

Mapping tree density at a global scale

T. W. Crowther¹, H. B. Glick¹, K. R. Covey¹, C. Bettigole¹, D. S. Maynard¹, S. M. Thomas², J. R. Smith¹, G. Hintler¹, M. C. Duguid¹, G. Amatulli³, M.-N. Tuanmu³, W. Jetz^{1,3,4}, C. Salas⁵, C. Stam⁶, D. Piotta⁷, R. Tavani⁸, S. Green^{9,10}, G. Bruce⁹, S. J. Williams¹¹, S. K. Wiser¹², M. O. Huber¹³, G. M. Hengeveld¹⁴, G.-J. Nabuurs¹⁴, E. Tikhonova¹⁵, P. Borchardt¹⁶, C.-F. Li¹⁷, L. W. Powrie¹⁸, M. Fischer^{19,20}, A. Hemp²¹, J. Homeier²², P. Cho²³, A. C. Vibrans²⁴, P. M. Umunay¹, S. L. Piao²⁵, C. W. Rowe¹, M. S. Ashton¹, P. R. Crane¹ & M. A. Bradford¹

The global extent and distribution of forest trees is central to our understanding of the terrestrial biosphere. We provide the first spatially continuous map of forest tree density at a global scale. This map reveals that the global number of trees is approximately 3.04 trillion, an order of magnitude higher than the previous estimate. Of these trees, approximately 1.39 trillion exist in tropical and subtropical forests, with 0.74 trillion in boreal regions and 0.61 trillion in temperate regions. Biome-level trends in tree density demonstrate the importance of climate and topography in controlling local tree densities at finer scales, as well as the overwhelming effect of humans across most of the world. Based on our projected tree densities, we estimate that over 15 billion trees are cut down each year, and the global number of trees has fallen by approximately 46% since the start of human civilization.

Forest ecosystems harbour a large proportion of global biodiversity, contribute extensively to biogeochemical cycles, and provide countless ecosystem services, including water quality control, timber stocks and carbon sequestration^{1–4}. Our current understanding of the global forest extent has been generated using remote sensing approaches that provide spatially explicit values relating to forest area and canopy cover^{3,5,6}. Used in a wide variety of global models, these maps have enhanced our understanding of the Earth system^{3,5,6}, but they do not currently address population numbers, densities or timber stocks. These variables are valuable for the modelling of broad-scale biological and biogeochemical processes^{7–9} because tree density is a prominent component of ecosystem structure, governing elemental processing and retention rates^{7,9,10}, as well as competitive dynamics and habitat suitability for many plant and animal species^{11–13}.

The number of trees in a given area can also be a meaningful metric to guide forest management practices and inform decision-making in public and non-governmental sectors^{14,15}. For example, international afforestation efforts such as the ‘Billion Trees Campaign’, and city-wide projects including the numerous ‘Million Tree’ initiatives around the world have motivated civil society and political leaders to promote environmental stewardship and sustainable land management by planting large numbers of trees^{14,16,17}. Establishing targets and evaluating the proportional contribution of such projects requires a sound baseline understanding of current and potential tree population numbers at regional and global scales^{16,17}.

The current estimate of global tree number is approximately 400.25 billion¹⁸. Generated using satellite imagery and scaled based on global forest area, this estimate engaged policy makers and environmental practitioners worldwide by suggesting that the ratio of trees-to-people is 61:1. This has, however, been thrown into doubt by a recent broad-scale inventory that used 1,170 ground-truthed measurements of tree density to estimate that there are 390 billion trees in the Amazon basin alone¹⁹.

Mapping tree density

Here, we use 429,775 ground-sourced measurements of tree density from every continent on Earth except Antarctica to generate a global map of forest trees. Forested areas are found in most of Earth’s biomes, even those as counterintuitive as desert, tundra, and grassland (Fig. 1a, b). We generated predictive regression models for the forested areas in each of the 14 biomes as defined by The Nature Conservancy (<http://www.nature.org>). These models link tree density to spatially explicit remote sensing and geographic information systems (GIS) layers of climate, topography, vegetation characteristics and anthropogenic land use (see Extended Data Table 1). Following almost all of the collected data sources, we define a tree as a plant with woody stems larger than 10 cm diameter at breast height (DBH)¹⁹.

