases, a number of candidate models nested within the global model that performed comparably well. We therefore employed weighted model averaging of the dredged models with cumulative AIC weights ≥ 0.95 (ref. 44).

We constructed a unique regression model for each biome or ecoregion that contained at least 50 tree density measurements (for rationale see Model validation and testing). We lacked sufficient plot data for two of the forested biomes: ‘Mangroves’ and ‘Tropical and subtropical coniferous forests’, primarily due to the limited availability of data for these ecosystems.

Figure 2. Statistical and spatial model validation. (a) The standard deviation of the predicted mean number of trees per biome as a function of sample size. As sample size increases, the variability of the predicted mean tree density reaches a threshold, beyond which an increase in sample size results in a minimal increase in precision. Standard deviations were calculated using a bootstrapping approach (see Statistical model validation), and smooth curves were modeled using standard linear regression with a log–log transformation. After Crowther et al. (2015) Fig. 3b. (b) Biome-level regression models predict the mean values of the omitted validation plot measurements in 12 biomes. Overall, the models underestimated mean tree density by ~3% (slope = 0.97) but this difference was not statistically significant (P = 0.51). Bars show ± one s.d. for the predicted mean and the dotted boundaries represent the 95% confidence interval for the mean. The values plotted here represent mean densities for the plot measurements (that is, for forested ecosystems), rather than those predicted for each entire biome. Figure is modified from Crowther et al. (2015) Fig. 3a.
to the relative rarity of these biomes worldwide (representing 0.23 and 0.48% of the global land surface, respectively). In both cases we used models from the most analogous biomes for which we had sufficient data, relying on similarity in geography and general ecological conditions (e.g., moist environment, broadleaf species). The ‘Tropical and subtropical moist broadleaf’ biome was substituted for the ‘Mangroves biome’, and ‘Temperate coniferous biome’ for the ‘Tropical and subtropical coniferous’ biome. Because we used ecological analogy, the biome-level estimates for these areas should be considered less reliable than those of other biomes. At the ecoregion level, the distribution of plot-level data prevented us from modelling a large number of global ecoregions. For each of the missing ecoregion models we used the spatially coincident biome-level model in its place, such that the final global ecoregion model of tree density is largely driven by biome-level regression models.

Spatial modelling

Our final biome- and ecoregion-level negative binomial regression models were applied in a map algebraic framework using an iterative looping structure in R. We relied on the doSnow and foreach packages to perform computations in an embarrassingly parallel manner, such that each computational task bore no dependency on any other computational task. For both models, random access memory (RAM) limitations were bypassed by individually processing more than 10,000 geographically distinct regions and mosaicking the results to create a final map of predicted global tree density.

Prior to making area-dependent calculations, mosaicked datasets were reprojected to the Interrupted Goode Homolosine projected coordinate system and outlying predictions were truncated to 10,000 trees ha⁻¹ based on biome-level variability and expert knowledge of forest structure. Density estimates were then scaled from per-hectare units to per-pixel units where each pixel was nominally 1 km² (897.27 m × 897.27 m, or 0.805 km² under Goode Homolosine projection). Since forest reference plots were predominantly located in moderately forested areas (63% ± 35% [1 s.d.] forested, on average), the original model had minimal predictive power in regions with markedly different land cover types than the reference plots (i.e., in grasslands, deserts, or densely forested areas). To improve the spatial mapping, we therefore used a basic ratio estimation approach to scale the raw model means by an auxiliary independent data set—the global 1-km consensus land cover data set of 2014 (ref. 21) —which provides an estimate of the percent forested area for each pixel globally. First, we scaled the raw model means by the average percent forest area in the reference plots, on a biome-by-biome basis. We then multiplied this ratio by the percent forested area in the non-reference pixels. This estimation improved the final map

