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Co-limitation towards lower latitudes shapes global forest diversity gradients

Liang Jingjing ^{1,*}, Gamarra Javier G. P. ², Picard Nicolas ³, Zhou Mo ¹, Pijanowski Bryan ⁴, Jacobs Douglass F. ⁴, Reich Peter B. ^{5,6,7}, Crowther Thomas W. ⁸, Nabuurs Gert-Jan ^{9,10}, De-Miguel Sergio ^{11,12}, Fang Jingyun ^{13,14}, Woodall Christopher W. ¹⁵, Svenning Jens-Christian ^{16,17}, Jucker Tommaso ¹⁸, Bastin Jean-Francois ¹⁹, Wisser Susan K. ²⁰, Slik Ferry ²¹, Herault Bruno ^{22,23}, Alberti Giorgio ^{24,25,26}, Keppel Gunnar ²⁷, Hengeveld Geerten M. ^{28,29}, Ibsch Pierre L. ³⁰, Silva Carlos A. ³¹, Ter Steege Hans ³², Peri Pablo L. ³³, Coomes David A. ³⁴, Searle Eric B. ³⁵, Von Gadow Klaus ^{36,37,38}, Jaroszewicz Bogdan ³⁹, Abbasi Akane O. ¹, Abegg Meinrad ⁴⁰, Yao Yves C. Adou ⁴¹, Aguirre-Gutierrez Jesus ^{42,43}, Zambrano Angelica M. Almeyda ⁴⁴, Altman Jan ^{45,46}, Alvarez-Davila Esteban ⁴⁷, Alvarez-Gonzalez Juan Gabriel ⁴⁸, Alves Luciana F. ⁴⁹, Amani Bienvenu H. K. ⁵⁰, Amani Christian A. ⁵¹, Ammer Christian ⁵², Ilondea Bhely Angoboy ⁵³, Anton-Fernandez Clara ⁵⁴, Avitabile Valerio ⁵⁵, Aymard Gerardo A. ⁵⁶, Azihou Akomian F. ⁵⁷, Baard Johan A. ⁵⁸, Baker Timothy R. ⁵⁹, Balazy Radomir ⁶⁰, Bastian Meredith L. ^{61,62}, Batumike Rodrigue ⁶³, Bauters Marijn ^{64,65}, Beeckman Hans ⁶⁶, Benu Nithanel Mikael Hendrik ⁶⁷, Bitariho Robert ⁶⁸, Boeckx Pascal ⁶⁵, Bogaert Jan ⁶⁹, Bongers Frans ¹⁰, Bouriaud Olivier ⁷⁰, Brancalion Pedro H. S. ⁷¹, Brandl Susanne ⁷², Brearley Francis Q. ⁷³, Briseno-Reyes Jaime ⁷⁴, Broadbent Eben N. ³¹, Bruelheide Helge ^{75,76}, Bulte Erwin ⁷⁷, Catlin Ann Christine ⁷⁸, Gatti Roberto Cazzolla ⁷⁹, Cesar Ricardo G. ⁷¹, Chen Han Y. H. ³⁵, Chisholm Chelsea ⁸⁰, Cienciala Emil ^{81,82}, Colletta Gabriel D. ⁸³, Corral-Rivas Jose Javier ⁷⁴, Cuchiatti Anibal ⁸⁴, Cuni-Sanchez Aida ^{85,86}, Dar Javid A. ^{87,88,89}, Dayanandan Selvadurai ^{90,91}, De Haulleville Thales ^{66,69}, Decuyper Mathieu ¹⁰, Delabye Sylvain ^{92,93}, Derroire Geraldine ⁹⁴, Devries Ben ⁹⁵, Diisi John ⁹⁶, Van Do Tran ⁹⁷, Dolezal Jiri ^{45,98}, Dourdain Aurelie ⁹⁴, Durrheim Graham P. ⁵⁸, Obiang Nestor Laurier Engone ⁹⁹, Ewango Corneille E. N. ¹⁰⁰, Eyre Teresa J. ¹⁰¹, Fayle Tom M. ^{93,102}, Feunang Lethicia Flavine N. ¹⁰³, Finer Leena ¹⁰⁴, Fischer Markus ¹⁰⁵, Fridman Jonas ¹⁰⁶, Frizzera Lorenzo ¹⁰⁷, De Gasper Andre L. ¹⁰⁸, Gianelle Damiano ¹⁰⁷, Glick Henry B. ¹⁰⁹, Gonzalez-Elizondo Maria Socorro ¹¹⁰, Gorenstein Lev ⁷⁸, Habonayo Richard ¹¹¹, Hardy Olivier J. ¹¹², Harris David J. ¹¹³, Hector Andrew ¹¹⁴, Hemp Andreas ¹¹⁵, Herold Martin ¹¹⁶, Hillers Annika ^{117,118}, Hubau Wannes ^{66,119}, Ibanez Thomas ¹²⁰, Imai Nobuo ¹²¹, Imani Gerard ¹²², Jagodzinski Andrzej M. ^{123,124}, Janecek Stepan ⁹², Johannsen Vivian Kvist ¹²⁵, Joly Carlos A. ¹²⁶, Jumbam Blaise ^{127,128}, Kabelong Banoho L. P. R. ¹⁰³, Kahsay Goytom Abraha ¹²⁹, Karminov Viktor ¹³⁰, Kartawinata Kuswata ¹³¹, Kassi Justin N. ¹³², Kearsley Elizabeth ¹³³, Kennard Deborah K. ¹³⁴, Kepfer-Rojas Sebastian ¹²⁵, Khan Mohammed Latif ¹³⁵, Kigomo John N. ¹³⁶, Kim Hyun Seok ^{137,138,139,140}, Klauberg Carine ³¹, Klomberg Yannick ⁹², Korjus Henn ¹⁴¹, Kothandaraman Subashree ^{88,89}, Kraxner Florian ¹⁴², Kumar Amit ¹⁴³, Kuswandi Relawan ⁶⁷, Lang Mait ^{141,144}, Lawes Michael J. ¹⁴⁵, Leite Rodrigo, V ¹⁴⁶, Lentner Geoffrey ⁷⁸, Lewis Simon L. ^{59,147}, Libalah Moses B. ^{103,148}, Lisingo Janvier ¹⁴⁹, Lopez-Serrano Pablito Marcelo ¹⁵⁰, Lu Huicui ¹⁵¹, Lukina Natalia, V ¹⁵², Lykke Anne Mette ¹⁵³, Maicher Vincent ^{92,93,154}, Maitner Brian S. ¹⁵⁵, Marcon Eric ^{94,156}, Marshall Andrew R. ^{157,158,159}, Martin Emanuel H. ¹⁶⁰, Martynenko Olga ¹³⁰, Mbayu Faustin M. ¹⁰⁰, Mbuvi Musingo T. E. ¹⁶¹, Meave Jorge A. ¹⁶², Merow Cory ¹⁶³, Miscicki Stanislaw ¹⁶⁴, Moreno Vanessa S. ⁷¹, Morera Albert ¹², Mukul Sharif A. ¹⁶⁵, Muller Jorg C. ^{166,167}, Murdjoko Agustinus ¹⁶⁸, Nava-Miranda Maria Guadalupe ¹⁵⁰, Ndiva Litonga Elias ¹⁶⁹, Neldner Victor J. ¹⁰¹, Nevenic Radovan, V ¹⁷⁰, Nforbelie Louis N. ¹⁰³, Ngoh Michael L. ^{171,172}, N'Guessan Anny E. ⁴¹, Ngugi Michael R. ¹⁰¹, Ngute Alain S. K. ^{165,173}, Njila Emile Narcisse N. ¹⁰³, Nyako Melanie C. ¹⁰³, Ochuodho Thomas O. ¹⁷⁴, Oleksyn Jacek ¹²³, Paquette Alain ¹⁷⁵, Parfenova Elena, I ¹⁷⁶, Park Minjee ⁴, Parren Marc ¹⁰

Parthasarathy Narayanaswamy⁸⁹, Pfausch Sebastian¹⁷⁷, Phillips Oliver L.⁵⁹, Piedade Maria T. F.¹⁷⁸,
 Piotto Daniel¹⁷⁹, Pollastrini Martina¹⁸⁰, Poorter Lourens¹⁰, Poulsen John R.¹⁵⁴,
 Poulsen Axel Dalberg¹¹³, Pretzsch Hans¹⁸¹, Rodeghiero Mirco^{107, 182}, Rolim Samir G.¹⁷⁹,
 Rovero Francesco^{183, 184}, Rutishauser Ervan¹⁸⁵, Sagheb-Talebi Khosro¹⁸⁶, Saikia Purabi¹⁸⁷,
 Sainge Moses Nsanyi^{171, 188}, Salas-Eljatib Christian^{189, 190, 191}, Salis Antonello², Schall Peter⁵²,
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 Seben Vladimir¹⁹⁵, Schongart Jochen¹⁷⁸, Sellan Giacomo^{73, 196}, Selvi Federico¹⁸⁰,
 Serra-Diaz Josep M.¹⁹⁷, Sheil Douglas^{10, 198}, Shvidenko Anatoly Z.¹⁴², Sist Plinio¹⁹⁹,
 Souza Alexandre F.²⁰⁰, Sullivan Martin J. P.⁷³, Sundarapandian Somaiah⁸⁹, Svoboda Miroslav⁴⁶,
 Swaine Mike D.²⁰¹, Targhetta Natalia¹⁷⁸, Tchebakova Nadja¹⁷⁶, Trethowan Liam A.²⁰²,
 Tropek Robert^{92, 93}, Mukendi John Tshibamba²⁰³, Umunay Peter Mbanda²⁰⁴, Usoltsev Vladimir A.²⁰⁵,
 Laurin Gaia Vaglio²⁰⁶, Valentini Riccardo²⁰⁶, Valladares Fernando²⁰⁷, Van Der Plas Fons²⁰⁸,
 Vega-Nieva Daniel Jose⁷⁴, Verbeeck Hans¹³³, Viana Helder^{209, 210}, Vibrans Alexander C.²¹¹,
 Vieira Simone A.²¹², Vleminckx Jason²¹³, Waite Catherine E.²¹⁴, Wang Hua-Feng²¹⁵,
 Wasingya Eric Katembo¹⁰⁰, Wekesa Chemuku²¹⁶, Westerlund Bertil¹⁰⁶, Wittmann Florian²¹⁷,
 Wortel Verginia²¹⁸, Zawila-Niedziwiecki Tomasz²¹⁹, Zhang Chunyu²²⁰, Zhao Xiuhai²²⁰, Zhu Jun²²¹,
 Zhu Xiao⁷⁸, Zhu Zhi-Xin²¹⁵, Zo-Bi Irie C.²²², Hui Cang^{223, 224}

¹ Purdue Univ, Dept Forestry & Nat Resources, Forest Adv Comp & Artificial Intelligence Lab FAC, W Lafayette, IN 47907 USA.

² Food & Agr Org United Nations, Forestry Div, Rome, Italy.

³ GIP ECOFOR, Paris, France.

⁴ Purdue Univ, Dept Forestry & Nat Resources, W Lafayette, IN 47907 USA.

⁵ Univ Michigan, Sch Environm & Sustainabil, Inst Global Change Biol, Ann Arbor, MI 48109 USA.

⁶ Univ Minnesota, Dept Forest Resources, St Paul, MN USA.

⁷ Western Sydney Univ, Hawkesbury Inst Environm, Penrith, NSW, Australia.

⁸ Swiss Fed Inst Technol, Dept Environm Syst Sci, Crowther Lab, Inst Integrat Biol, Zurich, Switzerland.

⁹ Wageningen Univ & Res, Wageningen Environm Res, Wageningen, Netherlands.

¹⁰ Wageningen Univ & Res, Forest Ecol & Forest Management Grp, Wageningen, Netherlands.

¹¹ Univ Lleida, Dept Crop & Forest Sci, Lleida, Spain.

¹² Joint Res Unit CTFC Agrotecnio CERCA, Solsona, Spain.

¹³ Peking Univ, Coll Urban & Environmental Sci, Inst Ecol, Minist Educ, Beijing, Peoples R China.

¹⁴ Peking Univ, Coll Urban & Environmental Sci, Key Lab Earth Surface Proc, Minist Educ, Beijing, Peoples R China.

¹⁵ US Forest Serv, Northern Res Stn, USDA, Durham, NH USA.

¹⁶ Aarhus Univ, Ctr Biodivers Dynam Changing World BIOCHANGE, Dept Biol, Aarhus C, Denmark.

¹⁷ Aarhus Univ, Dept Biol, Sect Ecoinformat & Biodivers, Aarhus C, Denmark.

¹⁸ Univ Bristol, Sch Biol Sci, Bristol, Avon, England.

¹⁹ Univ Liege, TERRA Teaching & Res Ctr, Gembloux Agrobiotech, Gembloux, Belgium.

²⁰ Manaaki Whenua Landcare Res, Lincoln, New Zealand.

²¹ Univ Brunei Darussalam, Fac Sci, Gadong, Brunei.

²² Ctr Cooperat Int Rech Agron Dev, Montpellier, France.

²³ Univ Montpellier, INP HB Inst Natl Polytech Felix Houphouet Boigny, Yamoussoukro, Cote Ivoire.

²⁴ Univ Udine, Dept Agr Food Environm & Anim Sci, Udine, Italy.

²⁵ Free Univ Bolzano, Fac Sci & Technol, Bolzano, Italy.

²⁶ CNR, Inst Bioecon, Sesto, Italy.

²⁷ Univ South Australia, Nat & Built Environm Res Ctr, Sch Nat & Built Environm, Adelaide, SA, Australia.

²⁸ Wageningen Univ & Res, Biometris, Wageningen, Netherlands.

²⁹ Wageningen Univ & Res, Forest & Nat Conservat Policy Grp, Wageningen, Netherlands.

³⁰ Eberswalde Univ Sustainable Dev, Ctr Econ & Ecosyst Management, Eberswalde, Germany.

³¹ Univ Florida, Sch Forest Fisheries & Geomat Sci, Inst Food & Agr Sci, Gainesville, FL USA.

³² Nat Biodivers Ctr, Leiden, Netherlands.

³³ Inst Nacl Tecnol Agr INTA, Santa Cruz, Argentina.