Incorporating plot-level measurements from more than 50 countries, the measured tree density values were inherently variable within and among biomes (Figs 1 and 2). However, the large number of tree density measurements ensured that the confidence in our mean (and total) estimates is high (Fig. 3). Furthermore, the scale of these data

¹Yale School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511, USA. ²Department of Environmental Sciences, University of Helsinki, Helsinki 00014, Finland. ³Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06511, USA. ⁴Department of Life Sciences, Silwood Park, Imperial College, London SL5 7PY, UK. ⁵Departamento de Ciencias Forestales, Universidad de La Frontera, Temuco 4811230, Chile. ⁶RedCastle Resources, Salt Lake City, Utah 84103, USA. ⁷Universidade Federal do Sul da Bahia, Ferradas, Itabuna 45613-204, Brazil. ⁸Forestry Department, Food and Agriculture Organization of the United Nations, Rome 00153, Italy. ⁹Operation Wallacea, Spilbsy, Lincolnshire PE23 4EX, UK. ¹⁰Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and Conservation (SAC), University of Kent, Canterbury ME4 4AG, UK. ¹¹Molecular Imaging Research Center MIRcen/CEA, CNRS URA 2210, 91401 Orsay Cedex, France. ¹²Landcare Research, Lincoln 7640, New Zealand. ¹³WSL, Swiss Federal Institute for Forest, Snow and Landscape Research, 8903 Birmensdorf, Switzerland. ¹⁴Environmental Science Group, Wageningen University & Research Centre, 6708 PB, The Netherlands. ¹⁵Center for Forest Ecology and Productivity RAS, Moscow 117997, Russia. ¹⁶CEN Center for Earth System Research and Sustainability, Institute of Geography, University of Hamburg, Hamburg 20146, Germany. ¹⁷Department of Botany and Zoology, Masaryk University, Brno 61137, Czech Republic. ¹⁸South African National Biodiversity Institute, Kirstenbosch Research Centre, Claremont 7735, South Africa. ¹⁹Institute of Plant Sciences, Botanical Garden, and Oeschger Centre for Climate Change Research, University of Bern, 3013 Bern, Switzerland. ²⁰Senckenberg Gesellschaft für Naturforschung, Biodiversity and Climate Research Centre (BKC-F), 60325 Frankfurt, Germany. ²¹Department of Plant Systematics, University of Bayreuth, 95447 Bayreuth, Germany. ²²Albrecht von Haller Institute of Plant Sciences, Georg August University of Göttingen, 37073 Göttingen, Germany. ²³Tropical Ecology Research Group, Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK. ²⁴Universidade Regional de Blumenau, Departamento de Engenharia Florestal, Blumenau/Santa Catarina 89030-000, Brazil. ²⁵Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China.

