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ForestGEO: Understanding forest diversity and dynamics through a global observatory network

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ABSTRACT

ForestGEO is a network of scientists and long-term forest dynamics plots (FDPs) spanning the Earth's major forest types. ForestGEO's mission is to advance understanding of the diversity and dynamics of forests and to strengthen global capacity for forest science research. ForestGEO is unique among forest plot networks in its large-scale plot dimensions, censusing of all stems $\geq$1 cm in diameter, inclusion of tropical, temperate and boreal forests, and investigation of additional biotic (e.g., arthropods) and abiotic (e.g., soils) drivers, which together provide a holistic view of forest functioning. The 71 FDPs in 27 countries include approximately 7.33 million living trees and about 12,000 species, representing 20% of the world's known tree diversity. With >1300 published papers, ForestGEO researchers have made significant contributions in two fundamental areas: species coexistence and diversity, and ecosystem functioning. Specifically, defining the major biotic and abiotic controls on the distribution and coexistence of species and functional types and on variation in species' demography has led to improved understanding of how the multiple dimensions of forest diversity are structured across space and time and how this diversity relates to the processes controlling the role of forests in the Earth system. Nevertheless, knowledge gaps remain that impede our ability to predict how forest diversity and function will respond to climate change and other stressors. Meeting these global research challenges requires major advances in standardizing taxonomy of tropical species, resolving the main drivers of forest dynamics, and integrating plot-based ground and remote sensing observations to scale up estimates of forest diversity and function, coupled with improved predictive models. However, they cannot be met without greater financial commitment to sustain the long-term research of ForestGEO and other forest plot networks, greatly expanded scientific capacity across the world's forested nations, and increased collaboration and integration among research networks and disciplines addressing forest science.

1. Introduction

Forests store about half of the world's carbon, take up 25% of all new anthropogenic carbon emissions (Keenan and Williams, 2018), and control climatic and hydrological cycles (Immerzeel et al., 2020). They house about 50% of the world's known species, providing medicines, food, and fuel for a huge fraction of humanity. Forests are in the midst of the greatest transformation since the last great extinction through the combined anthropogenic effects of deforestation, forest degradation through overexploitation, the deposition of pollutants, invasive pests, and climate and atmospheric change. How forests respond to the Anthropocene has profound consequences for life on Earth, yet understanding these responses has proved challenging due to the diversity and complexity of forest ecosystems and the long timeframes over which forests develop and change. The current state of knowledge of the underlying processes regulating species distributions, population and community dynamics, and the resistance and resilience of forests to perturbations provides an incomplete basis from which to predict the future of the world's forest biomes. Even the fundamental biology of many forest species is unknown, yet is essential to predicting and mitigating anthropogenic impacts on forests at a global scale.

The diversity, structure and functioning of forests vary across a wide range of spatial and temporal scales and involve a plethora of interacting species beyond trees. In other words, while trees make up forests, forests are more than trees. Tree species can persist across diverse climatic conditions, and forests vary by orders of magnitude in species diversity across the Earth. The same area that supports roughly ten tree species in a *Sequoia* forest can support over a thousand in Borneo or the Amazon (Lee et al., 2002; Duque et al., 2017). Yet, we remain ignorant of how the ecological niches and demographic characteristics of the vast majority of tree species determine their specific geographic and environmental distributions, which underpin patterns of diversity. The dynamics of tree growth, mortality, and recruitment vary dramatically among forests and through time. Abiotic environmental drivers, like climate, soil, and disturbances, and biotic drivers, involving interactions with other taxa, shape the vital rates of trees, which ultimately determine carbon, water, and nutrient storage and fluxes. Yet, these processes and interactions remain obscure. Nowhere is this more true than in tropical forests, where knowledge of the myriad ways in which animals and microbiota interact with trees, and consequently forests, is in its infancy. A challenge for defining these interaction networks is not only identifying which taxa live in forests, but also quantifying what ecological roles they play and when, and with what impact. Integrating the entire forest biota into a holistic understanding of forest ecosystem function is daunting, yet is key to predicting the resilience or vulnerability of forests to change.

The enormous challenge for forest science is determining the controls on the structure, function, and diversity of forests across large spatial and temporal scales and linking these processes to the functioning of the Earth system. Meeting this challenge requires integration across levels of organization from the molecular to the ecosystem levels using detailed standardized data collected around the world and over decades to centuries. While ambitious, this knowledge is essential for building better predictive models and improving space-borne observation platforms that can be used to monitor and predict the future of forested biomes globally. Such advances cannot be accomplished by a single research group, institution, or even country, but rather require a distributed network of scientists, representing many disciplines, and engaging in long-term collaborations, who are committed to capacity-strengthening in forest science globally and to seeking long-term financial support for these essential endeavors. The mission of the Forest Global Earth Observatory (ForestGEO) is to advance these fundamental and pressing research and training needs.

2. ForestGEO

The Forest Global Earth Observatory (ForestGEO), administered by the Smithsonian Tropical Research Institute (STRI), is a worldwide network of scientists and long-term forest dynamics plots (FDPs) spread across Earth's major forests. ForestGEO is dedicated to understanding the diversity and dynamics of forests and strengthening global capacity for forest science research. Since 1980, the network has grown from a single forest research site in Panama into a collaboration of 71 sites in 27 tropical and temperate countries, including >100 partner organizations. ForestGEO collects standardized data on the recruitment, growth, and death of over 7 million trees of 12,000 unique species, approximately 20% of the world's known tree diversity (Table 1, Fig. 1). ForestGEO FDPs represent a very wide range of environmental conditions spanning ever-wet tropical to arid to boreal climates (see Fig. 1 in Anderson-Teixeira et al., 2015). FDPs are distributed across gradients of soil fertility, topography, rainfall intensity and seasonality, and disturbance regimes. ForestGEO FDPs in the tropics are largely confined to intact "old-growth" forests. In the temperate zone, many ForestGEO FDPs are in regenerating forests of 30–150 years post-disturbance, though several in the western US are in old-growth forests (e.g., Yosemite). ForestGEO FDPs are also representative of global woody plant diversity. A recent analysis of 63 of the 71 FDP species lists found that 59% of all plant families and 35% of all plant genera that contain woody species are found within the network (Fig. 2). The sample of families and genera is unbiased with respect to the phylogeny of woody plants (Monks, Davies & Swenson, *unpublished data*). However, certain woody families are underrepresented by ForestGEO, for example, families constrained to geographical areas not currently sampled by ForestGEO (e.g., Nothofagaceae and Araucariaceae), or primarily herbaceous families (e.g., Caryophyllaceae and Geraniaceae). A future goal of ForestGEO is to expand sampling to underrepresented areas, including Australia, southern Africa, and southern South America.

Each ForestGEO FDP is in a protected area and is led and managed by one or more principal investigators based at host-country partner organizations. Principal scientists in each country lead the regular, long-term data collection, implement all research activities at the sites, and represent their sites in network-wide discussions and collaborative activities. An FDP is a large-scale forest plot with all stems ≥1 cm in diameter measured approximately every five years to obtain longitudinal data on the growth, survival, and recruitment of individual trees. This standardized protocol is essential to addressing a wide range of research questions in ecology, evolution, and conservation because it captures much of the tree lifespan, as well as temporal variation in the community structure of forests across relatively large contiguous areas that encompass local diversity gradients.

The pivotal strengths of the ForestGEO network are: (1) standardized data and measurement protocols – the core tree data and ancillary data are collected and managed uniformly, facilitating data sharing and comparative analyses among sites; and (2) the strengthening of global scientific capacity – by engaging forest researchers from across all participating nations, the network has been able to train hundreds of scientists and build an integrated, collaborative community of forest ecologists in some of the most diverse and threatened forests in the world. ForestGEO researchers have published >1300 papers that have made significant contributions and novel discoveries in forest science (Fig. 3, Section 7). In this paper, we provide a brief overview of the ForestGEO network, including a short history, a description of the measurements and protocols implemented in the FDPs, a description of our approach to training, strengthening capacity and creating opportunities for early-career scientists, a brief overview of some of the key scientific achievements of the network, and suggestions for future priorities, opportunities, and challenges in forest science.

3. History

The first large-scale forest dynamics plot was initiated on Barro Colorado Island (BCI) in Panama by Stephen Hubbell and Robin Foster in 1980 (Fig. 1). The goals of this novel and ambitious undertaking were clearly stated in the first recensus grant proposal for the BCI 50-ha plot:

> "The long-range objectives are: (1) to obtain statistically adequate samples of many tropical trees species for horizontal life table analysis using large cohorts of individually tagged and mapped trees; (2) to document changes in forest composition directly with a sufficient data base to test competing equilibrium and non-equilibrium theories of tropical forest organization and dynamics; and (3) to provide detailed maps of tree populations to other researchers interested in diverse aspects of the biology of tropical tree species." Excerpt from: Hubbell and Foster (1982) unpublished NSF proposal "*The Structure and Dynamics of a Tropical Forest: A Demographic Analysis*."

FDPs in Pasoh Forest Reserve, Malaysia, and Mudumalai Wildlife Sanctuary, India, soon followed through partnerships with the Forest Research Institute of Malaysia and the Indian Institute of Sciences, respectively. In 1989, Peter Ashton, then Professor at the Arnold Arboretum of Harvard University, orchestrated a USAID and NSF-supported meeting of regional forest scientists in Bangkok, Thailand, during which a plan for expanding FDPs across edaphic, rainfall and

Table 1

Characteristics of 71 ForestGEO FDPs spanning the world's forest types, including total number of trees (trees #), species (species #) and censuses (censuses #), and mean annual temperature (MAT) and mean annual precipitation (MAP). Elevation is the average elevation across each plot. Data for each plot are derived from the most recent census. For Santa Cruz, the plot started as 6 ha in 2007 and was expanded to 16 ha in 2012.

