Article:
(2018) Phylogenetic classification of the world's tropical forests. Proceedings of the National Academy of Sciences of the United States of America. 1837–1842. ISSN 1091-6490

https://doi.org/10.1073/pnas.1714977115

CLASSIFICATION: BIOLOGICAL SCIENCES, Ecology

TITLE: A phylogenetic classification of the world's tropical forests

SHORT TITLE: Tropical forest classification

AUTHORS: J. W. Ferry Slik[1], Janet Franklin[51], Víctor Arroyo-Rodríguez[2], Richard Field[3], Salomon Aguilar[4], Nikolay Aguirre[5], Jorge Ahumada[6], Shin-Ichiro Aiba[7], Luciana F. Alves[8], Anitha K[9], Andres Avella[10], Francisco Mora Ardila[2], Gerardo A. Aymard C.[11, 12], Selene Báez[13], Patricia Balvanera[2], Meredith L. Bastian[14], Jean-François Bastin[15], Peter J. Bellingham[16], Eduardo van den Berg[17], Polyanna da Conceição Bispo[18], Pascal Boeckx[19], Katrin Boehning-Gaese[20, 21], Frans Bongers[22], Brad Boyle[23], Fabian Brambach[24], Francis Q. Brearley[25], Sandra Brown[26], Shauna-Lee Chai[27], Robin L. Chazdon[28], Shengbin Chen[29], Phourin Chhang[30], George Chuyong[31], Ewango Corneille[32], Indiana M. Coronado[33], Jurgi Cristóbal-Azkarate[34], Heike Culmsee[35], Kipiro Damas[36], HS Dattaraja[37], Priya Davidar[38], Saara J. DeWalt[39], Hazimah Din[1], Donald R. Drake[40], Alvaro Duque[41], Giselda Durigan[42], Karl Eichhorn[43], Eduardo Schmidt Eler[44], Tsutomu Enoki[45], Andreas Ensslin[46], Adandé Belarmain Fandohan[47], Nina Farwig[48], Kenneth J. Feeley[49], Markus Fischer[46], Olle Forshed[50], Queila Garcia[52], Satish Chandra Garkoti[53], Thomas W. Gillespie[54], Jean-Francois Gillet[55], Christelle Gonmadje[56, 57], Iñigo Granzow-de la Cerda[58], Daniel M. Griffith[59], James Grogan[60], Khalid Rehman Hakeem[61], David J. Harris[62], Rhett D. Harrison[63], Andy Hector[64], Andreas Hemp[65], Jürgen Homeier[66], M. Shah Hussain[67], Guillermo Ibarra-Manríquez[2], Faridah Hanum Ibrahim[68], Nobuo Imai[69], Patrick A. Jansen[4, 22], Shijo Joseph[9, 70], Kuswata Kartawinata[71, 72], Elizabeth Kearsley[73], Daniel Kelly[74], Michael Kessler[75], Timothy J. Killeen[76], Robert Kooyman[77, 78], Yves Laumonier[9], Susan Laurance[79], William Laurance[79], Michael J. Lawes[80], Susan Letcher[81], Jeremy Lindsell[82], Jon Lovett[83, 140], Jose Lozada[84], Xinghui Lu[85], Anne Mette Lykke[86], Khairil Bin Mahmud[87], Ni Putu Diana Mahayani[88], Asyraf Mansor[89, 90], Andrew R. Marshall[91, 92, 161], Emanuel

H. Martin[93], Darley Calderado Leal Matos[94], Jorge A. Meave[95], Felipe P. L. Melo[96], Zhofre Huberto Aguirre Mendoza[97], Faizah Metali[1], Vincent Metjibe[98], Jean Paul Metzger[99], Thiago Metzker[52,100], D. Mohandass[38, 101], Miguel A. Munguía-Rosas[102], Rodrigo Muñoz[95], Eddy Nurtjahya[103], Eddie Lenza de Oliveira[104], Onrizal[105], Pia Parolin[106, 107], Marc Parren[108], N Parthasarathy[38], Ekananda Paudel[109], Rolando Perez[4], Eduardo A. Pérez-García[95], Ulf Pommer[20], Lourens Poorter[22], Lan Qie[83], Maria Teresa F. Piedade[44], José Roberto Rodrigues Pinto[110], Axel Dalberg Poulsen[62], John Poulsen[111], Jennifer S. Powers[112], Rama Chandra Prasad[113], Jean-Philippe Puyravaud[114], Orlando Rangel[10], Jan Reitsma[115], Diogo S. B. Rocha[116], Samir Rolim[117], Francesco Rovero[118], Andes Rozak[119], Kalle Ruokolainen[120], Ervan Rutishauser[4], Gemma Rutten[46], Mohd. Nizam Mohd. Said[121], Felipe Z. Saiter[122], Philippe Saner[123], Braulio Santos[124], João Roberto dos Santos[125], Swapan Kumar Sarker[126], Christine B. Schmitt[127, 160], Jochen Schoegart[44], Mark Schulze[128], Douglas Sheil[129], Alexandre F. Souza[130], Wilson Roberto Spironello[44], Tereza Sposito[52, 100], Robert Steinmetz[131], Tariq Stevart[132], Marcio Seiji Suganuma[133], Rahayu Sukri[1], Aisha Sultana[134], Raman Sukumar[37], Terry Sunderland[9], Supriyadi[88], Suresh H. S.[37], Eizi Suzuki[7], Marcelo Tabarelli[135], Jianwei Tang[136], Ed V. J. Tanner[137], Natalia Targhetta[44], Ida Theilade[138], Duncan Thomas[139], Jonathan Timberlake[140], Márcio de Morisson Valeriano[141], Johan van Valkenburg[142], Tran Van Do[143], Sam Van Hoang[144], John H. Vandermeer[145], Hans Verbeeck[73], Ole Reidar Vetaas[146], Victor Adekunle[147], Simone A. Vieira[148], Campbell Webb[149], Edward Webb[150], Tim Whitfeld[151], Serge Wich[152, 153], John Williams[154], Susan Wiser[16], Florian Wittmann[155], Xiaobo Yang[156], C. Yves Adou Yao[157], Sandra Yap[158], Rakan A. Zahawi[159], Rahmad Zakaria[89], Runguo Zang[85]

AFFILLIATIONS: 1. Environmental Life Sciences, Faculty of Science, Universiti Brunei Darussalam, Gadong, Brunei Darussalam; **2.** Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, 58190 Morelia, Michoacán, Mexico; **3.** School of Geography, University of Nottingham, NG7 2RD, UK; **4.** Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Ancon, Panama; **5.** Biodiversity and Ecosystem Services Research Program. Universidad Nacional de Loja, Ecuador; **6.** The Moore Center for Science, Conservation International, Arlington VA, USA; **7.** Graduate School of Science and Engineering, Kagoshima University, Kagoshima 890-0065, Japan; **8.** Center for Tropical Research, Institute of the Environment and Sustainability, University of California, Los Angeles, CA, USA; **9.** Forest and Environment Program, Center for International Forestry Research (CIFOR), Bogor, Indonesia; **10.** Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Sede Bogotá, Colombia; **11.** UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Mesa de Cavacas, Estado Portuguesa 3350, Venezuela; **12.** Compensation International Progress S.A.– Ciprogress Greenlife, Calle 86A N0. 15–31, P.O. Box 260161, Bogotá D. C., Colombia; **13.** Instituto de Ciencias Biológicas, Escuela Politécnica Nacional del Ecuador, Quito – Ecuador; **14.** Smithsonian's National Zoo, Animal Care Sciences, Primates, MRC 5507 PO Box 37012, Washington DC 20013-7012, USA; **15.** Landscape Ecology and Plant Production Systems Unit, Université libre de Bruxelles, CP264-2, B-1050 Bruxelles, Belgium; **16.** Landcare Research Manaaki Whenua, PO Box 69040, Lincoln 7640, New Zealand; **17.** Universidade Federal de Lavras, Av. Doutor Sylvio Menicucci, 1001 - Kennedy, Lavras - MG, 37200-000, Brazil; **18.** Centre for Landscape and Climate Research, Department of Geography, University of Leicester, University Road, Leicester LE1 7RH, UK; **19.** Isotope Bioscience Laboratory (ISOFYS), Department of Applied Analytical and Physical Chemistry, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, B-9000 Ghent, Belgium; **20.** Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt (Main), Germany; **21.** Goethe, University Frankfurt, Institute for Ecology, Evolution & Diversity, Max von Laue Str. 13, 60439 Frankfurt (Main), Germany; **22.** Forest Ecology and Forest Management (FEM), Centre for Ecosystem Studies, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands;

23. Hardner & Gullison Associates, 206 - 1875 Lansdowne Rd, Victoria, BC, Canada V8P 1A9; **24.** Ecology and Ecosystem Research, Georg-August-University Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany; **25.** School of Science and the Environment, Manchester Metropolitan University, Chester Street, Manchester, M1 5GD, UK; **26.** Environment Group, Winrock International, 6 Bryngwyn Estates, St Dogmaels, SA43 3 DT, UK; **27.** Ecosystem Management Unit, InnoTech Alberta, Bag 4000, Hwy 16A & 75 Street, Vegreville, AB T9C 1T4, Canada; **28.** Dept. of Ecology & Evolution, Biology, Unit 3043, University of Connecticut, Storrs, CT 06269-3043, USA; **29.** College of Environment, Chengdu University of Technology, Chengdu 610059, China; **30.** Forest and Wildlife Research Institute, Hanoi St. (1019), Phnom Penh, Cambodia; **31.** Department of Botany and Plant Physiology, University of Buea, PO Box 63 Buea, Cameroon; **32.** Wildlife Conservation Society-Program DR Congo & Centre de Formation et de Recherche en Conservation Forestiere (CEFRECOF), Epulu-DR Congo; **33.** Universidad Nacional Autónoma de Nicaragua, Facultad de Ciencias y Tecnología, Departamento de Biología, Herbario HULE, León Nicaragua; **34.** Division of Biological Anthropology, University of Cambridge, Cambridge, UK; **35.** DBU Naturerbe GmbH, An der Bornau 2, 49090 Osnabrück, Germany; **36.** PNG Forest Research Institute, P.O . Box 314, Lae, Morobe Province, Papua New Guinea; **37.** Centre for Ecological Sciences, TE-13, 3rd Floor, Biological Sciences Building, Indian Institute of Science (IISc.), Bangalore-560012, India; **38.** Department of Ecology & Environmental Sciences, Pondicherry University, Puducherry- 605 014, India; **39.** Department of Biological Sciences, Clemson University, Clemson, SC 29634, USA; **40.** Botany Department, University of Hawaii, 3190 Maile Way, Honolulu, HI 96822, USA; **41.** Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Address: Calle 59A #63-20, Medellín, Colombia; **42.** Laboratório de Ecologia e Hidrologia Florestal, Floresta Estadual de Assis, Instituto Florestal de SP, Caixa Postal 104, 19802-970 Assis, SP, Brasil; **43.** Eichhorn Ecologie, Melis Stokestaat 29, 3702 BK Zeist, The

Netherlands; **44.** Instituto Nacional de Pesquisas da Amazônia – INPA, CDAM, MAUA, Av. André, Araújo, 2.936 - Petrópolis - CEP 69067-375 - Manaus -AM, Brazil; **45.** Kasuya Research Forest, Kyushu University, 394 Tsubakuro, Sasaguri, Fukuoka 811-2415, Japan; **46.** Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland; **47.** Ecole de Foresterie et Ingénierie du Bois, Université Nationale d'Agriculture, BP 45, Kétou, République du Bénin; **48.** Conservation Ecology, Faculty of Biology, Philipps-Universität Marburg, Karl-von-Frisch-Str. 8, 35032 Marburg, Germany; **49.** International Center for Tropical Botany, Department of Biological Sciences; Florida International University; Miami FL USA 33199; **50.** WWF-Sweden/Världsnaturfonden WWF, Ulriksdals Slott, S-170 81 Solna, Sweden; **51.** Department of Botany and Plant Sciences, University of California – Riverside, 900 University Ave, Riverside CA 92521; **52.** Departamento de Botânica, Universidade Federal de Minas Gerais, Brazil; **53.** School of Environmental Sciences, Jawaharlal Nehru University, New Delhi 110067, India; **54.** Department of Geography, UCLA, Los Angeles, CA, 90095, USA; **55.** Nature Forest Environment, Consultant Indépendant, Foresterie Tropicale, 7c Rue du Moulin, 6929 Porcheresse, Belgium; **56.** Department of Plant Biology, Faculty of Sciences - University of Yaounde I, PO BOX 812, Yaounde, Cameroun; **57.** National Herbarium, P.O BOX 1601, Yaoundé, Cameroon; **58.** CREAF – Univ. Autònoma de Barcelona, Cerdanyola del Vallès 08193, Spain; **59.** Universidad Técnica Particular de Loja, Loja, Ecuador; **60.** Mount Holyoke College Botanic Garden, South Hadley, MA 01075 USA; **61.** Department of Biological Sciences, Faculty of Science, King Abdulaziz University, Jeddah, Saudi Arabia; **62.** Royal Botanical Garden Edinburgh, Edinburgh, UK; **63.** World Agroforestry Centre, East & Southern Africa Region, 13 Elm Road, Woodlands, Lusaka, Zambia; **64.** Department of Plant Sciences, University of Oxford, OX1 3RB, UK; **65.** Dept. of Plant Systematics, University of Bayreuth, Universitaetsstr. 30-31, 95440 Bayreuth, Germany; **66.** Plant Ecology, Albrecht von Haller Institute of Plant Sciences, Georg August University of