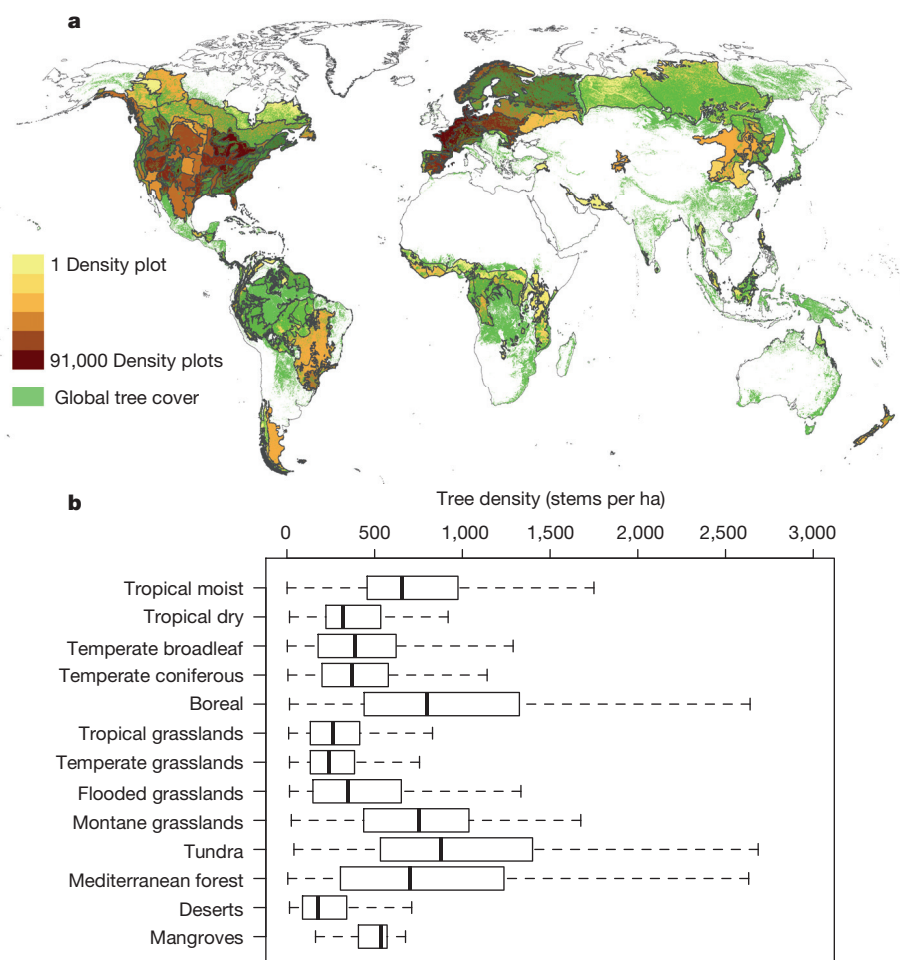


Figure 1 | Map of data points and raw biome-level forest density data.
a, Image highlighting the ecoregions (shapefiles provided by The Nature Conservancy (<http://www.nature.org>)) from which the 429,775 ground-sourced measurements of tree density were collected. Shading indicates the

total number of plot measurements collected in each ecoregion. A global forest map was overlaid in green to highlight that collected data span the majority of forest ecosystems on a global scale. **b**, The median and interquartile range of tree density values collected in the forested areas of each biome.

ensures that our modelled estimates are unlikely to be influenced significantly by recent forest loss, reforestation or natural forest regeneration, which are responsible for a net global change of <1% of the

global forest area each year³. Biome-level validation estimates indicate that our models have high precision when predicting the mean tree densities of omitted validation plots (Fig. 3a). Although the accuracy

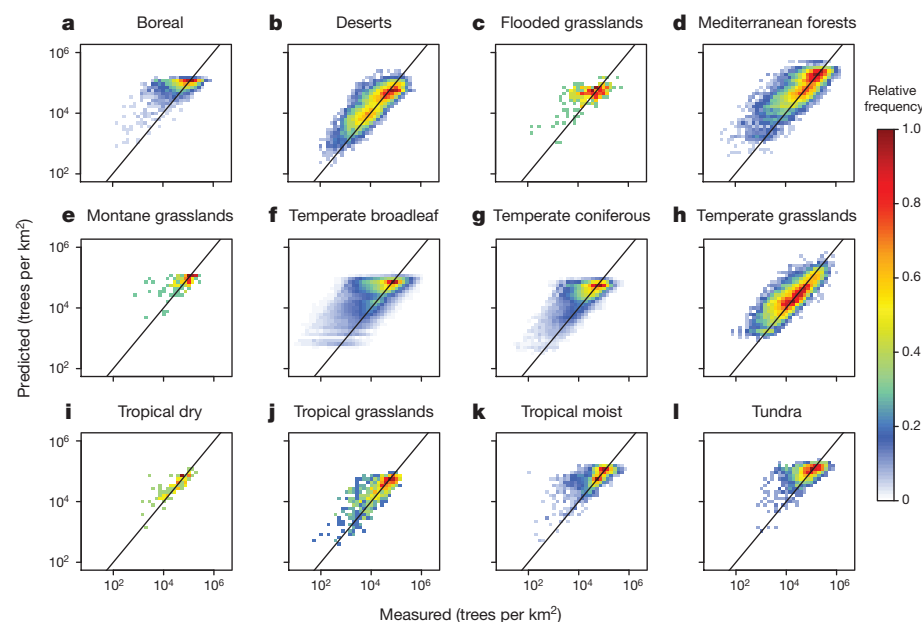


Figure 2 | Heat plots showing the relationships between predicted and measured tree density data. **a–l**, Predictions were generated using generalized linear models ($n = 429,775$). Diagonal lines indicate 1:1 lines (perfect correspondence) between predicted and observed points, scaled to the kilometre level. Colours indicate the proportion of data points from that biome that fall within each pixel. Biomes with a greater number of plot measurements have greater variability but higher confidence in the mean estimates, highlighting the trade-off between broad-scale precision and fine-scale accuracy. Axes are log-transformed to account for exceptionally high variability in tree density.

