

REVIEW

CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change

KRISTINA J. ANDERSON-TEIXEIRA^{1,2}, STUART J. DAVIES^{1,3}, AMY C. BENNETT², ERIKA B. GONZALEZ-AKRE², HELENE C. MULLER-LANDAU¹, S. JOSEPH WRIGHT¹, KAMARIAH ABU SALIM⁴, ANGÉLICA M. ALMEYDA ZAMBRANO^{2,5,6}, ALFONSO ALONSO⁷, JENNIFER L. BALTZER⁸, YVES BASSET¹, NORMAN A. BOURG², EBEN N. BROADBENT^{2,5,6}, WARREN Y. BROCKELMAN⁹, SARAYUDH BUNYAVEJCHEWIN¹⁰, DAVID F. R. P. BURSLEM¹¹, NATHALIE BUTT^{12,13}, MIN CAO¹⁴, DAIRON CARDENAS¹⁵, GEORGE B. CHUYONG¹⁶, KEITH CLAY¹⁷, SUSAN CORDELL¹⁸, HANDANAKERE S. DATTARAJA¹⁹, XIAOBAO DENG¹⁴, MATTEO DETTO¹, XIAOJUN DU²⁰, ALVARO DUQUE²¹, DAVID L. ERIKSON³, CORNEILLE E.N. EWANGO²², GUNTER A. FISCHER²³, CHRISTINE FLETCHER²⁴, ROBIN B. FOSTER²⁵, CHRISTIAN P. GIARDINA¹⁸, GREGORY S. GILBERT^{26,1}, NIMAL GUNATILLEKE²⁷, SAVITRI GUNATILLEKE²⁷, ZHANQING HAO²⁸, WILLIAM W. HARGROVE²⁹, TERESE B. HART³⁰, BILLY C.H. HAU³¹, FANGLIANG HE³², FORREST M. HOFFMAN³³, ROBERT W. HOWE³⁴, STEPHEN P. HUBBELL^{1,35}, FAITH M. INMAN-NARAHARI³⁶, PATRICK A. JANSEN^{1,37}, MINGXI JIANG³⁸, DANIEL J. JOHNSON¹⁷, MAMORU KANZAKI³⁹, ABDUL RAHMAN KASSIM²⁴, DAVID KENFACK^{1,3}, STALINE KIBET^{40,41}, MARGARET F. KINNAIRD^{42,43}, LISA KORTE⁷, KAMIL KRAL⁴⁴, JITENDRA KUMAR³³, ANDREW J. LARSON⁴⁵, YIDE LI⁴⁶, XIANKUN LI⁴⁷, SHIRONG LIU⁴⁸, SHAWN K.Y. LUM⁴⁹, JAMES A. LUTZ⁵⁰, KEPING MA²⁰, DAMIAN M. MADDALENA³³, JEAN-REMY MAKANA⁵¹, YADVINDER MALHI¹³, TOBY MARTHEWS¹³, RAFIZAH MAT SERUDIN⁵², SEAN M. MCMAHON^{1,53}, WILLIAM J. MCSHEA², HERVÉ. MEMIAGHE⁵⁴, XIANGCHENG MI²⁰, TAKASHI MIZUNO³⁹, MICHAEL MORECROFT⁵⁵, JONATHAN A. MYERS⁵⁶, VOJTECH NOVOTNY^{57,58}, ALEXANDRE A. DE OLIVEIRA⁵⁹, PERRY S. ONG⁶⁰, DAVID A. ORWIG⁶¹, REBECCA OSTERTAG⁶², JAN DEN OUDEN⁶³, GEOFFREY G. PARKER⁵³, RICHARD P. PHILLIPS¹⁷, LAWREN SACK³⁵, MOSES N. SAINGE⁶⁴, WEIGUO SANG²⁰, KRIANGSAK SRI-NGERNYUANG⁶⁵, RAMAN SUKUMAR¹⁹, I-FANG SUN⁶⁶, WITCHAPHART SUNGPALAE⁶⁵, HEBBALALU SATHYANARAYANA SURESH¹⁹, SYLVESTER TAN⁶⁷, SEAN C. THOMAS⁶⁸, DUNCAN W. THOMAS⁶⁹, JILL THOMPSON^{70,71}, BENJAMIN L. TURNER¹, MARIA URIARTE⁷², RENATO VALENCIA⁷³, MARTA I. VALLEJO⁷⁴, ALBERTO VICENTINI⁷⁵, TOMÁŠ VRŠKA⁴⁴, XIHUA WANG⁷⁶, XUGAO WANG³⁰, GEORGE WEIBLEN⁷⁷, AMY WOLF⁷⁸, HAN XU⁴⁶, SANDRA YAP⁶⁰ and JESS ZIMMERMAN⁷¹

¹Center for Tropical Forest Science-Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Panama, Republic of Panama, ²Conservation Ecology Center, Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal, VA, USA, ³Department of Botany, National Museum of Natural History, Washington, DC, USA, ⁴Environmental and Life Sciences, Faculty of Science, Universiti of Brunei Darussalam, Tungku Link Road, Bandar Seri Begawan, BE 1410, Brunei Darussalam, ⁵Stanford Woods Institute for the Environment, Stanford University, Stanford, CA, USA, ⁶Department of Geography, University of Alabama, Tuscaloosa, AL, USA, ⁷Center for Conservation Education and Sustainability, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC, USA, ⁸Department of Biology, Wilfrid Laurier University, Waterloo, ON, N2L 3C5, Canada, ⁹Department of Biology, Mahidol University, Bangkok, Thailand, ¹⁰Research Office, Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand, ¹¹School of Biological Sciences, University of Aberdeen, Aberdeen, UK, ¹²School of Biological Sciences, University of Queensland, St. Lucia 4072, Australia, ¹³Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK, ¹⁴Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 88 Xuefu Road, Kunming 650223, China, ¹⁵Instituto Amazónico de Investigaciones Científicas Sinchi, Bogotá, Colombia, ¹⁶Department of Botany and Plant Physiology, University of Buea, Buea, Cameroon, ¹⁷Department of Biology, Indiana University, Bloomington, IN, USA, ¹⁸Institute of Pacific Islands Forestry, USDA Forest Service, Hilo, HI, USA, ¹⁹Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India, ²⁰Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China, ²¹Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Medellín, Colombia, ²²Centre de Formation et de Recherche en Conservation Forestière (CEFRECOCF) Epulu, Ituri Forest, Reserve de Faune a Okapis, Epulu, Democratic Republic of Congo, ²³Kadoorie Farm and Botanic Garden, Tai Po, Hong Kong, ²⁴Forest

Research Institute Malaysia, Selangor, Malaysia,²⁵Botany Department, The Field Museum, Chicago, IL, USA,²⁶Environmental Studies Department, University of California, Santa Cruz, Santa Cruz, CA, USA,²⁷Faculty of Science, Department of Botany, University of Peradeniya, Peradeniya, Sri Lanka,²⁸State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, China,²⁹Eastern Forest Environmental Threat Assessment Center, USDA-Forest Service Station Headquarters, Asheville, NC, USA,³⁰Tshuapa-Lomami-Lualaba Project, Lukuru Wildlife Research Foundation, Kinshasa BP 2012, Democratic Republic of the Congo,³¹Kadoorie Institute and School of Biological Sciences, The University of Hong Kong, Pokfulam, Hong Kong,³²Department of Renewable Resources, University of Alberta, Edmonton, AB, Canada,³³Computational Earth Sciences Group, Oak Ridge National Laboratory, Oak Ridge, TN, USA,³⁴Department of Natural and Applied Sciences, University of Wisconsin-Green Bay, Green Bay, WI 54311, USA,³⁵Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA, USA,³⁶College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa, Honolulu, HI, USA,³⁷Resource Ecology Group, Wageningen University, Wageningen, The Netherlands,³⁸Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China,³⁹Graduate School of Agriculture, Kyoto University, Kyoto, Japan,⁴⁰National Museums of Kenya, P.O. Box 40658 -00100, Nairobi, Kenya,⁴¹Land Resource Management & Agricultural Technology Department, University of Nairobi, P.O. Box 29053-00625 Nairobi, Kenya,⁴²Mpala Research Centre, PO Box 555, Nanyuki 10400, Kenya,⁴³Global Conservation Programs, Wildlife Conservation Society, 2300 Southern Blvd., Bronx, NY 10460, USA,⁴⁴Department of Forest Ecology, Silva Tarouca Research Institute, Brno, Czech Republic,⁴⁵Department of Forest Management, College of Forestry and Conservation, The University of Montana, Missoula, MT, USA,⁴⁶Research Institute of Tropical Forestry, Chinese Academy of Forestry, Guangzhou, China,⁴⁷Guangxi Institute of Botany, Chinese Academy of Sciences, Guilin, Guangxi, China,⁴⁸Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing, China,⁴⁹Natural Sciences & Science Education Academic Group, National Institute of Education, Nanyang Technological University, Singapore,⁵⁰Wildland Resources Department, Utah State University, Logan, UT, USA,⁵¹Wildlife Conservation Society, Brazzaville, Democratic Republic of the Congo,⁵²Environmental and Life Sciences, Faculty of Science, Universiti of Brunei Darussalam, Tungku Link Road, BE 1410, Bandar Seri Begawan, Brunei Darussalam,⁵³Forest Ecology Group, Smithsonian Environmental Research Center, Edgewater, MD, USA,⁵⁴Institut de Recherche en Ecologie Tropicale/Centre National de la Recherche Scientifique et Technologique, Libreville, GABON,⁵⁵Natural England, Sheffield, England, UK,⁵⁶Department of Biology, Washington University in St. Louis, St. Louis, MO, USA,⁵⁷New Guinea Binatang Research Centre, PO Box 604, Madang, Papua New Guinea,⁵⁸Biology Centre, Academy of Sciences of the Czech Republic and Faculty of Science, University of South Bohemia, Branisovska 31, Ceske Budejovice 370 05, Czech Republic,⁵⁹Departamento Ecologia, Universidade de São Paulo, Instituto de Biociências, Cidade Universitária, São Paulo, SP, Brazil,⁶⁰Institute of Biology, University of the Philippines Diliman, Quezon City, Philippines,⁶¹Harvard Forest, Harvard University, Petersham, MA, USA,⁶²Department of Biology, University of Hawaii, Hilo, HI, USA,⁶³Forest Ecology and Forest Management Group, Wageningen University, Wageningen, The Netherlands,⁶⁴Tropical Plant Exploration Group (TroPEG), P.O. Box 18 Mundemba, Southwest Region, Cameroon,⁶⁵Faculty of Architecture and Environmental Design, Maejo University, Chiang Mai Province, Thailand,⁶⁶Department of Natural Resources and Environmental Studies, National Dong Hwa University, Hualien, Taiwan,⁶⁷Sarawak Forest Department, Kuching, Sarawak, Malaysia,⁶⁸Faculty of Forestry, University of Toronto, 33 Willcocks St., Toronto, ON M5S 3B3, Canada,⁶⁹School of Biological Sciences, Washington State University, Vancouver, WA, USA,⁷⁰Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK,⁷¹Institute for Tropical Ecosystem Studies, Department of Environmental Science, University of Puerto Rico, Rio Piedras Campus, PO Box 70357, San Juan 00936-8377, Puerto Rico,⁷²Department of Ecology, Evolution & Environmental Biology, Columbia University, New York, NY, USA,⁷³Department of Biological Sciences, Pontifical Catholic University of Ecuador, Apartado Postal 17-01-2184, Quito, Ecuador,⁷⁴Calle 37, Instituto Alexander von Humboldt, Number 8-40 Mezzanine, Bogotá, Colombia,⁷⁵Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil,⁷⁶School of ecological and environmental sciences, East China Normal University, Shanghai, China,⁷⁷Department of Plant Biology, University of Minnesota, St. Paul, MN, USA,⁷⁸Departments of Biology & Natural & Applied Sciences, Lab Sciences 435, UW-Green Bay, Green Bay, WI 54311, USA