Site	Area (ha)	First census (yr)	Trees #	Species #	Fisher's alpha	Censuses #	Elevation (m)	MAT (°C)	MAP (mm/yr)
Ailaoshan, Yunnan	20	2014	44,168	104	12.8	2	2550	11.3	1778
Amacayacu, Colombia	25	2006	123,790	1133	172.2	2	94	25.8	3215
Badagongshan, Hunan	25	2011	186,000	238	26.9	2	1420	15.9	1410
Baishanzu, Zhejiang	25	2014	207,178	177	19.0	1	1527	12.8	2342
Baotianman, Henan	25	2009	59,569	126	15.2	2	.	15.1	886
Barro Colorado Island, Panama	50	1981	208,400	299	34.3	8	120	27.1	2551
Bidoup, Vietnam	25	2012	204,684	215	23.7	1	1557	17.3	1533
Bukit Timah, Singapore	4	1993	17,239	408	75.0	6	99	26.9	2473
Changbaishan, Jilin	25	2004	36,904	52	6.0	4	801	2.9	700
Cocoli, Panama	4	1994	3200	176	40.1	3	50	26.6	1950
Danum Valley, Malaysia	50	2010	256,729	694	86.8	2	150	26.7	2822
Daxinganling, Heilongjiang	25	2011	209,785	18	1.5	1	897	−4.0	458
Dinghushan, Guangdong	20	2005	71,617	210	26.6	2	350	20.9	1985
Doi Inthanon, Thailand	15	1997	73,269	162	19.7	4	1670	20.9	1908
Donglingshan, Beijing	20	2010	52,136	58	6.4	2	1400	4.7	570
Fushan, Taiwan	25	2004	110,595	101	11.0	4	667	18.2	4271
Gutianshan, Zhejiang	24	2005	140,087	159	17.7	3	581	15.3	1964
Hainan, Hainan	60	2012	439,676	290	30.3	2	942	19.8	2381
Haliburton, Canada	13.5	2007	46,339	30	3.1	2	434	5.0	1070
Harvard Forest, MA, USA	35	2010	116,200	51	5.1	1	354	9.0	1050
Heishiding, Guangdong	50	2013	218,513	236	26.1	2	567	22.0	1744
Hong Kong, Hong Kong	20	2012	81,021	172	20.8	1	201	23.3	2399
Huai Kha Khaeng, Thailand	50	1992	72,500	251	32.6	6	596	23.5	1476
Ilha do Cardoso, Brazil	10.2	2004	40,000	106	13.2	2	6	22.4	2100
Indian Cave, NE, USA	18.4	2019	15,786	49	6.3	1	315	11.2	876
Ituri, D.R. Congo	40	1994	288,000	445	51.6	4	775	24.3	1682
Kenting, Taiwan	10	1996	39,093	95	11.7	1	275	25.4	1964
Khao Chong, Thailand	24	2000	121,500	593	81.1	4	235	27.1	2611
Korup, Cameroon	50	1996	329,000	494	57.0	3	195	26.6	5272
Belalong, Brunei Darussalam	25	2009	155,901	1266	188.4	1	240	26.5	5203
La Planada, Colombia	25	1997	105,400	240	29.3	2	1818	19.0	4087
Lambir, Malaysia	52	1991	359,600	1182	152.2	5	174	26.6	2664
Laupahoehoe, USA	4	2008	14,641	21	2.4	2	1160	16.0	3440
Lienhuachih, Taiwan	25	2008	153,268	144	15.7	1	754	20.8	2211
Lilly Dickey Woods, IN, USA	25	2012	27,993	35	3.9	2	267	11.6	1203
Luquillo, Puerto Rico, USA	16	1990	39,160	138	17.9	6	381	22.8	3548
Manaus, Brazil	25	2004	154,177	1519	234.0	2	60	26.7	2600
Michigan Big Woods, MI, USA	23	2014	33,690	45	5.1	1	288	8.6	857
Mo Singto, Thailand	30.5	2000	134,942	264	31.6	3	770	23.5	2100
Mpala, Kenya	120	2011	139,259	68	6.9	2	1730	17.9	657
Mudumalai, India	50	1988	25,500	72	9.1	8	1050	22.7	1255
Nanjenshan, Taiwan	5.88	1989	36,400	125	16.2	4	320	23.5	3582
Ngardok, Palau	4	2017	14,216	70	9.6	1	39	28.0	3734
Ngel Nyaki, Nigeria	20.28	2014	41,031	106	13.2	1	1639	19.0	1800
Niobrara, NE, USA	20.16	2018	8293	26	3.3	1	687	8.7	597
Nonggang, Guangxi	15	2011	68,010	223	28.7	2	275	22.0	1376
Ordway-Swisher, FL, USA	23.04	2019	9935	11	1.2	1	38	20.0	1280
Palamanui, HI, USA	4	2008	15,652	15	1.6	2	265	20.0	835
Palanan, Philippines	16	1994	78,205	335	44.9	5	97	26.1	3380
Pasoh, Malaysia	50	1986	300,211	814	101.9	7	80	27.9	1788
Rabi, Gabon	25	2010	178,447	342	40.8	2	41	26.0	2282
San Lorenzo, Panama	6	1996	1935	238	71.3	5	140	26.2	3030
Santa Cruz, CA, USA	6/16	2007/2012	20,892	33	3.8	3/2	323	14.8	778
Scotty Creek, Canada	9.6	2013	38,050	11	1.0	2	266	−3.2	369
Sinharaja, Sri Lanka	25	1993	193,400	204	22.5	5	500	22.5	5016
SCBI, VA, USA	25.6	2008	49,285	65	7.4	3	306	12.9	1001
SERC, MD, USA	16	2007	24,961	79	10.1	3	8	13.2	1068
Speulderbos, Netherlands	27	2013	9350	13	1.5	2	56	10.1	833
Tiantongshan, Zhejiang	20	2008	94,603	153	17.8	2	453	16.2	1375
Traunstein, Germany	25	2015	15,758	29	3.4	1	605	7.6	1240
Tyson Res. Center, MO, USA	20.16	2013	30,333	42	5.3	2	205	13.5	957
UMBC, MD, USA	12.5	2012	7782	79	12.2	2	50	12.8	1063
Utah, UT, USA	13.64	2014	23,177	17	1.8	1	3084	2.7	850
Wabikon, WI, USA	25.2	2008	50,130	42	4.5	3	498	4.2	805
Wanang, Papua New Guinea	50	2009	285,825	527	62.5	2	140	26.0	3500
Wind River, WA, USA	27.2	2010	30,973	26	2.8	2	369	9.2	2495
Wytham Woods, UK	18	2008	16,313	23	2.6	3	134	10.0	717
Xishuangbanna, Yunnan	20	2007	95,834	468	64.0	3	789	21.8	1493
Yasuni, Ecuador	50	1995	297,778	1114	146.2	2	230	28.3	3081
Yosemite Nat. Park, CA, USA	25.6	2009	34,458	23	2.4	3	1843	10.2	1065
Zofin, Czech Republic	25	2012	72,846	13	1.4	2	780	6.2	866

Fig. 1. Global map of 71 ForestGEO Forest Dynamics Plots.

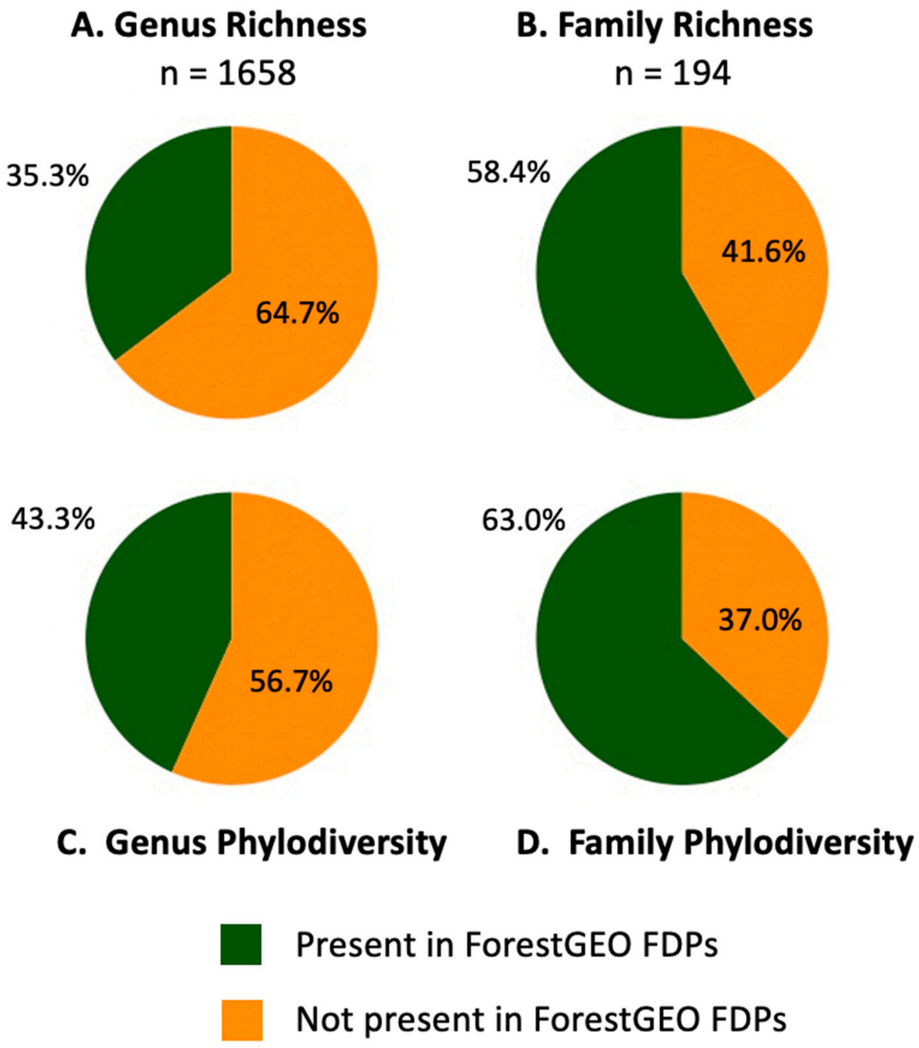


Fig. 2. Representation of woody plant diversity in ForestGEO FDPs. The percent of known woody plant genera (A) and families (B) recorded within ForestGEO plots based of the global woody plant database (Zanne et al., 2014). Percent of global woody plant phylogenetic diversity (phylodiversity) of genera (C) and families (D) recorded in ForestGEO FDPs. Phylodiversity is the sum all branch lengths for the phylogeny of genera or families (Faith, 1992). The phylodiversity percent is the fraction of branches on the phylogeny that occur in ForestGEO FDPs. The analysis was based on 63 FDPs (Monks, Davies & Swenson, *unpublished data*), so underestimates the actual diversity found in the ForestGEO network. n is the total number of woody genera and families.