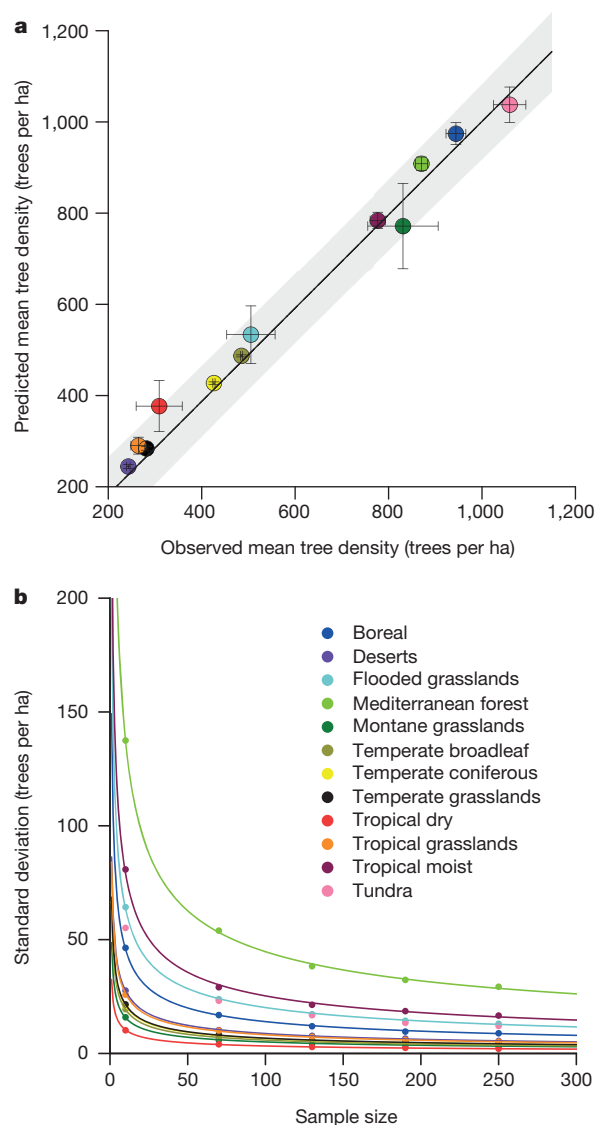


Figure 3 | Validation plots for biome-level predictions. **a**, Biome-level regression models predict the mean values of the omitted validation plot measurements in 12 biomes. Overall, the models underestimated mean tree density by $\sim 3\%$ (slope = 0.97) but this difference was not statistically significant ($P = 0.51$). Bars show \pm one standard deviation for the predicted mean and the grey area represents 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. **b**, The standard deviation of the predicted mean values 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 Methods), and smooth curves were modelled using standard linear regression with a log–log transformation.

of our models is limited at the level of an individual hectare, the precision of the mean density estimates is high (± 40 trees ha^{-1}) beyond a threshold of ~ 200 plots (Fig. 3b).

Global-level and biome-level patterns

Together, the biome-level models provide the first spatially continuous map of global tree densities at a 1- km^2 (30 arc-seconds) resolution (Fig. 4a). Based on this map, we estimate that the global number of trees is approximately 3.04 trillion (± 0.096 trillion, 95% confidence intervals (CI)). An order of magnitude higher than the previous global estimate¹⁸, the scale of our projection is consistent with recent large-scale inventories

in Europe, North America and the Amazon basin¹⁹ (Fig. 4d). With a human population of 7.2 billion, our estimate of global tree density revises the ratio of trees per person from 61:1 to 422:1.

At the biome-level, the highest tree densities exist in forested regions of the Boreal and Tundra zones (Fig. 1b). In these northern latitudes, limited temperature and moisture lead to the establishment of stress-tolerant coniferous tree species that can reach the highest densities on Earth (Fig. 1). However, the tropical regions contain a greater proportion of the world's forested land. A total of 42.8% of the planet's trees exist in tropical and subtropical regions, with another 24.2% and 21.8% in boreal and temperate biomes, respectively (Fig. 4a).