- ³⁴ Univ Cambridge, Dept Plant Sci, Cambridge, England.
- ³⁵ Lakehead Univ, Fac Nat Resources Management, Thunder Bay, ON, Canada.
- ³⁶ Univ Gottingen, Gottingen, Germany.
- ³⁷ Beijing Forestry Univ, Beijing, Peoples R China.
- ³⁸ Univ Stellenbosch, Stellenbosch, South Africa.
- ³⁹ Univ Warsaw, Fac Biol, Bialowieza Geobot Stn, Bialowieza, Poland.
- ⁴⁰ Swiss Fed Inst Forest Snow & Landscape Res WSL, Swiss Natl Forest Inventory, Birmensdorf, Switzerland.
- ⁴¹ Univ Felix Houphouet Boigny, UFR Biosci, Abidjan, Cote Ivoire.
- ⁴² Univ Oxford, Sch Geog & Environm, Environm Change Inst, Oxford, England.
- ⁴³ Nat Biodivers Ctr, Biodivers Dynam, Leiden, Netherlands.
- ⁴⁴ Univ Florida, Ctr Latin Amer Studies, Gainesville, FL USA.
- ⁴⁵ Acad Sci Czech Republ, Inst Bot, Trebon, Czech Republic.
- ⁴⁶ Czech Univ Life Sci Prague, Fac Forestry & Wood Sci, Prague, Czech Republic.
- ⁴⁷ Natl Open Univ & Distance Colombia UNAD, Escuela ECAPMA, Bogota, Colombia.
- ⁴⁸ Univ Santiago de Compostela, Dept Ingn Agroforestal, Lugo, Spain.
- ⁴⁹ Univ Calif Los Angeles, Ctr Trop Res, Inst Environm & Sustainabil, Los Angeles, CA USA.
- ⁵⁰ Univ Jean Lorougnon Guede, Daloa, Cote Ivoire.
- ⁵¹ Univ Officielle Bukavu, Bukavu, DEM REP CONGO.
- ⁵² Univ Gottingen, Silviculture & Forest Ecol Temperate Zones, Gottingen, Germany.
- ⁵³ Inst Natl Etud & Rech Agron, Kinshasa, DEM REP CONGO.
- ⁵⁴ Norwegian Inst Bioecon Res NIBIO, Div Forestry & Forest Resources, As, Norway.
- ⁵⁵ European Commiss, Joint Res Ctr, Ispra, Italy.
- ⁵⁶ Compensat Int Progress SA, Bogota, Colombia.
- ⁵⁷ Univ Abomey Calavi, Lab Appl Ecol, Cotonou, Benin.
- ⁵⁸ South African Natl Pk, Sci Serv, Knysna, South Africa.
- ⁵⁹ Univ Leeds, Sch Geog, Leeds, W Yorkshire, England.
- ⁶⁰ Forest Res Inst, Dept Geomat, Raszyn, Poland.
- ⁶¹ Proceedings Natl Acad Sci, Washington, DC USA.
- ⁶² Duke Univ, Dept Evolutionary Anthropol, Durham, NC USA.
- ⁶³ Univ Cinquantenaire Lwiro, Dept Environm, Bukavu, DEM REP CONGO.
- ⁶⁴ Univ Ghent, Dept Environm, Ghent, Belgium.
- ⁶⁵ Univ Ghent, Dept Green Chem & Technol, Ghent, Belgium.
- ⁶⁶ Royal Museum Cent Africa, Serv Wood Biol, Tervuren, Belgium.
- ⁶⁷ Balai Penelitian & Pengembangan Lingkungan Hidup, Manokwari, Indonesia.
- ⁶⁸ Mbarara Univ Sci & Technol, Inst Trop Forest Conservat, Mbarara, Uganda.
- ⁶⁹ Univ Liege, Gembloux Agrobio Tech, Gembloux, Belgium.
- ⁷⁰ Univ Stefan Cel Mare Suceava, Integrated Ctr Res Dev & Innovat Adv Mat Nanotech, Suceava, Romania.
- ⁷¹ Univ Sao Paulo, Luiz de Queiroz Coll Agr, Dept Forestry Sci, Piracicaba, Brazil.
- ⁷² Bavarian State Inst Forestry, Freising Weihenstephan, Germany.
- ⁷³ Manchester Metropolitan Univ, Dept Nat Sci, Manchester, Lancs, England.
- ⁷⁴ Univ Juarez Estado Durango, Fac Ciencias Forestales, Durango, Mexico.
- ⁷⁵ Martin Luther Univ Halle Wittenberg, Inst Biol & Bot Garden, Halle, Saale, Germany.
- ⁷⁶ German Ctr Integrat Biodivers Res iDiv, Leipzig, Germany.
- ⁷⁷ Wageningen Univ, Dev Econ Grp, Wageningen, Netherlands.
- ⁷⁸ Purdue Univ, Rosen Ctr Adv Comp RCAC, W Lafayette, IN 47907 USA.
- ⁷⁹ Univ Bologna, Dept Biol Geol & Environm Sci BiGeA, Bologna, Italy.
- ⁸⁰ Swiss Fed Inst Technol, Inst Integrat Biol, Zurich, Switzerland.
- ⁸¹ IFER Inst Forest Ecosyst Res, Jilove, Czech Republic.
- ⁸² CAS, Global Change Res Inst, Brno, Czech Republic.
- ⁸³ Univ Estadual Campinas, Inst Biol, Programa Posgrad Biol Vegetal, Campinas CEP, Campinas, Brazil.
- ⁸⁴ Minist Ambiente & Desarrollo Sostenible MAyDS, Direcc Nacl Bosques DNB, Buenos Aires, DF, Argentina.
- ⁸⁵ Norwegian Univ Life Sci NMBU, Fac Landscape & Soc, Dept Int Environm & Dev Studies Noragric,

As, Norway.

- ⁸⁶ Univ York, Dept Environm & Geog, York, N Yorkshire, England.
- ⁸⁷ SRM Univ AP, Sch Engn & Sci, Dept Environm Sci, Guntur, Andhra Pradesh, India.
- ⁸⁸ Dr Harisingh Gour Vishwavidyalaya Cent Univ, Dept Bot, Sagar, Madhya Pradesh, India.
- ⁸⁹ Pondicherry Univ, Dept Ecol & Environm Sci, Pondicherry, India.
- ⁹⁰ Concordia Univ, Ctr Struct & Funct Genom, Biol Dept, Montreal, PQ, Canada.
- ⁹¹ Concordia Univ, Quebec Ctr Biodivers Sci, Biol Dept, Montreal, PQ, Canada.
- ⁹² Charles Univ Prague, Fac Sci, Dept Ecol, Prague, Czech Republic.
- ⁹³ Czech Acad Sci, Inst Entomol, Biol Ctr, Ceske Budejovice, Czech Republic.
- ⁹⁴ Univ Antilles, Univ Guyane, Inrae, Cirad,UMR EcoFoG,AgroParistech,CNRS, Campus Agron, Kourou, French Guiana.
- ⁹⁵ Univ Guelph, Dept Geog Environm & Geomat, Guelph, ON, Canada.
- ⁹⁶ Natl Forest Author, Kampala, Uganda.
- ⁹⁷ Vietnamese Acad Forest Sci, Dept Silviculture Fdn, Silviculture Res Inst, Hanoi, Vietnam.
- ⁹⁸ Univ South Bohemia, Fac Sci, Dept Bot, Bohemia, Czech Republic.
- ⁹⁹ CENAREST, IRET, IPHAMETRA, Libreville, Gabon.
- ¹⁰⁰ Univ Kisangani, Fac Gest Ressources Nat Renouvelables, Kisangani, DEM REP CONGO.
- ¹⁰¹ Dept Environm & Sci, Queensland Herbarium, Toowong, Qld, Australia.
- ¹⁰² Queen Mary Univ London, Sch Biol & Behav Sci, London, England.
- ¹⁰³ Univ Yaounde I, Fac Sci, Dept Plant Biol, Yaounde, Cameroon.
- ¹⁰⁴ Nat Resources Inst Finland, Joensuu, Finland.
- ¹⁰⁵ Univ Bern, Inst Plant Sci, Bern, Switzerland.
- ¹⁰⁶ Swedish Univ Agr Sci, Dept Forest Resource Management, Umea, Sweden.
- ¹⁰⁷ Fdn Edmund Mach, Res & Innovat Ctr, San Michele All Adige, Italy.
- ¹⁰⁸ Univ Reg Blumenau, Herbario Dr Roberto Miguel Klein, Blumenau, Brazil.
- ¹⁰⁹ Glick Designs LLC, Hadley, MA USA.
- ¹¹⁰ Inst Politecn Nacl, CIIDIR Durango, Durango, Mexico.
- ¹¹¹ Univ Burundi, Dept Sci & Technol Environm, Bujumbura, Burundi.
- ¹¹² Univ Libre Bruxelles, Fac Sci, Evolutionary Biol & Ecol Unit, Brussels, Belgium.
- ¹¹³ Royal Bot Garden Edinburgh, Edinburgh, Midlothian, Scotland.
- ¹¹⁴ Univ Oxford, Dept Plant Sci, Oxford, England.
- ¹¹⁵ Bayreuth Univ, Dept Plant Systemat, Bayreuth, Germany.
- ¹¹⁶ Helmholtz GFZ German Res Ctr Geosci, Sect Remote Sensing & Geoinformat 1 4, Potsdam, Germany.
- ¹¹⁷ Wild Chimpanzee Fdn, Liberia Representat, Monrovia, Liberia.
- ¹¹⁸ Royal Soc Protect Birds, Ctr Conservat Sci, Sandy, Beds, England.
- ¹¹⁹ Univ Ghent, Dept Environm, Lab Wood Technol UGent Woodlab, Ghent, Belgium.
- ¹²⁰ Univ Montpellier, INRAE, CNRS, CIRAD,IRD,AMAP, Montpellier, France.
- ¹²¹ Tokyo Univ Agr, Dept Forest Sci, Tokyo, Japan.
- ¹²² Univ Officielle Bukavu, Biol Dept, Bukavu, DEM REP CONGO.
- ¹²³ Polish Acad Sci, Inst Dendrol, Kornik, Poland.
- ¹²⁴ Poznan Univ Life Sci, Fac Forestry & Wood Technol, Dept Game Management & Forest Protect, Poznan, Poland.
- ¹²⁵ Univ Copenhagen, Dept Geosci & Nat Resource Management, Copenhagen, Denmark.
- ¹²⁶ Univ Campinas UNICAMP, Biol Inst, Plant Biol Dept, Campinas, SP, Brazil.
- ¹²⁷ Purdue Univ, Dept Bot & Plant Pathol, W Lafayette, IN 47907 USA.
- ¹²⁸ Minist Sci Res & Innovat, Inst Agr Res Dev IRAD, Nkolbisson, Yaounde, Cameroon.
- ¹²⁹ Univ Copenhagen, Dept Food & Resource Econ, Copenhagen, Denmark.
- ¹³⁰ Bauman Moscow State Tech Univ, Forestry Fac, Mytishchi, Russia.
- ¹³¹ Field Museum, Integrat Res Ctr, Chicago, IL USA.
- ¹³² Univ Felix Houphouet Boigny, Labo Bot, Abidjan, Cote Ivoire.
- ¹³³ Univ Ghent, Computat & Appl Vegetat Ecol Lab, Ghent, Belgium.
- ¹³⁴ Colorado Mesa Univ, Dept Phys & Environm Sci, Grand Junction, CO USA.
- ¹³⁵ Dr Harisingh Gour Vishwavidyalaya Cent Univ, Dept Bot, Sagar, India.
- ¹³⁶ Kenya Forestry Res Inst, Dept Forest Resource Assessment, Nairobi, Kenya.
- ¹³⁷ Seoul Natl Univ, Dept Forest Sci, Seoul, South Korea.

- 138 Seoul Natl Univ, Interdisciplinary Program Agr & Forest Meteorol, Seoul, South Korea.
- 139 Natl Ctr Agro Meteorol, Seoul, South Korea.
- 140 Seoul Natl Univ, Res Inst Agr & Life Sci, Seoul, South Korea.
- 141 Estonian Univ Life Sci, Inst Forestry & Engn, Tartu, Estonia.
- 142 Int Inst Appl Syst Anal, Laxenburg, Austria.
- 143 Cent Univ Jharkhand, Dept Geoinformat, Ranchi, Bihar, India.
- 144 Univ Tartu, Tartu Observ, Toravere, Estonia.
- 145 Univ KwaZulu Natal, Sch Life Sci, Pietermaritzburg, South Africa.
- 146 Fed Univ Vicosa UFV, Dept Forest Engn, Vicosa, MG, Brazil.
- 147 UCL, Dept Geog, London, England.
- 148 Univ Yaounde I, Higher Teachers Training Coll, Plant Systemat & Ecol Lab LaBosystE, Yaounde, Cameroon.
- 149 Univ Kisangani, Dept Ecol & Gest Ressources Vegetales, Lab Col & Amenagement Forestier, Kisangani, DEM REP CONGO.
- 150 Univ Juarez Estado Durango, Inst Silvicultura & Ind Madera, Durango, Mexico.
- 151 Qingdao Agr Univ, Fac Forestry, Qingdao, Peoples R China.
- 152 Ctr Forest Ecol & Prod RAS CEPF RAS, Moscow, Russia.
- 153 Aarhus Univ, Dept Ecosci, Silkeborg, Denmark.
- 154 Duke Univ, Nicholas Sch Environm, Durham, NC 27708 USA.
- 155 Univ Arizona, Dept Ecol & Evolutionary Biol, Tucson, AZ USA.
- 156 Univ Montpellier, AgroParisTech, UMR AMAP, CIRAD, CNRS, INRAE, IRD, Montpellier, France.
- 157 Univ Sunshine Coast, Sippy Downs, Qld, Australia.
- 158 Univ York, York, N Yorkshire, England.
- 159 Flamingo Land Ltd, Kirby Misperton, N Yorkshire, England.
- 160 Coll African Wildlife Management, Dept Wildlife Management, Mweka, Tanzania.
- 161 Kenya Forestry Res Inst, Nairobi, Kenya.
- 162 Univ Nacl Autonoma Mexico, Fac Ciencias, Dept Ecol & Recursos Nat, Mexico City, DF, Mexico.
- 163 Univ Connecticut, Ecol & Evolutionary Biol, Storrs, CT USA.
- 164 Warsaw Univ Life Sci, Dept Forest Management & Forest Econ, Warsaw, Poland.
- 165 Univ Sunshine Coast, Trop Forests & People Res Ctr, Maroochydore, Qld, Australia.
- 166 Julius Maximilians Univ Wurzburg, Fieldstn Fabrikschleichach, Wurzburg, Germany.
- 167 Bavarian Forest Nationalpk, Grafenau, Germany.
- 168 Univ Papua, Fak Kehutanan, Jalan Gunung Salju Amban, Manokwari Papua Barat, Indonesia.
- 169 Limbe Bot Garden, Limbe, Cameroon.
- 170 Inst Forestry, Belgrade, Serbia.
- 171 Trop Plant Explorat Grp TroPEG, Buea, Cameroon.
- 172 Univ Tennessee, Dept Ecol & Evolutionary Biol, Knoxville, TN USA.
- 173 Univ Dschang, Appl Biol & Ecol Res Unit, Dschang, Cameroon.
- 174 Univ Kentucky, Dept Forestry & Nat Resources, Lexington, KY USA.
- 175 Univ Quebec Montreal, Ctr Forest Res, Montreal, PQ, Canada.
- 176 FRC KSC SB RAS, VN Sukachev Forest Inst, Krasnoyarsk, Russia.
- 177 Western Sydney Univ, Sch Social Sci, Urban Management & Planning, Penrith, NSW, Australia.
- 178 Inst Nacl Pesquisas Amazonia INPA, Grp Ecol Monitoramento & Uso Sustentavel Areas Um, Manaus, Amazonas, Brazil.
- 179 Univ Fed Sul Bahia, Ctr Formacao Ciencias Agroflorestais, Ilheus, BA, Brazil.
- 180 Univ Firenze, Dept Agr Food Environm & Forestry, Florence, Italy.
- 181 Tech Univ Munich, Sch Life Sci Weihenstephan, Chair Forest Growth & Yield Sci, Munich, Germany.
- 182 Univ Trento, Ctr Agr Alimenti Ambiente, San Michele All Adige, Italy.
- 183 Univ Florence, Dept Biol, Sesto Fiorentino, Italy.
- 184 MUSE Museo Sci, Trento, Italy.
- 185 Bot Garden Geneva, Infoflora, Geneva, Switzerland.
- 186 Agr Res Educ & Extens Org AREEO, Res Inst Forests & Rangelands RIFR, Tehran, Iran.
- 187 Cent Univ Jharkhand, Dept Environm Sci, Ranchi, Bihar, India.
- 188 One World Trade Ctr, Inst Int Educ Scholar Rescue Fund IIE SRF, New York, NY USA.
- 189 Univ Mayor, Fac Ciencias, Ctr Modelac & Monitoreo Ecosistemas, Santiago, Chile.
- 190 Univ La Frontera, Vicerrector Invest & Postgrad, Temuco, Chile.