Göttingen, 37073 Göttingen, Germany; **67.** Biodiversity Parks Programme, Centre for Environmental Management of Degraded Ecosystems (CEMDE), University of Delhi, Delhi-110007, India; **68.** Faculty of Forestry, Universiti Putra Malaysia, Serdang-43400, Selangor, Malaysia; **69.** Department of Forest Science, Tokyo University of Agriculture, Japan; **70.** GIS and Remote Sensing Department, Kerala Forest Research Institute (KFRI), Peechi, Kerala, India; **71.** Integrative Research Center, The Field Museum, 1400 Lake Shore Drive, Chicago, IL 60605, USA; **72.** Herbarium Bogoriense, Research Center for Biology, Indonesian Institute of Sciences, Cibinong Science Center (CSC), Jl. Raya Jakarta - Bogor Km. 46, Cibinong – 16911, Indonesia; **73.** Computational and Applied Vegetation Ecology (CAVElab), Department of Applied Ecology and Environmental Biology, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, B-9000 Ghent, Belgium; **74.** Trinity Center for Bioengineering, Trinity College Dublin, the University of Dublin, College Green, Dublin 2, Ireland; **75.** Department of Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland; **76.** Agteca-Amazonica, Santa Cruz, Bolivia; **77.** Department of Biological Sciences, Macquarie University, North Ryde, NSW, Australia; **78.** National Herbarium of NSW, Royal Botanic, Gardens and Domain Trust, Sydney, NSW, Australia; **79.** Centre for Tropical Environmental and Sustainability Science & College of Science and Engineering, James Cook University, Cairns, Queensland 4878, Australia; **80.** School of Life Sciences, University of KwaZulu-Natal, Scottsville, 3209, South Africa; **81.** College of the Atlantic, 105 Eden St., Bar Harbor, ME 04609, USA; **82.** The RSPB Centre for Conservation Science, Sandy, Bedfordshire SG19 2DL, UK; **83.** School of Geography, University of Leeds, Leeds, LS2 9JT, UK; **84.** Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes, Venezuela; **85.** Key Laboratory of Forest Ecology and Environment of State Forestry Administration, Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091, China; **86.** Department of Bioscience, Aarhus University, Vejlsøvej 25, 8600 Silkeborg, Denmark; **87.** Faculty of Bioresources and Food Sciences, Universiti Sultan Zainal Abidin, 20300, Besut Campus, Terengganu, Malaysia; **88.** Faculty of Forestry, Universitas Gadjah Mada, Yogjakarta, Indonesia; **89.** School of Biological Sciences, Universiti Sains Malaysia, 11800 Penang. Malaysia; **90.** Centre for Marine and Coastal Studies, Universiti Sains Malaysia, 11800 Penang. Malaysia; **91.** CIRCLE, University of York, UK; **92.** Flamingo Land, North Yorkshire, UK; **93.** College of African Wildlife Management, Department of Wildlife Management, P.O. Box 3031, Moshi – Tanzania; **94.** PPGBionorte/MPEG Bióloga – UFPA, CRBio 73013/06-D, Brazil; **95.** Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, C.P. 04510, Mexico; **96.** Center for Biosciences, Federal University of Pernambuco, Brazil; **97.** Herbario LOJA, Universidad Nacional de Loja, Ecuador; **98.** Mesure et Suivi du Carbone Forestier, Projet Régional REDD+, COMIFAC - GEF-Banque Mondiale, BP 20818 Yaoundé - République du Cameroun; **99.** Department of Ecology, Institute of Bioscience – University of São Paulo, Rua do Matão, 321, travessa 14, 05508-900, São Paulo, SP, Brazil; **100.** Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre (ECMVS), IBAM - Instituto Bem Ambiental, Centauro, 231, Belo Horizonte - Minas Gerais, Brazil; **101.** Root & Soil Biology Laboratory, Department of Botany, Bharathiar University, Coimbatore – 641 046, India; **102.** Laboratorio de Ecología Terrestre, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (CINVESTAV), Antigua Carretera a progreso Km 6, C.P. 27310, Mérida, México; **103.** Universitas Bangka Belitung, Jl. Kampus Terpadu UBB, Kel. Balunijuk, Kec. Merawang, Balun Ijuk, Merawang, Kabupaten Bangka, Kepulauan Bangka Belitung 33172, Indonesia; **104.** Universidade do Estado de Mato Grosso – UNEMAT, Av. Tancredo Neves, 1095 - Cavalhada II - 78200-000 - Cáceres - Mato Grosso, Brazil; **105.** Faculty of Forestry, University of Sumatera Utara, Indonesia; **106.** Dept. Biodiversity, Evolution and Ecology of Plants, Biocentre Klein Flottbek, University of

Hamburg, Ohnhorststrasse 18, D-22609 Hamburg, Germany; **107.** INRA, University of Nice Sophia Antipolis, CNRS, UMR 1355-7254 Institut Sophia Agrobiotech, 06903, Sophia Antipolis, France; **108.** World Resource Institute, 10 G Street NE Suite 800, Washington, DC 20002, USA; **109.** Centre for Mountain Ecosystem Studies, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China; **110.** Departamento de Engenharia Florestal, Universidade de Brasília (UnB), P.O. Box 4357, 70910-900, Brasília, Distrito Federal, Brazil; **111.** Nicholas School of the Environment, Duke University, P.O. Box 90328, Durham, NC 27708, USA; **112.** Depts. of Ecology, Evolution, & Behavior and Plant Biology, University of Minnesota, 1479 Gortner Ave, St. Paul, MN 55108 USA; **113.** International Institute of Information Technology, Gachibowli, Hyderabad, Telangana 500032, India; **114.** Sigur Nature Trust, Chadapatti, Masinagudi PO Nilgiris, TN 643223, India; **115.** Bureau Waardenburg bv, P.O. Box 365, 4100 AJ, Culemborg, The Netherlands; **116.** Universidade Estadual de Santa Cruz, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Ilhéus, Bahia, Brazil; **117.** Laboratório de Restinga e Floresta Atlântica, Universidade Federal do Espírito Santo, São Mateus, ES, Brazil; **118.** Tropical Biodiversity Section, MUSE – Museo delle Scienze, Trento, Italy; **119.** Cibodas Botanic Gardens, Indonesian Institute of Sciences (LIPI), Cipanas, Cianjur, West Java 43253, Indonesia; **120.** Department of Geography and Geology, University of Turku, Turku, 20014 Turun yliopisto, Finland; **121.** School of Environmental and Natural Resource Sciences, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, 43600 UKM Bangi, Selangor, Malaysia; **122.** Instituto Federal de Educação, Ciência e Tecnologia do Espírito Santo - Campus Santa Teresa, Rodovia ES 080, Km 93, São João de Petrópolis - Santa Teresa – ES, Brazil; **123.** Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland; **124.** Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, Brazil 58051-900; **125.** Remote Sensing Department (DSR), National Institute for Space Research (INPE), Av. dos Astronautas, 1.758, Jd. da Granja, São José dos Campos, São Paulo, 12227-010, Brazil; **126.** Institute of Biodiversity, Animal Health & Comparative Medicine, University of Glasgow, UK; **127.** Center for Development Research (ZEF), University of Bonn, Germany; **128.** H.J. Andrews Experimental Forest, PO Box 300, Blue River, Oregon OR 97413, USA; **129.** Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Box 5003, 1432 Ås, Norway; **130.** Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, Brazil; **131.** WWF Thailand, 92/2 Phaholyothin Road, Bangkok, Thailand 10400; **132.** Missouri Botanical Garden, Africa & Madagascar Department, 4344 Shaw Blvd, St. Louis, MO 63110; USA; **133.** Federal University of Technology - Paraná, Marcílio Dias Street, 635, Zip Code: 86812-460, Apucarana, PR, Brazil; **134.** Biodiversity Parks Programme, Centre for Environmental Management of Degraded Ecosystems (CEMDE), University of Delhi, Delhi – 110007, India; **135.** Universidade Federal de Pernambuco, Departamento de Botânica, Recife, Brazil; **136.** , Key Laboratory of Tropical Plant Resources and Sustainable Use, CAS, Xishuangabanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun Town, Mengla County, Yunnan Province, P. R. China 666303; **137.** Dept Plant Sciences, University of Cambridge CB2 3EA, UK; **138.** Department of Food and Ressource Economics, University of Copenhagen, Denmark; **139.** Department of Biological Sciences, Washington State University, Vancvouver, Washington, USA; **140.** Herbarium, Royal Botanic Gardens Kew, Richmond, Surrey TW9 3AB, UK; **141.** Remote Sensing Department (DSR), National Institute for Space Research (INPE), Av. dos Astronautas, 1.758, Jd. da Granja, São José dos Campos, São Paulo, 12227-010, Brazil; **142.** Netherlands Food and Consumer Product Safety, Authority, National Reference Centre (NRC), P.O. Box 9102 6700HC Wageningen, The Netherlands; **143.** Research Institute for Sustainable Humanosphere, Kyoto University, Uji, Kyoto, Japan; **144.** Science Technology & International Cooperation Department, Vietnam National University of

Forestry, Hanoi, Vietnam; **145.** Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA; **146.** Department of Geography, University of Bergen, PB 7802, N-5020 Bergen, Norway; **147.** Department of Forestry & Wood Technology, The Federal University of Technology, P.M.B. 704, Akure, Nigeria; **148.** UNICAMP, Cidade Universitária Zeferino Vaz - Barão Geraldo, Campinas - SP, 13083-970, Brazil; **149.** Arnold Arboretum, Harvard University, 125 Arborway, Boston, MA 02130, USA; **150.** Department of Biological Sciences, National University of Singapore, 14 Science Drive 4. Singapore 117543, Singapore; **151.** Brown University, 34 Olive Street, Box G-B225, Providence, RI, 02912, USA; **152.** School of Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom street L33AF, Liverpool, UK; **153.** Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Sciencepark 904, Amsterdam 1098, The Netherlands; **154.** Instituto Politécnico Nacional, CIIDIR-Unidad Oaxaca, Santa Cruz Xoxocotlán, CP 71230, Oaxaca, México; **155.** Institute of Floodplain Ecology, Dep. of Geography and Geoecology, Karlsruhe Institute of Technology – KITF, Josefstr.1, D-76437 Rastatt, Germany; **156.** College of Agriculture and Forestry, Hainan University, Hainan Province, China; **157.** U.F.R. Biosciences, Université Félix Houphouet-Boigny, 22 B.P. 1682, Abidjan 22, Ivory Coast; **158.** Far Eastern University, Nicanor Reyes Sr. St., Sampaloc, Manila, Sampaloc, Philippines; **159.** Department of Biology, American University of Beirut, Riad El-Solh, Beirut 1107 2020, Lebanon; **160.** Chair of Nature Conservation and Landscape Ecology, University of Freiburg, Germany; **161.** Tropical Forests and People Research Centre, University of the Sunshine Coast, QLD 4556, Australia.

CORRESPONDING AUTHOR: Janet Franklin, Department of Botany and Plant Sciences, University of California – Riverside, 900 University Ave, Riverside CA 92521. Telephone: 951-827-7020; Email: janet.franklin@ucr.edu

KEYWORDS: Biogeography, Biogeographic legacies, Forest classification, Forest functional similarity, Pan-tropical, Phylogenetic community distance.

Knowledge about the biogeographic affinities of the world's tropical forests helps to better understand regional differences in forest structure, diversity, composition and dynamics. Such understanding will enable anticipation of region specific responses to global environmental change. Modern phylogenies, in combination with broad coverage of species inventory data, now allow for global biogeographic analyses that take species evolutionary distance into account. Here we present the first classification of the world's tropical forests based on their phylogenetic similarity. We identify five principal floristic regions and their floristic relationships: (1) Indo-Pacific, (2) Subtropical, (3) African, (4) American, and (5) Dry forests. Our results do not support the traditional Neo- versus Palaeo-tropical forest division, but instead separate the combined American and African forests from their Indo-Pacific counterparts. We also find indications for the existence of a global dry forest region, with representatives in America, Africa, Madagascar and India. Additionally, a northern hemisphere Subtropical forest region was identified with representatives in Asia and America, providing support for a link between Asian and American northern hemisphere forests.

Significance

Identifying and explaining regional differences in tropical forest dynamics, structure, diversity and composition is critical for anticipating region specific responses to global environmental change. Floristic classifications are of fundamental importance for these efforts. Here we provide the first global tropical forest classification that is explicitly based on community evolutionary similarity, resulting in the identification of five major tropical forest regions and their relationships: (1) Indo-Pacific, (2) Subtropical, (3) African, (4) American, and (5) Dry forests. African and American forests are grouped, reflecting their former western Gondwanan connection, while Indo-Pacific forests range from eastern Africa and Madagascar to Australia and Pacific. The connection between northern hemisphere Asian and American forests is confirmed, while dry forests are identified as a single tropical biome.

\body

The biogeographic origin of species, in combination with dispersal limitation and environmental filtering, are the principal determinants of spatial variation in the species composition of tropical forests (1, 2). Despite evidence of long-distance dispersal (1, 3, 4, 5), tropical forests maintain conspicuous regional differences in species composition. For example, only ~4% of tropical tree species are shared among Africa, America and Asia (6). The lack of species overlap between continents makes global inference of relationships among tropical forests problematic because such classifications depend on comparison of amount of shared species. Therefore, pan-tropical biogeographic analyses have been based on comparison of compositional patterns at higher taxonomic levels, i.e. genus or family (6, 7, 8). However, such analyses treat taxa as independent units, while in reality taxa vary in their degree of phylogenetic relatedness and as a consequence their morphological and ecological similarity (1, 2). Taking phylogenetic relatedness in consideration enhances our ability to delimit phytogeographical boundaries that characterize functional and biogeographic affinities among forest regions (1, 2, 9, 10). Here we include phylogenetic relationships in a floristic analysis to provide such insight.

We compiled a standardized dataset of old-growth tropical forest inventories of angiosperm trees (trunk diameter ≥ 10 cm) for 406 1° latitude/longitude grid cells (hereafter referred to as locations) originally dominated by natural forests across the (sub-)tropics **(Table S1)**. These locations represented all major tropical forest regions and had broad environmental amplitude, including low to high elevations and dry to wet forests **(Fig. 1, Fig. S1)**. To determine the phylogenetic distance between locations we constructed a dated phylogenetic tree that was resolved to genus level and contained all taxa used for our classification analyses **(File S1)**. Location pair-wise phylogenetic distance matrices were constructed using 20 randomly drawn tree taxa per location. We used 20 taxa as this maximized the number of locations that could be included in the classification analyses while still providing a reliable classification result. In total, we generated 20 phylogenetic distance matrices, each with a different set of 20 randomly drawn taxa per location, which served as input for 20 cluster analyses **(Fig. S2)**. The final classification of each location depended on the frequency with which it was classified in a particular cluster across all 20 cluster analyses **(Fig. S3)**. Relationships between the clusters were represented by a majority rule consensus tree **(Fig. 1)**.

Results & Discussion

Mean pairwise phylogenetic distance analysis, which emphasizes ancient lineages in phylogenetic community comparisons, detected almost no spatial patterns in community phylogenetic similarity across the tropics, indicating that all tropical forest locations consist of more or less the same set of ancient plant lineages. This is in accordance with recent findings that the whole present day tropics are dominated by similar high levels of Late-Cretaceous aged phylogenetic lineages (11). Only when we used mean nearest taxon distance, which emphasizes recent lineages in phylogenetic community comparisons, did we detect clear spatial patterns across the tropics. Therefore, current day biogeographic patterns in the tropics seem to mainly reflect Cenozoic speciation events when Gondwanan breakup was already well on its way.

Using the mean nearest taxon distance, our phylogenetic cluster analyses showed that the world's tropical forests are divided into two major floristic regions: a combined American-African versus Indo-Pacific region **(Fig. 1)**. This division contradicts previous hypotheses about major global realms, which either recognized Neo- versus Palaeo-tropical regions or several separate continental regions (4, 12, 13, 14). However, Gentry (7) already noted the high generic level similarity of tropical American and African forests. He attributed this to Cretaceous and Cenozoic plate tectonic history (4, 15). Subsequent studies have shown that despite the severing of direct land connections between the African and South American plates ca. 96 Mya, long distance dispersal continued throughout the Late Cretaceous and Early Tertiary across the widening Atlantic Ocean (4, 5). The combined effect of shared origin with trans-Atlantic migration may explain the detected connection between South American and African forests.