Within-biome trends

Our models also provide mechanistic insights into potential controls on tree density within biomes (Fig. 5). For example, various climatic parameters correlate with mean forest density within all ecosystem types. Tree density generally increases with temperature (mean annual temperature and temperature seasonality) and moisture availability (precipitation regimes, evapotranspiration or aridity). These patterns are consistent with previous broad-scale tree inventory studies and support the idea that, within ecosystem types, moist, warm conditions are generally optimal for tree growth^{11,12}.

Given the generally positive effects of moisture availability and warmth on tree density within biomes, the negative relationships observed in some regions may seem surprising (Fig. 5). This highlights the complex suite of population- and community-level selection pressures that can obscure the expected effects of climate across landscapes. For example, in colder (boreal or tundra) biomes, increasing moisture levels can cause hydric and permafrost conditions in lower lying topographies, which then limit nutrient availability for tree development²⁰. In addition, current and historical anthropogenic land use decisions have the potential to drive these relationships in several regions. The negative relationships between tree density and moisture availability in flooded grasslands and tropical dry forests are, for example, likely to be driven by preferential use of moist, productive land for agriculture²¹. As a result, forest ecosystems are often relegated to drier regions, reversing the expected within-biome relationships between moisture availability and tree density. Such effects will vary among countries, depending on human population densities, alternative resource availability and socio-economic status^{22,23}.

Along with these indirect effects of human activity, the direct effect of human development (percentage developed and managed land)⁶ on tree density represented the only common mechanism across all biomes (Fig. 5). The negative relationships between tree density and anthropogenic land use exemplify how humans contend directly with natural forest ecosystems for space. Whereas the negative effect of human activity on tree numbers is highly apparent at local scales, the present study provides a new measure of the scale of anthropogenic effects, relative to other environmental variables. Current rates of global forest cover loss are approximately 192,000 km^2 each year³. By combining our tree density information with the most recent spatially explicit map of forest cover loss over the past 12 years³, we estimate that deforestation, forest management, disturbances and land use change are currently responsible for a gross loss of approximately 15.3 billion trees on an annual basis. Although these rates of forest loss are currently highest in tropical regions³, the scale and consistency of this negative human effect across all forested biomes highlights how historical land use decisions have shaped natural ecosystems on a global scale. Using the projected maps of current and historic forest cover provided by the United Nations Environment Programme (<http://geodata.grid.unep.ch>), our map reveals that the global number of trees has fallen