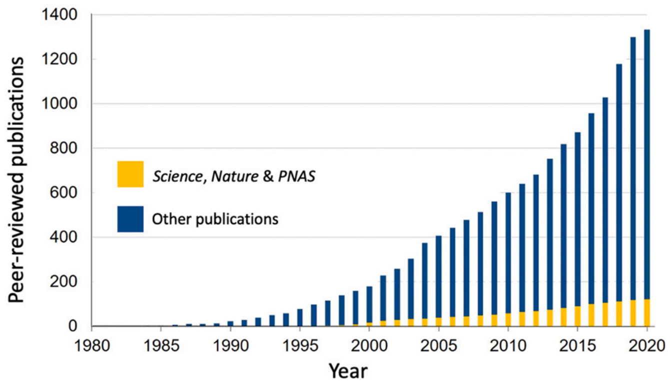


Fig. 3. Cumulative growth of ForestGEO peer-reviewed publications since the start of the first plot on Barro Colorado Island in Panama in 1981. Publications included up to August 2020.

biogeographic gradients within tropical Asia was discussed (Ashton et al., 1999). Recognizing the rapid transformation of Asian forests going on at that time, a key motivation for the meeting was to develop the knowledge base needed to improve sustainable forest management of Asia's rapidly dwindling forests (Anon, 1989), or, to:

> "design a plan for utilizing the available scientific skills of the region in conducting policy-oriented research at the minimum level required for sound policy decision-making, covering the major tropical forest … ecosystems of the region."
> excerpt from: Anon. (1989 unpublished USAID-NSF workshop report). "*Funding Priorities for Research Towards Effective Sustainable Management of Biodiversity Resources in Tropical Asia.*"

Over the next few years, through opportunistic funding successes and the inspired leadership of site principal investigators, FDPs were initiated in Sri Lanka (Sinharaja), Thailand (Huai Kha Khaeng), Singapore (Bukit Timah), the Philippines (Palanan), and an additional site in East Malaysia (Lambir Hills). It was a busy time for plot development, with new sites also being established in Africa and the Neotropics (Fig. 4). Researchers in Cameroon (Korup), the Democratic Republic of Congo (Ituri), Puerto Rico (Luquillo) and Ecuador (Yasuní) all initiated FDPs. While international partnerships were important for all of these developments, highly motivated individual researchers were critical to this phase of plot expansion.

In 1990, STRI and the Arnold Arboretum (AA) jointly established the Center for Tropical Forest Science (CTFS) to coordinate the expanding network of FDPs and help advance science and training opportunities among research partners. A series of graduate students working on the newly established plots helped drive the science output – perhaps serendipitously, this turned out to be a key element in the future strength of the network, as many of these students and fellows became future plot PIs and science leaders. In 1993, CTFS established a regional headquarters in Singapore at the National Institute for Education of Nanyang Technological University. The partnership with NTU, now through the recently formed Asian School of the Environment, continues today. Ashton (2014) and Ashton and Lee (2020) provide a thorough overview of research achievements of the CTFS network in Asia in a physical and biogeographic context.

Throughout the 1990s, CTFS expanded, developing new partnerships across the tropics, obtaining funding to establish new plots in southern Thailand and Manaus, Brazil, and to recensus earlier established plots (BCI and Pasoh). An overview of the expanding network was published in 2004 (Losos and Leigh Jr, 2004). Despite the progress, the challenge of securing continued funding remained. In 2003, STRI and the Arnold Arboretum, with critical support from the Frank Levinson Family Foundation, signed a new memorandum of understanding in which the institutions would co-fund the expanding CTFS network, with the Arboretum forming the CTFS-AA Asia program based at Harvard, and STRI continuing to lead the global network. Confirmed annual funding led to much greater security for core CTFS staff, continued plot censuses, funds for postdoctoral fellowships and grants to early-career scientists, and supported the implementation of field courses in the Asian tropics, which helped develop further interest in long-term ecological research across that region.

In 2005, the headquarters of CTFS moved from AA to STRI in Panama. With the encouragement and financial support of the Frank Levinson Family Foundation, CTFS embarked on a scientific review. A series of workshops were held with the goal of defining broad new scientific directions for the network. Specifically, the idea was to build on the core tree censuses to transform CTFS into a global forest observatory, providing a more holistic view of all the biotic and abiotic drivers that combine to produce a functioning forest. The idea was that the FDPs had collected a small fraction of the data that were needed to transform forest science into a more predictive endeavor, encompassing interdisciplinary ecology, evolution, conservation, and Earth system functioning. Workshops covered abiotic conditions (e.g., climate and soils), paleobiology, ecosystem processes (including carbon dynamics and functional traits), genetic approaches, and monitoring of several animal groups (e.g., arthropods and vertebrates). Several of these initiatives were rapidly implemented across the network with standardized data collection (Section 5). In 2007, the central Smithsonian endorsed the

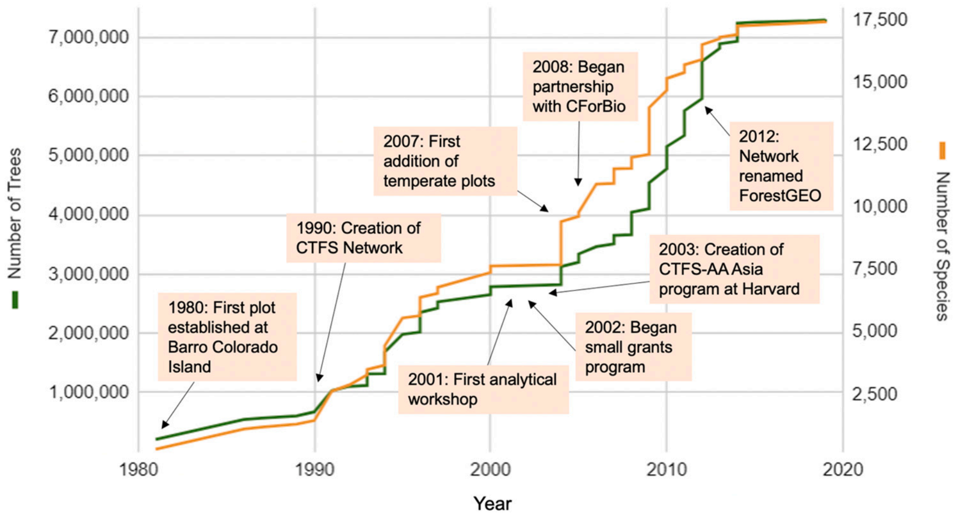


Fig. 4. Growth of the ForestGEO network in terms of numbers of species and trees being monitored by the FDPs. The number of species is the sum of all recorded species at each plot, so species occurring in more than one plot are counted twice. The number of unique species is approximately 12,000. The number of trees reflects the number of living trees at the most recent census of each plot. Over time the number of tree measurements has grown to over 20 million due to many plots having multiple censuses (Table 1).

network, and by 2010 helped secure core federal funds from the US government in support of the network's expanding science mission.

Building on a workshop held in Beijing in 2004, ForestGEO also began a formal partnership with the Chinese Forest Biodiversity Monitoring Network (CForBio) in 2008. By this time, several plots in China were already established and participating in the ForestGEO network, including in the far south (Xishuangbanna) and north (Changbaishan). The CForBio team was rapidly building new plots to sample the great diversity of forest types across China (Feng et al., 2016). Matching grants in 2010 from the NSF-US, under the International Research Coordination Networks program, and NSF-China led to a series of analytical workshops in both countries that greatly advanced collaborative activities among participating researchers.

The network expanded beyond the tropics beginning in 2007 (Fig. 4). The initial impetus for this expansion was through an initiative called the Global Climate Partnership, led and funded by HSBC Bank, UK. This led to the establishment of seven plots in North America and the UK. Soon after that, the core protocol, designed largely to answer questions about high-biodiversity tropical forests, proved valuable in extra-tropical forests. Long-term forest research employing large plots with measurements of small stems was a new approach in temperate forest monitoring. The initial seven temperate forest sites have grown to >25, including some of the highest biomass forests (Western US). Many of these new plots leveraged existing data by colocation with plots or other organized national environmental networks (e.g., NEON and LTER in the US). The expansion also enabled new synthetic investigations comparing forests at the global scale, in which fundamental ecological hypotheses (e.g., the diversity-ecosystem function relationship, the strength of species coexistence mechanisms, and determinants of life history variation), could be tested with comparable data, in many cases for the first time.

The Frank Levinson Family Foundation endowed the directorship of ForestGEO in 2013. This was timely as the Arnold Arboretum decided to end its support of the Asia program. To emphasize its global reach and expanding research scope, the network was renamed the Forest Global Earth Observatory (ForestGEO). Its mission is to build and sustain a global network of large-scale forest dynamics plots and associated research activities to monitor and understand the ecology, evolution, and conservation of forest biodiversity and its impact on Earth's functioning, to strengthen science capacity globally through professional training, and to develop scientific input for forest policy, conservation and management. Today, the strength of the network is a direct outcome of the dual mission of science and training. The continued commitment to early-career scientists across the world helps ensure continuity of the science and the individual FDPs, but is also the key source of the innovations required to tackle the challenges confronting forests.

4. The ForestGEO forest dynamics plot: core plot methods

A ForestGEO Forest Dynamics Plot (FDP) consists of a surveyed and mapped grid of typically 16–50 ha (average = 26 ha) in which all woody stems with a diameter ≥ 1 cm at 1.3 m above the ground (diameter at breast height, DBH) are mapped, measured, and identified to species (Manokaran et al., 1990; Condit, 1998). This census is repeated at approximately five-year intervals, during which all prior stems are remeasured or recorded as dead, and all new stems ≥1 cm in DBH (recruits) are tagged, mapped, measured, and identified as in the original census. ForestGEO FDPs now collectively cover 1833 ha (Table 1). In several sites, FDPs are smaller than 16-ha due either to local funding limitations or to constraints on available forest area, however, all other aspects of standardized data collection are followed in these sites. There have been 189 censuses among the 71 plots. The oldest plot, BCI, is in the midst of its ninth census. There are approximately 7.33 million living trees within the FDPs today, and there have been over 21 million tree measurements across the plots. To publicize the core plot data and provide detailed site-specific information on local field protocols, climate and soils, species identification, and other species information, many sites have published books describing the FDPs (Manokaran et al., 1993; Lee et al., 2003; Thomas et al., 2003; Gunatilleke et al., 2004; LaFrankie et al., 2005; Co et al., 2006; Su et al., 2007; Cao et al., 2008; Bunyavejchewin et al., 2009; Chen et al., 2009; Li et al., 2010; Chang et al., 2012; Ding et al., 2013; Cao et al., 2013; Pérez et al., 2014; Lu et al., 2016; Wang et al., 2016; Xu et al., 2017; Yang et al., 2019). Several of these are also published online (https://forestgeo.si.edu/research-programs/publications/forestgeo-stand-books).

Species identification is one of the key imperatives in the ForestGEO methodology. A core goal of the FDP is to document the population dynamics of as many species as possible, so the FDPs all go to great lengths to identify their constituent species as thoroughly as possible using extensive collections, comparisons with herbarium specimens, and consultation with taxonomists specializing in particular taxonomic groups. While most species can be identified, 10–15% of species, including mostly rare tropical species that account for a small fraction of stems in the tropical FDPs, remain classified as distinct morphospecies but without a confirmed binomial.

