

## Article (refereed) - postprint

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1 **TITLE:**

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3 *ForestGEO: Understanding Forest Diversity and Dynamics through a Global Observatory*  
4 *Network*

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## 1 **Abstract**

2

3 ForestGEO is a network of scientists and long-term forest dynamics plots (FDPs) spanning the  
4 Earth's major forest types. ForestGEO's mission is to advance understanding of the diversity and  
5 dynamics of forests and to strengthen global capacity for forest science research. ForestGEO is  
6 unique among forest plot networks in its large-scale plot dimensions, censusing of all stems  $\geq 1$  cm  
7 in diameter, inclusion of tropical, temperate and boreal forests, and investigation of additional  
8 biotic (e.g., arthropods) and abiotic (e.g., soils) drivers, which together provide a holistic view of  
9 forest functioning. The 71 FDPs in 27 countries include approximately 7.33 million living trees  
10 and about 12,000 species, representing 20% of the world's known tree diversity. With more than  
11 1,300 published papers, ForestGEO researchers have made significant contributions in two  
12 fundamental areas: species coexistence and diversity, and ecosystem functioning. Specifically,  
13 defining the major biotic and abiotic controls on the distribution and coexistence of species and  
14 functional types and on variation in species' demography has led to improved understanding of  
15 how the multiple dimensions of forest diversity are structured across space and time and how this  
16 diversity relates to the processes controlling the role of forests in the Earth system. Nevertheless,  
17 knowledge gaps remain that impede our ability to predict how forest diversity and function will  
18 respond to climate change and other stressors. Meeting these global research challenges requires  
19 major advances in standardizing taxonomy of tropical species, resolving the main drivers of forest  
20 dynamics, and integrating plot-based ground and remote sensing observations to scale up estimates  
21 of forest diversity and function, coupled with improved predictive models. However, they cannot  
22 be met without greater financial commitment to sustain the long-term research of ForestGEO and  
23 other forest plot networks, greatly expanded scientific capacity across the world's forested nations,  
24 and increased collaboration and integration among research networks and disciplines addressing  
25 forest science.

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27

28 *Keywords:* capacity strengthening, demography, forest plots, network science, species diversity,  
29 tree growth and mortality, tropical forests.

30



## 31 **Introduction**

32

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

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

65 The enormous challenge for forest science is determining the controls on the structure,  
66 function, and diversity of forests across large spatial and temporal scales and linking these  
67 processes to the functioning of the Earth system. Meeting this challenge requires integration across  
68 levels of organization from the molecular to the ecosystem levels using detailed standardized data  
69 collected around the world and over decades to centuries. While ambitious, this knowledge is  
70 essential for building better predictive models and improving space-borne observation platforms

71 that can be used to monitor and predict the future of forested biomes globally. Such advances  
72 cannot be accomplished by a single research group, institution, or even country, but rather require  
73 a distributed network of scientists, representing many disciplines, and engaging in long-term  
74 collaborations, who are committed to capacity-strengthening in forest science globally and to  
75 seeking long-term financial support for these essential endeavors. The mission of the Forest Global  
76 Earth Observatory (ForestGEO) is to advance these fundamental and pressing research and  
77 training needs.

## 78 **ForestGEO**

79  
80 The Forest Global Earth Observatory (ForestGEO), administered by the Smithsonian Tropical  
81 Research Institute (STRI), is a worldwide network of scientists and long-term forest dynamics  
82 plots (FDPs) spread across Earth's major forests. ForestGEO is dedicated to understanding the  
83 diversity and dynamics of forests and strengthening global capacity for forest science research.  
84 Since 1980, the network has grown from a single forest research site in Panama into a collaboration  
85 of 71 sites in 27 tropical and temperate countries, including more than 100 partner organizations.  
86 ForestGEO collects standardized data on the recruitment, growth, and death of over 7 million trees  
87 of 12,000 unique species, approximately 20% of the world's known tree diversity (Table 1, Figure  
88 1). ForestGEO FDPs represent a very wide range of environmental conditions spanning ever-wet  
89 tropical to arid to boreal climates (see Figure 1 in Anderson-Teixeira et al. 2015). FDPs are  
90 distributed across gradients of soil fertility, topography, rainfall intensity and seasonality, and  
91 disturbance regimes. ForestGEO FDPs in the tropics are largely confined to intact "old-growth"  
92 forests. In the temperate zone, many ForestGEO FDPs are in regenerating forests of 30-150 years  
93 post-disturbance, though several in the western US are in old-growth forests (e.g., Yosemite).  
94 ForestGEO FDPs are also representative of global woody plant diversity. A recent analysis of 63  
95 of the 71 FDP species lists found that 59% of all plant families and 35% of all plant genera that  
96 contain woody species are found within the network (Figure 2). The sample of families and genera  
97 is unbiased with respect to the phylogeny of woody plants (Monks, Davies & Swenson,  
98 *unpublished data*). However, certain woody families are underrepresented by ForestGEO, for  
99 example, families constrained to geographical areas not currently sampled by ForestGEO (e.g.,  
100 Nothofagaceae and Araucariaceae), or primarily herbaceous families (e.g., Caryophyllaceae and  
101 Geraniaceae). A future goal of ForestGEO is to expand sampling to underrepresented areas,  
102 including Australia, southern Africa, and southern South America.

103 Each ForestGEO FDP is in a protected area and is led and managed by one or more  
104 principal investigators based at host-country partner organizations. Principal scientists in each  
105 country lead the regular, long-term data collection, implement all research activities at the sites,  
106 and represent their sites in network-wide discussions and collaborative activities. An FDP is a  
107 large-scale forest plot with all stems  $\geq 1$  cm in diameter measured approximately every five years  
108 to obtain longitudinal data on the growth, survival, and recruitment of individual trees. This  
109 standardized protocol is essential to addressing a wide range of research questions in ecology,

110 evolution, and conservation because it captures much of the tree lifespan, as well as temporal  
111 variation in the community structure of forests across relatively large contiguous areas that  
112 encompass local diversity gradients.

113 The pivotal strengths of the ForestGEO network are: (1) standardized data and  
114 measurement protocols – the core tree data and ancillary data are collected and managed  
115 uniformly, facilitating data sharing and comparative analyses among sites; and (2) the  
116 strengthening of global scientific capacity – by engaging forest researchers from across all  
117 participating nations, the network has been able to train hundreds of scientists and build an  
118 integrated, collaborative community of forest ecologists in some of the most diverse and threatened  
119 forests in the world. ForestGEO researchers have published more than 1,300 papers that have made  
120 significant contributions and novel discoveries in forest science (Figure 3, *Section 5*). In this paper,  
121 we provide a brief overview of the ForestGEO network, including a short history, a description of  
122 the measurements and protocols implemented in the FDPs, a description of our approach to  
123 training, strengthening capacity and creating opportunities for early-career scientists, a brief  
124 overview of some of the key scientific achievements of the network, and suggestions for future  
125 priorities, opportunities, and challenges in forest science.

## 126 **1. History**

127  
128 The first large-scale forest dynamics plot was initiated on Barro Colorado Island (BCI) in Panama  
129 by Stephen Hubbell and Robin Foster in 1980 (Figure 1). The goals of this novel and ambitious  
130 undertaking were clearly stated in the first recensus grant proposal for the BCI 50-ha plot:

131  
132 "The long-range objectives are: (1) to obtain statistically adequate samples of many tropical  
133 trees species for horizontal life table analysis using large cohorts of individually tagged  
134 and mapped trees; (2) to document changes in forest composition directly with a sufficient  
135 data base to test competing equilibrium and non-equilibrium theories of tropical forest  
136 organization and dynamics; and (3) to provide detailed maps of tree populations to other  
137 researchers interested in diverse aspects of the biology of tropical tree species."

138 excerpt from: S.P. Hubbell & R.B. Foster (1982) unpublished NSF proposal "*The*  
139 *Structure and Dynamics of a Tropical Forest: A Demographic Analysis.*"

140  
141 FDPs in Pasoh Forest Reserve, Malaysia, and Mudumalai Wildlife Sanctuary, India, soon followed  
142 through partnerships with the Forest Research Institute of Malaysia and the Indian Institute of  
143 Sciences, respectively. In 1989, Peter Ashton, then Professor at the Arnold Arboretum of Harvard  
144 University, orchestrated a USAID and NSF-supported meeting of regional forest scientists in  
145 Bangkok, Thailand, during which a plan for expanding FDPs across edaphic, rainfall and  
146 biogeographic gradients within tropical Asia was discussed (Ashton et al. 1999). Recognizing the  
147 rapid transformation of Asian forests going on at that time, a key motivation for the meeting was

148 to develop the knowledge base needed to improve sustainable forest management of Asia's rapidly  
149 dwindling forests (Anon. 1989), or, to:

150  
151 “design a plan for utilizing the available scientific skills of the region in conducting policy-  
152 oriented research at the minimum level required for sound policy decision-making,  
153 covering the major tropical forest ... ecosystems of the region.”

154 excerpt from: Anon. (1989 unpublished USAID-NSF workshop report). “*Funding*  
155 *Priorities for Research Towards Effective Sustainable Management of Biodiversity*  
156 *Resources in Tropical Asia.*”

157  
158 Over the next few years, through opportunistic funding successes and the inspired leadership of  
159 site principal investigators, FDPs were initiated in Sri Lanka (Sinharaja), Thailand (Huai Kha  
160 Khaeng), Singapore (Bukit Timah), the Philippines (Palanan), and an additional site in East  
161 Malaysia (Lambir Hills). It was a busy time for plot development, with new sites also being  
162 established in Africa and the Neotropics (Figure 4). Researchers in Cameroon (Korup), the  
163 Democratic Republic of Congo (Ituri), Puerto Rico (Luquillo) and Ecuador (Yasuní) all initiated  
164 FDPs. While international partnerships were important for all of these developments, highly  
165 motivated individual researchers were critical to this phase of plot expansion.