- 191 Univ Chile, Dept Silvicultura & Conservac Naturaleza, Santiago, Chile.
- 192 Peoples Friendship Univ Russia RUDN Univ, Moscow, Russia.
- 193 Univ Freiburg, Fac Biol, Freiburg, Germany.
- 194 Univ Zurich, Inst City, Dept Geog, Zurich, Switzerland.
- 195 Natl Forest Ctr, Zvolen, Slovakia.
- 196 CNRS UMR LEEISA, Campus Agron, Kourou, French Guiana.
- 197 Univ Lorraine, INRA, AgroParisTech, Nancy, France.
- 198 Ctr Int Forestry Res CIFOR, Situ Gede, Bogor Barat, Indonesia.
- 199 Univ Montpellier, Cirad, Montpellier, France.
- 200 Univ Fed Rio Grande do Norte, Dept Ecol, Natal, RN, Brazil.
- 201 Univ Aberdeen, Sch Biol Sci, Aberdeen, Scotland.
- 202 Royal Bot Gardens Kew, Herbarium Kew, London, England.
- 203 Univ Mbujimayi, Fac Sci Appl, Mbujimayi, DEM REP CONGO.
- 204 Yale Sch Forestry & Environm Studies, New Haven, CT USA.
- 205 Ural State Forest Engrn Univ, Russian Acad Sci, Bot Garden, Ural Branch, Ekaterinburg, Russia.
- 206 Tuscia Univ, DIBAF Dept, Viterbo, Italy.
- 207 CSIC, MNCN, LINCGlobal, Madrid, Spain.
- 208 Wageningen Univ, Plant Ecol & Nat Conservat Grp, Wageningen, Netherlands.
- 209 Polytech Inst Viseu, Agr High Sch, ESAV, IPV, Viseu, Portugal.
- 210 UTAD, Ctr Res & Technol Agroenvironm & Biol Sci, CITAB, Vila Real, Portugal.
- 211 Univ Reg Blumenau, Dept Forest Engrn, Blumenau, Brazil.
- 212 Univ Estadual Campinas, Nucleo Estudos & Pesquisas Ambientais, Campinas UNICAMP, Campinas, SP, Brazil.
- 213 Florida Int Univ, Int Ctr Trop Bot, Dept Biol Sci, Miami, FL USA.
- 214 Univ Sunshine Coast, Forest Res Inst, Sippy Downs, Qld, Australia.
- 215 Hainan Univ, Sanya Nanfan Res Inst, Hainan Yazhou Bay Seed Lab, Sanya, Peoples R China.
- 216 Taita Taveta Res Ctr, Kenya Forestry Res Inst, Wundanyi, Kenya.
- 217 Karlsruhe Inst Technol, Inst Geog & Geoecol, Dept Wetland Ecol, Rastatt, Germany.
- 218 Ctr Agr Res Suriname, Dept Forest Management, Paramaribo, Suriname.
- 219 Polish State Forests Coordinat Ctr Environm Proje, Warsaw, Poland.
- 220 Beijing Forestry Univ, Res Ctr Forest Management Engrn, State Forestry & Grassland Adm, Beijing, Peoples R China.
- 221 Univ Wisconsin, Dept Stat, Madison, WI 53706 USA.
- 222 DFR Eaux Forests & Environm, Inst Natl Polytech Felix Houphouet Boigny, Yamoussoukro, Cote Ivoire.
- 223 Stellenbosch Univ, Ctr Invas Biol, Dept Math Sci, Matieland, South Africa.
- 224 African Inst Math Sci, Muizenberg, South Africa.

* Corresponding author : Jingjing Liang, email address : albeca.liang@gmail.com; chui@sun.ac.za

Abstract

The latitudinal diversity gradient (LDG) is one of the most recognized global patterns of species richness exhibited across a wide range of taxa. Numerous hypotheses have been proposed in the past two centuries to explain LDG, but rigorous tests of the drivers of LDGs have been limited by a lack of high-quality global species richness data. Here we produce a high-resolution (0.025 degrees x 0.025 degrees) map of local tree species richness using a global forest inventory database with individual tree information and local biophysical characteristics from similar to 1.3 million sample plots. We then quantify drivers of local tree species richness patterns across latitudes. Generally, annual mean temperature was a dominant predictor of tree species richness, which is most consistent with the metabolic theory of biodiversity (MTB). However, MTB underestimated LDG in the tropics, where high species richness was also moderated by

topographic, soil and anthropogenic factors operating at local scales. Given that local landscape variables operate synergistically with bioclimatic factors in shaping the global LDG pattern, we suggest that MTB be extended to account for co-limitation by subordinate drivers.

Main text

Identifying which mechanisms moderate global biodiversity patterns^{1,2} has perplexed the scientific community for more than two centuries^{3,4}. The most noticeable pattern, the latitudinal diversity gradient (LDG), is a trend of declining local species richness (alpha diversity) from low to high latitudes. This trend has been observed for many taxonomic groups and across land, freshwater and marine environments^{5,6}. More than 30 hypotheses have been proposed^{3,4,7,8} to explain LDG⁹, but few can be reconciled with existing observational data for predicting biodiversity decline towards the poles. To test these varied hypotheses, biodiversity data must be assembled that are global in scope with sufficient sample coverage across all ecoregions and biomes.

In addition to biodiversity data, testing these varied hypotheses also requires data on a wide spectrum of potential drivers that may moderate biodiversity at local scales^{9,10}, such as climate, soil and land features and anthropogenic factors. For instance, environmental temperature (that is, ambient temperature of the air, represented by annual mean temperature) is largely responsible for the generation and maintenance of biodiversity through the effects of solar radiation on demographic rates (for example, growth and mortality), ecological interactions (for example, predation and competition) and evolutionary rates of change (for example, speciation and

extinction)^{11,12}. Soil and topographic heterogeneity facilitate niche partitioning via inducing microclimatic variation, contributing to compositional variation¹³ and biodiversity maintenance^{14,15}. Furthermore, humans have a long history of reshaping biodiversity through the selective use of natural resources and the modification of native species composition¹⁶. In addition, multiple subordinate factors jointly affecting biodiversity could potentially increase the diversity of niche opportunities, thereby resulting in species rich assemblages.

Here we quantified the relative contribution of a wide range of environmental factors across space on local tree species richness in forested areas around the world. To accomplish this, we standardized a global tree species richness (that is, as alpha diversity) database (Fig. 1) and quantified the relative contribution of 47 explanatory variables including bioclimatic conditions (for example, annual mean temperature), vegetation and survey attributes (for example, sample plot size), topographic covariates (for example, terrain roughness), soil covariates (for example, bulk density) and anthropogenic spatial features (for example, size of roadless areas) in an attempt to test whether local co-limitation exists when multiple subordinate drivers co-dominate (Figs. 2 and 3). We conducted a three-stage analysis (Fig. 1 and Methods in Supplementary Information for details) based on two independent ground-sourced forest inventory datasets (Phase I and Phase II; Extended Data Fig. 1). The main dataset (Phase I) consisted of 1,255,444 sample plots, while the validating dataset (Phase II) consisted of 22,131 sample plots, most of which are located in unsampled and under-sampled regions of the Phase I dataset. Together, our sample data covered 424 of the 435 (97%) forested ecoregions worldwide (Extended Data Fig. 1), with a total of ~55 million sample trees representing more than 32,000 species.

Results and discussion

Global patterns of local tree species richness and LDG.

Our analyses confirmed, with a high level of accuracy, one general spatial trend in local tree species richness worldwide that has led us to three conclusions regarding the mechanisms underlying patterns of tree species richness. We found that LDG for tree species richness was consistent with that of most other groups of organisms, with a decline from the tropics to the poles (Figs. 2 and 4). In the Northern Hemisphere, tree species richness dropped sharply from the equator (98 species per ha) to 10° N with an average rate of decline of 6 species per ha per 1° increase in latitude, after which the decline diminished and stabilized at 4 species per ha at 50° N. In the Southern Hemisphere, tree species richness declined from the equator to 25° S on average by 3 species per ha per 1° increase in latitude, after which tree species richness fluctuated before another steep drop from 25 species per ha (43° S) to 4 species per ha (50° S). We were able to detect and map regional patterns and global peaks of tree species diversity, with a high spatial resolution (0.025° × 0.025°). The Amazonian, Southeast Asian and Melanesian rainforests are the regions with the greatest local tree species richness worldwide, containing >200 tree species per ha above the 5 cm diameter-at-breast-height (DBH) threshold, confirming previous findings^{17,18}. Tropical African rainforests generally contain 50% fewer tree species per hectare than Amazonian rainforests. In the temperate forests of the Northern Hemisphere, the Changbai Mountains in Northeast Asia (up to ~28 species per ha) and the Central Appalachian forests in the Eastern United States (up to ~20 species per ha) display high local species richness. In the Southern Hemisphere, the sclerophyllous and *Nothofagus*-dominated forests in south-central Chile are among the most species-rich temperate communities (up to 50 species per ha). Boreal forest communities are consistently low in local tree species richness, with typically five or fewer tree species per hectare.

The above LDG pattern of tree species richness was generally consistent with the metabolic theory of biodiversity (MTB)^{19,20}, except at low latitudes (Fig. 5). According to MTB, environmental temperature is largely responsible for the generation and maintenance of biodiversity^{12,21,22}, and the natural logarithm of species richness is linearly associated with $1,000 T^{-1}$, where T is the absolute environmental temperature in Kelvin (mean annual temperature +273.15 K), with a slope ranging

from -7.5 K to -9.0 K. Our global tree species richness gradient was largely consistent with MTB, with a slope of -8.0 K ($P < 0.001$) and a coefficient of determination of 0.82 (Metabolic Theory of Biodiversity in Methods), indicating that environmental temperature is generally a good predictor of LDG. However, at low latitudes, MTB substantially underestimated LDG. In fact, near the equator where the actual LDG peaked (98 species per ha), observed tree species richness was almost twice as high as predicted by MTB (56 species per ha) (Fig. 4a). Our results suggest that within this low latitudinal range, other factors are also important to the maintenance of biodiversity.

The under-estimation of local tree species richness by MTB at low latitudes is attributable, in part, to the lack of a definite dominant environmental factor, suggesting a co-limitation of multiple subordinate drivers at low latitudes (Fig. 5). In general, bioclimatic factors predominantly determined species richness in 82.6% of the forested areas, while co-limitation (that is, absence of any dominating factor) occurred in 11.7% of forested areas globally. However, in the low-latitude range between 5° N and 15° S, the percentage area of co-limitation increased to 37.1%, more than three times the global average. Furthermore, forested areas under co-limitation contained on average 81.1 ± 0.1 species per ha, much higher than the average local tree species richness of forested areas predominantly determined by topographic (43.9 ± 0.1), anthropogenic (35.6 ± 0.2), soil (33.9 ± 0.2) and bioclimatic (19.4 ± 0.02) factors (Fig. 5b). This suggests that the pattern of co-limitation is pervasive in species-rich tropical forests. In South America, transitional areas between Amazonia and savanna formations nearby are subject to co-limitation that is partly attributable to a dynamic equilibrium between closed forest and savanna²³, edaphic conditions and natural fire regimes²⁴. In Africa, anthropogenic influences such as selective timber extraction and fuelwood collection, together with large-scale degradation²⁵ affect local tree species richness (Fig. 5 and Extended Data Fig. 7). In Central Africa, the evolution of anthropogenic influences from prehistoric to present times has imposed a substantial effect on species diversity²⁶ and resulted in the development of a complex system of mixes with light-demanding and old-growth tree species.

Bioclimatic dominance and co-limitation.

In addition to an overall positive response of local tree species richness to the rise of annual mean temperature (partial dependence plot of C1 in Fig. 3 and Extended Data Fig. 3), the importance of environmental temperature (2.7%) was topped by the total annual precipitation (C12, 7.6%) (Fig. 3). Our findings are consistent with previous discoveries of a joint role of water and temperature/energy—as a proxy for net primary productivity²⁷—on plant species richness, with water dominating particularly at warmer, lower latitudes^{22,28}. Predicted tree species richness accelerated exponentially with temperature and rainfall, although independently, as shown in the cold–dry quadrant and the convex contours of the 2D partial dependence plot (Extended Data Fig. 3), until each has reached its respective threshold (1,500 mm for total annual precipitation and 10° C for annual mean temperature). Beyond one of these thresholds, species richness is limited only by the predictor below its threshold (that is, by annual mean temperature in the cold–wet quadrant or by annual precipitation in the hot–dry quadrant). When both predictors have reached their thresholds, that is, in the hot–wet quadrant, co-limitation predominates in most tropical forests. Net primary productivity in the tropics, thus, requires co-limitation of other factors besides only temperature and rainfall²⁹. As the response of carbon flux mirror the low-latitude co-limitation pattern for tree species diversity, the matching determinants for both diversity and productivity may explain the similar latitudinal gradient in productivity and the positive diversity–productivity relationship^{30,31}. Our findings also indicate that under climate change, intensified droughts coupled with increased annual mean temperature³² can potentially trigger declines of tree species richness, although possible increases in water-use efficiency from elevated CO₂ and the dominance of highly contingent co-limiting factors may partially buffer this effect in the tropics³³.