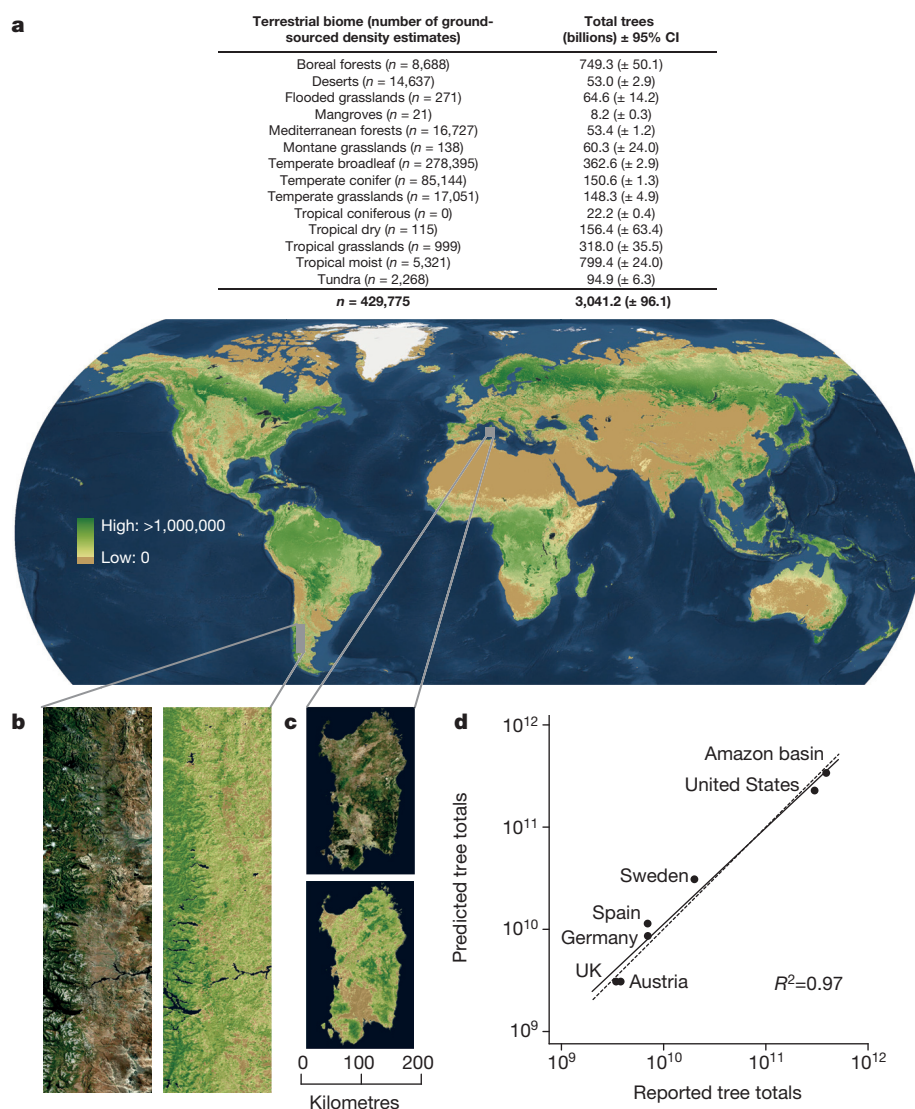


Figure 4 | The global map of tree density at the 1-km² pixel (30 arc-seconds) scale. a, The scale refers to the number of trees in each pixel. **b, c**, We highlight the map predictions for two areas (South American Andes (**b**) and Sardinia (**c**)) and include the corresponding images for visual comparison. All maps and images were generated using ESRI basemap imagery. **d**, A scatterplot as

validation for our broad-scale estimates of total tree number. This shows the relationship between our predicted tree estimates and reported totals for regions with previous broad-scale tree inventories (see Methods for details). The straight line and the dotted line are the predicted best fit line and the 1:1 line, respectively.

by approximately 45.8% since the onset of human civilization (post-Pleistocene).

Discussion

The global map of tree density can facilitate ongoing efforts to understand biogeochemical Earth system dynamics^{3,6,7,9} by incorporating ecosystem features that relate to elemental cycling rates^{9,10}. For example, tree abundance can help to explain some of the variation in carbon storage and productivity within ecosystem types^{7,9}, but the strength of these effects remain untested across biomes⁸. We assessed the relationship between tree density and plant carbon storage at a global scale by regressing our plot-level tree counts against modelled estimates of plant biomass carbon in those sites²⁴. This revealed a positive effect of tree density on plant carbon storage ($P < 0.001$). However, the strength of the relationship is weak ($r^2 = 0.14$), reflecting the vast array of local ecological forces that can obscure such global trends. For example, the effect of tree density is likely to interact strongly with tree size. Larger trees contain the greatest proportion of carbon in woodlands²⁵, but the highest tree densities within a given ecosystem type are often associated with young or recovering forests

characterized by many small trees^{13,20}. A thorough understanding of total vegetative carbon storage requires information about both the size and the number of individual trees.

A dense forest environment is a fundamentally different ecosystem from a sparse one and this influences a vast array of biotic and abiotic processes^{10–12}. Current remote sensing tools capture some, but not all of this information. The tree density layer that we provide can therefore augment the currently available layers by providing unique insights into ecological dynamics that are not represented by estimates of forest cover or biomass^{3,5,6}. It can inform biodiversity estimates and species distribution models by capturing perceivable environmental characteristics that determine habitat suitability for a wide variety of plants and animals^{11–13}. Baseline estimates of tree populations are also critical for projecting population- and community-level tree demographics under current and future climate change scenarios²⁶, and for guiding local, national, and international reforestation/afforestation efforts^{14–17}. Finally, by allowing us to comprehend the global forest extent in terms of tree numbers, this map contributes to our fundamental understanding of the Earth's terrestrial system.