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

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

188 In 2005, the headquarters of CTFS moved from AA to STRI in Panama. With the  
189 encouragement and financial support of the Frank Levinson Family Foundation, CTFS embarked  
190 on a scientific review. A series of workshops were held with the goal of defining broad new  
191 scientific directions for the network. Specifically, the idea was to build on the core tree censuses  
192 to transform CTFS into a global forest observatory, providing a more holistic view of all the biotic  
193 and abiotic drivers that combine to produce a functioning forest. The idea was that the FDPs had  
194 collected a small fraction of the data that were needed to transform forest science into a more  
195 predictive endeavor, encompassing interdisciplinary ecology, evolution, conservation, and Earth  
196 system functioning. Workshops covered abiotic conditions (e.g., climate and soils), paleobiology,  
197 ecosystem processes (including carbon dynamics and functional traits), genetic approaches, and  
198 monitoring of several animal groups (e.g., arthropods and vertebrates). Several of these initiatives  
199 were rapidly implemented across the network with standardized data collection (*Section 3*). In  
200 2007, the central Smithsonian endorsed the network, and by 2010 helped secure core federal funds  
201 from the US government in support of the network's expanding science mission.

202 Building on a workshop held in Beijing in 2004, ForestGEO also began a formal  
203 partnership with the Chinese Forest Biodiversity Monitoring Network (CForBio) in 2008. By this  
204 time, several plots in China were already established and participating in the ForestGEO network,  
205 including in the far south (Xishuangbanna) and north (Changbaishan). The CForBio team was  
206 rapidly building new plots to sample the great diversity of forest types across China (Feng et al.  
207 2016). Matching grants in 2010 from the NSF-US, under the International Research Coordination  
208 Networks program, and NSF-China led to a series of analytical workshops in both countries that  
209 greatly advanced collaborative activities among participating researchers.

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

223 The Frank Levinson Family Foundation endowed the directorship of ForestGEO in 2013.  
224 This was timely as the Arnold Arboretum decided to end its support of the Asia program. To  
225 emphasize its global reach and expanding research scope, the network was renamed the Forest  
226 Global Earth Observatory (ForestGEO). Its mission is to build and sustain a global network of  
227 large-scale forest dynamics plots and associated research activities to monitor and understand the

228 ecology, evolution, and conservation of forest biodiversity and its impact on Earth's functioning,  
229 to strengthen science capacity globally through professional training, and to develop scientific  
230 input for forest policy, conservation and management. Today, the strength of the network is a direct  
231 outcome of the dual mission of science and training. The continued commitment to early-career  
232 scientists across the world helps ensure continuity of the science and the individual FDPs, but is  
233 also the key source of the innovations required to tackle the challenges confronting forests.

## 234 **2. The ForestGEO Forest Dynamics Plot: core plot methods**

235  
236 A ForestGEO Forest Dynamics Plot (FDP) consists of a surveyed and mapped grid of typically  
237 16-50 hectares (average = 26 ha) in which all woody stems with a diameter  $\geq 1$  cm at 1.3 m above  
238 the ground (diameter at breast height, DBH) are mapped, measured, and identified to species  
239 (Manokaran et al. 1990, Condit 1998). This census is repeated at approximately five-year intervals,  
240 during which all prior stems are remeasured or recorded as dead, and all new stems  $\geq 1$  cm in DBH  
241 (recruits) are tagged, mapped, measured, and identified as in the original census. ForestGEO FDPs  
242 now collectively cover 1,833 ha (Table 1). In several sites, FDPs are smaller than 16-ha due either  
243 to local funding limitations or to constraints on available forest area, however, all other aspects of  
244 standardized data collection are followed in these sites. There have been 189 censuses among the  
245 71 plots. The oldest plot, BCI, is in the midst of its ninth census. There are approximately 7.33  
246 million living trees within the FDPs today, and there have been over 21 million tree measurements  
247 across the plots. To publicize the core plot data and provide detailed site-specific information on  
248 local field protocols, climate and soils, species identification, and other species information, many  
249 sites have published books describing the FDPs (Manokaran et al. 1993, Lee et al. 2003, Thomas  
250 et al. 2003, Gunatilleke et al. 2004, LaFrankie et al. 2005, Co et al. 2006, Su et al. 2007, Cao et al.  
251 2008, Bunyavejchewin et al. 2009, Chen et al. 2009, Li et al. 2010, Chang et al. 2012, Ding et al.  
252 2013, Cao et al. 2013, Lu et al. 2016, Wang et al. 2016, Xu et al. 2017, Yang et al. 2019). Several  
253 of these are also published online ([https://forestgeo.si.edu/research-](https://forestgeo.si.edu/research-programs/publications/forestgeo-stand-books)  
254 [programs/publications/forestgeo-stand-books](https://forestgeo.si.edu/research-programs/publications/forestgeo-stand-books)).

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

### 262 **(i) Why large plots with the inclusion of small stems?**

263  
264 The ForestGEO FDP methodology pioneered two relatively unique features in forest science: the  
265 very large-scale plot dimensions, and the complete censusing of all stems of at least 1 cm DBH.

266 Previous plot-based studies in tropical forests mostly employed plots of either 1 ha in area using a  
267 DBH cut-off of 10 cm, or 0.1 ha with  $DBH \geq 2.5$  cm (e.g., Gentry 1988, Malhi et al. 2002). Both  
268 of these methodological innovations have significant logistical and financial consequences: a 50-  
269 ha plot including all stems  $\geq 1$  cm DBH may include 250,000-450,000 stems, compared to an  
270 average of about 500 stems  $\geq 10$  cm DBH in a typical 1-ha plot. Establishing a 50-ha plot in diverse  
271 tropical forest with  $\sim 350,000$  stems typically takes a team of 15 technicians two years, followed  
272 by at least two years for expert plant identification, and data processing and quality control. While  
273 measuring, mapping and sampling small stems is straightforward, albeit laborious, the  
274 identification of small stems, which are often juveniles of locally occurring adults, can be  
275 exceedingly challenging, as trees often undergo dramatic changes in morphology as they grow  
276 from the understory to the canopy. However, sampling larger areas and including small stems  
277 provides a series of benefits for sampling forest diversity, dynamics, and demography.

278 The spatial and temporal scale, and intensity of sampling in the ForestGEO FDP is  
279 especially valuable for studying population and community ecology in forests. The dynamics of  
280 most forests are, barring episodic disturbances, slow. Mortality rates typically range from 1-4%  
281 per year among forests, so detecting trends in mortality rates, and especially differential trends  
282 among species, size classes or habitats requires lots of individuals to be monitored over long  
283 periods (McMahon et al. 2019). Most tropical tree species are rare, so large plots are needed to  
284 achieve the goal of building robust demographic data for a large fraction of species at a particular  
285 site. Furthermore, a considerable portion of woody plant diversity is present at diameters less than  
286 10 cm, so studying trees down to 1 cm is important for capturing forest diversity (Memiaghe et al.  
287 2016). Large plots are useful for advancing understanding of how disturbances influence the  
288 diversity and dynamics of tropical forests since many (though certainly not all) disturbances in  
289 tropical forests occur on the scale of 0.25–5 hectares (e.g., tree falls, landslides, lightning, etc.).  
290 Large mapped plots provide a valuable resource for exploring the spatial patterns in forests,  
291 especially for large-diameter trees that occur at relatively low densities (Lutz et al. 2018, Engone-  
292 Obiang et al. 2019). Many of the mechanisms posited to maintain diversity and drive patterns of  
293 species turnover are spatial, including abiotic components of edaphic, hydrologic and light  
294 variation, and interactions among neighboring con- and heterospecific individuals. The inclusion  
295 of small stems (1–10 cm DBH) provides a window into the early life stages of tree species, a stage  
296 at which mortality rates are often higher and individuals are more sensitive to competition,  
297 disturbance and biotic effects. Finally, large plots have a large footprint and can be more easily  
298 "seen" from satellites and other remote observing instruments (Réjou-Méchain et al. 2014).

## 299 **(ii) Data management & analysis**

300  
301 ForestGEO designed and developed a complete data system for storing and managing tree census  
302 results for the network. The ForestGEO database model follows theories of data normalization by  
303 minimizing data redundancy, which can lead to anomalies during updates and is the source of  
304 many common errors (Condit et al. 2014). The database runs on the open-source MySQL server,

305 with interfaces written in HTML, PHP and JavaScript for online access via web portals. The data  
306 entry interface can be configured to mirror the field forms for plots using paper forms. The system  
307 screens and uploads data to the MySQL plot database. All data are in a standard format, facilitating  
308 sharing of software for data analysis, and fostering comparative data analysis (e.g., LaManna et al.  
309 2017, Lutz et al. 2018). Metadata and version control are maintained to ensure that researchers can  
310 reliably reference datasets. A data request system is linked to the database, including descriptions  
311 of the terms and conditions for data access, and details for acknowledgement  
312 (<https://forestgeo.si.edu/explore-data>). Several plot datasets are now publicly accessible (e.g.,  
313 Bourg et al. 2013) and many other FDP data are available following acceptance of the terms and  
314 conditions for data sharing, as described on the site pages of the ForestGEO website. To ensure  
315 uniform data quality across the partner sites, ForestGEO provides technical support to plot PIs.  
316 The protocol for this system is detailed in the "*ForestGEO Database Handbook*"  
317 ([https://forestgeo.si.edu/sites/default/files/database\\_handbook-final.pdf](https://forestgeo.si.edu/sites/default/files/database_handbook-final.pdf)).

318 To facilitate comparative data analysis across FDPs, ForestGEO developed a package of  
319 analytical software in the R programming language designed specifically for use with census data  
320 from the FDPs (Condit 2012). The package is available as either the "CTFS R package"  
321 <https://forestgeo.si.edu/explore-data/r-package-0> or the "fgeo" R package  
322 <https://forestgeo.si.edu/explore-data/r-package>. The package includes many tutorials, broadening  
323 access to a wide range of data analytical tools and facilitating research by forest scientists with a  
324 broad range of levels of experience with analyses of large datasets. Long used in the annual  
325 network-wide analytical workshops (*Section 4*), the CTFS R package has also served as an entry  
326 point for many young forest scientists to learn to develop the bespoke statistical analytical code  
327 necessary for testing ecological hypotheses within and across the network. Although the functions  
328 in the CTFS R package are designed for use with ForestGEO data, the source code for each  
329 function is freely available, and can be modified to accommodate any data format, which enables  
330 capacity building in forest science beyond the ForestGEO network.