Within the American-African cluster, the first split separated the African from the American regions **(Fig. 1)**, suggestive of the west Gondwanan breakup associated with the formation of the Atlantic Ocean and the, over time, increasing difficulty for plants to disperse across the Atlantic (1, 15). Interestingly, the African region showed the highest consistency in clustering of all five identified floristic regions. On average, locations belonging to the African region were assigned to this cluster in 91.4% of cases, versus consistency values of 79.5%, 63.7%, 79.5% and 70.3% for the Indo-Pacific, Subtropical, American and Dry forest regions, respectively. This clustering consistency indicates high floristic similarity across tropical Africa, which is in accord with the relatively low beta diversity observed for these forests (6). Postulated repeated cycles of contraction and expansion of the tropical African forests from a few small forest refugia in combination with large scale species shifts during the Pleistocene glaciations may explain the relatively high compositional homogeneity of the forests within the African region (16, 17).

The tropical American forests were further divided into moist and dry forests **(Fig. 1; Fig S1)**, indicating that this division is primarily environmental (18). The American floristic region comprises humid forests, including the lowland forests of Central America, the Amazon basin, the Guianas, and the northern half of the Atlantic Forest. The Dry forest region encompasses the Caatinga and Cerrado regions as well as other dry forests throughout the Americas, but interestingly, and contrary to the non-phylogenetic pan-tropical analysis by Dexter et al. (8), also includes dry forests of Africa, Madagascar and India. Further research is needed to confirm whether this indicates the existence of a global dry forest region with a shared biogeographic origin, or whether selection for drought- and fire-resistance has favored the dominance of similar plant lineages in tropical dry forests around the world (8, 18, 19).

The Indo-Pacific floristic region occupies the humid areas of Eastern Africa, Madagascar, India, Southeast Asia, Australia and the Pacific islands **(Fig. 1)**. With the exception of SE Asia which is of Laurasian origin, this floristic region combines all areas that once comprised eastern Gondwana (4, 15). Given the diverse geologic history of Asia and the Indo-Pacific (20), it is surprising to find a similar forest type covering most of the region. Nevertheless, there is strong evidence of significant plant migration within this region that likely had a homogenizing effect, notably the biotic exchange between India and Southeast Asia starting from ca. 45 Mya (21), and between Southeast Asia and Australia, New Guinea and the Pacific islands that commenced ca. 15 Mya (4). Presence of Indo-Pacific forests in eastern continental Africa may either reflect eastern Gondwanan origin, or dispersal within the Indo-Pacific region.

We also identified a group of locations in Asia and America that occupies cooler climates and higher elevations relative to the other identified forest clusters **(Fig 1; Fig. S1)**, and which we therefore termed Subtropical region. This Subtropical floristic region confirms the floristic link between Asia and North America, reflecting a shared Boreotropical affinity (22). Within Asia, the Subtropical region is mostly restricted to the subtropics, with the exception of high elevation forests of Java. In the Americas, by contrast, this floristic region extends from the subtropics deep into the tropics, probably because the cooler montane climate of the Central American highlands and South American Andes has facilitated the southward migration of cold-adapted plant lineages. The absence of continuous, North-South oriented mountain chains in Asia may have limited the dispersal of such lineages into lower latitudes.

Conclusion

We provide the first phylogenetic distance based biogeographic classification of the world's tropical forests, using the most extensive sampling scheme for the tropics currently in existence. Our results uncover novel floristic patterns which will help in the development of region specific models for forest structure, diversity and dynamics as well as possible responses of tropical forest regions to global environmental change. Our results may necessitate reconsideration of established biogeographic ideas. For example, Madagascar and New Guinea have often been considered two separate major tropical regions, ecologically and biogeographically distinct from tropical America, Africa and Southeast Asia (23, 24). However, despite their highly endemic species compositions, we show that they are both part of the widespread Indo-Pacific floristic region. Finally, our analysis can serve as a model for classifying regional floras.

Materials & Methods

Tree inventory data set

Individual angiosperm trees (diameter at breast height ≥ 10 cm) from old-growth forest inventories throughout the (sub-)tropics (between -35°S and 35°N latitudes) were pooled within their respective one degree latitude/longitude grid cells (henceforth called locations). These locations represented all major tropical forest regions and had broad environmental amplitude, including low to high elevations and dry to wet forests **(Fig. S1)**. Monocots and Cactaceae were excluded because these were not consistently surveyed in all data sets. This dataset originally included 439 locations, containing 925,009 individual trees belonging to 15,012 taxa. Species names were standardized using 'The Plant List' (www.theplantlist.org), 'Taxonomic Name Resolution Service' (trns.iplantcollaborative.org/TNRSapp.html) and 'The Asian Plant Synonym Lookup' (phylodiversity.net/fslik/synonym_lookup.htm). On average, 1.4% of individual stems per location remained unidentified. These unidentified individuals were excluded from further analyses.

Community phylogenetic tree

The APG-III classification (25) served as the family-level backbone of our community phylogenetic tree. Recent updates in APG-IV (26) are mostly of nomenclatural nature and did not affect our analyses. This tree was further resolved up to genus level using the species level phylogeny (32,223 species included) published by Zanne et al. (27), which covered most genera in our dataset **(File S1)**. Genera present in our dataset, but not in Zanne et al. (27), were placed at the base of their respective families. Genera that had disjunct species occurrences in the phylogeny of Zanne et al. (27) were placed at the most basal node connecting the disjunct species. This phylogeny was subsequently dated using the BLADJ function in PHYLOCOM v4.2 (28), using taxon ages given in Magallon et al. (29) for the age file.

Phylogenetic distance analysis

Phylogenetic distance between all pairs of locations was calculated using the options COMDIST and COMDISTNT in PHYLOCOM v4.2 (28). COMDIST uses the mean pairwise phylogenetic distance (MPPD); for each taxon in a location, it finds the average phylogenetic distance to all taxa in the other location, and calculates the mean. COMDISTNT uses the mean nearest taxon distance (MNTD); for each taxon in location 1, it finds the nearest phylogenetic neighbor in location 2, records this and calculates the mean. Both functions return a symmetrical matrix of locations versus locations with their pairwise phylogenetic distances. Principal Coordinate (PCO) analyses (in Multi Variate Statistical Package v3.13, Kovach Computing Services) on resulting location versus location matrices showed that the MPPD matrices had almost no explanatory power (generally the first five PCO axes explained less than 5% of data variance), meaning that detected patterns were mostly random. The MNTD matrices, however, explained considerable amounts of data variance in the first five axes of the PCO. Therefore, we used only MNTD for further analysis.

Correcting for taxon richness bias in MNTD

Taxon richness differed considerably between locations, varying between 4 and 1466. MNTD may be sensitive to such differences in taxon richness because the chance of finding a close relative between two locations may increase when their taxon richness increases. Applying MNTD to determine phylogenetic distance between locations with differing taxon numbers could therefore result in taxon-rich locations being grouped together in the cluster analysis simply because they are more taxon-rich. To determine the impact of this effect, we created five 'location by taxon' matrices, each with a lower number of taxa per location (320, 160, 80, 40, and 20 taxa per location, respectively), using the 41 locations containing more than 320 taxa. For each location, taxa were ranked according to abundance, so that the 'location by taxon' matrix based on, for example, 320 taxa consisted only of the 320 most abundant taxa per location. Where tied abundances exceeded the predefined number of taxa, we randomly selected the appropriate number of taxa from among those with tied minimum abundance. We then calculated the MNTD matrices for each of these five 'location by taxon' matrices and found that with increasing taxon richness of locations, MNTD (as averaged over all locations) decreased with increasing taxon richness per location following a power function ($y = 310.4x-0.194$ **[Fig. S4]**), demonstrating that MNTD is indeed sensitive to taxon richness.

Determining the optimal number of taxa per location for further analysis

To avoid taxon richness bias when using MNTD, locations had to be compared based on similar numbers of taxa. Minimum variance clustering, based on the five 'location by taxon' matrices described earlier, consistently recovered the same major clusters in the same configuration (African and American locations clustered on one main branch and Asian locations clustered on the other), although the relationships between locations within these main clusters could vary **(Fig. S5)**. Only in the 20 taxon analysis, was one American location (location no. 165 from the Brazilian Atlantic Forest) placed in the Asian cluster. The amount of variance captured in the first five axes of a Principal Coordinate (PCO) analysis (using the same MNTD distance matrices) declined by only ~20%, from 83.3% to 60.7%, between the 320 and 20 taxa analysis, respectively. We decided to use 20 taxa per location in the final analyses **(Table S1)** because of this limited loss of information in the PCO and similarity of cluster results. In addition, we were able to use most of our locations (406 of the initial 439), including locations on remote islands and extreme habitats that would have been excluded if we had set the minimum number of taxa too high.

Forest classification analyses

For the final analyses we produced 20 location by taxon data sets. In these data sets, each location was represented by 20 randomly drawn taxa (from that location). Random draws were irrespective of taxon abundance as abundance is a spatially and temporally labile taxon trait that likely reflects contemporary environmental conditions rather than historical biogeographic signal. For each of these 20 location by taxon data sets we calculated the corresponding symmetrical location by location matrices with their pairwise phylogenetic distances (MNTD). These matrices were then used as input for cluster analyses.

Locations were grouped in clusters using the Ward's minimum variance method (30), using Multi Variate Statistical Package v. 3.13. This is a centroid-based clustering technique that identifies cluster centers (centroids) by minimizing the overall squared distances of the objects (in this case locations) to the centroids at each cluster level. This clustering technique identified spatially clearly defined location groupings **(Fig. S2)**. The optimal number of clusters for defining floristic regions across the tropics was determined by calculating the cophenetic correlation coefficient at each cluster level, starting at the first split (K2) in the dendrogram. The cophenetic correlation coefficient calculates the correlation between the distance of the clusters as calculated by the clustering algorithm and the distance based on observed MNTD values between clusters. The higher the cophenetic correlation, the better the cluster result reflects the patterns present in the original distance matrix. We applied this method to each of our 20 data sets, calculated the average cophenetic correlation coefficient for each cluster level, and found a steep increase in cophenetic correlation up to K5, after which it slowly declined **(Fig. S6)**. Therefore we chose K5 as the optimum level for defining our main floristic regions across the tropics.

For each location, at cluster level K5, we determined the cluster in which it was classified for each of the 20 cluster analyses that we performed. The location was then assigned to the cluster in which it had the highest proportion of observations. A 'Single Proportion Test' (31), which calculates the probability of an observed (sample) proportion (in the range 0-1) against a hypothetical proportion, was then used to determine if the observed proportions were significantly higher than expected by random (Paleontological Statistics [PAST] v3.08). For example, for K5, the expected random proportion of locations per cluster is 0.2. For a sample size of 20, a proportion has to be at least 0.38 to be significantly higher ($p < 0.05$) than the random expectation. The resulting classification success rates of locations for K5 are shown in **Figure S3 and Table S1**. The final classification (K5) of the clusters was based on the majority consensus rule (**Fig. 1**).

ACKNOWLEDGEMENTS This study benefited greatly from data contributed by Patricia Alvarez-Loayza, Ana Andrade, Peter Ashton, Julian Bayliss, Luis Bernacci, Lilian Blanc, J. Bogaert, Matt Bradford, Mireille Breuer Ndoundou Hockemba, C. De Cannière, Miguel Castillo, Eduardo Catharino, Connie Clark, David Clark, Deborah Clark, Gilles Dauby, Jean-Louis Doucet, Pedro Eisenlohr, Leandro Ferreira, Christine Fletcher, Geraldo Franco, Gabriella Frederikson, Satish Chandra Garkoti, Girirai, Nimal Gunatilleke, Terese Hart, Miriam van Heist, Zhila Hemati, M. A. Hernández-Ruedas, David Kenfack, Kanehiro Kitayama, Eileen Larney, Ieda Leao do Amaral, Jean-Remy Makana, Punchi Manage Saranga Amila Ruwan, Antti Marjokorpi, Olga Martha Montiel, Miguel Martínez-Ramos, Henrik Meilby, Jerome Millet, Cao Min, Kazuki Miyamoto, Xiaoxue Mo, Juan Carlos Montero, Badru Mugerwa, Pantaleo Munishi, Helen Murphy, Hidetoshi Nagamasu, David Newbery, Rueben Nilus, Meyner Nusalawo, Susana Ochoa-Gaona, Atila Oliveira, Navendu Page, Andrea Permana, Nigel Pitman, Jean Razafimahaimodison, Rocío Rojas, Hugo Romero, Rozainah M.Z., Fernanda Santos, Manichanh Satdichanh, Lars Schmidt, Lila Nath Sharma, Kade Sidiyasa, Eduardo da Silva Pinheiro, Plinio Sist, Peguy Tchouto, Johanna Urtado, Renato Valencia, Luis Valenzuela, Rodolfo Vasquez, Thorsten Wiegand, Guadelupe Williams-Linera, Hansjoerg Woll, Tsuyoshi Yoneda, and Nicole Zweifel. We also acknowledge contributed financial support from European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 660020, Instituto Bem Ambiental

(IBAM), Myr Projetos Sustentáveis, IEF and CNPq, CAPES FAPEMIG, German Research Foundation (DFG, grants CRC 552, CU127/3-1, HO 3296/2-2, HO3296/4-1 and RU 816), UNAM-PAPIIT IN218416 and Semarnat-CONACYT 128136, Conselho Nacional de Desenvolvimento Científico e Tecnoloógico (CNPq, Brazil), Fundação Grupo Boticário de Proteção à Natureza /Brazil. PAPIIT-DGAPA-UNAM (project IN-204215), National Geographic Society, National Foundation For Scientific and Technology Development Vietnam (grant number 106.11-2010.68), and Core funding for Crown Research Institutes from the New Zealand Ministry of Business, Innovation and Employment's Science and Innovation Group. Some data in this publication were provided by the Tropical Ecology Assessment and Monitoring (TEAM) Network, a collaboration between Conservation International, the Missouri Botanical Garden, the Smithsonian Institution, and the Wildlife Conservation Society, and partially funded by these institutions, the Gordon and Betty Moore Foundation, and other donors.

REFERENCES

1. Cavender-Bares J, Ackerly DD, Hobbie SE, Townsend PA (2016) Evolutionary legacy effects on ecosystems: biogeographic origins, plant traits, and implications for management in the era of global change. *Annu. Rev. Ecol. Evol. Syst.* 47: 433–462.

2. Donoghue MJ (2008) A phylogenetic perspective on the distribution of plant diversity. *Proc. Natl. Acad. Sci. U. S. A.* 105(S1): 11549-11555.

3. Weigelt P et al. (2015) Global patterns and drivers of phylogenetic structure in island floras. *Sci. Rep.* 5: 12213.

4. Morley RJ (2003) Interplate dispersal paths for megathermal angiosperms. *Perspect. Plant Ecol. Evol. Syst.* 6: 5-20.

5. Pennington RT, Dick CW (2004) The role of immigrants in the assembly of the South American rainforest tree flora. *Phil. Trans. R. Soc. Lond. B* 359: 1611–1622.

6. Slik JWF et al. (2015) An estimate of the number of tropical tree species. *Proc. Natl. Acad. Sci. U. S. A.* 112: 7472-7477.

7. Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Mo. Bot. Gard.* 75: 1-34.

8. Dexter KG et al. (2015) Floristics and biogeography of vegetation in seasonally dry tropical regions. *Int. For. Rev.* 17: 10-22.

9. Holt BG et al. (2013) An update of Wallace's zoographic regions of the world. *Science* 339: 74-78.

10. Webb CO et al. (2002) Phylogenies and community ecology. *Ann. Rev. Ecol. Syst.* 33: 475-505.

11. Proches S et al. (2015) Global hotspots in the present-day distribution of ancient animal and plant lineages. *Sci. Rep.* 5: 15457.

12. Takhtajan AL (1986) *The floristic regions of the world.* (UC Press, Berkeley) pp 1-401.

13. Chang HT (1994) An outline on the regionalisation of the global flora. *Acta Sci. Nat. Univ. Sunyatseni* 33: 73-80.

14. Cox CB (2001) The biogeographic regions reconsidered. *J. Biogeogr.* 28: 511-523.

15. McLoughlin S (2001) The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Aust. J. Bot.* 49: 271-300.

16. McClean CJ et al. (2005) African plant diversity and climate change. *Ann. Mo. Bot. Gard.* 92: 139-152.

17. Anhuf D et al. (2006) Paleo-environmental change in Amazonian and African rainforest during the LGM. *Palaeogeogr. Palaeocl.* 239: 510–527.

18. DRYFLOR: Banda-RK et al. (2016) Plant diversity patterns in neotropical dry forests and their conservation implications. *Science* 353: 1383-1387.

19. Ratnam J et al. (2016) Savannahs of Asia: antiquity, biogeography, and an uncertain future. *Phil. Trans. R. Soc. Lond. B* 371: 20150305.

20. Hall R (2001) Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. *Faunal and floral migrations and evolution in SE Asia-Australasia,* eds Metcalfe I, Smith JMB, Morwood M, Davidson ID (Swets & Zeitlinger Publishers, Lisse) pp 35-56.

21. Klaus S et al. (2016) Biotic interchange between the Indian subcontinent and mainland Asia through time. *Nat. Commun.* 7: 12132.

22. Qian H et al. (2017) Phylogenetic diversity anomaly in angiosperms between eastern Asia and eastern North America. *Proc. Natl. Acad. Sci. U. S. A.* 114: 11452–11457.

23. Primack RB, Corlett RT (2005) *Tropical rainforests: an ecological and biogeographical comparison.* (Wiley-Blackwell, Hoboken, NJ).

24. Corlett RT, Primack RB (2006) Tropical rainforests and the need for cross-continental comparisons. *Trends Ecol. Evol.* 21: 105–110.

25. APG-III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161: 105-121.

26. APG-IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181: 1-20.

27. Zanne AE et al. (2014) Three keys to the radiation of angiosperms into freezing environments. *Nature* 506: 89-92.

28. Webb CO et al. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24: 2098-2100.

29. Magallon S et al. (2015) A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytol.* 207: 437-453.

30. Ward JH Jr (1963) Hierarchical grouping to optimize an objective function. *JASA* 58: 236–244 (1963).

31. Clopper C, Pearson ES (1934) The use of confidence or fiducial limits illustrated in the case of the binomial. *Biometrika* 26: 404–413.

32. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25: 1965-1978.

FIGURE LEGENDS

Figure 1. Classification maps of the world's tropical forests, showing from two (a) to five (d) clusters. Cluster result represents a majority rule consensus tree, with percentage of times that each grouping was observed in the 20 separate cluster analyses shown in (d). Only locations that could be classified with certainty ($p < 0.05$) are shown ($n = 392$).

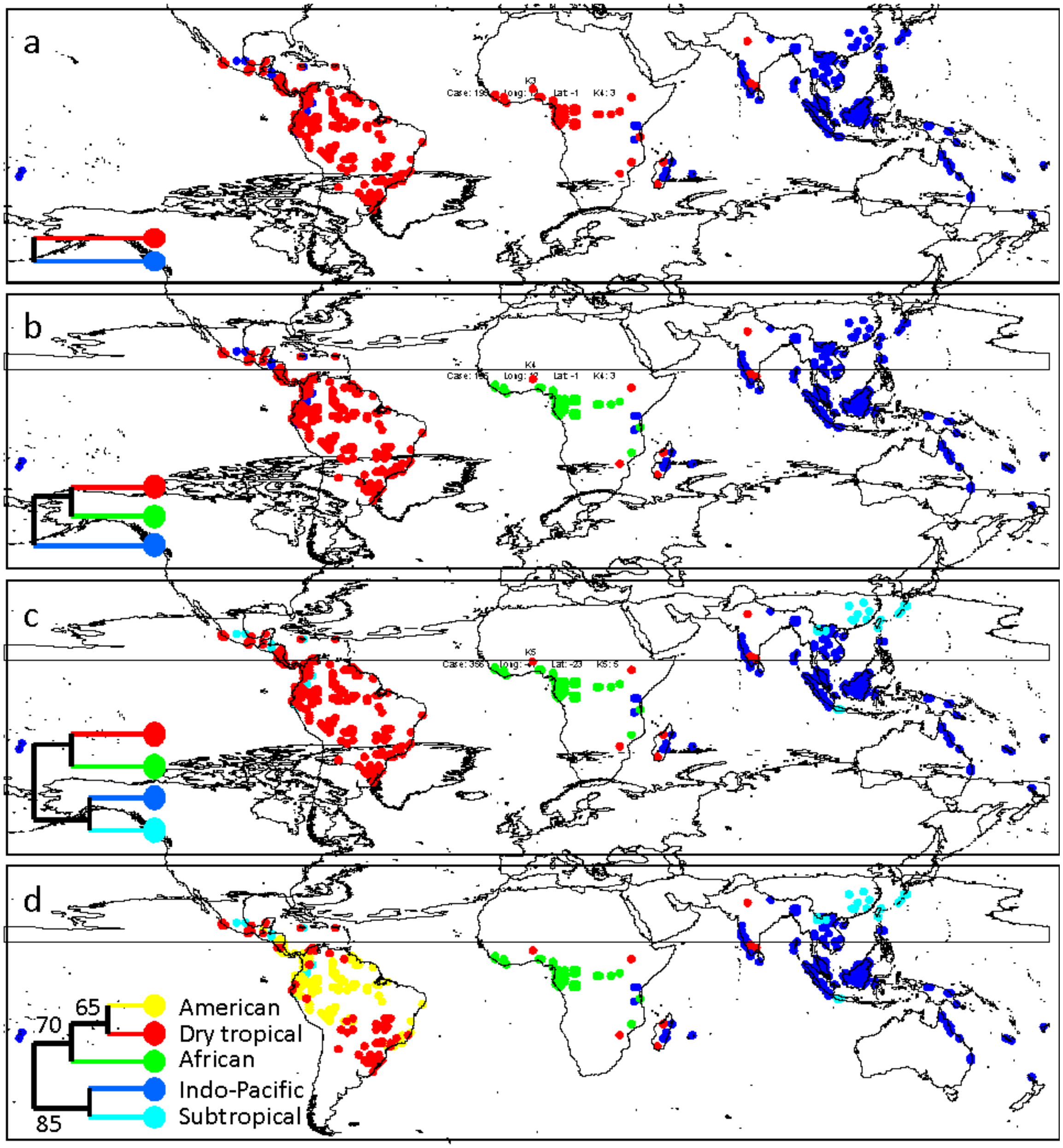

a
b
c
d
65
70
85
American
Dry tropical
African
Indo-Pacific
Subtropical

Figure 1

SUPPLEMENTARY INFORMATION

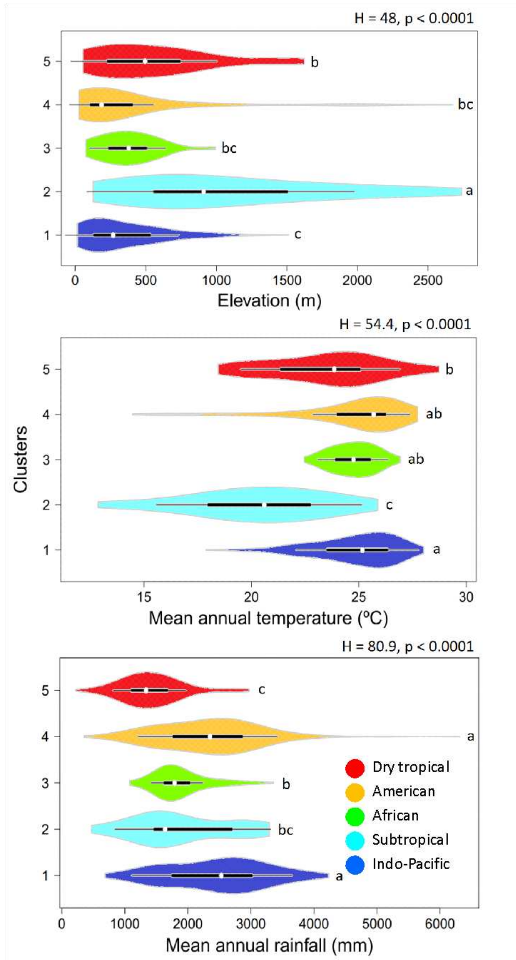
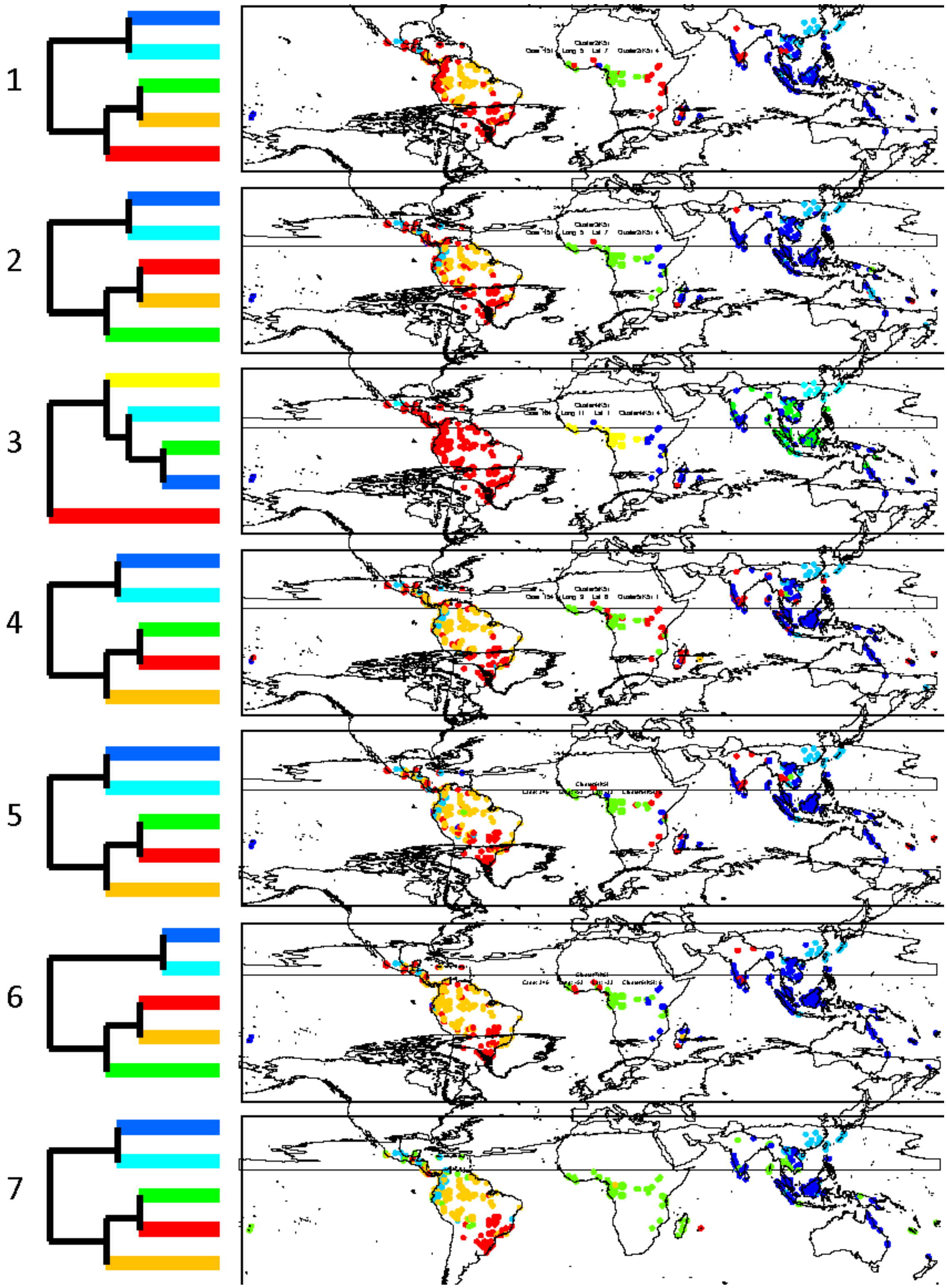
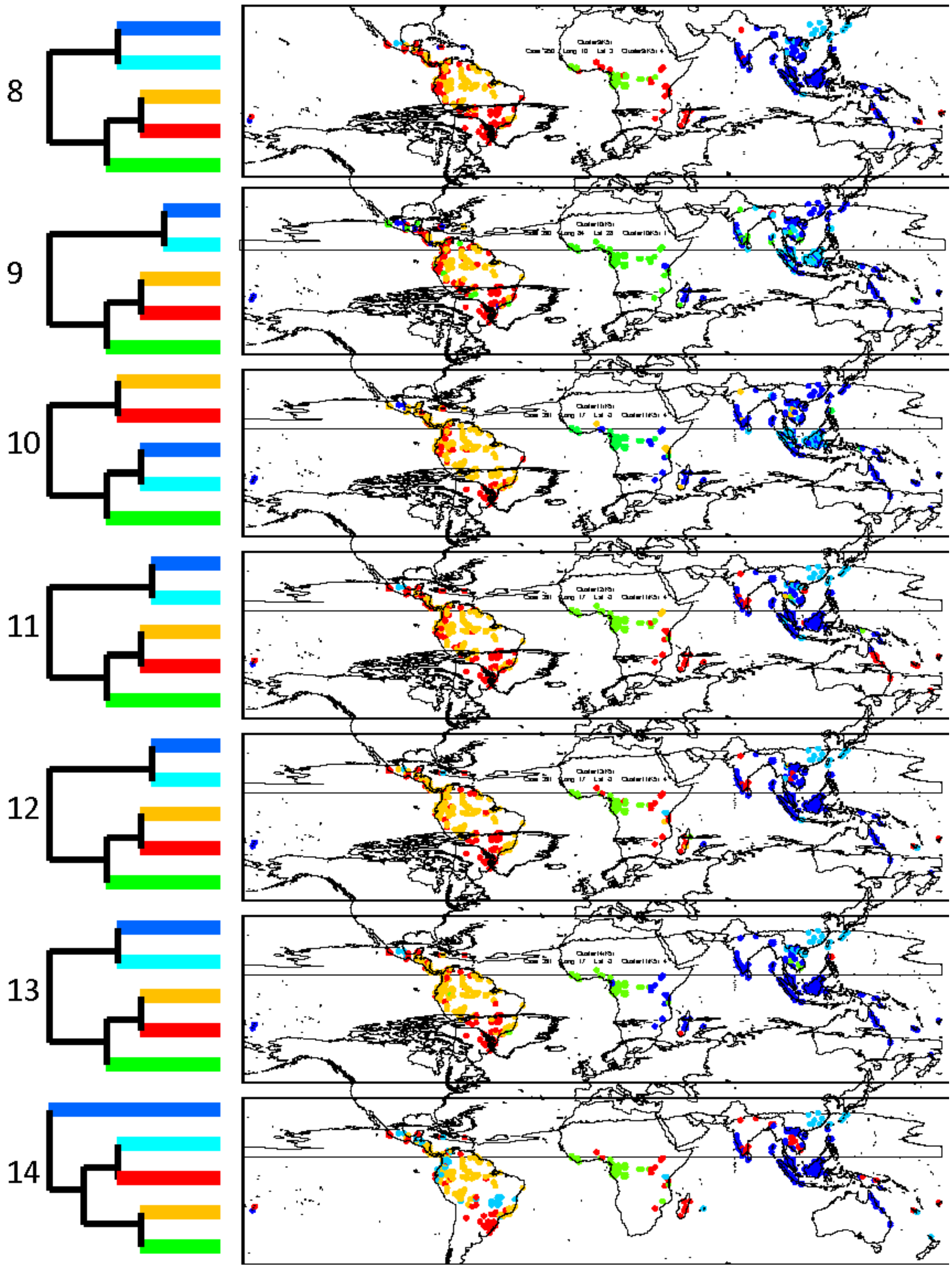