<table>
<thead>
<tr>
<th>Terrestrial Biome</th>
<th>n</th>
<th>Pred. Mean</th>
<th>Obs. Mean</th>
<th>SD</th>
<th>Pred. Sum</th>
<th>Obs. Sum</th>
<th>SD Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreal forests</td>
<td>1,116</td>
<td>98.157</td>
<td>94.459</td>
<td>1.168</td>
<td>109,542,928</td>
<td>105,416,204</td>
<td>1,303,046</td>
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<td>Deserts</td>
<td>2,921</td>
<td>28.315</td>
<td>24.337</td>
<td>2.255</td>
<td>82,122,745</td>
<td>71,089,686</td>
<td>685,260</td>
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<tr>
<td>Flooded grasslands</td>
<td>55</td>
<td>47.691</td>
<td>50.576</td>
<td>2.984</td>
<td>2,623,006</td>
<td>2,781,658</td>
<td>159,169</td>
</tr>
<tr>
<td>Mangroves</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Mediterranean forests</td>
<td>3,333</td>
<td>99.681</td>
<td>87.080</td>
<td>902</td>
<td>332,235,677</td>
<td>290,238,564</td>
<td>3,006,751</td>
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<tr>
<td>Montane grasslands</td>
<td>28</td>
<td>88.356</td>
<td>83.125</td>
<td>6.583</td>
<td>2,473,968</td>
<td>2,327,500</td>
<td>184,467</td>
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<tr>
<td>Temperate broadleaf</td>
<td>54,681</td>
<td>49.524</td>
<td>48.548</td>
<td>108</td>
<td>2,708,012,198</td>
<td>2,654,674,881</td>
<td>5,892,683</td>
</tr>
<tr>
<td>Temperate conifer</td>
<td>16,808</td>
<td>43.864</td>
<td>42.661</td>
<td>132</td>
<td>737,265,239</td>
<td>717,049,203</td>
<td>2,224,122</td>
</tr>
<tr>
<td>Tropical coniferous</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Tropical dry</td>
<td>17</td>
<td>48.525</td>
<td>30.938</td>
<td>4.083</td>
<td>824,925</td>
<td>525,938</td>
<td>69,415</td>
</tr>
<tr>
<td>Tropical grasslands</td>
<td>148</td>
<td>32.038</td>
<td>26.304</td>
<td>1.130</td>
<td>4,741,584</td>
<td>3,922,320</td>
<td>167,305</td>
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<tr>
<td>Tropical moist</td>
<td>1,017</td>
<td>80.839</td>
<td>77.722</td>
<td>795</td>
<td>82,212,834</td>
<td>79,043,004</td>
<td>808,476</td>
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<tr>
<td>Tundra</td>
<td>430</td>
<td>105.216</td>
<td>105.973</td>
<td>1.813</td>
<td>45,242,812</td>
<td>45,568,300</td>
<td>3,892,698</td>
</tr>
<tr>
<td>Total</td>
<td>83,969</td>
<td>752,410</td>
<td>708,137</td>
<td>4,211,133,091</td>
<td>4,068,990,550</td>
<td>4,068,990,550</td>
<td>3.5%</td>
</tr>
</tbody>
</table>

Table 3. Summary table showing the results of model validation. n = number of withheld plots, ~20% of total; Pred. Mean = Predicted mean number of trees per pixel, post scaling, at locations of withheld 20% of plots; Obs. Mean = Observed mean number of trees per plot × 100, for withheld 20% of plots; s.d. = Standard deviation of pixel-level predictions at withheld 20% of plot locations; Pred. Sum = Sum of predicted number of trees per pixel at all plot locations within each biome, post scaling; Obs. Sum = Sum of observed number of trees per plot × 100, for all plots within each biome; SD Sum = Standard deviation of predicted number of trees per pixel for all plot locations within each biome; % Difference = Percent difference in the total number of trees predicted (by pixel) and observed (plot × 100) at all plot locations within each biome.
characteristics by ensuring that pixels with 0% forests were assigned a value of zero trees, and that the difference in tree totals between two pixels with identical covariate values was directly proportional to their relative difference in percent forest cover. More importantly, this approach ensured that the global and biome-level marginal tree totals were approximately unbiased (see Fig. 2, Table 3).

**Code availability**

We used custom scripting to automate a variety of tasks in the production of our global models of tree density. Covariate pre-processing was partially automated using R (v. 3.1.x, R Core Development Team 2015) and the *raster* package. Hierarchical clustering and model selection were fully automated using R’s ClustOfVar and MuMln packages, as was the spatial application of statistical models in parallel using the raster, doSnow, and foreach packages. See the above portions of Methods for additional details. At the time of publication, we have no plans to distribute the scripts used in our analysis.