4.1. *Why large plots with the inclusion of small stems?*

The ForestGEO FDP methodology pioneered two relatively unique features in forest science: the very large-scale plot dimensions, and the complete censusing of all stems of at least 1 cm DBH. Previous plot-based studies in tropical forests mostly employed plots of either 1 ha in area using a DBH cut-off of 10 cm, or 0.1 ha with DBH ≥ 2.5 cm (e.g., Gentry, 1988; Malhi et al., 2002). Both of these methodological innovations have significant logistical and financial consequences: a 50-ha plot including all stems ≥1 cm DBH may include 250,000–450,000 stems, compared to an average of about 500 stems ≥10 cm DBH in a typical 1-ha plot. Establishing a 50-ha plot in diverse tropical forest with ~350,000 stems typically takes a team of 15 technicians two years, followed by at least two years for expert plant identification, and data processing and quality control. While measuring, mapping and sampling small stems is straightforward, albeit laborious, the identification of small stems, which are often juveniles of locally occurring adults, can be exceedingly challenging, as trees often undergo dramatic changes in morphology as they grow from the understory to the canopy. However, sampling larger areas and including small stems provides a series of benefits for sampling forest diversity, dynamics, and demography.

The spatial and temporal scale, and intensity of sampling in the ForestGEO FDP is especially valuable for studying population and community ecology in forests. The dynamics of most forests are, barring episodic disturbances, slow. Mortality rates typically range from 1 to 4% per year among forests, so detecting trends in mortality rates, and especially differential trends among species, size classes or habitats requires lots of individuals to be monitored over long periods (McMahon et al., 2019). Most tropical tree species are rare, so large plots are needed to achieve the goal of building robust demographic data for a large fraction of species at a particular site. Furthermore, a considerable portion of woody plant diversity is present at diameters <10 cm, so studying trees down to 1 cm is important for capturing forest diversity (Memiaghe et al., 2016). Large plots are useful for advancing understanding of how disturbances influence the diversity and dynamics of tropical forests since many (though certainly not all) disturbances in tropical forests occur on the scale of 0.25–5 ha (e.g., tree falls, landslides, lightning, etc.). Large mapped plots provide a valuable resource for exploring the spatial patterns in forests, especially for large-diameter trees that occur at relatively low densities (Lutz et al., 2018; Engone-Obiang et al., 2019). Many of the mechanisms posited to maintain diversity and drive patterns of species turnover are spatial, including abiotic components of edaphic, hydrologic and light variation, and interactions among neighboring con- and heterospecific individuals. The inclusion of small stems (1–10 cm DBH) provides a window into the early life stages of tree species, a stage at which mortality rates are often higher and individuals are more sensitive to competition, disturbance and biotic effects. Finally, large plots have a large footprint and can be more easily "seen" from satellites and other remote observing instruments (Réjou-Méchain et al., 2014).

4.2. Data management & analysis

ForestGEO designed and developed a complete data system for storing and managing tree census results for the network. The ForestGEO database model follows theories of data normalization by minimizing data redundancy, which can lead to anomalies during updates and is the source of many common errors (Condit et al., 2014). The database runs on the open-source MySQL server, with interfaces written in HTML, PHP and JavaScript for online access via web portals. The data entry interface can be configured to mirror the field forms for plots using paper forms. The system screens and uploads data to the MySQL plot database. All data are in a standard format, facilitating sharing of software for data analysis, and fostering comparative data analysis (e.g., LaManna et al., 2017; Lutz et al., 2018). Metadata and version control are maintained to ensure that researchers can reliably reference datasets. A data request system is linked to the database, including descriptions of the terms and conditions for data access, and details for acknowledgement (https://forestgeo.si.edu/explore-data). Several plot datasets are now publicly accessible (e.g., Bourg et al., 2013) and many other FDP data are available following acceptance of the terms and conditions for data sharing, as described on the site pages of the ForestGEO website. To ensure uniform data quality across the partner sites, ForestGEO provides technical support to plot PIs. The protocol for this system is detailed in the "*ForestGEO Database Handbook*" (https://forestgeo.si.edu/sites/default/files/database_handbook-final.pdf).

To facilitate comparative data analysis across FDPs, ForestGEO developed a package of analytical software in the R programming language designed specifically for use with census data from the FDPs (Condit, 2012). The package is available as either the "CTFS R package" https://forestgeo.si.edu/explore-data/r-package-0 or the "fgeo" R package https://forestgeo.si.edu/explore-data/r-package. The package includes many tutorials, broadening access to a wide range of data analytical tools and facilitating research by forest scientists with a broad range of levels of experience with analyses of large datasets. Long used in the annual network-wide analytical workshops (Section 6), the CTFS R package has also served as an entry point for many young forest scientists to learn to develop the bespoke statistical analytical code necessary for testing ecological hypotheses within and across the network. Although the functions in the CTFS R package are designed for use with ForestGEO data, the source code for each function is freely available, and can be modified to accommodate any data format, which enables capacity building in forest science beyond the ForestGEO network.

5. ForestGEO as a platform for forest research

The transition from CTFS to ForestGEO was motivated by the idea that a full understanding of the functioning of forests requires an integrated set of observations with greater biotic coverage, coupled with detailed measurements of the abiotic drivers that strongly influence forests. This led to greatly expanded data collection at many ForestGEO FDPs. The focus of the expanded field data collection program included sampling animal and microbial diversity, monitoring life stages from flowering through seedling recruitment, quantifying components of carbon stocks and fluxes, using genome-based approaches to forest diversity and lineage interactions, as well as detailed assessment of climatic and edaphic variation within sites. As with the core plot censuses, protocols for expanded data collection were standardized to facilitate local, regional and global comparative analyses. Here we present some examples of data being collected across the FDPs that are opening new avenues of forest science discovery. Full descriptions of these and other standardized protocols and their implementation across ForestGEO FDPs are described in Anderson-Teixeira et al. (2015) and available on the ForestGEO website (https://forestgeo.si.edu/protocols; see also).

5.1. Arthropods

Arthropods influence key forest functions, including nutrient cycling, seed predation and dispersal, herbivory, and pollination. Given recent concerns about global insect decline (Sánchez-Bayo and Wyckhuys, 2019; Wagner, 2020), high quality data on the population dynamics of tropical arthropods are urgently needed to understand their responses to global changes and the functional implications for their ecosystems (Basset and Lamarre, 2019; Wagner, 2020). In 2009, ForestGEO developed a standardized protocol (https://forestgeo.si.edu/node/145661/) for monitoring common arthropod species with methods that can be applied consistently across the network. The protocol is now implemented in seven tropical FDPs representing a rare effort to monitor key arthropod assemblages in tropical forests (Lamarre et al., 2020; WWF, 2020). Monitoring data now represent >600,000 records, >6000 species, 14,000 DNA barcoding sequences, and 100,000 vouchered specimens. Taxonomic resolution is improved by building reference collections and DNA barcode libraries (e.g., Basset et al., 2015). Species traits (e.g., thermal tolerance) are being used to delineate functional groups to monitor population trends and overcome the challenge of studying thousands of individual species (Basset et al., 2017; Lamarre et al., 2020). DNA metabarcoding is also being used to monitor community dynamics (Gripenberg et al., 2019). The data are being used for a wide range of monitoring and interactions studies, including responses of insects to climate change (Basset et al., 2013, 2015, 2017; Lucas et al., 2016; Luk et al., 2019), and studies of seed predators (Basset et al., 2018; Gripenberg et al., 2019).

5.2. Completing the tree life cycle from reproduction to recruitment

The core monitoring program at all ForestGEO FDPs focuses on trees and begins when a tree enters the 1 cm DBH size class and ends when the tree dies. Key aspects of a tree's life-history are overlooked with this protocol. Stems of 1 cm DBH may be decades old (Delissio et al., 2002), key processes affecting individual survival may be most intense in the smallest size classes, and patterns of flowering, fruiting, seed dispersal, germination, and recruitment strongly affect when and where species will occur. In 1987, the collection of data on seed production, seedling recruitment and seedling growth and survival was initiated on BCI to build complete life cycle information for tropical tree species using seedling plots and seed traps (Wright et al., 2005, https://forestgeo.si.edu/research-programs/flowers-seeds-and-seedlings-initiative). The implementation of these field protocols, coupled with intensive monitoring of the reproductive status of thousands of individual trees, has led to a new generation of studies that have integrated all life stages from seed to adult to evaluate: (1) relationships between vital rates and functional traits across the tree life cycle (Iida et al., 2014; Visser et al., 2016), (2) costs and benefits of dioecy (Bruijning et al., 2017), (3) the impact of lianas on population growth rates of host trees (Visser et al., 2017), and (4) the processes that underlie liana-tree interactions including colonization, shedding, baseline mortality, and increased lethality (Visser et al., 2018). Today 26 FDPs have established seed/seedling monitoring programs using these standardized protocols (e.g., Chen et al., 2010, Chen et al., 2018, Jin et al., 2017).

Additional seedling plots have been added to many FDPs to improve spatial coverage and sample size for early-life stage demographic analyses (e.g., Comita et al., 2010). Seed traps, by collecting all fallen leaf and reproductive material have also been a source of information on seed dispersal patterns (Hubbell et al., 1999; Du et al., 2009; Marchand et al., 2020), and the phenology of reproduction and tissue turnover (e.g., Detto et al., 2018). Repeated observations of individual trees have also been implemented at ForestGEO FDPs, providing insights into patterns of vegetative and reproductive phenology (e.g., Williams et al., 2008; Kurten et al., 2018).

5.3. Biomass and carbon storage and fluxes

ForestGEO FDP data have provided an excellent resource for quantifying aboveground woody biomass carbon stocks (AGB), woody productivity and woody mortality fluxes. The core ForestGEO FDP carbon measurement is tree diameter at breast height (DBH). These measurements are used in combination with allometric equations and sometimes also measurements of tree height and wood density, to estimate individual tree biomass (Chave et al., 2014; Réjou-Méchain et al., 2017; Gonzalez-Akre et al., in review). Individual tree and stem AGB are then summed over area to estimate total AGB stocks per area. Repeat census data together with biomass allometric equations can be used to quantify woody productivity and woody mortality fluxes at the stand level. Numerous studies have quantified biomass stocks and fluxes in ForestGEO plots, and their variation over space and time (Chave et al., 2003; Chave et al., 2008; Valencia et al., 2009; Lin et al., 2012; Yuan et al., 2016, 2019; Zuleta et al., 2017; Ma et al., 2019; Rutishauser et al., 2019). A key advantage of ForestGEO plots for these studies is that their large size reduces sampling errors in these biomass stocks and fluxes, sampling errors which remain substantial even at the 1-ha scale (Wagner et al., 2010; Muller-Landau et al., 2014; Réjou-Méchain et al., 2014).