Figure S1. *Elevation and climatic variables (temperature and rainfall) of each of the five floristic clusters. Each violin plot indicates the probability density of the data at different values, the median (white dots), 1st and 3rd quartiles (black thick lines) and range. Climate data were taken from WorldClim (32). Overall differences between clusters were tested with Kruskal-Wallis (H) test. The differences between pairs of clusters were assessed with Mann-Whitney tests with Bonferroni corrected p values (indicated with different letters in each plot). Sample sizes: Indo-Pacific 138; Subtropical 34; African 46; American 105; Dry forest 69.*


1
2
3
4
5
6
7


8
9
10
11
12
13
14

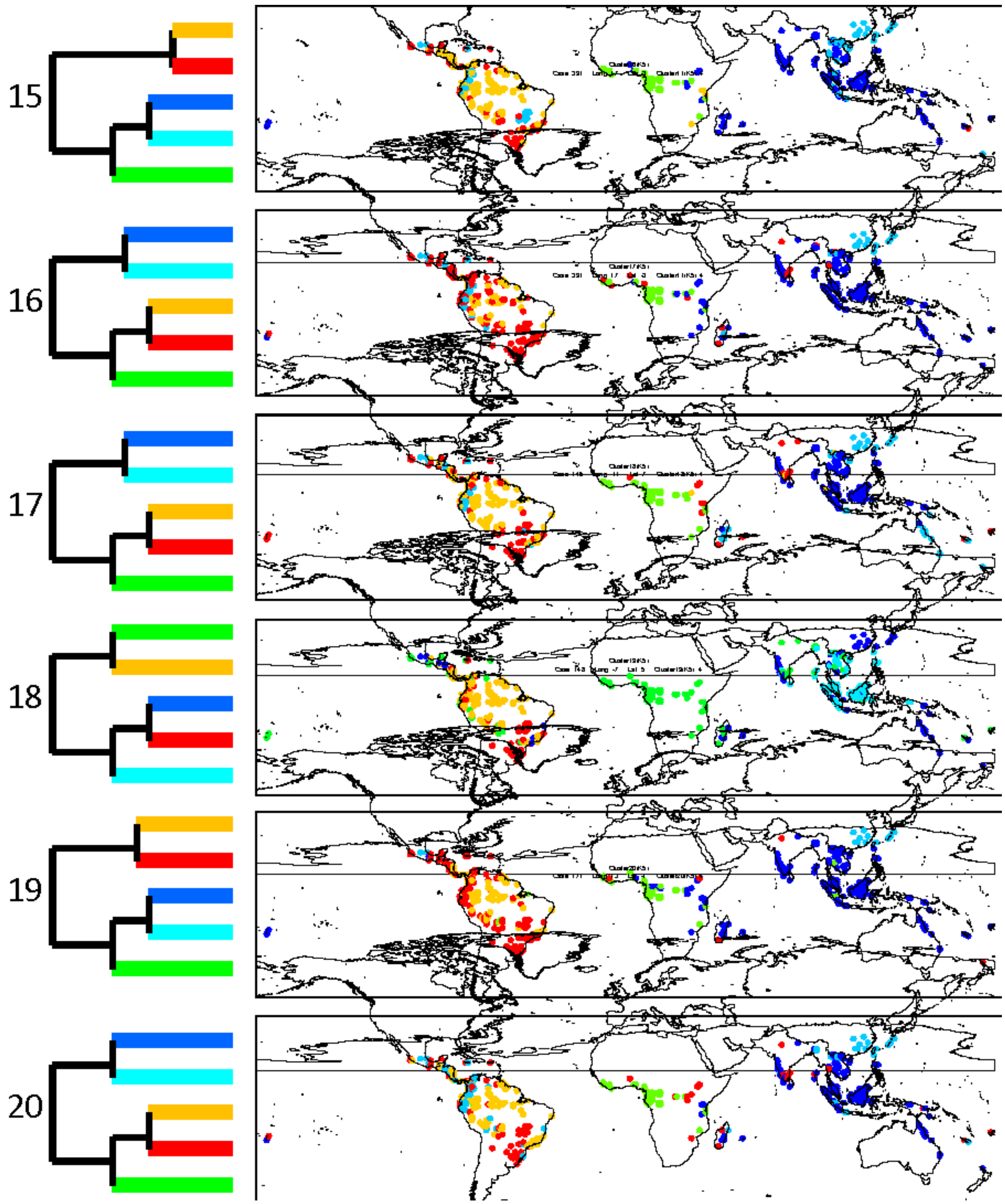


Figure S2. *Clustering results for the 20 datasets based on Mean Nearest Taxon Distance. Each data set is based on a random draw of 20 taxa for each location (n = 406).*

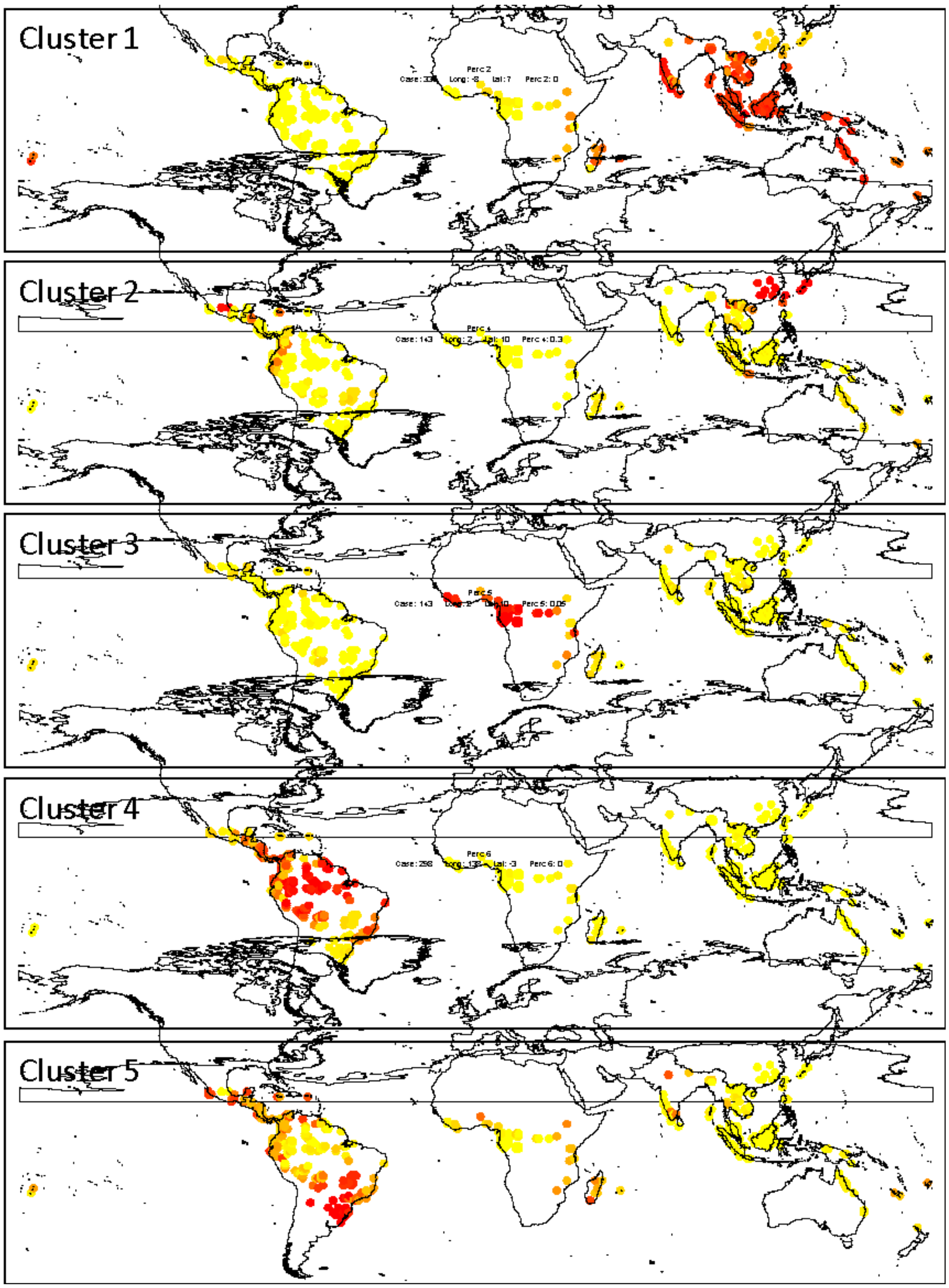


Figure S3. *The classification frequency of each location in one of the five identified clusters, based on the 20 classifications shown in Extended Data Figure 4. Colours range from yellow (zero) to red (one). Cluster numbers correspond to those indicated in Extended Data Table 1.*

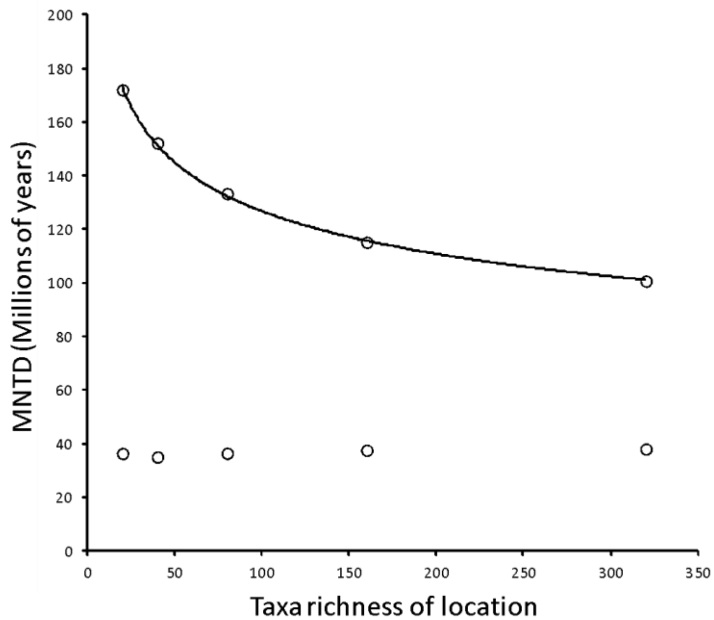


Figure S4. *Relationship between 'Mean Nearest Taxon Distance' (MNTD) and taxa richness of locations (black dots), based on 41 locations which had more than 320 taxa. With increasing taxa richness of locations, MNTD decreased following a power-function ($y = 310.4x^{-0.194}$). Standard deviation (white dots) was not influenced by taxa richness.*

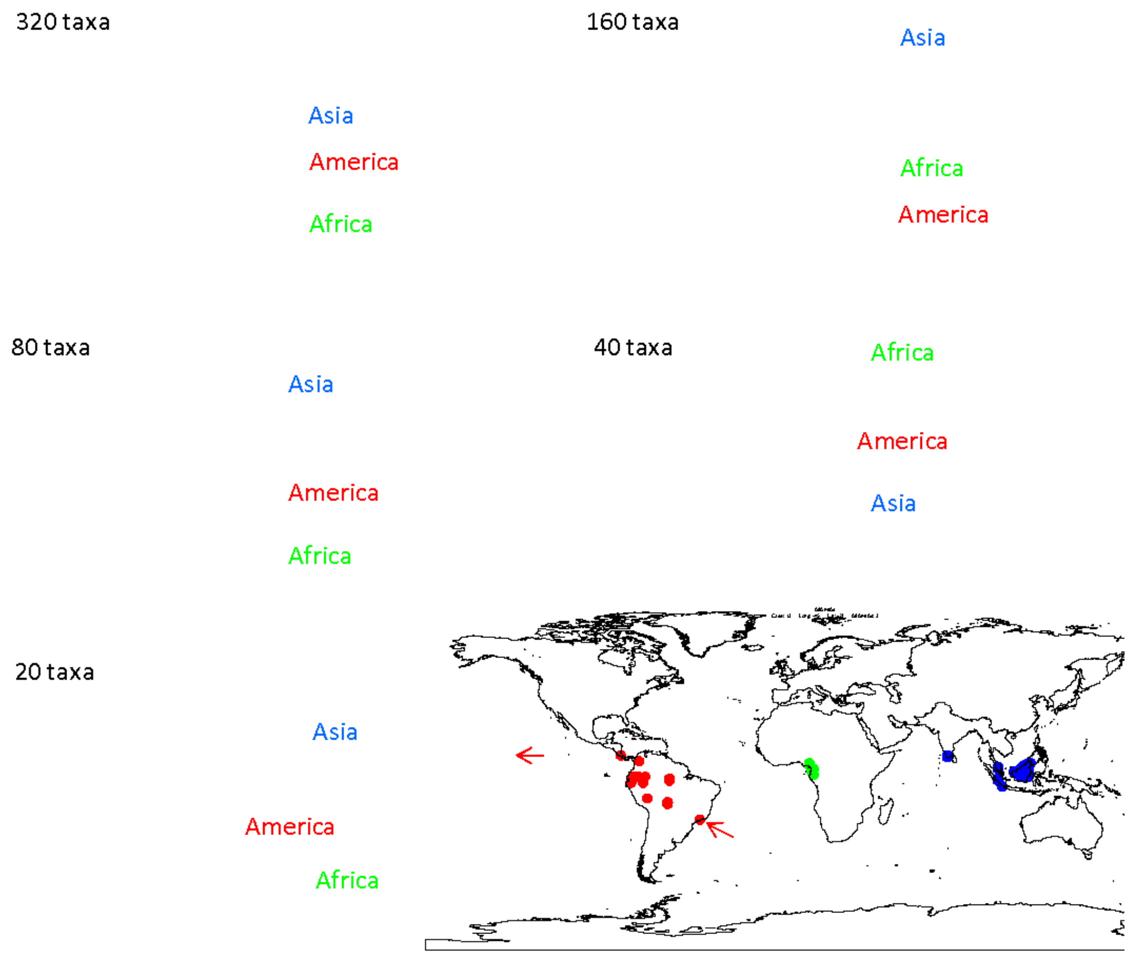


Figure S5. *Cluster results for 41 locations (indicated in lower right map) using decreasing numbers of taxa per location (320, 160, 80, 40 and 20 from top to bottom). All analyses recovered the same three main groups of locations in the same configuration (African and American versus Asian locations), although one American location (indicated with red arrow) was grouped with the Asian cluster in the 20 taxon analysis.*