Abstract

Global change is impacting forests worldwide, threatening biodiversity and ecosystem services including climate regulation. Understanding how forests respond is critical to forest conservation and climate protection. This review describes an international network of 59 long-term forest dynamics research sites (CTFS-ForestGEO) useful for characterizing forest responses to global change. Within very large plots (median size 25 ha), all stems ≥ 1 cm diameter are identified to species, mapped, and regularly recensused according to standardized protocols. CTFS-ForestGEO spans 25°S–61°N latitude, is generally representative of the range of bioclimatic, edaphic, and topographic conditions experienced by forests worldwide, and is the only forest monitoring network that applies a standardized protocol to

each of the world's major forest biomes. Supplementary standardized measurements at subsets of the sites provide additional information on plants, animals, and ecosystem and environmental variables. CTFs-ForestGEO sites are experiencing multifaceted anthropogenic global change pressures including warming (average 0.61 °C), changes in precipitation (up to $\pm 30\%$ change), atmospheric deposition of nitrogen and sulfur compounds (up to 3.8 g N m⁻² yr⁻¹ and 3.1 g S m⁻² yr⁻¹), and forest fragmentation in the surrounding landscape (up to 88% reduced tree cover within 5 km). The broad suite of measurements made at CTFs-ForestGEO sites makes it possible to investigate the complex ways in which global change is impacting forest dynamics. Ongoing research across the CTFs-ForestGEO network is yielding insights into how and why the forests are changing, and continued monitoring will provide vital contributions to understanding worldwide forest diversity and dynamics in an era of global change.

Keywords: biodiversity, Center for Tropical Forest Science (CTFS), climate change, demography, forest dynamics plot, Forest Global Earth Observatory (ForestGEO), long-term monitoring, spatial analysis

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Introduction

Forests play key roles in biodiversity maintenance and climate regulation. Globally, they support over half of all described species and provide a range of valuable ecosystem services (Groombridge, 2002; Pan *et al.*, 2013). Forests play a particularly significant role in climate regulation; they contain ~45% of carbon (C) in the terrestrial biosphere and influence climate on local to global scales through their low albedo and high rates of evapotranspiration (Snyder *et al.*, 2004; Bonan, 2008; Anderson-Teixeira *et al.*, 2012; Pan *et al.*, 2013). Global change pressures – including climate change, pollution, agricultural expansion, logging, nontimber forest product extraction, hunting, and the spread of invasive species – are affecting forests worldwide, threatening biodiversity, altering community composition, and driving feedbacks to climate change (Foley *et al.*, 2005; Chapin *et al.*, 2008; Wright, 2010). Understanding and predicting such changes will be critical to biodiversity conservation, management of ecosystem services, and climate protection.

The Center for Tropical Forest Science (CTFS) – Forest Global Earth Observatory (ForestGEO) is a global network of forest research sites that is strategically poised for monitoring, understanding, and predicting forest responses to global change. This international partnership currently includes 59 long-term forest dynamics research sites in 24 countries (Fig. 1), which have been monitored continuously since as early as 1981 (Barro Colorado Island; Condit, 1995). The network applies a unique standardized tree census protocol across all of the world's major forest biomes, allowing comparison across sites (e.g., Condit, 2000; Muller-Landau *et al.*, 2006a,b; Chave *et al.*, 2008; Chisholm *et al.*, 2013, 2014). Supplementary measurements, also following standardized procedures, provide additional information on plants, animals, and ecosystem

processes, making it possible to identify ecological interactions that might otherwise be missed (e.g., Harrison *et al.*, 2013). This review describes the defining features of a CTFs-ForestGEO plot, the distribution and representativeness of CTFs-ForestGEO sites, supplementary measurements and their applications, global change pressures across the CTFs-ForestGEO network, and the impacts of these drivers documented to date.

Attributes of a CTFs-ForestGEO plot

The unifying measurement at all CTFs-ForestGEO sites is an intensive census of all freestanding woody stems ≥ 1 cm diameter at breast height (DBH), typically repeated every 5 years, that characterizes forest structure, diversity and dynamics over a large spatial area (Table 1). Plot sizes are large, ranging from 2 to 120 ha, with a median size of 25 ha and 90% ≥ 10 ha (Table 2). Following standardized methodology, each individual (genet) is mapped, tagged, and identified to species when it first enters the census. In the case of multi-stemmed individuals, each stem ≥ 1 cm DBH (ramet) is censused. On each stem, diameter is measured at breast height (1.3 m) or above stem irregularities (Manokaran *et al.*, 1990; Condit, 1998). The census includes both trees and shrubs; henceforth, the term “trees” will refer to all individuals in the census. An accompanying fine-scale topographic survey allows identification of topographically defined habitat types (e.g., ridges, valleys, slopes; Condit, 1998). This core CTFs-ForestGEO protocol has proved useful for a wide range of analyses (Table 1).

Site distribution and representativeness

This core tree census protocol has been applied to 59 sites distributed among all of the world's major forest biomes, making CTFs-ForestGEO the only international forest monitoring network with global distribution (Fig. 1; Table 2). In total, 1653 ha of forest (>5.68

Correspondence: Kristina J. Anderson-Teixeira,
tel. 1 540 635 6546, fax 1 540 635 6506, e-mail: teixeirak@si.edu

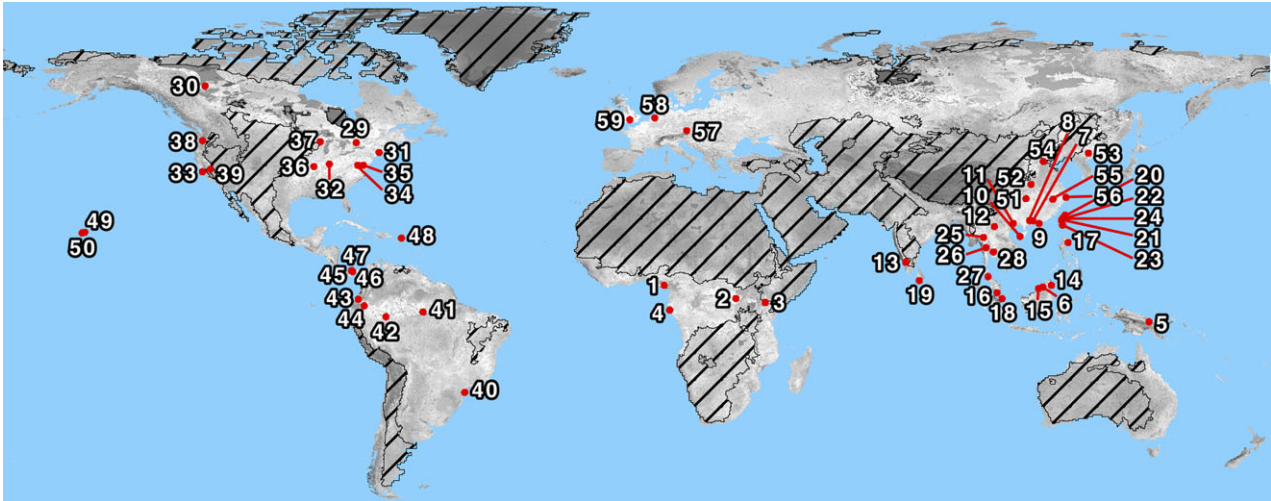


Fig. 1 Map of the CTFS-ForestGEO network illustrating its representation of bioclimatic, edaphic, and topographic conditions globally. Site numbers correspond to ID# in Table 2. Shading indicates how well the network of sites represents the suite of environmental factors included in the analysis; light-colored areas are well-represented by the network, while dark colored areas are poorly represented. Stippling covers nonforest areas. The analysis is described in Appendix S1.

Table 1 Attributes of a CTFS-ForestGEO census

Attribute	Utility
Very large plot size	Resolve community and population dynamics of highly diverse forests with many rare species with sufficient sample sizes (Losos & Leigh, 2004; Condit <i>et al.</i> , 2006); quantify spatial patterns at multiple scales (Condit <i>et al.</i> , 2000; Wiegand <i>et al.</i> , 2007a,b; Detto & Muller-Landau, 2013; Lutz <i>et al.</i> , 2013); characterize gap dynamics (Feeley <i>et al.</i> , 2007b); calibrate and validate remote sensing and models, particularly those with large spatial grain (Mascaro <i>et al.</i> , 2011; Réjou-Méchain <i>et al.</i> , 2014)
Includes every freestanding woody stem ≥ 1 cm DBH	Characterize the abundance and diversity of understory as well as canopy trees; quantify the demography of juveniles (Condit, 2000; Muller-Landau <i>et al.</i> , 2006a,b).
All individuals identified to species	Characterize patterns of diversity, species-area, and abundance distributions (Hubbell, 1979, 2001; He & Legendre, 2002; Condit <i>et al.</i> , 2005; John <i>et al.</i> , 2007; Shen <i>et al.</i> , 2009; He & Hubbell, 2011; Wang <i>et al.</i> , 2011; Cheng <i>et al.</i> , 2012); test theories of competition and coexistence (Brown <i>et al.</i> , 2013); describe poorly known plant species (Gereau & Kenfack, 2000; Davies, 2001; Davies <i>et al.</i> , 2001; Sonké <i>et al.</i> , 2002; Kenfack <i>et al.</i> , 2004, 2006)
Diameter measured on all stems	Characterize size-abundance distributions (Muller-Landau <i>et al.</i> , 2006b; Lai <i>et al.</i> , 2013; Lutz <i>et al.</i> , 2013); combine with allometries to estimate whole-ecosystem properties such as biomass (Chave <i>et al.</i> , 2008; Valencia <i>et al.</i> , 2009; Lin <i>et al.</i> , 2012; Ngo <i>et al.</i> , 2013; Muller-Landau <i>et al.</i> , 2014)
Mapping of all stems and fine-scale topography	Characterize the spatial pattern of populations (Condit, 2000); conduct spatially explicit analyses of neighborhood influences (Condit <i>et al.</i> , 1992; Hubbell <i>et al.</i> , 2001; Uriarte <i>et al.</i> , 2004, 2005; Rüger <i>et al.</i> , 2011, 2012; Lutz <i>et al.</i> , 2014); characterize microhabitat specificity and controls on demography, biomass, etc. (Harms <i>et al.</i> , 2001; Valencia <i>et al.</i> , 2004; Chuyong <i>et al.</i> , 2011); align on the ground and remote sensing measurements (Asner <i>et al.</i> , 2011; Mascaro <i>et al.</i> , 2011).
Census typically repeated every 5 years	Characterize demographic rates and changes therein (Russo <i>et al.</i> , 2005; Muller-Landau <i>et al.</i> , 2006a,b; Feeley <i>et al.</i> , 2007a; Lai <i>et al.</i> , 2013; Stephenson <i>et al.</i> , 2014); characterize changes in community composition (Losos & Leigh, 2004; Chave <i>et al.</i> , 2008; Feeley <i>et al.</i> , 2011; Swenson <i>et al.</i> , 2012; Chisholm <i>et al.</i> , 2014); characterize changes in biomass or productivity (Chave <i>et al.</i> , 2008; Banin <i>et al.</i> , 2014; Muller-Landau <i>et al.</i> , 2014)

Table 2 Characteristics of the CTFS-ForestGEO sites. Sites are ordered alphabetically by biogeographic zone (*sensu* Olson *et al.*, 2001), then by country, and finally by site name. More site data are given in the appendix (Tables S1–S7) and online (<http://www.ctfs.si.edu/Data>)

No.	Site	Country	Köppen Climate zone†	MAT (°C)‡	MAP (mm yr ⁻¹)‡	Dominant Soil order(s)§	Dominant vegetation type(s)**	Natural Dist. Regime††	N species	Plot Size (ha)	Year established‡‡
<i>Afrotropics</i>											
1	Korup	Cameroon	Am	26.6	5272	Ult, Ox	BE	W	494	55	1996
2	Ituri (Eldoro and Lenda)	Democratic Republic of Congo	Af	24.3	1682	Ox	BE	W; A	445	40	1994
3	Rabi	Gabon	Aw	26.0	2282	Ox	BE	W	342	25	2010
4	Mpala	Kenya	Cfb	17.9	657	Alf; Ve	BdD	Fi, A	22	120	2011
<i>Australasia</i>											
5	Wanang	Papua New Guinea	Af	26.0	3500	Alf; In	BE	L; E	500*	50	2009
<i>Indo-Malaya</i>											
6	Kuala Belalong	Brunei Darussalam	Af	26.5	5203	Ult	BE	L	850–1050*	25	2009
7	Dinghushan	China	Cfa	20.9	1985		BE		210	20	2005
8	Heishiding	China	Cfa	22.0	1744		BE		245	50	2013
9	Hong Kong	China	Cwa	23.3	2399	Ox	BE	H	67–147*	21	2012
10	Jianfengling	China	Aw	19.8	1657	Ult	BE	H	291	60	2012
11	Nonggang	China	Cwa	22.0	1376	Ox	BE; BdD	D	223	15	2011
12	Xishuangbanna	China	Cwa	21.8	1493	Ox	BE	W; D	468	20	2007
13	Mudumalai	India	Aw	22.7	1255	Alf	BdD	Fi; A; D	72	50	1987
14	Danum Valley	Malaysia	Af	26.7	2822	Ult	BE	D; A	*	50	2010
15	Lambir	Malaysia	Af	26.6	2664	Ult	BE	L; D	1182	52	1991
16	Pasoh	Malaysia	Af	27.9	1788	Ult	BE	W	814	50	1986
17	Palanan	Philippines	Af	26.1	3380	Ult; In	BE	H	335	16	1994
18	Bukit Timah	Singapore	Af	26.9	2473	Ult	BE	A	347	4	1993
19	Sinhharaja	Sri Lanka	Af	22.5	5016	Ult	BE	W	204	25	1993
20	Fushan	Taiwan	Cfa	18.2	4271	Ult; In	BE	H	110	25	2004
21	Kenting	Taiwan	Am	25.4	1964		BE	H	95	10	1996
22	Lienhuachih	Taiwan	Cwb	20.8	2211	Ult	BE	H; L	144	25	2008
23	Nanjenshan	Taiwan	Aw	23.5	3582	Ult	BE; BdD	W; H	125	6	1989
24	Zenlun	Taiwan	Am	22.7	2620	Ult	NE	H		12	2005
25	Doi Inthanon	Thailand	Aw	20.9	1908	Ult	BE	–	162	15	1997
26	Huai Kha Khaeng (HKK)	Thailand	Aw	23.5	1476	Alf	BE; BdD	Fi; D	251	50	1992
27	Khao Chong	Thailand	Am	27.1	2611	Ult; In	BE	W; L	593	24	2000
28	Mo Singto	Thailand	Aw	23.5	2100		BE; BdD	W	262	30.5	2000

Table 2 (continued)

No.	Site	Country	Köppen Climate zone†	MAT (°C)‡	MAP (mm yr ⁻¹)‡	Dominant Soil order(s)§	Dominant vegetation type(s)**	Natural Dist. Regime††	N species	Plot Size (ha)	Year established‡‡
<i>Nearctic</i>											
29	Haliburton	Canada	Dfb	4.2	962		BcD	–	30	13.5	2007
30	Scotty Creek	Canada	Dfc	–3.2	369	Ge	NE	PT; Fi	12–15*	21	2013
31	Harvard Forest	USA	Dfb	9.0	1050	In	BdD	H	60	35	2010
32	Lilly Dickey Woods	USA	Cfa	11.6	1203	In; Ult; Alf	BcD	W; D; Ic	35	25	2009
33	Santa Cruz	USA	Csb	14.8	778	Mo	BE; NE	Fi, W	33	16	2007
34	Smithsonian Conservation Biology Institute (SCBI)	USA	Cfa	12.9	1001	Alf	BcD	W, Ic	64	25.6	2008
35	Smithsonian Environmental Research Center (SERC)	USA	Cfa	13.2	1068	Ult; In; En	BcD	H; W	79	16	2007
36	Tyson Research Center	USA	Cfa	13.5	957	Alf	BcD	D; Fi; Ic; W	42	20	2013
37	Wabikon	USA	Dfb	4.2	805	Alf	BcD	W	42	25.6	2008
38	Wind River	USA	Csb	9.2	2495	An	NE	Fi; W; In	26	25.6	2010
39	Yosemite National Park	USA	Csb	10.2	1065	Alf	NE	Fi; W; D; In	23	25.6	2009
<i>Neotropics</i>											
40	Ilha do Cardoso	Brazil	Cfa	22.4	2100	S	BE		106	10.2	2004
41	Manaus	Brazil	Af	26.7	2600	Ox	BE	W	1440*	25	2004
42	Amacayacu	Colombia	Af	25.8	3215	Ult	BE	FI	1133	25	2006
43	La Planada	Colombia	Cfb	19.0	4087	An	BE	W	240	25	1997
44	Yasuni	Ecuador	Af	28.3	3081	Ult	BE	–	1114	50	1995
45	Barro Colorado Island (BCI)	Panama	Am	27.1	2551	Ox	BdD; BE	D; W	299	50	1981
46	Cocoli	Panama	Am	26.6	1950	Ox; In	BdD; BE	D; W	176	4	1994
47	San Lorenzo/ Sherman	Panama	Am	26.2	3030		BE	D; W	238	6	1996
48	Luquillo	Puerto Rico, USA	Am	22.8	3548	Ox; Ult	BE	H; L	138	16	1990
<i>Oceania</i>											
49	Laupahoehoe	USA	Cfb	16.0	3440	An	BE	W	21	4	2008
50	Palamani	USA	Cfb	20.0	835	Hi	BE	W	15	4	2008
<i>Paleartic</i>											

Table 2 (continued)

No.	Site	Country	Köppen Climate zone†	MAT (°C)‡	MAP (mm yr ⁻¹)‡	Dominant Soil order(s)§	Dominant vegetation type(s)**	Natural Dist. Regime††	N species	Plot Size (ha)	Year established‡‡
51	Badagongshan	China	Cfa	15.9	1410	In	BE, BbD	FI	238	25	2011
52	Baotianman	China	Cwa	15.1	886		BbD	A; D	126	25	2009
53	Changbaishan	China	Dwb	2.9	700	Alf	NE; BcD		52	25	2004
54	Donglingshan	China	Dwb	4.7	570	Alf	BcD	Fi	58	20	2010
55	Gutianshan	China	Cfa	15.3	1964	Ult	BE; BbD	Ic	159	24	2005
56	Tiantongshan	China	Cfa	16.2	1375	Ox	BE	H; D	153	20	2008
57	Zofin	Czech Republic	Cfb	6.2	866	S; In; Hi	BcD; NE	W; In	12	25	2012
58	Speulderbos	Netherlands	Cfb	10.1	833	In	BcD	W; A	13	27	2013
59	Wytham Woods	UK	Cfb	10.0	717	E	BcD		23	18	2008

*Measurement in progress.

†Af: Tropical with significant precipitation year-round; Am: Tropical monsoon; Aw: Tropical wet and dry; Csb-Dry-summer subtropical/mid-latitude climate with dry summers (a.k.a.: Warm-summer Mediterranean); Cfa: Humid subtropical/mid-latitude climate with significant precipitation year-round; Cwa: Humid subtropical/mid-latitude climate with dry winters; Cfb: Oceanic with significant precipitation year-round; Cwb: Oceanic with dry winters; Dfc: Subarctic.

‡Climate data are the best available for each site (based on judgment of site Pls; years vary). For sites where local data are not available or not reported, values (*italicized*) are mean 1950–2000 climate from WorldClim at 30 arcsecond resolution (Table S4; Hijmans *et al.*, 2005).

§Categorical following the USDA Soil Taxonomy System (Soil Survey Staff, 1999): Alf, Alfisols; An, Andisols; E, Entisols; Ge, Gelisols; Hi, Histosols; In, Inceptisols; Ox, Oxisols; Ult, Ultisols; S, Spodosols; Ve, Vertisols.

**BE, broadleaf evergreen; BbD, broadleaf drought deciduous; BcD, broadleaf cold deciduous; NE, needleleaf evergreen.

††A, animal activity (destructive); D, Drought; E, Erosion; Fi, Fire; FI, flood; H, hurricane/typhoon; Ic, Ice storms; Ininsect outbreaks; L, landslides; PT, permafrost thaw; W, wind storms (local); '-', no major natural disturbances.

‡‡When census spanned multiple years, the first year is listed.

million individuals) are currently monitored, with a cumulative sum of >17 000 ha-years of forest monitoring.

CTFS-ForestGEO sites cover a wide diversity of physical and biotic environments (Figs 1 and 2; Table 1, Table S1). The network spans latitudes 25°S–61°N, with sites in every biogeographic realm (*sensu* Olson *et al.*, 2001; Table 1, Table S1). Climate varies widely (Fig. 2; Table 1, Table S2): mean annual temperature (MAT) ranges from –3.2 °C (Scotty Creek, Canada) to 28.3 °C (Yasuni, Ecuador), and mean annual precipitation (MAP) from 369 mm yr^{–1} (Scotty Creek, Canada) to 5272 mm yr^{–1} (Korup, Cameroon). Elevation ranges from 3 m.a.s.l. (Ilha do Cardoso, Brazil) to 1911 m.a.s.l. (Yosemite, USA), and relief from 4 m (SERC, USA) to 298 m (Tiantongshan, China; Table S1). According to the Soil Survey Staff (1999) soil classification, 11 of the world's 12 soil orders are represented (the exception is Aridisols; Table 1), with corresponding marked variation in fertility.

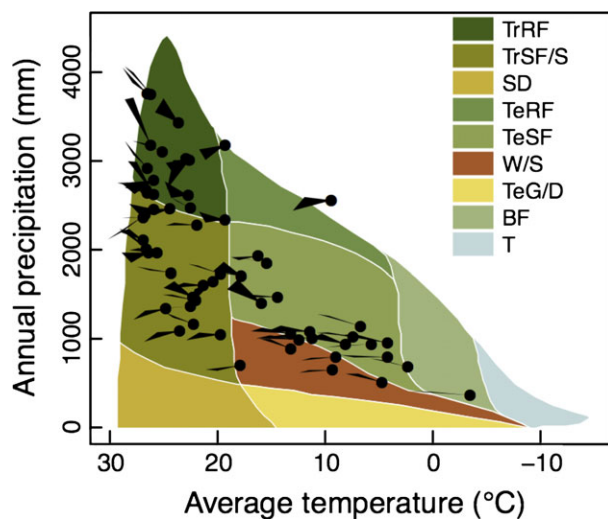


Fig. 2 Current and projected future (2050) mean annual temperature and precipitation of CTFS-ForestGEO sites superimposed upon Whittaker's classic climate-biomes diagram (Whittaker, 1975; Ricklefs, 2007). Dots represent average climate from 1950 to 2000. Wedges represent the range of projected climates through 2050 as projected by the HADGEM2-ES model; specifically, smaller and larger temperature increases represent IPCC's RCP 2.6 and RCP 8.5 scenarios, respectively. Biome codes are as follows: TrRF, tropical rain forest; TrSF/S, tropical seasonal forest/savanna; SD, subtropical desert; TeRF, temperate rain forest; TeSF, temperate seasonal forest; W/S, woodland/shrubland; TeG/D, temperate grassland/desert; BF, boreal forest; T, tundra. Data from WorldClim (worldclim.org); recent climate data differ from those in Table 1. Details on climate data and analysis are given in Appendix S1; data are listed in Table S4.

The CTFS-ForestGEO network is generally representative of the range of bioclimatic, edaphic, and topographic conditions experienced by forests globally (Fig. 1), as evidenced by a multivariate spatial clustering analysis with 4 km resolution (Hargrove *et al.*, 2003; Hoffman *et al.*, 2013; Maddalena *et al.*, 2014; Appendix S1). Particularly well-represented regions include tropical rain forests on upland or 'tierra firme' habitats – especially in the Indo-Malay biogeographic zone – and temperate forests of Eastern China and Eastern North America. Underrepresented regions include temperate forests in the Southern Hemisphere; seasonal forests and woodland savannas south and east of the Amazon and in Africa; the Rocky Mountains of North America; and boreal forests – particularly in the Palearctic biogeographic zone. On a finer scale, many of the CTFS-ForestGEO sites in Asia, Europe, and North America are on more topographically complex terrain compared to the original forest distribution, as are most remaining intact forests in these regions. Forests with extreme edaphic conditions – for example, mangrove, swamp, and peat forests – remain almost completely unrepresented.

Dominant vegetation types of the CTFS-ForestGEO sites include broadleaf evergreen, broadleaf drought deciduous, broadleaf cold deciduous, and needle-leaf evergreen forests (Table 1). Floristically, the network has extensive coverage, with >10 000 tree and shrub species (and >14 000 unique site-species combinations). Unique tree floras that are not yet represented include the high-endemism forests of Madagascar; southern temperate forests in New Zealand, Australia, and southern South America; and dry forests in Africa and the southern and eastern Amazon.

The sites are generally in old-growth or mature secondary forests and are commonly among the most intact, biodiverse, and well-protected forests within their region. They are subjected to a range of natural disturbances (Table 1), and a number of sites have experienced significant natural disturbances in recent years (e.g., fire at Yosemite, typhoons at Palanan). In addition, most sites have experienced some level of anthropogenic disturbance (discussed below; Table S5).

Supplementary measurements and applications

At all sites, the core census is complemented by one or more supplementary measurements that provide further basis for standardized comparisons across the world's major forest biomes. Supplementary measurements provide additional information on plants, animals, and ecosystem and environmental variables (Table 3). In this section, we review CTFS-ForestGEO-specific protocols and other relatively standard

Table 3 Summary of supplementary CTFs-ForestGEO measurement protocols applied at five or more sites

Measurement	N sites*	Description	Utility
Plants			
Lianas	7 (15)	Lianas are included as part of the core census; they are mapped, identified to species, and measured at breast height (1.3 m)	Characterize liana abundance and diversity and changes therein (Schnitzer, 2005; DeWalt <i>et al.</i> , 2015; Thomas <i>et al.</i> , 2015); understand liana impacts on tree community (Ingwell <i>et al.</i> , 2010).
Functional traits	33 (39)†	Traits characterized include three dimensions (maximum height and crown diameter); leaf traits [size, specific leaf area, thickness, (N), (P), dry matter content]; wood traits (stem wood density, C content); and reproductive traits (dispersal mode; fruit, diaspore, and seed fresh and dry masses).	Characterize species' differences in physiology and ecological roles (Condit <i>et al.</i> , 1996; Santiago & Wright, 2007; Muller-Landau <i>et al.</i> , 2008; Kraft <i>et al.</i> , 2010; Wright <i>et al.</i> , 2010; Westbrook <i>et al.</i> , 2011; Katabuchi <i>et al.</i> , 2012; Liu <i>et al.</i> , 2012); detect directional changes in functional composition (Feeley <i>et al.</i> , 2011; Hietz <i>et al.</i> , 2011; Swenson <i>et al.</i> , 2012; Harrison <i>et al.</i> , 2013); improve inventory-based C stock estimates (Martin & Thomas, 2011; Cushman <i>et al.</i> , 2014); parameterize models
High-precision diameter growth	28 (32)	Diameter growth is measured weekly to annually using dendrometer bands on a subset of trees.	Understand effects of tree size, species, and environmental conditions on growth; characterize seasonal growth patterns (McMahon & Parker, 2014); estimate the woody stem growth component of aboveground net primary productivity (ANPP _{wood})
Flower & seed production	24 (33)	Species-level flower & seed production are quantified using weekly to bimonthly censuses of 60–336 0.5-m ² traps.	Quantify reproductive phenology (Zimmerman <i>et al.</i> , 2007); infer seed dispersal distances (Muller-Landau <i>et al.</i> , 2008); quantify interannual variation and its ecological implications (Wright <i>et al.</i> , 1999, 2005; Harms <i>et al.</i> , 2000; Usinowicz <i>et al.</i> , 2012); detect directional changes (Wright & Calderon, 2006)
Seedling performance	21 (30)	Seedling establishment, growth and survival are quantified annually in three 1-m ² plots associated with each seed trap.	Characterize density- and distance-dependent effects on con- and hetero-specific seedling recruitment (Harms <i>et al.</i> , 2000; Comita <i>et al.</i> , 2010; Lebrija-Trejos <i>et al.</i> , 2013); Understand postdisturbance successional dynamics (Dalling <i>et al.</i> , 1998; Dalling & Hubbell, 2002)
DNA barcoding	27 (28)	Short DNA sequences from a standard position within the genome are used to construct phylogenies and distinguish individual species from one another. Can be applied to all tissues of the plants (e.g., roots, pollen, leaves, and bark) or animals. Over 3000 plant species have been barcoded to date.	Build phylogenetic trees of local community relationships and investigate constraints on the assembly of communities (Pei <i>et al.</i> , 2011; Swenson <i>et al.</i> , 2011; Lebrija-Trejos <i>et al.</i> , 2013); identify tree roots to species (Jones <i>et al.</i> , 2011); reconstruct networks of feeding, pollination, and parasitism – (Hrcek <i>et al.</i> , 2011)
Animals			
Arthropods	5 (13)		

Table 3 (continued)

Measurement	N sites*	Description	Utility
		A variety of key taxa are monitored 1–4 times annually†using a variety of techniques (light traps, Winkler extractors, McPhail traps, butterfly transects, termite transects, and bee baits).	Elucidate the role of arthropods in forest ecosystems (Novotny <i>et al.</i> , 2002; Novotny & Basset, 2005); evaluate the impact of global change on the full range of forest trophic levels
Vertebrates	14 (34)	Camera trapping is used to monitor terrestrial mammals.	Elucidate the role of vertebrates in forest ecosystems; detect directional changes
Ecosystem & Environmental			
Aboveground biomass	59	Ground based: Biomass is estimated from core census data using best available allometries, often in combination with site-specific height and wood density data.	Characterize spatial variation in biomass within sites in relation to environmental gradients and species diversity (Valencia <i>et al.</i> , 2009; Chisholm <i>et al.</i> , 2013); detect directional changes in C stocks (Chave <i>et al.</i> , 2008; Muller-Landau <i>et al.</i> , 2014); calibrate and evaluate models of biomass based on airborne LiDAR (Asner <i>et al.</i> , 2011; Mascaro <i>et al.</i> , 2011; Réjou-Méchain <i>et al.</i> , 2014)
	(15)	Airborne: LiDAR flights (one-time or repeated) provide data on biomass and tree architecture.	
Dead wood/CWD	21 (25)	Standing dead wood and fallen coarse woody debris are surveyed by transect or comprehensive survey.	Quantify C stocks in dead wood and changes therein
Fine root biomass & soil carbon	16 (32)	Measured to 3 m depth on every hectare, with additional replicates to shallower depths.	Understand the role of associations between plants and mycorrhizal fungi in driving soil carbon storage (Peay <i>et al.</i> , 2010; Averill <i>et al.</i> , 2014)
Soil nutrients	23 (26)	Extractable soil cations, available N, nitrogen mineralization rates, and extractable phosphorus at 0 to 10-cm depths are measured at high spatial resolution.	Characterize species' microhabitat associations (Lee <i>et al.</i> , 2002; Davies <i>et al.</i> , 2003; John <i>et al.</i> , 2007; Tan <i>et al.</i> , 2009; Baldeck <i>et al.</i> , 2013a,b,c; De Oliveira <i>et al.</i> , 2014); characterize plant performance in relation to soil nutrients (Russo <i>et al.</i> , 2005, 2013)
Litterfall	21 (29)	Litter is collected biweekly to monthly from traps, oven-dried, sorted (to leaves, woody, reproductive, and other), and weighed.	In combination with woody growth data, quantify aboveground net primary productivity (ANPP) and its phenology and environmental drivers
Bio-micrometeorology	(13)	Eddy-covariance technique is used to continuously measure CO ₂ , H ₂ O, and energy exchange between ecosystem and the atmosphere.	Understand forest ecophysiology and C cycling on half-hourly to multiannual time scales
Meteorology	5(33)	Some sites have local meteorological stations within 10 km of the plot.	Characterize climatic controls on forest processes such as flower and fruit production, tree growth and mortality, and ecosystem-atmosphere gas exchange (Condit <i>et al.</i> , 2004; Wright & Calderon, 2006; Feeley <i>et al.</i> , 2007a; Dong <i>et al.</i> , 2012; Li <i>et al.</i> , 2012)

*Numbers indicate sites where measurements have been made or are in progress following a specific CTFS Forest GEO protocol. Numbers in parentheses indicate total number of sites with measurements using any protocol.

†Varies by trait. Number indicates sites with measurements of one or more functional traits.

‡Varies by protocol. See Appendix S1 for details.

measurements that are comparable across sites. The Supplementary Information section provides further information on methodologies (Appendix S2) and details which measurements have been made at each site (Tables S6 and S7).

Plants

Supplementary measurements on plants include liana abundance and diversity, functional traits, high-precision diameter growth, flower and seed production, seedling performance, and DNA barcoding (Table 3). Liana censuses help to characterize the important role of lianas in forest dynamics. Measurements of functional traits – well-defined, measurable properties of organisms that are strongly associated with ecological performance – provide information on key attributes and ecological roles of the species included in the census. High-precision growth measurements provide fine-scale understanding of temporal and spatial variation in tree growth and forest productivity. Flower, seed and seedling censuses enable study of complete tree life cycles, which are critically important for forest regeneration and long-term species persistence. DNA barcoding provides a powerful means of species identification that allows elucidation of phylogenetic relationships and ecological roles (Dick & Kress, 2009; Kress *et al.*, 2009, 2010).

Animals-

Arthropod and vertebrate initiatives (Table 3) yield understanding of the roles of these taxa in forest dynamics through their roles as herbivores, pollinators, seed dispersers, predators, ecosystem engineers, and vectors of microbial diversity. In a unique effort to monitor multitaxon assemblages in tropical rainforests (Basset *et al.*, 2013; but see Leidner *et al.*, 2010 for long-term monitoring of a single taxon), key arthropod groups are being monitored to better understand how interactions between arthropods and plants affect forest dynamics and to evaluate the impact of global change on the full range of forest trophic levels. Vertebrate monitoring is helping to elucidate how mammals differentially affect tree species and how modification of the fauna may impact the future forest (e.g., Wright *et al.*, 2007; Harrison *et al.*, 2013; see below).

Ecosystem and environmental

Supplementary measurements of ecosystem and environmental variables include major aboveground C stocks and fluxes (aboveground biomass, standing dead wood and coarse woody debris, ANPP_{wood}, litter-

fall, net ecosystem exchange); soil nutrients, C, and fine root biomass; bio-micrometeorology, and meteorology (Table 3). These measurements provide a basis for understanding environmental and biotic controls on C stocks and fluxes within forest ecosystems and how these may respond to global change. Soils measurements provide a basis for understanding the critical role of soils in determining species composition, forest structure, and primary productivity, as well as their globally significant role as an important C reservoir. Bio-micrometeorological measurements further elucidate the important role of forests in climate regulation through ongoing exchange of CO₂, H₂O, and energy between the ecosystem and the atmosphere. Meteorological data are critical for understanding how the biotic community and whole ecosystem processes respond to climate variables over half-hourly to multiannual time scales.

Combined applications

In combination, the core tree census and supplementary measurements enable unique analyses of the many interacting components of forest ecosystems, yielding a holistic picture of forest dynamics. For instance, core census data have been combined with data on lianas, vertebrates, seeds, seedlings, and reproductive functional traits to link decreasing populations of seed dispersers to changing patterns of plant reproduction, liana abundance, and tree growth and survival (Wright & Calderon, 2006; Wright *et al.*, 2007; Ingwell *et al.*, 2010; Harrison *et al.*, 2013). Core census, functional trait, and DNA barcoding data have been combined to understand the roles of phylogeny and functional traits in shaping habitat associations and diversity in space and time (Pei *et al.*, 2011; Swenson *et al.*, 2011). The combination of core census data, plant functional traits, ecosystem measurements, soils data, and weather data lend themselves to parameterizing and evaluating ecosystem and earth system models. Thus, the broad suite of standardized measurements at CTFs-ForestGEO sites (Tables 1 and 3) provides opportunities to address a multitude of questions on forest dynamics and their responses to global change pressures.

Global change pressures at CTFs-ForestGEO sites

All ecosystems on Earth – including CTFs-ForestGEO's relatively intact forests – are affected by anthropogenic influences (Fig. 3). Human appropriation of land and water for agriculture and other purposes; emission of extraneous compounds to the atmosphere (e.g., CO₂, CH₄, N₂O, NO_y, NH_x, SO₂) and water (e.g., NO₃⁻, PO₄³⁻); extraction of food, fuel, and fiber from natural

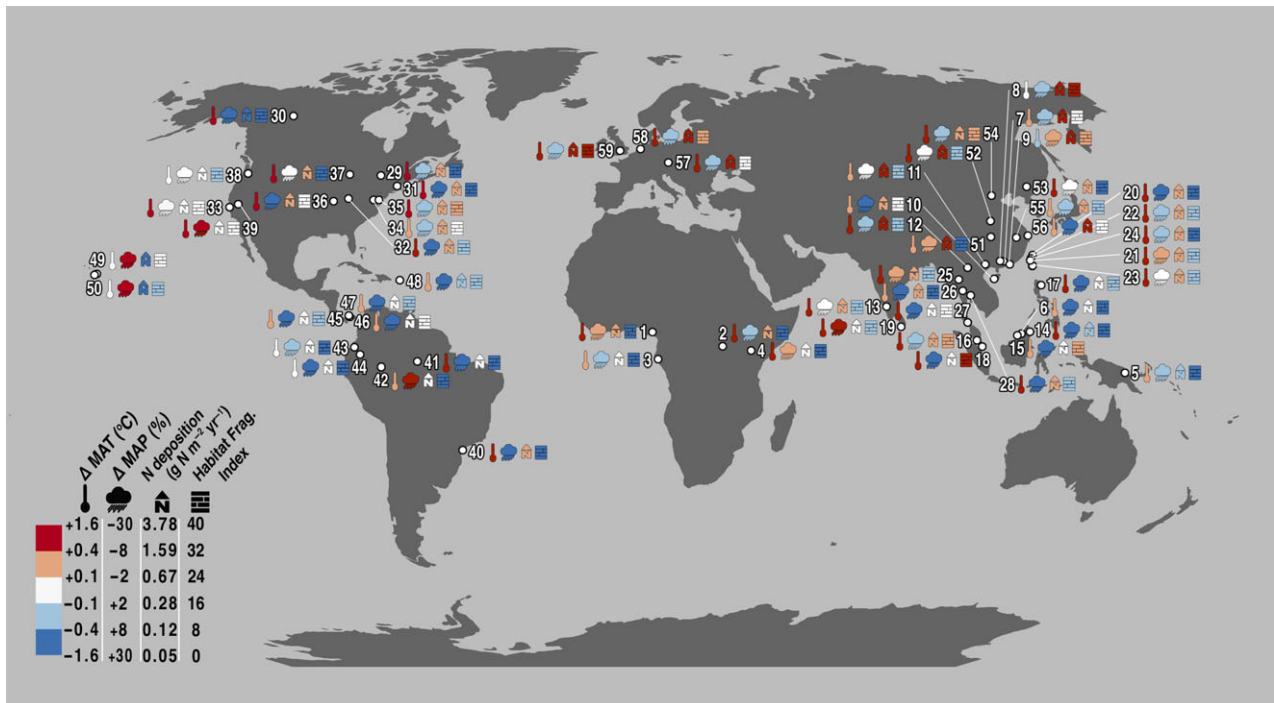


Fig. 3 Map of CTFS-ForestGEO sites illustrating the severity of four global change pressures: changes in mean annual temperature and precipitation relative to the 1951–1980 climatic average (MAT and MAP, respectively; Table S3), total N deposition (Table S5), and an index of habitat fragmentation (see Appendix S1; Table S5). Numbers correspond to ID#s in Table 2. Analyses are detailed in Appendix S1.

ecosystems; and transport of species around the globe has so pervasively influenced Earth's climate, hydrology, biogeochemistry, land cover, and species diversity as to warrant classification of a new geologic period in Earth's history – the Anthropocene (Schlesinger, 2012; Vitousek *et al.*, 1997a; Zalasiewicz *et al.*, 2010, 2011).

Over the lifetime of the CTFS-ForestGEO network, atmospheric CO₂ has increased 16%, from 340 ppm in 1981 to 396 ppm in 2013 (Tans & Keeling, 2014), with variable effects on climate globally. Over a similar time frame, temperatures have increased across the network by an average of 0.61 °C, with greater increases at colder sites (Figs 3 and 4; Table S3; details on data and analysis in Appendix S1). On both annual and daily time scales, minimum temperatures have increased more than maximum temperatures, leading to decreases in the diurnal temperature range. Frost-day frequency has decreased at sites that experience frost. Potential evapotranspiration (PET) has increased slightly on average (+2.5%) – particularly at low-PET sites. A tendency for increased cloud cover has offset the increases in PET that would be expected based on temperature increases alone, and high-PET sites have therefore experienced little change in PET on average (Fig. 4). Changes in mean annual precipitation (MAP) and wet-day frequency have been variable, with an

overall tendency toward increases (averaging 6.0% and 2.7%, respectively) – particularly at high-precipitation sites (Fig. 4). Changes to the difference between annual MAP and PET have also been variable, with a tendency for wet sites (high MAP-PET) to become wetter – particularly in the Neotropical and Indo-Malay biogeographic zones – and low MAP-PET sites to become drier (Fig. 4). Changes in seasonality and the number of months with precipitation < PET have been variable across the network. In summary, CTFS-ForestGEO sites have experienced warming and variable changes in precipitation and aridity.

Ongoing climate change is inevitable, with its course dependent upon future greenhouse gas emissions and land use patterns (IPCC, 2013). The IPCC AR5 examines four representative concentration pathways (RCP's), the most optimistic of which has greenhouse gas emissions going to zero before 2100 (RCP 2.6) and the most pessimistic of which denotes continuously increasing emissions leading to a radiative forcing of 8.5 W m⁻² by 2100 (RCP 8.5; IPCC, 2013). Across this range of future scenarios, the HADGEM2-ES model predicts MAT increases averaging 2.0 °C under RCP 2.6 (range: 1.2–3.6 °C) to 3.0 °C under RCP 8.5 (range: 1.9–5.7 °C) across the CTFS-ForestGEO sites (Fig. 2; Table S4). This warming will push some tropical forests

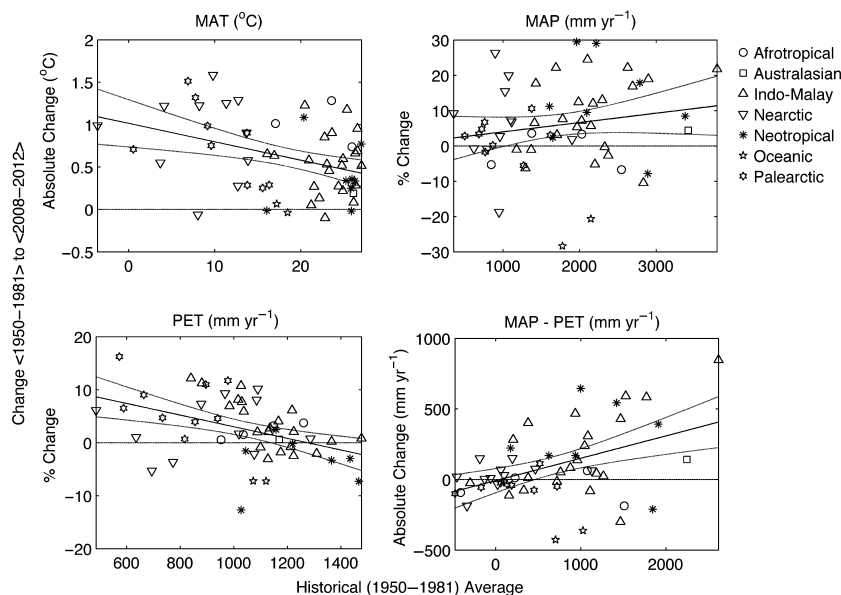


Fig. 4 Recent climate change at CTFs-ForestGEO sites. Specifically, shown is the change from the 1951–1981 average to the 2008–2012 average plotted as a function of the historical (1950–1981) average for four variables: mean annual temperature (MAT), mean annual precipitation (MAP), mean annual potential evapotranspiration (PET), and the difference between mean annual precipitation and potential evapotranspiration (MAP–PET). Solid and dotted lines represent the linear fit and its 95% CI, respectively; dashed horizontal lines represent zero change. Based on CGIAR-CSI climate data (www.cgiar-csi.org/data; CRU-TS v3.10.01 Historic Climate Database and PET estimates from Zomer, 2007; Zomer *et al.*, 2008). Analyses are detailed in Appendix S1.

into climates with no current analog (Fig. 2). Predicted changes in annual precipitation at these sites range from -8.6% to $+19.0\%$ under RCP 2.6 and -13.6% to $+7.3\%$ under RCP 8.5 (Fig. 2; Table S4). When coupled with predicted warming and associated increases in potential evapotranspiration, constant or decreasing precipitation – which is predicted for approximately half the sites (Fig. 2, Table S4) – implies that conditions will become more arid. At most CTFs-ForestGEO sites, soil moisture and relative humidity are predicted to decline in the near-term (i.e., 2016–2035), even under a modest emissions scenario (Kirtman *et al.*, 2013; Sherwood & Fu, 2014).

The biogeochemistry of these sites has also been modified by human activities. The global nitrogen (N) cycle has been dramatically transformed by human activities (Schlesinger, 2012; Vitousek *et al.*, 1997a; Galloway *et al.*, 2008; Canfield *et al.*, 2010). Atmospheric deposition of reactive N can fertilize forests that are N limited (Magnani *et al.*, 2007; Yu *et al.*, 2014), and can also impair ecosystem function through soil acidification and N saturation (Aber *et al.*, 1989; Schlesinger, 2012; Vitousek *et al.*, 1997b). At CTFs-ForestGEO sites, current N deposition has a median value of $0.9 \text{ g N m}^{-2} \text{ yr}^{-1}$ and ranges from 0.05 (Scotty Creek) to $3.8 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Badagongshan, China; Fig. 3), implying that N deposition at many sites may exceed

critical loads for soil acidification (Bouwman *et al.*, 2002). In addition, sulfuric acid deposition reduces soil fertility (e.g., Likens *et al.*, 1996) and increases tree mortality (Dietze & Moorcroft, 2011). Across the network, annual SO_x deposition has a median value of $0.5 \text{ g S m}^{-2} \text{ yr}^{-1}$ (range $0.08 \text{ g S m}^{-2} \text{ yr}^{-1}$ at Mpala, Kenya to $3.1 \text{ g S m}^{-2} \text{ yr}^{-1}$ at Tiantongshan, China; Table S5; data from Dentener *et al.*, 2006; see Appendix S1 for details). Nitrogen and sulfur deposition is predicted to continue to increase in the future (Dentener *et al.*, 2006).

At the local level, CTFs-ForestGEO sites have also been directly exposed to a range of past and ongoing anthropogenic perturbations. Some sites and their surrounding areas were partially to fully logged in the past, and in some cases the land was used for farming or pasture (Table S5). Historical and contemporary forest loss (through deforestation or natural stand-clearing disturbance) in surrounding areas has exposed some sites to severe habitat fragmentation, whereas others are surrounded by vast expanses of near-pristine forest (Figs 3 and 5; Table S5). By the year 2012, 27 sites (primarily in Europe, North America, and Asia) had tree cover within a 5 km radius reduced by more than 10% relative to tree cover in the plot, and seven sites even had reductions $>40\%$. Generally speaking, percent tree cover on the landscape decreases with distance from the site, while recent (2000–2012) forest loss rates and

forest fragmentation increase (Fig. 5; data from Hansen *et al.*, 2013; see Appendix S1 for details). In addition to forest loss in the surrounding landscapes, the majority of sites have been exposed to past and/or ongoing extraction of timber or nontimber forest products, hunt-

ing, or invasive species (Table S5). A few sites are have high human population density in the surrounding areas and are affected by urbanization.

Forest responses to global change

As described above, all CTFS-ForestGEO sites are experiencing multifaceted global change pressures (Fig. 3). With spatially explicit dynamic tree data for large forest dynamics plots and the additional measurements summarized above (Table 2), the network is poised to advance mechanistic understanding of the impact of global and environmental change on the world's forests.

Are forests changing?

Change is the natural condition of forests (e.g., Baker *et al.*, 2005; Laurance *et al.*, 2009), which makes it challenging to detect and attribute directional responses to global change pressures. A key finding from the network is that forests generally, and in particular tropical forests, are highly dynamic; for instance, in the first 18 years of monitoring at BCI, >40% of trees ≥ 1 cm DBH (or 34% ≥ 10 cm DBH) turned over, and 75% of all species changed in abundance by >10% (Leigh *et al.*, 2004). Superimposed upon this dynamism, forests are responding to global change pressures. Data from the network reveal some generalities and long-term trends of change in forests worldwide.

Forest composition in terms of species and functional groups has changed at multiple sites across the network, in different directions at different sites (Condit *et al.*, 1996; Chave *et al.*, 2008; Feeley *et al.*, 2011; Makana *et al.*, 2011; Swenson *et al.*, 2011). An analysis of data from twelve CTFS-ForestGEO sites reveals that environmental variability – as opposed to demographic stochasticity – is the most important factor driving tree population dynamics on decadal time scales (Chisholm *et al.*, 2014). Across relatively undisturbed tropical forests, the dominance of slow-growing species increased at nine of ten sites analyzed (significantly so at five sites), indicating that these forests may be recovering from past disturbances, even as they are impacted by a variety of global change pressures (Chave *et al.*, 2008). In addition, at six tropical sites monitored over more than 10 years, there have been long term increases in the proportions of flowers and seeds produced by lianas (Fig. 6; Wright & Calderon, 2006; Wright, unpublished analysis) – a trend that corresponds with long term increases in the abundance of lianas observed on BCI (Panama) and elsewhere in the tropics (Ingwell *et al.*, 2010; Schnitzer & Bongers, 2011). While community change appears to be the rule rather than the

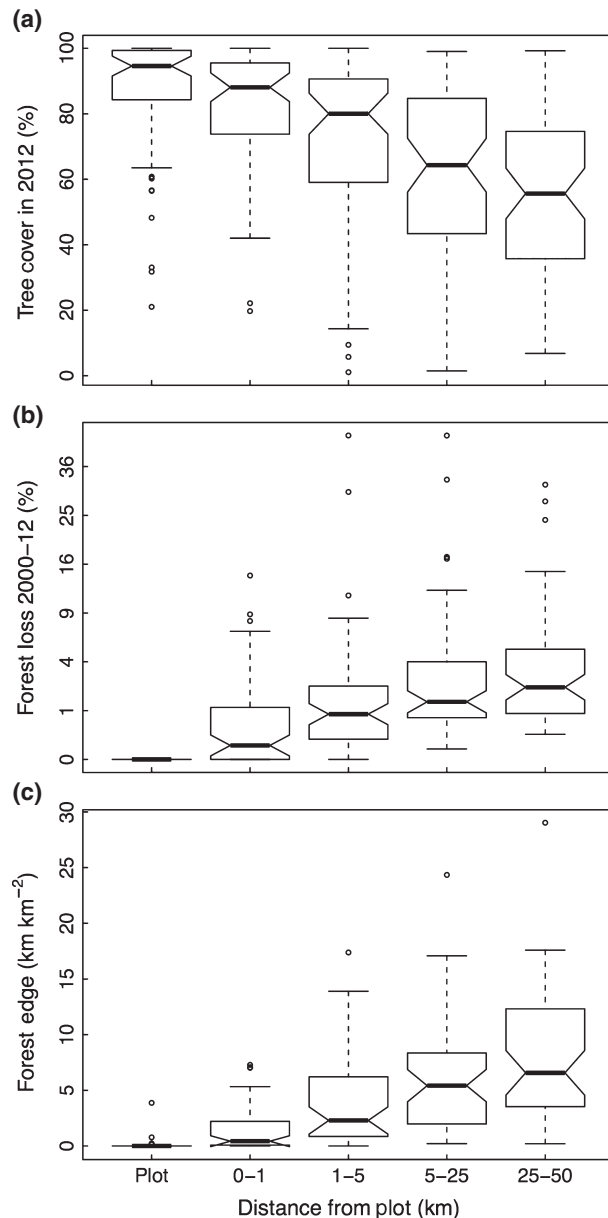


Fig. 5 Characterization of forest cover, fragmentation, and loss in the landscapes surrounding CTFS-ForestGEO sites, with distance zones describing concentric circles centered at each site. (a) Average % tree cover in year 2012; (b) % loss of existing tree cover from 2000 to 2012 (note the vertical scale is the square of forest loss); (c) Forest fragmentation, as characterized by forest edge: area ratio in year 2012. Note that 'forest' can include agroforestry areas. Data from (Hansen *et al.*, 2013). Analysis methods given in Appendix S1. Data for each site given in Table S5.

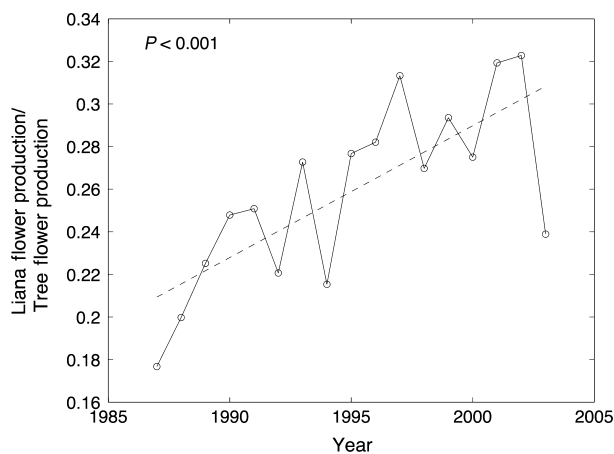


Fig. 6 Ratio of flower production by lianas (33 species) to that of trees (48 species) over 17 years on Barro Colorado Island, Panama. Redrawn from Wright & Calderon (2006).

exception across the network, and while there have been some instances of rapid change in forest composition (e.g., Condit *et al.*, 1995; Chave *et al.*, 2008), there have not been any hugely dramatic changes such as a forest die-off affecting the majority of large trees at the network sites.

Trends in various components of aboveground net primary productivity (ANPP) have also been monitored at some sites. Across the network, the woody component of NPP ($ANPP_{wood}$) has increased or decreased, as a function of both climate change and succession. Forests globally are mixed in terms of their productivity trends (Laurance *et al.*, 2004; Clark *et al.*, 2010; Gedalof & Berg, 2010; Wright, 2010). For instance, decreases in $ANPP_{wood}$ were observed in tropical forests in Panama (BCI) during 1981–2005 and Malaysia (Pasoh) during 1990–2000 (Feeley *et al.*, 2007b) and increases in $ANPP_{wood}$ were observed in secondary forests in Maryland, USA (SERC; McMahon *et al.*, 2010). Notably lacking is evidence of consistent increases in ANPP, as might be expected based solely on increasing atmospheric CO_2 concentration (e.g., Norby *et al.*, 2005). In the tropics, allocation of NPP to reproduction appears to have shifted; at five of six tropical sites where flower and seed production has been monitored for more than 10 years, there has been a long-term increase in flower production but not seed production (Wright & Calderon, 2006; Wright, unpublished analysis). Ongoing monitoring of NPP and flower and seed production will be vital to characterizing trends in productivity and C allocation.

Finally, changes in standing biomass over time have been detected. Across ten relatively undisturbed tropical forests, highly resolved estimates of net

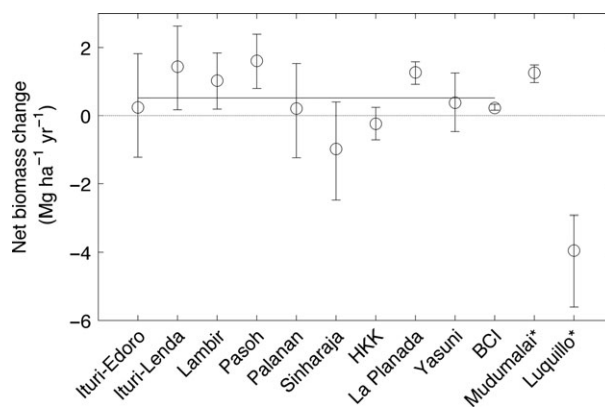


Fig. 7 Aboveground biomass change in twelve tropical forests. Solid line represents mean for ten undisturbed sites; *indicates disturbed plots. Replotted from Chave *et al.* (2008) with an updated value for BCI (Muller-Landau *et al.*, 2014; K.C. Cushman, personal communications).

biomass change show that aboveground biomass increased on average $0.24 \pm 0.16 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Fig. 7; Chave *et al.*, 2008). This value is comparable to (though slightly lower than) values recorded for networks of small forest plots in Amazonia ($0.62 \pm 0.23 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; Baker *et al.*, 2004), and Africa ($0.63 \pm 0.36 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; Lewis *et al.*, 2009a). Combining published data for the CTFS-ForestGEO, RAINFOR, and AfriTRON tropical forest sites leads to an overall average of $0.34 \pm 0.11 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ based on a total of 8243 ha-years of monitoring (Muller-Landau *et al.*, 2014). Ongoing monitoring will be important for quantifying trends in biomass in the global forests represented by CTFS-ForestGEO.

What are the mechanisms by which global change impacts forests?

While data from the CTFS-ForestGEO network add to abundant evidence that forests globally are changing (e.g., Soja *et al.*, 2007; Lewis *et al.*, 2009b; Allen *et al.*, 2010; Wright, 2010), it is difficult to identify the mechanisms underlying such changes given ubiquitous and simultaneous changes in multiple global change drivers (Fig. 3). The information-rich nature of CTFS-ForestGEO sites has yielded insights into the mechanisms of response to global change pressures.

Warming is expected to alter forest dynamics, but predicting effects at the ecosystem scale remains a major scientific challenge (e.g., U.S. DOE, 2012). Monitoring, physiological measurements, and nearby warming experiments combine to yield insights into how warming may impact forest dynamics. The effects of warming are perhaps most dramatic at Scotty Creek, Canada – the highest latitude site, which is experienc-

ing rapid warming (Figs 2 and 3; Tables S3 and S4) – where accelerating permafrost thaw is resulting in tree functional decline near forested plateau edges (i.e., reduced sap flow, radial growth, and leaf area) and driving loss of forest area at a rate of $0.5\% \text{ yr}^{-1}$ (Baltzer *et al.*, 2014). At another Canadian site (Haliburton Forest), a heat wave event during spring leaf-out in 2010 resulted in a $>50\%$ decline in leaf area of the dominant tree species (Filewod & Thomas, 2014), and a large net ecosystem carbon loss in the same year (Geddes *et al.*, 2014). However, at most temperate and tropical sites, the impacts of warming are less obvious and tend to be confounded by other aspects of global change (Fig. 3). Data from four tropical forest sites (BCI, Huai Kha Khaeng, Lambir, and Pasoh) indicate that tree growth rate correlates negatively with nighttime temperature, as expected from increased respiration rates causing a reduced carbon balance (Feeley *et al.*, 2007a; Dong *et al.*, 2012) – a trend that has also been observed at an external site in Costa Rica (Clark *et al.*, 2010). In contrast, warming experiments associated with two of the sites reveal that warming may also directly or indirectly increase woody productivity; specifically, soil warming at Harvard Forest has increased tree growth through increased N mineralization (Melillo *et al.*, 2011), and chamber warming experiments in Panama revealed that increased nighttime temperatures increased seedling growth rates (Cheesman & Winter, 2013). Ongoing monitoring, experimentation, and modeling will be necessary to disentangle the diverse productivity responses of forests to warming. Warming may also shift C allocation to reproduction; flower production at BCI, Panama has increased with increasing temperature (Pau *et al.*, 2013). Future warming (Fig. 2) will inevitably impact forests, and ongoing monitoring at CTFS-ForestGEO sites should help to document and explain these changes.

Changes in aridity and drought severity have the potential to impact forests worldwide, including those in wet climates (Allen *et al.*, 2010; Choat *et al.*, 2012). Across the tropics, increases in aridity or the occurrence of severe droughts have led to forest “browning”, mortality episodes, or fires (Van Nieuwstadt & Sheil, 2005; Lewis *et al.*, 2011; Zhou *et al.*, 2014), and there is concern that potential future increases in aridity in some parts of the tropics could result in severe tropical forest dieback (e.g., U.S. DOE, 2012). Research across the CTFS-ForestGEO network has yielded insights into the role of aridity in shaping tropical forest dynamics. Droughts in Panama (BCI, San Lorenzo, and Cocoli) and Malaysia (Lambir) have revealed differential drought sensitivity by size class, microhabitat association, and functional type (Condit *et al.*, 1995, 2004; Potts, 2003). In Panama, mild or even fairly strong

drought increased both woody productivity and production of flowers and seeds – presumably because of increased solar radiation (Condit *et al.*, 2004; Wright & Calderon, 2006). At a tropical dry forest in India (Mudumalai), drought increased mortality rate, but with a 2–3 year lag for larger trees (Suresh *et al.*, 2010). These findings yield insight into how moist tropical forests may respond to predicted changes in aridity (Fig. 2; Table S4; IPCC, 2013).

Beyond climate, impacts of other global change drivers have been observed across the CTFS-ForestGEO network. Nitrogen deposition (Fig. 1; Table S5) has altered forest biogeochemistry across the globe. Temperate forests are typically N limited; however, high N deposition at Haliburton Forest, Canada, has caused a shift from N to P limitation (Gradowski & Thomas, 2006, 2008), providing evidence of constraints on increases in temperate forest productivity driven by elevated CO_2 and/or nitrogen deposition. Because tropical forests are typically limited by elements other than N, N deposition is not expected to increase the productivity of these forests (Matson *et al.*, 1999). At the two tropical CTFS-ForestGEO sites where relevant measurements have been made, increased ^{15}N concentrations in plant tissues suggests substantial N deposition and altered N cycles (Hietz *et al.*, 2011). Specifically, on BCI, leaf N and $\delta^{15}\text{N}$ in recent (2007) samples were elevated relative to herbarium samples (~1968) (Hietz *et al.*, 2011). These changes have been mechanistically linked to increased N availability through a nearby fertilization experiment, which increased foliar N concentrations and $\delta^{15}\text{N}$ by similar amounts but did not affect productivity (Wright *et al.*, 2011; Mayor *et al.*, 2014a,b). A similar increase in $\delta^{15}\text{N}$ was observed in wood from Huai Kha Khaeng, Thailand (Hietz *et al.*, 2011). These results imply that, in tropical forests, N deposition is accelerating N cycling without increasing productivity, and reduced cation availability resulting from N deposition may be one potential explanation for observed declines in tree growth rates at some tropical sites (see above; Matson *et al.*, 1999).

Habitat fragmentation (Fig. 5) and faunal degradation have also been linked to altered dynamics at CTFS-ForestGEO sites. The CTFS-ForestGEO site near Manaus, Brazil, is part of the Biological Dynamics of Forest Fragments Project (BDFFP), which has revealed that forest fragmentation rapidly and profoundly alters tree, arthropod, bird, and primate communities, reducing species diversity and shifting composition toward dominance of more disturbance-adapted species (Laurance *et al.*, 2006). Across the network, more highly fragmented sites (e.g., Witham Woods, UK; Bukit Timah, Singapore; Lambir, Malaysia; Heishiding, China;

Fig. 3; Table S5) tend to have degraded faunas, as indicated by the absence of apex predators and larger vertebrates that were present historically, whereas faunal communities tend to remain more intact in unfragmented forests such as Yasuni (Ecuador), Rabi (Gabon), and Scotty Creek (Canada) (Turner & T Corlett, 1996; LaFrankie *et al.*, 2005; Laurance *et al.*, 2012; Harrison *et al.*, 2013; W.F. Laurance, personal communication). As detailed below, faunal degradation – whether caused by habitat fragmentation, hunting, or other pressures – has strong impacts on forest structure and dynamics.

The strong influence of fauna on forest composition and dynamics (e.g., Wright, 2010; Estes *et al.*, 2011; Schmitz *et al.*, 2013) has been documented at several CTFS-ForestGEO sites. At Mpala, Kenya, an experiment excluding herbivores of different sizes and replicated across a rainfall gradient revealed that herbivores of different sizes influence the biomass and growth rates of trees and understory plants, plant community composition, and small mammal communities (Goheen *et al.*, 2013). At Mudumalai, elephants (*Elephas maximus*) cause high mortality among the small- to medium-sized stems, particularly in a few favored forage species (Sukumar *et al.*, 2005). At SCBI (Virginia, USA), where white-tailed deer (*Odocoileus virginianus*) populations greatly exceed their historical levels, 20 years of deer exclusion from a 4-ha subsection of the CTFS-ForestGEO plot has resulted in a >4-fold increase in sapling abundance relative to heavily browsed forest outside the exclosure (McGarvey *et al.*, 2013). Large impacts of mammalian herbivores have also been found in an exclosure study adjacent to the Pasoh plot site in Malaysia (Ickes *et al.*, 2001), where native pigs (*Sus scrofa*) have a dramatic effect on tree recruitment. In Panama, comparison of forest plots protected from bushmeat hunting with those exposed to poachers revealed that by reducing the abundance of frugivores and seed dispersers, hunting decreases the abundance of plant species with seeds dispersed by these animals while increasing the abundance of species with seeds dispersed by bats, small birds, or mechanical means (Wright *et al.*, 2007). The latter includes lianas whose seeds are much more likely to be dispersed by wind (60% of liana species vs. 25% of canopy trees and <10% of midstory and understory trees and shrubs). Lianas have thus increased disproportionately in abundance where hunters remove the frugivores that disperse the seeds of most tree species, hence hunting may have unforeseen consequences for carbon sequestration (Jansen *et al.*, 2010). Directional change in tree communities driven by faunal degradation has also been demonstrated. At Lambir, where populations of large mammals and birds have been severely impacted by hunting, tree community dynamics changed

profoundly from 1992 to 2008 (Harrison *et al.*, 2013). Specifically, sapling densities increased and regeneration of tree species with animal-dispersed seeds decreased and became more spatially clustered (Harrison *et al.*, 2013). Thus, ongoing faunal degradation due to hunting and habitat fragmentation in many forests globally is expected to alter forest community composition, tree dispersal and regeneration, species diversity, forest structure, and carbon cycling.

CTFS-ForestGEO research has also shed light on community interactions that will act to either magnify or buffer forest responses to global change. Species are linked to one another through complex webs of interaction. For example, mapping of quantitative trophic foodwebs at Wanang (Papua New Guinea) and current efforts to document tritrophic foodwebs of seeds, seed predators and parasitoids at this same location, at Khao Chong (Thailand) and Barro Colorado Island (Panama) demonstrates the complexity of ecological interactions in forest ecosystems (Novotny *et al.*, 2010). Studies of seed dispersal and seedling recruitment demonstrate the critical role of vertebrates and insects in tree reproduction and the composition of future forests (e.g., Wright *et al.*, 2007; Harrison *et al.*, 2013). It is therefore unsurprising that global change impacts on one group cascade through the ecosystem. For example, as described above, dramatic reduction in large mammal and bird populations at Lambir, Malaysia has altered the dynamics of tree dispersal and regeneration (Harrison *et al.*, 2013). Similarly, in the light-limited moist tropical forests of Panama, El Niño events bring relatively cloud free, sunny conditions that enhance fruit production while subsequent La Niña events bring rainy, cloudy conditions, and lower levels of fruit production that can lead to famines, particularly among terrestrial frugivores and granivores (Wright *et al.*, 1999; Wright & Calderon, 2006). Climate change is bringing changes in cloud cover and atmospheric transmissivity to PAR (Table S3) with cascading effects on frugivores, granivores, and the plant species with which they interact.

At the same time, the diversity and complexity of forest communities may serve to provide some resilience to global change. A diversity of tree physiological strategies implies a wide range of responses to global change that helps to provide ecosystem resilience (e.g., Isbell *et al.*, 2011; Mori *et al.*, 2013). For example, Panamanian tree species have displayed a wide range of physiological responses to temperature variation (Cheesman & Winter, 2013; Slot *et al.*, 2014), and trees of different species have generally responded differently to experimental manipulation of CO₂, temperature, or precipitation globally (Anderson-Teixeira *et al.*, 2013). The resilience enabled by species diversity may be exemplified by the stability of biomass, size struc-

ture, and functional composition of the BCI forest (Chave *et al.*, 2008; Swenson *et al.*, 2012) despite severe droughts that impacted drought-sensitive species (Condit *et al.*, 1995, 1996). In addition, in the tropics, pervasive negative density dependence – i.e., elevated mortality of a plant species in areas where it is abundant – may buffer change because as a species becomes rare, it will suffer less from negative density dependence (Comita *et al.*, 2010). Thus, accounting for biodiversity in ecosystem models will be important for predicting forest responses to climate change. While such complexity makes it challenging to predict forest responses to global change, it may serve to partially buffer forest response to global change, which might otherwise be more dramatic.

Conclusions

The CTFS-ForestGEO forest dynamics sites are representative of the world's more intact forests, covering a diversity of geographical, climatic, edaphic, topographic, and biotic environments (Figs 1 and 2; Table 2). Yet, even this selection of the world's more intact forests is being impacted by multifaceted global change drivers (Figs 2–5). Because many interacting species and processes are simultaneously being affected by a variety of global change pressures, extracting a mechanistic understanding of observed forest changes is challenging, requiring a holistic understanding of the abiotic setting, site history, demography for all tree life stages, trophic interactions, and ecosystem-level processes. The broad suite of measurements made at CTFS-ForestGEO sites (Tables 1 and 3) makes it possible to understand the complex ways in which global change is impacting forest dynamics.

Ongoing research across the CTFS-ForestGEO network is yielding insights into how and why the forests are changing. As global change pressures inevitably intensify (Fig. 2; IPCC, 2013), ongoing monitoring across the network should prove valuable for documenting and understanding multifaceted forest responses and feedbacks to the climate system. To project into the future, broad suite of variables measured at CTFS-ForestGEO sites (Tables 1 and 3) will be invaluable for parameterizing and evaluating ecosystem and earth system models, particularly those that characterize forest demography and differences among species or functional groups (e.g., Moorcroft *et al.*, 2001; Medvigy *et al.*, 2009). Together, CTFS-ForestGEO's unique standardized core census (Table 1) and supplementary measurements (Table 3), applied across all of the world's major forest biomes (Fig. 1; Table 1), will provide mechanistic insight as forests change in the 21st century.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Data sources and analysis methods.

Appendix S2. CTFS-ForestGEO measurement protocols.

Table S1. Geographic coordinates, elevation data, and references to site descriptions for all CTFS-ForestGEO sites.

Table S2. Climate data for all CTFS-ForestGEO sites: average for 1980–2012 from CGIAR-CSI climate data.

Table S3. Recent climate change at CTFS-ForestGEO sites (difference between 2008–2012 and 1951–1980 average) calculated from CGIAR-CSI climate data.

Table S4. Climate Change Projections for CTFS-ForestGEO sites.

Table S5. Atmospheric deposition; forest degradation, loss, and fragmentation; and local anthropogenic disturbances at CTFS-ForestGEO sites.

Table S6. Record of supplementary measurements at CTFS-ForestGEO sites.

Table S7. Record of arthropod sampling at CTFS-ForestGEO sites.

Table S8. Acknowledgement of funding to individual CTFS-ForestGEO sites.