While woody productivity and mortality can be well characterized with a 5-yearly recensus interval, their responses to short-term environmental fluctuations, including droughts, storms and pest outbreaks require more frequent measurements (Lutz, 2015; McMahon et al., 2019). To better characterize the causes and directionality of changes in growth and mortality rates, many ForestGEO plots have implemented annual or subannual measurements of growth and mortality. For growth, plots have subsampled trees with dendrometer bands at temporal frequencies ranging down to weeks (McMahon and Parker, 2015) or even minutes (Herrmann et al., 2016), and many have also developed tree-ring chronologies that provide histories of annual growth over decades to centuries (e.g., Šamonil et al., 2013; Sniderhan and Baltzer, 2016; Alfaro-Sánchez et al., 2017; Helcoski et al., 2019). For mortality in tropical FDPs, ForestGEO established a protocol for the assessment of tree damage and death (Arellano et al., in review), complementing existing surveys in temperate FDPs (Furniss et al., 2020), and currently conducts annual mortality censuses at >10 sites.

Because living trees may account for less than half of total ecosystem carbon stocks (Anderson-Teixeira et al., 2018), and their woody productivity can represent <10% of gross primary production (Anderson-Teixeira et al., 2016), many FDPs are also censusing carbon stocks and/or fluxes in soil, fine roots, dead wood and lianas (Ngo et al., 2013; Wright et al., 2015; Gora et al., 2019; Janik et al., 2019). Annual or subannual measurements of litterfall and soil respiration are being used to estimate interannual variation in associated carbon fluxes in numerous plots (Rubio and Detto, 2017; Detto et al., 2018).

5.4. Soils and climate

Soils and climate drive many aspects of the diversity and dynamics of forests. ForestGEO has designed protocols to assess their spatial and temporal variation. At the scale of a 50-ha plot there is often dramatic spatial heterogeneity in soil properties driven by variation in underlying parent material, topographic position, and water table depth and flow paths (Fig. 5). This edaphic variation impacts spatial variation in carbon and biomass stocks and fluxes, and strongly affects species distributions (Section 7). ForestGEO has implemented a standard protocol to measure the physical and chemical properties of soils in over 25 tropical and temperate FDPs (https://forestgeo.si.edu/protocols/soils). Soils are sampled across the entire FDP resulting in maps of soil chemical and physical characteristics (John et al., 2007). Soil carbon is being quantified in FDPs to improve our understanding of factors controlling

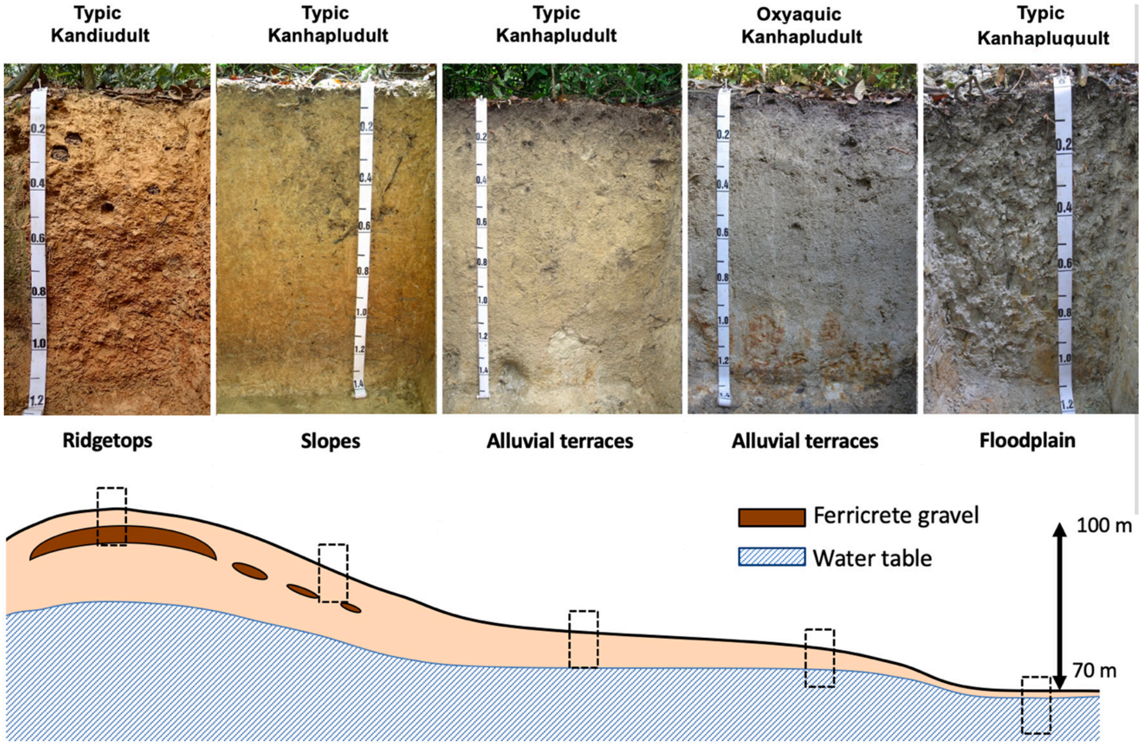


Fig. 5. Pictorial representation of soil, topographic and hydrological variation within the 50-ha FDP at Pasoh, Malaysia, illustrating the dramatic variation in edaphic conditions that are often included within a typical large-scale ForestGEO FDP. USDA soil taxonomic names listed at the top of each photo which were taken within soil pits sampled along the soil *catena* (hatched boxes) spanning just 30 m of elevation difference between the highest and lowest points within the plot. Like most FDPs this edaphic and topographic gradient results in significant turnover in species composition across the plot (Davies et al., 2003).

carbon stocks globally, and how this might change with future shifts in climate. Maps of soils and topography are also being used to investigate demographic patterns of individual tree species (e.g., Russo et al., 2005).

Meteorological data are collected at or near various ForestGEO sites. This information is fully described in Anderson-Teixeira et al. (2015) and is curated in the open-access ForestGEO Climate Data Portal (https://forestgeo.github.io/Climate/; DOI: https://doi.org/10.5281/zenodo.4041609), along with climate records extracted specifically for ForestGEO sites from global databases (e.g., CRU, Harris et al., 2020). The portal also hosts historical records of atmospheric pollution (CO_2, NO_x and SO_2 emissions, Hoesly et al., 2020).

5.5. Genome-based approaches to diversity and dynamics

The identification of species remains an impediment to advancing forest science. For trees, the available sample may have no flowers or fruits to enable a confirmed identification. For many other organisms, they may be microscopic (e.g., bacteria, fungi, etc.), they may be taxonomically very poorly known (e.g., many arthropod groups), and in still many cases, they remain unknown to science (Cardoso et al., 2017). By harnessing advances in molecular genetics, sequencing technology, and bioinformatics, DNA barcoding has become a valuable tool for exploring diversity in ForestGEO FDPs and has potential value in tracking changes in biodiversity (Kress et al., 2009). More than 3,000 tree species in 25 ForestGEO FDPs and 14,000 arthropods in seven FDPs have now been DNA barcoded (Erickson et al., 2014; Basset et al., 2015). These barcodes are being used for the identification of tree roots (Jones et al., 2011) and seed predators (Gripenberg et al., 2019), and to build community-level phylogenies (Swenson et al., 2012, 2013; Erickson et al., 2014).

Metabarcoding, barcoding applied to mixed community samples, is now being widely used in ForestGEO plots to explore plant-animal and plant-microbe interactions, including studies of mycorrhizal symbionts in dipterocarp-dominated FDPs in Malaysia (Peay et al., 2010, 2015), microbial diversity along habitat gradients and in relation to the tree community (Russo et al., 2012; Barberán et al., 2015; Song et al., 2018) and food plant diversity in fecal material of vertebrate herbivores (Erickson et al., 2017; McShea et al., 2019). The potential to explore the functional basis of tree interactions with the environment are being further enhanced through the use of genomic approaches in FDPs (Swenson et al., 2017a), for example, to investigate the genetic basis of drought tolerance differences among tree species (Swenson et al., 2017b).

6. ForestGEO education and training initiatives

Recognizing the global need for strengthening capacity in forest science, ForestGEO is deeply committed to training early-career scientists from all over the world spanning diverse professions in forest science, including researchers, academics, conservation biologists, and managers. By cultivating new skills, gaining research experience, and increasing accessibility to a network of data and shared expertise, ForestGEO's education and training initiatives ensure that benefits derived from the global syntheses are shared among diverse groups. Regular analytical and data workshops, individual research grants, internships, and postdoctoral fellowships are designed to train the next generation of scientists who will be the future stewards of Earth's forests.

For ForestGEO's hundreds of collaborating researchers around the world, dedicated time to meet in-person to share research findings, learn new analytical techniques, and discuss multi-plot research is invaluable. ForestGEO's analytical and data workshops bring researchers together to define global-scale science questions, address data gaps and network needs, and expand interdisciplinary collaboration. ForestGEO has convened 17 analytical workshops since 2001, each bringing together scientists from >20 countries (Fig. 7). Analytical workshops consist of hands-on training, seminars, and discussions for approximately 60 individuals over two to three weeks in a location near a ForestGEO plot. Workshop participants consist of approximately 70% students and early-career scientists who are grouped by research interest with a designated mentor to foster research collaborations and receive direct training and support. These workshops have provided >350 early-career scientists with opportunities to gain international research experience, improve writing and editing skills, and expand data analysis expertise. The analytical workshops have resulted in peer-reviewed papers in a wide array of journals spanning disciplines, with 255 workshop-derived papers published since 2011. Many of the papers are coauthored by participants from multiple plots, reflecting the value of data sharing and analysis that is fostered through the workshops. The connections cultivated at analytical workshops continue and develop into enduring mentorships and collaborations that allow workshop attendees to be conduits of research mentorship to others in their home institutions, exponentially expanding the network's training impact.

ForestGEO also holds focused data management workshops that cover a range of topics from basic data entry techniques and management utilizing Structured Query Language (SQL), to training in statistical analyses with the R programming language. ForestGEO database staff and scientists provide individual attention and training to plot managers, early-career scientists, and students, who then bring this knowledge back to their local plots and institutions.

To create direct opportunities for graduate students and postdoctoral fellows to conduct research in ForestGEO sites in collaboration with site Principal Investigators, ForestGEO holds an annual research grants program. Small grants enable investigations of a wide range of forest science questions and give opportunities to those who have not previously been involved in the network to build working relationships with senior scientists and begin long-term collaborations. These projects benefit the individual's continued training and education, and at the same time improve the depth of research at individual FDPs. Since 2002, >700 researchers have applied for these competitive grants, and ForestGEO has awarded more than $1.1 million to 183 individuals. These novel projects give ForestGEO the opportunity to fund innovative research that advances the strength of the ForestGEO network as a whole.

In addition to funding short-term grant projects, ForestGEO supports postdoctoral fellowships. These are independent research projects designed to answer a specific research question relevant to ForestGEO's science goals. Between two and five postdoctoral fellows per year conduct research on a variety of topics related to advancing the science of forest structure and dynamics, including plant-water relations and forest function, tree mortality, and above-ground biomass dynamics.