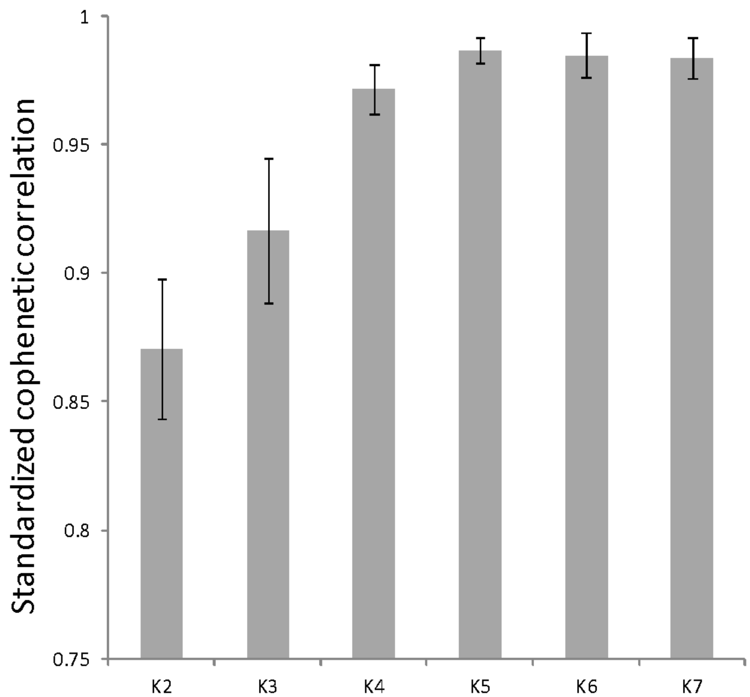


Figure S6. *Standardized cophenetic correlation coefficients for cluster levels K2 to K7 (mean with confidence interval of 20 cluster analyses). Cophenetic correlation coefficients show how well the distance data in the original data matrix fits the cluster dendrogram, i.e. the higher the value, the better the fit. Cophenetic correlation increased to cluster level 5 (K5).*

Table S1. *The 406 locations with 20 or more species that were used in this study (contributor abbreviations given at end of table). Cluster assignment is given along with cluster success (percentage of times that each location was assigned to the same cluster based on 20 cluster analyses, each time with a different random set of 20 species per location). Environmental conditions represent the average for each location (1 x 1 degree latitude/longitude grid cell).*

Location	Country	Long.	Lat.	Cluster assignment	Cluster assignment success (%)	Species (n)	Elev. (m)	Mean Temp. (°C)	Annual rain (mm)	Contributor
8	Mexico	-105	19	4	50	145	199	25.7	1015	JW; PB; FMA
9	Mexico	-105	20	4	50	163	733	23.1	1299	JW; AG; PB;FMA
12	Mexico	-97	20	2	60	22	781	21	1514	AG; GW
13	Mexico	-96	16	4	50	154	1004	22.1	982	JW
14	Mexico	-96	17	4	45	61	1307	19.3	1596	BB
15	Mexico	-96	18	4	40	82	213	24.8	2317	BB
16	Mexico	-95	19	4	65	127	201	24.7	2841	AG; FB; JVA; VAR
18	Mexico	-91	16	4	60	292	687	23.2	2983	MC; MMR; SOG; VAR
19	Mexico	-91	17	4	70	120	282	25.2	2175	JM; SOG
20	Honduras	-88	15	4	40	91	693	23	1684	DK
21	Honduras	-88	16	2	40	131	160	25.9	2083	DK
22	Costa Rica	-86	11	4	55	60	111	26	1685	JP
23	Nicaragua	-86	13	4	60	22	682	22.7	1431	AG
24	Costa Rica	-85	10	4	70	159	269	25.3	2323	AG; JH; JP

25	Costa Rica	-85	11	4	50	108	180	25.5	2290	AG; BB
26	Nicaragua	-85	12	4	65	36	195	25.2	1980	AG
27	Nicaragua	-85	14	4	75	93	329	24.7	2237	DG
28	Costa Rica	-84	9	4	75	84	447	24.2	3582	AG
29	Costa Rica	-84	10	4	65	521	978	21.2	3216	AG; BB; DC; SL; TEAM
30	Costa Rica	-84	11	4	80	158	91	25.6	4072	RC
31	Nicaragua	-84	12	4	90	132	66	25.3	3710	IGC; JVM
32	Nicaragua	-84	13	4	85	47	37	25.7	2866	IGC; JVM
33	Costa Rica	-83	9	4	60	129	962	21.3	3179	ZZ
36	Peru	-81	-4	4	50	22	291	23.1	216	AG
37	Ecuador	-81	-2	4	65	45	141	24	352	AG
40	Ecuador	-80	-4	4	60	105	814	22.8	925	JH; NA; SB; ZA
41	Ecuador	-80	-2	4	55	27	67	25	962	AG
42	Ecuador	-80	-1	4	90	27	134	24.9	1374	AG
43	Peru	-80	-5	2	45	26	942	21.6	467	AG
44	Panama	-80	9	4	85	311	148	26.3	2694	AG; RCo; TEAM
46	Peru	-79	-6	2	45	51	1888	18	811	AG
47	Peru/Ecuador	-79	-5	4	40	176	1817	19	1278	AG; SB
48	Ecuador	-79	-4	4	45	537	1923	17.8	1536	AG; JH; SB
49	Ecuador	-79	-1	4	90	78	2073	15.5	1512	AG
50	Ecuador	-79	0	2	45	41	1125	20.3	2424	AG
51	Peru	-78	-6	4	55	53	2152	16.7	1004	AG
52	Ecuador	-78	-3	4	60	40	847	22.9	2608	AG
53	Ecuador	-78	-1	4	90	593	2093	15.7	2635	AG; JH
54	Ecuador	-78	0	2	45	21	2742	12.8	1470	AG; BB
55	Ecuador/Colombia	-78	1	4	45	220	2012	16.4	2209	AG; BB; CTFS; SB
56	Jamaica	-78	18	4	45	37	234	24.6	1865	AG
57	Ecuador	-77	0	4	75	122	450	24	3329	AG; NP

58	Colombia	-77	4	4	85	145	412	24.6	5138	AG
59	Colombia	-77	6	4	90	46	172	25.8	6369	AG
60	Colombia	-77	7	4	70	40	140	26.5	4075	AG
61	Jamaica	-77	18	2	45	56	311	24	1686	ET; SC; PB
62	Peru	-76	-7	4	50	38	540	25.4	1646	AG
63	Ecuador	-76	-1	4	95	534	235	25.3	2921	TEAM
64	Colombia	-76	2	2	45	32	1802	17.8	1896	AG
65	Colombia	-76	4	2	40	36	2002	17.4	1608	AG
66	Colombia	-76	5	2	45	88	1326	20.8	2934	AD; AG
67	Colombia	-76	7	2/4	35	101	1536	19.9	2681	AD; AG
68	Colombia	-76	8	4	90	201	256	26.1	2162	AA; AG; AV; JC; HA; HM; MLB; OR
69	Peru	-75	-11	4	70	39	1727	18.8	1771	AG
70	Peru	-75	-10	4	75	206	578	24.3	2292	AG; TEAM
71	Peru	-75	-9	4	95	39	322	25.7	2612	AG
72	Peru	-75	-2	4	95	198	185	25.8	2794	NP
73	Peru	-75	-1	4	95	433	202	25.8	2748	NP
74	Colombia	-75	5	4	50	44	1624	19.2	2053	AG
75	Colombia	-75	8	4	80	183	111	27.8	3288	AD; AG
76	Colombia	-75	10	4	60	59	84	27.6	1217	AG
78	Peru	-74	-5	4	95	111	117	26.9	2451	AG; KR
79	Peru	-74	-4	4	95	182	133	26.3	2676	AG; KR
80	Peru	-74	-3	4	90	285	148	26.1	3147	NP
81	Peru	-74	-2	4	95	240	163	26.1	3072	NP
82	Colombia	-74	5	2	45	40	2395	15	1371	AG
83	Colombia	-74	11	4	60	111	1125	21	1839	AG
84	Peru	-73	-4	4	80	493	120	26.2	2742	AG; KR
85	Peru	-73	-3	4	90	154	132	26.2	2956	AG
86	Colombia	-73	0	4	90	160	224	26.3	2808	AD
87	Colombia	-73	10	4	45	69	744	23.6	1860	AG
88	Colombia	-73	11	4	70	27	610	24.4	1391	AG

89	Peru	-72	-4	4	90	65	117	26	2727	KR
90	Colombia	-72	-1	4	95	527	160	26.4	2911	AD
91	Colombia	-72	0	4	95	139	186	26.5	2885	AD; AG
92	Peru	-71	-12	4	75	463	389	24.8	2698	AG; TEAM
94	Peru	-70	-13	4	85	107	378	24.4	3713	AG
96	Bolivia	-69	-14	4	85	98	1459	20	2145	AG
97	Peru	-69	-13	4	90	143	235	25.3	2373	AG
98	Bolivia	-68	-16	4	45	61	2679	14.5	1028	AG
99	Bolivia	-68	-15	4	60	52	1052	22	1560	AG
100	Bolivia	-68	-14	4	85	149	526	24.2	1852	SDW
101	Bolivia	-68	-12	4	95	48	207	25.8	1763	FW; JCM
102	Bolivia	-68	-11	4	80	111	213	25.8	1802	FW; JCM
103	Venezuela	-68	9	4	50	24	86	27.3	1325	AG
104	Bolivia	-67	-12	4	90	36	177	26.2	1601	FW, JCM
105	Bolivia	-67	-11	4	80	139	175	26.2	1729	AG; FW; JCM
106	Brazil	-67	-3	4	95	139	72	25.7	2954	A; FW; MP
108	Bolivia	-66	-10	4	90	40	153	26.3	1743	AG
109	Brazil	-66	-3	4	90	192	70	25.9	2904	A; FW; JS; MP
110	Venezuela	-66	1	4	75	39	380	25.3	3068	AG
111	Puerto Rico	-66	18	4	50	36	185	24.6	1773	AG
112	Argentina	-65	-25	4	40	28	1083	17.9	611	AG
113	Brazil	-65	-4	4	90	182	77	26.7	2483	A; FW; MP
114	Brazil	-65	-3	4	90	289	57	26.6	2950	FW, JS, MP
115	Brazil	-65	0	4	95	66	104	26.5	2628	FW, JCM, MP
117	Bolivia	-64	-18	4	65	108	1440	19.7	907	MK
118	Brazil	-64	0	4	95	85	52	26.8	2613	FW, JCM; MP
120	Bolivia	-63	-15	4	80	29	242	25.1	1285	AG

121	Brazil	-63	-1	4	95	71	44	26.8	2339	FW, JCM; MP
122	Venezuela	-63	7	4	60	159	318	25.8	1582	KF
124	Bolivia	-62	-19	4	50	26	343	24.8	566	AG
125	Bolivia	-62	-15	4	60	56	261	24.4	1245	TK
126	Brazil	-62	-4	4	90	164	35	26.7	2517	A; FW; MP
127	Bolivia	-61	-15	4	90	348	254	24	1342	AG; TK
128	Bolivia	-61	-14	4	85	383	312	23.4	1599	TK
129	Brazil	-61	-3	4	95	113	43	27.1	2439	FW; JCM; MP, PP
131	Bolivia	-60	-18	4	50	40	378	24.5	1217	AG
132	Bolivia	-60	-15	4	75	70	299	23.9	1443	TK
133	Bolivia	-60	-14	4	60	99	347	23.2	1752	TK
134	Brazil	-60	-3	4	95	677	53	27.3	2260	AG; PP; TEAM
135	Brazil	-60	-2	4	95	976	99	27	2635	AAn; SLa; TEAM; WL
137	Guyana	-60	7	4	95	44	126	25.9	2172	SBr
138	Guyana	-60	8	4	95	34	41	26.2	2546	SBr
139	Brazil	-59	-2	4	90	171	99	27	2273	FW; NT
140	Guyana	-59	5	4	95	32	213	25.9	2650	SBr
141	Guyana	-59	6	4	95	46	101	26	2415	SBr
142	Guyana	-59	7	4	95	34	69	26.3	2267	SBr
143	Argentina	-58	-27	4	40	20	62	22.1	1291	AG
144	Guyana	-58	5	4	95	23	82	26.7	2351	SBr
145	Guyana	-58	6	4	95	55	36	26.6	1931	AG; SBr
146	Paraguay	-56	-24	4	40	24	214	22.4	1475	AG
147	Brazil	-55	-4	4	90	169	172	25.9	1876	PBi; JRS
148	Brazil	-55	-3	4	80	179	101	25.8	1955	AG; PBi; JRS
149	French Guiana	-53	4	4	90	42	159	25	2901	AG
150	Brazil	-52	-23	4	40	24	431	20.9	1297	GD; MSS
153	Brazil	-52	-2	4	85	277	37	26.9	2267	TEAM