### 331 **3. ForestGEO as a platform for forest research**

332  
333 The transition from CTFS to ForestGEO was motivated by the idea that a full understanding of the  
334 functioning of forests requires an integrated set of observations with greater biotic coverage,  
335 coupled with detailed measurements of the abiotic drivers that strongly influence forests. This led  
336 to greatly expanded data collection at many ForestGEO FDPs. The focus of the expanded field  
337 data collection program included sampling animal and microbial diversity, monitoring life stages  
338 from flowering through seedling recruitment, quantifying components of carbon stocks and fluxes,  
339 using genome-based approaches to forest diversity and lineage interactions, as well as detailed  
340 assessment of climatic and edaphic variation within sites. As with the core plot censuses, protocols  
341 for expanded data collection were standardized to facilitate local, regional and global comparative  
342 analyses. Here we present some examples of data being collected across the FDPs that are opening  
343 new avenues of forest science discovery. Full descriptions of these and other standardized



344 protocols and their implementation across ForestGEO FDPs are described in Anderson-Teixeira  
345 et al. (2015) and available on the ForestGEO website (<https://forestgeo.si.edu/protocols>; see also).

### 346 **(i) Arthropods**

347  
348 Arthropods influence key forest functions, including nutrient cycling, seed predation and dispersal,  
349 herbivory, and pollination. Given recent concerns about global insect decline (Sánchez-Bayo &  
350 Wyckhuys 2019; Wagner 2020), high quality data on the population dynamics of tropical  
351 arthropods are urgently needed to understand their responses to global changes and the functional  
352 implications for their ecosystems (Basset & Lamarre 2019; Wagner 2020). In 2009, ForestGEO  
353 developed a standardized protocol (<https://forestgeo.si.edu/node/145661/>) for monitoring common  
354 arthropod species with methods that can be applied consistently across the network. The protocol  
355 is now implemented in seven tropical FDPs representing a rare effort to monitor key arthropod  
356 assemblages in tropical forests (Lamarre et al. 2020; WWF, 2020). Monitoring data now represent  
357 more than 600,000 records, >6,000 species, 14,000 DNA barcoding sequences, and 100,000  
358 vouchered specimens. Taxonomic resolution is improved by building reference collections and  
359 DNA barcode libraries (e.g., Basset et al. 2015). Species traits (e.g., thermal tolerance) are being  
360 used to delineate functional groups to monitor population trends and overcome the challenge of  
361 studying thousands of individual species (Basset et al. 2017, Lamarre et al. 2020). DNA  
362 metabarcoding is also being used to monitor community dynamics (Gripenberg et al. 2019). The  
363 data are being used for a wide range of monitoring and interactions studies, including responses  
364 of insects to climate change (Basset et al. 2013, 2015, 2017; Lucas et al. 2016; Luk et al. 2019),  
365 and studies of seed predators (Basset et al. 2018, Gripenberg et al. 2019).

### 366 **(ii) Completing the tree life cycle from reproduction to recruitment**

367  
368 The core monitoring program at all ForestGEO FDPs focuses on trees and begins when a tree  
369 enters the 1 cm DBH size class and ends when the tree dies. Key aspects of a tree's life-history are  
370 overlooked with this protocol. Stems of 1 cm DBH may be decades old (Delissio et al. 2002), key  
371 processes affecting individual survival may be most intense in the smallest size classes, and  
372 patterns of flowering, fruiting, seed dispersal, germination, and recruitment strongly affect when  
373 and where species will occur. In 1987, the collection of data on seed production, seedling  
374 recruitment and seedling growth and survival was initiated on BCI to build complete life cycle  
375 information for tropical tree species using seedling plots and seed traps (Wright et al. 2005,  
376 <https://forestgeo.si.edu/research-programs/flowers-seeds-and-seedlings-initiative>). The  
377 implementation of these field protocols, coupled with intensive monitoring of the reproductive  
378 status of thousands of individual trees, has led to a new generation of studies that have integrated  
379 all life stages from seed to adult to evaluate: (1) relationships between vital rates and functional  
380 traits across the tree life cycle (Iida et al. 2014, Visser et al. 2016), (2) costs and benefits of dioecy  
381 (Bruijning et al. 2017), (3) the impact of lianas on population growth rates of host trees (Visser et

382 al. 2017), and (4) the processes that underlie liana-tree interactions including colonization,  
383 shedding, baseline mortality, and increased lethality (Visser et al. 2018). Today 26 FDPs have  
384 established seed/seedling monitoring programs using these standardized protocols (e.g., Chen et  
385 al. 2010, Chen et al. 2018, Jin et al. 2018).

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

### 393 **(iii) Biomass and carbon storage and fluxes**

394  
395 ForestGEO FDP data have provided an excellent resource for quantifying aboveground woody  
396 biomass carbon stocks (AGB), woody productivity and woody mortality fluxes. The core  
397 ForestGEO FDP carbon measurement is tree diameter at breast height (DBH). These  
398 measurements are used in combination with allometric equations and sometimes also  
399 measurements of tree height and wood density, to estimate individual tree biomass (Chave et al.  
400 2014, Réjou- Méchain et al. 2017; Gonzalez-Akre et al. *in review*). Individual tree and stem AGB  
401 are then summed over area to estimate total AGB stocks per area. Repeat census data together with  
402 biomass allometric equations can be used to quantify woody productivity and woody mortality  
403 fluxes at the stand level. Numerous studies have quantified biomass stocks and fluxes in  
404 ForestGEO plots, and their variation over space and time (Chave et al. 2003, Chave et al. 2008,  
405 Valencia et al. 2009, Lin et al. 2012, Yuan et al. 2016, 2019, Zuleta et al. 2017, Ma et al. 2019,  
406 Rutishauser et al. 2019). A key advantage of ForestGEO plots for these studies is that their large  
407 size reduces sampling errors in these biomass stocks and fluxes, sampling errors which remain  
408 substantial even at the 1-ha scale (Wagner et al. 2010, Muller-Landau et al. 2014, Réjou-Méchain  
409 et al. 2014).

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

421 existing surveys in temperate FDPs (Furniss et al. 2020), and currently conducts annual mortality  
422 censuses at more than 10 sites.

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

#### 430 **(iv) Soils and climate**

431  
432 Soils and climate drive many aspects of the diversity and dynamics of forests. ForestGEO has  
433 designed protocols to assess their spatial and temporal variation. At the scale of a 50-ha plot there  
434 is often dramatic spatial heterogeneity in soil properties driven by variation in underlying parent  
435 material, topographic position, and water table depth and flow paths (Figure 5). This edaphic  
436 variation impacts spatial variation in carbon and biomass stocks and fluxes, and strongly affects  
437 species distributions (*Section 5*). ForestGEO has implemented a standard protocol to measure the  
438 physical and chemical properties of soils in over 25 tropical and temperate FDPs  
439 (<https://forestgeo.si.edu/protocols/soils>). Soils are sampled across the entire FDP resulting in maps  
440 of soil chemical and physical characteristics (John et al. 2007). Soil carbon is being quantified in  
441 FDPs to improve our understanding of factors controlling carbon stocks globally, and how this  
442 might change with future shifts in climate. Maps of soils and topography are also being used to  
443 investigate demographic patterns of individual tree species (e.g., Russo et al. 2005).

444 Meteorological data are collected at or near various ForestGEO sites. This information is  
445 fully described in Anderson-Teixeira et al. (2015) and is curated in the open-access ForestGEO  
446 Climate Data Portal (<https://forestgeo.github.io/Climate/>; DOI: 10.5281/zenodo.4041609), along  
447 with climate records extracted specifically for ForestGEO sites from global databases (e.g., CRU,  
448 Harris et al. 2020). The portal also hosts historical records of atmospheric pollution (CO<sub>2</sub>, NO<sub>x</sub>  
449 and SO<sub>2</sub> emissions, Hoesly et al. 2020).

#### 450 **(v) Genome-based approaches to diversity and dynamics**

451  
452 The identification of species remains an impediment to advancing forest science. For trees, the  
453 available sample may have no flowers or fruits to enable a confirmed identification. For many  
454 other organisms, they may be microscopic (e.g., bacteria, fungi, etc.), they may be taxonomically  
455 very poorly known (e.g., many arthropod groups), and in still many cases, they remain unknown  
456 to science (Cardoso et al. 2017). By harnessing advances in molecular genetics, sequencing  
457 technology, and bioinformatics, DNA barcoding has become a valuable tool for exploring diversity  
458 in ForestGEO FDPs and has potential value in tracking changes in biodiversity (Kress et al. 2009).

459 More than 3,000 tree species in 25 ForestGEO FDPs and 14,000 arthropods in seven FDPs have  
460 now been DNA barcoded (Erickson et al. 2014, Basset et al. 2015). These barcodes are being used  
461 for the identification of tree roots (Jones et al. 2011) and seed predators (Gripenberg et al. 2019),  
462 and to build community-level phylogenies (Swenson et al. 2012, 2013, Erickson et al. 2014).

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

#### 472 **4. ForestGEO Education and Training Initiatives**

473  
474 Recognizing the global need for strengthening capacity in forest science, ForestGEO is deeply  
475 committed to training early-career scientists from all over the world spanning diverse professions  
476 in forest science, including researchers, academics, conservation biologists, and managers. By  
477 cultivating new skills, gaining research experience, and increasing accessibility to a network of  
478 data and shared expertise, ForestGEO's education and training initiatives ensure that benefits  
479 derived from the global syntheses are shared among diverse groups. Regular analytical and data  
480 workshops, individual research grants, internships, and postdoctoral fellowships are designed to  
481 train the next generation of scientists who will be the future stewards of Earth's forests.

482 For ForestGEO's hundreds of collaborating researchers around the world, dedicated time  
483 to meet in-person to share research findings, learn new analytical techniques, and discuss multi-  
484 plot research is invaluable. ForestGEO's analytical and data workshops bring researchers together  
485 to define global-scale science questions, address data gaps and network needs, and expand  
486 interdisciplinary collaboration. ForestGEO has convened 17 analytical workshops since 2001,  
487 each bringing together scientists from more than 20 countries (Figure 7). Analytical workshops  
488 consist of hands-on training, seminars, and discussions for approximately 60 individuals over two  
489 to three weeks in a location near a ForestGEO plot. Workshop participants consist of  
490 approximately 70% students and early-career scientists who are grouped by research interest with  
491 a designated mentor to foster research collaborations and receive direct training and support. These  
492 workshops have provided more than 350 early-career scientists with opportunities to gain  
493 international research experience, improve writing and editing skills, and expand data analysis  
494 expertise. The analytical workshops have resulted in peer-reviewed papers in a wide array of  
495 journals spanning disciplines, with 255 workshop-derived papers published since 2011. Many of  
496 the papers are coauthored by participants from multiple plots, reflecting the value of data sharing  
497 and analysis that is fostered through the workshops. The connections cultivated at analytical

498 workshops continue and develop into enduring mentorships and collaborations that allow  
499 workshop attendees to be conduits of research mentorship to others in their home institutions,  
500 exponentially expanding the network's training impact.