ForestGEO is also committed to training undergraduate students in learning new skills and gaining access to a network of data and shared expertise. In addition to training fellows, ForestGEO offers internships in fieldwork, data analysis, or data management at network sites or at ForestGEO offices. ForestGEO is committed to training interns from countries with developing forest science capacity, stationing them at plots with opportunities to develop their skills and expertise. Strengthening capacity through analytical and data workshops, individual research grants, and internships and fellowships are essential for ensuring network continuity and continued progress in forest science.

7. Advances in understanding forest diversity

The ForestGEO network has made major contributions in two broad areas of forest science: (i) Species coexistence and diversity, and (ii) Ecosystem processes and forest functioning. Other articles in this special issue have addressed many key accomplishments of the long-term tropical forest plot networks in the area of forest functioning and the impacts of altered climatic and atmospheric conditions (e.g., Phillips et al. *this volume*). Anderson-Teixeira et al. (2015) described how the broad suite of measurements being made at ForestGEO sites is critical for addressing the complex responses of ecosystem processes and forest functioning to diverse global change drivers. What has been covered less are the insights gained from ForestGEO FDPs on the processes regulating species diversity, coexistence and dynamics. Here, we highlight a series of key findings linked to the biology of species and the role they play in forests. These findings are not exclusively attributable to the ForestGEO approach, however in several cases it is clear that the unique large-scale sampling of the FDP has provided critical insights in these areas. The following selection is also not intended to be comprehensive with respect to the diversity of topics addressed using the ForestGEO plots. Key areas of species diversity research conducted using ForestGEO FDPs that are not covered below include: geographical patterns of diversity among plots (e.g., Ren et al., 2013; Ricklefs and He, 2016; Sreekar et al., 2018; Chu et al., 2018), patterns of phylogenetic diversity (e.g., Mi et al., 2012), and relationships between biodiversity and ecosystem function (e.g., Chisholm et al., 2013). A complete list of ForestGEO publications is available (https://forestgeo.si.edu/research-programs/publications; and https://scholar.google.com/citations?user=RFULppIAAAAJ&hl=en).

7.1. Spatial distribution of tree species and functional types with respect to habitat

ForestGEO FDPs have demonstrated that forests consist of highly spatially structured assemblages of species. The majority of tree species have strongly aggregated spatial distributions. Analyses across many ForestGEO plots have shown that 30–75% of species in any one plot have spatial distributions significantly aggregated with respect to soil nutrients, topographic position, moisture availability, and the history of local disturbance (e.g., Fig. 6). This finding, first documented on BCI and several plots in Asia (Condit et al., 2000; Harms et al., 2001), has now been confirmed in many plots across the network (Davies et al., 2005; Gunatilleke et al., 2006; Lai et al., 2009; Chuyong et al., 2011; Lan et al., 2012; Bunyavejchewin et al., 2019). With the obvious exception of the distribution of pioneer species in relation to light gaps, the details of what specific resource requirements, e.g., water availability, soil nutrients, wind exposure, constrain species distributions across these topographic and edaphic gradients remains poorly understood, as many factors covary (John et al., 2007; Baldeck et al., 2013; Kupers et al., 2019). However, recent studies in BCI and across the Isthmus of Panama demonstrate the key roles played by soil moisture and phosphorus availability (Condit et al., 2013; Zemunik et al., 2018). It is an area where experimentation needs to be coupled with long-term monitoring (Engelbrecht et al., 2007; Baltzer et al., 2008). In addition to having fundamental consequences for the theories of species diversity in forests, the observation of pervasive habitat associations in tropical tree species has direct importance for forest conservation and management. Species-site matching remains an important requirement for successful ecological restoration by tree planting (Shono et al., 2007).

The patchy distribution of species across edaphic and topographic gradients is reflected in functional differences of the constituent species. Analyses of functional trait variation in species across many FDPs show strong relationships with underlying edaphic and hydrological conditions. For example, within the extremely diverse 25-ha plot at Yasuní, Ecuador, species with lower average specific leaf area, smaller leaves and heavier seeds were more common on ridges (Valencia et al., 2004, 2009, Kraft et al., 2008). Analogous patterns have been observed in many other large FDPs around the world (e.g., Katabuchi et al., 2012; Liu et al., 2013; Yang et al., 2014). Patterns of species-level functional trait covariance across habitat gradients provides a way of pooling hundreds of species into a smaller number of life-history types that can be more easily parameterized in Earth System Models (Scheiter et al., 2013; Fisher et al., 2015; Koven et al., 2020).

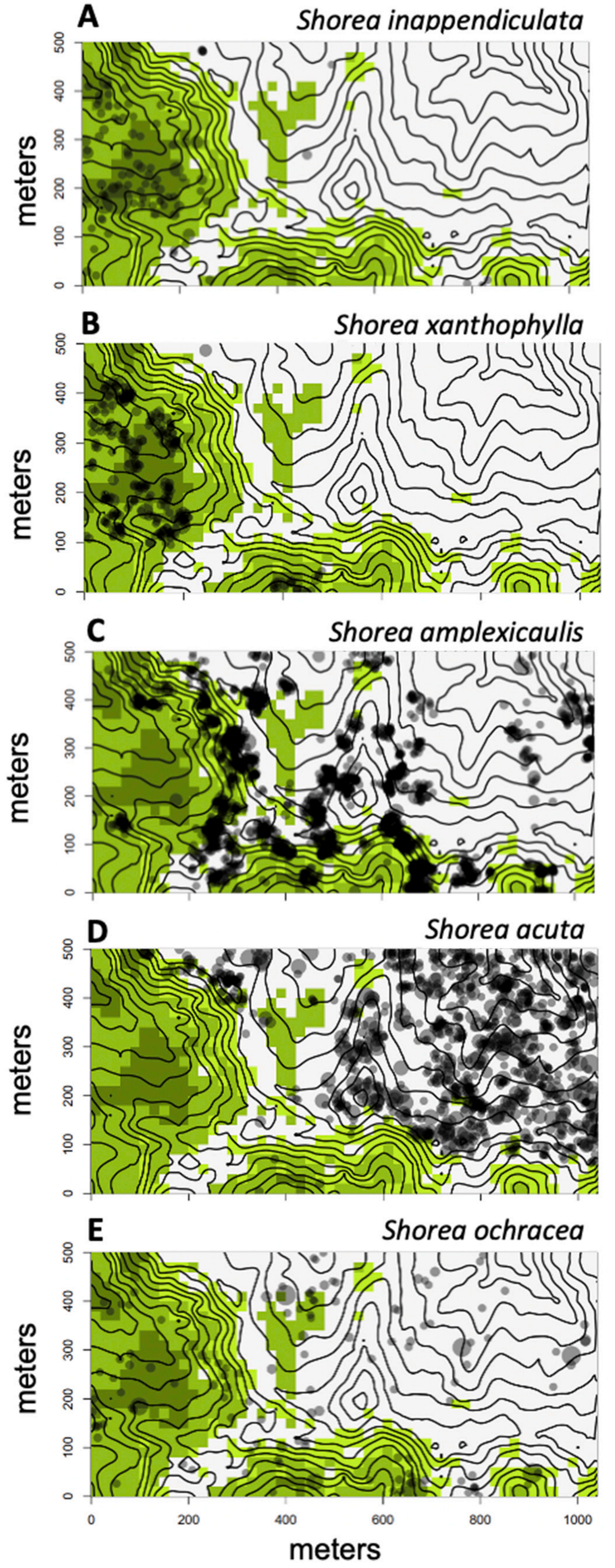
7.2. Seed dispersal, seedling recruitment and patterns of spatial aggregation

Seed dispersal controls the ability of plants to reach preferred regeneration sites and to colonize new habitats. The seed trapping program implemented at many ForestGEO FDPs has demonstrated that mean seed dispersal distance varies by more than an order of magnitude among coexisting tree species (Muller-Landau et al., 2008). Life-history tradeoffs involving seed dispersal and fecundity can contribute to species niche differentiation and coexistence (Muller-Landau, 2008; Muller-Landau, 2010; Bin et al., 2019). Species dispersal strategies vary not only in distance distributions but also in directionality, efficacy in reaching canopy gaps, and clumping (Muller-Landau and Hardesty, 2005; Wright et al., 2008; Puerta-Piñero et al., 2013; van Putten et al., 2012). Limited seed dispersal distances and clumped seed dispersal, often combined with low adult abundance, mean that many species fail to arrive in any given regeneration site (Hubbell et al., 1999; Li et al., 2012; Chen et al., 2014), which can make overall community dynamics more stochastic (Hurtt and Pacala, 1995).

Since most seeds of most species fall close to the mother tree (Marchand et al., 2020), species-level spatial aggregation at local scales is in large part attributable to limited seed dispersal and is associated with seed dispersal syndromes (Condit et al., 2000, Seidler and Plotkin, 2006, Shen et al., 2009, Shen et al., 2013, Detto and Muller-Landau, 2013, Clark et al., 2017, Wang et al., 2018), which are often phylogenetically conserved (Russo et al., 2007). This has significant consequences for subsequent seedling recruitment and survival (Janzen, 1970; Beckman et al., 2012). While habitat suitability may be higher close to a parent tree, high conspecific seedling density and proximity to a conspecific adult may increase intraspecific competition and exposure to pest pressure, shifting seedling distributions farther from adults (Janzen, 1970; Uriarte et al., 2005; Murphy et al., 2017). Seed dispersal and seedling recruitment dynamics play important roles in regulating the diversity of tree communities.

