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Diversity and carbon storage across the tropical forest biome

Martin J. P. Sullivan^{1,*}, Joey Talbot^{1,*}, Simon L. Lewis^{1,2,*}, Oliver L. Phillips^{1,*}, Lan Qie¹, Serge K. Begne^{1,3}, Jérôme Chave⁴, Aida Cuni-Sanchez², Wannex Hubau¹, Gabriela Lopez-Gonzalez¹, Lera Miles⁵, Abel Monteagudo-Mendoza^{6,7}, Bonaventure Sonké³, Terry Sunderland^{8,9}, Hans ter Steege^{10,11}, Lee J. T. White^{12,13,14}, Kofi Affum-Baffoe¹⁵, Shin-ichiro Aiba¹⁶, Everton Cristo de Almeida¹⁷, Edmar Almeida de Oliveira¹⁸, Patricia Alvarez-Loayza¹⁹, Esteban Álvarez Dávila²⁰, Ana Andrade²¹, Luiz E. O. C. Aragão²², Peter Ashton²³, Gerardo A. Aymard C.²⁴, Timothy R. Baker¹, Michael Balinga²⁵, Lindsay F. Banin²⁶, Christopher Baraloto²⁷, Jean-Francois Bastin^{28,29}, Nicholas Berry³⁰, Jan Bogaert³¹, Damien Bonal³², Frans Bongers³³, Roel Brienen¹, José Luís C. Camargo³⁴, Carlos Cerón³⁵, Victor Chama Moscoso⁷, Eric Chezeaux³⁶, Connie J. Clark³⁷, Álvaro Cogollo Pacheco³⁸, James A. Comiskey^{39,46}, Fernando Cornejo Valverde⁴⁰, Eurídice N. Honorio Coronado⁴¹, Greta Dargie¹, Stuart J. Davies⁴², Charles De Canniere⁴³, Marie Noel Djuikouo K.⁴⁴, Jean-Louis Doucet⁴⁵, Terry L. Erwin⁴⁶, Javier Silva Espejo⁷, Corneille E. N. Ewango^{47,48}, Sophie Fauset^{1,49}, Ted R. Feldpausch²², Rafael Herrera^{50,51}, Martin Gilpin¹, Emanuel Gloor¹, Jefferson S. Hall⁵², David J. Harris⁵³, Terese B. Hart^{54,55}, Kuswata Kartawinata^{56,57}, Lip Khoo Kho⁵⁸, Kanehiro Kitayama⁵⁹, Susan G. W. Laurance⁶⁰, William F. Laurance⁶⁰, Miguel E. Leal⁶¹, Thomas Lovejoy⁶², Jon C. Lovett¹, Faustin Mpanya Lukasu⁶³, Jean-Remy Makana⁴⁷, Yadvinder Malhi⁶⁴, Leandro Maracahipes⁶⁵, Beatriz S. Marimon¹⁸, Ben Hur Marimon Junior¹⁸, Andrew R. Marshall^{66,67}, Paulo S. Morandi¹⁸, John Tshibamba Mukendi⁶³, Jaques Mukinzi^{47,68}, Reuben Nilus⁶⁹, Percy Núñez Vargas⁷, Nadir C. Pallqui Camacho⁷, Guido Pardo⁷⁰, Marielos Peña-Claros^{33,71}, Pascal Pétronelli⁷², Georgia C. Pickavance¹, Axel Dalberg Poulsen⁷³, John R. Poulsen³⁷, Richard B. Primack⁷⁴, Hari Priyadi^{75,76}, Carlos A. Quesada²¹, Jan Reitsma⁷⁷, Maxime Réjou-Méchain⁴, Zorayda Restrepo⁷⁸, Ervan Rutishauser⁷⁹, Kamariah Abu Salim⁸⁰, Rafael P. Salomão⁸¹, Ismayadi Samsuodin⁸², Douglas Sheil^{8,83}, Rodrigo Sierra⁸⁴, Marcos Silveira⁸⁵, J. W. Ferry Slik⁷⁹, Lisa Steel⁸⁶, Hermann Taedoumg³, Sylvester Tan⁸⁷, John W. Terborgh³⁷, Sean C. Thomas⁸⁸, Marisol Toledo⁷¹, Peter M. Umunay⁸⁹, Luis Valenzuela Gamarra⁶, Ima Célia Guimarães Vieira⁸¹, Vincent A. Vos^{70,90}, Ophelia Wang⁹¹, Simon Willcock^{92,93} & Lise Zemagho³

Tropical forests are global centres of biodiversity and carbon storage. Many tropical countries aspire to protect forest to fulfil biodiversity and climate mitigation policy targets, but the conservation strategies needed to achieve these two functions depend critically on the tropical forest tree diversity-carbon storage relationship. Assessing this relationship is challenging due to the scarcity of inventories where carbon stocks in aboveground biomass and species identifications have been simultaneously and robustly quantified. Here, we compile a unique pan-tropical dataset of 360 plots located in structurally intact old-growth closed-canopy forest, surveyed using standardised methods, allowing a multi-scale evaluation of diversity-carbon relationships in tropical forests. Diversity-carbon relationships among all plots at 1 ha scale across the tropics are absent, and within continents are either weak (Asia) or absent (Amazonia, Africa). A weak positive relationship is detectable within 1 ha plots, indicating that diversity effects in tropical forests may be scale dependent. The absence of clear diversity-carbon relationships at scales relevant to conservation planning means that carbon-centred conservation strategies will inevitably miss many high diversity ecosystems. As tropical forests can have any combination of tree diversity and carbon stocks both require explicit consideration when optimising policies to manage tropical carbon and biodiversity.