154	Brazil	-51	-23	4	45	65	462	21.4	1319	GD; MSS
155	Brazil	-51	-6	4	90	40	291	25	1915	AG
156	Brazil	-51	-2	4	95	290	28	26.7	2382	TEAM
157	Brazil	-50	-23	4	60	77	511	20.9	1322	ESP; GD
158	Brazil	-50	-22	4	40	27	486	21.2	1223	ESP; GD
159	Brazil	-50	-8	4	85	123	231	25.8	1851	JG; MS
160	Brazil	-48	-24	4	65	35	545	19.3	1380	AG
161	Brazil	-48	-1	4	90	39	25	26.7	2547	AG
162	Brazil	-47	-24	4	50	291	570	18.9	1885	ELMC; LB
163	Brazil	-47	-23	4	60	23	724	18.9	1336	AG
164	Brazil	-46	-24	4	70	38	504	19.1	2300	AG
165	Brazil	-45	-23	4	60	395	794	18.4	1666	LA
166	Brazil	-45	-21	4	60	81	930	19.9	1511	EB
167	Brazil	-43	-23	4	65	48	122	22.6	1365	AG
168	Brazil	-41	-20	4	60	279	576	21.7	1248	FS
169	Brazil	-40	-19	4	80	304	77	24	1203	AG; SR
170	Brazil	-36	-9	4	90	125	372	22.8	1319	BS; FM; MT
172	Sierra Leone	-11	7	3	95	82	104	25.9	3364	JL
173	Sierra Leone	-11	8	3	90	142	244	25.7	2663	JL
175	Liberia	-8	6	3	90	110	235	26.1	2076	FB; HW; LP
178	Ivorycoast	-7	5	3	80	144	104	25.7	1794	AY; FB
179	Benin	2	10	3	40	52	382	26.5	1135	BF
180	Nigeria	4	7	3	70	108	104	26.9	1497	AVi
181	Nigeria	5	7	3	65	115	198	26.2	1592	AG, AVi
183	Cameroon	9	4	3	90	36	395	23.3	2951	AG
184	Cameroon	9	5	3	90	345	270	25.1	2883	AG, CTFS, TEAM
185	Cameroon	9	6	3	80	351	213	26.2	2379	AG; TS
186	Gabon	10	-2	3	90	313	100	25.5	1961	GD; JFG
187	Gabon	10	-1	3	95	44	73	25.8	2054	GD
188	Gabon	10	0	3	90	209	76	25.9	2378	GD; TS
189	Eq.Guinea/Gabon	10	1	3	95	252	287	24.1	2580	TS

190	Cameroon	10	2	3	95	424	297	23.9	2284	PT
191	Gabon	11	-3	3	95	308	228	24.7	1627	JFG; JR
192	Gabon	11	-2	3	95	78	264	25.3	1957	GD
193	Gabon	11	-1	3	95	186	393	24.6	2047	GD; TSt
194	Gabon	11	0	3	95	339	310	24.9	1953	GD; JFG; JLD; JR; TSt
195	Gabon	11	1	3	90	200	596	22.9	2016	JR; TS
196	Cameroon	11	2	3	95	63	596	23.1	1940	PT
197	Cameroon	11	3	3	95	485	611	23.7	1941	CG; MPa
198	Gabon	12	-2	3	95	67	610	23.3	1900	TSt
199	Gabon	12	-1	3	95	282	453	24.5	1798	JFG; JLD
200	Gabon	12	0	3	95	245	377	25	1611	JFG; JLD; GD
201	Gabon	12	1	3	95	202	546	23.9	1646	JFG; JLD
202	Gabon	13	-1	3	95	226	394	24.7	1731	JFG; JLD
203	Gabon	13	0	3	95	223	490	24.1	1656	GD; JR; VM
204	Gabon	13	1	3	95	54	528	23.8	1625	AG
205	Gabon	13	2	3	95	183	577	23.6	1612	JVV
206	Cameroon	13	3	3	85	119	657	23.4	1631	TS
207	CAR/Congo	16	2	3	95	302	425	24.6	1650	AG; CC; DH; JPo; TEAM; TS
208	CAR	16	3	3	75	63	518	24.4	1601	TS
209	Congo	17	2	3	90	71	380	24.8	1717	TS
210	Congo	17	3	3	95	112	473	24.3	1668	TEAM
211	Congo	24	1	3	90	144	420	24.9	1802	EK
212	Congo	25	1	3	90	151	457	24.9	1789	EK
213	Congo	29	1	3	90	259	883	23.9	1600	CTFS
214	Uganda	30	-1	1/3	35	103	1597	19.1	1105	TEAM
215	Uganda	30	1	1/3	35	42	1060	22.5	1319	ML
216	Uganda	32	2	3	60	92	994	23.6	1244	KB; NF
217	Ethiopia	35	6	1	40	26	945	23.8	998	CS
218	Ethiopia	36	7	1	35	48	1576	20.1	1673	CS

219	Tanzania	37	-8	1	45	181	445	24.1	1374	AM; JLo; PM; TEAM
220	Tanzania	39	-7	3	80	32	106	25.8	1073	AG
221	Madagascar	45	-24	4	45	27	396	23.9	687	AG
222	Madagascar	47	-21	1	70	157	1271	17.9	1345	TEAM
223	Madagascar	47	-16	1	40	22	81	26.7	1509	AG
224	Madagascar	48	-21	1	65	108	316	21.9	2358	TEAM
225	Madagascar	48	-19	1	45	39	1150	18.5	1628	AG
226	Madagascar	50	-16	1	60	48	214	23.2	2516	AG
227	Mauritius	57	-20	1	75	31	181	22.6	1709	AG
228	India	74	15	1	95	87	228	26.3	3062	NP; R
229	India	74	16	1	100	40	413	25.5	2856	NP
230	India	74	17	1	100	31	534	25	2033	NP
231	India	74	19	1	100	20	652	24.6	1017	NP
232	India	75	12	1	100	40	115	26.7	3994	NP
233	India	75	13	1	100	152	242	26	4237	JPP; NP; P; R
234	India	75	14	1	90	221	487	24.8	3153	JPP; NP; R
235	India	75	15	1	95	106	560	25.2	1554	R
236	India	76	11	1	95	116	173	26.7	2871	AG, NP
237	India	76	12	1	80	193	688	23.7	2494	NP; SJ
238	India	76	13	1	95	110	872	23.2	1402	NP; Pa; R
240	India	77	8	1	100	74	144	26.7	1308	PD
241	India	77	9	1	100	389	294	26.1	1973	G; NP; P; PD
242	India	77	10	1	95	405	702	24	2247	MO; NP; P; SJ; VSR
243	India	77	11	1	55	210	542	25.4	1065	AG; AK; MO; NP
244	India	77	12	1	30	134	753	24.3	728	AG; RS; SJ
245	India	78	10	1	65	29	282	27.7	850	P; PD
246	India	78	11	1	90	62	232	28	684	P
247	India	79	10	1	45	48	53	28.8	932	P
248	India	79	11	1	40	46	98	28.6	939	P

250	Sri Lanka	80	6	1	95	159	88	26.4	3122	CTFS
252	India	80	13	1	45	22	59	28.5	1100	P
254	Andamans	92	10	1	85	147	38	26.8	2791	P
255	Andamans	92	12	1	80	86	47	26.5	2880	P
256	Andamans	93	13	1	90	156	50	26.7	2829	RP
257	Sumatra	96	5	1	95	103	562	24.3	2556	SW
258	Sumatra	97	3	1	100	38	462	24.6	2784	AP
260	Sumatra	98	3	1	95	104	670	23.3	2767	O
261	Sumatra	98	4	1	85	142	501	24.4	2328	SW
262	Sumatra	99	1	1	95	167	296	25.1	3392	KK
263	Sumatra	99	2	1	95	309	886	21.9	2608	GF; O
264	Thailand	99	16	1	80	238	618	24.6	1460	CTFS
265	Sumatra	100	-1	1	90	158	250	25.8	3390	TY
266	Pen. Malaysia	100	6	1	95	117	48	27.2	2364	MKo
267	Pen. Malaysia	100	7	1	95	70	93	26.9	2096	AMa; RZ
268	Yunnan	100	21	2	55	114	983	21.8	1435	EP; RH
269	Yunnan	100	22	2	55	190	1297	19.5	1460	EP; RH
270	Sumatra	101	-1	1	75	122	620	23.7	2416	TY
271	Pen. Malaysia	101	5	1	95	221	427	25	2719	AMa; RZ; MNMS
272	Pen. Malaysia	101	6	1	95	53	287	25.9	2238	AMa; RZ
273	Yunnan	101	21	2	55	50	879	21.9	1608	EP; RH
274	Yunnan	101	22	1	80	259	1026	20.4	1501	EP; JT; RH; XM
275	Sumatra	102	-3	1	90	623	621	23.5	2931	YL
276	Sumatra	102	-2	1	85	683	466	24.4	2737	YL
277	Pen. Malaysia	102	3	1	95	799	181	26.1	2212	AG; CTFS; KN; TEAM
278	Pen. Malaysia	102	4	1	95	546	308	24.9	2484	AG; AMa; KN; MNMS; RZ
279	Thailand	102	14	1	100	37	212	26.7	1577	AG

280	Thailand	102	15	1/3	40	38	239	26.7	1155	AG
281	Laos	102	18	1	85	47	312	25.2	1549	MS; JMi
282	Yunnan	102	21	1	90	83	884	21.4	1581	JT
283	Yunnan	102	22	1	65	298	1014	20.2	1681	CTFS; JT
284	Sumatra	103	-4	1	90	247	607	23.5	2947	YL
285	Pen. Malaysia	103	3	1	95	223	70	26.4	2409	AMa; KM; RZ
286	Pen. Malaysia	103	4	1	95	67	170	25.5	2801	AMa; RZ
287	Pen. Malaysia	103	5	1	95	124	220	25.4	3053	AMa; RZ
288	Laos	103	18	1	80	235	227	25.4	2031	MS; JMi
289	Vietnam	103	21	1	50	59	872	20.9	1667	TVD
290	Sumatra	104	-6	1	95	489	107	26.3	2961	TEAM; YL
291	Sumatra	104	-5	1	90	236	541	23.9	2854	YL
292	Singapore	104	1	1	95	164	12	26.7	2530	CTFS
293	Vietnam	104	21	1	60	56	862	20.1	1476	TVD
294	Vietnam	105	20	1	80	69	516	21.8	1519	SVH
295	Vietnam	105	21	1	95	103	430	21.6	1580	TVD
296	Vietnam	105	22	1	95	98	254	22.4	1751	TVD
297	Sumatra	106	-2	1	100	28	21	27.3	2810	EN
298	Cambodia	106	13	1	85	176	84	26.9	1811	IT
299	Vietnam	106	20	1	85	84	28	24.2	1723	SVH
300	Java	107	-7	1	60	124	553	23.8	3114	AR; H; Y
301	Vietnam	107	11	1	70	104	69	26.3	2112	LBl
302	Java	108	-7	1	60	42	636	23.5	2790	AR
303	Vietnam	108	14	1	95	110	580	23.5	2107	TVD
304	Borneo	109	1	1	85	189	48	26.6	2915	ES
305	Hainan	109	19	1	70	212	269	23.8	1318	RZ; SBC; XL; XY
306	Borneo	110	-1	1	95	303	44	26.9	3195	CW
307	Borneo	110	0	1	95	65	43	27	3057	AMk
308	Borneo	110	1	1	95	334	161	26	3318	ES
309	Borneo	110	2	1	95	390	68	26.5	3790	AG, PA

310	Borneo	111	0	1	95	55	106	26.5	3150	AMk
311	Borneo	113	-1	1	95	403	222	25.6	3118	PW
312	Borneo	113	2	1	95	572	236	25.5	3791	PA
313	Borneo	113	3	1	95	986	64	26.4	3812	PA
314	Borneo	114	-2	1	95	212	35	26.5	2690	KMi; MB; NZ
315	Borneo	114	-1	1	95	176	110	26.1	3364	SRi
316	Borneo	114	0	1	95	304	464	24.2	3627	FBr; JPr
317	Borneo	114	2	1	95	309	525	24	4056	PA
318	Borneo	114	3	1	95	261	328	25.1	4021	PA
319	Borneo	114	4	1	95	1466	45	26.9	3319	CTFS; HN; PA
320	Borneo	115	1	1	90	154	658	23.2	3662	ER
321	Borneo	115	2	1	95	264	900	22	3773	JVV; SWu
322	Borneo	115	3	1	95	89	778	22.9	3895	SWu
323	Borneo	115	4	1	95	539	505	24.6	3446	M; JPr
324	Borneo	115	5	1	95	609	91	27.1	3424	Apo; FMe; HD; RSu; TCB Y
325	Borneo	116	-2	1	95	45	135	25.8	2672	FSl
326	Borneo	116	-1	1	95	276	150	25.7	2616	FSl
327	Borneo	116	2	1	95	42	891	22.1	3264	SWu
328	Borneo	116	3	1	90	630	518	24.4	1601	DS; SWu
329	Borneo	117	-1	1	90	990	57	26.4	2265	CEB; FSl; KE; KK; MVN; SRi
330	Borneo	117	0	1	95	201	42	26.5	2037	SRi
331	Borneo	117	2	1	95	675	245	25.5	2586	FSl; PS
332	Borneo	117	3	1	95	374	155	26.2	3089	DS
333	Borneo	117	5	1	95	401	401	25	2461	AH; NI; OF; PSa
334	Borneo	117	6	1	95	390	423	24.8	2636	KKi; SIA
335	Borneo	118	5	1	90	293	164	26.2	2346	DN

336	Borneo	118	6	1	95	485	19	27	3019	RN
337	Sulawesi	120	-2	1	85	242	1287	20	2235	FBra; HC; MK
338	Sulawesi	120	-1	1	95	311	691	23.2	1754	HC; MK
339	Taiwan	121	22	1/2	45	62	298	23.1	2894	AG
340	Philippines	122	17	1	95	247	259	25.7	2423	CTFS
341	Taiwan	122	25	2	60	73	440	19.9	3079	CTFS
342	Philippines	123	17	1	85	58	88	26.5	2740	AG
343	Okinawa	128	27	2	60	57	83	21.9	2221	TE
344	Ryukyu	129	28	2	60	50	124	21.2	2660	TY
345	Yakushima	130	30	2	60	58	154	19.7	2916	SIA
346	New Guinea	138	-3	1	90	119	334	25.4	3136	DS; MVH
347	New Guinea	145	-5	1	95	190	360	25.2	3548	KD; TW
348	Australia	146	-17	1	85	256	372	22.6	2619	AG; HMu; MBr
349	New Guinea	146	-5	1	90	37	197	25.8	3335	AG
351	New Guinea	148	-9	1	95	44	963	21.9	3024	AG
352	Australia	153	-29	1	90	74	132	18.9	1297	RK
353	Australia	153	-28	1	90	85	53	19.9	1174	RK
354	New Caledonia	165	-21	1	50	27	252	22	1666	TG
356	Fiji	178	-17	1	50	25	74	25	2266	TG
357	Mexico	-100	20	2	60	35	2471	14.7	804	AG
358	Ecuador	-80	1	4	80	59	132	24.9	1428	AG
360	Yakushima	131	30	2	60	57	154	19.7	2916	SIA
361	New Guinea	139	-3	1	80	94	322	25.6	2880	DS; MVH
362	New Caledonia	167	-22	1	60	43	261	21.6	1943	AG
363	Australia	145	-17	1	85	148	530	22.7	1301	HM; MBra
364	Australia	146	-19	1	85	69	389	22.6	1034	HM; MBra
365	Australia	146	-18	1	85	43	321	22.6	2284	HM; MBra
366	Australia	145	-16	1	85	191	378	24	1539	HM; MBra
367	Australia	143	-14	1	85	46	178	25.6	1272	HM; MBra
368	Australia	149	-21	1	90	26	169	22.1	1471	HM; MBra