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

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

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

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

## 530 **5. Advances in Understanding Forest Diversity**

531  
532 The ForestGEO network has made major contributions in two broad areas of forest science: (i)  
533 Species coexistence and diversity, and (ii) Ecosystem processes and forest functioning. Other  
534 articles in this special issue have addressed many key accomplishments of the long-term tropical  
535 forest plot networks in the area of forest functioning and the impacts of altered climatic and  
536 atmospheric conditions (e.g., Phillips et al. *this volume*). Anderson-Teixeira et al. (2015) described

537 how the broad suite of measurements being made at ForestGEO sites is critical for addressing the  
538 complex responses of ecosystem processes and forest functioning to diverse global change drivers.  
539 What has been covered less are the insights gained from ForestGEO FDPs on the processes  
540 regulating species diversity, coexistence and dynamics. Here, we highlight a series of key findings  
541 linked to the biology of species and the role they play in forests. These findings are not exclusively  
542 attributable to the ForestGEO approach, however in several cases it is clear that the unique large-  
543 scale sampling of the FDP has provided critical insights in these areas. The following selection is  
544 also not intended to be comprehensive with respect to the diversity of topics addressed using the  
545 ForestGEO plots. Key areas of species diversity research conducted using ForestGEO FDPs that  
546 are not covered below include: geographical patterns of diversity among plots (e.g., Ren et al.  
547 2013, Ricklefs & He 2016, Sreekar et al. 2018, Chu et al. 2018), patterns of phylogenetic diversity  
548 (e.g., Mi et al. 2012), and relationships between biodiversity and ecosystem function (e.g.,  
549 Chisholm et al. 2013). A complete list of ForestGEO publications is available  
550 (<https://forestgeo.si.edu/research-programs/publications>;  
551 <https://scholar.google.com/citations?user=RFULppIAAAAJ&hl=en>).

#### 552 **(i) Spatial distribution of tree species and functional types with respect to habitat**

553  
554 ForestGEO FDPs have demonstrated that forests consist of highly spatially structured assemblages  
555 of species. The majority of tree species have strongly aggregated spatial distributions. Analyses  
556 across many ForestGEO plots have shown that 30-75% of species in any one plot have spatial  
557 distributions significantly aggregated with respect to soil nutrients, topographic position, moisture  
558 availability, and the history of local disturbance (e.g., Figure 6). This finding, first documented on  
559 BCI and several plots in Asia (Condit et al. 2000, Harms et al. 2001), has now been confirmed in  
560 many plots across the network (Davies et al. 2005, Gunatilleke et al. 2006, Lai et al. 2009, Chuyong  
561 et al. 2011, Lan et al. 2012, Bunyavejchewin et al. 2019). With the obvious exception of the  
562 distribution of pioneer species in relation to light gaps, the details of what specific resource  
563 requirements, e.g., water availability, soil nutrients, wind exposure, constrain species distributions  
564 across these topographic and edaphic gradients remains poorly understood, as many factors covary  
565 (John et al. 2007, Baldeck et al. 2013, Kupers et al. 2019). However, recent studies in BCI and  
566 across the Isthmus of Panama demonstrate the key roles played by soil moisture and phosphorus  
567 availability (Condit et al. 2013, Zemunik et al. 2018). It is an area where experimentation needs to  
568 be coupled with long-term monitoring (Engelbrecht et al. 2007, Baltzer et al. 2008). In addition to  
569 having fundamental consequences for the theories of species diversity in forests, the observation  
570 of pervasive habitat associations in tropical tree species has direct importance for forest  
571 conservation and management. Species-site matching remains an important requirement for  
572 successful ecological restoration by tree planting (Shono et al. 2007).

573 The patchy distribution of species across edaphic and topographic gradients is reflected in  
574 functional differences of the constituent species. Analyses of functional trait variation in species  
575 across many FDPs show strong relationships with underlying edaphic and hydrological conditions.

576 For example, within the extremely diverse 25-ha plot at Yasuní, Ecuador, species with lower  
577 average specific leaf area, smaller leaves and heavier seeds were more common on ridges  
578 (Valencia 2004, 2009, Kraft et al. 2008). Analogous patterns have been observed in many other  
579 large FDPs around the world (e.g., Katabuchi et al. 2012, Liu et al. 2013, Yang et al. 2014).  
580 Patterns of species-level functional trait covariance across habitat gradients provides a way of  
581 pooling hundreds of species into a smaller number of life-history types that can be more easily  
582 parameterized in Earth System Models (Scheiter et al. 2013, Fisher et al. 2015, Koven et al. 2020).  
583

### 584 **(ii) Seed dispersal, seedling recruitment and patterns of spatial aggregation**

585

586 Seed dispersal controls the ability of plants to reach preferred regeneration sites and to colonize  
587 new habitats. The seed trapping program implemented at many ForestGEO FDPs has demonstrated  
588 that mean seed dispersal distance varies by more than an order of magnitude among coexisting  
589 tree species (Muller-Landau et al. 2008). Life-history tradeoffs involving seed dispersal and  
590 fecundity can contribute to species niche differentiation and coexistence (Muller-Landau 2008,  
591 Muller-Landau 2010, Bin et al. 2019). Species dispersal strategies vary not only in distance  
592 distributions but also in directionality, efficacy in reaching canopy gaps, and clumping (Muller-  
593 Landau & Hardesty 2005, Wright et al. 2008, Puerta-Piñero et al. 2013, van Putten et al. 2012).  
594 Limited seed dispersal distances and clumped seed dispersal, often combined with low adult  
595 abundance, mean that many species fail to arrive in any given regeneration site (Hubbell et al.  
596 1999; Li et al. 2012; Chen et al. 2014), which can make overall community dynamics more  
597 stochastic (Hurtt & Pacala 1995).

598 Since most seeds of most species fall close to the mother tree (Marchand et al. 2020),  
599 species-level spatial aggregation at local scales is in large part attributable to limited seed dispersal  
600 and is associated with seed dispersal syndromes (Condit et al. 2000, Seidler & Plotkin et al. 2006,  
601 Shen et al. 2009, Shen et al. 2013, Detto & Muller-Landau 2013, Clark et al. 2017, Wang et al.  
602 2018), which are often phylogenetically conserved (Russo et al. 2007). This has significant  
603 consequences for subsequent seedling recruitment and survival (Janzen 1970, Beckman et al.  
604 2012). While habitat suitability may be higher close to a parent tree, high conspecific seedling  
605 density and proximity to a conspecific adult may increase intraspecific competition and exposure  
606 to pest pressure, shifting seedling distributions farther from adults (Janzen 1970, Uriarte et al.  
607 2005, Murphy et al. 2017). Seed dispersal and seedling recruitment dynamics play important roles  
608 in regulating the diversity of tree communities.

### 609 **(iii) Neighborhood composition and the impacts on individual performance**

610

611 Given that most tree species exhibit spatially clumped distributions (Condit et al. 2000), ultimately  
612 owing to limited seed dispersal (Clark et al. 2017), tree local neighborhoods have enormous effects  
613 on recruitment, growth, and survival. Such neighborhood effects are not only mediated by  
614 competitive interactions with other plants, but also strongly by interactions with natural enemies

615 and mutualists. This is particularly the case when trees are surrounded by conspecifics or close  
616 relatives, which are more likely to share natural enemies (Gilbert 2002, Janzen 1970, Connell  
617 1971). Tropical forests are notorious for their long-tailed species rank-abundance distributions  
618 (Whittaker 1965), with most species being rare. A key focus of ForestGEO research has been the  
619 identification of possible mechanisms that facilitate a “rare species advantage”, ensuring no single  
620 tree species can “take over the world” or at least a local tree community on the scale of a 50-ha plot  
621 (Wills et al. 2006). In theory, this occurs when all species have positive invasion growth rates  
622 (Chesson 2000), a condition that is met when each species density affects itself more than it affects  
623 other species (Broekman et al. 2019). Although it has proven challenging to robustly measure such  
624 conspecific density effects (Detto et al. 2019), evidence of conspecific negative density  
625 dependence (CNDD) has been reported in many tropical, subtropical and temperate FDPs for  
626 growth and survival (e.g., Hubbell & Condit 1990, Harms et al. 2000, Uriarte et al. 2004, Jia et al.  
627 2020). In addition, rare species in at least one tropical FDP have been found to have stronger  
628 negative effects on their own growth or survival than common species, suggesting the hypothesis  
629 that rare species are rare at least in part because they suffer more from intraspecific competition or  
630 species-specific natural enemies (Comita et al. 2010, Mangan et al. 2010). However, results from  
631 manipulation studies on the prevalence of negative density dependence are mixed (Song et al. *in*  
632 *review*) and the hypothesis that species suffer more CNDD when rare has been challenged in other  
633 forests (e.g., Liu et al. 2015).

634         There is clearly much to learn regarding how species' populations are regulated and thereby  
635 prevent dominance. For example, soil microorganisms, including fungal and oomycete pathogens,  
636 are thought to be principal mediators of conspecific density dependence (Bever et al. 2015), but  
637 plant-soil feedback studies have shown that being near close relatives is not always bad,  
638 particularly for tree species hosting ectomycorrhizal fungi (Segnitz et al. 2020). While numerous  
639 factors contribute to variation in species' abundances in space and time, the prevalence of negative  
640 density dependence and interspecific variation in its strength has profound consequences for the  
641 maintenance of diversity in forests (Johnson et al. 2012, Stump & Comita 2018, Chisholm & Fung  
642 2020, Comita & Stump 2020).