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¹School of Geography, University of Leeds, Leeds, UK. ²Department of Geography, University College London, London, UK. ³Plant Systematic and Ecology Laboratory, University of Yaounde I, Cameroon. ⁴Université Paul Sabatier CNRS, Toulouse, France. ⁵United Nations Environment Programme World Conservation Monitoring Centre, Cambridge, UK. ⁶Jardín Botánico de Missouri, Oxapampa, Perú. ⁷Universidad Nacional de San Antonio Abad del Cusco, Cusco, Perú. ⁸CIFOR, Bogor, Indonesia. ⁹College of Marine and Environmental Sciences, James Cook University, Cairns, Australia. ¹⁰Naturalis Biodiversity Center, Leiden, Netherlands. ¹¹Ecology and Biodiversity Group, Utrecht University, Utrecht, Netherlands. ¹²Agence Nationale des Parcs Nationaux, Libreville, Gabon. ¹³Institut de Recherche en Ecologie Tropicale, Libreville, Gabon. ¹⁴School of Natural Sciences, University of Stirling, Stirling, UK. ¹⁵Mensuration Unit, Forestry Commission of Ghana, Kumasi, Ghana. ¹⁶Graduate School of Science and Engineering, Kagoshima University, Japan. ¹⁷Instituto de Biodiversidade e Floresta, Universidade Federal do Oeste do Pará, Santarém, Brazil. ¹⁸Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil. ¹⁹Center for Tropical Conservation, Duke University, Durham, NC, USA. ²⁰Red para la Mitigación y Adaptación al Cambio Climático de la UNAD, Bogota, Colombia. ²¹Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. ²²Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK. ²³Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA. ²⁴Programa de Ciencias del Agro y el Mar, Herbario Universitario, Barinas, Venezuela. ²⁵CIFOR, Conakry, Guinea. ²⁶Centre for Ecology and Hydrology, Penicuik, UK. ²⁷International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL, USA. ²⁸UMR AMAP, IRD, Montpellier, France. ²⁹UPR BSEF, CIRAD, Montpellier, France. ³⁰The University of Edinburgh, School of GeoSciences, Edinburgh, UK. ³¹Biodiversity and Landscape Unit, Gembloux Agro-Bio Tech, Université de Liège, Gembloux, Belgium. ³²INRA, UMR EEF, Champenoux, France. ³³Forest Ecology and Forest Management group, Wageningen University, Wageningen, The Netherlands. ³⁴Instituto Nacional de Pesquisas da Amazônia, Projeto Dinâmica Biológica de Fragmentos Florestais, Manaus, Brazil. ³⁵Herbario Alfredo Paredes, Universidad Central del Ecuador, Quito, Ecuador. ³⁶Rougier-Gabon, Libreville, Gabon. ³⁷Nicholas School of the Environment, Duke University, Durham, NC, USA. ³⁸Jardín Botánico Joaquín Antonio Uribe, Medellín, Colombia. ³⁹Inventory & Monitoring Program, National Park Service, Fredericksburg, VA, USA. ⁴⁰Andes to Amazon Biodiversity Program, Puerto Maldonado, Perú. ⁴¹Instituto de Investigaciones de la Amazonia Peruana, Iquitos, Perú. ⁴²Smithsonian Tropical Research Institute, Washington, DC, USA. ⁴³Landscape Ecology and Vegetal Production Systems Unit, Université Libre de Bruxelles, Brussels, Belgium. ⁴⁴Department of Botany & Plant Physiology, Faculty of Science, University of Buea, Buea, Cameroon. ⁴⁵Forest Resources Management, Gembloux Agro-Bio Tech, University of Liege, Belgium. ⁴⁶Smithsonian Institution, Washington, DC, USA. ⁴⁷Wildlife Conservation Society-DR Congo, Kinshasa I, Democratic Republic of Congo. ⁴⁸Centre de Formation et de Recherche en Conservation Forestiere (CEFRECOCF), Democratic Republic of Congo. ⁴⁹Institute of Biology, UNICAMP, Campinas, Brazil. ⁵⁰Centro de Ecologia, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela. ⁵¹Institut für Geographie und Regionalforschung, Geoökologie, University of Vienna, Vienna, Austria. ⁵²Smithsonian Tropical Research Institute, Panamá, Republic of Panama. ⁵³Royal Botanic Garden Edinburgh, Edinburgh, UK. ⁵⁴Lukuru Wildlife Research Foundation, Kinshasa, Gombe, Democratic Republic of Congo. ⁵⁵Division of Vertebrate Zoology, Yale Peabody Museum of Natural History, New Haven, CT, USA. ⁵⁶Herbarium Bogoriense, Indonesian Institute of Sciences, Bogor, Indonesia. ⁵⁷Integrative Research Center, The Field Museum, Chicago, IL, USA. ⁵⁸Tropical Peat Research Institute, Biological Research Division, Malaysian Palm Oil Board, Selangor, Malaysia. ⁵⁹Kyoto University, Kyoto, Japan. ⁶⁰Centre for Tropical Environmental and Sustainability Sciences and College of Science and Engineering, James Cook University, Cairns, Australia. ⁶¹Wildlife Conservation Society, Kampala, Uganda. ⁶²Department of Environmental Science and Policy, George Mason University, Fairfax, VA, USA. ⁶³Faculté des Sciences Agronomiques, Université de Kisangani, Kisangani, Democratic Republic of Congo. ⁶⁴School of Geography and the Environment, University of Oxford, Oxford, UK. ⁶⁵Universidade Federal de Goiás, Goiânia, Brazil. ⁶⁶Flamingo Land Ltd, Kirby Misperton, UK. ⁶⁷CIRCLE, Environment Department, University of York, York, UK. ⁶⁸Salonga National Park, Kinshasa I, DR Congo. ⁶⁹Sabah Forestry Department, Sabah, Malaysia. ⁷⁰Universidad Autónoma del Beni, Riberalta, Bolivia. ⁷¹Instituto Boliviano de Investigación Forestal, Santa Cruz de la Sierra, Bolivia. ⁷²CIRAD, UMR Ecologie des Forêts de Guyane, Sinamary, French Guiana, France. ⁷³Natural History Museum, University of Oslo, Oslo, Norway. ⁷⁴Department of Biology, Boston University, Boston, MA, USA. ⁷⁵CIFOR, Bogor, Indonesia. ⁷⁶Southern Swedish Forest Research Center, Swedish University of Agricultural Sciences, Alnarp, Sweden. ⁷⁷Bureau Waardenburg, The Netherlands. ⁷⁸Fundación Con Vida, Medellín, Colombia. ⁷⁹Carboforexpert, Geneva, Switzerland. ⁸⁰Environmental and Life Sciences, Faculty of Science, Universiti Brunei Darussalam, Brunei, Darussalam. ⁸¹Museu Paraense Emilio Goeldi, Belém, Brazil. ⁸²FORDA, The Ministry of Forestry and Environment, Bogor, Indonesia. ⁸³Norwegian University of Life Sciences, Aas, Norway. ⁸⁴GeoS, Quito, Ecuador. ⁸⁵Museu Universitário, Universidade Federal do Acre, Brazil. ⁸⁶World Wildlife Fund, Washington, DC, USA. ⁸⁷CTFS-AA Asia Program, Harvard University, Cambridge, MA, USA. ⁸⁸Faculty of Forestry, University of Toronto, Toronto, Canada. ⁸⁹Yale School of Forestry & Environmental Studies, New Haven, CT, USA. ⁹⁰Centro de Investigación y Promoción del Campesinado - Regional Norte Amazónico, Riberalta, Bolivia. ⁹¹School of Earth Sciences and Environmental Sustainability, Northern Arizona University, Flagstaff AZ, USA. ⁹²Biological Sciences, University of Southampton, Southampton, UK. ⁹³School of Environment, Natural Resources and Geography, Bangor University, Bangor, UK. *These authors contributed equally to this work. Correspondence and requests for materials should be addressed to M.J.P.S. (email: m.j.sullivan@leeds.ac.uk)

Biodiversity is threatened by the loss of natural habitats and climate change^{1–3}. Tropical forests are under particular pressure, whilst also being the most diverse biomes on the planet⁴. By legally protecting areas, tropical countries can safeguard ecosystems with high biodiversity value⁵, and so address their policy targets to reduce biodiversity loss⁶. Likewise, carbon losses from the conversion of forest to other land-uses represent major emission sources for many tropical countries⁷, and so incentives such as the UN REDD+ policy framework have emerged to help safeguard areas with high carbon stocks⁸. Yet the potential for protection of carbon-rich areas to directly benefit

Study	Geographical scope	Number of plots		Number of sampling locations				Taxonomic level	Diversity measures	Minimum identification level	Diversity-carbon relationship	
		1 ha	0.04 ha	Total	Amazon	Congo	Borneo				Within stand	Among stands
This study	Tropics	360	6536	166	77	52	18	Species, genus and family	Richness, rarefied richness, Shannon diversity, Simpson diversity, Fisher's alpha and functional diversity	80% stems to genus, 60% to species	+	None
Ref. 22	Tropical and temperate	688 ^a	17200 ^a	25	2	1	1	Species	Richness ^b	None given	+	[None]
Ref. 24	Tropics	59	NA	11	3	2	0	Genus	Richness, Shannon diversity, functional diversity	80% stems to family	NA	+
Ref. 23	Tropical America	294	1975 ^d	59	47	0	0	Species	Richness, rarefied richness and Shannon diversity	None given	+	+ ^e