Here we articulate evidence for co-limitation in LDG. Resource co-limitation is a common concept in ecology (for example, refs. 34,35), often used to describe how the synergistic interactions of two or more factors limit ecological productivity³⁶. Our use of the term co-limitation emphasizes

the reduced effect of bioclimate on tree species richness at low latitudes, although bioclimate is the globally predominant driver of species richness, recognizing that several local subordinate factors synergistically contribute to increased tree species richness in this latitudinal range. We thus argue that the inclusion of co-limitation could substantially improve the explanatory power of biodiversity models in estimating alpha diversity by considering multiple subordinate factors where single-factor dominance is lacking, especially in the tropics. At high latitudes, bioclimatic conditions, particularly environmental temperature, are the major limiting factors and thus the dominant drivers of tree species diversity. As the latitude declines, the influence of bioclimatic conditions dwindles and the maintenance of tree species richness is moderated by many interacting drivers without a clear dominance, which is especially well expressed between 5° N and 15° S (Fig. 5). This prevalence of co-limiting factors is thus not a mere coincidence as to why the observed LDG at low latitudes is almost double that predicted by MTB (Fig. 2). While each of the existing hypotheses underpinning LDG addresses a certain process^{10,12} (for example, selection, drift, dispersal or speciation), the evidence of co-limitation highlights synergistic interactions of local processes across the latitudinal gradient.

Concluding remarks.

More research is needed to fully elucidate patterns of LDG driven by climatic and other influences, especially those outlined in competing hypotheses. First, our analyses lack explicit consideration of some evolutionary, ecological and historical factors. These include mid-domain stochastic effects³⁷, the legacies of the poleward expansion of tree species after the Last Glacial Maximum^{38,39} and recent human land use/management. Alternative hypotheses, such as niche conservatism or climatic history, are more difficult to test due to data limitations. In addition, long-term effects at geological and millennial time scales also play a role, but it is difficult to disentangle these effects due to collinearity⁴⁰. A major source of uncertainty in our results (Fig. 4b) came from an uneven sample coverage between developed and developing countries (Extended Data Fig. 1). To address this gap, we argue that there needs to be a shared responsibility among forestry agencies at various levels of government, scientists, indigenous communities and other biodiversity monitoring groups to improve sample coverage of forest inventories in developing countries. Innovative biodiversity funding mechanisms, for example, forest inventories funded by carbon initiatives such as REDD+, should be incorporated into a comprehensive global forest biodiversity database. Meanwhile, the severe shortage of experts and database management infrastructures, especially in developing countries, poses another major challenge to address this gap⁴¹. The education and training of new generations of forest scientists, taxonomists and foresters can bring tangible benefits to biodiversity monitoring while improving local economies as well. Considering co-limitation in addition to MTB enables a refined description of the biogeographic distribution of biodiversity and mechanisms underlying LDG. Our analysis has resulted in the production of a high-resolution map of tree species richness across the global forest range, along with visuals of those factors responsible for the moderation of local tree species richness. Such tools are necessary for conservation management which requires assessments of factors responsible for biodiversity patterns at multiple scales that matter—from local and regional to global scales. Patterns of local tree species richness and associated drivers may provide insights into how and why the diversity of other forest flora, fauna and microbes^{42,43} vary across space and time. Furthermore, the high-resolution map of local tree species richness presented here provides a benchmark for evaluating the impact of biodiversity loss on the productivity and functioning of forest ecosystems^{31,44}. Finally, aligned with current international calls for spatially explicit monitoring of ecosystem attributes⁴⁵, this study delivers detailed biogeographic information to support international endeavours⁴⁶ focused on valuing natural capital and advancing global conservation.

Methods

As illustrated in Fig. 1, we conducted data analyses and modelling in three stages.

Stage 1. For this study, we compiled individual in situ tree data from all the regional and national GFBi forest inventory datasets (Supplementary Table 2) into a standardized GFBi dataframe, that is, the GFBi tree list. In this standardized GFBi dataframe, each row represents an individual tree, and columns represent nine key tree- and plot-level attributes. These attributes are tree ID (FID), a unique number assigned to each individual tree; plot ID (PLT), a unique string assigned to each plot; plot coordinates (LAT and LON); tree species name (SPCD); DBH or above buttress; year of measurement; and dataset name (DSN), a unique number assigned to each forest inventory dataset (Supplementary Table 2). With a total of 56 million trees surveyed, GFBi individual-based dataframe represents 1/50,000 of the approximately 2.7 trillion trees⁴⁷ worldwide. Because all trees in each sample plot were identified and measured, GFBi data make it possible to quantify forest community structure, composition and species distribution. To ensure consistency and maximum accuracy in species names, we standardized observations from different forest inventory datasets with the following protocol. First, all multi-stem trees were divided so that each stem represents an individual tree. The scientific names were extracted from original datasets, keeping only the genus and species (authority names were removed). Next, all the species names were compiled into five general species lists, one for each continent. We verified individual species names against 23 online taxonomic databases or web application programming interfaces (API) using the `gnr_resolve()` function from the 'taxize' package⁴⁸ of R⁴⁹. We then manually verified and corrected all the names that did not match with the majority of the online taxonomic databases, that is, the names with a matching score lower than 0.9. For individuals denoted by morphospecies, we assigned each a unique name comprising the genus name and a unique species code. The unique species code consisted of the string 'spp', plus the dataset name followed by a unique number denoting if two individuals belong to the same species. For example, 'Aidia sppCDi1' and 'Aidia sppCDi2' represented two different species under the genus 'Aidia', and both species have been observed in a forest inventory of the Democratic Republic of the Congo named 'CDi'. To maximize our species coverage, a tree was defined in this study as a perennial plant with an elongated woody stem that supports branches and leaves, including woody angiosperms, gymnosperms and taller palms (Arecaceae). Tree ferns (Cyatheales) and bamboos (Bambusoideae) were excluded from our analysis.

From the GFBi individual tree-level dataframe, we derived a global species abundance matrix. The global species abundance matrix consisted of the number of individuals by species (column vectors) within individual sample plots (row vectors). The global species abundance matrix consisted of two complementary datasets: Phase I dataset contained 1,255,444 sample plots and Phase II dataset contained 22,131 sample plots, most of which are located in unsampled and under-sampled regions of Phase I dataset. Phase I sample plots cover 394 ecoregions across the world, and Phase II sample plots cover an additional 30 ecoregions in Africa, South America, Southeast Asia, Mexico, India and Japan. Together, our ground-based forest sample plots cover 424 of 435 (97.5%) forested ecoregions across the world. The global species abundance matrix contains ~1.3 million rows (plots) by 32,608 columns (species). Key plot-level information was added to the matrix, including PLT, DSN, plot coordinates, basal area (B), the total cross-sectional areas (m²) of living trees per ha calculated from DBH and TPH (expansion factor) and the year of measurement. TPH denotes the number of trees per hectare represented by each sampled individual. It ranged from 1 to 5,244 across the GFBi data, with a mean of 48 trees per ha.

We quantified for each sample plot tree species richness (S), which is the total number of tree species in a community. Due to the difference in plot size (standard deviation = 0.09 ha) and threshold DBH values (standard deviation = 2.52 cm) across GFBi sample plots, we developed machine learning models to standardize tree species richness for a common basis of 1 ha in area and 5 cm in threshold DBH. The models incorporated both plot area (A) and threshold DBH (D) as predictors to account for the underlying species-area relationship^{50–52} and species-individual size distribution⁵³ in a rarefaction-based approach⁵⁴. This standardization approach justifies compiling direct tree species diversity estimates from GFBi in situ data of different sources and sampling protocols^{55–57}, an issue highlighted in earlier large-scale—although less extensive—forest

biodiversity studies^{57,58}. To evaluate the accuracy of this standardization approach, we tested the machine learning models using cross-sample validation and compared our global maps of estimated tree species diversity against other standardization approaches based on sample completeness (Model Evaluation below).

The machine learning models employed 47 environmental covariates to predict tree species richness. These covariates, derived from satellite-based remote sensing and ground-based survey data, can be summarized into five general categories: bioclimatic (for example, annual mean temperature, total annual precipitation, potential evapotranspiration and indexed annual aridity); soil (bulk density, pH, electrical conductivity, C/N ratio and total nitrogen); topographic, including elevation, slope, aspect and terrain features; vegetation and survey attributes (plot size, basal area, threshold diameter and percent forest canopy cover); and anthropogenic variables (human footprint, roadless areas and size of protected areas) (Supplementary Table 1). We extracted all geospatial covariate values from raster datasets to point locations of GFBi plots using ArcMap 10.3 (ref. 59) and R 3.4.1 (ref. 49), to build a standardized plot-level dataframe.

Stage 2. We trained random forests (RF)⁶⁰, an ensemble learning method that detects general trends present in the data using a multitude of decision trees, to estimate standardized community-level tree species diversity. The RF algorithm applies the general technique of bootstrap aggregating (bagging) with a modified tree learning algorithm that selects at each candidate split in the learning process a random subset of the features (that is, feature bagging). Because a random subset of variables is chosen for each tree, the RF algorithm based on bagged tree ensembles avoids overfitting⁶⁰ and mitigates the multicollinearity issue⁶¹ posed by high correlations between some of the predictors variables (Fig. 3). Using subsamples of GFBi data as the training set (that is, training dataframe) with response S , bagging repeatedly for B times selects a random sample with replacement of the training set and trains a regression tree f_b . After training, RF can predict for unseen samples X' with the response variable S being tree species richness per ha:

$$S = \frac{1}{B} \sum_{b=1}^B f_b(X') \quad (1)$$

For rigorous model evaluation, we employed three very different cross validation approaches: randomized cross validation (RCV), spatial cross validation (SCV) and post-sample validation (PSV). In RCV, a model was trained for each continent with a random subsample that accounted for 90% of the training data from that continent, and the remaining 10% of the training data were used as the testing set. This process was repeated 20 times with sample replacement to examine the accuracy of estimated tree species diversity values. In SCV, all sample data from an ecoregion⁶² were reserved for testing the model that was trained with the remaining samples from the larger continent within which the ecoregion is situated. We decided to use ecoregions as spatial blocks because (1) unlike political units such as countries and provinces, ecoregions are delineated based on ecological and bioclimatic conditions; and (2) with a total of ~700 terrestrial ecoregions across the world, each ecoregion encompasses 1,800 sample plots on average, which is a large enough sample size for training RF models. This process was repeated until all the forested ecoregions across the world had been tested. SCV was more rigorous than RCV because samples from an entire ecoregion rather than random samples were withheld for validation. PSV was the most rigorous among the three validation processes. For PSV, we have collated an independent sample dataset from 22,131 forest sample plots, which we named Phase II sample plots to highlight their independence from the original GFBi dataset (that is, Phase I sample plots). In PSV, we used Phase II data as the testing set to evaluate the accuracy of the predictive models that were trained for each continent with the Phase I data.

Using these three cross validation processes, we also evaluated the performance of the RF model against two other predictive models, including multiple regression with ordinary least squares (OLS) and Extreme Gradient Boosting (XGBoost). For each model, we derived predicted values of tree species richness of the testing sets and compared these predicted values against observed data using

mean absolute error, root-mean-squared error (RMSE), and coefficient of determination (R²) (ref. 63). The process was repeated 20 times to select the best model for each continent.

The OLS model estimated values of standardized point diversity for non-sampled point location s , based on spatially explicit values of covariates:

$$Y(s) = \alpha \cdot X(s) + e(s) \quad (2)$$

where $Y(s)$ is tree species richness at location s ; X a design matrix for the predictor variables at location s ; α is a vector of coefficients; and e is a random vector following a Gaussian probability density function, with an expected value of zero and variance of σ^2 . Spatial autocorrelation⁶⁴ was not accounted for here due to computational limitations. GFBi data collected from sample plots of various sizes were harmonized to represent local forest community populations per ha using the expansion factor⁶⁵, and we used the standardized species richness per ha values for the response variables. We fit a model (2) for each continent. To mitigate the multicollinearity issue⁶⁶, we selected for the OLS model the best subset of predictor variables for each continent from the predictor variables used in the RF models, using step-wise regression and Akaike information criterion⁶⁷.

XGBoost is a scalable machine learning system⁶⁸ that implements the gradient boosting decision tree algorithm⁶⁹. With this ensemble technique, an initial model was trained, with new models added sequentially to correct for errors made by each existing model until no further improvements could be made. Then, new and initial models were merged to make a final prediction that minimized errors. With its algorithm engineered for efficiency in computing time and memory resources, XGBoost is widely used by data scientists to achieve state-of-the-art results on a number of machine learning challenges⁶⁸. In this study, the XGBoost model estimated tree species diversity values in three steps. First, an initial model F_0 was defined to predict the target variable Y . This model was associated with a residual ($Y - F_0$). Second, a new model h_1 was fit to the residuals from the previous step, and F_0 and h_1 were combined to form the boosted model F_1 :

$$F_1(x) = F_0(x) + h_1(x) \quad (3)$$

of which the mean squared error was lower than that from F_0 . Finally, to improve the performance of F_1 , we modelled after the residuals of F_1 to create a new model, F_2 , and repeated it for m iterations until the mean squared error converged:

$$F_m(x) = F_{m-1}(x) + h_m(x) \quad (4)$$

Before training RF and XGBoost models, we fine tuned four key hyper-parameters, two for each model. Using 20 bootstrapping iterations on random training sets consisting of 90% of the samples, we first evaluated the sensitivity of RMSE of the testing sets (consisting of the remaining 10% of the samples) to the number of trees to grow and the number of variables randomly sampled as candidates at each split for the RF model and selected the optimal hyper-parameter values (Extended Data Fig. 5). Similarly, we selected the optimal values of the maximum number of boosting iterations (that is, number of rounds) and the maximum depth of a tree for the XGBoost model (Extended Data Fig. 6). As a result, we obtained a preliminary RF model.

Because the RF model emerged as the most accurate model from all three cross validation processes (Extended Data Fig. 2), we selected the RF as the final model, and re-calibrated the final RF model using all the sample data (Phase I and Phase II data).

Stage 3. Global map of local tree species richness. To map community-level tree species richness over the global forest range, we first derived the global forest range map from version 1.3 of the Global Forest Change database⁷⁰ (years 2000–2015). To ensure consistency with the definition of forest⁷¹ by the Food and Agriculture Organization of the United Nations (FAO), the global forest range in this study was defined as forested areas with $\geq 10\%$ tree crown coverage per unit area. The tiled ‘treecover2000’, ‘loss’ and ‘gain’ datasets were integrated to obtain current forest cover estimates for the year 2015. To minimize processing artefacts, the ~ 1 arcsecond spatial resolution tiles were

spatially aggregated to an even multiple of their native resolution that approximated the resolution of our covariates. The datasets were then converted to vector point files before being reconverted to raster format with the exact resolution and origin of our covariates. After mosaicking each set of tiles, we computed ‘tree cover’ (scaled) – ‘loss’ + ‘gain’ to obtain the 2015 global forest cover, represented as percent forest cover per ~30 arcsecond pixel. Artefacts in the original data led to 0.08% of all terrestrial pixels having forest cover estimates greater than 100% and 1.9% of terrestrial pixels having estimates less than 0%. These values were truncated to 100% and inflated to 0%, respectively. Finally, the global forest range consisted of those pixels with a percent forest cover $\geq 10\%$ in 2015. In total, each map consisted of 9,944,908 pixels of $0.025^\circ \times 0.025^\circ$ (hereafter, the pixel) of forested areas. This range is rather conservative and potentially underestimates many remnant forests in drylands and grasslands⁷².

We then estimated tree species richness at a 1 ha scale for all pixels within a continent based on the final RF model trained for that continent, using both Phase I and Phase II data. Spatially explicit local environmental covariate data across the global forest range were used for the imputation, except that plot size and threshold DBH were set as 1 ha and 5 cm, respectively. For ecoregions with extremely low sample coverage, we further fine tuned the RF model using samples of similar environment characteristics from other continents. More specifically, we first identified two ecoregions of extremely low sample coverage, that is, the temperate forests in South America and the tropical forests in Oceania, as there were fewer than 1,000 sample plots for the entire biome on those continents. We then trained a new RF model for each ecoregion, using all the sample data from the same biome across the world and fine tuned the mapping data for that ecoregion using the biome-specific RF model.

We computed and mapped the width of the 95% confidence interval for our local estimates of tree species richness per ha across the global forest range. To this end, we employed a rigorous spatial-block approach, analogous to the spatial cross validation, to derive the 95% confidence interval. More specifically, we computed the width of the 95% confidence interval for each $0.025^\circ \times 0.025^\circ$ mapping pixel by ecoregion. For a pixel p in ecoregion e , we trained 20 RF models using random subsamples that accounted for 90% of the training data from the same continent, which included all samples except those from ecoregion e . We then derived the standard error and the width of the 95% confidence interval for this pixel p in ecoregion e from the predictions of the 20 RF models trained for this ecoregion. This process was repeated until all the forested ecoregions across the world had been assessed and mapped.

Uncertainty in our global diversity estimates was caused by two types of error. The first was measurement error from in situ forest inventories. We mitigated this type of error by implementing stringent species name check and data standardization protocols (Stage 1 Data Standardization). The second arose from the imputation process to map tree species diversity. We minimized this type of error using the three cross validation approaches introduced in Stage 2.

Metabolic theory of biodiversity. Using the global standardized tree species richness values predicted from the final RF models, we quantified the global LDG of tree species richness and tested the effect of environmental temperature based on the MTB19:

$$\ln(S) = \alpha \frac{1,000}{T_{env}} + \beta \quad (5)$$

where S represents species richness and T_{env} here represents absolute environmental temperature (mean annual temperature +273.15 K); α and β represent coefficients to be estimated by ordinary least squares. According to both the original and extended MTB19,20, the slope α is expected to range between -7.5 K and -9.0 K, under the assumption that tree community abundance per area does not vary with latitude.

Variance partitioning. We used variance partitioning⁷³ based on the sample data from ~1.3 million plots to quantify the unique and joint fractions of spatial variance in tree species richness explained

by environmental factors and latitude. Due to the correlation between species and environment and between the spatially explicit environmental factors, the variance partitioning approach mitigates type I error inflated by spatial autocorrelation⁷⁴. With variance partitioning, we tested the significance of environmental effects on tree species richness in a series of nested RF models. (A) The full model (Extended Data Fig. 4a) consisted of latitude and 47 environmental variables (including 21 bioclimatic ones). (B) The reduced model I (Extended Data Fig. 4b) consisted of all but the 21 bioclimatic variables. (C) The reduced model II (Extended Data Fig. 4c) consisted of only a zero constant. The overall significance of all environmental factors plus latitude was tested in an one-tailed F-test by comparing the residual sum of squares of error (RSS) of model (A) and model (C):

$$F = \frac{\frac{RSS_C - RSS_A}{n_C - n_A}}{\frac{RSS_A}{n - n_A}}, \quad (6)$$

where $n - n_A$ and $n_C - n_A$ stand for the degree of freedom for the full model and the difference in the degrees of freedom between the full model and the reduced model II, respectively.

The significance of bioclimatic factors, with the effect of latitude being controlled, was tested in an one-tailed F-test by comparing RSS of model (A) and model (B):

$$F = \frac{\frac{RSS_B - RSS_A}{n_B - n_A}}{\frac{RSS_A}{n - n_A}}, \quad (7)$$

where $n_B - n_A = 21$ stands for the difference in the degrees of freedom between the full model and the reduced model I.

We partitioned the spatial variance in observed species richness into four components: a represents the fraction of variance uniquely explained by environmental factors (that is, bioclimatic, topographic, anthropogenic and soil variables), after latitudinal effects have been taken into account; b represents the fraction of variance jointly explained by environmental factors and latitudinal effects; c represents the fraction of variance explained by latitudinal effects after removing environmental effects; and d represents the fraction of variance not explained by the full RF model. Then, the total fraction of variance explained by both environmental factors and latitude was $a + b + c$, the fraction of variance explained by environmental factors was $a + b$, and the fraction of variance explained by latitude was $b + c$. Components $a + b + c$, $a + b$ and $b + c$ were estimated by the R^2 statistics from the RF models trained for each continent using all factors, environmental factors and latitude, respectively (Stage 2 Model Training and Evaluation). Components a , b and c were computed from the previous components using arithmetic relationships that ensure that $a + b + c + d = 100\%$.

Model sensitivity. Based on the final RF models and sample data from ~ 1.3 million plots, we mapped the dominant drivers of tree species richness with a $0.025^\circ \times 0.025^\circ$ resolution (that is, global map of co-limitation), following a standard procedure for model sensitivity analysis⁷⁵:

Step 1: using the full RF model, and the values of environmental factors $X(s)$ specific to a 0.025° -pixel s , we had already estimated local tree species richness $S_{full}(s)$:

$$S_{full}(s) = f(X(s)), \quad (8)$$

where $f()$ represents the RF model, and $X(s)$ environmental factors in four categories, namely E1: bioclimatic, E2: topographic, E3: anthropogenic and E4: soil.

Step 2: for the above-mentioned pixel, we estimated a new local tree species richness value $S_{-E1}(s)$, using a reduced RF model in which all E1 (bioclimatic) variables were removed:

$$S_{-E1}(s) = f_{-E1}((X - E1)(s)), \quad (9)$$

where $f_{-E1}()$ represents the RF model trained with all but 21 bioclimatic variables, and $(X - E1)(s)$ encompassed environmental factors in three categories, namely E2: topographic, E3: anthropogenic and E4: soil.

Step 3: for a given pixel, we calculated the relative sensitivity of predicted species richness to E1:

$$R(E1) = |S_{full}(s) - S_{-E1}(s)| / S_{full}(s) . \quad (10)$$

Step 4: we repeated steps 2 and 3 to calculate, for a given pixel, the relative sensitivity of each of the following categories (that is, E2: topographic, E3: anthropogenic and E4: soil), respectively. The dominant driver (that is, limiting factor) for this pixel was then the category with the highest relative sensitivity, provided that this relative sensitivity was greater than or equal to 0.2.

Step 5: if the relative sensitivities were less than 0.2 for all categories, we considered that this was a scenario of joint effects of multiple categories of factors (that is, co-limitation), rather than dominance of a single category. Where clear dominance of a single category was lacking, we denoted the dominant driver of this pixel as 'E5: co-limitation.'

Step 6: we repeated the steps above to calculate, for all the remaining pixels of the global grid, the relative sensitivity of each of the five categories of environmental factors, namely E1: bioclimatic, E2: topographic, E3: anthropogenic, E4: soil and E5: co-limitation. On the basis of these values, we created a wall-to-wall map of dominant drivers of tree species richness across the global forest range by labelling the category with the highest relative sensitivity for each pixel (Fig. 5a).

Step 7: on the basis of the relative sensitivity obtained from the steps 1–6, we computed percent prevalence (0–100%) of bioclimatic, topographic, anthropogenic and soil factors and a lack of dominance (co-limitation) in all the forested pixels along each latitudinal band.

Data availability

The global map of tree species richness is available under license CC BY 4.0, with the identifier: 10.6084/m9.figshare.17232491. This map can be downloaded in two formats. One is a geoTIFF file (S_mean_raster.tif) containing the fully geo-referenced map of tree species richness worldwide at a $0.025^\circ \times 0.025^\circ$ resolution. The other is a comma-separated file (S_mean_grid.csv) with the following attributes: S is local average tree species richness per ha and x, y are centroid coordinates of all $0.025^\circ \times 0.025^\circ$ pixels. The global map of co-limitation is available under license CC BY 4.0, with the identifier: 10.6084/m9.figshare.17234339. The metadata of the entire training dataframe— including the characteristics and references of all the in situ Phase I and Phase II datasets and the definitions, units and summary statistics of the environmental covariates—is available under license CC BY 4.0 with the identifier: 10.6084/m9.figshare.19733449.v1. The public version of the training dataframe, including the plot-level species richness and all the covariates, which is needed to reproduce the models and results presented here, is available at: <https://doi.org/10.6084/m9.figshare.20055488>. The maps and dataframe are also available on the international web research platform: Science-i (<https://science-i.org/>). Raw forest inventory data are commonly subject to a wide array of confidentiality clauses in regard to open access policies. Despite recent efforts to make some of these data fully open^{76,77}, some governments and private data owners, especially those from the developing countries generally have decided to keep their data confidential. This decision is based on well-founded arguments to protect certain trees or forests (because of their large size or protected taxonomic status) from illegal logging or trespassing and to protect landowners' privacy against the misuse of plot information such as the geographic coordinates. The sensitive information in the training dataframe, including the plot coordinates and tree-level information, will be available from the corresponding author (albeca.liang@gmail.com) upon a request via Science-i (<https://science-i.org/>) or GFBI (<https://www.gfbinitiative.org/>) and an approval from data contributors.

Code availability

All the models in this study were constructed using command line applications written in the R programming language, which processed and restructured the input data, trained the model and

performed cross validation. Due to the massive amount of data, we used Purdue University's Brown supercomputing cluster to accelerate the training process. The development of the GFBi database, tabular data cleaning, creation of species abundance matrices, evaluation of diversity determinants and geostatistical imputation were conducted in R49 (v.3.4.2) through the use of several Linux-based high-performance computing resources at Purdue University and a custom HPC interface developed using Amazon Web Services, each designed for batch processing, scalable resource distribution, embarrassingly parallel computations and/or large RAM jobs. Compute nodes with up to 1 TB of RAM and clusters of up to 64 nodes were employed in this study. Portions of the covariate preparation, mapping and quality control assessment were conducted on Windows-based operating systems with up to 128 GB of RAM. Final continental-level RF models and the R codes we developed to train the models are available under license MIT with the identifier: 10.6084/m9.figshare.17234729.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41559-022-01831-x>.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41559-022-01831-x>.

Figures

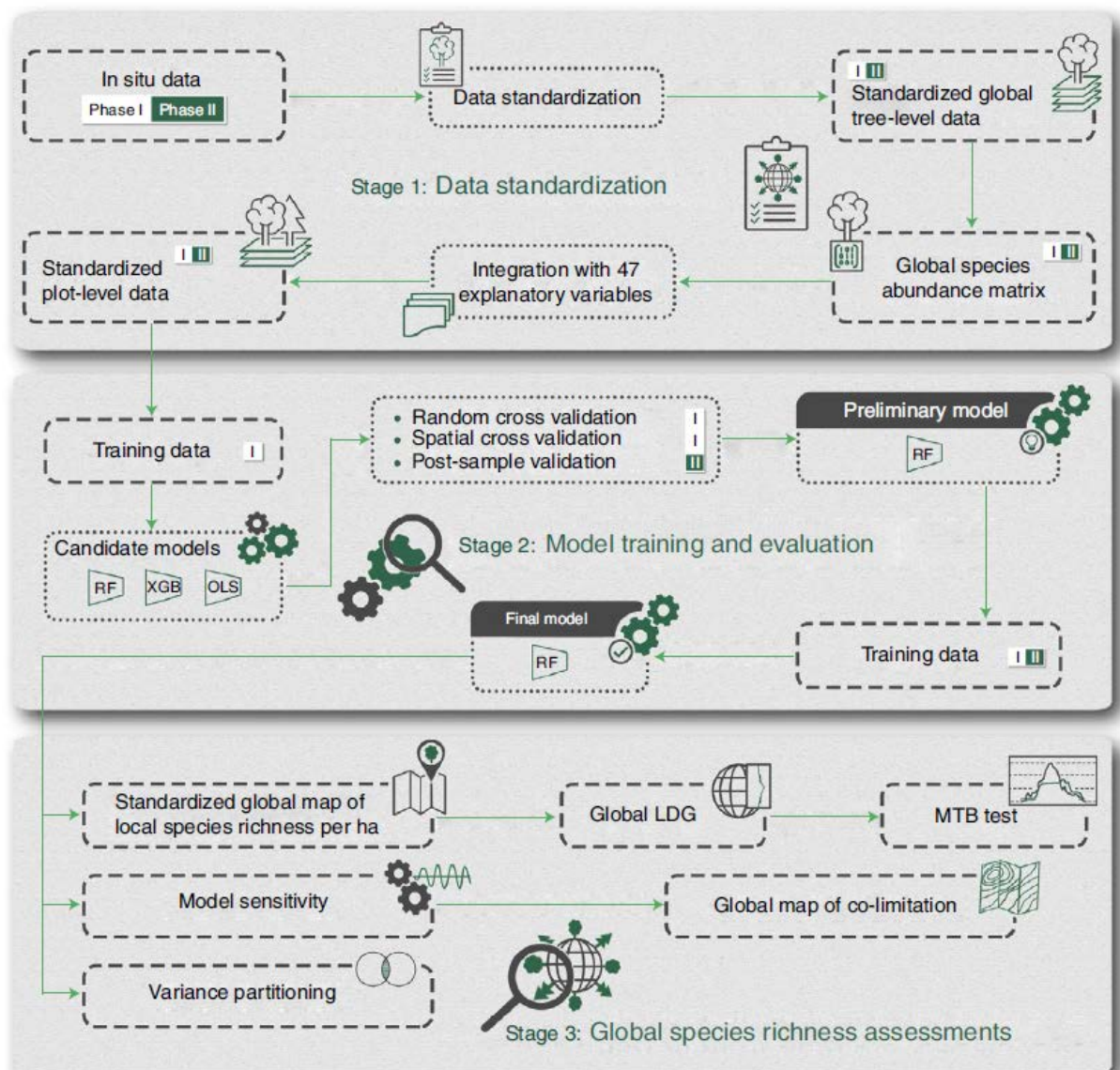


Fig. 1. A conceptual diagram of the three-stage process employed in the study.

Stage 1: Two independent global forest biodiversity individual-based (GFBI) datasets (Phase I and Phase II; Extended Data Fig. 1) were standardized into a global tree-level dataframe and aggregated into a global species abundance matrix. On the basis of plot locations, we merged the abundance matrix with 47 explanatory variables (Fig. 3) into a standardized plot-level dataframe. Stage 2: We compared three candidate models (RF, random forests; XGB, XGBoost; OLS, ordinary least squares) trained from the Phase I plot-level dataframe, using random and spatial cross validation based on Phase I data and post-sample validation based on Phase II data (Extended Data Fig. 2). The final model was then selected and re-calibrated with both Phase I and Phase II data. Stage 3: Using the final model, we standardized and mapped local tree species richness per hectare across the global forest range. On the basis of this globally continuous map, we quantified the associated LDG (Fig. 4a) and tested for the MTB (Fig. 2). We further developed the global map of co-limitation (Fig. 5a) based on model sensitivity analysis and quantified the contribution of key factors to local species richness patterns using variance partitioning (Fig. 6). Dotted boxes represent processes or models and dashed ones represent data or results. Methods provide details.

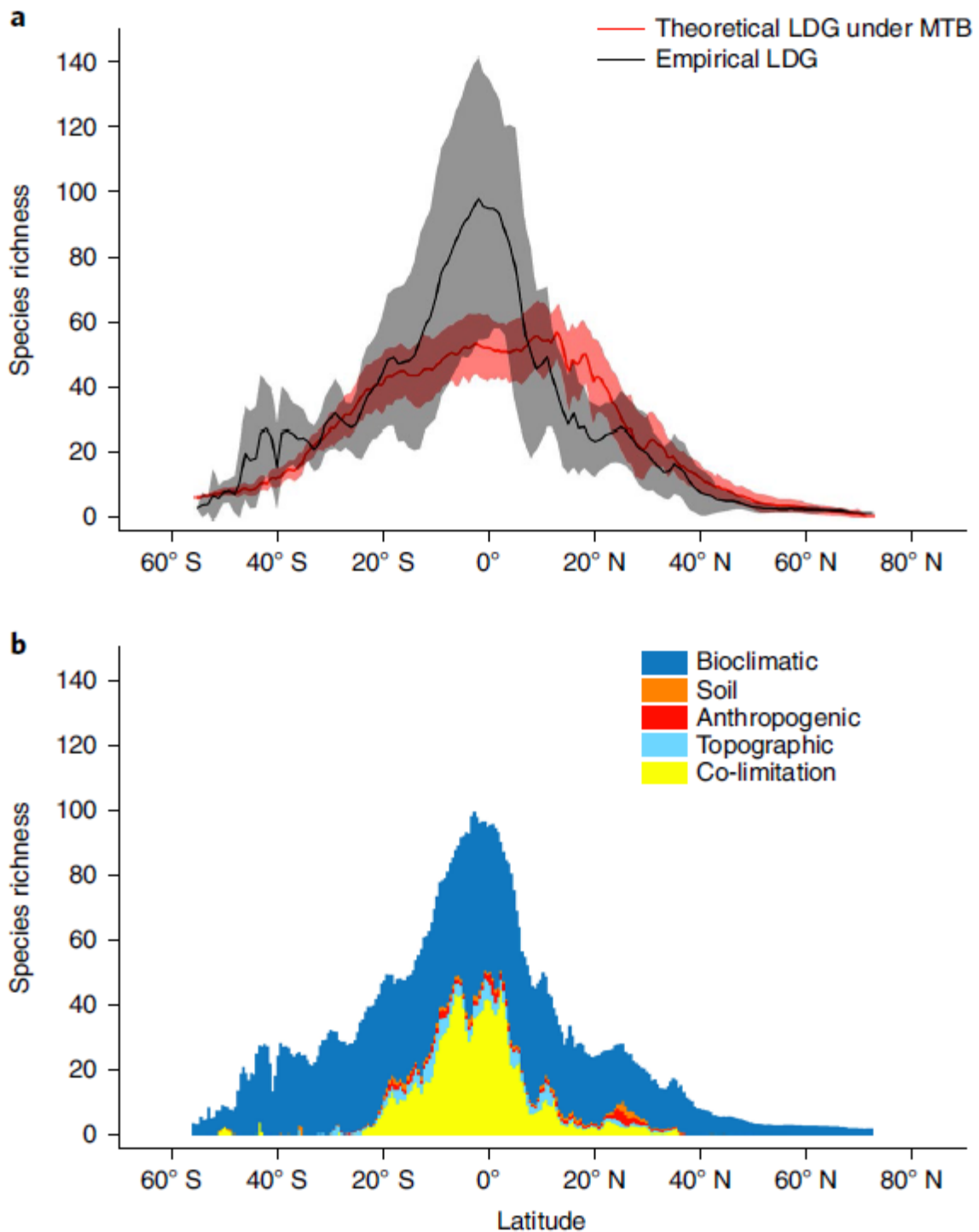


Fig. 2. Latitudinal gradients of estimated tree species richness and co-limitation of drivers.

a, The LDG of tree species richness per hectare was first empirically derived for all 0.025° pixels within the global forest range and aggregated by latitude (Methods). Data are presented as mean values (solid lines) \pm standard deviation (shaded areas) and then compared to LDG predicted by the MTB based on local mean annual temperatures.

b, The co-limitation illustrated here was the product of LDG and the percentage prevalence of dominant drivers by latitude (Fig. 5).

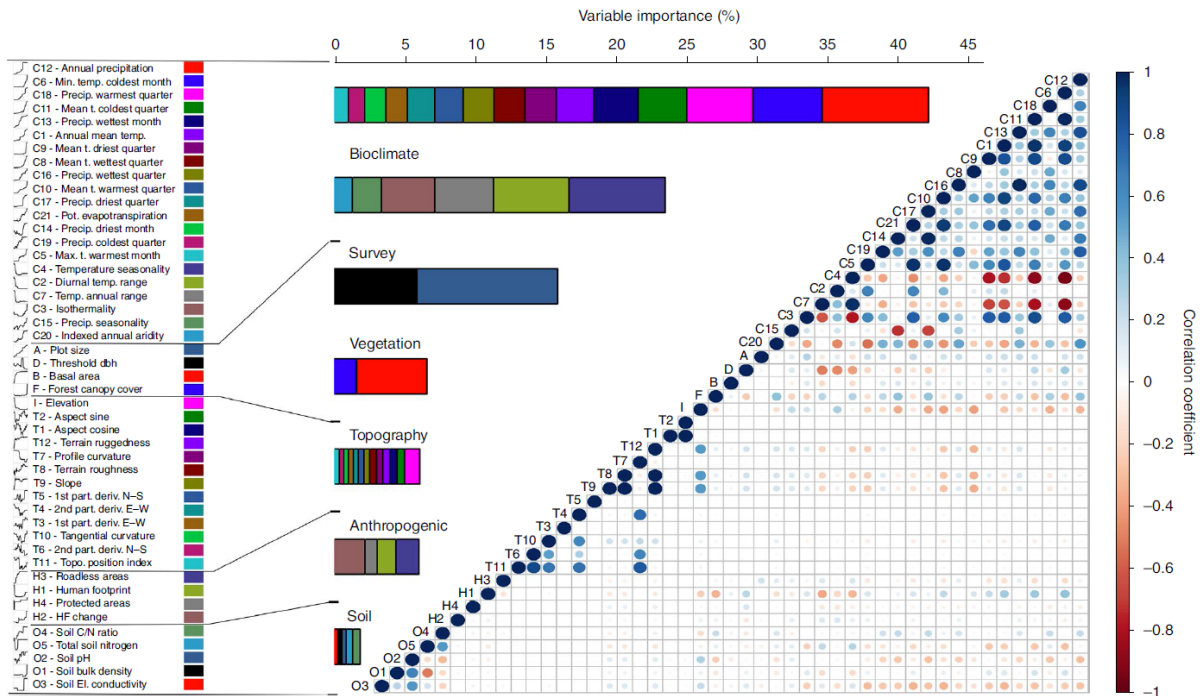


Fig. 3. A total of 47 explanatory variables in five categories were used in random forests models to predict local tree species richness and quantify LDG.

According to standardized variable importance values (horizontal bar plots to the left), bioclimatic variables contributed the most to LDG, followed by vegetation and survey, topographic, anthropogenic and soil variables. The correlogram to the right illustrates correlations between any two variables by the colour and size of a disk. The partial dependence plots to the left (see Extended Data Fig. 3) show the effect of each predictor variable on the species richness, while all the other predictors remained constant at their sample mean. The metadata of the training dataframe provide a detailed description of the explanatory variables. Min., minimum; Temp., temperature; Precip., precipitation; t., temperature; Pot., potential; Max., maximum; dbh, diameter at breast height; part. deriv., partial derivative; Topo., topographic; HF, human footprint; El., electrical.

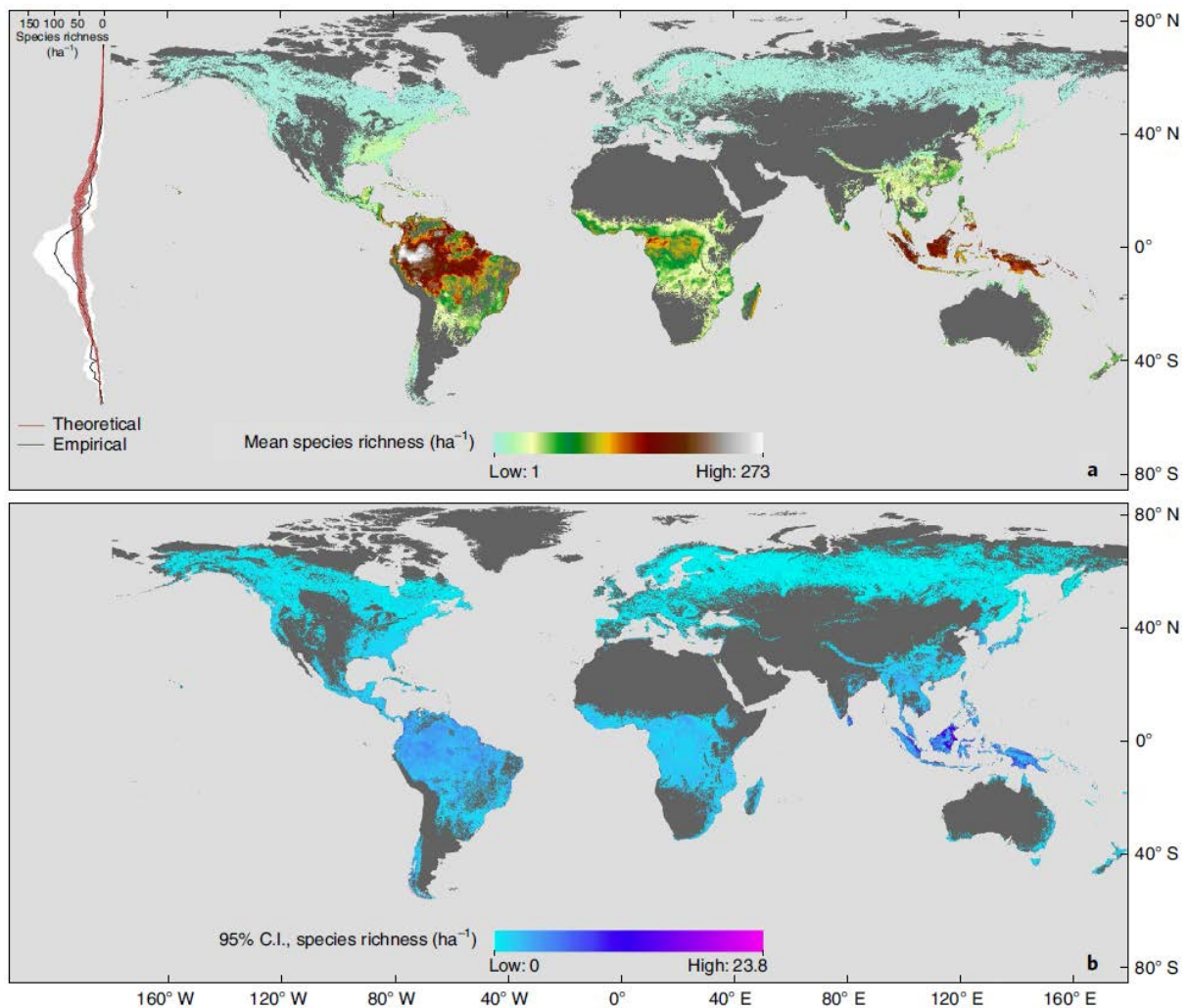


Fig. 4. Estimated tree species richness per hectare in forested areas worldwide.

a, Tree species richness per hectare was first derived for the ~1.3 million GFBi plots across the world and then imputed to the global forest extent. Top left, curves (solid lines representing the mean and shaded areas representing the standard deviation of the mean) represent the observed LDG (black) of tree species diversity in comparison with LDG (red) predicted by the MTB based on local mean annual temperatures (Fig. 2a).

b, Width of the 95% confidence interval (C.I.) for the estimated tree species richness per hectare. All map layers are displayed at a $0.025^\circ \times 0.025^\circ$ resolution with an equirectangular projection (Plate-Carrée) for better illustration of the latitudinal gradients.