#### 643 **(iv) Tree life-histories: demographic variation within- and among- forests**

644  
645 The balance between growth, recruitment and mortality largely determines the variation in carbon,  
646 water, and nutrient cycles, affects above and belowground trophic interactions, and underpins the  
647 coexistence and abundance of species. Quantifying how demographic rates vary within- and  
648 among- sites and through time is therefore important for predicting the future of Earth's forests  
649 and their role in regulating the Earth system. The ForestGEO FDPs have enabled the  
650 characterization of growth, mortality, and recruitment rates for thousands of tree species across the  
651 world's forests (e.g., Rüger et al. 2011, Johnson et al. 2018, Russo et al. 2020). Analyses of many  
652 plots have found an interspecific trade-off between a tree species' ability to grow fast in high  
653 resource conditions versus to survive in low resource conditions due to species' differences in



654 allocation (Russo et al. 2008, Wright et al. 2010, Rüger et al. 2018, Medeiros et al. 2019). The  
655 strength of this trade-off varies among edaphic habitats within a forest, reinforcing resource-based  
656 species' distribution patterns (Russo et al. 2008). The trade-off, however, is not equally strong in  
657 all forests. Although it was observed across tropical forests at the global scale, it was not observed  
658 in some forests where the local disturbance regime (e.g., frequent hurricane exposure) appears to  
659 have restricted the adaptive resource allocation strategies to a narrow range of those possible  
660 (Russo et al. 2020). While the growth-mortality trade-off can promote species' coexistence, the  
661 range of species' growth and mortality rates in a forest does not explain the massive differences in  
662 species richness of forests across the tropics: species-rich tropical forests actually have a narrower  
663 range of demographic variation and finer demographic niches than species-poor forests (Condit et  
664 al. 2006).

665         Analysis of the BCI FDP in Panama revealed an additional demographic trade-off  
666 contributing to tree species coexistence, a 'stature–recruitment' trade-off distinguishing between  
667 small-statured species with high recruitment success and large-statured species with low  
668 recruitment success (Rüger et al. 2018). In combination, the growth-mortality and stature-  
669 recruitment trade-offs have been used to accurately predict basal area and compositional changes  
670 during forest succession at BCI (Rüger et al. 2020), illustrating the importance of demographic  
671 data collected in ForestGEO plots for understanding and predicting consequences of human  
672 impacts on forest ecosystems.

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

683

#### 684 **(v) Neutral Theory and the maintenance of species diversity in tropical forests**

685

686 Observations from ForestGEO FDPs and other tropical forests inspired the neutral theory of  
687 biodiversity (Hubbell 1979a, 1979b, 2001), which makes the bold assertion that many observed  
688 patterns in nature can be explained without invoking species differences. An initial wave of  
689 enthusiasm for neutral theory stemmed from its successful explanation of empirical patterns such  
690 as species abundance distributions (Volkov et al. 2003) and species–area relationships (Rosindell  
691 & Chisholm 2020). But this enthusiasm waned upon discovery that other predictions of neutral  
692 theory were less accurate, in particular its predictions of temporal change on both ecological and

693 evolutionary timescales (Nee 2005, Leigh 2007, Chisholm & O'Dwyer 2014). A study of 12  
694 ForestGEO sites revealed that fluctuations in the abundance of common tree species over  
695 timescales of 6–28 years were orders of magnitude larger than neutral predictions (Chisholm et al.  
696 2014).

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

#### 709 **(vi) Temporal change in the species composition of old-growth tropical forests**

710  
711 The idea that the species composition of old-growth tropical forests is stable over time has been  
712 comprehensively refuted by the unique long-term data of ForestGEO plots. Forests are surprisingly  
713 dynamic with large changes due to annual mortality rates ranging from 1-4% per year (see Wright,  
714 *this volume*). Analyzing the dynamics of over 4,000 species in 12 ForestGEO FDPs, the largest  
715 and most comprehensive sample of species-level population dynamics from tropical forests across  
716 Africa, Asia and the Americas, Chisholm et al. (2014) found that the abundance of a majority of  
717 species is increasing or decreasing more than expected under a neutral model of community  
718 change. Natural disturbances, including fires, landslides, droughts, and hurricanes are a major  
719 cause of temporal fluctuations in species composition on decadal timescales in many tropical  
720 forests (Hubbell & Foster 1992, Hogan et al. 2018, Bunyavejchewin et al. 2019). Species-level  
721 studies across many ForestGEO FDPs have demonstrated differential sensitivity to drought (e.g.,  
722 Condit et al. 1995, Engelbrecht et al. 2007, Itoh et al. 2012, Zuleta et al. 2017). On century time  
723 scales, dendrochronological studies provide increasing evidence that current community  
724 composition of some ForestGEO FDPs reflects historical disturbance events (e.g., Baker et al.  
725 2005). Despite these cases, in many forests there is no obvious factor driving differential  
726 abundance changes among species (Chisholm et al. 2014). Further work is needed to understand  
727 whether these population changes are linked to specific shifts in climatic conditions, biotic  
728 interactions, or other drivers. Given the potential for climate-related changes at these sites, large  
729 FDPs are a critical baseline for understanding the impact of future natural and anthropogenic  
730 change on species populations.

731 **(vii) Impact of changes in vertebrate populations on forest diversity and dynamics**

732

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

750 **6. Future Directions and Research Opportunities**

751

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

762 **(i) Standardizing tree taxonomies for improved understanding of tropical forest species**  
763 **diversity and distributions**

764

765 The total number of tropical tree species remains unknown, and many species remain unnamed by  
766 science (Slik et al. 2016, Cardoso et al. 2017). Moreover, the ecological roles, geographic  
767 distributions, and demographic characteristics of the vast majority of tropical tree species remain  
768 unknown (e.g., Chua et al. 2010, ter Steege et al. 2013, Johnson et al. 2018). Many prior findings

769 on tropical tree species' responses to abiotic and biotic conditions, such as soil nutrient availability  
770 or pathogen incidence, are derived from studies in single forests (e.g., John et al. 2007, Comita et  
771 al. 2010). Comparisons among sites are typically done at higher taxonomic levels (e.g., Esquivel-  
772 Muelbert, et al. 2019) or using functional traits (ter Steege et al. 2006) due to the lack of taxonomic  
773 standardization among sites. Studies at higher taxonomic levels provide more limited insights into  
774 ecological, evolutionary and biogeographic processes. Consequently, very little is known about  
775 the degree of phenotypic (e.g., ecological drought tolerance traits) or genotypic variation across  
776 species' geographic ranges in tropical forests (Brousseau et al. 2019). It therefore remains unclear  
777 whether individual species can adapt to global change in ways that would limit their risks of  
778 extinction (Fauset et al. 2012, Levine et al. 2016). This lack of knowledge impedes basic  
779 understanding of the diversity and distributions of tropical forests, and consequently, of how they  
780 are responding to changing environmental conditions (Baker et al. 2017). A range of new tools in  
781 taxonomy, imaging spectroscopy, genomics, and artificial intelligence and machine learning, will  
782 facilitate taxonomic standardization among plots, as well as greatly accelerating species discovery  
783 (e.g., Boyle et al. 2013, Durgante et al. 2013, Christin et al. 2019, Draper et al. 2020). Resolving  
784 these taxonomic issues would provide essential baseline data on the diversity of tropical forests,  
785 the distributions of individual species, and is fundamental to addressing how species composition  
786 in tropical forests is changing.

## 787 **(ii) Resolving the main drivers of forest dynamics**

788  
789 A robust understanding of how forest dynamics depend on environmental drivers like climate, soil  
790 properties, disturbance, and interactions with other taxa, such as seed-dispersing animals, is a  
791 critical precursor to predicting the future of forests under global change. Studies based on clusters  
792 of plots have documented patterns at local to regional scales, but results sometimes diverge across  
793 studies. For example, within the tropics some studies have found that forest biomass increases with  
794 soil fertility and others found that it decreases (Lewis et al. 2009, Schiatti et al. 2016, Laurance et  
795 al. 1999, Slik et al. 2010, Muller-Landau et al. 2020). Similarly, some studies have found elevated  
796 tree mortality in dry years (Phillips et al. 2010, Zuleta et al. 2017), and others in wet years or  
797 seasons (Aubry-Kientz et al. 2015, Fontes et al. 2018). Evidence for recent directional changes in  
798 tropical forest dynamics, potentially due to direct and indirect anthropogenic effects, is also mixed.  
799 Physiology-based hypotheses propose that rising atmospheric carbon dioxide and other aspects of  
800 global change should increase tropical forest productivity, turnover, and biomass (Lewis et al.  
801 2009). Consistent with this hypothesis, regional plot networks in Africa (Lewis et al. 2013), Asia  
802 (Qie et al. 2017) and Amazonia (Brienen et al. 2015) have found evidence for a substantial carbon  
803 sink in tropical forests. However, whether these plot networks are representative has been debated  
804 (Wright 2013, McMichael et al. 2017), and other studies have found little or no evidence of a  
805 carbon sink (Chave et al. 2008, Clark et al. 2013, Rutishauser et al. 2019, Walker et al. 2020).  
806 Likewise, lianas have been shown to be increasing in some, but not all, tropical forests, a pattern  
807 also hypothesized to be linked to global change (e.g., Phillips et al. 2002, Schnitzer & Bongers

808 2011, Wright et al. 2015). The degree to which these divergent results reflect differences in  
809 methodology, sampling error, or biologically meaningful variation among sites is unclear. This  
810 uncertainty impedes progress in forest science because it reduces the ability to make more  
811 generally applicable inferences that are necessary to advance understanding of the role of forests  
812 in the Earth System. Collaboration among forest plot networks would help resolve these  
813 conflicting findings through the synthesis of much larger datasets and the development and  
814 application of more powerful analytical techniques (e.g., Rutishauser et al. 2019).

815 **(iii) Scaling-up ground plots with remote sensing to assess forest biomass and diversity at a**  
816 **global scale**

817  
818 Projections of the feedbacks between forests and climate require accurate and precise estimates of  
819 current and future forest carbon stocks and fluxes (Friedlingstein et al. 2014). Carbon stocks vary  
820 enormously across tropical and temperate forests in relation to a range of environmental and  
821 anthropogenic drivers. While ground plots have advanced understanding of forest carbon stocks,  
822 they cover far less than 0.01% of forest area (Schimel et al. 2015). Remote-sensing technologies  
823 provide the potential to scale up ground-based observations of forest biomass (Avitabile et al.  
824 2016), structure (Yang et al. 2016, Krůček et al. 2020), productivity (Liu et al. 2017), and mortality  
825 (Clark et al. 2004) from local-to-global scales, and to be a key solution for estimating global carbon  
826 stocks and fluxes, and consequently, forest responses to anthropogenic change (Schimel et al.  
827 2015, Randin et al. 2020). Airborne remote sensing of hyperspectral reflectance can enable  
828 mapping of tree functional composition and diversity (Antonarakis et al. 2014, Asner et al. 2017,  
829 Durán et al. 2019), and quantification of their responses to anthropogenic impacts (Swinfield et al.  
830 2019). Future hyperspectral instruments on satellites will enable global surveys of plant functional,  
831 and perhaps even, species diversity (Schimel et al. 2013).