369	Australia	143	-13	1	100	53	130	25.7	1678	HM; MBra
370	Bangladesh	92	24	1	85	66	132	24.6	2408	SKS
371	Bangladesh	92	25	1	80	61	19	24.8	3395	SKS
372	Brazil	-56	-29	4	40	27	84	20.1	1567	AS
373	Brazil	-55	-30	4	40	28	119	19.1	1665	AS
375	Brazil	-54	-29	4	40	45	375	19	1771	AS
377	Brazil	-54	-27	4	40	62	396	19.4	1788	AS
378	Brazil	-53	-30	4	40	31	139	19.3	1459	AS
379	Brazil	-53	-29	4	40	119	430	18.6	1593	AS
380	Brazil	-52	-31	4	40	23				AS
381	Brazil	-52	-29	4	45	98	488	18	1584	AS
382	Brazil	-51	-30	4	40	71	97	19	1510	AS
383	Brazil	-51	-29	4	45	104	709	16.8	1824	AS
384	Brazil	-51	-28	4	40	134	862	16.4	1696	AS
385	Brazil	-51	-27	4	40	47	979	15.7	1735	AS
386	Brazil	-50	-29	4/5	35	238	647	16.5	1670	AS
387	Brazil	-53	-33	4	40	34				AS
388	Brazil	-43	-20	4	80	170	636	21.1	1285	TM
389	New Zealand	174	-35	1	65	39				PBe
390	Ivorycoast	-8	7	3	80	84	322	25.2	1817	N
391	Cameroon	10	3	3	90	251	156	25.3	2509	CG
392	Mozambique	36	-16	3	50	37	668	22.5	1712	JB; JTi
393	Congo	16	-2	3	95	52	382	25.3	1704	JFB
394	Congo	16	-3	3	95	82	496	24.5	1620	JFB
395	Congo	17	-2	3	95	84	339	25.6	1558	JFB
396	Tanzania	39	-5	3	45	114	227	25	1155	AM; JLo; PM
397	Tanzania	37	-3	1	50	51	1513	19	881	AE; AHe; GR; MF
398	Tanzania	38	-3	1	50	27	968	22.3	777	AE; AHe; GR; MF
399	Zimbabwe	32	-20	3	35	38	744	20.9	606	JTi
400	Brazil	-40	-15	4	60	151	405	22.4	941	DR

401	Ecuador	-78	-2	2	45	97	1506	19.1	2850	SB
404	Mexico	-90	20	4	50	30	60	26.4	1074	MMRo
405	Venezuela	-61	8	4	70	129	105	26.1	1834	JLoz
406	Venezuela	-61	7	4	90	117	196	26	1623	JLoz
407	Borneo	114	5	1	95	136	14	27.3	2937	TCB; Y
408	Mexico	-104	19	4	55	156	531	24.5	1011	GIM
409	Mexico	-95	17	4	50	83	283	24.6	1941	JM
410	India	76	27	4	35	36	398	25.1	593	ASu; MSH
413	Cambodia	103	12	1	85	101	379	25.2	2735	IT
415	Tonga	-175	-21	1	85	74	43	23.5	1597	DD; JF; SWi
416	Tonga	-174	-19	1	55	62	26	25	2170	JF
417	Pen. Malaysia	103	6	1	95	116	72	26.4	2966	MNMS
418	Pen. Malaysia	101	4	1	95	76	148	26.4	2479	MNMS
419	Pen. Malaysia	102	6	1	90	137	180	26.1	2613	MNMS
420	Thailand	104	16	1	85	30	153	26.7	1394	T
421	Colombia	-77	9	4	90	167	77	26.1	1923	AD
422	Colombia	-77	8	4	85	97	187	25.7	2536	AD
423	Colombia	-76	6	2	40	190	1498	20.4	3297	AD
425	Colombia	-75	7	4	60	348	1008	23	3358	AD
426	Colombia	-75	6	4	85	186	1178	22.1	2730	AD
428	Thailand	99	15	1	50	217	555	24.6	1747	EW; RSt
429	Brazil	-48	-14	4	45	66	685	24.2	1682	ELO; JPi
430	Brazil	-49	-18	4	40	54	654	23.7	1303	ELO; JPi
431	Brazil	-47	-14	4	40	76	652	24.7	1407	ELO; JPi
432	Brazil	-48	-17	4	40	64	871	22.4	1369	ELO; JPi
433	Brazil	-49	-16	4	40	79	881	22.9	1514	ELO; JPi
434	Brazil	-49	-14	4	40	67	495	25.2	1775	ELO; JPi
435	Brazil	-52	-18	4	45	82	727	23.3	1582	ELO; JPi
436	Brazil	-50	-17	4	35	57	614	24.1	1455	ELO; JPi
437	Brazil	-52	-16	4	45	69	409	25.1	1559	ELO; JPi
438	Nepal	84	28	1	75	21	1147	19	2113	LNS; ORV
439	Congo	17	-3	3	95	55	346	25.5	1523	JFB

440	Venezuela	-67	2	4	95	66	108	26.4	3390	GA
441	Venezuela	-66	2	4	90	144	165	26.4	3042	GA
442	Venezuela	-67	6	4	80	224	373	26.1	2526	GA
443	Venezuela	-67	3	4	95	59	110	26.8	3225	GA
444	Venezuela	-67	5	4	95	156	630	24.7	2964	GA
445	China	117	25	2	55	73	584	18.9	1706	SBC
446	China	118	28	2	60	50	486	16.9	1935	SBC
447	China	111	30	2	60	61	471	15.5	1344	SBC
448	China	109	18	1	50	45	125	25	1339	SBC
449	China	114	27	2	60	49	372	16.8	1592	SBC
450	China	112	25	2	60	37	524	18	1525	SBC
451	China	113	25	2	60	37	569	18	1570	SBC
452	China	116	31	2	60	33				SBC
453	India	93	25	1	65	127	198	24.1	2771	SCG
454	India	93	24	1	90	47	644	22.1	2170	SCG

Abbreviations of data holders (contributors): A (Assis); AA (Andres Avella); AAn (Anna Andrade); AD (Alvaro Duque); AE (Andreas Ensslin); AG (Al Gentry); AH (Andy Hector); AHe (Andreas Hemp); AK (Anitha K); AM (Andrew Marshall); AMa (Asyraf Mansor); AMk (Antti Marjokorpi); AP (Andrea Permana); APo (Axel Poulsen); AR (Andes Rozak); AS (Alexandre Souza); ASu (Aisha Sultana); AV (Adela Vasquez); AVi (Adekunle Victor); AY (Adou Yao); BB (Brad Boyle); BF (Belarmain Fandohan); BS (Braulio Santos); CC (Connie Clark); CEB (Clara Eijk-Bos); CG (Christelle Gonmadje); CS (Christine Schmitt); CTFS (Center for Tropical Forest Studies); CW (Campbell Webb); DC (Deborah Clark); DD (Don Drake); DG (Daniel Griffith); DH (David Harris); DK (Daniel Kelly); DN (David Newbery); DR (Diogo Rocha); DS (Douglas Sheil); EB (Eduardo van den Berg); EK (Elisabeth Kearsley); ELMC (Eduardo Luis Martins Catharino); ELO (Eddie Lenza de Oliveira); EN (Eddy Nurtjahya); EP (Enkananda Paudel); ER (Ervan Rutishauser); ES (Eizi Suzuki); ESP (Eduardo da Silva Pinheiro); ET (Edward Tanner); EW (Edward Webb); FB (Frans Bongers); FBr (Francis Brearley); FBra (Fabian Brambach); FM (Felipe Melo); FMe (Faizah Metalli); FMA (Francisco Mora

Ardila); FS (Felipe Saiter); FSl (Ferry Slik); FW (Florian Wittmann); G (Girirai); GA (Gerardo Aymard); GD (Giselda Durigan); GD (Gilles Dauby); GF (Gabriella Fredriksson); GIM (Guillermo Ibarra-Manriquez); GR (Gemma Rutten); GW (Guadelupe Williams); H (Helmi et al. 2009); HA (Henry Arellano); HC (Heike Culmsee); HD (Hazimah Din); HM (Heyda Mandoza); HMu (Helen Murphy); HN (Hidetoshi Nagamasu); HW (Hansjoerg Woll); IGC (Inigo Granzo de la Cerda); IT (Ida Theilade); JB (Julian Bayliss); JC (Juan Garcia); JCA (Jurgi Cristobal-Azkarate); JCM (Juan Carlos Montero); JF (Janet Franklin); JFB (Jean-Francois Bastin); JFG (Jean-Francois Gillet); JG (James Grogan); JH (JorgenHomeier); JL (Jeremy Lindsell); JLD (Jean-Louis Doucet); JLo (John Lovett); JLoz (Jose Lozada); JM (Jorge Meave); JMi (Jerome Millet); JP (Jennifer Powers); JPi (Jose Roberto Rodrigues Pinto); JPo (John Poulsen); JPr (John Proctor); JR (Jan Reitsma); JRS (Joao Roberto dos Santos); JS (Jochen Schoengart); JT (Jiangwei Tang); JTi (Jonathan Timberlake); JVM (John VanderMeer); JVV (Johan van Valkenburg); JW (John Williams); KB (Katrin Boehning); KD (Kipiro Damas); KE (Karl Eichhorn); KF (Ken Feeley); KK (Kuswata Kartawinata); KKi (Kanehiro Kitayama); KM (Khairil bin Mahmud); KMi (Kazuki Miyamoto); KN (K. Niiyama et al 2014); KR (Kalle Ruokolainen); LA (Luciana Alves); LB (Luis Bernacci); LBl (Lilian Blanc); LNS (Lila Nath Sharma); LP (Lourens Poorter); M (Martin, 1977); MB (Meredith Bastian); MBr (Matt Bradford); MC (Miguel Castillo); MF (Markus Fischer); MK (Michael Kessler); MKo (M Kohira et al. 2001); ML (Michael Lawes); MLB (Mary Lee Berdugo); MMR (Miguel Martinez-Ramos); MMRo (Miguel Munguia-Rosas); MNMS (Mohd. Nizam Mohd. Said); MO (Mohandas); MP (Maria Piedade); MPa (Marc Parren); MS (Mark Schulze); MSa (Manichanh Satdichanh); MSH (Mohd. Shah Hussain); MSS (Marcio Seiji Suganuma); MT (Marcello Tabarelli); MVH (Miriam van Heist); MVN (Mark van Nieuwstadt); N (Nusbaumer, 2003); NA (Nikolay Aguirre); NF (Nina Farwig); NI (Nobuo Imai); NP (Navendu Page); NT (Natalia Targheta); NP (Nigel Pitman); NZ (Nicole Zweifel); O (Onrizal); OF (Olle Forshed); OR (Orlando Rango); ORV (Ole Reidar Vetaas); P (Parthasarathy); Pa (Pascal &

Pelissier, 1996); PA (Peter Ashton); PB (Patricia Balvanera); PBe (Peter Bellingham); PBi (Polyana Bispo); PD (Priya Davidar); PM (Pantaleo Munishi); PP (Pia Parolin); PS (Plinio Sist); PSa (Phillipe Saner); PT (Peguy Tchouto); PW (Peter Wilkie); R (Ramesh et al. 2010); RC (Robin Chazdon); RCo (Richard Conditt); RH (Rhett Harrison); RK (Robert Kooyman); RN (Rueben Nilus); RP (Rama Prasad); RS (Raman Sukumar); RSt (Robert Steinmetz); RSu (Rahayu Sukri); RZ (Rahmad Zakaria); SB (Selene Baez); SBr (Sandra Brown); SBC (Shengbin Chen); SC (Shauna Chai); SCG (Satish Chandra Garkoti); SDW (Saara DeWalt); SIA (Shin-Ichiro Aiba); SJ (Shijo Joseph); SKS (Swapan Kumar Sarker); SL (Susan Letcher); Sla (Susan Laurance); SOG (Susana Ochoa-Gaona); SR (Samir Rolim); SRi (Soedarsono Riswan); SVH (Sam Van Hoang); SW (Serge Wich); SWi (Susan Wiser); SWu (Stefan Wulffraat); T (Tabuchi et al. 2014); TCB (Truebridge Callender Beach, 1992); TE (Tsutomu Enoki); TEAM (Tropical Ecology Assessment and Monitoring); TG (Thomas Gillespie); TK (Tim Killeen); TM (Thiago Metzker); TS (Terry Sunderland); TSt (Tariq Stevart); TVD (Tran Van Do); TW (Tim Whitfeld); TY (Tsuyoshi Yoneda);VAR (Victor Arroyo-Rodrigues); VM (Vincent Metjibe); VSR (V.S.Ramachandran); WL (William Laurance); XM (Xiaoxue Mo); XL (Xinghui Lu); XY (XiaoboYang); Y (Yamada, 1977 & 1986); YL (Yves Laumonier); ZA (Zhofre Aguirre); ZZ (Zak Zahawi).

Helmi, N., K. Kartawinata, et al. (2009). "An undescribed lowland natural forest at Bodogol, the Gunung Gedeh Pangrango National Park, Cibodas Biosphere Reserve, West Java, Indonesia." Reinwardtia 13(1): 33-44.

Kohira M, Ninomiya I, Ibrahim AZ & Latiff A (2001) Diversity, diameter structure and spatial pattern of trees in a semi-evergreen rain forest on Langkawi Island, Malaysia. Journal of Tropical Forest Science 13(3): 460-476.

Martin, P.J., 1977. The altitudinal zonation of forests along the west ridge of Gunung Mulu. Report Forestry Department Sarawak, Kuching, Malaysia.

Niiyama, K. and Abd Rhaman, K. (2014) Tree Census Data 1993: Pasoh. Datasets. Available on-line [http://www.ffpri.affrc.go.jp/labs/EA-FDPN/] from Forestry and Forest Products Research Institute, Tsukuba, Japan.

Nusbaumer, L. (2003) Structure et composition floristique de la Foret Classee du Scio (Côte d'Ivoire). Etude descriptive et comparative. Thesis Universite de Geneve, Switzerland.

Pascal, J.-P. & Pélissier, R. 1996. Structure and floristic composition of a tropical evergreen forest in southwest India. Journal of Tropical Ecology 12: 195-218.

Ramesh et al. (2010) Forest stand structure and composition in 96 sites along environmental gradients in the central Western Ghatts of India. Ecology 91: 3118.

Tabuchi, R., Patanaponpaiboon, P. and Poungparn, S. (2014) Tree Census Data 2005-2009: Lam Se Buy. Datasets. Available on-line [http://www.ffpri.affrc.go.jp/labs/EA-FDPN/] from Forestry and Forest Products Research Institute, Tsukuba, Japan.

Truebridge Callender Beach, 1992. Establishment of teaching and research plots for biology. Report, Brunei Darussalam.

Yamada, I. (1977). "Forest ecological studies of the montane forest of Mt. Pangrango, West Java. IV. Floristic composition along the altitude." South East Asian Studies 15(2): 226-254.

Yamada 1987. Report on the forest research in Negara Brunei Darussalam from 1984 through 1986. Forest Research Note in Brunei Darussalam no. 3.