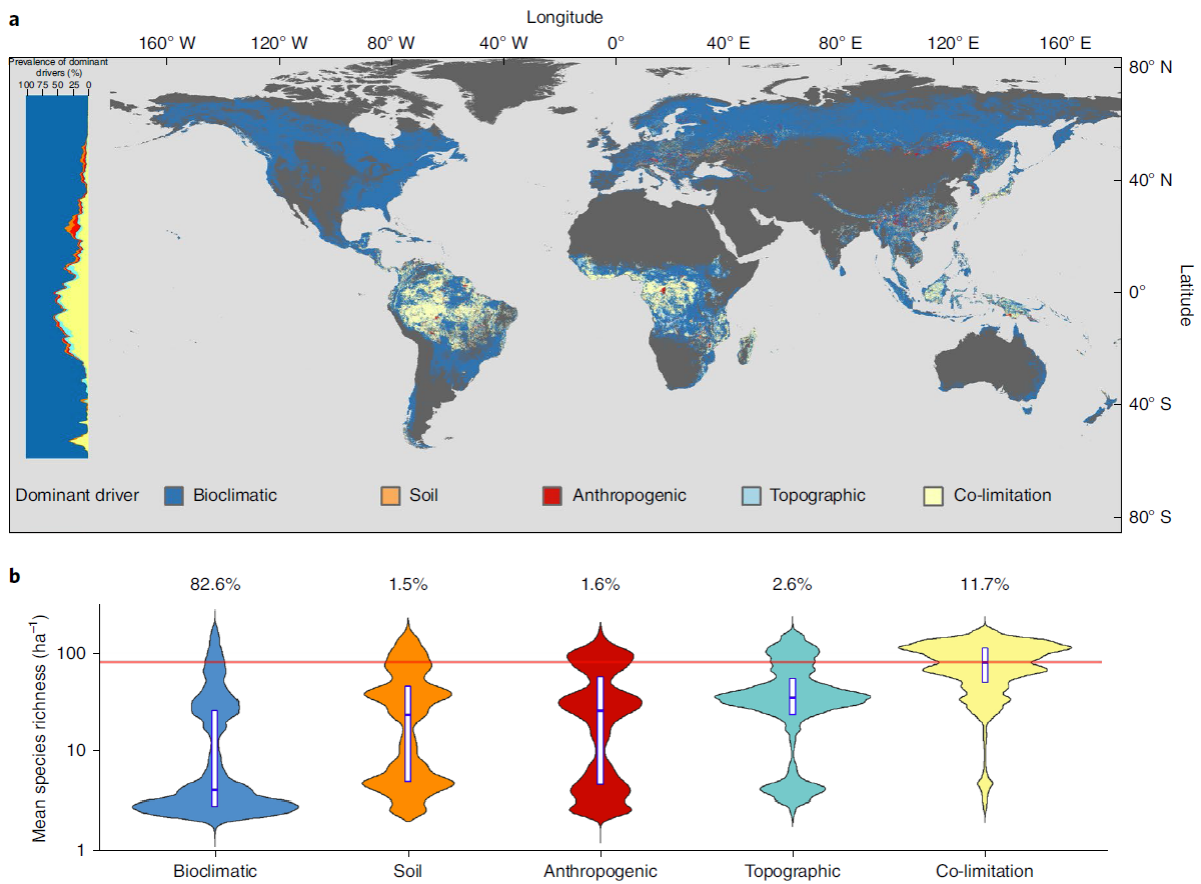


Fig. 5 | Dominant drivers of tree species richness in forested areas worldwide.

a, Driver dominance was derived for each pixel from four driver categories (that is, bioclimatic, topographic, anthropogenic and soil) and co-limitation, which represents a lack of clear dominance among the four foregoing categories. The pixel-level drivers were then aggregated by 0.5° latitudinal bins to show the percentage prevalence of dominant drivers by latitude (top left).

b, The violin charts show the kernel probability density of tree species richness per ha for different drivers. Inside boxes indicate the median (line in the centre) and interquartile range (bounds of boxes). The numbers on top of the violin charts indicate the percentage of forested pixels globally that corresponds to each driver category. The red line represents the mean and 95% confidence interval of tree species richness per ha (81.1 ± 0.1) for all the $0.025^\circ \times 0.025^\circ$ pixels of co-limitation. The vertical axis is on a logarithmic scale for better illustration.

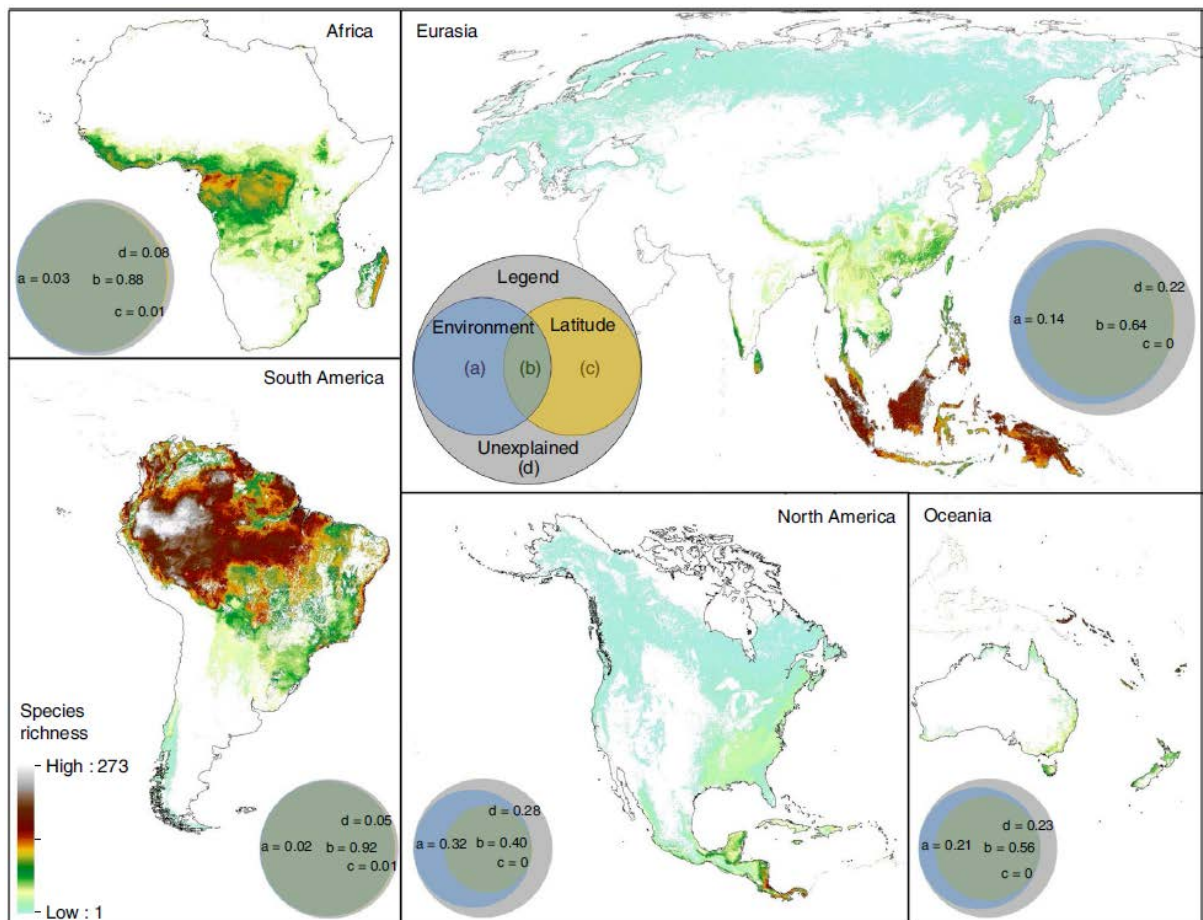


Fig. 6. Patterns and variance of local tree species richness per ha by continent.

The collage of maps shows the zoomed-in view of the distribution of predicted local tree species richness per ha (Fig. 4a) by continent. Circular Venn diagrams (with the legend in the centre) show, for each continent, the spatial variance in observed tree species richness partitioned as follows: a (mean = 14.3%) represents the fraction of variance uniquely explained by environmental factors (that is, bioclimatic, topographic, anthropogenic and soil variables) after latitudinal effects had been accounted for. b (mean = 68.2%) stands for the fraction of variance jointly explained by environmental factors and latitudinal effects. c (mean = 0.3%) represents the fraction of variance explained by latitudinal effects after removing environmental effects. d (mean = 17.2%) represents the fraction of unexplained variance in tree species richness. The fractions were based on contrasting the amount of local richness variations in sample data from ~1.3 million plots explained by the R² statistics from the continental-scale random forest models with the full set of factors versus those with targeted factors removed.

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Affiliations

- 1 Forest Advanced Computing and Artificial Intelligence Laboratory (FACAI), Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA.
- 2 Forestry Division, Food and Agriculture Organization of the United Nations, Rome, Italy.
- 3 GIP ECOFOR, Paris, France.
- 4 Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA.
- 5 Institute for Global Change Biology, School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA.
- 6 Department of Forest Resources, University of Minnesota, St. Paul, MN, USA.
- 7 Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia.
- 8 Crowther Lab, Department of Environmental Systems Science, Institute of Integrative Biology, ETH Zürich, Zürich, Switzerland.
- 9 Wageningen Environmental Research, Wageningen University and Research, Wageningen, Netherlands.
- 10 Forest Ecology and Forest Management Group, Wageningen University and Research, Wageningen, Netherlands.
- 11 Department of Crop and Forest Sciences, University of Lleida, Lleida, Spain.
- 12 Joint Research Unit CTFC—Agrotecnio—CERCA, Solsona, Spain.
- 13 Institute of Ecology and Key Laboratory for Earth Surface Processes of the Ministry of Education, College of Urban and Environmental Sciences, Peking University, Beijing, China.
- 14 Northern Research Station, USDA Forest Service, Durham, NH, USA.
- 15 Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Biology, Aarhus University, Aarhus C, Denmark.
- 16 Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus C, Denmark.
- 17 School of Biological Sciences, University of Bristol, Bristol, UK.
- 18 TERRA Teaching and Research Centre, Gembloux Agro Bio-Tech, University of Liege, Gembloux, Belgium.
- 19 Manaaki Whenua Landcare Research, Lincoln, New Zealand.
- 20 Environmental and Life Sciences, Faculty of Science, Universiti Brunei Darussalam, Gadong, Brunei Darussalam.
- 21 Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Montpellier, France.
- 22 INP-HB (Institut National Polytechnique Félix Houphouët-Boigny), University of Montpellier, Yamoussoukro, Ivory Coast.
- 23 Department of Agricultural, Food, Environmental and Animal Sciences, University of Udine, Udine, Italy.
- 24 Faculty of Science and Technology, Free University of Bolzano, Bolzano, Italy.
- 25 Institute of Bioeconomy, CNR, Sesto, Italy.
- 26 Natural and Built Environments Research Centre, School of Natural and Built Environments, University of South Australia, Adelaide, South Australia, Australia.
- 27 Biometris, Wageningen University and Research, Wageningen, Netherlands.
- 28 Wageningen University & Research, Forest and Nature Conservation Policy Group, Wageningen, Netherlands.
- 29 Centre for Econics and Ecosystem Management, Eberswalde University for Sustainable Development, Eberswalde, Germany.
- 30 School of Forest, Fisheries, and Geomatics Sciences, Institute of Food & Agricultural Sciences, University of Florida, Gainesville, FL, USA.
- 31 Naturalis Biodiversity Center, Leiden, Netherlands.
- 32 Instituto Nacional de Tecnología Agropecuaria (INTA), Santa Cruz, Argentina.

- 33 Department of Plant Sciences, University of Cambridge, Cambridge, UK.
- 34 Faculty of Natural Resources Management, Lakehead University, Thunder Bay, Ontario, Canada.
- 35 University of Göttingen, Göttingen, Germany.
- 36 Beijing Forestry University, Beijing, China.
- 37 University of Stellenbosch, Stellenbosch, South Africa.
- 38 Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, Białowieża, Poland.
- 39 Swiss National Forest Inventory/Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland.
- 40 UFR Biosciences, University Félix Houphouët-Boigny, Abidjan, Ivory Coast.
- 41 Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK.
- 42 Biodiversity Dynamics, Naturalis Biodiversity Center, Leiden, Netherlands.
- 43 Center for Latin American Studies, University of Florida, Gainesville, FL, USA.
- 44 Institute of Botany, Academy of Sciences of the Czech Republic, Trebon, Czech Republic.
- 45 Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, Praha-Suchdol, Czech Republic.
- 46 Escuela ECAPMA, National Open University and Distance (Colombia) | UNAD, Bogotá, Colombia.
- 47 Departamento de Ingeniería Agroforestal, Universidad de Santiago de Compostela, Lugo, Spain.
- 48 Center for Tropical Research, Institute of the Environment and Sustainability, University of California, Los Angeles, CA, USA.
- 49 Université Jean Lorougnon Guédé, Daloa, Ivory Coast.
- 50 Université Officielle de Bukavu, Bukavu, Democratic Republic of Congo.
- 51 Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Goettingen, Germany.
- 52 Institut National pour l'Etude et la Recherche Agronomiques, Kinshasa, Democratic Republic of Congo.
- 53 Norwegian Institute of Bioeconomy Research (NIBIO), Division of Forestry and Forest Resources, Ås, Norway.
- 54 European Commission, Joint Research Centre, Ispra, Italy.
- 55 Compensation International Progress S.A., Bogotá, Colombia.
- 56 Laboratory of Applied Ecology, University of Abomey-Calavi, Cotonou, Benin.
- 57 Scientific Services, South African National Parks, Knysna, South Africa.
- 58 School of Geography, University of Leeds, Leeds, UK.
- 59 Department of Geomatics, Forest Research Institute, Sekocin Stary, Raszyn, Poland.
- 60 Proceedings of the National Academy of Sciences, Washington, DC, USA.
- 61 Department of Evolutionary Anthropology, Duke University, Durham, NC, USA.
- 62 Department of Environment, Université du Cinquanteaire de Lwiro, Bukavu, Democratic Republic of Congo.
- 63 Department of Environment, Ghent University, Ghent, Belgium.
- 64 Department of Green Chemistry and Technology, Ghent University, Ghent, Belgium.
- 65 Service of Wood Biology, Royal Museum for Central Africa, Tervuren, Belgium.
- 66 Balai Penelitian dan Pengembangan Lingkungan Hidup dan Kehutanan, Manokwari, Indonesia.
- 67 Institute of Tropical Forest Conservation, Mbarara University of Science and Technology, Mbarara, Uganda.
- 68 Université de Liège, Gembloux Agro-Bio Tech, Gembloux, Belgium.
- 69 Integrated Center for Research, Development and Innovation in Advanced Materials, Nanotechnologies, and Distributed Systems for Fabrication and Control (MANSiD), University Stefan cel Mare of Suceava, Suceava, Romania.
- 70 Department of Forestry Sciences, 'Luiz de Queiroz' College of Agriculture, University of São Paulo, Piracicaba, Brazil.
- 71 Bavarian State Institute of Forestry, Freising, Germany.
- 72 Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK.