832 US and international space agencies are making significant investments in space-based  
833 global biomass and diversity monitoring (e.g., GEDI, Dubayah 2019, BIOMASS, Quegan et al.  
834 2019). Despite these investments, there has been limited coordination with coincident ground-  
835 based observations (Chave et al. 2019, but see Schepaschenko et al. 2019), which are essential for  
836 calibration and validation of remotely-sensed biomass and diversity estimates (NASA-ESA-  
837 Smithsonian workshop 2016, Duncanson et al. 2019). ForestGEO and other tropical plot networks  
838 have systematically collected the data needed for this calibration and validation, including data on  
839 tree size, growth, diversity and functional traits. Collaboration between remote sensing scientists  
840 and forest ecologists has the potential to transform our ability to monitor forest biomass and  
841 biodiversity at the global scale.

842 **(iv) Improving predictions of future tropical forest structure and function**

843  
844 Historically, Earth System Models (ESMs) have done a poor job of capturing patterns in tropical  
845 forest structure and dynamics (e.g., Johnson et al. 2016, Muller-Landau et al. 2020), and have

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

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

## 874 **7. Conclusions: Addressing the challenges**

875  
876 Long-term networks of forest plots like ForestGEO, and many others in both tropical and  
877 temperate regions, have created an unprecedented knowledge base, a greatly expanded capacity  
878 for forest science, and a wide range of new data with which to advance the science of forests at a  
879 global scale. Solving the grand scientific challenges outlined in Section 6, requires four interrelated  
880 developments:

881  
882         (i) *Financial support*: In the tropics, more than anywhere, the future of the advances made  
883 by ForestGEO is at serious risk. Successfully maintaining the networks of FDPs, while a minor  
884 fraction of the cost of installing Earth-observing satellites (Phillips et al., *this volume*), is

885 expensive, labor-intensive, logistically complex and remains a major challenge for ForestGEO and  
886 other forest plot networks. Building on the successes of ForestGEO and sustaining the network of  
887 FDPs will require much more secure, long-term financial support. Despite the enthusiasm and  
888 willingness to continue this program, many ForestGEO partner sites have no long-term financial  
889 security for continued data collection. They do not have the resources to engage young scholars to  
890 use the existing data, and very few have the resources to advance and expand the science conducted  
891 at their sites. Without committed support for sites and the research teams that make up these sites,  
892 the long-term sustainability of ForestGEO is in jeopardy.

893  
894 *(ii) Training and capacity strengthening:* The future of the ForestGEO network requires  
895 continued and expanded commitment to strengthening scientific capacity across the network,  
896 particularly in the tropics. Leadership is required in each and every site to maintain and expand  
897 science at the sites. The benefits accrued by networks like ForestGEO need to be more broadly  
898 shared among sites, with increased opportunities for diverse participation in network activities.  
899 Without a concerted effort to fund and train new generations of scientists and science leaders  
900 within the partner countries of the ForestGEO network, the future conservation and sustainable  
901 management of the world's forests is at risk.

902  
903 *(iii) Collaboration among forest plot networks:* We recently estimated that there are  
904 currently in excess of 11,000 forest plots currently maintained around the tropics. These plots are  
905 coordinated through networks that span gradients in geography, elevation, land-use history, and  
906 scientific focus. No plot network individually provides the spatial intensity and extent required for  
907 global inferences about the structure, functioning and diversity of forests. It is therefore essential  
908 that the ground-based networks work together to address the major challenges outlined in Section  
909 6. The US NSF has recently awarded ForestGEO and partner networks with a grant to help advance  
910 a multi-network collaboration through the AccelNet Program. The opportunity exists to rapidly  
911 advance understanding of tropical (and temperate) forest science through network-network  
912 collaboration.

913  
914 *(iv) Interdisciplinary collaboration:* ForestGEO and the other networks of forest plots, on  
915 their own, are not sufficient to address scientific challenges outlined in Section 6. The diversity,  
916 structure, functioning and dynamics of tropical forests are currently being investigated by several  
917 largely independent scientific disciplines: biogeography, ecology, remote sensing, and modeling.  
918 These disciplines operate at different but complementary spatial and temporal scales. Greatly  
919 increased integration among these disciplines is urgently needed to achieve novel inferences about  
920 tropical forests that will accelerate our understanding of their role in the functioning of the Earth  
921 System.

922

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2342 induced mortality patterns and rapid biomass recovery in a terra firme forest in the Colombian  
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2345

2346 **Table 1.** Characteristics of 71 ForestGEO FDPs spanning the world's forest types, including total number of trees (trees #), species (species #) and  
 2347 censuses (censuses #), and mean annual temperature (MAT) and mean annual precipitation (MAP). Elevation is the average elevation across each  
 2348 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  
 2349 2012.

2351	Site	Area	First census	Trees	Species	Fisher's	Censuses	Elevation	MAT	MAP
2352		(ha)	(yr)	#	#	alpha	#	(m)	(°C)	(mm/yr)
2353										
2354										
2355	Ailaoshan, Yunnan	20	2014	44168	104	12.8	2	2550	11.3	1778
2356	Amacayacu, Colombia	25	2006	123790	1133	172.2	2	94	25.8	3215
2357	Badagongshan, Hunan	25	2011	186000	238	26.9	2	1420	15.9	1410
2358	Baishanzu, Zhejiang	25	2014	207178	177	19.0	1	1527	12.8	2342
2359	Baotianman, Henan	25	2009	59569	126	15.2	2	.	15.1	886
2360	Barro Colorado Island, Panama	50	1981	208400	299	34.3	8	120	27.1	2551
2361	Bidoup, Vietnam	25	2012	204684	215	23.7	1	1557	17.3	1533
2362	Bukit Timah, Singapore	4	1993	17239	408	75.0	6	99	26.9	2473
2363	Changbaishan, Jilin	25	2004	36904	52	6.0	4	801	2.9	700
2364	Cocoli, Panama	4	1994	3200	176	40.1	3	50	26.6	1950
2365	Danum Valley, Malaysia	50	2010	256729	694	86.8	2	150	26.7	2822
2366	Daxinganling, Heilongjiang	25	2011	209785	18	1.5	1	897	-4.0	458
2367	Dinghushan, Guangdong	20	2005	71617	210	26.6	2	350	20.9	1985
2368	Doi Inthanon, Thailand	15	1997	73269	162	19.7	4	1670	20.9	1908
2369	Donglingshan, Beijing	20	2010	52136	58	6.4	2	1400	4.7	570
2370	Fushan, Taiwan	25	2004	110595	101	11.0	4	667	18.2	4271
2371	Gutianshan, Zhejiang	24	2005	140087	159	17.7	3	581	15.3	1964
2372	Hainan, Hainan	60	2012	439676	290	30.3	2	942	19.8	2381
2373	Haliburton, Canada	13.5	2007	46339	30	3.1	2	434	5.0	1070
2374	Harvard Forest, MA, USA	35	2010	116200	51	5.1	1	354	9.0	1050
2375	Heishiding, Guangdong	50	2013	218513	236	26.1	2	567	22.0	1744
2376	Hong Kong, Hong Kong	20	2012	81021	172	20.8	1	201	23.3	2399
2377	Huai Kha Khaeng, Thailand	50	1992	72500	251	32.6	6	596	23.5	1476
2378	Ilha do Cardoso, Brazil	10.2	2004	40000	106	13.2	2	6	22.4	2100
2379	Indian Cave, NE, USA	18.4	2019	15786	49	6.3	1	315	11.2	876
2380	Ituri, D.R. Congo	40	1994	288000	445	51.6	4	775	24.3	1682



2381	Kenting, Taiwan	10	1996	39093	95	11.7	1	275	25.4	1964
2382	Khao Chong, Thailand	24	2000	121500	593	81.1	4	235	27.1	2611
2383	Korup, Cameroon	50	1996	329000	494	57.0	3	195	26.6	5272
2384	Belalong, Brunei Darussalam	25	2009	155901	1266	188.4	1	240	26.5	5203
2385	La Planada, Colombia	25	1997	105400	240	29.3	2	1818	19.0	4087
2386	Lambir, Malaysia	52	1991	359600	1182	152.2	5	174	26.6	2664
2387	Laupahoehoe, USA	4	2008	14641	21	2.4	2	1160	16.0	3440
2388	Lienhuachih, Taiwan	25	2008	153268	144	15.7	1	754	20.8	2211
2389	Lilly Dickey Woods, IN, USA	25	2012	27993	35	3.9	2	267	11.6	1203
2390	Luquillo, Puerto Rico, USA	16	1990	39160	138	17.9	6	381	22.8	3548
2391	Manaus, Brazil	25	2004	154177	1519	234.0	2	60	26.7	2600
2392	Michigan Big Woods, MI, USA	23	2014	33690	45	5.1	1	288	8.6	857
2393	Mo Singto, Thailand	30.5	2000	134942	264	31.6	3	770	23.5	2100
2394	Mpala, Kenya	120	2011	139259	68	6.9	2	1730	17.9	657
2395	Mudumalai, India	50	1988	25500	72	9.1	8	1050	22.7	1255
2396	Nanjenshan, Taiwan	5.88	1989	36400	125	16.2	4	320	23.5	3582
2397	Ngardok, Palau	4	2017	14216	70	9.6	1	39	28.0	3734
2398	Ngel Nyaki, Nigeria	20.28	2014	41031	106	13.2	1	1639	19.0	1800
2399	Niobrara, NE, USA	20.16	2018	8293	26	3.3	1	687	8.7	597
2400	Nonggang, Guangxi	15	2011	68010	223	28.7	2	275	22.0	1376
2401	Ordway-Swisher, FL, USA	23.04	2019	9935	11	1.2	1	38	20.0	1280
2402	Palamanui, HI, USA	4	2008	15652	15	1.6	2	265	20.0	835
2403	Palanan, Philippines	16	1994	78205	335	44.9	5	97	26.1	3380
2404	Pasoh, Malaysia	50	1986	300211	814	101.9	7	80	27.9	1788
2405	Rabi, Gabon	25	2010	178447	342	40.8	2	41	26.0	2282
2406	San Lorenzo, Panama	6	1996	1935	238	71.3	5	140	26.2	3030
2407	Santa Cruz, CA, USA	6/16	2007/2012	20892	33	3.8	3/2	323	14.8	778
2408	Scotty Creek, Canada	9.6	2013	38050	11	1.0	2	266	-3.2	369
2409	Sinharaja, Sri Lanka	25	1993	193400	204	22.5	5	500	22.5	5016
2410	SCBI, VA, USA	25.6	2008	49285	65	7.4	3	306	12.9	1001
2411	SERC, MD, USA	16	2007	24961	79	10.1	3	8	13.2	1068
2412	Speulderbos, Netherlands	27	2013	9350	13	1.5	2	56	10.1	833
2413	Tiantongshan, Zhejiang	20	2008	94603	153	17.8	2	453	16.2	1375
2414	Traunstein, Germany	25	2015	15758	29	3.4	1	605	7.6	1240
2415	Tyson Res. Center, MO, USA	20.16	2013	30333	42	5.3	2	205	13.5	957