7.3. Neighborhood composition and the impacts on individual performance

Given that most tree species exhibit spatially clumped distributions (Condit et al., 2000), ultimately owing to limited seed dispersal (Clark et al., 2017), tree local neighborhoods have enormous effects on recruitment, growth, and survival. Such neighborhood effects are not only mediated by competitive interactions with other plants, but also strongly by interactions with natural enemies and mutualists. This is particularly the case when trees are surrounded by conspecifics or close relatives, which are more likely to share natural enemies (Gilbert, 2002; Janzen, 1970; Connell, 1971). Tropical forests are notorious for their long-tailed species rank-abundance distributions (Whittaker, 1965), with most species being rare. A key focus of ForestGEO research has been the identification of possible mechanisms that facilitate a “rare species advantage”, ensuring no single tree species can “take over the world” or at least a local tree community on the scale of a 50-ha plot (Wills et al., 2006). In theory, this occurs when all species have positive invasion growth rates (Chesson, 2000), a condition that is met when each species density affects itself more than it affects other species (Broekman et al., 2019). Although it has proven challenging to robustly measure such conspecific density effects (Detto et al., 2019), evidence of conspecific negative density dependence (CNDD) has been reported in many tropical, subtropical and temperate FDPs for growth and survival (e.g., Hubbell et al., 1990, Harms et al., 2000, Uriarte et al., 2004, Jia et al., 2020). In addition, rare species in at least one tropical FDP have been found to have stronger negative effects on their own growth or survival than common species, suggesting the hypothesis that rare species are rare at least in part because they suffer more from intraspecific competition or species-specific natural enemies (Comita et al., 2010; Mangan et al., 2010). However, results from manipulation studies on the



(caption on next column)

Fig. 6. The striking habitat-related variation in spatial distributions of individuals of five species of *Shorea* (Dipterocarpaceae) in the 52-ha FDP at Lambir, Sarawak, Malaysia. The pattern of sympatric congeneric species occupying different habitats within the same plot is a repeated feature of many ForestGEO FDPs. Habitats, defined by soil chemistry and texture, range from most nutrient-poor sandy loams (white) to least nutrient-poor clays (dark green). Contour lines span 140 m of elevation change within the plot. Dot sizes are scaled to tree size. Species and habitat specialization include: (A) *Shorea inappendiculata* - clay, B. *Shorea xanthophylla* - fine loam; C. *Shorea amplexicaulis* - loam; D. *Shorea acuta* - sandy loam; E. *Shorea ochracea* - a generalist species without habitat specialization within the plot. Figure adapted from Russo et al. (2005). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

prevalence of negative density dependence are mixed (Song et al., in review) and the hypothesis that species suffer more CNDD when rare has been challenged in other forests (e.g., Liu et al., 2015).

There is clearly much to learn regarding how species' populations are regulated and thereby prevent dominance. For example, soil microorganisms, including fungal and oomycete pathogens, are thought to be principal mediators of conspecific density dependence (Bever et al., 2015), but plant-soil feedback studies have shown that being near close relatives is not always bad, particularly for tree species hosting ectomycorrhizal fungi (Segnitz et al., 2020). While numerous factors contribute to variation in species' abundances in space and time, the prevalence of negative density dependence and interspecific variation in its strength has profound consequences for the maintenance of diversity in forests (Johnson et al., 2012; Stump and Comita, 2018; Chisholm and Fung, 2020; Comita and Stump, 2020).

7.4. Tree life-histories: demographic variation within- and among- forests

The balance between growth, recruitment and mortality largely determines the variation in carbon, water, and nutrient cycles, affects above and belowground trophic interactions, and underpins the coexistence and abundance of species. Quantifying how demographic rates vary within- and among- sites and through time is therefore important for predicting the future of Earth's forests and their role in regulating the Earth system. The ForestGEO FDPs have enabled the characterization of growth, mortality, and recruitment rates for thousands of tree species across the world's forests (e.g., Rüger et al., 2011; Johnson et al., 2018; Russo et al., 2020). Analyses of many plots have found an interspecific trade-off between a tree species' ability to grow fast in high resource conditions versus to survive in low resource conditions due to species' differences in allocation (Russo et al., 2008; Wright et al., 2010; Rüger et al., 2018; Medeiros et al., 2019). The strength of this trade-off varies among edaphic habitats within a forest, reinforcing resource-based species' distribution patterns (Russo et al., 2008). The trade-off, however, is not equally strong in all forests. Although it was observed across tropical forests at the global scale, it was not observed in some forests where the local disturbance regime (e.g., frequent hurricane exposure) appears to have restricted the adaptive resource allocation strategies to a narrow range of those possible (Russo et al., 2020). While the growth-mortality trade-off can promote species' coexistence, the range of species' growth and mortality rates in a forest does not explain the massive differences in species richness of forests across the tropics: species-rich tropical forests actually have a narrower range of demographic variation and finer demographic niches than species-poor forests (Condit et al., 2006).

Analysis of the BCI FDP in Panama revealed an additional demographic trade-off contributing to tree species coexistence, a 'stature–recruitment' trade-off distinguishing between small-statured species with high recruitment success and large-statured species with low recruitment success (Rüger et al., 2018). In combination, the growth-mortality and stature-recruitment trade-offs have been used to accurately predict basal area and compositional changes during forest

Fig. 7. Photo of network participants at the annual ForestGEO analytical workshop in July 2018 in Boubin old-growth forest, Czech Republic; the oldest known forest plot with mapped stems in the world.

succession at BCI (Rüger et al., 2020), illustrating the importance of demographic data collected in ForestGEO plots for understanding and predicting consequences of human impacts on forest ecosystems.

The extensive demographic data from ForestGEO FDPs offer an alternative route to simplifying the challenge of high species diversity in dynamic vegetation models (e.g., Koven et al., 2020). These models typically rely on trait data to characterize plant functional types, a task that can be challenging in species-rich forests. Tree species across ForestGEO FDPs have been shown to cluster into demographic groups based on variation in size-dependent growth and survival. At least for survival, the relative abundance of these demographic groups varies among plots and is associated with climatic variation (Johnson et al., 2018). Size-structured demographic groupings are also likely to prove useful for extrapolating demography across unsampled forest regions to predict ecosystem processes, such as biomass change and response to climate (Johnson et al., 2018; Needham et al., 2018).

7.5. Neutral theory and the maintenance of species diversity in tropical forests

Observations from ForestGEO FDPs and other tropical forests inspired the neutral theory of biodiversity (Hubbell, 1979a, 1979b, 2001), which makes the bold assertion that many observed patterns in nature can be explained without invoking species differences. An initial wave of enthusiasm for neutral theory stemmed from its successful explanation of empirical patterns such as species abundance distributions (Volkov et al., 2003) and species–area relationships (Rosindell and Chisholm, 2020). But this enthusiasm waned upon discovery that other predictions of neutral theory were less accurate, in particular its predictions of temporal change on both ecological and evolutionary timescales (Nee, 2005; Leigh, 2007; Chisholm and O'Dwyer, 2014). A study of 12 ForestGEO sites revealed that fluctuations in the abundance of common tree species over timescales of 6–28 years were orders of magnitude larger than neutral predictions (Chisholm et al., 2014).

These latter limitations of neutral theory are perhaps not surprising, given the lack of evidence for the species equivalence assumption. Nevertheless, neutral theory has played a valuable role in ecology in several ways. First, it serves as a null model for detecting when important non-neutral processes are operating. Second, it provides a rigorous mathematical framework for making falsifiable predictions about biodiversity patterns—a framework into which other processes, including non-neutral processes, can be incorporated. Lastly, neutral theory has shown that diversity of local communities, specifically tree communities in ForestGEO plots, can easily be maintained by immigration from beyond the plot boundaries, without invoking local niche stabilizing mechanisms (Condit et al., 2012). This latter point, though often overlooked, transcends the theory's assumptions about species equivalence and is arguably its greatest contribution to our understanding of forest dynamics–one that only emerged from the interplay of theory with ForestGEO data.

7.6. Temporal change in the species composition of old-growth tropical forests

The idea that the species composition of old-growth tropical forests is stable over time has been comprehensively refuted by the unique long-term data of ForestGEO plots. Forests are surprisingly dynamic with large changes due to annual mortality rates ranging from 1 to 4% per year (see Wright, *this volume*). Analyzing the dynamics of over 4000 species in 12 ForestGEO FDPs, the largest and most comprehensive sample of species-level population dynamics from tropical forests across Africa, Asia and the Americas, Chisholm et al. (2014) found that the abundance of a majority of species is increasing or decreasing more than expected under a neutral model of community change. Natural disturbances, including fires, landslides, droughts, and hurricanes are a major cause of temporal fluctuations in species composition on decadal timescales in many tropical forests (Hubbell and Foster, 1992; Hogan et al., 2018; Bunyavejchewin et al., 2019). Species-level studies across many ForestGEO FDPs have demonstrated differential sensitivity to drought (e.g., Condit et al., 1995; Engelbrecht et al., 2007; Itoh et al., 2012; Zuleta et al., 2017). On century time scales, dendrochronological studies provide increasing evidence that current community composition of some ForestGEO FDPs reflects historical disturbance events (e.g., Baker et al., 2005). Despite these cases, in many forests there is no obvious factor driving differential abundance changes among species (Chisholm et al., 2014). Further work is needed to understand whether these population changes are linked to specific shifts in climatic conditions, biotic interactions, or other drivers. Given the potential for climate-related changes at these sites, large FDPs are a critical baseline for understanding the impact of future natural and anthropogenic change on species populations.

7.7. Impact of changes in vertebrate populations on forest diversity and dynamics

Hunting-induced defaunation is driving major changes in the diversity and functioning of forests around the world (Dirzo et al., 2014; Malhi et al., 2016; Osuri et al., 2016; Peres et al., 2016). However, defaunation outcomes are often idiosyncratic and site-specific because of the unique impacts of locally dominant vertebrates on herbivory, seed dispersal, predation and physical disturbance at each site (Wright, 2003). For example, defaunation in three ForestGEO FDPs in Asia resulted in substantially different ecological outcomes. Defaunation of seed-dispersers in Khao Yai, Thailand, has reduced tree recruitment (Chanthorn et al., 2019). In Lambir, Malaysia, defaunation of seed predators and herbivores led to a dramatic increase in tree recruitment and shifts in the spatial aggregation of recruiting saplings (Harrison et al., 2013). In Pasoh, Malaysia, the loss of predators coupled with augmented food supplies from neighboring oil palm plantations have led to a hyperabundance of wild boar resulting in a 62% decline in sapling abundances (Ickes et al., 2005; Luskin et al., 2017) and an increase in the relative abundance of lianas, which are less preferred by wild boar (Luskin et al., 2019). Both the loss of and shifts in the relative abundance of top predators and megaherbivores results in trophic cascades that are severely affecting both tropical and temperate forests (Terborgh, 2001; Estes et al., 2011; McGarvey et al., 2013). The long-term impacts of changes in faunal communities need to be explored more widely with increased standardized monitoring of vertebrate communities coupled with more manipulative experiments.

8. Future directions and research opportunities

The ForestGEO network is one of many networks of forest plots that have collectively developed a powerful system of ground observations with which to monitor the dynamics of the world's forests and develop a detailed understanding of how the underlying drivers regulate the structure, composition and dynamics of these critical ecosystems (e.g., Malhi et al., 2002; Sist et al., 2015). In this section, we describe some of the most urgent challenges preventing a more complete understanding of the role of forests in the Earth System. While the focus in this discussion is on tropical forests, the arguments apply similarly to forests outside the tropics. A key element of our argument is that progress in understanding patterns and processes operating among forests will be greatly enhanced with much greater collaboration among forest plot networks, as well as broader integration among science disciplines actively engaged in the study of forests.