- 73 Facultad de Ciencias Forestales, Universidad Juárez del Estado de Durango, Durango, Mexico.
- 74 Institute of Biology and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany.
- 75 German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany.
- 76 Development Economics Group, Wageningen University, Wageningen, Netherlands.
- 77 Rosen Center for Advanced Computing (RCAC), Purdue University, West Lafayette, IN, USA.
- 78 Department of Biological, Geological and Environmental Sciences (BiGeA), University of Bologna, Bologna, Italy.
- 79 Institute of Integrative Biology, ETH Zürich, Zürich, Switzerland.
- 80 IFER – Institute of Forest Ecosystem Research, Jilove u Prahy, Czech Republic.
- 81 Global Change Research Institute of the CAS, Brno, Czech Republic.
- 82 Programa de Pós-graduação em Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas CEP, Biologia, Brazil.
- 83 Dirección Nacional de Bosques (DNB), Ministerio de Ambiente y Desarrollo Sostenible (MAyDS), Ciudad Autónoma de Buenos Aires, Buenos Aires, Argentina.
- 84 Department of International Environment and Development Studies (Noragric), Faculty of Landscape and Society, Norwegian University of Life Sciences (NMBU), Ås, Norway.
- 85 Department of Environment and Geography, University of York, York, UK.
- 86 Department of Environmental Science, School of Engineering and Sciences, SRM University-AP, Guntur, India.
- 87 Department of Botany, Dr. Harisingh Gour Vishwavidyalaya (A Central University), Madhya Pradesh, India.
- 88 Department of Ecology and Environmental Sciences, Pondicherry University, Puducherry, India.
- 89 Centre for Structural and Functional Genomics & Quebec Centre for Biodiversity Science, Biology Department, Concordia University, Montreal, Quebec, Canada.
- 90 Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic.
- 91 Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic.
- 92 Cirad, UMR EcoFoG (AgroParistech, CNRS, Inrae, Université des Antilles, Université de la Guyane), Campus Agronomique, Kourou, French Guiana.
- 93 Department of Geography, Environment and Geomatics, University of Guelph, Guelph, Ontario, Canada.
- 94 National Forest Authority, Kampala, Uganda.
- 95 Department of Silviculture Foundation, Silviculture Research Institute, Vietnamese Academy of Forest Sciences, Hanoi, Vietnam.
- 96 Department of Botany, Faculty of Science, University of South Bohemia, Bohemia, Czech Republic.
- 97 IPHAMETRA, IRET, CENAREST, Libreville, Gabon.
- 98 Faculté de Gestion de Ressources Naturelles Renouvelables, Université de Kisangani, Kisangani, Democratic Republic of Congo.
- 99 Queensland Herbarium, Department of Environment and Science, Toowong, Queensland, Australia.
- 100 School of Biological and Behavioural Sciences, Queen Mary University of London, London, UK.
- 101 Department of Plant Biology, Faculty of Science, University of Yaoundé I, Yaoundé, Cameroon.
- 102 Natural Resources Institute Finland, Joensuu, Finland.
- 103 Institute of Plant Sciences, University of Bern, Bern, Switzerland.
- 104 Department of Forest Resource Management, Swedish University of Agricultural Sciences, Umea, Sweden.
- 105 Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, Italy.
- 106 Herbário Dr. Roberto Miguel Klein, Universidade Regional de Blumenau, Blumenau, Brazil.
- 107 Glick Designs, LLC, Hadley, MA, USA.
- 108 CIIDIR Durango, Instituto Politécnico Nacional, Durango, Mexico.

- 109 Département des Sciences et Technologies de l'Environnement, Université du Burundi, Bujumbura, Burundi.
- 110 Faculté des Sciences, Evolutionary Biology and Ecology Unit, Université Libre de Bruxelles, Brussels, Belgium.
- 111 Royal Botanic Garden Edinburgh, Edinburgh, UK.
- 112 Department of Plant Sciences, University of Oxford, Oxford, UK.
- 113 Department of Plant Systematics, Bayreuth University, Bayreuth, Germany.
- 114 Helmholtz GFZ German Research Centre for Geosciences, Section 1 .4 Remote Sensing and Geoinformatics, Potsdam, Germany.
- 115 Wild Chimpanzee Foundation, Liberia Representation, Monrovia, Liberia.
- 116 Centre for Conservation Science, The Royal Society for the Protection of Birds, Sandy, UK.
- 117 Department of Environment, Laboratory for Wood Technology (UGent-Woodlab), Ghent University, Ghent, Belgium.
- 118 AMAP, University of Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France.
- 119 Department of Forest Science, Tokyo University of Agriculture, Tokyo, Japan.
- 120 Biology Department, Université Officielle de Bukavu, Bukavu, Democratic Republic of Congo.
- 121 Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland.
- 122 Poznan University of Life Sciences, Faculty of Forestry and Wood Technology, Department of Game Management and Forest Protection, Poznan, Poland.
- 123 Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark.
- 124 Plant Biology Department, Biology Institute, University of Campinas (UNICAMP), Campinas, Brazil.
- 125 Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN, USA.
- 126 Institute of Agricultural Research for Development (IRAD), Nkolbisson, Ministry of Scientific Research and Innovation, Yaounde, Cameroon.
- 127 Department of Food and Resource Economics, University of Copenhagen, Copenhagen, Denmark.
- 128 Forestry Faculty, Bauman Moscow State Technical University, Mytishi, Russia.
- 129 Integrative Research Center, The Field Museum, Chicago, IL, USA.
- 130 Labo Botanique, Université Félix Houphouët-Boigny, Abidjan, Ivory Coast.
- 131 Computational and Applied Vegetation Ecology Lab, Ghent University, Ghent, Belgium.
- 132 Department of Physical and Environmental Sciences, Colorado Mesa University, Grand Junction, CO, USA.
- 133 Department of Botany, Dr. Harisingh Gour Vishwavidyalaya (A Central University), Sagar, India.
- 134 Kenya Forestry Research Institute, Department of Forest Resource Assessment, Nairobi, Kenya.
- 135 Department of Forest Sciences, Seoul National University, Seoul, Republic of Korea.
- 136 Interdisciplinary Program in Agricultural and Forest Meteorology, Seoul National University, Seoul, Republic of Korea.
- 137 National Center for Agro Meteorology, Seoul, Republic of Korea.
- 138 Research Institute for Agriculture and Life Sciences, Seoul National University, Seoul, Republic of Korea.
- 139 Institute of Forestry and Engineering, Estonian University of Life Sciences, Tartu, Estonia.
- 140 International Institute for Applied Systems Analysis, Laxenburg, Austria.
- 141 Department of Geoinformatics, Central University of Jharkhand, Ranchi, India.
- 142 Tartu Observatory, University of Tartu, Tõravere, Estonia.
- 143 School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa.
- 144 Department of Forest Engineering, Federal University of Viçosa (UFV), Viçosa, Brazil.
- 145 Department of Geography, University College London, London, UK.
- 146 Plant Systematics and Ecology Laboratory (LaBosystE), Higher Teacher's Training College, University of Yaoundé I, Yaoundé, Cameroon.
- 147 Laboratoire d'Écologie et Aménagement Forestier, Département d'Ecologie et de Gestion des Ressources Végétales, Université de Kisangani, Kisangani, Democratic Republic of Congo.

- 148 Instituto de Silvicultura e Industria de la Madera, Universidad Juarez del Estado de Durango, Durango, Mexico.
- 149 Faculty of Forestry, Qingdao Agricultural University, Qingdao, China.
- 150 Center for Forest Ecology and Productivity RAS (CEPF RAS), Moscow, Russia.
- 151 Department of Ecoscience, Aarhus University, Silkeborg, Denmark.
- 152 Nicholas School of the Environment, Duke University, Durham, NC, USA.
- 153 Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA.
- 154 AgroParisTech, UMR AMAP, University of Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France.
- 155 University of the Sunshine Coast, Sippy Downs, Queensland, Australia.
- 156 University of York, York, UK.
- 157 Flamingo Land Ltd., North Yorkshire, UK.
- 158 Department of Wildlife Management, College of African Wildlife Management, Mweka, Tanzania.
- 159 Kenya Forestry Research Institute, Headquarters, Nairobi, Kenya.
- 160 Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico.
- 161 Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA.
- 162 Department of Forest Management and Forest Economics, Warsaw University of Life Sciences, Warsaw, Poland.
- 163 Tropical Forests and People Research Centre, University of the Sunshine Coast, Maroochydore DC, Queensland, Australia.
- 164 Fieldstation FabrikSchleichach, Julius-Maximilians University Würzburg, Würzburg, Germany.
- 165 Bavarian Forest Nationalpark, Grafenau, Germany.
- 166 Fakultas Kehutanan, Universitas Papua, Jalan Gunung Salju Amban, Manokwari Papua Barat, Indonesia.
- 167 Limbe Botanic Garden, Limbe, Cameroon.
- 168 Institute of Forestry, Belgrade, Serbia.
- 169 Tropical Plant Exploration Group (TroPEG), Buea, Cameroon.
- 170 Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN, USA.
- 171 Applied Biology and Ecology Research Unit, University of Dschang, Dschang, Cameroon.
- 172 Department of Forestry and Natural Resources, University of Kentucky, Lexington, KY, USA.
- 173 UQAM, Centre for Forest Research, Montreal, Quebec, Canada.
- 174 V.N. Sukachev Forest Institute of FRC KSC SB RAS, Krasnoyarsk, Russia.
- 175 Urban Management and Planning, School of Social Sciences, Western Sydney University, Penrith, New South Wales, Australia.
- 176 Instituto Nacional de Pesquisas da Amazônia—INPA, Grupo Ecologia. Monitoramento e Uso Sustentável de Áreas Úmidas MAUA, Manaus, Brazil.
- 177 Centro de Formação em Ciências Agroflorestais, Universidade Federal do Sul da Bahia, Ilhéus, Brazil.
- 178 Department of Agriculture, Food, Environment and Forestry, University of Firenze, Firenze, Italy.
- 179 Technical University of Munich, School of Life Sciences Weihenstephan, Chair of Forest Growth and Yield Science, Munich, Germany.
- 180 Centro Agricoltura, Alimenti, Ambiente, University of Trento, San Michele all'Adige, Italy.
- 181 Department of Biology, University of Florence, Sesto Fiorentino, Italy.
- 182 MUSE—Museo delle Scienze, Trento, Italy.
- 183 Infoflora c/o Botanical Garden of Geneva, Geneva, Switzerland.
- 184 Agricultural Research, Education and Extension Organization (AREEO), Research Institute of Forests and Rangelands (RIFR), Tehran, Iran.
- 185 Department of Environmental Sciences, Central University of Jharkhand, Ranchi, India.
- 186 Institute of International Education Scholar Rescue Fund (IIE-SRF), One World Trade Center, New York, NY, USA.
- 187 Centro de Modelación y Monitoreo de Ecosistemas, Facultad de Ciencias, Universidad Mayor, Santiago, Chile.

- 188 Vicerrectoría de Investigación y Postgrado, Universidad de La Frontera, Temuco, Chile.
- 189 Departamento de Silvicultura y Conservación de la Naturaleza, Universidad de Chile, Santiago, Chile.
- 190 Peoples Friendship University of Russia (RUDN University), Moscow, Russia.
- 191 University of Freiburg, Faculty of Biology, Freiburg, Germany.
- 192 Institution with City, Department of Geography, University of Zurich, Zurich, Switzerland.
- 193 National Forest Centre, Zvolen, Slovak Republic.
- 194 CNRS-UMR LEEISA, Campus Agronomique, Kourou, French Guiana.
- 195 Université de Lorraine, AgroParisTech, INRA, Nancy, France.
- 196 Center for International Forestry Research (CIFOR), Situ Gede, Bogor Barat, Indonesia.
- 197 Cirad, University of Montpellier, Montpellier, France.
- 198 Universidade Federal do Rio Grande do Norte, Departamento de Ecologia, Natal, Brazil.
- 199 School of Biological Sciences, University of Aberdeen, Aberdeen, UK.
- 200 Herbarium Kew, Royal Botanic Gardens Kew, London, UK.
- 201 Faculté des Sciences Appliquées, Université de Mbujimayi, Mbujimayi, Democratic Republic of Congo.
- 202 Yale School of Forestry and Environmental Studies, New Haven, CT, USA.
- 203 Ural State Forest Engineering University, Botanical Garden, Ural Branch of the Russian Academy of Sciences, Yekaterinburg, Russia.
- 204 DIBAF Department, Tuscia University, Viterbo, Italy.
- 205 LINCGlobal, MNCN, CSIC, Madrid, Spain.
- 206 Plant Ecology and Nature Conservation Group, Wageningen University, AA Wageningen, Netherlands.
- 207 Agricultural High School, ESAV, Polytechnic Institute of Viseu, IPV, Viseu, Portugal.
- 208 Centre for the Research and Technology of Agro-Environmental and Biological Sciences, CITAB, UTAD, Quinta de Prados, Vila Real, Portugal.
- 209 Department of Forest Engineering, Universidade Regional de Blumenau, Blumenau, Brazil.
- 210 Nucleo de Estudos e Pesquisas Ambientais, Universidade Estadual de Campinas, Campinas (UNICAMP), SP, Campinas, Brazil.
- 211 International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL, USA.
- 212 Forest Research Institute, University of the Sunshine Coast, Sippy Downs, Queensland, Australia.
- 213 Sanya Nanfan Research Institute, Hainan Yazhou Bay Seed Laboratory, Hainan University, Sanya, China.
- 214 Kenya Forestry Research Institute, Taita Taveta Research Centre, Wundanyi, Kenya.
- 215 Department of Wetland Ecology, Institute for Geography and Geoecology, Karlsruhe Institute for Technology, Rastatt, Germany.
- 216 Department of Forest Management, Centre for Agricultural Research in Suriname, Paramaribo, Suriname.
- 217 Polish State Forests–Coordination Centre for Environmental Projects, Warsaw, Poland.
- 218 Research Center of Forest Management Engineering of State Forestry and Grassland Administration, Beijing Forestry University, Beijing, China.
- 219 Department of Statistics, University of Wisconsin–Madison, Madison, WI, USA.
- 220 Institut National Polytechnique Félix Houphouët-Boigny, DFR Eaux, Forêts et Environnement, BP, Yamoussoukro, Ivory Coast.
- 221 Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Matieland, South Africa.
- 222 African Institute for Mathematical Sciences, Muizenberg, South Africa.