Table 1. Pan-tropical and continental studies assessing the diversity-carbon relationship. Sampling locations are groups of plots in close proximity to each other (individual large plots in ref. 22, TEAM study sites in ref. 24, “forest sites” in ref. 23, groups of plots within 5 km of each other in this study). The number of sampling locations in the largest blocs of forest in each continent are given, these are the Amazon basin and surrounding contiguous forest, the Congo basin and surrounding contiguous forest, and Borneo. + indicates a positive diversity-carbon relationship, NA indicates the relationship was not studied at the given scale. In this study, ref. 22 and ref. 24 all stems ≥ 10 cm d.b.h. were measured, in ref. 23 the minimum stem diameter measured varied among plots (either 5 cm or 10 cm). ^aSample size not stated, so maximum possible number of 1 ha and 0.04 ha subplots given. ^bStem density was included as a covariate in analysis. ^cRelationship analysed among 1 ha plots within sampling locations, not among sampling locations. ^d0.1 ha not 0.04 ha. ^eRelationship among sampling locations.

biodiversity, and vice versa, depends critically on the relationship between biomass carbon and tree diversity, at relevant scales. A positive relationship would indicate potential synergies while a negative relationship would indicate difficult trade-offs between biodiversity and carbon conservation⁹. In the absence of any relationship, optimal solutions for protected area placement need to carefully and separately consider the distribution of carbon stocks and the distribution of biodiversity¹⁰. Understanding these distributions and potential carbon-biodiversity trade-offs is important, as protecting some forest can divert threats onto other unprotected areas¹¹.

The expected form of diversity-carbon relationships in tropical forests and the strength and scale-dependence of any underlying mechanisms are uncertain. Numerous experimental studies have demonstrated that plant diversity promotes biomass production, with niche partitioning and positive species interactions allowing diverse communities to exploit available resources more efficiently^{12,13}. Diversity can also increase productivity through selection effects, where communities that contain a larger sample of the species pool are more likely to contain high functioning species that contribute strongly to ecosystem productivity¹⁴. Positive diversity-productivity relationships have been found in low diversity mid-latitude forests^{15–17}, potentially due to increased canopy packing through complimentary canopy architecture in higher diversity forests¹⁸. Yet, it is unclear how significant such mechanisms are in diverse tropical forests, as experimental and theoretical work indicates that the positive effect of diversity may saturate at high species richness^{12,19}. Furthermore, additional traits associated with high-productivity species could conceivably lead to a positive diversity-biomass mortality relationship, as highly productive stands tend to be composed of trees with shorter biomass residence times²⁰. Overall, this alongside high-productivity stands consisting of smaller, lighter-wooded trees²¹, may lead to a negative diversity-biomass carbon storage relationship.

Previous studies investigating the tree diversity-carbon stock relationship in tropical forests have reported a positive relationship at fine spatial scales^{22,23}. However, the form of the relationship at the stand-level (i.e. among 1 ha plots) is less clear (Table 1), as some studies report a continued positive diversity-carbon relationship among sampling locations^{23–25}, while one other did not detect a relationship among 1 ha subplots within 25 larger plots²². Thus, while there is some evidence that higher tree diversity promotes higher carbon stocks per unit area in diverse tropical forests^{22–24}, it is unknown whether any positive effect is strong enough for carbon and diversity to co-vary at scales relevant to conservation planning.

Here we analyse a unique dataset of 360 inventory plots across the three major tropical forest blocs in the Americas, Africa, and the Sundaland biogeographic region in Southeast Asia (subsequently referred to as Asia). Importantly, this dataset greatly improves sampling of the two most extensive contiguous areas of tropical forest in the world, centred on the Amazon and Congo Basins (Table 1). Each plot was surveyed by standardised methods and is of uniform size, allowing robust quantification of co-located aboveground live carbon and tree diversity estimates. We analyse this standardised, multi-continental dataset at three spatial scales. Firstly, we explore forest carbon and diversity patterns within South America, Africa and Asia, in order to characterise among-continent variations in tree alpha diversity, beta diversity, and carbon stocks. Secondly, we assess diversity-carbon relationships across each of the continents, initially by looking at the bivariate association of tree diversity metrics and carbon stocks per unit area, and then re-examining the relationships after controlling for potentially confounding environmental variation and residual spatial autocorrelation. Finally, we investigate fine-scale relationships

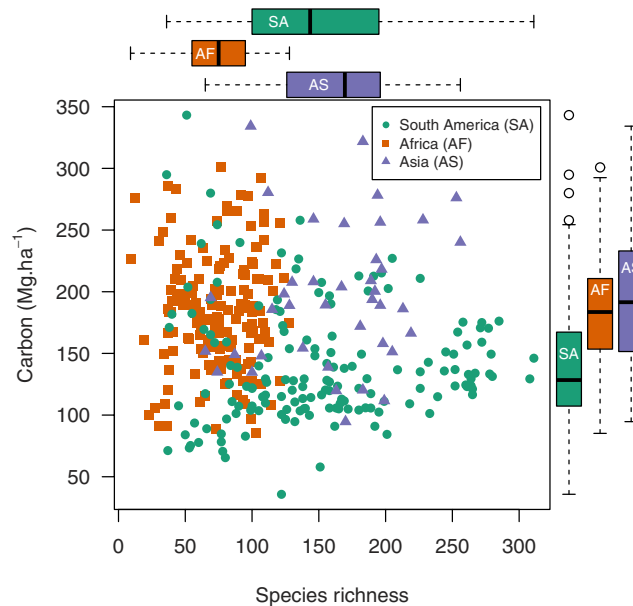


Figure 1. No relationship across the tropical forest biome between carbon stocks per unit area and tree species richness. Green circles = plots in South America ($n = 158$), orange squares = Africa ($n = 162$) and purple triangles = Asia ($n = 40$). Boxplots show variation in species richness and biomass carbon stocks in each continent. Both carbon and species richness differed significantly between continents (Table 2), but no significant correlation exists between carbon and species richness, neither within each continent ($\tau \leq 0.132$, $P \geq 0.12$), nor across all three (linear regression weighted by sampling density in each continent, $\beta < -0.001$, $t = 0.843$, $P = 0.4$, weights = 1.2 for South America, 0.6 for Africa and 1.8 for Asia). Results for other diversity metrics are similar (Supplementary Fig. S13).

between tree diversity and carbon within 0.04 ha subsections of 1 ha plots, where environmental differences that may obscure a positive diversity effect on carbon are accounted for. This approach allows us to (1) examine basic patterns of diversity and carbon across the biome, (2) test if more diverse tropical forests are also in fact more carbon dense, and (3) explore whether relationships between diversity and carbon-storage, after accounting for the effect of potentially confounding variables, are consistent with tree diversity having a positive effect on carbon in tropical forests. We conduct additional analyses to assess support for the operation of selection effects and niche complementarity at different spatial scales. We focus on carbon in aboveground live biomass derived using allometric relationships, and diversity metrics relating to taxon richness. We also repeat analyses using alternative diversity metrics that consider species abundance and functional diversity for which results and inferences are similar (see Supplementary Information).