**Technical Validation**

**Statistical model validation**

Using two cross-validation schemes to assess the bias and precision of our tree density estimates at plot locations, we evaluated biome-level regression models prior to applying them in a spatial context. In the

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**Figure 3.** Global models of tree density. Tree density as portrayed through biome- (a) and ecoregion-level (b) models where values represent number of trees per ~1 km² pixel. Actual pixel size, 897.27 m by 897.27 m in the Goode Homolosine projection. All computations based on areal measurements were made using Goode Homolosine. Maps were produced using ESRI basemap imagery.
first scheme, 20% of plot locations within each biome were withheld at random as an independent testing dataset and regression models were generated (dredged) from the remaining 80% using the hierarchically clustered results noted above. These models were then used to predict tree density at the withheld plot locations and the predicted densities were regressed against the observed densities (see Fig. 2 in (ref. 1)). Table 3 provides a summary of model validation results. The 80% models were constructed independently of the full models (see Statistical Modeling), however the additional 20% of plot locations in the full models only reduced bias in relation to the 80% models.

A second validation scheme evaluated the number of field plots required to maximize the precision of density estimates. Following ref. 50, we used a bootstrapping function to evaluate the incremental decrease in standard deviation of our density estimates as a function of sample size for each biome. From the 20% pool of withheld plots noted above, we used simple random sampling with replacement to obtain a sample of size \( n \) (\( n = 10, 20, \ldots, 500 \) plots). We next applied the fitted regression models from the retained 80% of plots to the sample to model density at the \( n \) omitted plots, from which we computed and stored the standard deviation of estimated densities. To obtain a reliable estimate of the standard deviation of tree densities for each \( n \), this process was repeated 10,000 times for each sample size. We then plotted standard deviation as a function of sample size to evaluate the point at which an increase in the number of field plots no longer increased the precision of estimated densities (Fig. 2a). Beyond 50 field plots the inclusion of additional data produced only minor increases in precision. This led us to use 50 field plots as the threshold for whether or not to develop a unique regression model for a given geographic area (see Statistical modelling).

Spatial model validation
To evaluate the effect of scale on global predictions, spatial models were generated at both the biome and ecoregion levels (Fig. 3). Where our models were sensitive to the proportion of forested land cover within each pixel, we generated independent biome-level models using the consensus land cover dataset and the map of Global Forest Change 2000–2013 (ref. 19). The former was available at 1 km\(^2\) spatial resolution while the latter required spatial aggregation from 30 m\(^2\) to 1 km\(^2\) to make it compatible with our models. We also compared our predicted tree densities to published country-scale estimates to ensure agreement (Fig. 4).

The close agreement of the biome- and ecoregion-level global models of tree density led us to compute margins of error associated with the biome-level model, which we believed to be more robust given the broader geographic regions over which it was built. We used a Taylor series approximation to estimate the variance in the global and biome-specific totals, accounting for collinearity among predicted values and the log-link negative binomial regression structures (Fig. 2b, Table 4).

Data Records
Due to data sharing agreements, we are unable to provide direct access to the forest inventory plot data used in model development. However, biome- and ecoregion-level spatial models (maps) of tree density

![Figure 4](https://www.nature.com/sdata/)

**Figure 4.** Correlation of predicted and published numbers of trees per country. The dotted line is a 1:1 line, while the solid line is the ordinary least squares line of best fit. Figure is modified from Crowther et al (2015) Fig. 4d.
coniferous biomes, respectively. Given data limitations, and Tropical coniferous biome predictions rely on models derived from Tropical moist and Temperateconsidered less reliable than those for the other biomes.

To increase the number of field plots within each ecologically-meaningful region, and to account for local-level variability in vegetative structure, we modeled tree density at large spatial scales. Through this approach we were able to obtain high precision in our global estimates of mean tree density and total number of trees. However, it is important to note that precision decreases with a concomitant reduction in spatial extent. Both biome- and ecoregion-level models are less accurate than their global counterparts, country-level estimates are less accurate than their biome- and ecoregion-level counterparts, and pixel-level estimates are less accurate than all other scales of estimation. With this in mind, we are explicit in stating that the spatial models we present here are not intended to provide accurate or precise estimates of tree density at the 1 km² scale, nor even at the scale of small countries. Spatial models are presented without restriction. See Data collection and standardization for known limitations in field plot information.