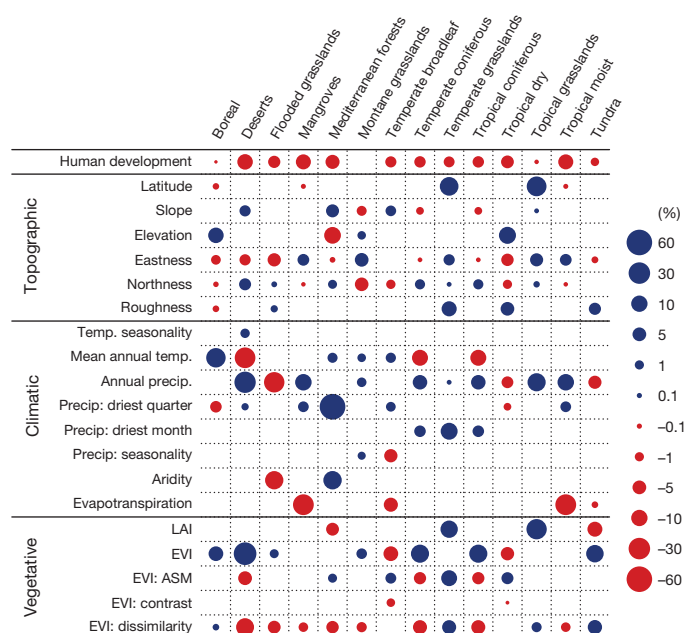


Figure 5 | Standardized coefficients for the variables included in final biome-level regression models. Coefficients represent relative per cent change in tree density for one standard deviation increase in the variable. Red and blue circles indicate negative and positive effects on tree density, respectively. Circle size indicates the magnitude of effects. All layers are available at the global scale. Human development = per cent developed and managed land; LAI = leaf area index; EVI = enhanced vegetation index; EVI: ASM = angular second moment of EVI; EVI: contrast = contrast of EVI; and EVI: dissimilarity = dissimilarity of EVI (see Extended Data Table 1).

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

Received 6 May; accepted 23 July 2015.

Published online 2 September; corrected online 9 September 2015
(see full-text HTML version for details).

- Pan, Y. *et al.* A large and persistent carbon sink in the world's forests. *Science* **333**, 988–993 (2011).
- Crowther, T. W. *et al.* Predicting the responsiveness of soil biodiversity to deforestation: a cross-biome study. *Glob. Change Biol.* **20**, 2983–2994 (2014).
- Hansen, M. C. *et al.* High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013).
- Bonan, G. B. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* **320**, 1444–1449 (2008).
- Pfeifer, M., Disney, M., Quaife, T. & Marchant, R. Terrestrial ecosystems from space: a review of earth observation products for macroecology applications. *Glob. Ecol. Biogeogr.* **21**, 603–624 (2012).
- Tuanmu, M.-N. & Jetz, W. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Glob. Ecol. Biogeogr.* **23**, 1031–1045 (2014).
- Walker, A. P. *et al.* Predicting long-term carbon sequestration in response to CO₂ enrichment: how and why do current ecosystem models differ? *Glob. Biogeochem. Cycles* **29**, 476–495 (2015).
- Asner, G. P. *et al.* A universal airborne LiDAR approach for tropical forest carbon mapping. *Oecologia* **168**, 1147–1160 (2012).
- Fauset, S. *et al.* Hyperdominance in Amazonian forest carbon cycling. *Nature Commun.* **6**, 6857 (2015).
- Slik, J. W. F. *et al.* Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Glob. Ecol. Biogeogr.* **19**, 50–60 (2010).