8.1. Standardizing tree taxonomies for improved understanding of tropical forest species diversity and distributions

The total number of tropical tree species remains unknown, and many species remain unnamed by science (Slik et al., 2016; Cardoso et al., 2017). Moreover, the ecological roles, geographic distributions, and demographic characteristics of the vast majority of tropical tree species remain unknown (e.g., Chua et al., 2010; ter Steege et al., 2013; Johnson et al., 2018). Many prior findings on tropical tree species' responses to abiotic and biotic conditions, such as soil nutrient availability or pathogen incidence, are derived from studies in single forests (e.g., John et al., 2007; Comita et al., 2010). Comparisons among sites are typically done at higher taxonomic levels (e.g., Esquivel-Muelbert et al., 2019) or using functional traits (ter Steege et al., 2006) due to the lack of taxonomic standardization among sites. Studies at higher taxonomic levels provide more limited insights into ecological, evolutionary and biogeographic processes. Consequently, very little is known about the degree of phenotypic (e.g., ecological drought tolerance traits) or genotypic variation across species' geographic ranges in tropical forests (Brousseau et al., 2019). It therefore remains unclear whether individual species can adapt to global change in ways that would limit their risks of extinction (Fauset et al., 2012; Levine et al., 2016). This lack of knowledge impedes basic understanding of the diversity and distributions of tropical forests, and consequently, of how they are responding to changing environmental conditions (Baker et al., 2017). A range of new tools in taxonomy, imaging spectroscopy, genomics, and artificial intelligence and machine learning, will facilitate taxonomic standardization among plots, as well as greatly accelerating species discovery (e.g., Boyle et al., 2013; Durgante et al., 2013; Christin et al., 2019; Draper et al., 2020). Resolving these taxonomic issues would provide essential baseline data on the diversity of tropical forests, the distributions of individual species, and is fundamental to addressing how species composition in tropical forests is changing.

8.2. Resolving the main drivers of forest dynamics

A robust understanding of how forest dynamics depend on environmental drivers like climate, soil properties, disturbance, and interactions with other taxa, such as seed-dispersing animals, is a critical precursor to predicting the future of forests under global change. Studies based on clusters of plots have documented patterns at local to regional scales, but results sometimes diverge across studies. For example, within the tropics some studies have found that forest biomass increases with soil fertility and others found that it decreases (Lewis et al., 2009; Schietti et al., 2016; Laurance et al., 1999; Slik et al., 2010; Muller-Landau et al., 2020). Similarly, some studies have found elevated tree mortality in dry years (Phillips et al., 2010; Zuleta et al., 2017), and others in wet years or seasons (Aubry-Kientz et al., 2015; Fontes et al., 2018). Evidence for recent directional changes in tropical forest dynamics, potentially due to direct and indirect anthropogenic effects, is also mixed. Physiology-based hypotheses propose that rising atmospheric carbon dioxide and other aspects of global change should increase tropical forest productivity, turnover, and biomass (Lewis et al., 2009). Consistent with this hypothesis, regional plot networks in Africa (Lewis et al., 2013), Asia (Qie et al., 2017) and Amazonia (Brienen et al., 2015) have found evidence for a substantial carbon sink in tropical forests. However, whether these plot networks are representative has been debated (Wright, 2013; McMichael et al., 2017), and other studies have found little or no evidence of a carbon sink (Chave et al., 2008; Clark et al., 2013; Rutishauser et al., 2019; Walker et al., 2020). Likewise, lianas have been shown to be increasing in some, but not all, tropical forests, a pattern also hypothesized to be linked to global change (e.g., Phillips et al., 2002; Schnitzer and Bongers, 2011; Wright et al., 2015). The degree to which these divergent results reflect differences in methodology, sampling error, or biologically meaningful variation among sites is unclear. This uncertainty impedes progress in forest science because it reduces the ability to make more generally applicable inferences that are necessary to advance understanding of the role of forests in the Earth System. Collaboration among forest plot networks would help resolve these conflicting findings through the synthesis of much larger datasets and the development and application of more powerful analytical techniques (e.g., Rutishauser et al., 2019).

8.3. Scaling-up ground plots with remote sensing to assess forest biomass and diversity at a global scale

Projections of the feedbacks between forests and climate require accurate and precise estimates of current and future forest carbon stocks and fluxes (Friedlingstein et al., 2014). Carbon stocks vary enormously across tropical and temperate forests in relation to a range of environmental and anthropogenic drivers. While ground plots have advanced understanding of forest carbon stocks, they cover far <0.01% of forest area (Schimel et al., 2015). Remote-sensing technologies provide the potential to scale up ground-based observations of forest biomass (Avitabile et al., 2016), structure (Yang et al., 2016; Krůček et al., 2020), productivity (Liu et al., 2017), and mortality (Clark et al., 2004) from local-to-global scales, and to be a key solution for estimating global carbon stocks and fluxes, and consequently, forest responses to anthropogenic change (Schimel et al., 2015; Randin et al., 2020). Airborne remote sensing of hyperspectral reflectance can enable mapping of tree functional composition and diversity (Antonarakis et al., 2014; Asner et al., 2017; Durán et al., 2019), and quantification of their responses to anthropogenic impacts (Swinfield et al., 2019). Future hyperspectral instruments on satellites will enable global surveys of plant functional, and perhaps even, species diversity (Schimel et al., 2013).

US and international space agencies are making significant investments in space-based global biomass and diversity monitoring (e.g., GEDI, Dubayah, 2019, BIOMASS, Quegan et al., 2019). Despite these investments, there has been limited coordination with coincident ground-based observations (Chave et al., 2019, but see Schepaschenko et al., 2019), which are essential for calibration and validation of remotely-sensed biomass and diversity estimates (NASA-ESA-Smithsonian Workshop, 2016; Duncanson et al., 2019). ForestGEO and other tropical plot networks have systematically collected the data needed for this calibration and validation, including data on tree size, growth, diversity and functional traits. Collaboration between remote sensing scientists and forest ecologists has the potential to transform our ability to monitor forest biomass and biodiversity at the global scale.

8.4. *Improving predictions of future tropical forest structure and function*

Historically, Earth System Models (ESMs) have done a poor job of capturing patterns in tropical forest structure and dynamics (e.g., Johnson et al., 2016; Muller-Landau et al., 2020), and have diverged greatly in their predictions for tropical forest responses to novel atmospheric and climate scenarios (Cavaleri et al., 2015). This is in part because most models represented vegetation as a "big leaf" and represented the diversity of tropical tree species with one or a few plant functional types (Levine et al., 2016). In recent years, ESMs have increasingly adopted vegetation demographic approaches that explicitly model size-structured competition, growth, survival, and reproduction of trees or cohorts of trees of different functional types (Fisher et al., 2018). These models have succeeded in better reproducing patterns within individual tropical sites, as well as general trends in among-site variation with precipitation (Seiler et al., 2014; Levine et al., 2016; Xu et al., 2016; Koven et al., 2020; Longo et al., 2019). Simulations with these models have also demonstrated the critical importance of better representing tropical tree functional diversity: models with more functional types have higher productivity and biomass, and greater resilience to environmental perturbations (Sakschewski et al., 2016; Koven et al., 2020). However, these models still require further development and improvements to remove large systematic errors (e.g., excessively high tree mortality rates, Longo et al., 2019), and to better capture spatial and temporal variation in tropical forest dynamics in relation to environmental conditions and disturbance patterns (Powell et al., 2013).

Resolving key uncertainties in vegetation demographic models requires strong integration between model development and testing with plot-based observations of vegetation structure, dynamics, and composition (Fisher et al., 2018). Specifically, these models, with their higher-fidelity representation of vegetation structure, need to be evaluated against benchmark data for tree size distributions, growth, mortality, and recruitment, and their variation with site conditions and species traits. These are exactly the kinds of data that ForestGEO maintains. Recognizing the need for model development and integration with field data, the US Department of Energy funded the "*Next Generation Ecosystem Experiment - Tropics*" in 2015 to build a new process-rich tropical forest ecosystem model that accurately represents forest structure and function, and provides robust projections of tropical forest responses to global change. The first version of this model, the Functionally Assembled Terrestrial Ecosystem Simulator (FATES), was recently published and is currently undergoing rapid development (Koven et al., 2020).

9. Conclusions: addressing the challenges

Long-term networks of forest plots like ForestGEO, and many others in both tropical and temperate regions, have created an unprecedented knowledge base, a greatly expanded capacity for forest science, and a wide range of new data with which to advance the science of forests at a global scale. Solving the grand scientific challenges outlined in Section 8, requires four interrelated developments:

9.1. *Financial support*

In the tropics, more than anywhere, the future of the advances made by ForestGEO is at serious risk. Successfully maintaining the networks of FDPs, while a minor fraction of the cost of installing Earth-observing satellites (Phillips et al., *this volume*), is expensive, labor-intensive, logistically complex and remains a major challenge for ForestGEO and other forest plot networks. Building on the successes of ForestGEO and sustaining the network of FDPs will require much more secure, long-term financial support. Despite the enthusiasm and willingness to continue this program, many ForestGEO partner sites have no long-term financial security for continued data collection. They do not have the resources to engage young scholars to use the existing data, and very few have the resources to advance and expand the science conducted at their sites. Without committed support for sites and the research teams that make up these sites, the long-term sustainability of ForestGEO is in jeopardy.

9.2. *Training and capacity strengthening*

The future of the ForestGEO network requires continued and expanded commitment to strengthening scientific capacity across the network, particularly in the tropics. Leadership is required in each and every site to maintain and expand science at the sites. The benefits accrued by networks like ForestGEO need to be more broadly shared among sites, with increased opportunities for diverse participation in network activities. Without a concerted effort to fund and train new generations of scientists and science leaders within the partner countries of the ForestGEO network, the future conservation and sustainable management of the world's forests is at risk.

9.3. *Collaboration among forest plot networks*

We recently estimated that there are currently in excess of 11,000 forest plots currently maintained around the tropics. These plots are coordinated through networks that span gradients in geography, elevation, land-use history, and scientific focus. No plot network individually provides the spatial intensity and extent required for global inferences about the structure, functioning and diversity of forests. It is therefore essential that the ground-based networks work together to address the major challenges outlined in Section 8. The US NSF has recently awarded ForestGEO and partner networks with a grant to help advance a multi-network collaboration through the AccelNet Program. The opportunity exists to rapidly advance understanding of tropical (and temperate) forest science through network-network collaboration.

9.4. *Interdisciplinary collaboration*

ForestGEO and the other networks of forest plots, on their own, are not sufficient to address scientific challenges outlined in Section 8. The diversity, structure, functioning and dynamics of tropical forests are currently being investigated by several largely independent scientific disciplines: biogeography, ecology, remote sensing, and modelling. These disciplines operate at different but complementary spatial and temporal scales. Greatly increased integration among these disciplines is urgently needed to achieve novel inferences about tropical forests that will accelerate our understanding of their role in the functioning of the Earth System.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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