Usage Notes
To increase the number of field plots within each ecologically-meaningful region, and to account for local-level variability in vegetative structure, we modeled tree density at large spatial scales. Through this approach we were able to obtain high precision in our global estimates of mean tree density and total number of trees. However, it is important to note that precision decreases with a concomitant reduction in spatial extent. Both biome- and ecoregion-level models are less accurate than their global counterparts, country-level estimates are less accurate than their biome- and ecoregion-level counterparts, and pixel-level estimates are less accurate than all other scales of estimation. With this in mind, we are explicit in stating that the spatial models we present here are not intended to provide accurate or precise estimates of tree density at the 1 km² scale, nor even at the scale of small countries.
Spatial models are presented without restriction. See Data collection and standardization for known limitations in field plot information.

References

<table>
<thead>
<tr>
<th>Terrestrial Biome</th>
<th>Number of field plots</th>
<th>Predicted number of trees (billions)</th>
<th>± 2 s.d. (billions)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreal forests</td>
<td>8,688</td>
<td>749.3</td>
<td>50.1</td>
</tr>
<tr>
<td>Deserts</td>
<td>14,637</td>
<td>53.0</td>
<td>2.9</td>
</tr>
<tr>
<td>Flooded grasslands</td>
<td>271</td>
<td>64.6</td>
<td>14.2</td>
</tr>
<tr>
<td>Mangroves</td>
<td>21</td>
<td>8.2*</td>
<td>0.3*</td>
</tr>
<tr>
<td>Mediterranean forests</td>
<td>16,727</td>
<td>53.4</td>
<td>1.2</td>
</tr>
<tr>
<td>Montane grasslands</td>
<td>138</td>
<td>60.3</td>
<td>24.0</td>
</tr>
<tr>
<td>Temperate broadleaf</td>
<td>278,395</td>
<td>362.6</td>
<td>2.9</td>
</tr>
<tr>
<td>Temperate coniferous</td>
<td>85,144</td>
<td>150.6</td>
<td>1.3</td>
</tr>
<tr>
<td>Temperate grasslands</td>
<td>17,051</td>
<td>148.3</td>
<td>4.9</td>
</tr>
<tr>
<td>Tropical coniferous</td>
<td>—</td>
<td>22.2*</td>
<td>0.4*</td>
</tr>
<tr>
<td>Tropical dry</td>
<td>115</td>
<td>156.4</td>
<td>63.4</td>
</tr>
<tr>
<td>Tropical grasslands</td>
<td>999</td>
<td>318.0</td>
<td>35.5</td>
</tr>
<tr>
<td>Tropical moist</td>
<td>5,321</td>
<td>799.4</td>
<td>24.0</td>
</tr>
<tr>
<td>Tundra</td>
<td>2,268</td>
<td>94.9</td>
<td>6.3</td>
</tr>
<tr>
<td>Global</td>
<td>429,775</td>
<td>3041.2</td>
<td>96.1</td>
</tr>
</tbody>
</table>

Table 4. Summary table showing the number of field plots, estimates for the total number of predicted trees at those plots, and 95% confidence intervals on the estimates at biome and global scales. *Mangroves and Tropical coniferous biome predictions rely on models derived from Tropical moist and Temperate coniferous biomes, respectively. Given data limitations, figures associated with these biomes should be considered less reliable than those for the other biomes.
46. S. Package ‘doSNOW’ (Revolution Analytics, CRAN, Comprehensive R Archive Network, 2015).
47. S. Package ‘qforeach’ (Revolution Analytics, CRAN, Comprehensive R Archive Network, 2015).
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Data Citations

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Author Contributions
The conceptual framework for the technical analysis was developed by H.B.G., C.B., D.S.M., and J.R.S. The conceptual framework for the broader project was developed by T.W.C., H.B.G., K.R.C., C.B., and D.S.M. The manuscript was written by H.B.G., D.S.M., and T.W.C. with input from K.R.C., C.B., and J.R.S. Technical analysis was completed by H.B.G., D.S.M., C.B., and J.R.S.

Additional Information
Table 1 is only available in the online version of this paper.

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