Taking the Pulse of Earth's Tropical Forests using Networks of Highly Distributed Plots

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Abstract

Tropical forests are the most diverse and productive ecosystems on Earth. While better understanding of these forests is critical for our collective future, until quite recently efforts to measure and monitor them have been largely disconnected. Networking is essential to discover the answers to questions that transcend borders and the horizons of funding agencies. Here we show how a global community has responded to the challenges of tropical ecosystem research with diverse teams measuring forests tree-by-tree in hundreds of long-term plots. We review the major scientific discoveries of this work and show how this process is changing tropical forest science. Our core approach involves linking long-term grassroots initiatives with standardized protocols and data management to generate robust scaled-up results. By connecting tropical researchers and elevating their status, our Social Research Network model recognises the key role of the data originator in scientific discovery. Conceived in 1999 with RAINFOR (South America), our permanent plot networks have been adapted to Africa (AfriTRON) and Southeast Asia (T-FORCES) and widely emulated worldwide. Now these multiple initiatives are integrated via ForestPlots.net cyber-infrastructure, linking colleagues from 54 countries across 24 plot networks. Collectively these are transforming understanding of tropical forests and their biospheric role. Together we have discovered how, where and why forest carbon and biodiversity are responding to climate change, and how they feedback on it. This long-term pan-tropical collaboration has revealed a large long-term carbon sink and its trends, as well as making clear which drivers are most important, which forest processes are affected, where they are changing, what the lags are, and the likely future responses of tropical forests as the climate continues to change. By leveraging a remarkably old technology, plot networks are sparking a very modern revolution in tropical forest science. In the future, humanity can benefit greatly by nurturing the grassroots communities now collectively capable of generating unique, long-term understanding of Earth's most precious forests.

Key Words: Amazonia, Africa, Southeast Asia, rainforest, RAINFOR, AfriTRON, species richness, forest plots, permanent sample plots, monitoring, dynamics, carbon sink, global change, ecology, biodiversity.

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Introduction

As the most diverse and productive ecosystems on Earth, tropical forests play essential roles in the carbon and water cycles and maintenance of global biodiversity. Tropical forest lands are also home to more than a billion people and thousands of cultures. Having first provided the environments and germplasm that sustained foragers and farmers since the earliest days of humanity, today they underpin a large fraction of our globalized diet and intense demand for water, food and clean air. They also affect our health in multiple ways, providing rich pharmacopeias to traditional and modern societies, and capable of changing the course of history when pandemic zoonotic pathogens emerge as forests and wildlife are exploited. Tropical forests are also critical to determining the degree and impact of anthropogenic climate change. Because of their extent, carbon density and productivity, they may both slow global heating by absorbing carbon into their biomass and soils, or accelerate it as deforestation and high temperatures damage forests and release carbon to the atmosphere.

Tropical carbon and biodiversity are therefore critical targets for environmental measurement and monitoring. While vital to our past and future, efforts to measure and monitor them have until recently been localised and largely disconnected. Although aspects of their ecology can be sensed remotely on-the-ground, tree-by-tree measurement is essential. Indeed ground measurements are irreplaceable – whether to address a plethora of ecological questions (e.g., Wright, this volume), inform and validate ecosystem models (e.g., Malhi et al., this volume), or assist with interpreting remotely acquired data (e.g., Chave et al. 2019, Duncanson et al. 2019, Phillips et al. 2019). Yet the very features that enhance tropical forests' ecological value, such as remoteness, diversity and high rainfall, make fieldwork challenging. Tropical forest science and scientists from forest-rich countries are often under-resourced and academically marginalised. Often colonized from afar and distant from economic centres, tropical nature and many who explore it remain peripheral to national and global academic and political priorities.

The focus of this paper is specifically about the power of new collaborative networks to transform tropical forest science – *what* we do, *how* we do it, and eventually *who* does it - to understand tropical forest functioning and dynamics over large temporal and spatial scales. Conceived and funded starting in South America in 1999 (RAINFOR, Malhi et al. 2002) and later adapted to Africa (AfriTRON, Lewis et al. 2009) and Southeast Asia (T-FORCES, Qie et al. 2017) our approach encourages international grassroots initiatives and links them with standardized field methods and data management. Now, with ForestPlots.net (Lopez-González et al. 2011, 2015) we support multiple networks with cyber-infrastructure that enables tropical scientists to do together what was previously impossible alone. Providing tools to ensure tropical scientists can manage, share and analyse their data themselves, ForestPlots.net is a global platform where data originators are in control and free to collaborate, support, or lead as much as they like. However, while much has been accomplished the wider challenges still run deep. Our aim of supporting the best possible science within a model of equitable access to data and other resources, remains as much an aspiration as a claim of achievements already made.

Here we first review how the continental networks and ForestPlots.net emerged, in terms of collaborators, institutions, people and plots. Next we focus on key scientific achievements of the combined networks, including a comprehensive understanding of the variation in biomass carbon stock, growth rates, and carbon residence time among continents. We also review multiple discoveries concerning large-scale changes over time, with insights emerging from hundreds of permanent plots that have transformed our understanding of the role that tropical forests play in the biosphere. Finally, we return to the challenges of building and sustaining long-term science networks in the tropics and outline key priorities for the future.

1. Network Development

Tropical research plots that tag, measure, identify and follow forests tree-by-tree have existed for decades. They long precede any continental or global network, but no plot survives since before 1939 and few predate 1970. The earliest efforts were closely connected to the imperial- and post-imperial projects of European nations. As such, these were largely motivated by questions of timber inventory and wood production, and only later diversity and wider ecological questions. The very first permanent sample plots we are aware of in the tropics were installed in 1857 by the German forester Brandis, who worked for the British in Burma (now Myanmar) and later other parts of India (Dawkins and Philip, 1998). **In India** a few extant Forest Department plots date to 1939 (Pomeroy et al. 2003). Important early work in **Southeast Asia** included plots installed by Don Nicholson and J.E.D. Fox in the 1950s through to the 1970s, as well as Peter Ashton since the 1960s and John Proctor since the 1970s. **In Africa**, early permanent plots include those installed by William Eggeling in Uganda in the 1930s. Among plots surviving today are one in Mpanga Forest, Uganda, set up by Alan Hamilton in 1968, and those established by Mike Swaine in Ghana and Hans Woell in Liberia in the 1970s, and later plots by Jan Reistma and Lee White (Gabon), Bonaventure Sonké (Cameroon), Kofi Affum Baffoe (Ghana), and Henri-Félix Maître and colleagues (Gabon, Congo, C.A.R.). **In Australia**, North Queensland saw the first plot sampling, for timber, in the 1930s, with many sites from the 1970s still maintained today by the national science agency (CSIRO). Separately Joe Connell, co-originator of the influential Janzen-Connell hypothesis, installed and expanded long-term ecological plots in 1963.

In the tropical Americas, T.A.W. Davis and Paul Richards installed ecological plots in Guyana in the 1930s (Davis and Richards 1933) but these do not survive, while Frank Wadsworth established long-term plots in Puerto Rico's subtropical forests starting in 1943 (e.g. Drew et al. 2009). In Suriname, Schulz and colleagues established silvicultural studies in the 1950s and 60s that were used to design the CELOS Management System (Werger 2011). Neotropical ecological plots that persist today include many in Venezuela by Jean-Pierre Veillon in the 1950s, 60s and 70s (Vilanova et al. 2018) and Rafael Herrera, Ernesto Medina and colleagues in the 1970s, as well as a few in Brazilian Amazonia by João Murça Pires, H. Dobzhansky and G.A. Black and later Ghillean Prance, and several in Costa Rica since 1969 by Diana and Milton Lieberman. Elsewhere, Alwyn Gentry, John Terborgh, Terry Erwin, Gary Hartshorn, David Neill and Rodolfo Vásquez set up the first long-term plots in western Amazon in the late 1970s and 80s (Gentry 1988a, Monteagudo et al. 2020). Eastern and central Amazon plots survive established by Ima Vieira and Rafael Salomão in Pará (Salomão 1991, Pires and Salomão 2000), Tom Lovejoy, Niro Higuchi and colleagues near Manaus, Henri-Félix Maître in French Guiana, and by Marcelo Nascimento and colleagues in Roraima. The earliest extant plots in southern Amazonia originate with Tim Killeen, Luzmila Arroyo, Beatriz Marimon and José Roberto Rodrigues. The first long-term tropical large plot was established in Costa Rica (Hubbell 1979), which represented a separate innovation that permitted plot-level analysis of multi-species demography, followed soon after by the first 50-ha plot in Panama (Hubbell and Foster 1983, Wright this volume) and later developments by the Smithsonian Institution and the ForestGEO network (e.g. Anderson-Teixeira et al. 2015).

RAINFOR (Red Amazónica de Inventarios Forestales) is the first international tropical forest network encompassing hundreds of long-term plots. At root, RAINFOR was inspired by Alwyn Gentry, a virtuoso tropical botanist who established the first globally standardized floristic inventories. In the 1970s Gentry developed a 0.1-ha sampling design to rapidly inventory diversity in species-rich tropical forests, capturing all stems $\geq$2.5 cm diameter. He and his colleagues applied it throughout the tropical

Americas as well as parts of Africa, India, Southeast Asia, Australasia, and some northern and southern temperate forests. By the time of his untimely death at the age of 48 in 1993, Gentry had completed 226 of these samples, comprising an inventory of thousands of tree and liana species including many new to science. His legacy lives on in multiple ways. After studying with Walter Lewis and recruited by Peter Raven in the early 1970's, Gentry was a key figure in the Missouri Botanical Garden's golden age of tropical botany. He collected more than 80,000 plant specimens, approximately half of which are tropical trees and lianas. He pioneered a new approach to the challenge of identifying plants in the world's most diverse forests (Gentry and Vásquez 1993) which has inspired generations of botanists throughout Latin America. Perhaps most importantly, it was Gentry who embodied the ambition of combining efficient ecological sampling with high-quality identifications and replicating these to create highly distributed measurements of the world's forests (e.g. Gentry 1988b, Clinebell et al. 1995, Phillips and Miller 2002, Phillips and Raven 1997). He also established permanent plots (Gentry 1988a) that feature in the first continental and pan-tropical analyses of forest carbon and dynamics (Phillips and Gentry 1994, Phillips et al. 1994, Phillips et al. 1998), which in turn led to the creation of RAINFOR (Malhi et al. 2002, López-Gonzalez and Phillips 2012) and its protocols (e.g. Phillips et al. 2002). Originating in 1999 from a small nucleus of researchers and plots and supported by EU funding to Brazil's LBA initiative and UK scientists, RAINFOR grew to tackle the challenge of analysing Amazonian forests and climate responses tree-by-tree from the ground-up. By bringing different groups together RAINFOR facilitated the development of long-term international collaborations to measure and understand not only forest dynamics and diversity but also biogeochemistry and carbon fluxes.