Results

Pantropical forest carbon and diversity. Our standardised methods of inventory reveal great variation in both aboveground live carbon stocks and tree diversity within continents and across the humid tropical forest biome. While it is possible to find almost any combination of both parameters (Fig. 1), the plots reveal large differences in carbon and diversity amongst the three continents (Table 2). African tropical forests are characterised by high carbon storage per unit area and consistently low alpha-diversity (even the most species-rich African plot had fewer species than the median species richness recorded in South America and Asia). By contrast, in South American plots carbon storage per unit area was lower than in African forests (Fig. 1). Nevertheless both diversity and carbon vary greatly within South America, as reflects previously reported gradients in species richness²⁶ and biomass^{27,28}, with some stands in the Guiana Shield region containing carbon stocks comparable to forests in the paleotropics (Fig. 1). Asian forests differ again, having on average both high carbon storage per unit area and high tree diversity. These differences in diversity amongst continents remain when diversity metrics are standardised per 300 stems (Table 2), and when the analysis was repeated only including plots with >90% of stems identified to species level (Supplementary Table 3), thus are robust to differing stem numbers (lower in Africa, negative binomial GLM $\chi^2 = 188.6$, $P < 0.001$), and are unaffected by our levels of tree identification (not different amongst continents, Kruskal-Wallis test $H = 2.1$, $P = 0.335$). This pantropical assessment of forest carbon stocks and diversity is consistent with previous reports from individual continents, indicating high biomass in forests in Africa²⁹ and Borneo^{30,31}, high diversity in central and western Amazonia³² and low diversity in Africa^{33,34}. Our analysis demonstrates that forests across the Sundaland region of Southeast Asia are not only amongst the most diverse in the tropics, as noted elsewhere³³, but also amongst the most carbon-dense.

Beta-diversity also showed contrasting patterns amongst continents. Tree communities in neighbouring forests were least similar in Asia and most similar in Africa, where diversity rapidly saturates over geographic distance and plots (Fig. 2, Supplementary Fig. 11). However while similarity in species composition decayed most

Variable	South America	Africa	Asia
Carbon (Mg ha ⁻¹)	140 (133–148) ^A	183 (176–190) ^B	197 (180–215) ^B
Fisher's α	80 (71–88) ^B	28 (26–30) ^A	84 (73–96) ^B
Species richness (ha ⁻¹)	152 (141–163) ^B	74 (70–78) ^A	162 (147–177) ^B
(300 stems ⁻¹)	109 (102–116) ^B	65 (62–69) ^A	120 (111–130) ^B
Genus richness (ha ⁻¹)	91 (86–96) ^B	59 (56–62) ^A	87 (81–93) ^B
(300 stems ⁻¹)	72 (68–75) ^B	54 (51–56) ^A	71 (66–75) ^B
Family richness (ha ⁻¹)	38 (37–39) ^B	28 (27–28) ^A	40 (38–42) ^B
(300 stems ⁻¹)	33 (32–34) ^B	26 (25–27) ^A	35 (34–37) ^B

Table 2. Mean carbon stocks per unit area and tree diversity in forest inventory plots in South America (n = 158), Africa (n = 162) and Asia (n = 40). 95% confidence limits derived from 10,000 bootstrap resamples of the data (sampling with replacement) are shown in parentheses. Different letters indicate significant differences between continents (ANOVA and subsequent Tukey's all-pair comparison, $P < 0.05$). Data for other diversity metrics shown in Supplementary Table 2.

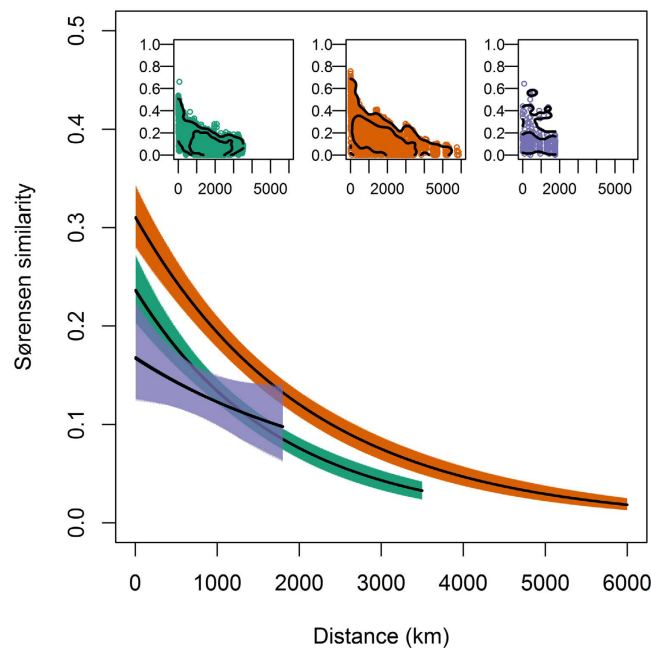


Figure 2. Decay in similarity (Sørensen index) of tree communities with distance in South America (green), Africa (orange) and Asia (purple). Solid lines show fitted relationships of the form $\ln(\text{similarity}) = \alpha + \beta \times \text{distance} + \epsilon$. Estimated α and β parameters for each continent are given in Supplementary Fig. S12, ϵ denotes binomial errors. Differences in the α parameter indicate differences in the similarity of neighbouring stands, while differences in the β parameter indicate differences in the distance decay of tree community similarity. Filled polygons show 95% confidence intervals derived from 10000 bootstrap resamples. Data underlying these relationships are shown in insets, with contours (0.05 and 0.25 quantiles) overlain to show the density of points following kernel smoothing.

strongly with distance in South America, there was weaker distance decay in Asia (Fig. 2, Supplementary Fig. 12). As a result, while adjacent stands differ most in Asia, at distances $> 1,000$ km plots in Asia are no more dissimilar than equidistant plot pairs in South America. Differences in beta diversity could have been driven by differences in gamma diversity³⁵. However, local tree communities remained more similar in Africa than other continents when null models were used to account for variation in gamma diversity (Supplementary Fig. 13). Gamma diversity was comparable in South America and Asia³³, so was also unlikely to drive differences in the distance decay of tree community similarity in those continents.

Large-scale diversity-carbon relationships. Notably, aboveground carbon stocks in live biomass per unit area was unrelated to tree species richness amongst 1 ha plots, whether analysed within continents or when combining all data in a pan-tropical analysis (Fig. 1, Table 3). Correlations with other diversity metrics varied in sign but were also non-significant (Table 3, Supplementary Fig. 14). Thus, in tropical forests high values of diversity and biomass carbon are associated neither at the biome nor the continental scale; instead they vary independently. We note that while in both South America and Africa there is sufficient statistical power to detect even small effects of diversity had they existed, in Asia power was only sufficient to detect relatively large effect sizes (Table 2).