2416	UMBC, MD, USA	12.5	2012	7782	79	12.2	2	50	12.8	1063
2417	Utah, UT, USA	13.64	2014	23177	17	1.8	1	3084	2.7	850
2418	Wabikon, WI, USA	25.2	2008	50130	42	4.5	3	498	4.2	805
2419	Wanang, Papua New Guinea	50	2009	285825	527	62.5	2	140	26.0	3500
2420	Wind River, WA, USA	27.2	2010	30973	26	2.8	2	369	9.2	2495
2421	Wytham Woods, UK	18	2008	16313	23	2.6	3	134	10.0	717
2422	Xishuangbanna, Yunnan	20	2007	95834	468	64.0	3	789	21.8	1493
2423	Yasuni, Ecuador	50	1995	297778	1114	146.2	2	230	28.3	3081
2424	Yosemite Nat. Park, CA, USA	25.6	2009	34458	23	2.4	3	1843	10.2	1065
2425	Zofin, Czech Republic	25	2012	73457	13	1.2	2	780	6.2	866
2426										
2427										

2428 **List of Figures.**

2429

2430 **Figure 1.** Global map of 71 ForestGEO Forest Dynamics Plots.

2431

2432 **Figure 2.** Representation of woody plant diversity in ForestGEO FDPs. The percent of known woody plant  
2433 genera (A) and families (B) recorded within ForestGEO plots based of the global woody plant database  
2434 (Zanne et al. 2014). Percent of global woody plant phylogenetic diversity (phylodiversity) of genera (C)  
2435 and families (D) recorded in ForestGEO FDPs. Phylodiversity is the sum all branch lengths for the  
2436 phylogeny of genera or families (Faith 1992). The phylodiversity percent is the fraction of branches on the  
2437 phylogeny that occur in ForestGEO FDPs. The analysis was based on 63 FDPs (Monks, Davies & Swenson,  
2438 *unpublished data*), so underestimates the actual diversity found in the ForestGEO network. n is the total  
2439 number of woody genera and families.

2440

2441 **Figure 3.** Cumulative growth of ForestGEO peer-reviewed publications since the start of the first plot on  
2442 Barro Colorado Island in Panama in 1981. Publications included up to August 2020.

2443

2444 **Figure 4.** Growth of the ForestGEO network in terms of numbers of species and trees being monitored by  
2445 the FDPs. The number of species is the sum of all recorded species at each plot, so species occurring in  
2446 more than one plot are counted twice. The number of unique species is approximately 12,000. The number  
2447 of trees reflects the number of living trees at the most recent census of each plot. Over time the number of  
2448 tree measurements has grown to over 20 million due to many plots having multiple censuses (Table 1).

2449

2450 **Figure 5.** Pictorial representation of soil, topographic and hydrological variation within the 50-ha FDP at  
2451 Pasoh, Malaysia, illustrating the dramatic variation in edaphic conditions that are often included within a  
2452 typical large-scale ForestGEO FDP. USDA soil taxonomic names listed at the top of each photo which  
2453 were taken within soil pits sampled along the soil catena (hatched boxes) spanning just 30 m of elevation  
2454 difference between the highest and lowest points within the plot. Like most FDPs this edaphic and  
2455 topographic gradient results in significant turnover in species composition across the plot (Davies et al.  
2456 2003).

2457

2458 **Figure 6.** The striking habitat-related variation in spatial distributions of individuals of five species of  
2459 *Shorea* (Dipterocarpaceae) in the 52-ha FDP at Lambir, Sarawak, Malaysia. The pattern of sympatric  
2460 congeneric species occupying different habitats within the same plot is a repeated feature of many  
2461 ForestGEO FDPs. Habitats, defined by soil chemistry and texture, range from most nutrient-poor sandy  
2462 loams (white) to least nutrient-poor clays (dark green). Contour lines span 140 m of elevation change within  
2463 the plot. Dot sizes are scaled to tree size. Species and habitat specialization include: (A) *Shorea*  
2464 *inappendiculata* - clay, B. *Shorea xanthophylla* - fine loam; C. *Shorea amplexicaulis* - loam; D. *Shorea*  
2465 *acuta* - sandy loam; E. *Shorea ochracea* - a generalist species without habitat specialization within the plot.  
2466 Figure adapted from Russo et al. (2005).

2467

2468 **Figure 7.** Photo of network participants at the annual ForestGEO analytical workshop in July 2018 in  
2469 Boubin old-growth forest, Czech Republic; the oldest known forest plot with mapped stems in the world.