While RAINFOR has grown steadily, other plot networks later emerged with complementary foci in South America. Some are daughter initiatives to RAINFOR, others were formed separately, but most share a similar ethos and strongly overlapping protocols. To the extent that they can be combined together these networks represent an impressive Observatory for Neotropical Forests. Below (Table 1) we report key information about many vibrant networks worldwide that specifically contribute to ForestPlots.net, while here we briefly enumerate national and international neotropical networks, the majority of which ForestPlots.net supports. These include (with dates when plots were censused or consolidated as a network) Tropical Ecology Assessment and Monitoring (TEAM, 2002), Amazon Tree Diversity Network (ATDN, 2003), Programa de Pesquisa em Biodiversidade (PPBio, 2004, Brazil), Red Colombiana de Monitoreo de los Bosques (COL-TREE, 2004), Global Ecosystems Monitoring (GEM, 2010; Malhi et al. this volume), Latin American Seasonally Dry Tropical Forest Network (DryFlor, 2012), Red de Investigación y Monitoreo del Bosque Seco Tropical en Colombia (Red BST-Col, 2014), Secondary Forest Network (2ndFOR, 2015), Peru Monitoring Network (MonANPerú, 2017), sANDES (Tree Diversity, Composition and Carbon in Andean Montane Forests, 2019), and Red de Bosques Andinos (RBA, 2020), as well as global networks and meta-networks including ForestGEO (Anderson-Teixeira et al. 2015), GFBI (Steidinger er al. 2019), sPlot (Bruelheide et al. 2019), FOS (Schepaschenko et al. 2019) and TmFO in logged forests (Sist et al. 2015). Each of these has notable achievements of their own and at the time of writing this in 2020 almost all have active research programmes.

In Africa, our early networking focussed on assessing whether there were similar patterns of changes in carbon stocks as observed in South American forests and the causes of such changes. Efforts began in 2001 to recensus many of the earlier plots installed in post-independence Africa (UK funding to O. Phillips, Y. Malhi and S. Lewis), which were later formalised as the African Tropical Rainforest Observation Network (AfriTRON; Lewis et al. 2009), and catalysing a tripling of the African multi-census plot dataset over the last decade (Hubau et al. 2020). These span 12 African countries with moist forests from Sierra Leone in the west to Tanzania in the east. Like RAINFOR in Amazonia, AfriTRON pools expertise and data to tackle long-term, large-scale questions relating to the ecology and biogeochemistry of tropical forests. Networks sharing a similar ethos with programmes in Africa now include TEAM, DynAfFor (Gourlet-Fleury et al. 2013), TmFO and ForestGEO. Recently, the SEOSAW (Ryan et al. in review) and AfriMont networks have been established, extending long-term plots into the extensive southern woodlands and savannas and Africa's distinctive montane forests.

Our work in Southeast Asia began in 2001 to assess forest carbon balance and later developed into a network once Lan Qie undertook fieldwork and networking. European Research Council investment (T-FORCES 2012 grant to Phillips, Malhi and Lewis) enabled intensive campaigns to develop long-term plot networking in Borneo (Qie et al. 2017), and supported African recensuses (Hubau et al. 2020). While smaller than its Amazonian and African counterparts the Asian network builds on plots installed by a number of foresters and botanists as long as 60 years ago. Critically, RAINFOR, AfriTRON, T-FORCES and TmFO use the same field and analytical protocols.

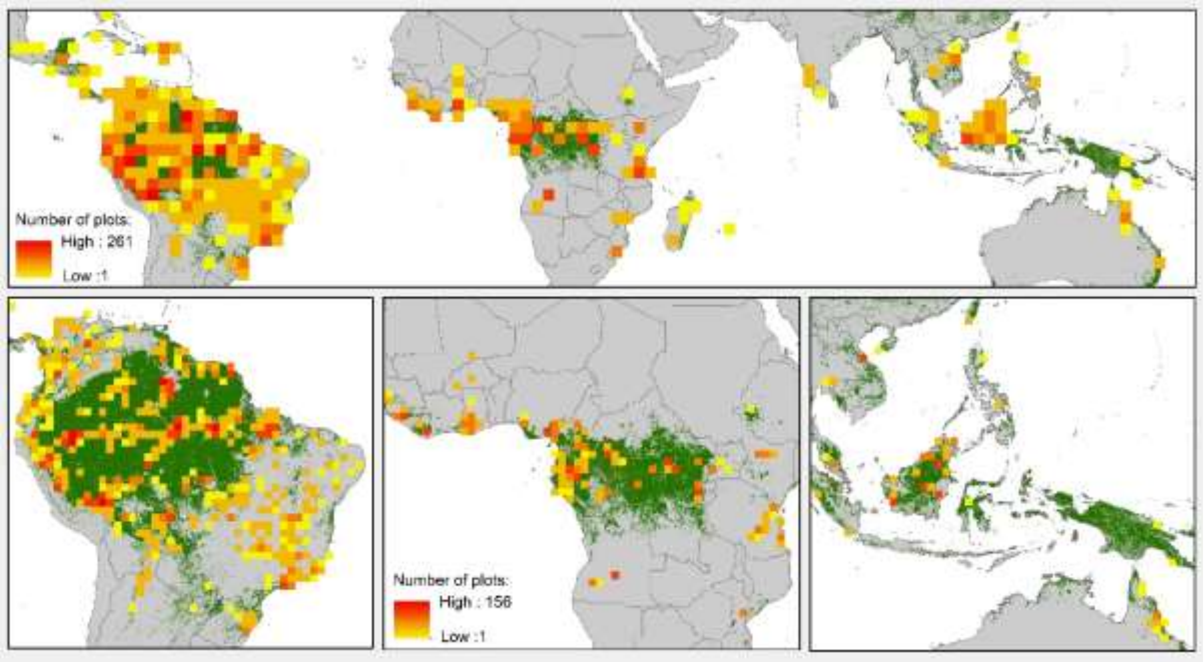
Insert Table 1 here: **Table 1. Networks contributing to ForestPlots.net (September 2020).**

How can we combine the different strengths of these and other initiatives to maximise their impact on science and society? To achieve this requires shared data management tools and horizontal organisational structures that foster leadership by tropical scientists. Our plot data management scheme was originally conceived in 2000 as a desktop database to support the first RAINFOR analyses of spatial variation in wood density, biomass, productivity, and changes in biomass over time (Baker et al. 2004a, b; Malhi et al. 2004). This was expanded to draw together inventory data from more than 100 sites in Amazonia and then African forest plots, including some of the longest running monitoring sites worldwide (Peacock et al. 2007).

Since 2009 we have developed a Structured Query Language web application with sophisticated programming, providing a one-stop platform to a growing global community of contributors and users (López-Gonzalez et al. 2011). Now, ForestPlots.net supplies ecological informatics to colleagues in scientist-led networks from 54 countries working across 44 tropical nations (Fig. 1). Key advances in this platform include the ability to manage complex time-series data, to track species linked to high-quality botanical records, and to analyse records with common BiomasaFP R-language protocols (López-Gonzalez et al. 2015). While focussed on species identity, tree growth, mortality and carbon dynamics, ForestPlots.net encompasses many related forest attributes including lianas, soils, and plant traits.

At their heart long-term plots are an intensely human enterprise and so we also document the personal contributions to plot establishment and continued monitoring. By tracking who did what, and when, we also honour the inter-generational aspect of plots that allows modern analysts to stand on the shoulders of giants. With ForestPlots.net data contributors retain control and are able to manage, share and analyse their records using a common toolset. If new projects requesting to use their data are proposed they can agree to collaborate, or not, as they wish. Contributors often propose their own multi-site projects. ForestPlots.net can provide DOIs to datasets, further ensuring that contributors are properly acknowledged. Developing this functionality has supported a surge in multi-site and multi-national analyses that are increasingly initiated by scientists from the tropics, gradually supplanting the traditional model where researchers from the Global North lead. In sum, ForestPlots.net enables the level of control and collaboration that individual researchers wish for while underpinning network and multi-network integration. In turn, this is empowering data owners and networks and helping to transform the face of tropical ecological science.

Figure 1. Current extent of ForestPlots.net



Top: Pantropical plot sampling density per 2.5 degree square with the 4.062 multiple- and single-inventory plots hosted at ForestPlots.net. These plots contribute to 24 networks including RAINFOR, AfriTRON, T-FORCES, ATDN, BIOTA, COL-TREE, FATE, GEM, Nordeste, PELD, PPBio, RAS, RBA and SEOSAW. Forest cover based on the Global Land Cover 2000 database (JRC, 2003) with tree cover categories: broad-leaved evergreen; mixed leaf type; and regularly flooded. Our plots also extend into neotropical and African savannas; ***Bottom:*** The same plot sampling but displayed at higher-resolution (1-degree grid cells) for each focal continent, South America, Africa, and Southeast Asia and Australia.

The networks and ForestPlots share a 20-year history, but as already seen the history of plot monitoring is much longer. The first recorded census in ForestPlots.net dates from 1939 in Budongo, Uganda. Forty years later, 676 censuses had been completed from 90 plots, but since 1979 fieldwork has accelerated greatly with more than 10,000 censuses completed across 4,000 plots by 2020 (Fig. 2a). This acceleration is reflected by the growing community of contributors, which by 2020 had reached 2,000 individuals (Fig. 2b). ForestPlots.net itself has grown steadily both in terms of censuses uploaded and in outputs (Fig. 3). The neotropics dominate much of this inventory and monitoring effort as well as the growth of ForestPlots.net in particular, but contributions from Africa and other continents are increasing (Figs. 2, 3). Scientific outputs emerging from this collective effort have always spanned local to global scales but now have an increasingly pan-tropical theme (Fig. 3b).