Diversity metric	South America		Africa		Asia	
	τ	<i>P</i> -value	τ	<i>P</i> -value	τ	<i>P</i> -value
Fisher's α	0.083	0.12	0.012	0.821	0.115	0.302
Species richness	0.084 (0.092)	0.12 (0.087)	0.014 (0.031)	0.788 (0.573)	0.132 (0.151)	0.230 (0.174)
Genus richness	0.066 (0.059)	0.223 (0.272)	-0.016 (0.01)	0.765 (0.859)	-0.006 (-0.051)	0.954 (0.652)
Family richness	-0.007 (-0.042)	0.893 (0.43)	-0.051 (-0.036)	0.35 (0.519)	0.087 (0.021)	0.434 (0.862)
Detectable effect size	$\tau = 0.14$ $r = 0.22$		$\tau = 0.14$ $r = 0.22$		$\tau = 0.28$ $r = 0.43$	

Table 3. Correlations (Kendall's τ) between carbon and tree diversity in South America (n = 158 plots), Africa (n = 162) and Asia (n = 40). Power analysis was used to estimate the minimum effect size (presented as both τ and Pearson's r) detectable with 80% power. Correlations with taxon richness per 300 stems are shown in parentheses. Correlations with other diversity metrics shown in Supplementary Table 4.

Since confounding environmental variables might obscure any underlying effect of tree diversity on carbon stocks, we next applied multiple regression including climate and edaphic variables as covariates to statistically control for environmental variation that might otherwise obscure the effect of diversity. In ordinary least squares multiple regression models, there was a consistent negative relationship between diversity and carbon in South America, and no significant relationship in Africa and Asia (Fig. 3b). When the analysis was repeated using simultaneous autoregressive error models to account for spatial autocorrelation, diversity was not supported as a predictor in South America or Africa (Fig. 3c). In Asia, while there were significant positive relationships between carbon and both Fisher's α and species richness (Fig. 3c), environmental variables were more important predictors of carbon stocks based on their occurrence in low AIC_C models (Supplementary Table 5) and other diversity metrics were not supported as predictors of carbon stocks (Fig. 3c). Thus, overall no consistent pan-tropically applicable relationship between diversity and carbon stocks was observed. Instead, carbon stocks per unit area was influenced by climate and soil (Supplementary Fig. 15, Supplementary Table 5). In South America and Africa annual cumulative water deficit was the strongest environmental predictor of carbon stocks, as indicated by high \sum AIC_C weights (≥ 0.98), and in South America a positive effect of soil fertility was also evident (Supplementary Fig. 15, Supplementary Table 5). In Asia, where no plots experienced cumulative water deficit, carbon stocks per unit area increased with mean annual precipitation (\sum AIC_C weights = 1) and declined with mean annual temperature (\sum AIC_C weights = 0.65).

Carbon stocks per unit area was also related to structural attributes, increasing with basal area and basal area-weighted mean wood density, but not with stem density (Supplementary Fig. 16). While consistent with previous studies²³, this is hardly surprising as both wood density and basal area are constituents of biomass estimates. Critically, these two structural attributes of carbon stocks per unit area were themselves largely unrelated to species richness (Supplementary Fig. 16), indicating that diversity is not a correlate of the key structural factors that lead to high biomass in some tropical forest stands. Stem size inequality, which has been posited as a mechanism linking diversity and carbon in boreal forests³⁶, was positively related to carbon but unrelated to species richness (Supplementary Fig. 17). Inclusion of mean wood density (a proxy for stem turnover) in multiple regression models did not affect diversity-carbon relationships (Supplementary Table 6), indicating that the lack of a consistent diversity-carbon relationship is unlikely to be due to variation in mortality. Finally, we also used structural equation modelling to examine the relationship between diversity and carbon while explicitly modelling the effect of climate and soil on both tree species richness and carbon stocks. In this modelling framework, there were non-significant positive relationships between species richness and carbon in Africa and Asia and a significant negative relationship in South America (Supplementary Figure 18).

Fine-scale diversity-carbon relationships. Amongst 0.04 ha subplots within each plot most environmental differences in climate and soil are implicitly accounted for. Here, relationships between species richness and carbon were on average significantly positive when considering all 266 \times 1 ha plots for which we had subplot-scale data (one-sample Wilcoxon test, $P = 0.007$), and significant for plots within Africa ($n = 111$ plots, one-sample Wilcoxon test, $P = 0.022$) and South America alone ($n = 118$ plots, one-sample Wilcoxon test, $P = 0.013$, Fig. 4). Within these plots, 148 (55.6%) had a positive richness-carbon relationship and 118 (44.4%) a negative relationship (Fig. 4). Overall the richness-carbon relationship was weak but positive ($\beta = 0.096 \pm 0.048$ SE). This implies that doubling species richness per 0.04 ha would increase carbon stocks by 6.9%, with similar relationships for other diversity metrics (Supplementary Table 7). This is consistent with an independent within-plot study of 25 plots which showed a 7% effect size of diversity on aboveground biomass at the 0.04 ha spatial scale, but no relationship at the 1 ha scale²².

Examining support for niche complementarity and selection effects. There was a statistically significant positive relationship between a multivariate metric of functional diversity incorporating wood density and maximum diameter traits and carbon stocks at the 0.04 ha scale (linear mixed effects model, $P < 0.001$, Supplementary Figure 1), but this relationship was not significant in any continent at the 1 ha scale (linear regression models, $P \geq 0.139$, Supplementary Figure 1). Carbon stocks increased with the community weighted means of both wood density and maximum diameter traits at both 0.04 ha (linear mixed effects models, $P < 0.001$, Supplementary Figure 4) and 1 ha scales (linear regression models, $P \leq 0.049$, Supplementary Figure 4), indicating that carbon stocks was positively related to the functional dominance of potentially large and dense wooded species. The probability of sampling a species with large maximum size or dense wood increased through the

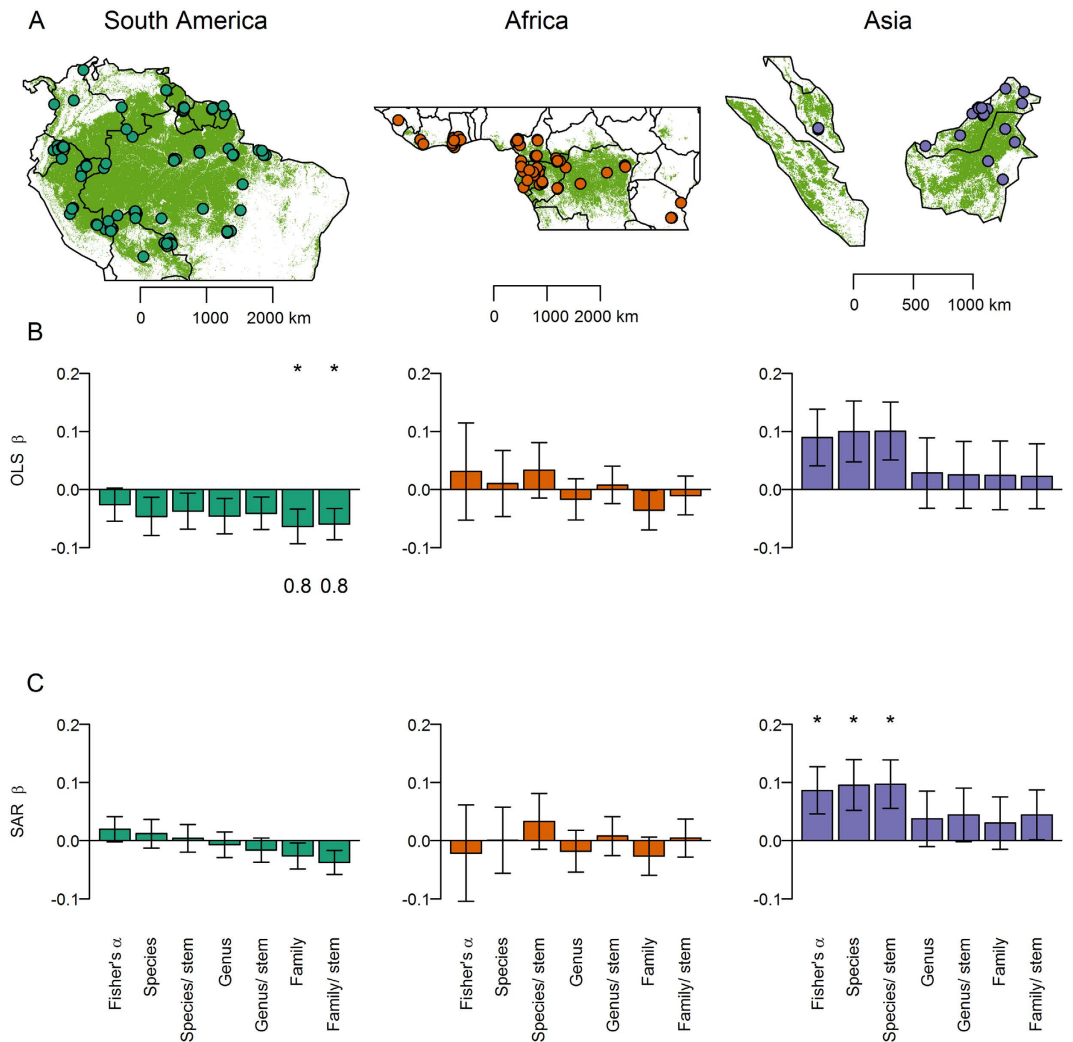


Figure 3. Stand-level effect of diversity on carbon stocks per unit area. (A) Location of clusters of forest inventory plots in South America ($n = 158$ plots), Africa ($n = 162$ plots) and Asia ($n = 40$ plots) (some cluster centroids are not visible due to over plotting). (B & C) Diversity metric coefficients in multiple regressions relating carbon to diversity, climate and soil. Results have been presented for (B) non-spatial (OLS) and (C) simultaneous autoregressive error (SAR) models. Bars show model-averaged parameter estimates, with error bars showing standard errors. Asterisks denote variables that were significant in the average model ($P < 0.05$), with the summed AIC_C weights of models in which a variable appears shown beneath bars (where > 0.75). Taxa/stem denotes richness estimates per 300 stems. SAR models indicate that increasing species richness by 1 SD (from 86 to 151 species.ha⁻¹) increased carbon by 1.5 Mg.ha⁻¹ in South America, 0.2 Mg.ha⁻¹ in Africa and 15.8 Mg.ha⁻¹ in Asia (note only the relationship in Asia was statistically significant). Green shading in (A) shows the extent of broadleaved evergreen and fresh water regularly flooded forest classes from⁵². Model coefficients are given in Supplementary Table 5. Maps were created in R version 3.02 (<http://www.R-project.org/>)⁵³ using base maps from maps package version 2.3–9 (<http://CRAN.R-project.org/package=maps>)⁵⁴.

range of species richness values typical of 0.04 ha subplots, but tended to saturate by the species richness values typical of 1 ha plots, with the exact form of this relationship depending on the threshold used to define a large or dense wooded species and whether the null model used to sample species randomly selected species from the pool available within a continent or sampled species according to their relative frequency of occurrence (Supplementary Figures 5–10). For example, the expected probability of sampling a tree species with maximum diameter ≥ 70 cm, as assessed using a null model randomly selecting species from the pool of species recorded in plots within each continent, increased from 0.760 to 0.878 over the interquartile range of species richness found in 0.04 ha subplots (i.e. 11 to 18 species), but was 0.999 by the lower quartile of species richness in 1 ha plots (i.e. 72 species). Likewise, there was a positive relationship between the observed occurrence of potentially large tree species and species richness in 0.04 ha subplots (binomial generalised linear mixed effects models, $P < 0.001$, Supplementary Figure 6), while at 1 ha scale this relationship was no longer evident as all but one 1 ha plot contained a potentially large species. Further details and interpretation of these analyses are given in Supplementary Discussion.

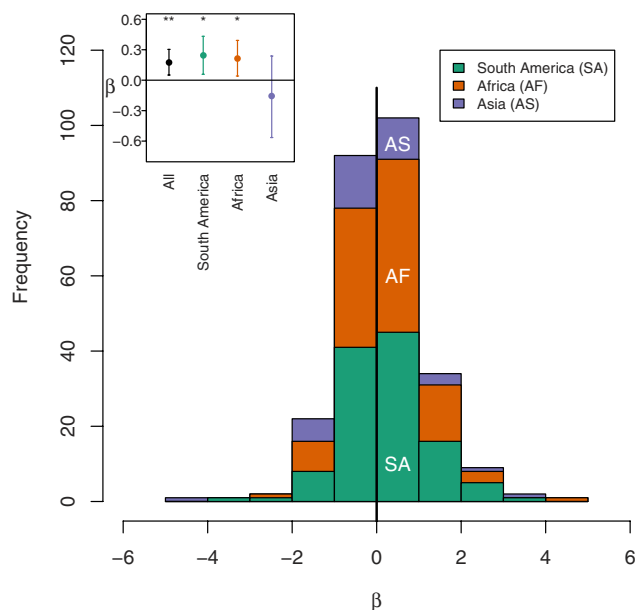


Figure 4. Variation in the coefficient (β) of the relationship between species richness and carbon among 0.04 ha subplots within 266 1 ha plots. Coefficients come from multiple regression models also containing the number of stems as a second-order polynomial term to allow for a saturating relationship. Coefficients from plots in South America are shown in green, Africa in orange and Asia in purple. Mean values of coefficients are shown in the inset, with error bars showing 95% confidence intervals derived from 10000 bootstrap resamples (with replacement) of the dataset, with asterisks denoting significant differences from zero (one-sample Wilcoxon test, $**P < 0.01$, $*P < 0.05$). Across all plots, doubling species richness in 0.04 ha subplots increased carbon by 6.9%. The horizontal line in the inset and bold vertical line in the main figure show where coefficients = 0. β is in units of $\ln(\text{Mg}\cdot\text{ha}^{-1} \text{ carbon})$ per $\ln(\text{tree species})$.

Discussion

By analysing a large, standardised, pan-tropical dataset of inventory plots we were able to explore large-scale patterns in tropical forest above-ground carbon stocks per unit area and tree diversity, and the large-scale and fine-scale relationships between the two. Carbon and diversity both exhibit remarkable variation across the tropical forest biome. Each continent has a distinctive signature of alpha diversity, beta diversity and carbon-density, and tropics-wide it is possible to find all combinations of diversity and carbon. Yet, these two fundamental attributes of tropical forests are also found to be largely unrelated to one another among stands, whether analysed among-continent or within each one.

Our results contrast with those from an earlier examination of pan-tropical diversity-biomass relationships reporting a positive relationship with genus level diversity²⁴ (Table 1). Although both studies statistically control for the effect of climate, we also restricted our analysis to lowland plots and statistically controlled for the effect of soil, which may have improved our ability to account for the effect of environmental variation when examining the effect of diversity on carbon stocks. Additionally, our results are based on an order of magnitude more extensive sampling of the biome (166 locations and 360 plots in this study, compared to 11 locations and 59 plots in ref. 24). Positive stand-scale diversity-carbon stock per unit area relationships have also been reported in the neotropics²³ and in some Central African forests²⁵, but these positive relationships were once again not evident with improved sampling across the whole domain and once spatial autocorrelation is accounted for. Our neotropical dataset differs from Ref. 23 by being concentrated in the Amazon basin rather than including Central America and the Caribbean Islands, and by excluding plots in dry forest; these differences may have reduced the effects of environmental and biogeographic variation in our data.

Our best sampled regional domains - the world's two largest contiguous regions of tropical forest - show no within-continent diversity-carbon relationship at the 1 ha scale. In our dataset, tropical carbon remained positively but weakly related to diversity in Asia, and this was the exception among major tropical forest regions. Importantly, this lack of a consistent positive relationship between diversity and carbon is robust to analysis method, persisting whether data are analysed using simple bivariate correlations, or with multiple regressions to account for environmental drivers, or by simultaneous autoregressive models to also account for spatial autocorrelation, or when constructing structural equation models to account for environmental effects on diversity. Instead, we found that moisture availability (annual cumulative water deficit in South America and Africa, mean annual precipitation in Asia where plots did not experience cumulative water deficit) was the most important and pantropically consistent environmental driver of spatial variation in aboveground biomass carbon stocks per unit area.

Although tree diversity and carbon stocks were uncorrelated at the stand-level, they were positively correlated within forest stands, so our results are consistent with tree diversity having a positive local effect on carbon in tropical forests, supporting previous studies documenting positive fine-scale relationships^{22,23} (Table 1). The presence

of a weakly positive (overall, South America, Africa) relationship at 0.04 ha but not at 1 ha scale (overall, South America, Africa) could indicate that the mechanisms driving the diversity-carbon relationship are scale dependent, or could be due to environmental variation acting at larger spatial scales obscuring the mechanistic effects of diversity²². Although our multiple regression models applied at 1 ha scale statistically control for important variation in climate, soil texture and soil chemistry, it is clearly not possible to capture all environmental variation that may influence carbon stocks, such as local disturbance history, so we cannot rule out the latter explanation. However, we conducted additional analyses (full details in Supplementary Discussion) to examine possible mechanisms underlying the diversity effects and explore their putative scale-dependency. Carbon stocks increased with the functional dominance of species with high wood density and large maximum diameter at both 0.04 ha and 1 ha scales (Supplementary Figure 4). The effect of functional dominance at 1 ha scale has been found before in tropical forests^{24,37}, and has been interpreted to support the role of selection effects^{16,24}. However, this analysis by itself is a test of the biomass ratio hypothesis³⁷. For selection effects to operate, the probability of sampling a high functioning species should also increase with species richness. We found that the probability of sampling species with high maximum diameters or high wood density increases with species richness at diversity levels found in 0.04 ha subplots, but saturates at diversity levels below those of 1 ha plots (Supplementary Figures 5–10), indicating that selection effects, as expected, appear to be scale-dependent. Additionally, the effects of niche complementarity may also saturate, as we found a positive relationship between a multivariate functional diversity metric (incorporating wood density and maximum diameter traits) and carbon only at the 0.04 ha scale (Supplementary Figure 1). The absence of a significant relationship between tree functional diversity and carbon stocks per unit area at 1 ha scale is consistent with a previous analysis from three neotropical rainforests³⁷. Although the saturating probability of sampling a high functioning species with increasing species richness and the absence of carbon – functional diversity relationships at 1 ha are consistent with both selection effects and niche complementarity being scale-dependent, they are based on correlative analysis of observational data so causal inferences need to be made cautiously. Neither do our analyses test other potentially important ecosystem impacts of diversity, such as on the resistance and resilience of biomass production to climate extremes³⁸. Long-term large-scale experiments that manipulate tree diversity in tropical forests³⁹ may provide additional mechanistic insights into potential positive effects of tree diversity and their potential saturation with scale.

A caveat with this and other studies using allometric equations to estimate above-ground biomass carbon is that allometric equations do not allow variation in tree architecture with forest structure. For example, Banin *et al.*⁴⁰ found a weak negative relationship between tree height and stem density, meaning that allometric equations may overestimate carbon stocks in plots where stem density is highest. This could increase the chances of finding a spurious positive relationship between diversity and carbon, as we find a weak positive relationship between stem density and species richness (Supplementary Figure 16). This potential bias is unlikely to have impacted our results, as we still find a weak positive diversity-carbon relationship within plots and no relationship among plots when diversity metrics are standardised per *n* stems (Table 3, Supplementary Table 7). Such potential biases could be evaluated in the future if co-located LiDAR based aboveground biomass carbon estimates and ground-based tree diversity measurements are made at sufficient sites. The uncertainty in biomass carbon estimates due to using allometric equations could reduce the chance of finding diversity-carbon relationships by adding noise to the data. Whilst this highlights the need to maximise statistical power with large datasets, we note that the two largest studies investigating diversity-carbon relationships (this study by number of sampling locations across the biome, Ref. 22, by area sampled, see Table 1) converge on a similar result with independent datasets; diversity and carbon are positively related at the 0.04 ha scale but unrelated at the 1 ha scale.

Conservation implications. Despite the absence of a stand-level diversity-carbon relationship, some forest stands certainly do combine high tree diversity and biomass (Fig. 1), indicating that high value carbon and biodiversity conservation can be simultaneously achieved, but only with confidence if both are considered^{9,10}. We note that conservation strategies will also need to consider biodiversity of taxa other than trees, which may also be unrelated to carbon stocks⁴¹, the conservation value of specific species assemblages³, belowground carbon stores such as in tropical peat swamps⁴², and spatial variation in opportunity costs⁴³. Methods to select protected areas that consider multiple metrics of conservation value (e.g. aboveground biomass carbon and aspects of biodiversity) are available¹⁰. Our results support the use of such an approach over carbon-dominated prioritisation incentivised under REDD+⁹. Applying this in practice is challenging as it requires knowledge of spatial variation in tree diversity, composition and carbon stocks, highlighting the importance of careful identifications to species level during forest inventories. As tropical forests can have any combination of tree diversity and carbon both will require explicit consideration when optimising policies to manage tropical carbon and biodiversity.

In sum, our large, pan-tropical analysis reveals that at small scales of less than 1 ha tree diversity is weakly positively correlated with aboveground carbon stocks, potentially due to both niche complementarity and sampling effects. Yet our results show that these processes do not translate to patterns at scales that matter practically for conservation: tree diversity and carbon vary independently among sites, both within continents and across the whole tropical forest biome. Despite the general lack of association between diversity and carbon, our analysis demonstrates that forests in Asia are not only amongst the most diverse in the tropics but also amongst the most carbon-dense. Thus at a global scale a clear synergy emerges, with forests in Asia being both highly speciose and extremely carbon-dense. Asian forests are under substantial threat, particularly from conversion to oil palm plantations and more intensive logging than elsewhere in the tropics. As a triple hotspot for biodiversity, carbon and threat, there is a compelling global case for prioritising their conservation.

Methods

To permit comparisons among and within continents we utilised 360 forest inventory plots, surveyed using uniform standardised protocols, from three networks, RAINFOR (Amazon Forest Inventory Network; www.

rainfor.org, ref. 44), AfriTRON (African Tropical Rainforest Observatory Network; www.afritron.org, ref. 29) and T-FORCES (Tropical Forests in the Changing Earth System; www.tforces.net). The plots were all within closed-canopy lowland (maximum altitude 1217 m above sea level) humid *terra firme* forest (mean annual temperature, MAT, $\geq 20^\circ\text{C}$ and mean annual precipitation, MAP, $\geq 1300\text{ mm}$), all were 1 ha, except four of 0.96 ha, and none exceeded 500 m in maximum dimension. The rationale for restricting the environmental domain sampled was to minimise the environmental differences among plots and thus reduce the confounding effect of environmental variation on the diversity-carbon relationship; this approach contrasts with previous studies that have sampled along larger elevation (and thus temperature)²⁴ and precipitation²³ gradients. In each plot at least 80% of stems were identified to genus and at least 60% to species (mean = 90.3% stems identified to species; 84% of plots had at least 80% stems identified to species, 63% had at least 90% of stems identified to species). All stem diameter measurements follow standard (above buttress) methods (see Supplementary Methods for full protocols). All stems $\geq 10\text{ cm d.b.h.}$ were measured. Sampling was distributed across the world's three largest tropical humid forest blocs, with 158 plots in South America, 162 in Africa and 40 in Asia (Fig. 3). These came from 166 discrete localities (South America 80, Africa 67, Asia 19), where a 'locality' is defined as clusters of plots with maximum inter-plot distance of 5 km. Plot data were curated in ForestPlots.net⁴⁵ or using equivalent offline procedures, with each plot following the same quality control and subsequent calculation protocol. Aboveground biomass (AGB) was estimated for each stem using the allometric equation $\text{AGB} = 0.0673 \times (\rho D^2 H)^{0.976}$, from⁴⁶, where ρ is stem wood density (in g cm^{-3}) obtained from a world database^{47,48}, D is stem diameter (in cm) at 1.3 m or above buttresses, and H is height (in m), the latter estimated using regional height-diameter Weibull equations⁴⁹. AGB values were converted to estimates of carbon using the mean carbon fraction for tropical angiosperms, 47.1%, from⁵⁰. Taxon richness was estimated as the sum of identified species and morphospecies plus the estimated number of unidentified taxa based on observed richness per stem ratios (details in Supplementary Methods). Richness per 300 stems was estimated using individual based rarefaction.

Differences in diversity and carbon among continents were assessed using analysis of variance. To meet model assumptions, carbon stocks per unit area was log-transformed and Fisher's alpha square-root transformed, while taxon richness was modelled using a negative binomial error distribution to account for overdispersion. We used log-linear generalised linear models with binomial errors to model the relationship between Sørensen index (beta diversity) and geographical distance between plots in each continent, restricting this analysis to plots with $>90\%$ of stems identified to species level (227 plots). Relationships among 1 ha plots were assessed using [1] bivariate Kendall's τ correlations and [2] multiple regressions of carbon as a function of diversity, climate (cumulative water deficit, MAT, MAP; 1 km resolution) and soil (total exchangeable bases, C:N ratio, soil texture; 0–30 cm depth). We ran all predictor subsets and averaged models where cumulative AIC_C weights summed to 0.95. Residual spatial autocorrelation was present, so we repeated the analysis using simultaneous autoregressive error models to explicitly model spatially autocorrelated errors. We also repeated the analysis using structural equation models implemented in the R package lavaan⁵¹. Relationships amongst 0.04 ha subplots in the 266 plots where subplot level data were also available were examined using multiple regressions of $\ln(\text{carbon})$ against $\ln(\text{diversity})$ and $\ln(\text{stem density})$ for each plot individually, as well as for all plots using a random coefficients mixed effect model with plot identity as a random effect. Finally, we conducted a series of analyses to assess support for possible mechanisms driving diversity-carbon relationships, which are described in full in the Supplementary Discussion. Briefly, we produced separate models of carbon stocks as a function of the community weighted mean (CWM) of wood density, the CWM of maximum stem diameter, the standard deviation of wood density and a functional diversity metric including both these traits. Relationships at 1 ha were modelled using linear regression, relationships at 0.04 ha were modelled using linear mixed effects models with plot identity as a random effect. We related the expected probability of sampling a species with large potential size or high wood density (defined as maximum diameter $\geq 70\text{ cm}$ or wood density $\geq 0.8\text{ g cm}^{-3}$ respectively, other thresholds were also examined) to species richness using null models, and also used binomial generalised linear mixed-effects models to relate the occurrence of these species in 0.04 ha subplots to species richness. Significance testing is based on two-tailed tests, with $\alpha = 0.05$ used to determine statistical significance. See Supplementary Methods for full details of methods.

Data availability. Data are available from http://dx.doi.org/10.5521/FORESTPLOTS.NET/2016_3.

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Author Contributions

O.L.P., S.L.L. and Y.M. conceived the RAINFOR, AfriTRON and T-FORCES forest census network programmes. J. Talbot, O.L.P., S.L.L. and L. Miles conceived and designed the study. O.L.P., R.J.W.B., T.R.F., T.R.B., A.M.M. (South America), S.L.L., B.S., L.J.T.W., W.H., A.C.S., S.K.B., T.S. (Africa), L.Q., S.L.L., O.L.P., T.S., L.F.B. and F.S. (Asia) coordinated data collection with the help of most co-authors. G.L.G., S.L.L., O.L.P., T.R.B. and G.C.P. contributed tools to analyse and curate data. J. Talbot, S.L.L., O.L.P., L.Q., S.K.B., J.C., A.C.S., W.H., G.L.G., A.M.M., B.S., T.S., H.t.S., L.J.T.W., K.A.B., S.I.A., E.C.A., A.A., L.E.O.C.A., P.A., G.A.A.C., T.R.B., M.B., L.F.B., C.B., J.F.B., N.B., J.B., D.B., F.B., R.B., N.C.P.C., J.L.C.C., C.C., E.C., C.J.C., J.A.C., E.N.H.C., Z.R.C., G.D., S.J.D., E.A.D., C.D.C., M.N.D.K., J.L.D., T.L.E., J.S.E., C.E.N.E., S.F., T.R.F., R.H., L.V.G., M.G., J.H., D.J.H., T.B.H., K.K., K.H.O.L.K., K. Kitayama, S.G.W.L., W.F.L., M.E.L., P.A.L., T.L., J.C.L., F.M.L., J.R.M., Y.M., L.M., B.S.M., B.H.M.J., A.R.M., P.S.M., V.C.M., J.T.M., J.M., R.N., E.A.O., A.C.P., G.P., M.P.C., P.P., G.C.P., A.D.P., J.R.P., R.B.P., H.P., C.A.Q., J.R., M.R.M., E.R., K.A.S., R.P.S., I.S., D.S., R.S., M.S., L.S., H.T., S.T., J.W.T., S.C.T., M.T., P.U., F.C.V., P.N.V., I.C.G.V., V.A.V., O.W., S.W. and L.Z. collected field data. M.J.P.S. and J. Talbot carried out the data analysis. M.J.P.S., J. Talbot, O.L.P. and S.L.L. wrote the paper. All co-authors commented on or approved the manuscript.

Additional Information

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