- Leathwick, L. R. & Austin, M. P. Competitive interactions between tree species in New Zealand old-growth indigenous forests. *Ecology* **82**, 2560–2573 (2001).
- Oliver, C. D. & Larson, B. C. *Forest Stand Dynamics* (John Wiley & Sons, 1996).
- Riginos, C. & Grace, J. B. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology* **89**, 2228–2238 (2008).
- O'Neil-Dunne, J., MacFaden, S. & Royer, A. A versatile, production-oriented approach to high-resolution tree-canopy mapping in urban and suburban landscapes using GEObIA and data fusion. *Remote Sens.* **6**, 12837–12865 (2014).
- Guldin, R. W. Forest science and forest policy in the Americas: building bridges to a sustainable future. *For. Policy Econ.* **5**, 329–337 (2003).
- Cao, S. *et al.* Greening China naturally. *Ambio* **40**, 828–831 (2011).
- Oldfield, E. E. *et al.* Growing the urban forest: tree performance in response to biotic and abiotic land management. *Restoration Ecol.* (<http://dx.doi.org/10.1111/rec.12230>) (2015).
- Nadkarni, N. *Between Earth and Sky: Our Intimate Connections to Trees* (Univ. of California Press, 2008).
- ter Steege, H. *et al.* Hyperdominance in the Amazonian tree flora. *Science* **342**, 1243092 (2013).
- Bonan, G. B. & Shugart, H. H. Environmental factors and ecological processes in boreal forests. *Annu. Rev. Ecol. Syst.* **20**, 1–28 (1989).
- Meyfroidt, P. & Lambin, E. F. Global forest transition: prospects for an end to deforestation. *Annu. Rev. Environ. Resour.* **36**, 343–371 (2011).
- Rudel, T. K. The national determinants of deforestation in sub-Saharan Africa. *Phil. Trans. R. Soc. Lond. B* **368**, 20120405 (2013).
- Hengeveld, G. M. *et al.* A forest management map of European forests. *Ecol. Soc.* **17**, 53 (2012).
- Kindermann, G. E., McCallum, I., Fritz, S. & Obersteiner, M. A global forest growing stock, biomass and carbon map based on FAO statistics. *Silva Fennica* **42**, 387–396 (2008).
- Stephenson, N. L. *et al.* Rate of tree carbon accumulation increases continuously with tree size. *Nature* **507**, 90–93 (2014).
- Zhu, K., Woodall, C. W., Ghosh, S., Gelfand, A. E. & Clark, J. S. Dual impacts of climate change: forest migration and turnover through life history. *Glob. Change Biol.* **20**, 251–264 (2014).

Supplementary Information is available in the online version of the paper.

Acknowledgements We thank P. Peterkins for her support throughout the study. We also thank Plant for the Planet for initial discussions and for collaboration during the study. The main project was funded by grants to T.W.C. from the Yale Climate and Energy Institute and the British Ecological Society. We acknowledge various sources for tree density measurements and estimates: the Canadian National Forest Inventory (<https://nfi.nfis.org/index.php>), the US Department of Agriculture Forest Service for their National Forest Inventory and Analysis (<http://fia.fs.fed.us/>), the Taiwan Forestry Bureau (which provided the National Vegetation Database of Taiwan), the DFG (German Research Foundation), BMBF (Federal Ministry of Education and Science of Germany), the Floristic and Forest Inventory of Santa Catarina (IFFSC), the National Vegetation Database of South Africa, and the Chilean research grants FONDECYT no. 1151495. For Europe NFI plot data were brought together with input from J. Rondeux and M. Waterinckx, Belgium, T. Bélouard, France, H. Polley, Germany, W. Daamen and H. Schoonderwoerd, Netherlands, S. Tomter, Norway, J. Villanueva and A. Trasobares, Spain, G. Kempe, Sweden. New Zealand Natural Forest plot data were collected by the LUCAS programme for the Ministry for the Environment (New Zealand) and sourced from the National Vegetation Survey Databank (New Zealand) (<http://nvs.landcareresearch.co.nz>). We also acknowledge the BCI forest dynamics research project, which was funded by National Science Foundation grants to S. P. Hubbell, support from the Center for Tropical Forest Science, the Smithsonian Tropical Research Institute, the John D. and Catherine T. MacArthur Foundation, the Mellon Foundation, the Small World Institute Fund, numerous private individuals, the Ucross High Plains Stewardship Initiative, and the hard work of hundreds of people from 51 countries over the past two decades. The plot project is part of the Center for Tropical Forest Science, a global network of large-scale demographic tree plots.

Author Contributions The study was conceived by T.W.C. and G.H. and designed by T.W.C., K.R.C. and M.A.B. Statistical analyses were conducted by H.B.G., S.M.T., J.R.S., C.B., D.S.M. and T.W.C. and mapping was conducted by H.B.G. and C.B. The manuscript was written by T.W.C. with input from M.A.B., P.C., D.S.M., H.B.G. and C.B., with comments provided by all other authors. Tree density measurements or geospatial data from all over the world were contributed by K.R.C., S.M.T., M.C.D., G.A., M.N.T., W.J., C.Sa., C.St., D.P., T.T., S.G., G.B., S.J.W., S.K.W., M.O.H., G.M.H., G.J.N., E.T., P.B., C.F.L., L.W.P., M.F., A.H., J.H., P.C., A.C.V., P.M.U., S.L.P., C.W.R. and M.S.A.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to T.W.C. (thomas.crowther11@gmail.com).