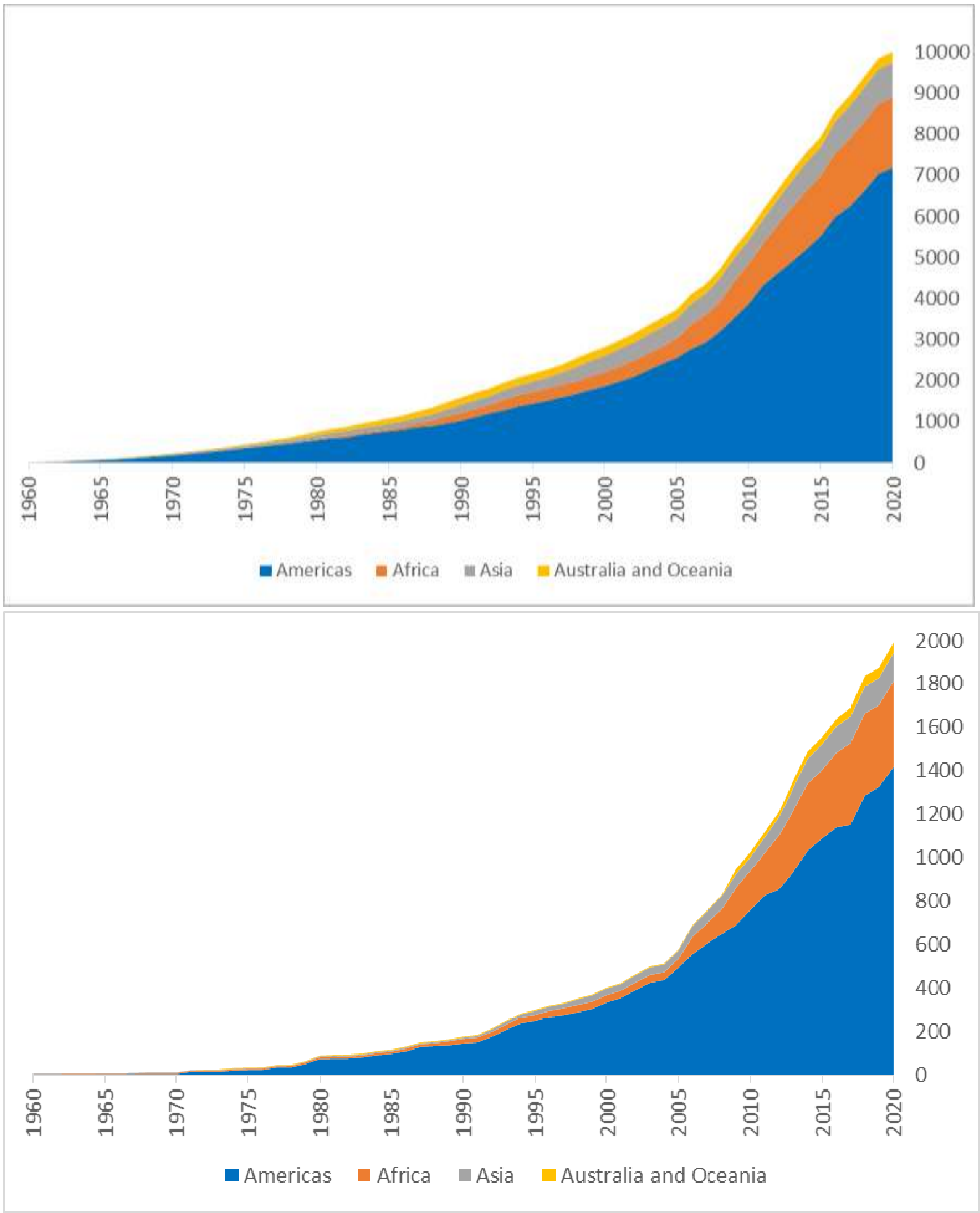
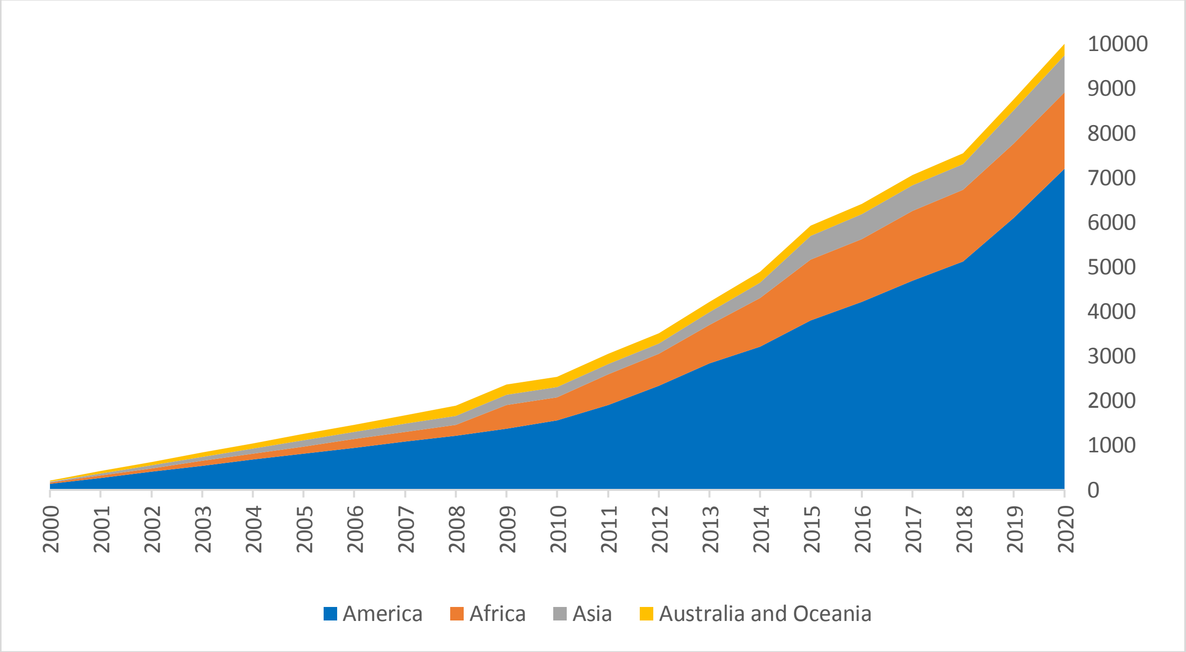


Figure 2. Growth of pan-tropical forest monitoring since the mid-twentieth-century.

Top: Plot-censuses curated at ForestPlots.net by date of census;
Bottom: Cumulative number of contributors to ForestPlots.net by date of first recorded fieldwork. Growth was slow following the first census in 1939, only reaching 100 censuses by 1969. For early censuses, records of field team personnel and leaders are often sparse or absent. Note that 'contributors' are defined inclusively to reflect members of indigenous communities, protected area guards, parataxonomists, students, and technicians, as well as principal investigators, botanists, and other specialists.



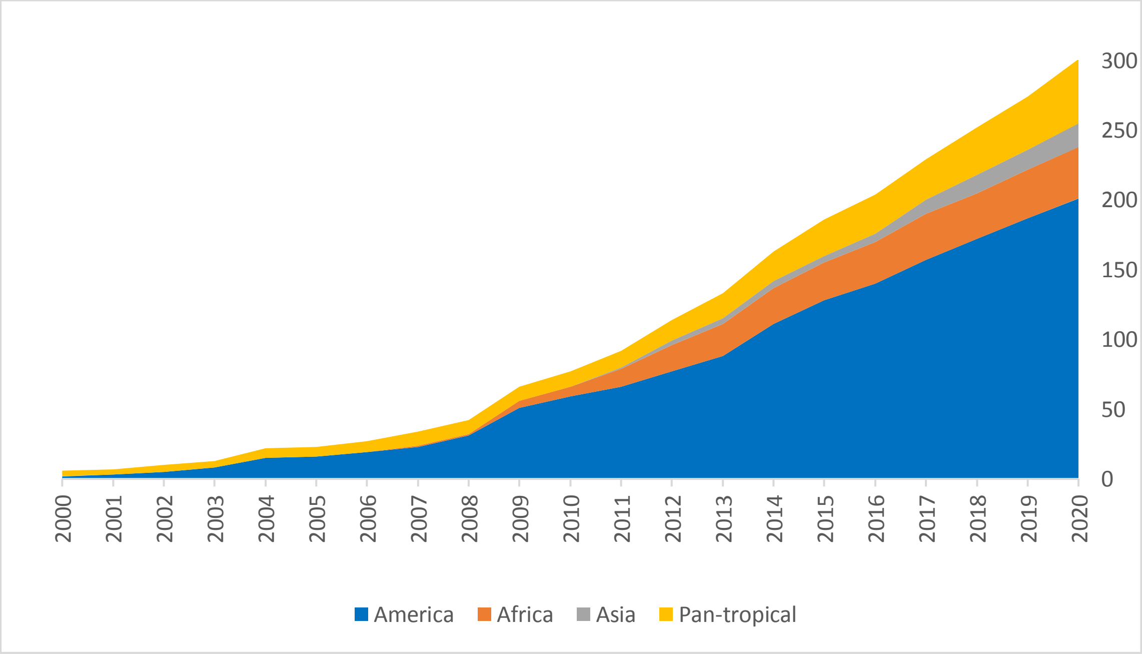


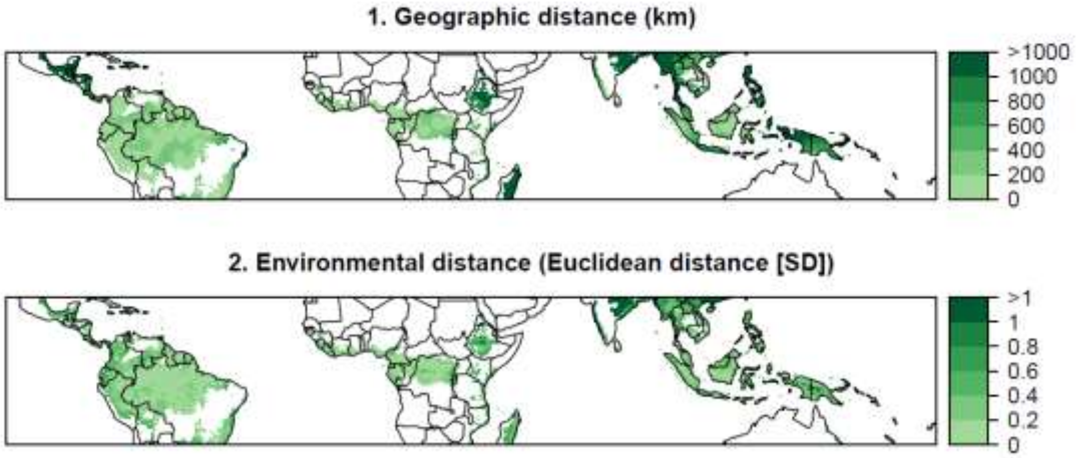
Figure 3. Growth of ForestPlots.net and its contributing networks since 2000.

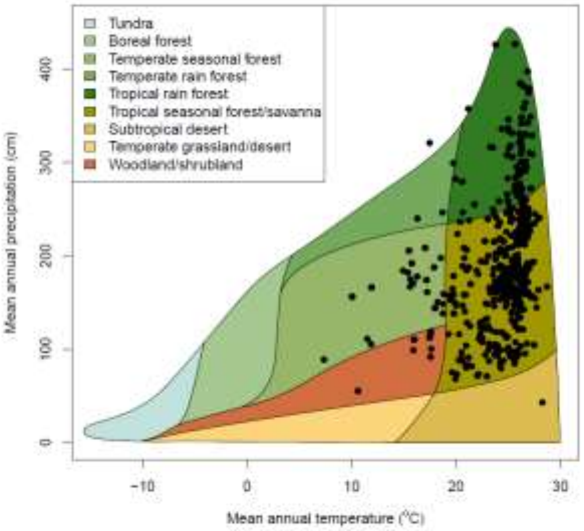
Top: Cumulative upload of unique plot censuses to ForestPlots.net by date of upload (pre-2009 uploads to pre-internet versions allocated evenly back to network beginnings);
Bottom: Cumulative peer-reviewed scientific articles based on network plots, excluding research based on single-plot studies.

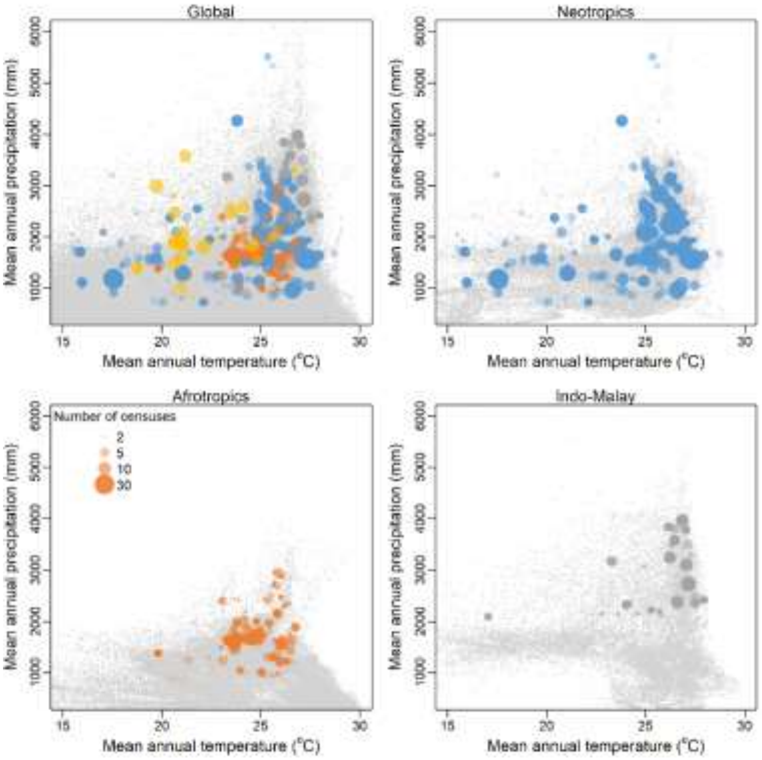
2. Environmental Representation

While it is not possible to intensively sample the whole tropical forest extent, in practice RAINFOR, AfriTRON and T-FORCES have managed to cover almost the entire climatic and geographic space across the humid tropics with permanent plots (Fig. 4a) as well as extensively sampling the biome space of the terrestrial tropics except for semi-arid biomes (Fig. 4b). Within each continent coverage has been focused on the moist tropical lowlands with sampling extending into montane and drier forest systems most effectively in South America (Fig 4c). Plots also cover the complex edaphic variation present in Amazonia (Quesada et al. 2012) where they encompass landscape-level variability within old-growth forests (Anderson et al. 2009, 2010). This effective representation of structurally intact moist forests provides good support for large-scale inferences from what is, inevitably, a limited sample of the domain. It is important to note that many tropical countries lack statistical inventories of forests, let alone long-term monitoring or historical baselines, so research plots fill critical gaps in global and national observations.

Yet significant work remains to be done to increase representativeness, better understand impacts of geological and edaphic variation, and expand sampling in remote areas especially in parts of Amazonia, the central Congo Basin, and New Guinea (c.f. Brearley et al. 2019, Fig 4. below). Fuller environmental coverage can help networks address challenges such as monitoring of protected area effectiveness (Baker et al. 2020) and providing calibration-validation of Earth Observation space-borne sensors (Chave et al. 2019). Beyond the lowland humid tropics, special effort is also needed for long-term, ground-based monitoring in particular environments. Expansion is especially required for: (i) secondary forests and those impacted by disturbance events such as logging, fragmentation, and wildfires (e.g. Chazdon et al. 2016, Elias et al. 2020, Villela et al. 2006); (ii) montane forests, which harbour exceptional concentrations of endemism and are at great risk of biodiversity loss due to deforestation and climate change and therefore represent urgent conservation opportunities (e.g. Malizia et al. 2020); (iii) Asian dry forests, and (iv) the wider extent of tropical dry forest and savanna biomes, which are home to distinctive biotas and significant carbon stocks of their own (DRYFLOR 2016, Pennington et al. 2018). ForestPlots.net partner groups are expanding research and monitoring in such critical areas beyond the structurally intact lowland forests that have been the main focus of RAINFOR and AfriTRON.


1. Geographic distance (km)
>1000
1000
800
600
400
200
0
2. Environmental distance (Euclidean distance [SD])
>1
1
0.8
0.6
0.4
0.2
0


Tundra
Boreal forest
Temperate seasonal forest
Temperate rain forest
Tropical rain forest
Tropical seasonal forest/savanna
Subtropical desert
Temperate grassland/desert
Woodland/shrubland
Mean annual precipitation (cm)
0
100
200
300
400
−10
0
10
20
30
Mean annual temperature (°C)


Global
Neotropics
Afrotropics
Indo-Malay
Number of censuses
2
5
10
30
Mean annual precipitation (mm)
1000
2000
3000
4000
5000
6000
15
20
25
30
Mean annual temperature (°C)

[Previous Page] Figure 4. Network coverage of geographical and climate space

Analyses include >1500 permanent plots managed at ForestPlots.net. **(a) Top panels**: (1) Geographic distance between multi-census plots across the humid tropical forest biome; and (2) Minimum climate dissimilarity (Euclidean distance on variables scaled by their standard deviation, accounting for mean annual temperature, temperature seasonality, mean annual precipitation and precipitation seasonality), where for each cell environmental distance represents how dissimilar a location is to the most climatically similar plot in the network. Note that some poorly sampled areas are mostly deforested, such as Central America, Madagascar, and much of tropical South and Southeast Asia. The baseline map depicts WWF terrestrial ecoregions (Olson et al. 2001). **(b) Middle panel**: Tropical plots displayed in global biome space (Whittaker diagram), showing the main concentration of plots from lowland wet through to moist forests and savanna, with some samples in cooler montane climates. **(c) Lower panels**: Plots displayed within tropical humid and sub-humid climate space, with plots displayed colour-coded by continent and symbol size corresponding to total census effort. Note the important differences in baseline climatic conditions between continents.

3. Discovery: Forest Ecology across the Tropical Continents

RAINFOR, AfriTRON and T-FORCES plots have generated ecological and biogeographical insights that have only been achievable via large-scale collaboration. RAINFOR has revealed that Amazonian forests differ substantially from one another, even those that share essentially identical climates. For example, basal-area weighted wood density of northeastern forests is 50% greater than that of southern and western forests. This reflects floristic differences (Baker et al. 2004, ter Steege et al. 2006, Honorio Coronado et al. 2009, Patiño et al. 2009), which, in turn, are associated with large differences in forest dynamics. Stem turnover is twice as fast in the west and south as the east (Phillips et al. 2004) due to younger soils with poorer structure providing less rooting support (Quesada et al. 2012, Schietti et al. 2016) and in spite of only modest productivity differences (Malhi et al. 2004, 2014). In contrast, biomass in north-eastern Amazonia is higher than elsewhere due to the reduced mortality risk and hence bigger trees and denser wood (Baker et al. 2004, Malhi et al. 2006, Marimon et al. 2014, Pallqui et al. 2014, Johnson et al. 2016, Alvarez et al. 2018, Phillips et al. 2019).

In Africa, AfriTRON plots also show that species-driven differences in wood density prevail at large scales. In mature forests, soil-related compositional differences cause significant variation in basal-area weighted wood density. Forests on younger and more fertile acrisols and cambisols have 10 and 20% lighter wood than those on arenosols and histosols, respectively (Lewis et al. 2013). Similarly to Amazonia, African forests growing on older, less fertile soils have higher biomass (Lewis et al. 2013). Local and regional variation in soils and forest attributes are important within both continents but the key difference is that only Amazonia has clear continental-scale gradients in wood density, due to the powerful influence of Andean orogeny in the west. This leads to young, geologically dynamic landscapes with fertile, less-developed soils, influencing speciation, immigration and extinction, and contrasts with the ancient, stable Brazilian and Guianan Shields of the east.

Large-scale analysis thus reveals how soils and species help control the carbon that tropical forests store. This has implications for monitoring carbon stocks using remotely-sensed data. In tropical forests neither soil nor tree composition is easily perceived from space. For example, RAINFOR plots show that LiDAR-derived biomass estimates of Amazonian forests are compromised because they do not perceive the critical large-scale floristic gradients (Mitchard et al. 2014). Accounting for such limitations by relating plot-derived woody density and allometry to LiDAR sampling shows that plots greatly improve biomass maps (Mitchard et al. 2014, Avitabile et al. 2016). Thus the role of soils and species composition in affecting biomass carbon is a key reason why ground data are essential for mapping forests (Chave et al. 2019). While Earth Observation has great benefits in terms of spatial coverage and ability to update frequently the incorporation of plot-derived compositional data greatly improves our understanding of carbon storage patterns over large scales.

When networks using the same protocols are combined it is also possible to discover and explore variation between continents too. Common protocols have revealed major pan-tropical variation in vertical structure, including tree height and height-diameter allometry (Feldpausch et al. 2011) which have impacts on biomass (Banin et al. 2012; Feldpausch et al. 2012; Sullivan et al. 2018). African forests average one-third higher biomass per unit area than Amazon forests (Lewis et al. 2013), yet have roughly one-third *fewer* stems >10 cm diameter per unit area. This may be driven by systematically lower tree mortality in these forests (Hubau et al. 2020, Sullivan et al. 2020). Similarly, comparing climatically and edaphically similar forests in parts of Borneo with northwest Amazonia reveals that Bornean forests produce much more wood, with trees growing up to 50% more rapidly than those of Amazonia. This suggests that differences in phylogenetic composition of tree communities, especially the dominance of the dipterocarp family in tropical Asia (Corlett and Primack 2011), determine the efficiency with which atmospheric carbon is converted to woody carbon (Banin et al. 2014).

Tree species composition and dominance strongly control forest function within continents too. For example, a recent RAINFOR study discovered that Amazon woody productivity is enhanced in more phylogenetically diverse forests (Coelho de Sousa et al. 2019). Yet while Amazonian forests are very diverse, remarkably few species dominate in terms of stems (ter Steege et al. 2013, research led by the ATDN network), while biomass stocks and woody productivity are dominated by a different set of species (Fauset et al. 2015, RAINFOR network). Evidence also suggests that some of these 'hyperdominants' may have been long favoured by indigenous people as part of wider human influences on old-growth Amazon forests (Levis et al. 2017, Oliveira et al. 2020). These and other studies show that identity matters. Dominant species and their evolutionary history thus affect forest ecology and forest values, whether in terms of storing carbon, converting solar energy into wood or sustaining whole cultures.

These insights show that two of the defining challenges of the twenty-first century, climate change and biodiversity loss, are closely linked. How then do we best devise conservation strategies to achieve the targets of biodiversity protection and climate mitigation and adaptation? Can we rely for example on carbon conservation via schemes like REDD+ to protect tropical diversity too? The answers to these questions depend on the relationship between diversity and carbon storage but assessing this has been challenging due to the scarcity of inventories in which both carbon stocks and species identifications have been reliably quantified. By combining RAINFOR, AfriTRON and T-FORCES plots we found that for tropical trees diversity-carbon storage relationships barely exist at all (Sullivan et al. 2017, Fig. 5). For example, South America, the continent with the richest forests, actually stores the least carbon per hectare, while within continents there is no association. Independent data from the RAS network data support this, showing that strong carbon-biodiversity relationships are only found in disturbed and secondary forests but not old-growth (Ferreira et al. 2018). As mature forests exhibit all possible combinations of tree diversity and carbon stocks it is clear that both need to be explicitly considered to protect the climate and biodiversity. In addition, long-term carbon storage is threatened by defaunation of large-bodied frugivores, often essential for dispersing large-seeded heavy-wooded tree species (Peres et al. 2016). *We cannot simply focus on carbon and achieve biodiversity conservation, and vice versa.*

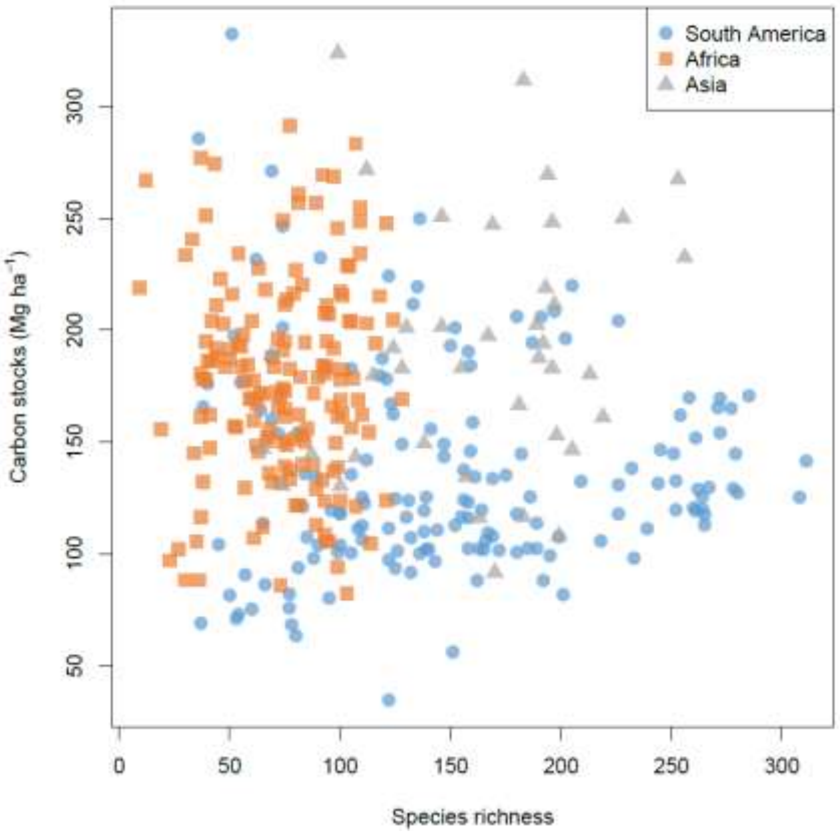


Figure 5. Pantropical forest carbon storage is independent of species richness.

There are no clear within-continent or pantropical relationships between carbon stocks and tree species richness per hectare in structurally intact old-growth tropical forests. Figure adapted from Sullivan et al. 2017.

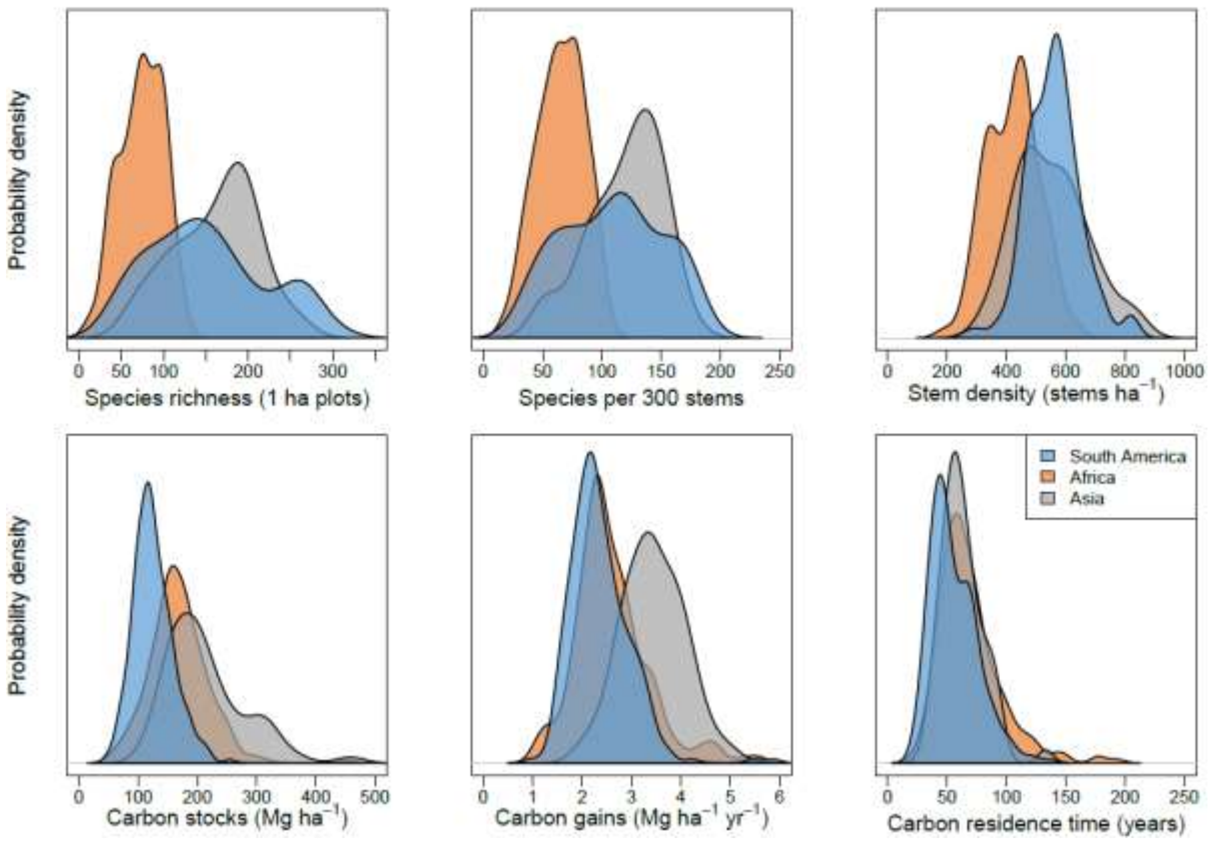


Figure 6. Tropical continental macroecology

Remarkable continental differences in species richness, stem density and carbon stocks emerge among lowland tropical moist forests when densely-sampled plot networks are combined. Graphics depict probability densities such that the whole area for each continent sums to 1. Note that the y-axis scale for each variable thus *itself varies depending on the range of the x-axis*: for continents with larger variation in x, the probability density at any point along the y axis is correspondingly smaller. Analysis adapted from Sullivan et al. 2017 and 2020.

When network data are combined surprisingly large and coherent continental-level differences emerge (Fig. 6). African forests are remarkably species-poor at the 1-ha scale whereas South American and Asian forests are more than twice as rich on average, but also vary much more in species-richness and diversity. The very richest forests in the world are located in parts of Western Amazonia, vindicating a claim by Gentry (Gentry 1988a, b) from more than three decades ago. African forests have many fewer stems than their Asian and South American counterparts, but South American forests have considerably less biomass. In terms of carbon gains Borneo’s forests are outliers, being up to twice as productive as other forests. Yet it is in South America where woody carbon turns over fastest. Fully half the carbon in neotropical trees has been replaced since 1970.

Overall these comparisons reveal remarkable differences between the tropical forest continents that are not strongly driven by rainfall, temperature or soil (Sullivan et al. 2020). The implication is that other factors related to the evolutionary and historical happenstance of each continent matter. We draw three higher level conclusions from this. *First, global-scale ecological modelling ignores biological composition at its peril. Second, if there was ever any doubt, each continent clearly needs its own robust research and monitoring programme. And third, each region likely responds to climate change in its own, idiosyncratic way.*

4. Discovery: Tropical Forest Change

The single most significant scientific impact of these multiple permanent plot networks has been to transform our understanding of how tropical forests function in the Earth system.

As the most diverse and carbon-rich tropical biome, the fate of humid tropical forests will impact the future of all life on Earth. Until quite recently it was axiomatic that old-growth tropical forests are at equilibrium when considered over sufficiently large scales, and that any changes observed at smaller scales are driven by natural disturbance-recovery processes. However, large-scale imbalances observed in the global carbon balance have cast doubt on this assumption (e.g. Taylor and Lloyd 1992). Over time, network analyses have helped to recast our understanding of contemporary old-growth tropical forests as being non-stationary systems. Their carbon, biodiversity and ecosystem processes are widely recognised as dynamic and continually responsive to multiple anthropogenic drivers (e.g. Lewis et al. 2004b, Pan et al. 2011, Malhi et al. 2014, Levis et al. 2017, Mcdowell et al. 2018, Reis et al. 2018). Key discoveries at this intersection between global change science and forest ecology and biodiversity include:

(1) **A pantropical increase in tree turnover rates, representing the first evidence for a widespread impact of global anthropogenic change on old-growth tropical forests** (Phillips and Gentry 1994). The finding that these forests were changing was controversial at the time - let alone the inference that global drivers were responsible - and contradicted established ecological orthodoxy. The debate that ensued helped generate new questions and analyses (e.g. Sheil 1996, Phillips and Sheil 1997) and address potential biases (e.g. Sheil 1995, Condit 1997, Lewis et al. 2004a, Gloor et al. 2009, Espirito-Santo 2014, Kohyama et al. 2019). A quarter of a century of research since then has rejected the notion that ‘intact’ tropical forests are unaffected by atmospheric changes and reinforced the central concept that all tropical forests are being influenced by a suite of large-scale contemporary anthropogenic drivers.

(2) **Biomass dynamics have also accelerated in Amazonia**. In parallel with the increases in stem dynamics, as RAINFOR grew it became clear that carbon fluxes via biomass growth and mortality were also increasing. Moreover, the increased gains in stems (recruitment) and biomass (woody productivity) clearly preceded increases in stem and biomass losses (mortality) (Lewis et al. 2004b, Phillips et al. 2004, 2008, Brienen et al. 2015, Nogueira et al. 2018). The mechanism underlying this acceleration of forest dynamics must therefore involve stimulated productivity via increased resources for plant growth, rather than direct stimulation of tree mortality such as by drought (Lewis, Phillips and Malhi 2004).

(3) **The Amazon forest carbon sink**. In conjunction with faster growth and turnover, the biomass density of Amazonian forests has increased (Phillips et al. 1998, Baker et al. 2004, Pan et al. 2011). Old-growth Amazonian forests have absorbed (net) atmospheric carbon for at least three decades now (Brienen et al. 2015), providing a true “subsidy from nature” with flux magnitude matching or exceeding net losses from neotropical deforestation (Aragão et al. 2014, Gatti et al. 2014). Thus, monitoring networks have shown that most Amazonian nations are on balance *not* net emitters of carbon (Espirito-Santo et al. 2014, Phillips and Brienen 2017). The location, magnitude and persistence of this old-growth carbon sink has important implications for guiding approaches to meeting nationally differentiated targets for controlling climate change (Vicuña Miñano et al. 2018).

(4) **The African forest carbon sink**. The AfriTRON network discovered a long-term net biomass increase similar in magnitude to that of the Amazon in the 1990s and early 2000s (Lewis et al. 2009). The consistency of these results on a second continent supports the idea that global drivers of change can affect even the most remote forests. The fact that biomass is increasing across the entire wood density spectrum of tree species implies that forests are responding to increasing atmospheric CO_2 concentrations (Lewis et al. 2009). The long-term increase in carbon stocks of African forests was recently updated and confirmed, with three times as many plots showing continued sink strength (Hubau et al. 2020).

(5) **The Pan-Tropical forest carbon sink**. Once the T-FORCES network allowed sufficient plot coverage across remaining Bornean forest a similar increase in aboveground biomass over recent decades was revealed (Qie et al. 2017). Thus the three continental networks discovered that old-growth tropical forests as a whole have been a long-term sink. Our ground measurements imply this totalled more than one billion tonnes of carbon each year over the 1990s and early 2000s, i.e. half the terrestrial global carbon sink (Pan et al. 2011), which is sufficient to significantly slow climate change. The fact that the main blocs of remaining tropical forests are *en masse* out-of-equilibrium and undergoing biomass increases of similar magnitude implies a common global driver of growth. Increasing atmospheric CO_2 is the most parsimonious candidate and is consistent with predictions from first principles (e.g., Phillips and Gentry 1994, Huntingford et al. 2013), inference from CO_2 fertilization experiments (Terrer et al. 2019), analyses of the global carbon budget (Ballantyne et al. 2012, Gaubert et al. 2019), observed greening of forests unaffected by land-use change (Piao et al. 2019), and recent plot analyses showing a significant role of CO_2 (Hubau et al. 2020).

(6) **The Amazon sink is slowing.** After 30 years of monitoring Amazonian forests, the RAINFOR plots show that the rate of increase in forest growth is declining. Tree mortality rates have increased in some regions, leading to a slow decline in the magnitude of the net biomass accumulation (Brienen et al. 2015, Phillips and Brienen 2017). The subsidy from nature provided by tropical forests may be time-limited.

(7) **Recent droughts in Amazonia have had large impacts**. Long-term plots also monitored immediately before and soon after droughts reveal that these forests can switch rapidly from being a major sink to a source of carbon. Both the 2005 and 2010 Amazon droughts had a net impact on the order of 1 Pg of carbon, driven primarily by drought-induced mortality (Phillips et al. 2009, Lewis et al. 2011; Doughty et al. 2015, Feldpausch et al. 2016). RAINFOR and GEM have quantified the drought sensitivity of the world's biggest rainforest and identified the key process affected: mostly tree mortality rather than growth, and not photosynthesis. The impact on the biomass carbon sink of the 2010 drought and non-drought years match independent inferences from measurements of atmospheric [CO_2] using aircraft (Gatti et al. 2014).

(8) **The African and Amazon sinks have diverged**. Thirty years of monitoring AfriTRON plots show that African forests have continued to function as a carbon sink, although the most intensively monitored plots suggest that the sink may be declining (Hubau et al. 2020). When analysed together with RAINFOR data, within-plot changes over time reveal a common set of drivers that suggest the sinks will decline, with African forests lagging behind Amazonian forests by 15-20 years (Hubau et al. 2020). Changes across both continents are best explained by a combination of the positive effects of increasing CO_2 enhancing productivity and negative effects of higher temperatures and droughts in suppressing growth and accelerating mortality, combined with the intrinsic properties of forests themselves. The time-lag of the African sink saturation is due to longer carbon residence times in African forests, so that mortality catches-up slower than in faster turnover forests. Amazonian forests are often harder hit because they are hotter and can be drought-prone (Hubau et al. 2020). Together, the pan-tropical plot networks have revealed long-term trends in carbon storage and determined which drivers matter, which processes are affected, where they are impacting, and what the lags are.

(9) **The future of the tropical forest carbon sink.** Monitoring the present and the recent past of forest behaviour can also reveal likely future scenarios as the climate continues to change. Our plot networks provide two powerful and independent lines of evidence. First, the *long-term sensitivity to climate* emerges from a space-for-time analysis based on 813 plots across the Earth's tropical forests. This shows how maximum temperature and dry season intensity combine to determine the equilibrium climate controls on forest carbon, acting on productivity and mortality to limit forest carbon storage in *the long-term* (Sullivan et al. 2020). Forests exhibit remarkable thermal resilience under low amounts of warming, but in the hottest forests (>32.2°C max. temp.) biomass carbon drops off rapidly. Most of the biome will exceed this value with one further degree of warming (approximately equivalent to a 2^{o}C increase above pre-industrial levels). Second, analysing recent changes in productivity and mortality as a function of recent climates, and coupling them with future climate scenarios, confirms that the carbon sink is likely to decline (Hubau et al. 2020). A key uncertainty with these latter projections is the extent to which local resilience due to shallow water-tables (Sousa et al. 2020) may mitigate effects, and whether more compositional changes will extend the carbon sink further if species better-adapted to the new conditions compensate for others' losses. The analysis by Sullivan et al. (2020) confirms that lagged species-related resilience is likely as long as forests do not experience substantial warming.

(10) **Tropical forest biodiversity is changing**. RAINFOR data show that an entire group of plants, lianas (woody vines), are increasing in dominance across Amazonia (Phillips et al. 2002). Large lianas in turn contribute to higher tree mortality (Phillips et al. 2005). Tree community composition is changing too. In the Andes, plots of ABERG, RBA and RedSPP show 'thermophilization' – communities becoming more warm-adapted (e.g Fadrique et al. 2018). Climate change is inducing large-scale change in tropical lowland trees too, as wet-adapted taxa in Amazonia face greater mortality

risks from drought (Esquivel Muelbert et al. 2017, 2019) while a shift towards drought-deciduous tree species is observed in west African plots experiencing a multi-decadal drought (Fauset et al. 2012, Aguirre-Gutiérrez et al. 2019, 2020). In both continents these community responses to drought coincided with biomass gains. Nonetheless, because of the long generation times of tropical trees the compositional change has not kept pace with the drying of Amazonia (Esquivel-Muelbert et al. 2019). This suggests that further community change is inevitable, even before accounting for losses driven by deforestation and disturbance of remaining forests (Barlow et al. 2016). Current models lack the capacity to account for variation in tropical woody plant biodiversity and demographic processes and their lagged responses to global change drivers.

In sum, highly distributed, long-term monitoring of the world's richest forests has profoundly increased our understanding of nature's sensitivity to climate change. It has shown that intact forests have been surprisingly resilient, but that many are now reaching the limits of their tolerance to global heating and drying. Looking forward, many of the key uncertainties that remain concern the responses of tropical biodiversity itself. This includes the extent to which the great biocomplexity of tropical forests themselves will provide an effective and timely insurance policy in the face of rapidly changing climates. To understand this, we must continue to monitor.

5. Challenges and the Future of Tropical Forest Monitoring

Large-scale plot networks have not only made a series of crucial scientific discoveries and advances, but even more profoundly the Social Research Network model pioneered by RAINFOR since 2000 has influenced how the science itself is being done. Tropical ecology has undergone a remarkable shift from a small cadre of researchers working in one or two sites to a more globalised and decentralised process with greatly increased contributions from tropical scientists. This has been made possible by supporting highly-distributed researchers and field sites, establishing mechanisms for shared data management, fostering an equitable concept of data ownership, and embracing groups who are often marginalised in research. Importantly, the network model is nurtured by researchers placing trust in the sharing of hard-won data to answer big questions and recognising the value of developing trusting relationships over time. Finally, the growth of interactive multi-site, multi-cultural science has benefited hugely from standardized field and analytical methods that have been agreed upon, formalised and promoted. The ForestPlots.net experience demonstrates that collaborative, multi-polar structures help ensure breadth and resilience, while supporting and encouraging the leaders of the future.

The transformative power of this approach has now led to the establishment of multiple plot-centred networks that are reshaping our understanding of tropical ecosystems. However, these networks face a number of key challenges to sustain the achievements made and enact even deeper transformational change, which we set out here.

1. How can networks support leadership in the Global South? Although no single project can reverse the impact of centuries of global inequality, tackling the barriers to a more equitable world is the responsibility of all. Ecology and conservation science remain biased towards temperate ecosystems in terms of funding and topical focus (Di Marco et al. 2017, Reboredo et al. 2020), while tropical ecology is often detached from policy-making processes and with most high-impact papers still led from the North. Together with open data-sharing and long-term collaboration, more leadership of forest science from tropical countries helps to address these disparities and achieve more impact on forest and carbon management (e.g., Vargas et al. 2017, Baker et al. 2020). Supporting tropical students at different levels up to PhD and mentoring beyond the doctoral degree is also important. To help, ForestPlots.net has made shared tools widely available, and especially data management and analytic tools that support data contributors as much as users. To ensure fieldwork is valued and leadership in tropical researchers is fostered, we have developed a Code of Conduct to encourage contributions, support scientists in tropical countries, and promote mentoring of junior scientists. To oversee this we created a diverse steering committee that currently supports more than 30 projects each year (http://www.forestplots.net/en/join-forestplots/research-projects). As a result, the proportion of ForestPlots.net research projects and products being led by tropical nationals has greatly increased, with less than 10% of publications as RAINFOR began (2000-2004), rising to 35% in 2009 and 50% by 2019. In spite of such gains diversifying leadership is a long-term process. Ultimately, sustained funding in and by tropical countries themselves will ensure they not only have strong training programmes to develop the core field and analytical skills scientists need, but equal opportunities for career development.

2. How should we value and recognise collaboration and leadership? Most of the obvious reward structures in science - job security, income, grant success, peer reputation and public acclaim – can favour a ‘me first’ approach. Credit accrues to individuals, but true collaboration involves trust, sharing and encouraging others. Collaboration is gratifying, but letting go of our egos can be challenging, and in larger groups there is greater risk that individuals feel their contributions go unnoticed. Likewise, the essential and major effort needed ‘backstage’ in ForestPlots.net to check data, update and develop data management, and support requests to utilize data, goes unseen. A partial developmental solution to this involves providing network contributors the opportunity to lead analyses with the expectation that *these new leaders then support others* with their analyses. Another approach is to reflect the diversity of contributions that underpin the success of networks by using a group author that shares credit amongst all, as in the current paper. These steps can promote the recognition of multiple contributions and development of tomorrow’s leaders.

3. How do we properly value the long-term? Project and thesis time-scales last from one to five years, but the lifespans of trees are measured in decades and centuries. What can seem vitally important in a hypothesis-driven research grant or a PhD may, in fact, have little relevance to the longer natural rhythms of nature. What if the dominant processes governing climate responses of forests turn out to involve lifetime accumulated ecophysiological stress, tree demography and species migration? Clearly very long-term research is essential to decode these processes. Meanwhile, maintaining permanent plots is as much an expression of hope in the future as a stake in an immediate scientific outcome, as rewards may accrue to others distant in time and space. Indeed, we have all benefited from researchers installing plots from the 1930s onwards. These pioneers never dreamt that their careful tree measurements and botanical identifications would help reveal the impacts of climate change on tropical forests, but look what they have achieved! *Long-term research programmes are simply irreplaceable, enabling us to discover, quantify, identify the causes of, and ultimately tackle environmental change.*

4. Can we ensure fieldwork and human skills are valued for what they are? Technology provides many benefits to the scientific endeavor, but there are risks too, particularly in a field where long-term measurements may be perceived as unfashionable (Ríos-Saldaña et al. 2018). A serious risk is that the tail wags the dog: when technological advance is an end in itself, it is unlikely that scientific and human progress will follow. We should never forget the basic truth that human beings and their skills are essential to measure and identify tropical trees. It is notable that those measuring, climbing and collecting tropical trees in permanent plots are among the least well-paid of all actors in the global scientific endeavour. Yet these true *key workers* are irreplaceable as tree measurement in many locations is completely dependent on such labour and skill (Fig. 7) and, more broadly, *combinations* of people and technology provide the best results (next section). Moreover, because tropical tree floras usually run into the thousands of species (e.g., >4,700 tree species in Peru, Vásquez et al. 2018), identification depends on the work of highly skilled climbers and botanists to collect material from canopies, make vouchers, and identify and permanently store them in herbaria. Without physical collections and the immense multi-cultural knowledge and skills that produce them, identifications are untestable hypotheses whose quality cannot be evaluated. But with vouchers, we have the names that are essential to test questions about diversity, composition, functional traits, and wood density and biomass.

5. How should we fund proven networks long-term? As the most pressing concern, this question intersects closely with all of the above. *Few organisations have the vision to support long-term endeavours where leadership and credit is shared diffusely, many benefits accrue after decades, and where the most exciting discoveries may be unforeseeable.* We recommend the following, potentially transformational changes to address the challenges and unlock the benefits of ambitious, long-term forest monitoring:

(i) *Science Agencies have the foresight to build long-term research capacity,* and consciously adopt the challenge of international ecosystem monitoring and tropical career development;

(ii) *Space Agencies recognise that tropical fieldwork can measure the things they cannot and validate the attributes that they can*, and contribute to the labour and unique skills of tropical field scientists and help overcome the challenges they face;

(iii) *Development and Conservation Agencies who depend on a robust understanding of the long-term health of forests*, recognise that high quality, long-term, on-the-ground monitoring of trees, and supporting these skills, is vital for their agenda;

(iv) *National and international climate adaptation and mitigation funders recognise that long-term, world-class forest monitoring is essential to assess both the mature forest carbon fluxes and the land-based emissions* which will together impact forest management, nature-based solutions, and nationally determined contributions (NDCs) to reducing greenhouse gases for decades to come.

Every one of these user groups requires successful networks with long-term, research-grade tropical forest plots to discern the status and change of biodiversity and to assess the stocks and flows of carbon.

Figure 7. Accurately measuring and identifying trees in remote tropical forests requires dedication, skill and courage.

To measure the diameter of this giant *Ceiba* (Malvaceae) tree in Colombia's Chocó, three people each needed to climb more than 10 meters. Such techniques can be the most practical and accurate options for measuring large trees. Here, like many of our sites, there is no electric power, let alone a field station, and chronic insecurity due to political and social conflicts and narcotrafficking means that aircraft and laser-scanners are not deployable. Images: Pauline Kindler.

6. Achievements, Impact and Potential

Despite the challenges, tropical forest science has come a very long way. Until recently, tropical ecology suffered from a massive data deficit. We had plenty of theory and conjecture, but few comparable observations over time and space to *deductively* put these ideas to the test or *inductively* generate new ones. Networks such as ForestGEO, RAINFOR, AfriTRON, and the wider ForestPlots community have contributed much to resolving this. *By leveraging a remarkably old technology, forest plot networks have sparked a modern revolution in tropical forest science*. They provide the means by which we have quantified the trajectory of tropical forest carbon balance, including its climate sensitivity, and now provide a Pan-Tropical Observatory for tracking these vital indicators of Earth’s health going forward.

Permanent plots are now the prism through which ecologists address a rich suite of ecological questions, but they have also changed the way *others* see forests. For example, well-identified permanent plots have proved fertile ground for botanists to discover new tree species and genera (e.g. Reitsma et al.

1988, Baker et al. 2017, Wurdack and Farfan Rios 2017, Vásquez et al. 2018, Gosline et al. 2019, Vásquez & Soto, 2020), ethnoecologists to quantify forest people's values (Phillips and Gentry 1993, Lawrence et al. 2005), atmospheric scientists to explore organic volatiles production (Harley et al. 2004), ecophysiologists to assess why trees die (Rowland et al. 2015, Mcdowell et al. 2018) and how necromass accumulates and decays (Chao et al. 2009), modelers to verify ecosystem simulations (Johnson et al. 2016), and foresters to predict and manage wood production and its impacts (Berry et al. 2008, Gourlet-Fleury et al. 2013). They provide critical infrastructure for whole-biodiversity and cross-taxa inventory, including exploration of cryptic canopy and soil faunal and microbial biodiversity (e.g., Nakamura et al. 2017). The impacts of these networks on policy are also growing. In Peru for example, ForestPlots.net, MonANPe and RAINFOR contribute to estimating National Forest Reference Emission Levels (NREF) since 2016, and our permanent plots are now being used to validate national contributions to the Paris Climate Accord via forest carbon sequestration (Vicuña et al 2018, Baker et al. 2020). In Ghana, plots were needed to quantify historical and current carbon stocks, helping to establish baseline forest reference levels for the flagship Cocoa Forest REDD+ Programme (FCPF, 2017). In Gabon stratified-random sampling of high-quality AfriTRON plots is now used for the National Forest Inventory (Poulsen et al. in press. Ecol. Apps). Internationally, RAINFOR, AfriTRON, T-FORCES and 2ndFor provide the new IPCC default values on old-growth and secondary forest carbon sequestration to assist countries develop their nationally determined contributions as part of the UNFCCC process (Requena Suarez et al. 2019).

What of the future? As new technologies for probing forests become available, the hundreds of standardised long-term plots and networks of skilled tropical researchers represent critical infrastructure to enhance and calibrate new insights as they arise. The benefits of working within established plots go beyond simply having confidence in species identifications and hence biomass. By leveraging their labour and insights, we can increase the scientific value of new technology. For example, the ability to match individual trees from laser-scanning surveys to tagged, censused individuals provides critical information on growth and identity (Disney et al. 2018). Integrating long-term botanical and ecological records of plots with terrestrial and airborne laser-scanning in designated *super-sites* (Chave et al. 2019) can help overcome limitations of different approaches, providing greater certainty to biomass estimates (e.g., Schepaschenko et al. 2019). Hence forest networks can help unlock the value of space-based efforts to monitor forests. Just as the constellation of Earth-observing environmental satellites is a public good, the plot constellation provides highly complementary, critical global infrastructure. And last, but not least, as intact tropical ecosystems continue to shrink, burn and fray at the edges, permanent plots provide the indispensable baseline for understanding biodiversity and ecosystem processes too. They should be our shining North Star for guiding sorely needed restoration efforts throughout this century.

So far this effort has relied on the goodwill of hundreds of colleagues and dozens of grants from many sources (see Acknowledgments). Only long-term funding will ensure that the vital public benefits of plot networks continue to flow. Such support is surprisingly difficult to obtain (see Box 1). Yet twenty years of hard-won scientific results show that reliable and highly distributed monitoring is irreplaceable. They underscore the importance of welcoming all contributors to this effort, and of valuing the diverse skills needed to understand tropical biodiversity and its dynamics. Ultimately, we will understand the nature of tropical forests best when the science is global, local skills are fairly valued, and when the development of tropical scientists is at its heart. Indeed, we know of no other model capable of achieving this.

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Box 1. What Does It Take?

Clearly long-term ground-based monitoring of tropical forests requires a sustained global team effort. But just how much does it take to deliver tropical forest plot data in practice? It requires both skilled people and their labour, and funds. So here we address this question in terms of *the human effort made thus far* and the *financial investment needed to monitor across continents.*

(a) The Human Contribution: Network efforts include not only in-country field campaigns but much besides. To deliver from conception to product, high-quality data collected over many years and in dozens of countries requires multiple teams that are well-led and consistently trained in the proper protocols, quality control, and data management. In RAINFOR and AfriTRON this includes national or local field-team members to establish and remeasure plots, others to collect and identify plants and collect and analyse soils, colleagues to organize and manage the data, and others to sustain and lead the process nationally and globally – not to mention those who support these processes with essential administration, herbarium assistance, database development, analytical packages, information technology support, technical training and so on. Naturally some individuals contribute in several ways and roles change over time as lives change. All these local, national and global efforts ultimately depend on funding.

The average effort *in the field, herbarium, and lab* to install a typically remote and diverse 1-ha tropical forest plot and analyse its species and soil sums to 98 person-days, with an additional effort of 38 person-days *to support and sustain these teams and data management*. Together a total of *136 person-days is needed on average to deliver high-quality data from a new plot.*

Recensusing a plot is usually less demanding (for example soil collection is not repeated and there are fewer plants to identify) but still considerable: 45 person-days in the field and herbarium, and 31 person-days to support and sustain. Therefore, *76 person-days are required to deliver high quality data from a recensused plot.* These represent long-term averages. These estimates are based on remeasuring plots within five years or less between each census, and assume the plot was installed using standard protocols. Naturally circumstances can vary from site-to-site and country-to-country.

Thus far our teams have established 4,062 plots in tropical forests of which 1,816 are recensused, from as little as once up to as many as 40 times each. Of the 4,062 plots the modal size is between 0.9 and 1.1 ha but there are smaller plots too (1,844 are $\geq$0.9 ha, and 2,216 are <0.9 ha). The recensused plots tend to be larger: of the 1,816 recensused plots, 62% are $\geq$0.9 ha (1,131) and 38% are <0.9 ha (675).

If we conservatively assume that plots $\geq$0.9 ha (average size = 1.2 ha) require 136 days to install and 76 days to recensus, and those <0.9ha require half this effort (also likely to be conservative due to fixed costs for even the smallest plots), then the total effort to install these plots has been 196,248 person-days, and recensusing them has taken 357,940 person-days. In total this comes to 1,518 years.

As if one remarkably talented and tireless individual had been working continuously since AD 502.

(b) Cost of Sustained Continental Monitoring: *How much does it cost to monitor Earth's remaining old-growth tropical forests with ground networks?* This is a critical question given the exceptional ecological value of these systems, the threats they are under, and the role they have and can play in modifying the rate of global climate change.

At first sight this question appears difficult to answer, or to even agree upon the terms of reference. Scientists would ask and likely argue: Monitoring what? For whom? With what precision, level of confidence, or spatial and temporal resolution? Recognising such difficulties we take a pragmatic approach and reframe the question. Instead we posit, *How much will it cost to monitor tropical forests using all the permanent plots that we have already remeasured?*

This question is tractable *practically* (these plots represent a known quantity: we know exactly *where* they are, *what* most of the species are, and to a large extent *who* can actually do the work – *each of which is critical*), it makes sense *scientifically* (the plots already have a baseline monitoring period against which we can assess any change, *which is essential*), and it is justifiable *quantitatively* (using somewhat smaller datasets than this we have already detected long-term changes in carbon balance, productivity and tree mortality on each continent, reported short-term changes in response to El Niño droughts and other climate anomalies, and attributed changes in carbon and biodiversity to climate drivers, *all of which establish proof-of-concept*). So here goes:

* There are 1,105 remeasured ForestPlots.net plots in tropical forest South America (422<0.9ha + 683>0.9ha), 462 in tropical forest Africa (109 + 353), 192 in tropical forest Asia (106 + 86) and 32 in tropical forest Australasia (22 + 10). With all 1,791 plots monitored on a four-year cycle this requires revisiting 448 plots annually, of which 165 are ≤0.9 ha and 283 are ≥0.9 ha.

* Recensus costs can vary from site-to-site. Botanical identification is especially challenging in most of South America due to the extraordinary diversity, while some African forests are exceptionally remote. Employment, social security and health costs vary but are rising almost everywhere. On average, considering all *the direct and indirect human effort required* (above) and *additional direct costs* (including consumables, equipment, travel, subsistence, insurance, visas, permits, shipping, training, IT), the current cost to deliver a high-quality tropical recensus is ≈ 18,000 USD for plots ≥0.9 ha, and at least half this for plots that are <0.9 ha. That's about 30 USD per tree.

[Similarly, to install plots is a significant operation but it requires more expert time to collect and identify hundreds of trees. The total cost to properly install a high-quality tropical forest plot is ≈ 27,000 USD for a 1 ha plot. When forests are recensused this start-up investment is leveraged as a contribution: this enables the subsequent monitoring of forest dynamics but it's not new spend.]

Thus, the annual delivery cost for a pantropical, practical ground-based *recensus programme* capable of tracking and attributing forest change to published standards is estimated as:

(283*18,000 + 165*9,000) ≈ 6.6 million US dollars.

This *annual investment is sufficient to ensure that ground-measurements track the biome-wide and continent-specific biomass carbon balance of the remaining intact tropical moist forests, as well as their climate sensitivity*. It also provides ground calibration and validation for remote estimates of biomass. It further enables us to detect whether the tropical sink is now disappearing as predicted, and where and why, and what the consequences for biodiversity are, and to determine how much intact ecosystems can contribute to countries' nationally determined contributions (NDCs) to climate mitigation.

While $6.6 million is a significant sum it is instructive to compare it to funding required for other large-scale science initiatives. The United States alone spends $80 million annually (i.e., *twelve times as much*) on its national forest inventory (Castillo and Alvarez, 2020). Space Agencies invest from ca. $80 million to 500 million Euros for a single mission to estimate biomass from space for a few years (i.e, *one to two orders of magnitude more*). And as we have seen, ground networks ultimately not only transcend the short-term time windows of such missions but add huge value to them.

In conclusion, the ongoing cost of monitoring Earth's remaining tropical forests on the ground is extraordinarily small compared to the great scientific and practical benefits it provides. Meanwhile, tropical forests themselves are in greater trouble than ever before, even while still providing tremendous and irreplaceable benefits to the people of the world. Now that the capacity to monitor tropical forests is established and proven it is surely incumbent on all of us to ensure this collective effort continues and grows.

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Author Contributions

All authors have contributed to ForestPlots.net-associated networks by leading, or collecting or supporting field data acquisition, or implementing and funding network development, data management, analyses and outputs. O.L.P. wrote the manuscript with contributions from most co-authors, M.J.S. contributed new analyses and M.J.S., G.L.P. and A.L.L. helped prepare the figures. O.L.P., T.R.B., G.L.-G. and S.L.L. conceived ForestPlots.net. R.B., T.F., D.G., E.G., E.H., W.H., A.E.-M., A.L., K.M., Y.M., G.C.P., B.S-M., L.Q., and M.J.P.S have additionally contributed tools, funding or management to its development since.

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Taking the Pulse of Earth's Tropical Forests using Networks of Highly Distributed Plots

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Table 1 of Contributing Networks

and

Table of Contributing Authors

Table 1. Networks contributing to ForestPlots.net

We report the 24 international, national, and regional plot networks contributing to and supported by ForestPlots.net in 2020, in order of date of affiliation. Note that some plots contribute to more than one network, in some cases the plots managed at ForestPlots.net are fewer than the total number of plots of the network, while others are not 'networked' but managed by individual researchers. Hence, cross-network totals do not correspond precisely to the number of plots managed. We include 20 tropical networks with multi-census plots plus four large-scale floristic-focussed networks (ATDN, CAO, sANDES, RedGentry) that work exclusively with single-census data. As an open collaborative project ForestPlots.net welcomes all contributors with carefully-managed plots.

Network[1]	**Geography**	**Main Purposes[2]**	**Joined ForestPlots.net**	**Initiated [e.g. plots censused as a network]**	**First census in ForestPlots.net**	**n (plots in ForestPlots.net)**	**n (plots recensued)**	**Modal plot**	**Mean size (ha)**	**Mean (maximum) years monitored**
RAINFOR	South America: tropical forests	B,D,F,M,T,V	2000	2000	1961	593	427	1-ha, >10cm d	0.8	15 (56)
DBTV	Venezuela: tropical forests	B,D,M,T	2004	1956	1961	48	48	0.25-ha, >10cm d	0.25	30 (55)
COL-TREE	Colombia	B,D,F,H,M,R,V	2004	2004	1992	61	55	1-ha, >10cm d	0.8	9 (25)
TROBIT	Pantropical: forest-savanna transition	B,D,F,H,R,T	2006	2006	2006	58	49	1-ha, >10cm d	1	12
AfriTRON	Africa: tropical forests	B,D,F,M	2009	2009	1939	575	407	1-ha, >10cm d	0.9	11 (69)
ABERG	Peru Andes: Kosñipata Valley	B,D,F,M,P,T	2011	2011	2003	23	23	1-ha, >10cm d	1	12 (16)
T-FORCES	Southeast Asia: tropical forests	B,D,F,H,M	2012	2012	1958	95	71	1-ha, >10cm d	1.3	22 (56)
GEM	Worldwide	D,H,M,P,R,T	2012	2010	2010	53	45	1-ha, >10cm d	0.8	5 (16)
PELD-TRAN	Brazil: Amazon-Cerrado transition	B,D,F,H,M,R,T,V	2012	2010	1996	48	45	1-ha, >10cm d	1	9 (22)
DRYFLOR	Latin America and Caribbean dry forests	B,D,F,H,M,R,T,V	2013	2012	2007	39	8	0.5-ha, >5cm d	0.3	7 (8)
ATDN	Amazonia: tropical forests	F,V	2014	2003	1974	413	N/A	1-ha, >10cm d	1	N/A
PPBio	Brazil: forests and savanna	B,D,F,H,M,T,V	2015	2004	2000	277	205	1-ha, >10cm d[3]	0.9	7 (17)
BIOTA	Brazil: São Paulo state, Atlantic forests	B,D,F,H,M,P,R,T,V	2016	2005	2005	20	18	1-ha, >10cm d	0.9	11 (14)

FATE	Brazil: Amazon fire-impacted	B,D,H,M,R,S,T	2016	2014	2009	57	38	0.25-ha, >10cm d[3]	0.3	4 (10)
RAS	Brazil: Para state	B,D,F,H,M,P,R,T,U,V	2016	2009	1999	256	59	0.25-ha, >10cm d[3]	0.26	6 (20)
MonANPeru	Peru	B,D,F,H,M,R,U,V	2017	2017	1974	128	103	1-ha, >10cm d	1	15 (43)
Nordeste	Brazil: Caatinga biome	B,D,F,H,M,R,T	2017	2017	2017	33	3	0.5-ha, >10cm d	0.5	3
SEOSAW	Southern Africa woodlands	B,D,F,H,M,R,S,T,U,V	2018	2018	2006	113	98	1-ha, >5cm d	0.5	9 (15)
Red BST-Col	Colombia: dry forests	B,D,F,H,M,R,U,V	2018	2014	2014	11	1	1-ha, >2.5cm d	1	3 (3)
CAO	Peru Amazon-Andes	B,F,S,T,V	2019	2009	2009	276	N/A	0.28-ha, >5cm d	0.28	N/A
RedSPP	Argentina: subtropical	B,D,F,H,M,R,V	2019	2019	1992	16	7	1-ha, >10cm d	1.4	10 (25)
RBA	South America: Andean forests	B,D,F,H,M,R,V	2020	2012	1992	46	34	1-ha, >10cm d	1	11 (25)
sANDES	South America: Andean forests	B,F,V	2020	2019	2003	191	N/A	0.1-ha, >2.5cm d	0.4	N/A
AfriMont	Africa: tropical montane forests	B,H,M,U,V	2020	2020	1939	105	N/A	1-ha, >10cm d	0.6	10 (69)
RedGentry	South America: Amazon forests	F,V	2020	2020	1983	350	N/A	0.1-ha, >2.5cm d	0.2	N/A

Footnotes

1 Full Network Names:

Red Amazónica de Inventarios Forestales (RAINFOR)
Dinámica y crecimiento del Bosque Tropical Venezolano (DBTV)
Tropical Biomes in Transition (TROBIT)
African Tropical Rainforest Observation Network (AfriTRON)
Andes Biodiversity and Ecosystem Research Group (ABERG)
Tropical Forests in the Changing Earth System (T-FORCES)
Red Colombiana de Monitoreo de los Bosques (COL-TREE)
Global Ecosystems Monitoring (GEM)
Programa Ecológico de Longa Duração (PELD-TRAN)
Amazon Tree Diversity Network (ATDN)
Programa de Pesquisa em Biodiversidade (PPBio)

Programa de Pesquisas em Caracterização, Conservação e Uso Sustentável da Biodiversidade (BIOTA)
Fire-Associated Transient Emissions (FATE)
Rede Amazônia Sustentável (RAS)
Monitoreo de las Areas Naturales Protegidos del Peru (MonANPeru)
Projeto Nordeste (Nordeste)
A Socio-Ecological Observatory for Southern African Woodlands (SEOSAW)
Red de Investigación y Monitoreo del Bosque Seco Tropical en Colombia (Red BST-Col)
Carnegie Airborne Observatory (CAO)
Red Subtropical de Parcelas Permanentes (RedSPP)
Red de Bosques Andinos (RBA)
Tree Diversity, Composition and Carbon in Andean Montane Forests (sANDES)
African tropical Montane forest network (AfriMont)
Red de parcelas Gentry (RedGentry)

2 Purpose: **B**iomass; **D**ynamics (mortality, recruitment, growth); **F**loristic composition; **H**uman-impacts (fire, logging, fragmentation); **M**onitoring carbon storage, sink, change; **P**roductivity and carbon-cycle; **R**ecovery and restoration, Remote-**S**ensing calibration/validation; **T**raits; Sustainable **U**se; Di**V**ersity

3 = with nested sub-plots for smaller stems

Taking the Pulse of Earth’s Tropical Forests using Networks of Highly Distributed Plots

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