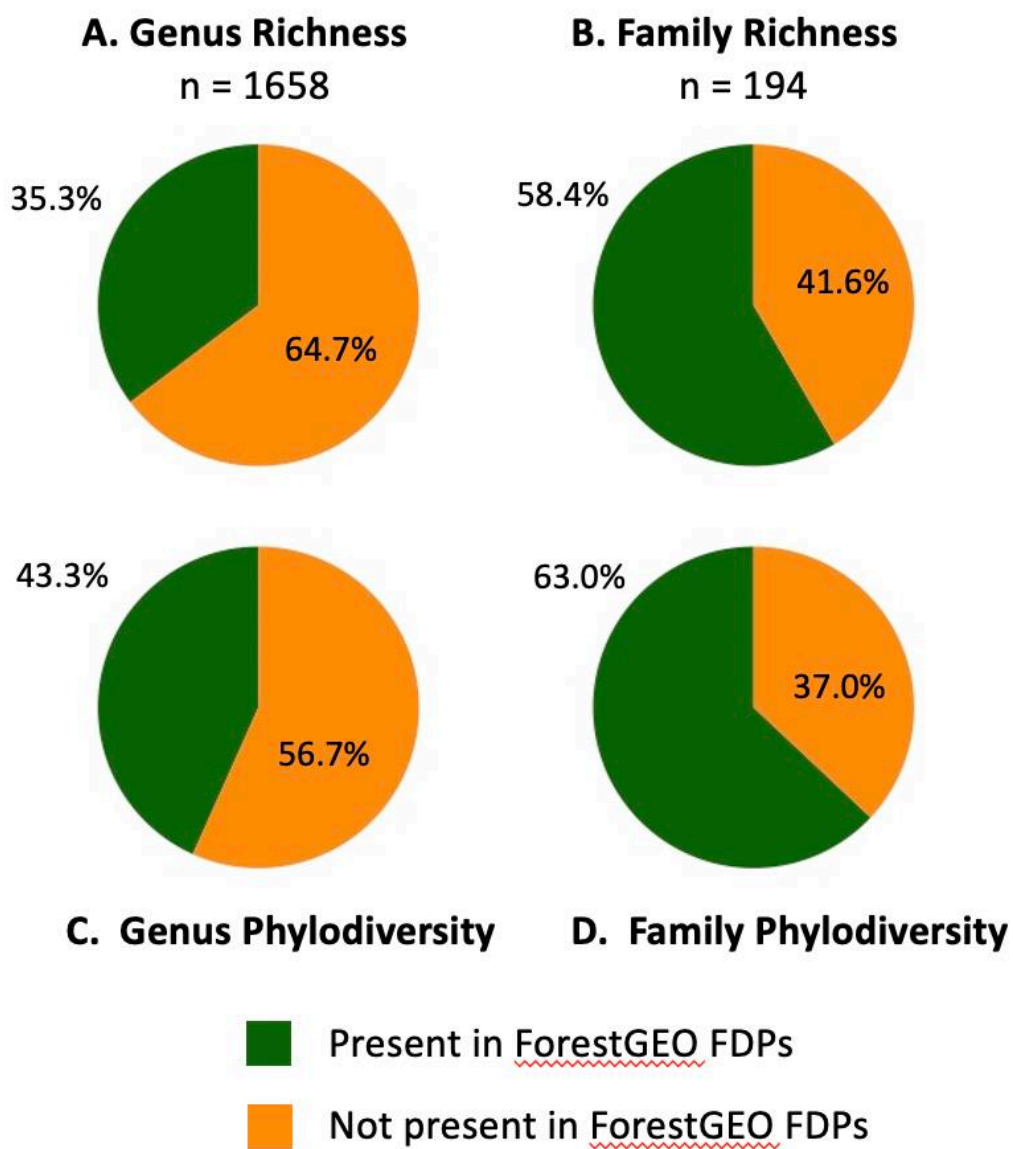
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2471 **Figure 1.**  
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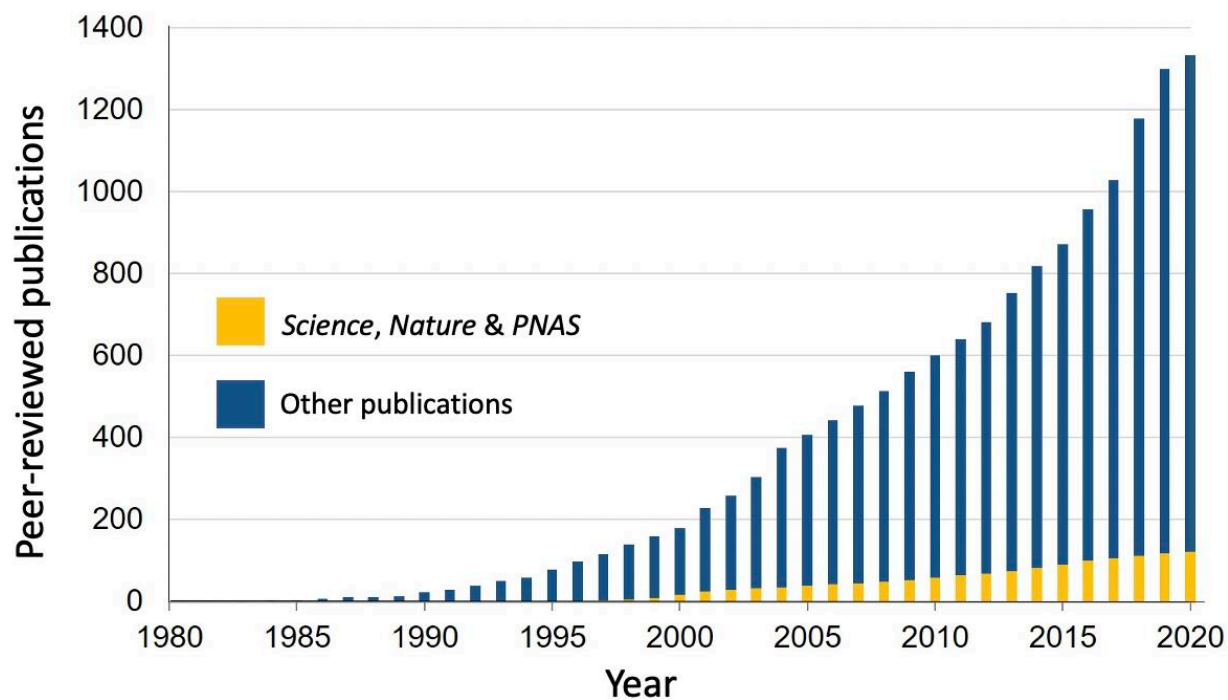
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2478 **Figure 2.**  
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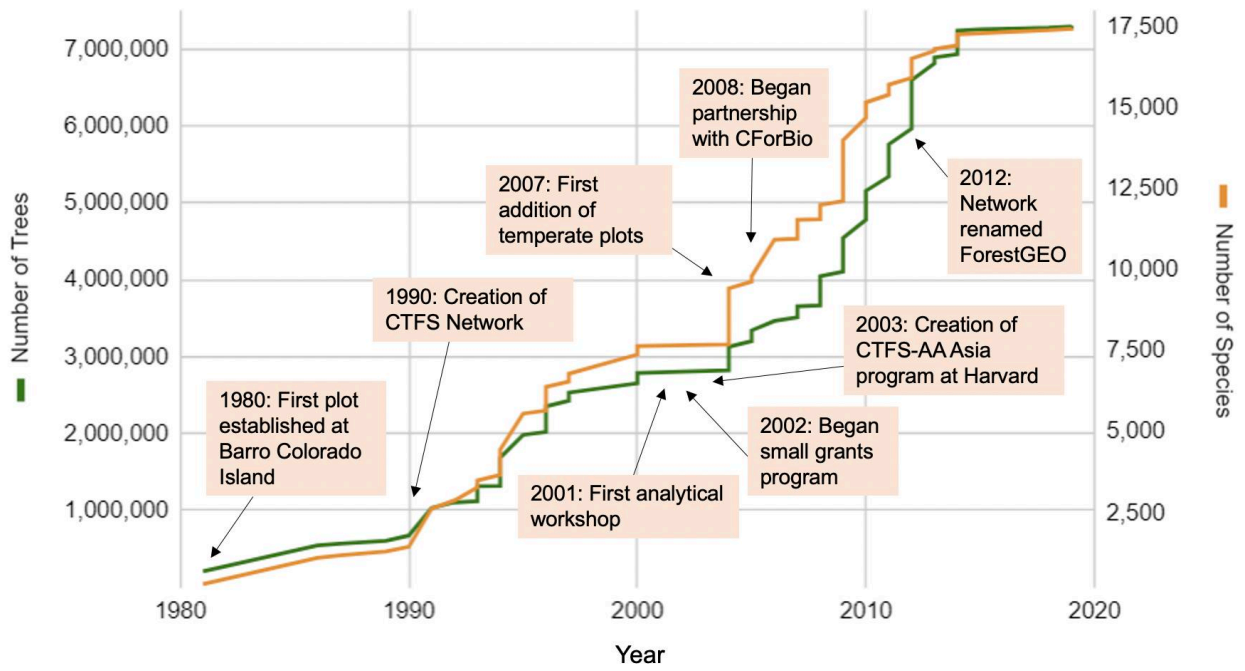
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2485 **Figure 3.**  
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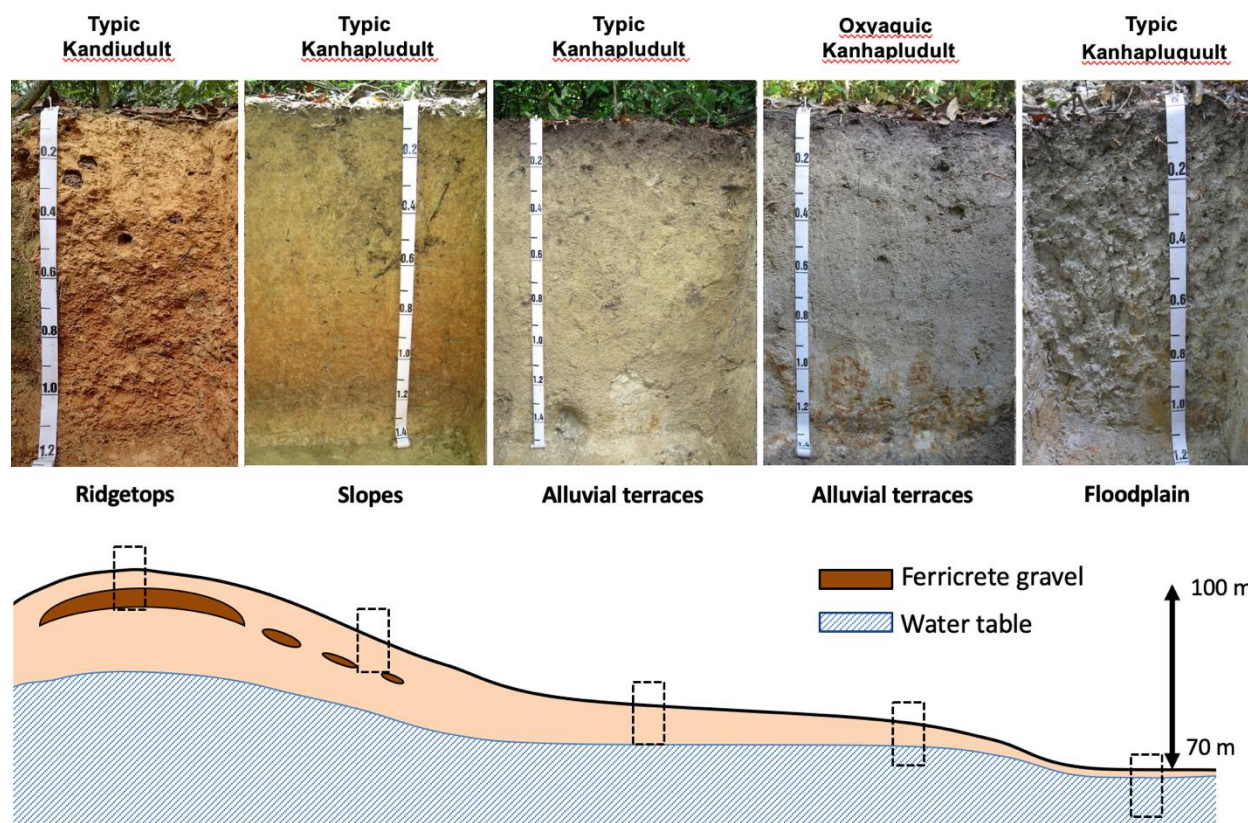
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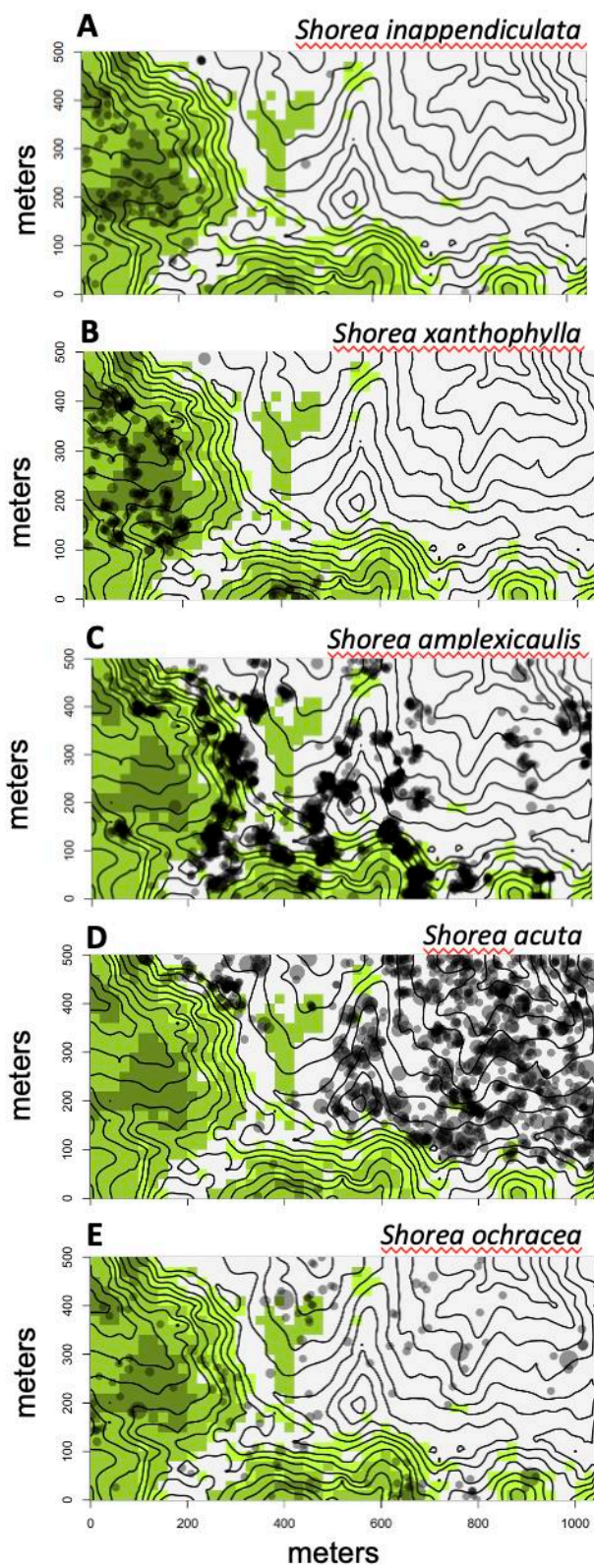
2499 Figure 5.  
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2506 **Figure 6.**  
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**Figure 7.**



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2519

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**Declaration of interests**

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.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: