Article:

Malhi, Y, Girardin, C, Metcalfe, DB et al. (18 more authors) (2021) The Global Ecosystems Monitoring network: Monitoring ecosystem productivity and carbon cycling across the tropics. Biological Conservation, 253. 108889. p. 108889. ISSN 0006-3207

https://doi.org/10.1016/j.biocon.2020.108889

The Global Ecosystems Monitoring network: monitoring ecosystem productivity and carbon cycling across the tropics

Yadvinder Malhi[1], Cécile Girardin[1], Dan Metcalfe[2], Chris Doughty[3], Luiz E.O. Aragão[4,5], Sami Rifai[6], Imma Oliveras[1], Alexander Shenkin[1], Jesus Aguirre-Gutiérrez[1,7], Cecilia Dahlsjö[1], Terhi Riutta[1], Erika Berenguer[1],[8], Sam Moore[1], Walter Huaraca Huasco[1], Norma Salinas[9], Antonio Carlos Lola da Costa[10], Lisa Patrick Bentley[11], Stephen Adu-Bredu[12], Toby R. Marthews[13], Patrick Meir[14,15], Oliver Phillips[16]

[1]Environmental Change Institute, School of Geography and the Environment, University of Oxford, OX1 3QY, UK
[2]Department of Physical Geography and Ecosystem Science, Lund University, SE 223 62, Lund, Sweden.
[3]School of Informatics, Computing and Cyber systems, Northern Arizona University, Flagstaff, Arizona, USA
[4]Divisão de Sensoriamento Remoto - DIDSR, Instituto Nacional de Pesquisas Espaciais, São Jose dos Campos, São Paulo, Brazil
[5]College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4RJ, United Kingdom
[6]ARC Centre of Excellence for Climate Extremes, University of New South Wales, Sydney, NSW 2052, Australia
[7]Biodiversity Dynamics, Naturalis Biodiversity Center, Leiden, The Netherlands
[8]Lancaster Environment Centre, University of Lancaster, UK
[9]Pontificial Catholic University of Peru, Lima, Peru
[10]Museu Paraense Emilio Goeldi, Belém, Pará, Brazil.
[11]Department of Biology, Sonoma State University, Rohnert Park, California, USA
[12]CSIR-Forestry Research Institute of Ghana, Kumasi, Ghana
[13]UK Centre for Ecology and Hydrology, Wallingford, Oxfordshire, UK
[14]Research School of Biology, Australian National University, Canberra, Australia
[15]School of Geosciences, University of Edinburgh, UK
[16]School of Geography, University of Leeds, UK

The Global Ecosystems Monitoring network: monitoring ecosystem productivity and carbon cycling across the tropics

Abstract

A rich understanding of the productivity, carbon and nutrient cycling of terrestrial ecosystems is essential in the context of understanding, modelling and managing the future response of the biosphere to global change. This need is particularly acute in tropical ecosystems, home to over 60% of global terrestrial productivity, over half of planetary biodiversity, and hotspots of anthropogenic pressure. In recent years there has been a surge of activity in collecting data on the carbon cycle, productivity, and plant functional traits of tropical ecosystems, most intensively through the Global Ecosystems Monitoring network (GEM). The GEM approach provides valuable insights by linking field-based ecosystem ecology with the needs of Earth system science. In this paper, we review and synthesize the context, history and recent scientific output from the GEM network. Key insights have emerged on the spatial and temporal variability of ecosystem productivity and on the role of temperature and drought stress on ecosystem function and resilience. New work across the network is now linking carbon cycling to nutrient cycling and plant functional traits, and subsequently to airborne remote sensing. We discuss some of the novel emerging patterns and practical and methodological challenges of this approach, and examine current and possible future directions, both within this network and as lessons for a more general terrestrial ecosystem observation scheme.

1. Introduction

The Global Ecosystems Monitoring (GEM) network is a network of sites where the productivity and carbon cycling of terrestrial ecosystems is tracked through a standard protocol, and frequently integrated with data on plant functional traits and broader environmental variables, such as tree species community composition, soil and climate. From its origins in 2005 focused on Amazonian and Andean forests, since 2010 it has expanded to cover all tropical continents, and to also cover a range of tropical savanna sites and some temperate forests.. To date (April 2020) there are at least 81 peer-reviewed publications resulting from this network, focussed on scales ranging from individual sites to regional and global syntheses. As of late 2020, the network spans 294 plots covering 178 hectares (Figure 1, Table S2). GEM has a detailed online manual (Marthews et al. 2014), as well as methods detailed in many papers. In this paper, we provide the context and history of the GEM network, its philosophy, its advantages and key contributions, experiences learned from both practical implementation and peer review comments, and lessons for future network development.

Specifically, we:
(i) describe the broader scientific context of tropical carbon cycle science and the motivation for establishing such a network;
(iii) describe the overall philosophy and features of the methodology and its key aspects;
(ii) describe the development of this network within the historical context of measurements of productivity and carbon cycling in the tropics;

(iv) summarise data analysis and processing protocols for the core GEM methodology, and discuss some key limitations and challenges;
(v) synthesise and highlight key discoveries thus far and present new areas for development;
(vi) discuss lessons learnt from the development and implementation of this network.

2. Background and History

2.1 Context

Attempts to describe the full carbon and energy budgets of ecosystems have been a feature of ecosystem ecology since the 1960s. Much effort has focused on northern temperate and boreal systems, which tended to have more convenient access for better-funded institutions. The first attempts to describe the carbon cycle of a tropical forest was conducted in Puerto Rico by Odum and Pigeon (1970) and in Thailand by Kira (1967). International programmes in the 1970s fuelled attempts at similar descriptions of ecosystems around the world, including a tropical forest site in Malaysia (Kira 1978). In parallel, the first attempts emerged to quantify the primary productivity of the biosphere, by scaling up from site-based estimates in a range of biomes {Lieth, 1975 #635}. These early attempts were constrained by limited tools for measuring carbon dioxide gas exchange (*e.g.*, absorbing chemicals were used at the time, rather than portable infrared gas analysers). Such activities fell into a lull in the late 1970s and early 1980s, but resurfaced in the 1990s with increased scientific interest in the global carbon cycle and its links with climate change, specifically to pinpoint the role of the terrestrial biosphere as either a source or a sink of carbon. This renewed interest was coupled with the development of micrometeorological tools and techniques, such as eddy covariance, to measure the net flux of carbon dioxide above vegetation canopies. At the same time, global biosphere models were advancing substantially, and there was increased demand for empirical ecosystem-level quantification of key aspects and processes of the biosphere carbon cycle to develop and test these models. Comprehensive measurements of the components of the carbon budgets provided a source of validation for models and micrometeorological studies, but also enabled a deeper process-level understanding of how different components of the system contributed to the magnitude and variability of the carbon budget.

Ecosystem flux measurements in the tropics tended to lag behind better-funded studies in North America and Europe. The first eddy covariance studies in the tropics were in Brazilian Amazonia in the late 1980s and early 1990s (Fan et al. 1990, Grace et al. 1995, Malhi et al. 1998) , from where they substantially expanded through the LBA (Large Scale Biosphere-Atmosphere study in Amazonia) programme. However, eddy covariance approaches remained limited in coverage in the tropics because of the specialised equipment required, and, on their own, only described the net exchange of carbon, water and energy between ecosystems and the atmosphere. Their large footprint (100s-1000s m^2), while an advantage in some aspects, also limit their utility in fragmented and patchy landscapes, or in sites with extreme topography.

In parallel with the spread of eddy covariance studies across the tropics, there was a renewed interest in calculating the Gross Primary Productivity (GPP) and

Net Primary Productivity (NPP) of tropical forests in the early 2000s. GPP is the total uptake of carbon by an ecosystem through photosynthesis, while NPP is the total rate of production of biomass (including leaves, reproductive organs, woody tissue, roots, and exudates and volatile compounds). The difference between GPP and NPP is accounted for by the metabolism (autotrophic respiration) of the plants themselves. Studies of NPP (or of its components such as litterfall and woody growth) in the tropics began in the 1960s and 1970s. Clark et al. synthesised both the limited available data at the start of this century, and the challenges in quantifying the NPP of tropical forests (Clark et al. 2001a, Clark et al. 2001b), and Chambers et al. (2004) presented a full NPP and respiration quantification of the carbon budget of a tropical forest plot near Manaus in Brazilian Amazonia. Similar site-based descriptions began to emerge in sites in tropical Asia. At the same time, broad networks of forest inventory plots were emerging, in particular the CTFS-ForestGEO network established repeatedly-censused plots, typically 50 ha (Anderson-Teixeira et al. 2015, Davies et al, this volume), and the RAINFOR forest inventory plot network (Malhi et al. 2002, Peacock et al. 2007) focused on 1-ha tree census plots across Amazonia, which later spawned the Forest Plots meta-network (Phillips et al. this volume). These networks built on a long tradition and expertise in assessment of tropical forest structure and biomass, and taxonomic expertise, and, by integrating these plots across regions and countries, provided new insights into spatial variability of forest structure, tree communities and dynamics, as well as revealing evidence for changes in biomass and in carbon dynamics and net biomass carbon balance over time (Lewis et al. 2009, Phillips et al. 2009, Hubau et al. 2020).

2.2. Motivation for development of the GEM network

A key objective of the GEM network has been to provide an interface between tropical forest ecology and Earth System science (ESS) (Malhi 2012). ESS is a scientific discipline that emerged in the 1970s that aims to provide an integrated systems view of planetary function, and quantifying and understanding the role of the biosphere is clearly pivotal in such understanding. Much of the early scientific revolution was driven by new observational tools (*e.g.* Galileo's use of one of the first telescopes, leading to the Copernican revolution, and Hooke's use of one of the first microscopes, leading to the cell theory of biology, among other things). Similarly, ESS has been driven by the development of two "macroscopes" in the late twentieth century: complex process-based models, enabled by advances in computing capacity, that can represent and integrate the processes of biosphere, atmosphere and hydrosphere; and satellite-based remote sensing, enabling mapping and monitoring of Earth processes at a comprehensive global scale.

Another key tool in biosphere-focussed ESS has been the development of field observation networks. The macroscopes need testing and ground-truthing against field observations that are embedded in a rich understanding of local ecosystem processes dynamics. Some networks such as the FLUXNET network of eddy covariance flux towers have tended to be focused on resource-rich regions such as North America, Europe, East Asia and Australia. Others, such as the Forest Plots and CTFS/ForestGEO networks mentioned above have developed impressive coverage of the old-growth tropical rainforest zones, while others (2ndFor and the Tropical Managed Forests Observatory) have focused on secondary and logged forests (Sist et al. 2015, Poorter et al. 2016). These networks have focused on forest inventories and yielded important insights into forest properties such as the net tropical forest carbon sink, continental variation in biodiversity and biomass dynamics, and rates of recovery from disturbance. However, integrating these results with the ESS macroscopes of modelling and remote sensing presents some challenges. Optical remote sensing focuses on canopy surface reflectance and fluorescence, often to infer fraction of absorbed photosynthetic radiation and hence GPP. Radar- or lidar-based remote sensing provides insights into structure and biomass, but does not directly capture the processes that generate that structure. Modelling of the carbon cycle has required representation of processes such as allocation, autotrophic respiration and soil carbon dynamics, aspects that are not immediately deducible from forest inventories alone. *GEM seeks to provide a bridge between the forest inventory networks and Earth system macroscopes*: it emerged out of the RAINFOR Amazonian forest plots network, but by focusing on a more holistic view of carbon cycling, it seeks to speak the "language" of biosphere carbon cycling models. Similarly, the recent focus on canopy functional traits under GEM-TRAITS (see below) seeks to act as a bridge between environment, tree community composition, ecosystem carbon cycling and remote sensing.

2.3 Network Development

The GEM network emerged gradually from the RAINFOR network, starting in 2005 with the introduction of detailed carbon budget studies at two relatively fertile RAINFOR plots in Tambopata, Peru, compared with two relatively infertile plots in Caxiuanã, Brazil. The impetus for this study was the discovery that the woody productivity of forests in western Amazonia appeared to be generally greater than that of eastern Amazonia (Malhi et al. 2004), a feature that appeared related to soil properties (Quesada et al. 2012). It was unclear whether this difference in woody growth rates reflected a difference in GPP (i.e. forests in lowland Peru were intrinsically more productive, perhaps because the leaves had higher nutrient concentrations), or whether there were differences in the allocation of captured carbon (*e.g.* a larger fraction of NPP goes to wood, or there is lower expenditure in autotrophic respiration). The results from this study were presented by Aragão et al. (2009) and Malhi et al. (2015), showing that the difference was mainly driven by lower autotrophic respiration in the Peruvian sites, with smaller influences from differences in allocation to wood and in overall GPP. This work highlighted the importance of understudied components of the carbon cycle, such as Carbon Use Efficiency (the ratio of NPP to GPP), or fractional allocation of NPP to canopy, wood and root tissue.

In parallel, the LBA (Large-Scale Biosphere-Atmosphere Programme in Amazonia) was collecting detailed carbon cycle measurements at a number of locations in Brazilian Amazonia, but the work was dispersed across multiple research organisations. Malhi et al. (2009) presented a compilation of data for three forest sites in Brazilian Amazonia, including Caxiuanã, gathered through LBA that helped provide an overall framework for providing a holistic carbon cycle description of forest ecosystems. This showed both the potential for detailed carbon cycle descriptions, how they cross-checked well with eddy covariance measurements, and the relatively small magnitude (in carbon budget terms) of some harder-to measure terms such as lateral dissolved inorganic carbon flows and methane and volatile organic carbon emissions. In addition, Metcalfe et al. (2010)presented a detailed carbon budget analysis for the drought and control forest plots in Caxiuanã, showing that long-term drought resulting in increased autotrophic respiration and hence a reduced proportion of GPP being allocated to biomass production.

In 2007, similar plots to those in Tambopata and Caxiuanã were established at multiple sites along a ~3500 m elevation gradient in south-eastern Peru (Girardin et al. 2010, Malhi et al. 2010), stretching upwards from the lowland rainforest site at Tambopata. The elevation transect had already been established by the Andes Biodiversity and Ecosystems Research Group (ABERG) in the early 2000s (Malhi et al. 2017) and has since become a major focus of interdisciplinary research into how elevation and temperature control ecosystem composition and function, and how these are changing under global warming.

A large boost to the nascent GEM network came with funding from the Gordon and Betty Moore Foundation over 2008-2014, which enabled establishment and monitoring of 16 plots across Amazonia and the Andes (Malhi et al. 2015, Malhi et al. 2017). This period of funding also enabled formalisation of this network, including development of a detailed protocol available online, training courses in South America, a website http://gem.tropicalforests.ox.ac.uk/ and the establishment and use of the name GEM. A key output from this period was the publication of eight site-based papers describing the carbon budget of each site in South America, in a special issue of *Plant Ecology and Diversity* in 2014 (Araujo-Murakami et al. 2014, da Costa et al. 2014, del Aguila-Pasquel et al. 2014, Doughty et al. 2014b, Galbraith et al. 2014, Girardin et al. 2014, Huasco et al. 2014, Malhi et al. 2014, Rocha et al. 2014). Many of these papers were led by local students and researchers, and provided a model for building local capacity in analysis and paper writing. For the first time, a library of detailed carbon cycle assessments was being assembled, each addressing locale-specific questions, but ultimately contribute to broader, biome-wide analyses (Doughty et al. 2015b, Malhi et al. 2015, Malhi et al. 2017).

The success of this model for an intensive carbon cycle plots network in South America led to similar project development in SE Asia and in Africa. A series of plots were established in Malaysian Borneo; first with two plots at Lambir, Sarawak in 2007 as part of a PhD project (Kho et al. 2013), then 7 plots were established in Sabah in 2010-11 in old-growth and logged forest under the auspices of the SAFE (Stability of Altered Forest Ecosystems) programme (Ewers et al. 2011, Riutta et al. 2018). In Africa, a NERC research grant enabled establishment in 2011 of 14 plots along a wet-dry gradient in Ghana and 6 plots in Gabon, providing the first measured NPP values for African lowland forests (Moore et al. 2018).

In addition to this pantropical coverage in old-growth systems, other trends in recent years have been increased coverage of human-modified forests (e.g. logged forests, burned forests and tree crops), and the beginnings of coverage in savanna and grassy ecosystems (Figure 1). For example, recent plots have been established in natural forest-cocoa agroforest gradients in Ghana (Morel et al. 2019), in natural forest-coffee agroforest gradients in Ethiopia (Morel et al, unpublished), in savannas in Brazil (Peixoto et al. 2017), Gabon and South Africa, and along gradient of human-disturbance in Brazilian Amazonia, including selectively-logged forests, burned forests, and secondary forests (Berenguer et al. 2018). A number of GEM sites also span control and treatment plots in experimental treatments, including the 20-year old drought experiment in the Caxiuana, Brazil (Rowland et al. 2015), the fire experiment in Tanguro, Brazil (Brando et al. 2016) and the Free Air Carbon Dioxide Enrichment experiment in Australia {Jiang, 2020 #637}.

Separate from the GEM network, there has been a surge of detailed NPP (and, to a lesser extent, GPP) measurements in tropical forests, particularly in SE Asia and in China and more recently in Central Africa (Rwanda and the Congos). Anderson-Teixeira et al. (2016) provide a summary of these data across the tropics, incorporated in the Global Forest Carbon (ForC) database (https://forc-db.github.io). In recent years GEM has also sought to be a convening hub for this wider tropical network of carbon cycling and productivity data, bringing in self-funded partners who wish to standardise data collection protocols, take advantage of the data management within the GEM network, and contribute to regional or global analyses.

Although the focus of core GEM activities has been predominantly tropical, there have been occasional forays into temperate forests while employing the same protocol. Fenn et al. (2015) applied this protocol in Wytham Woods, a long-established maritime broadleaf woodland near Oxford, UK. Urrutia-Jalabert et al. (2015) reported on the productivity and carbon dynamics of *Fitzroya*-dominated temperate rainforests in Chile ("the oldest, slowest rainforests on Earth") and more recently similar plots have been established in Ponderosa pine forests in Arizona (Doughty et al. 2020) and *Populus tremuloides* stands in Colorado (B. Blonder, *pers. comm.*).

In terms of climate space, the GEM network now covers substantial elevation gradients in the tropics, as well as spanning the lowlands of these regions (Figure 2a). Water stress gradients are also spanned, ranging from dry savannas in Ghana and South Africa, through mesic savannas, seasonally dry forests and aseasonal rainforests (Figure 2c). The coverage of some seasonal temperate sites provides some useful contrasts with high elevation tropical sites (Figure 2c), enabling exploration of the role of seasonality in shaping ecosystem carbon cycling and function. A selection of GEM sites are shown in Figure 3.

3. Features of the GEM Network

The core framework which defines the GEM network is the estimation of the key components of ecosystem productivity, through routine measurements at relatively high frequency (biweekly/monthly/trimonthly, depending on site and measurement type). A minimum requirement would be measurement of the main components of NPP (canopy litterfall, woody growth and fine root productivity). Many GEM sites also cover the main components of ecosystem respiration (woody stem respiration, leaf respiration and soil respiration partitioning into heterotrophic and autotrophic components), which enable estimations of total autotrophic respiration. The summation of autotrophic respiration and NPP gives an estimation of GPP (on annual or longer timescales, when the balance between photosynthesis and vegetation use of photosynthate can be assumed to be close to equilibrium).

An important attribute of the GEM protocol is the standardisation of sampling protocols. There is potential of much variation in protocols, and this standardisation facilitates comparisons across regions and ecosystems. Soils collected by the central GEM project are collected using the RAINFOR soil sampling protocol (Quesada et al. 2011). Such samples have largely been analysed in the cross-referenced soil laboratories of INPA in Manaus, Brazil (for most sites in Amazonia) or at the University of Leeds, UK (for most other sites).

An additional key feature of the GEM protocol is its emphasis on relatively low technology and low-cost approaches. Conversely, it is fairly heavy in human labour inputs, typically requiring field teams to spend a week every month at a cluster of field plots, and longer periods every three months. These features (low capital inputs and high labour inputs) have made it well-suited to many developing region contexts. This has facilitated its spread across multiple sites in low- and middle-income countries, where students and technicians are often available to conduct research but capital and equipment resources are low. Its application has been more challenged in high-income countries, where labour costs are higher (including tropical countries such as northern Australia). As a result, the GEM network has expanded well across the tropics, to the extent that there are currently more site-level NPP data available from tropical regions than from temperate regions. This is a remarkable reversal of the normal pattern of ecological data availability, where the tropics tend to have the strongest data deficits.

3.1 Plot location and size

Because of the requirement of frequent visits, ideal GEM plot locations are within easy reach (1-2 hours) of field stations or research institutes, which limits establishment in more remote and inaccessible settings. The standard GEM forest plot site is a 1 hectare square (100 x 100 m), which reflects its origins out of the RAINFOR forest plot network. One hectare is considered an adequate size to sample a range of trees (typically 500-800 trees > 10 cm dbh) and not be overly influenced by individual tree gap dynamics, while also being a tractable area to sample at high frequency. It is also a size that is useful for many current remote sensing technologies. In some low tree diversity sites, such as some savannas and a Pacific atoll, a “mini-GEM” plot size of 40 m x 40 m or 50 m x 50 m has been employed, and smaller plots are still welcomed in the network as providing useful information. Moreover, in the context of human-modified forests such as agroforests or burned/logged forest patches, the heterogeneous nature of the modified forest landscape can also favours a smaller plot size.

3.2 GEM field methodologies

An overview of the GEM sampling methodologies (Figure 4) is given in Table S1, and GEM methodologies are described in further detail in the GEM Manual (Marthews et al. 2014). Below we summarise some of the key features, challenges and limitations of these approaches.

A carbon (C) budgeting approach can be adopted to characterise the carbon cycle of an ecosystem from field data if it is possible to measure all C stocks and flows. Flows must be divided into flows into and out of the ecosystem (e.g. C fixation through photosynthesis vs, autotrophic respiration) and transfers between pools (e.g. litter fall, root decomposition). Hence summation of the components of NPP and the components of autotrophic respiration gives an estimate of GPP. Similarly, the difference between NPP and heterotrophic respiration gives an estimate of changes in net carbon balance.

3.2.1 Components of Net Primary Productivity

Woody production is calculated from forest censuses on an annual or multiannual scale, and from dendrometer bands at a seasonal scale. Growth rates are converted into woody biomass production rates using standardised tropical forest biomass allometries, adjusted to local regions (Chave et al. 2014).

Branch turnover is an additional component of woody production that attempts to capture the turnover of large branch material not associated with tree death. The assumption is that fallen branch material is compensated for by new branch growth.

Litterfall captures canopy productivity, and is collected through an array of litter traps that are sampled biweekly. In many sites, the material is separated into leaves, twigs and reproductive components. At some sites, *leaf herbivory* is estimated by scanning a subset of fallen litter and calculating what fraction of leaf area has been lost to herbivory (Metcalfe et al. 2014).

Many GEM sites derive seasonal canopy productivity by estimating *canopy leaf area index* on monthly timescales using hemispherical photos, coupled with measurements of Specific Leaf Area (leaf area per unit mass). This enables estimation of monthly changes in canopy leaf biomass stock. The leaf litterfall gives leaf outflow from the canopy, and the summation of the two provides an estimate of monthly leaf productivity.

Fine root productivity is a frequently neglected component of NPP measurements. It is a challenge to measure accurately, as any soil-based measurement involves disturbance of the study system. GEM adopts two approaches. Firstly, root-free ingrowth cores are installed and sampled after three months, to give a volume-based estimate of fine root productivity. In addition, at many sites screen rhizotrons are deployed that enable manual tracing of root growth at monthly timescales. They enable greater temporal resolution and also vertical profiles of root productivity. Where the two approaches have been compared, there has been good agreement in lowland tropical sites but some divergence in montane sites with rich organic soils very vulnerable to disturbance (Girardin et al. 2013)(Girardin, Aragao et al. 2013, Huaraca et al in prep).

Below-ground coarse root productivity is not directly measured (it is almost impossible to do so) but is estimated by multiplying above-ground woody productivity using biome-specific allometric relationships for biomass (Jackson et al. 1996).

At sites with a substantial and productive herbaceous layer (for example, savannas), *above-ground herbaceous productivity* (Oliveras et al. 2014, Moore et al. 2018) is estimated through seasonal biomass harvest of sample quadrats (protected from grazing where necessary). Below-ground herbaceous productivity is already incorporated into the fine root productivity estimates, which do not distinguish between trees and herbaceous plants.

3.2.2 Components of Ecosystem Respiration

The more complete GEM sites also measure the main components of ecosystem respiration. Summation of NPP and the autotrophic component of respiration enable the estimation of GPP, and the difference between above-ground NPP and total soil CO_2 efflux provides an estimate of net carbon balance.

Total soil CO_2 efflux is measured at monthly frequency in a grid across the plot, at fixed collar locations. Many GEM sites attempt to partition this efflux into components (litter layer, soil organic matter and fine roots) by installing a separate partitioning experiment (Metcalfe et al. 2018). Furthermore, at some sites a fine mesh treatment is employed, which enables passage of fungal hyphae but acts as a barrier to fine roots. This enables an estimation of the respiration associated with mycorrhizal fungi – as this respiration is derived from recent photosynthate transferred directly via plant roots, it can be considered an additional component of NPP.

Above ground, *woody tissue respiration* is measured at monthly frequency by installing similar collars on a subset of tree stems, scaling to the whole tree using tree surface area allometries, and then scaling to the full plot tree census.

Canopy foliar dark respiration is not measured regularly, but estimated in canopy sampling campaigns (either seasonally or in a one-off campaign associated with leaf traits collection, see below) by applying gas exchange measurements to leaves on cut branches. Frequently, *leaf photosynthetic parameters* are also measured in the same campaigns (photosynthesis under high light and/or high carbon dioxide), which can be employed in a canopy modelling framework to provide an independent estimate of GPP.

Respiration from dead wood is a term that is measured at a few GEM plots by attaching collars to dead trunks or placing small dead wood material in closed chambers. It can be a significant component of ecosystem heterotrophic respiration(Gurdak et al. 2014), especially so in logged forests.

3.2.3 Missing terms

There are a number of components of NPP that are challenging to quantify and are non-standard in NPP or carbon cycle assessments. These include, in likely declining order of importance: production of root exudates and transfer of photosynthate to mycorrhizae (although at some sites GEM estimates these through the soil respiration partitioning experiment, as described above), canopy productivity by epiphytes that senesce and decay *in situ* in the canopy, productivity of the herbaceous understory (not routinely measured in forest plots), release of volatile organic compounds such as isoprene or monoterpenes, methane fluxes from the soil, and lateral export of material as particulate or dissolved organic carbon. One cross check of whether these extra terms are significant is through constructing more complete carbon budgets where rich data streams enable this and cross-comparisons with independent eddy-covariance estimates of GPP (see below). Malhi et al. (2009) took advantage of the comprehensive range of research conducted in Brazilian Amazonia under the auspices of the LBA programme to quantify many of these terms for three old-growth *terra firme* Amazonian forests. VOC, methane and lateral carbon effluxes were found to be small in relation to the main carbon flux components above.

3.2.4 Functional traits collection

A key challenge in ecosystem ecology is linking biodiversity to ecosystem function and productivity. Over 2013-2018, an ERC Advanced Investigator Grant (GEM-TRAITS) enabled the further monitoring and databasing of the data emerging from the global network, and also a new focus on collecting tree functional traits across the network, with the aim to link community composition to ecosystem function.

Use of a plant functional traits framework has provided rich ground for theoretical and empirical analyses, particularly in high biodiversity tropical ecosystems where use of a few key functional traits is more tractable than engaging with thousands of plant species. To address this challenge, the GEM-TRAITS programme has been collecting leaf and wood functional traits for dominant canopy species in GEM sites across the tropics. The collection protocol is stratified according to basal area dominance, with tree species that contribute most of plot basal area (a proxy for canopy area) being prioritised. A goal of sampling the fewest species that contribute to 80% of the basal area is the target, although this is not always achieved in diverse lowland rainforest sites. Traits collected include leaf morphological, chemical and photosynthetic traits, and in some cases wood and leaf hydraulic traits. As with many features of GEM, the traits programme and methodology were initially developed along the Amazon-Andes transect in Peru, before being deployed across all tropical continents. These traits data have a variety of applications, including understanding the link between leaf and wood traits and ecosystem dynamics, parametrizing canopy parameters in biosphere models, and linking canopy traits to remote sensing data.

4 Challenges for the GEM approach

4.1 Uncertainty and Error Propagation

A key feature of the GEM approach is that it measures/estimates and then sums multiple components of the ecosystem carbon cycle. For example, an estimate of NPP involves at least four independent measurements (canopy litterfall, branch turnover, woody growth and fine root growth), an estimate of autotrophic respiration involves three independent measurements (canopy respiration, woody tissue respiration and autotrophic soil respiration). Estimation of GPP involves summing these two and hence requires at least seven independent measurements.

Each of these independent measurements carries uncertainties, either in random uncertainty sampling limitations, or systematic uncertainty arising from poorly understood biases or uncertainties in scaling. Examples of such systematic errors include uncertainties in local tree biomass or surface area allometries.

Each of these uncertainties can be accounted for by rigorous error propagation during summation. Random sampling errors can be estimated from the variance of observations (Metcalfe et al. 2008), but systematic errors are assigned (usually conservatively) from expert judgement.

Given the inherent uncertainty in each type of measurement, one remarkable feature is that overall uncertainty in estimated NPP or GPP can be fairly constrained, typically around ±10% (Malhi et al. 2016, 2017). This under-appreciated feature comes from the nature of error propagation: as each component measurement is independent, uncertainties propagate in quadrature, and hence relatively slowly compared to the summation. Hence, the biometric GEM approach can compare favourably against, for example, an eddy covariance approach to estimating GPP. The latter relies essentially only on one variable being measured (net carbon flux), and hence is more vulnerable to any systematic biases associated with that single measurement type.

4.2 Cross-checks with eddy covariance measurements

One useful cross-check for the GEM approach has been cross-checks with the independent "top-down" eddy-covariance approaches to estimate GPP. Eddy covariance is a tower-based approach that continuously measures the net turbulent exchange of carbon dioxide between the vegetation canopy and the atmosphere. Once suitable corrections are applied for estimating daytime ecosystem respiration (based on night-time ecosystem respiration rates), the total ecosystem photosynthesis (GPP) can be estimated. Eddy covariance comes with its own challenges, particularly under low turbulence night-time conditions. Nevertheless, good agreement between eddy covariance and GEM approaches provides some reassurance that no major carbon cycle components are being missed, and that measurement and scaling uncertainties are well-constrained.

At three sites in Brazilian Amazonia (Malhi et al. 2009), agreement between the two approaches has been good. Campioli et al. (2016) conducted a systematic cross-comparison of eddy covariance and biometric approaches across 18 forest sites (spanning boreal, temperate and the same three Brazilian tropical forests), and found no significant difference in estimation of annual mean GPP and total ecosystem respiration between the two approaches.

4.3 Logistics and management

The creation and management of a global observation network inevitably generates a number of management and logistical challenges. There has been a need to support central coordination, management and data cleaning, in addition to field data collection. The central coordination activities of GEM were supported by a number of funding initiatives, notably from the Gordon and Betty Moore Foundation (2008-2012) over the initial phase of developing a standardised network over the Amazon-Andes, from the European Research Council (2013-2018) that supported development and integration into a global network and the advance of the traits data collection, and from the Natural Environment Research Council (2016-2020) to continue this collection, analysis and databasing in the wake of the 2015/16 El Niño event. Both carbon cycle and traits data are stored in a dedicated GEM database {Shenkin, 2017 #640}, and made freely available to all users, subject to fair use agreements that acknowledge and protect the prior publication rights of data collectors and data providers ([DOI to be inserted in final proof])

One key advantage of GEM is the standardisation of data collection protocols across the global network, though inevitably there are some small local variations in protocols (sometimes inadvertent, sometimes deliberate because of locale-specific challenges or questions). For example, in sites with high elephant abundance such as in Gabon or Sabah, litter traps are frequently deliberately destroyed by elephants and an alternative or additional protocol of marking out discrete quadrants on the ground is employed, even though this risks higher rates of *in situ* decomposition prior to collection because of the activities of litter layer fauna. Small variations in protocols can also lead to substantial additional challenges in incorporation into the database.

4.4 Capacity-strengthening and training

The development of local research capacity is an essential feature of GEM. The basic research model is dependent on autonomous and long-term local collection of data, which requires the training of local students or technicians in both data collection and analysis. This is achieved through workshops and hands-on training *in situ* and online. A number of GEM students have gone on to Masters and PhD qualifications, in many cases using the GEM data they collected in the field. Local students are strongly encouraged and supported to lead scientific papers based on their local site data (e.g. Huasco et al. 2014, Peixoto et al. 2017, Addo-Danso et al. 2018, Ibrahim et al. 2020), though the challenges of writing a paper to international scientific journal standards are not to be underestimated.

A particularly exciting feature of GEM has been South-South training, where experienced field data collectors in one region have the opportunity to travel to other regions to train in plot installation and data collection. As an example, students and data technicians from Cusco, Peru (as the base for the Andes-Amazon transect, the oldest and most advanced of our GEM focal regions) have led training events and plot installation in Brazil, Belize, Chile, Gabon and Malaysia. Similarly, students from Ghana have collected traits data in Gabon, and students from Gabon have helped establish plots in South Africa. Such exchange enables flourishing cross-tropics relationships and collaborations amongst an emerging generation of tropical ecosystem ecologists.

4.5 Long term funding and prioritisation

A key challenge, as with all long-term observation networks, is maintaining long-term funding. In GEM the funding model to date has been dominated by a number of locale-focused grants centered on specific questions (*e.g.* temperature in the Andes, logging in Malaysia, fire in Amazonia), coupled with some large central grants that support network expansion, management and coordination. In some cases, notably in more prosperous tropical countries such as Brazil and Malaysia, this has led to locally sourced funding that enables continuation of measurements for the long-term. In most countries, however, continued data collection is dependent on centralised international funding. As the network has matured, additional partners have been brought into the network, who bring their own funding but would like their data to fit within the wider standardised network and contribute to large-scale analyses.

Dependency on centralised funding leads to a trade-off between supporting long-term time series, vs. expanding coverage of sites. How much information is gained from maintaining a site with monthly data collection for over a decade (e.g. the Tambopata, Peru plots were run over the period 2005-2017 (Malhi et al. 2014)) *vs.* investing in new collection of a few years of data from additional sites that enable better coverage of the heterogeneity of the tropical forest biome? The answer to this depends of course on the question being asked, and on the temporal and spatial variability being observed. Long-term time series have, for example, been immensely valuable in understanding the impacts of the 2015/6 El Niño (Rifai et al. 2018), and, in conjunction with forest inventories, may be the most cost-effective and practical way to collect long-term carbon flux time series and understanding global change impacts on forests. Broadly however, the focus in recent years has been to expand spatial coverage (either through setting up new plots or by bringing on board partners with new data collections), at the expense of long-term continuation of existing sites. However, it typically takes a few months to set up a new cluster of sites, and several months before all data collection protocols are properly underway and producing anything useful. Hence very short-term projects have a poor ratio between set-up phase and productive data output.

5. Key Discoveries

5.1 Variation of productivity and allocation across regions

A key contribution of GEM has been to provide a detailed description of how tropical ecosystem productivity varies across regions, and along environmental gradients, but also to show how woody growth (the most widely applied proxy for forest productivity) can be a poor indicator of overall ecosystem productivity. Malhi et al. (2015) showed how GPP declined along wet-dry rainfall gradients in Amazonia, as increasing dry season intensity limited productivity for part of the year. However, this decline was not as apparent in NPP, because the drier forests invested more in biomass production and less in autotrophic respiration, probably because they were lower biomass and younger tree age ecosystems (Doughty et al. 2015a). Furthermore, the wet-dry trend almost disappeared in woody growth, because drier forests invested disproportionately more in woody growth. Moore et al. (2018) reported a similar pattern along wet-dry gradients in Ghana, West Africa, though here the highest NPP was found in the centre of the gradient, possibly because of soil fertility effects.

Carbon use efficiency (CUE), the ratio of NPP to GPP, is a highly uncertain term in global biosphere modelling, yet has received much less attention than GPP. GEM has greatly increased the number of direct estimates of tropical CUE but found great site-to-site variability across lowland tropical forest sites. For example, CUE in lowland Amazonia averages 0.37 but ranges between ~0.25 and ~0.45 across Amazonian GEM sites. Overall, Amazonian forests have lower CUE in forest stands with slow growing trees and with lower fertility (Doughty et al. 2018a).

In contrast, along a 2800 m elevation gradient in the Andes, Malhi et al. (2017) reported no shifts in allocation or CUE along the gradient. GPP and NPP did decline at high elevations, but the cloud forest vegetation carbon cycle was simply a proportionately scaled-down version of the lowland rainforest one.

Moreover, the decline in productivity with elevation was not linear, but an abrupt change near cloud base (~ 1600 m a.s.l.), suggesting that mean temperature does not determine forest productivity. Oliveras et al. (2014) extended this transect higher beyond the cloud forest and into the *puna* grasslands, and showed no decline in NPP across this transition.

The GEM network has also revealed striking regional differences. Until around 2010, most understanding of tropical forest productivity and carbon cycling has emerged from the Neotropics, and in particular from eastern Amazonia, which was the focus of the LBA programme in Brazil. The wider GEM network has revealed that eastern Amazonia has amongst the lowest net primary productivity observed in the humid lowland tropics, probably because of its highly weathered soils. Higher values of productivity are observed in western Amazonia (Aragão et al. 2009, Malhi et al. 2015) , Borneo (Kho et al. 2013, Riutta et al. 2018) and most remarkably in West Africa (Moore et al. 2018), which has the highest recorded values for mature forests. The reasons for these contrasts is unclear, and are under investigation in an ongoing synthesis study across the network.

In old growth forests, GEM has also highlighted the relative importance of turnover time (mortality rates) in determining forest biomass and vegetation carbon stocks. Spatial gradients in biomass across the tropics are only weakly shaped by gradients in woody productivity, and much more strongly determined by gradients in mortality and turnover time (Galbraith et al. 2013, Malhi et al. 2015, Johnson et al. 2016). This presents a major challenge for terrestrial biosphere models, which have tended to prioritise the modelling of photosynthesis and productivity over the far less well-understood process of tree mortality (Friend et al. 2014).

5.2 Seasonal variation of productivity, allocation and phenology

Understanding the processes that govern seasonal carbon allocation strategies of humid and dry forests help provide a carbon and nutrient budget perspective on phenology. Many GEM sites collect bi-weekly data on fruit and flower fall. Focussing on tropical South American plots, Girardin et al. (2016) provided evidence that suggests solar irradiance may be a cue for flowering events governed by phylogeny. The energetic cost of reproduction was found to be trivial, suggesting that nutrient considerations are the predominant physiological constraint on timing and abundance of flowering and fruiting.
In terms of the overall allocation of NPP, two main seasonal allocation strategies were identified in Amazonian forests: trade-offs between allocation to wood and canopy in dry sites, and trade-offs between allocation to roots and canopy in humid sites (Doughty et al. 2014a, Girardin et al. 2016). When considering the full GPP, NPP and respiration budget, the data suggested that there is a temporal decoupling between total photosynthesis from eddy covariance and total carbon usage (from GEM studies) that indicates that nonstructural carbohydrates could be serving as seasonal stores of energy reserves that have a strong influence on shaping patterns of seasonality and interannual variability (Doughty et al. 2015a, Doughty et al. 2015b).

5.3 Logging, disturbance and the ecosystem carbon cycle

A whole-carbon-cycle approach has also yielded new insights into how logging and other forms of disturbance affect productivity and woody growth. It has long been known that logging and other forms of stand thinning tend to stimulate woody growth, but it has been unclear if this is due to an increase in overall GPP, a decrease in autotrophic respiration, or a shift in allocation of NPP to woody growth. Riutta et al. (2018) studied a logging gradient in Sabah, Malaysia, ranging from old growth to intensively logged forests. They showed that overall there was no increase in NPP between heavily logged and unlogged forest plots, but further examination showed strong increase in NPP in remaining patches of forest in the logged plots, offset by very low productivity in heavily degraded subplots, such as old logging platforms. The overall increase in woody growth was partially caused by a stimulation of NPP, and partially by increased allocation of NPP to woody growth, as a result of increased competition for light in the logged stands. Remarkably, the stimulation of growth did not result in net carbon accumulation in the logged forests, because of the ongoing release of carbon from dead wood and soil organic matter. Hence, logged forests can be net carbon sources to the atmosphere many decades after logging, a feature not visible if only tree biomass inventories are considered.

5.4 Response of carbon cycle to droughts

The rate of rise of atmospheric CO_2 shows strong interannual variability, and it is known that this variability is largely determined by the variability of the net carbon balance of the tropical terrestrial biosphere (Malhi et al. 2018b). Monitoring in the GEM network has now spanned a number of major drought events in the tropics, most notably the 2010 drought in Amazonia (Doughty et al. 2015a, Doughty et al. 2015b) and the 2015/16 El Niño, which was the strongest such event in decades. Moreover, these drought events sit on top of a long-term anthropogenic warming trend (Rifai et al. 2019), which means that every major drought event occurs under conditions of increasing peak temperature and atmospheric water stress.

Doughty et al. (2015a) examined impacts of the 2010 drought in 13 GEM sites across Amazonia. They found that, as expected, the drought caused a reduction in GPP but that, remarkably, there was no corresponding reduction in NPP and or woody growth; instead, there was a decline in autotrophic respiration. The study proposed that this indicated a decreased investment in plant maintenance and defence in favour of continued biomass growth, but that such a strategy may contribute to increased mortality in the years following drought. A worldwide analysis of GEM plots in the 2015/16 El Niño shows a similar pattern of little shift in NPP, but offers an additional insight in showing a strong pulse of increased soil respiration, suggesting that the interannual variability of the tropical forest carbon cycle is driven mainly by soil processes rather than plant processes (Malhi et al., unpublished analysis). Coupling traits data with the longer term forest inventories also enables an improved description of potential shifts in ecosystem function traits over time, as has been demonstrated by the Ghana rainfall gradient study (Aguirre-Gutierrez et al. 2019).

5.5 Linking canopy traits to ecosystem productivity and resilience through theory and models

A key goal of the traits-based research in GEM has been to link canopy functional traits to ecosystem productivity and resilience under climate change. Both theory and modelling approaches have been applied to this challenge, with an initial focus being the Andes-Amazon elevation gradient (Marthews et al. 2012, Enquist et al. 2017, Fyllas et al. 2017, Peng et al. 2020). Fyllas et al. (2017) showed that a traits-based model could accurately predict the magnitude and trends in forest productivity with elevation, with solar radiation and plant functional traits being sufficient to describe productivity variation. Remarkably, there was no need to explicitly represent temperature variation with elevation, as trait variation driven by species turnover appears to capture the effect of temperature. Enquist et al. (2017) applied a metabolic-theory-based approach to the same (Aguirre-Gutierrez et al. 2019) dataset, and arrived at a broadly similar conclusion, that the turnover in species results in an adaptive compensation for the effects of temperature on ecosystem productivity, a feature that current biosphere models struggle to represent. Peng et al. (2020) analysed the same rich dataset through a framework of optimisation of photosynthesis to temperature, and argued that an adjustment in leaf-level photosynthetic capacity was sufficient to explain ecosystem-level trends in nutrient stocks and productivity. While these interpretations differ in details, they all agree that the widely presumed sensitivity of ecosystem function to temperature is much less than expected, and demonstrated fundamental new insights into how temperature influences ecosystem function. Similar approaches and analyses are currently being applied to the very different context of the GEM rainforest-savanna gradient in Ghana (e.g. Aguirre-Gutierrez et al. 2019, Oliveras et al. 2020), and this is a fruitful direction where GEM can contribute to both theory and modelling. Previous studies using the GEM-trait database from the Peruvian elevation gradient suggest that leaf traits such as LMA may be changing in response to climate change (Enquist et al. 2017) and other studies have found that this could impact leaf reflectance by essentially darkening tropical leaves and changing the albedo of the tropical biosphere (Doughty et al. 2018b).

In a further model application, Fauset et al. (2019) applied a more advanced dynamic model that incorporated diverse tree strategies, realistic physiology and detailed forest structure. They explored the links between traits, demography (recruitment and mortality) forest structure and NPP and GPP, in the context of seasonal and aseasonal lowland forest GEM sites in Peru. The study found that in this case the differences in productivity between the two sites could be explained by climate alone and not by traits differences, but modelling the allocation of NPP to organs remained problematic. The rich allocation datasets now available from many GEM sites offer the opportunity for a better understanding of allocation strategies than can inform and test such models.

5.6 Linking field data to remote sensing

The link between ecosystem function and leaf traits opens the prospect for monitoring ecosystem function and health through airborne or satellite-based remote sensing. Long-established optical earth observation approaches are limited in the amount of information potentially contained in their few optical bands, and the tropical forest canopy is reduced to a largely uninformative green surface. However, new richer multispectral (> 5 bands) and hyperspectral (hundreds of distinct bands) approaches, coupled with information on ecosystem structure through Lidar and textural analysis, offer the promise of elucidating key canopy traits and structural features. Thereby, through the theoretical and modelling approaches outlined in the previous section, this opens up the potential of providing richly detailed maps and monitoring of tropical ecosystem function. Flights in 2011 and 2013 using hyperspectral and lidar sensors on board the Carnegie Airborne Observatory over much of the Andes-Amazon transect demonstrated the potential of linking canopy function to airborne remote sensing (Asner et al. 2014, Asner et al. 2017), thereby successfully predicting ecosystem productivity from remotely sensed functional diversity (Duran et al. 2019). Swinfield et al. (2020) used a similar combination of Lidar and imaging spectroscopy coupled with traits sampling in the GEM plots, to map nutrients in the matrix of intact and logged forests in Sabah, Malaysian Borneo. They showed that canopy foliar nitrogen and phosphorus concentrations decreased with elevation, a feature not detectable from the ground surveys alone. Once topography was controlled for, logged forests were found to have relatively depleted phosphorus concentrations as this limiting nutrient was extracted through harvest, highlighting long-term sustainability issues in repeated logging.

At a smaller scale, measurements of leaf spectroscopy along the Peruvian elevation gradient suggested that many new traits could be remotely sensed through correlations with other leaf traits, such as photosynthesis, leaf venation, wood density (Doughty et al. 2017). Another study, in Borneo, suggested that leaf spectroscopy has some potential in providing early warning of future tree mortality (Doughty et al., in review). Scaling up slightly more, drone-based hyperspectral remote sensing also showed potential in mapping canopy leaf nutrients and traits along the wet-dry ecosystem GEM gradient in Ghana (Thomson et al. 2018). An immediate goal of the GEM network is to exploit the latest generation of satellite-based sensors, such as the multispectral bands of the Sentinel-2 mission from the European Space Agency (ESA) or the Lidar on the GEDI mission, to develop the potential real-time remote sensing of canopy properties and ecosystem function (Aguirre-Gutierrez et al. 2020).

6. New scientific directions

The GEM network is continuing to deliver on its central goals of describing ecosystem productivity and carbon cycling, understanding their spatial and interannual variability, and their relationship to functional traits and remotely sensed properties. However, the network is also continuing to spawn new research directions, some of which are highlighted below.

6.1 GEM-Nutrients

The nutrient status of ecosystems is often described in static terms such as concentrations or stocks of nitrogen or phosphorus. However, the coupling of NPP (the signature feature of the GEM network) with the stoichiometry of leaves, wood and fine root tissue enables the quantification of ecosystem use and flows of nutrients, enabling direct assessment of ecosystem nutrient demand and use efficiency. This approach is currently being applied to GEM sites in Malaysia (Inagawa et al., in prep), Brazil (Scalon et al, in review), Ghana and South Africa, and offers the prospect of a network of standardised assessment of nutrient dynamics. In principle, the approach can be applied to any nutrient or organic compound: Feakins et al. (2016) applied such an approach to leaf wax *n*-alkane concentrations along the Andes-Amazon transect, and was thus able to uniquely quantify the variation of ecosystem wax production rates with elevation. They showed that ecosystem n-alkane production rates increased with elevation by more than an order of magnitude, most likely as a defence mechanism for long-lived montane-forest leaves. Such waxes are promising and important paleoindicators of ecosystem composition and function. This result shows the potential of new insights into the dynamics of ecosystem nutrients and complex organic compounds made possible through a network of NPP measurements.

6.2 *Tree architecture as a functional trait*

The consideration of plant functional traits has tended to focus on leaf or wood functional traits. However, consideration of tree architecture provides a series of traits that directly link species composition to ecosystem structure and biomass. It has been quite challenging to address architectural traits, as their collection has been laborious and often imprecise. This impediment has recently been largely removed with the advent of terrestrial laser scanning approaches (Malhi et al. 2018a) that enable digital extraction of detailed tree skeletons, from which a suite of architectural parameters can be derived. Recent field campaigns have collected such tree architectural data from a suite of GEM sites where NPP and traits data have been collected, including in Peru, Brazil, Ghana, South Africa, Malaysia and Australia. Immediate priorities are to understand the association between tree architecture and other plant functional traits, and the patterns of geographical and taxonomic variation in architecture. In addition, such data enable development of much more accurate descriptions and allometries of tree woody surface area, thereby enabling improved estimation of woody respiration, a key component of the GEM carbon cycle measurements (Meir et al. 2017).

6.3 GEM-Animals: a multitrophic view of ecosystems

A new direction for GEM is to combine the vegetation-focused conventional GEM focus with a holistic view of energy and nutrient flows through the fauna and multiple trophic levels of an ecosystem. These efforts link back to the earliest attempts in ecosystem ecology to describe whole ecosystem energy flow through both flora and fauna {Lindeman, 1942}. Such an approach is possible where there are rich data on the composition and abundance of faunal populations, where metabolic mass-based scaling approaches can be used to estimate energy needs and food consumption by each animal species or functional group. This can be complemented by direct estimates of herbivory, such as measuring what fraction of leaf area is consumed by insect herbivores. The advantage of using GEM sites is that the NPP and productivity data are available, enabling framing in terms of the fraction of total productivity and photosynthesis that is flowing through different populations and trophic levels. This approach is only possible at the few sites where detailed studies of animal populations are available. It is at an advanced stage at Wytham Woods, the UK GEM site with a rich history of animal research, and is also being developed at intact and logged forests in Sabah, Malaysia, where rich faunal datasets have been collected in the SAFE project (Ewers et al. 2011, Riutta et al. 2018), and also at the Wits Rural savanna sites in South Africa, where termite and ant exclusion experiments have been implemented. A recent study used combined the GEM methodology and large mammal data data (dung count and camera trap) to find forest thinning in North America appeared to increase energy flow from primary producers to primary consumers (Doughty et al. 2020).

7. Conclusions

This paper has sought to give an overview of the context and historical development of the GEM network, as well as providing a benchmark of the coverage and state of the network in 2020. It has highlighted the opportunities and challenges of developing such a network, and the potential it has to provide a stronger bridge between field ecology and Earth System Science. Synthetic analyses across the network offer the prospect of new broad insights into tropical ecosystem function, and new directions of research will result in richer understanding and scaling of ecosystem function. Whatever form the network continues in over the coming decade, we hope and believe that it has left a record of training, collaboration and scientific innovation, particularly in tropical nations, that will leave a positive legacy for many decades to come.

Acknowledgements

This paper is a product of the Global Ecosystems Monitoring (GEM) network. We thank the many hundreds of researchers, students and technicians who have contributed to data collection across the network, often in the face of many logistical challenges.

Funding

The core establishment of the GEM network has been supported by the Gordon and Betty Moore Foundation, and European Research Council Advanced Investigator Grant GEM-TRAIT (321131). Site development in individual locations have been supported by multiple grants from the UK Natural Environment Research Council, in particular NE/D014174/1, NE/J023418/1, NE/I014705/1, NE/K016369/1, NE/K016385/1, NE/F005776/1, NE/N012453/1, NE/P001092/1 and NE/S01084X/1. Activities in Africa have been additionally supported by Royal Society-Leverhulme and Royal Society-DFID Africa Capacity Building Awards. Work in Malaysia has been greatly supported by the Sime Darby Foundation. YM is supported by the Jackson Foundation.

Figures

Figure 1: The Global Ecosystems Monitoring Network, as of early 2020. Open circles indicate sites where detailed carbon cycle data alone have been collected; grey filled circles indicate where plant traits data and forest inventory data alone have been collected; filled circles where both detailed carbon cycle and plant functional traits data have been collected. Circles indicate sites that are centrally supported by the GEM network; triangles indicate sites primarily supported by external partners.

Figure 2: GEM plots in climate space. Colours indicate continent, and country of the sites are indicated, where they are not congested. The climate data are derived from TerraClimate (http://www.climatologylab.org/terraclimate.html) for the period 1982-2010 1(a) Mean annual solar radiation (W/m^2) vs Elevation (m); (b) Water stress: Potential evapotranspiration (mm/month) vs Maximum Climatological Water Deficit (mm); (c) Annual precipitation (mm) vs Mean annual temperature (^{o}C).

Figure 3: A selection of sites from the GEM network: (a) Fine root productivity measurements in Ivindo National Park, Gabon, Central Africa; (b) Measuring diameter of large trees with a ladder to reach above the buttress, Maliau Hills National park, Sabah, Malaysia; (c) Measuring leaf traits in montane cloud forest, Wayqecha, Peruvian Andes. (d) Measuring Leaf area Index in Bobiri Forest Reserve, Ghana; (e) Measuring herbaceous layer productivity in a savanna in Wits Rural Facility, South Africa; (f) Plot locations in a coral atoll in Tetiaroa, French Polynesia, looking at the impacts of invasive rat eradication on ecosystem functioning.

Figure 2: The key components of the GEM protocol. See main text for details.

Figure 1 The Global Ecosystems Monitoring Network, as of early 2020. Open circles indicate sites where detailed carbon cycle data alone have been collected; grey filled circles indicate where plant traits data and forest inventory data alone have been collected; filled circles where both detailed carbon cycle and plant functional traits data have been collected. Circles indicate sites that are centrally supported by the GEM network; triangles indicate sites primarily supported by external partners.

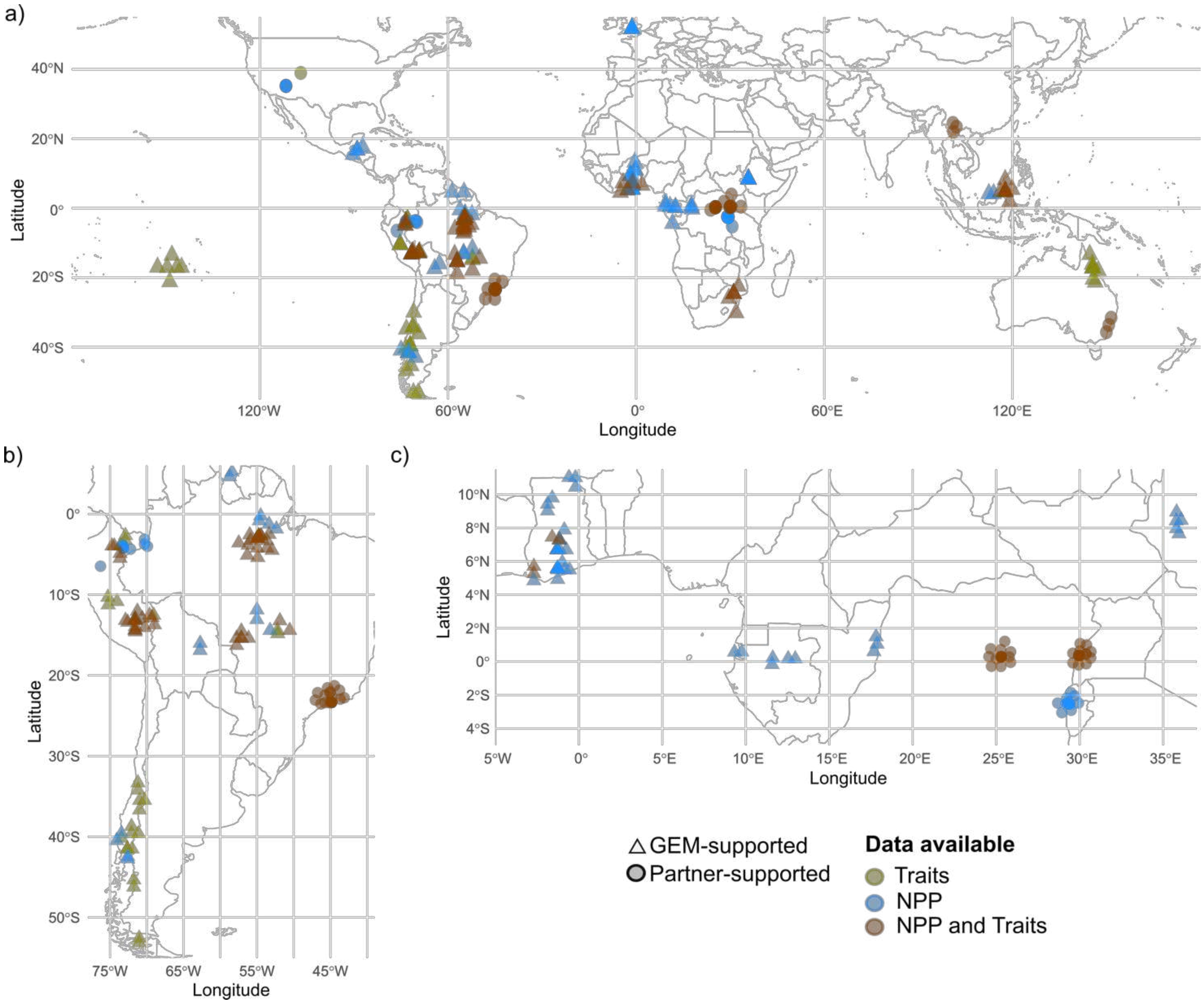


Figure 2: GEM plots in climate space. Colours indicate continent, and country of the sites are indicated, where they are not congested. The climate data are derived from TerraClimate (http://www.climatologylab.org/terraclimate.html) for the period 1982-2010 1(a) Mean annual solar radiation (W/m^2) vs Elevation (m); (b) Water stress: Potential evapotranspiration (mm/month) vs Maximum Climatological Water Deficit (mm); (c) Annual precipitation (mm) vs Mean annual temperature (^{o}C).

Figure 2(a)

1049 **Figure 2(b)**

1050

1051

Figure 2(c)

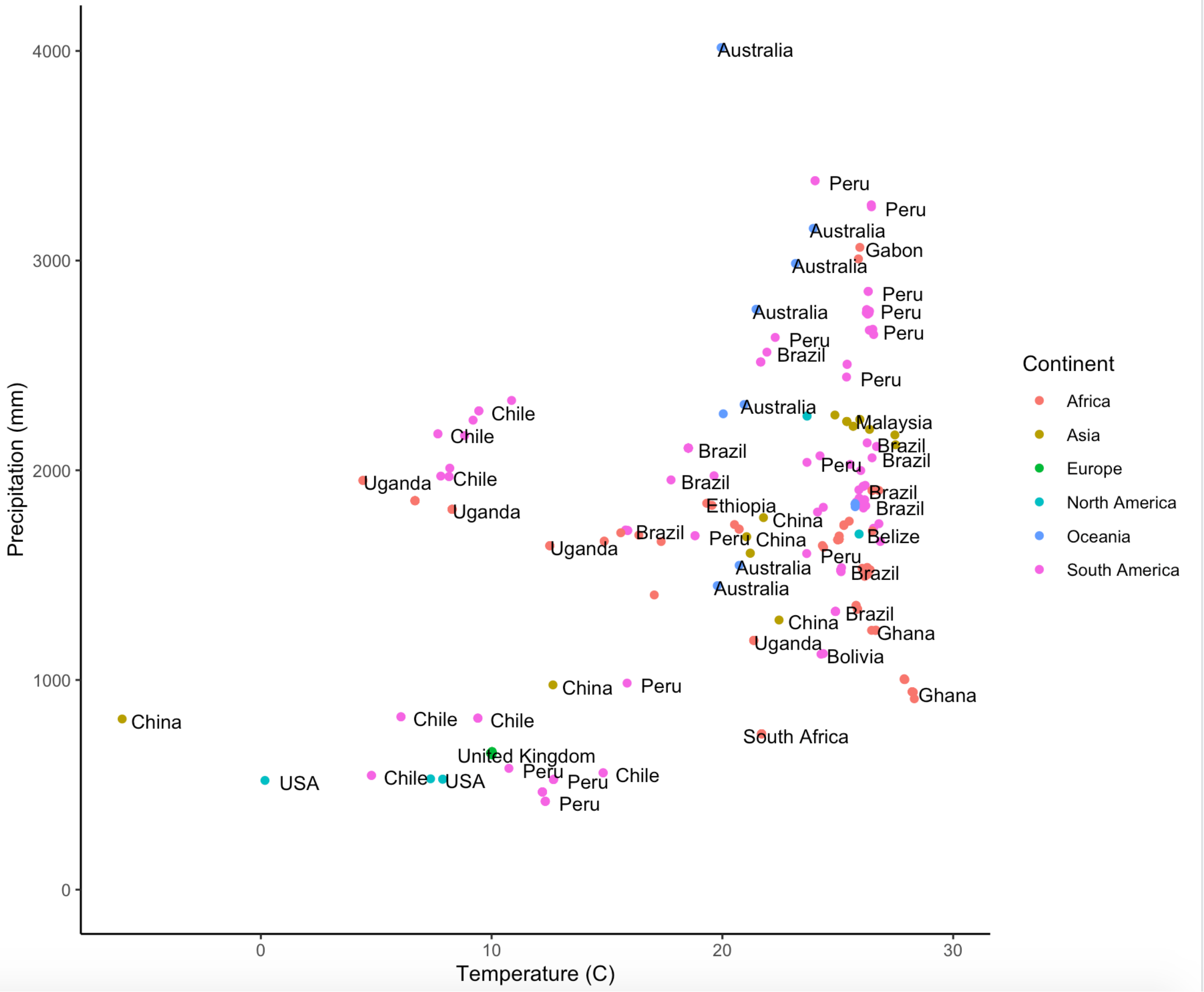
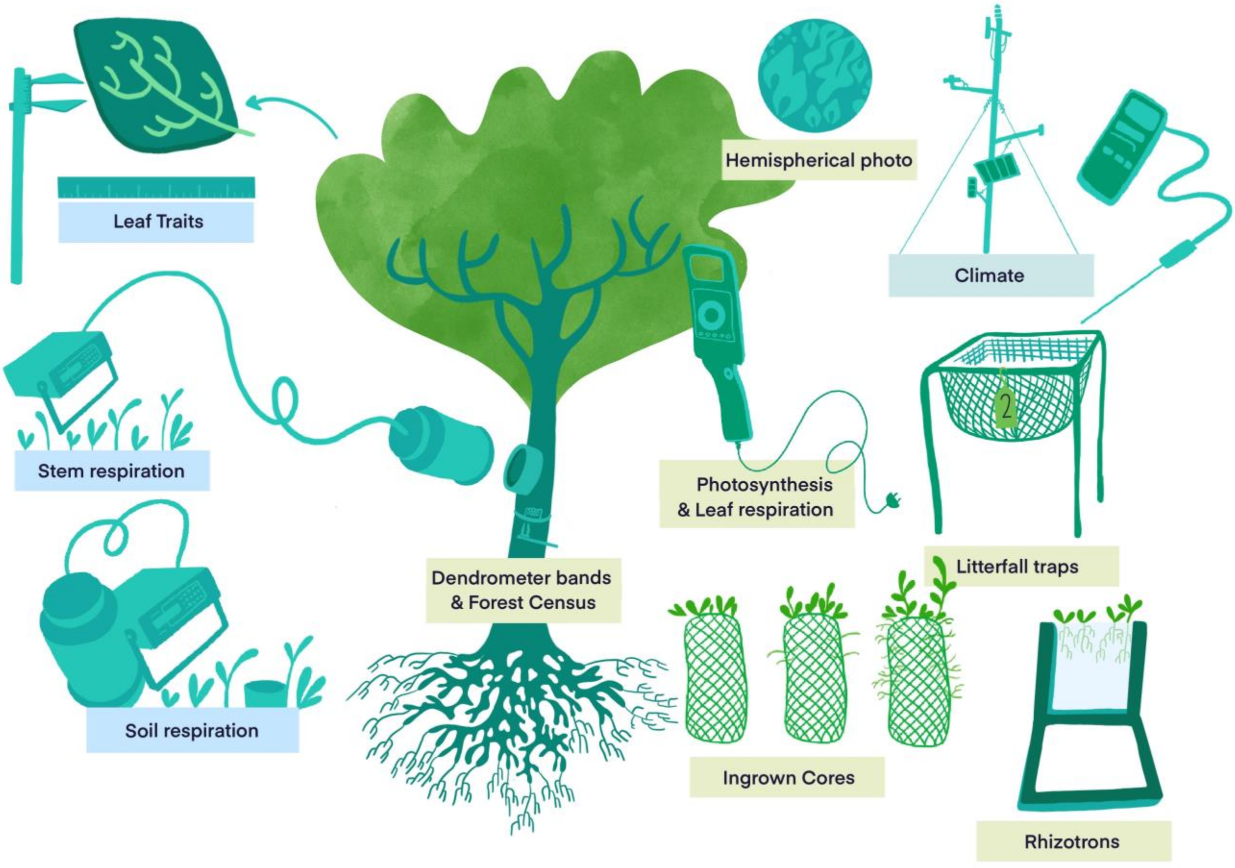

Precipitation (mm)
4000
3000
2000
1000
0
Temperature (C)
0
10
20
30
Continent
Africa
Asia
Europe
North America
Oceania
South America
Australia
Peru
Peru
Australia
Gabon
Australia
Peru
Australia
Peru
Peru
Peru
Brazil
Peru
Australia
Malaysia
Chile
Chile
Brazil
Brazil
Peru
Brazil
Uganda
Chile
Brazil
Uganda
Brazil
Ethiopia
China
Brazil
Brazil
Peru
China
Belize
Uganda
Peru
Australia
Brazil
Australia
Brazil
China
Ghana
Uganda
Bolivia
China
Peru
Ghana
China
Chile
Chile
South Africa
United Kingdom
USA
Chile
USA
Peru
Peru
Chile
Peru

Figure 3: A selection of sites from the GEM network: (a) Fine root productivity measurements in Ivindo National Park, Gabon, Central Africa; (b) Measuring diameter of large trees with a ladder to reach above the buttress, Maliau Hills National park, Sabah, Malaysia; (c) Measuring leaf traits in montane cloud forest, Wayqecha, Peruvian Andes. (d) Measuring Leaf area Index in Bobiri Forest Reserve, Ghana; (e) Measuring herbaceous layer productivity in a savanna in Wits Rural Facility, South Africa; (f) Plot locations in a coral atoll in Tetiaroa, French Polynesia, looking at the impacts of invasive rat eradication on ecosystem functioning.

Figure 4: The key components of the GEM protocol. See main text for details.



References

Addo-Danso, S. D., C. E. Prescott, S. Adu-Bredu, A. Duah-Gyamfi, S. Moore, R. D. Guy, D. I. Forrester, K. Owusu-Afriyie, P. L. Marshall, and Y. Malhi. 2018. Fine-root exploitation strategies differ in tropical old growth and logged-over forests in Ghana. Biotropica **50**:606-615.

Aguirre-Gutierrez, J., I. Oliveras, S. Rifai, S. Fauset, S. Adu-Bredu, K. Affum-Baffoe, T. R. Baker, T. R. Feldpausch, A. Gvozdevaite, W. Hubau, N. J. B. Kraft, S. L. Lewis, S. Moore, U. Niinemets, T. Peprah, O. L. Phillips, K. Zieminska, B. Enquist, and Y. Malhi. 2019. Drier tropical forests are susceptible to functional changes in response to a long-term drought. Ecology Letters **22**:855-865.

Anderson-Teixeira, K. J., S. J. Davies, A. C. Bennett, E. B. Gonzalez-Akre, H. C. Muller-Landau, S. J. Wright, K. Abu Salim, A. M. Almeyda Zambrano, A. Alonso, J. L. Baltzer, Y. Basset, N. A. Bourg, E. N. Broadbent, W. Y. Brockelman, S. Bunyavejchewin, D. Burslem, N. Butt, M. Cao, D. Cardenas, G. B. Chuyong, K. Clay, S. Cordell, H. S. Dattaraja, X. B. Deng, M. Detto, X. J. Du, A. Duque, D. L. Erikson, C. E. N. Ewango, G. A. Fischer, C. Fletcher, R. B. Foster, C. P. Giardina, G. S. Gilbert, N. Gunatilleke, S. Gunatilleke, Z. Q. Hao, W. W. Hargrove, T. B. Hart, B. C. H. Hau, F. L. He, F. M. Hoffman, R. W. Howe, S. P. Hubbell, F. M. Inman-Narahari, P. A. Jansen, M. X. Jiang, D. J. Johnson, M. Kanzaki, A. R. Kassim, D. Kenfack, S. Kibet, M. F. Kinnaird, L. Korte, K. Kral, J. Kumar, A. J. Larson, Y. D. Li, X. K. Li, S. R. Liu, S. K. Y. Lum, J. A. Lutz, K. P. Ma, D. M. Maddalena, J. R. Makana, Y. Malhi, T. Marthews, R. M. Serudin, S. M. McMahon, W. J. McShea, H. R. Memiaghe, X. C. Mi, T. Mizuno, M. Morecroft, J. A. Myers, V. Novotny, A. A. de Oliveira, P. S. Ong, D. A. Orwig, R. Ostertag, J. den Ouden, G. G. Parker, R. P. Phillips, L. Sack, M. N. Sainge, W. G. Sang, K. Sri-ngernyuang, R. Sukumar, I. F. Sun, W. Sungpalee, H. S. Suresh, S. Tan, S. C. Thomas, D. W. Thomas, J. Thompson, B. L. Turner, M. Uriarte, R. Valeorncia, M. I. Vallejo, A. Vicentini, T. Vrska, X. H. Wang, X. G. Wang, G. Weiblen, A. Wolf, H. Xu, S. Yap, and J. Zimmerman. 2015. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. Global Change Biology **21**:528-549.

Anderson-Teixeira, K. J., M. M. Wang, J. C. McGarvey, and D. S. LeBauer. 2016. Carbon dynamics of mature and regrowth tropical forests derived from a pantropical database (TropForC-db). Global Change Biology **22**:1690-1709.

Aragão, L., Y. Malhi, D. Metcalfe, J. Silva-Espejo, E. Jiménez, D. Navarrete, S. Almeida, A. Costa, N. Salinas, and O. Phillips. 2009. Above-and below-ground net primary productivity across ten Amazonian forests on contrasting soils. Biogeosciences **6**:2759-2778.

Araujo-Murakami, A., C. E. Doughty, D. B. Metcalfe, J. E. Silva-Espejo, L. Arroyo, J. P. Heredia, M. Flores, R. Sibler, L. M. Mendizabal, E. Pardo-Toledo, M. Vega, L. Moreno, V. D. Rojas-Landivar, K. Halladay, C. A. J. Girardin, T. J. Killeen, and Y. Malhi. 2014. The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia. Plant Ecology & Diversity **7**:55-69.

Asner, G. P., C. B. Anderson, R. E. Martin, D. E. Knapp, R. Tupayachi, F. Sinca, and Y. Malhi. 2014. Landscape-scale changes in forest structure and functional traits along an Andes-to-Amazon elevation gradient. Biogeosciences **11**:843-856.

Asner, G. P., R. E. Martin, C. B. Anderson, K. Kryston, N. Vaughn, D. E. Knapp, L. P. Bentley, A. Shenkin, N. Salinas, F. Sinca, R. Tupayachi, K. Q. Huaypar, M. M. Pillco, F. D. C. Alvarez, S. Diaz, B. J. Enquist, and Y. Malhi. 2017. Scale dependence of canopy trait distributions along a tropical forest elevation gradient. New Phytologist **214**:973-988.

Berenguer, E., Y. Malhi, P. Brando, A. C. N. Cordeiro, J. Ferreira, F. Franca, L. C. Rossi, M. M. M. de Seixas, and J. Barlow. 2018. Tree growth and stem carbon accumulation in human-modified Amazonian forests following drought and fire. Philosophical Transactions of the Royal Society B-Biological Sciences **373**.

Brando, P. M., C. Oliveria-Santos, W. Rocha, R. Cury, and M. T. Coe. 2016. Effects of experimental fuel additions on fire intensity and severity: unexpected carbon resilience of a neotropical forest. Global Change Biology **22**:2516-2525.

Campioli, M., Y. Malhi, S. Vicca, S. Luyssaert, D. Papale, J. Penuelas, M. Reichstein, M. Migliavacca, M. A. Arain, and I. A. Janssens. 2016. Evaluating the convergence between eddy-covariance and biometric methods for assessing carbon budgets of forests. Nature Communications **7**.

Chambers, J. Q., E. S. Tribuzy, L. C. Toledo, B. F. Crispim, N. Higuchi, J. d. Santos, A. C. Araújo, B. Kruijt, A. D. Nobre, and S. E. Trumbore. 2004. Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. Ecological applications **14**:72-88.

Chave, J., M. Rejou-Mechain, A. Burquez, E. Chidumayo, M. S. Colgan, W. B. Delitti, A. Duque, T. Eid, P. M. Fearnside, R. C. Goodman, M. Henry, A. Martinez-Yrizar, W. A. Mugasha, H. C. Muller-Landau, M. Mencuccini, B. W. Nelson, A. Ngomanda, E. M. Nogueira, E. Ortiz-Malavassi, R. Pelissier, P. Ploton, C. M. Ryan, J. G. Saldarriaga, and G. Vieilledent. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob Chang Biol **20**:3177-3190.

Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, and J. Ni. 2001a. Measuring net primary production in forests: concepts and field methods. Ecological applications **11**:356-370.

Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, J. Ni, and E. A. Holland. 2001b. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecological applications **11**:371-384.

da Costa, A. C. L., D. B. Metcalfe, C. E. Doughty, A. A. R. de Oliveira, G. F. C. Neto, M. C. da Costa, J. D. Silva, L. Aragao, S. Almeida, D. R. Galbraith, L. M. Rowland, P. Meir, and Y. Malhi. 2014. Ecosystem respiration and net primary productivity after 8-10 years of experimental through-fall reduction in an eastern Amazon forest. Plant Ecology & Diversity **7**:7-24.

del Aguila-Pasquel, J., C. E. Doughty, D. B. Metcalfe, J. E. Silva-Espejo, C. A. J. Girardin, J. A. C. Gutierrez, G. E. Navarro-Aguilar, C. A. Quesada, C. G. Hidalgo, J. M. R. Huaymacari, K. Halladay, D. D. Torres, O. Phillips, and Y. Malhi. 2014. The seasonal cycle of productivity, metabolism and carbon dynamics in a wet aseasonal forest in north-west Amazonia (Iquitos, Peru). Plant Ecology & Diversity **7**:71-83.

Doughty, C., A. Abraham, and T. Prys-Jones. 2020. Carbon fluxes and herbivory in ponderosa pines stands across a forest thinning chronosequence. Center for Open Science.

Doughty, C. E., G. R. Goldsmith, N. Raab, C. A. J. Girardin, F. Farfan-Amezquita, W. Huaraca-Huasco, J. E. Silva-Espejo, A. Araujo-Murakami, A. C. L. da Costa, W. Rocha, D. Galbraith, P. Meir, D. B. Metcalfe, and Y. Malhi. 2018a. What controls variation in carbon use efficiency among Amazonian tropical forests? Biotropica **50**:16-25.

Doughty, C. E., Y. Malhi, A. Araujo-Murakami, D. B. Metcalfe, J. E. Silva-Espejo, L. Arroyo, J. P. Heredia, E. Pardo-Toledo, L. M. Mendizabal, V. D. Rojas-Landivar, M. Vega-Martinez, M. Flores-Valencia, R. Sibler-Rivero, L. Moreno-Vare, L. J. Viscarra, T. Chuviru-Castro, M. Osinaga-Becerra, and R. Ledezma. 2014a. Allocation trade-offs dominate the response of tropical forest growth to seasonal and interannual drought. Ecology **95**:2192-2201.

Doughty, C. E., D. B. Metcalfe, M. C. da Costa, A. A. R. de Oliveira, G. F. C. Neto, J. A. Silva, L. Aragao, S. S. Almeida, C. A. Quesada, C. A. J. Girardin, K. Halladay, A. C. L. da Costa, and Y. Malhi. 2014b. The production, allocation and cycling of carbon in a forest on fertile terra preta soil in eastern Amazonia compared with a forest on adjacent infertile soil. Plant Ecology & Diversity **7**:41-53.

Doughty, C. E., D. B. Metcalfe, C. A. J. Girardin, F. F. Amezquita, D. G. Cabrera, W. H. Huasco, J. E. Silva-Espejo, A. Araujo-Murakami, M. C. da Costa, W. Rocha, T. R. Feldpausch, A. L.

M. Mendoza, A. C. L. da Costa, P. Meir, O. L. Phillips, and Y. Malhi. 2015a. Drought impact on forest carbon dynamics and fluxes in Amazonia. Nature **519**:78-U140.

Doughty, C. E., D. B. Metcalfe, C. A. J. Girardin, F. F. Amezquita, L. Durand, W. H. Huasco, J. E. Silva-Espejo, A. Araujo-Murakami, M. C. da Costa, A. C. L. da Costa, W. Rocha, P. Meir, D. Galbraith, and Y. Malhi. 2015b. Source and sink carbon dynamics and carbon allocation in the Amazon basin. Global Biogeochemical Cycles **29**:645-655.

Doughty, C. E., P. E. Santos-Andrade, G. R. Goldsmith, B. Blonder, A. Shenkin, L. P. Bentley, C. Chavana-Bryant, W. Huaraca-Huasco, S. Diaz, N. Salinas, B. J. Enquist, R. Martin, G. P. Asner, and Y. Malhi. 2017. Can Leaf Spectroscopy Predict Leaf and Forest Traits Along a Peruvian Tropical Forest Elevation Gradient? Journal of Geophysical Research-Biogeosciences **122**:2952-2965.

Doughty, C. E., P. E. Santos-Andrade, A. Shenkin, G. R. Goldsmith, L. P. Bentley, B. Blonder, S. Diaz, N. Salinas, B. J. Enquist, R. E. Martin, G. P. Asner, and Y. Malhi. 2018b. Tropical forest leaves may darken in response to climate change. Nature Ecology & Evolution **2**:1918-1924.

Duran, S. M., R. E. Martin, S. Diaz, B. S. Maitner, Y. Malhi, N. Salinas, A. Shenkin, M. R. Silman, D. J. Wieczynski, G. P. Asner, L. P. Bentley, V. M. Savage, and B. J. Enquist. 2019. Informing trait-based ecology by assessing remotely sensed functional diversity across a broad tropical temperature gradient. Science Advances **5**.

Enquist, B. J., L. P. Bentley, A. Shenkin, B. Maitner, V. Savage, S. Michaletz, B. Blonder, V. Buzzard, T. E. B. Espinoza, W. Farfan-Rios, C. E. Doughty, G. R. Goldsmith, R. E. Martin, N. Salinas, M. Silman, S. Diaz, G. P. Asner, and Y. Malhi. 2017. Assessing trait-based scaling theory in tropical forests spanning a broad temperature gradient. Global Ecology and Biogeography **26**:1357-1373.

Ewers, R. M., R. K. Didham, L. Fahrig, G. Ferraz, A. Hector, R. D. Holt, V. Kapos, G. Reynolds, W. Sinun, J. L. Snaddon, and E. C. Turner. 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. Philosophical Transactions of the Royal Society B-Biological Sciences **366**:3292-3302.

Fan, S. M., S. C. Wofsy, P. S. Bakwin, D. J. Jacob, and D. R. Fitzjarrald. 1990. Atmosphere-biosphere exchange of CO2 and O3 in the central Amazon forest. Journal of Geophysical Research: Atmospheres **95**:16851-16864.

Fauset, S., M. Gloor, N. M. Fyllas, O. L. Phillips, G. P. Asner, T. R. Baker, L. P. Bentley, R. J. W. Brienen, B. O. Christoffersen, J. del Aguila-Pasquel, C. E. Doughty, T. R. Feldpausch, D. R. Galbraith, R. C. Goodman, C. A. J. Girardin, E. N. H. Coronado, A. Monteagudo, N. Salinas, A. Shenkin, J. E. Silva-Espejo, G. van der Heijden, R. Vasquez, E. Alvarez-Davila, L. Arroyo, J. G. Barroso, F. Brown, W. Castro, F. C. Valverde, N. D. Cardozo, A. Di Fiore, T. Erwin, I. Huamantupa-Chuquimaco, P. N. Vargas, D. Neill, N. P. Camacho, A. P. Gutierrez, J. Peacock, N. Pitman, A. Prieto, Z. Restrepo, A. Rudas, C. A. Quesada, M. Silveira, J. Stropp, J. Terborgh, S. A. Vieira, and Y. Malhi. 2019. Individual-Based Modeling of Amazon Forests Suggests That Climate Controls Productivity While Traits Control Demography. Frontiers in Earth Science **7**.

Feakins, S. J., T. Peters, M. S. Wu, A. Shenkin, N. Salinas, C. A. J. Girardin, L. P. Bentley, B. Blonder, B. J. Enquist, R. E. Martin, G. P. Asner, and Y. Malhi. 2016. Production of leaf wax n-alkanes across a tropical forest elevation transect. Organic Geochemistry **100**:89-100.

Fenn, K., Y. Malhi, M. Morecroft, C. Lloyd, and M. Thomas. 2015. The Carbon Cycle of a Maritime Ancient Temperate Broadleaved Woodland at Seasonal and Annual Scales. Ecosystems **18**:1-15.

Friend, A. D., W. Lucht, T. T. Rademacher, R. Keribin, R. Betts, P. Cadule, P. Ciais, D. B. Clark, R. Dankers, P. D. Falloon, A. Ito, R. Kahana, A. Kleidon, M. R. Lomas, K. Nishina, S. Ostberg, R. Pavlick, P. Peylin, S. Schaphoff, N. Vuichard, L. Warszawski, A. Wiltshire, and F. I. Woodward. 2014. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO2. Proc Natl Acad Sci U S A **111**:3280-3285.

Fyllas, N. M., L. P. Bentley, A. Shenkin, G. P. Asner, O. K. Atkin, S. Diaz, B. J. Enquist, W. Farfan-Rios, E. Gloor, R. Guerrieri, W. H. Huasco, Y. Ishida, R. E. Martin, P. Meir, O. Phillips, N. Salinas, M. Silman, L. K. Weerasinghe, J. Zaragoza-Castells, and Y. Malhi. 2017. Solar radiation and functional traits explain the decline of forest primary productivity along a tropical elevation gradient. Ecology Letters **20**:730-740.

Galbraith, D., Y. Malhi, K. Affum-Baffoe, A. D. A. Castanho, C. E. Doughty, R. A. Fisher, S. L. Lewis, K. S. H. Peh, O. L. Phillips, C. A. Quesada, B. Sonke, and J. Lloyd. 2013. Residence times of woody biomass in tropical forests. Plant Ecology & Diversity **6**:139-157.

Galbraith, D., Y. Malhi, L. Aragao, and T. Baker. 2014. The ecosystem dynamics of Amazonian and Andean forests. Plant Ecology & Diversity **7**:1-6.

Girardin, C. A. J., L. Aragao, Y. Malhi, W. H. Huasco, D. B. Metcalfe, L. Durand, M. Mamani, J. E. Silva-Espejo, and R. J. Whittaker. 2013. Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. Global Biogeochemical Cycles **27**:252-264.

Girardin, C. A. J., J. E. S. Espejob, C. E. Doughty, W. H. Huasco, D. B. Metcalfe, L. Durand-Baca, T. R. Marthews, L. Aragao, W. Farfan-Rios, K. Garcia-Cabrera, K. Halladay, J. B. Fisher, D. F. Galiano-Cabrera, L. P. Huaraca-Quispe, I. Alzamora-Taype, L. Eguiluz-Mora, N. Salinas-Revilla, M. R. Silman, P. Meir, and Y. Malhi. 2014. Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. Plant Ecology & Diversity **7**:107-123.

Girardin, C. A. J., Y. Malhi, L. Aragao, M. Mamani, W. H. Huasco, L. Durand, K. J. Feeley, J. Rapp, J. E. Silva-Espejo, M. Silman, N. Salinas, and R. J. Whittaker. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. Global Change Biology **16**:3176-3192.

Girardin, C. A. J., Y. Malhi, C. E. Doughty, D. B. Metcalfe, P. Meir, J. del Aguila-Pasquel, A. Araujo-Murakami, A. C. L. da Costa, J. E. Silva-Espejo, F. F. Amezquita, and L. Rowland. 2016. Seasonal trends of Amazonian rainforest phenology, net primary productivity, and carbon allocation. Global Biogeochemical Cycles **30**:700-715.

Grace, J., J. Lloyd, J. McIntyre, A. C. Miranda, P. Meir, H. S. Miranda, C. Nobre, J. Moncrieff, J. Massheder, Y. Malhi, I. Wright, and J. Gash. 1995. CARBON-DIOXIDE UPTAKE BY AN UNDISTURBED TROPICAL RAIN-FOREST IN SOUTHWEST AMAZONIA, 1992 TO 1993. Science **270**:778-780.

Gurdak, D. J., L. Aragao, A. Rozas-Davila, W. H. Huasco, K. G. Cabrera, C. E. Doughty, W. Farfan-Rios, J. E. Silva-Espejo, D. B. Metcalfe, M. R. Silman, and Y. Malhi. 2014. Assessing above-ground woody debris dynamics along a gradient of elevation in Amazonian cloud forests in Peru: balancing above-ground inputs and respiration outputs. Plant Ecology & Diversity **7**:143-160.

Huasco, W. H., C. A. J. Girardin, C. E. Doughty, D. B. Metcalfe, L. D. Baca, J. E. Silva-Espejo, D. G. Cabrera, L. Aragao, A. R. Davila, T. R. Marthews, L. P. Huaraca-Quispe, I. Alzamora-Taype, L. E. Mora, W. Farfan-Rios, K. G. Cabrera, K. Halladay, N. Salinas-Revilla, M. R. Silman, P. Meir, and Y. Malhi. 2014. Seasonal production, allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. Plant Ecology & Diversity **7**:125-142.

Hubau, W., S. L. Lewis, O. L. Phillips, K. Affum-Baffoe, H. Beeckman, A. Cuní-Sanchez, A. K. Daniels, C. E. N. Ewango, S. Fauset, J. M. Mukinzi, D. Sheil, B. Sonké, M. J. P. Sullivan, T. C. H. Sunderland, H. Taedoumg, S. C. Thomas, L. J. T. White, K. A. Abernethy, S. Adu-Bredu, C. A. Amani, T. R. Baker, L. F. Banin, F. Baya, S. K. Begne, A. C. Bennett, F. Benedet, R. Bitariho, Y. E. Bocko, P. Boeckx, P. Boundja, R. J. W. Brienen, T. Brncic, E. Chezeaux, G. B. Chuyong, C. J. Clark, M. Collins, J. A. Comiskey, D. A. Coomes, G. C. Dargie, T. de Haulleville, M. N. D. Kamdem, J.-L. Doucet, A. Esquivel-Muelbert, T. R. Feldpausch, A. Fofanah, E. G. Foli, M. Gilpin, E. Gloor, C. Gonmadje, S. Gourlet-Fleury, J.

S. Hall, A. C. Hamilton, D. J. Harris, T. B. Hart, M. B. N. Hockemba, A. Hladik, S. A. Ifo, K. J. Jeffery, T. Jucker, E. K. Yakusu, E. Kearsley, D. Kenfack, A. Koch, M. E. Leal, A. Levesley, J. A. Lindsell, J. Lisingo, G. Lopez-Gonzalez, J. C. Lovett, J.-R. Makana, Y. Malhi, A. R. Marshall, J. Martin, E. H. Martin, F. M. Mbayu, V. P. Medjibe, V. Mihindou, E. T. A. Mitchard, S. Moore, P. K. T. Munishi, N. N. Bengone, L. Ojo, F. E. Ondo, K. S. H. Peh, G. C. Pickavance, A. D. Poulsen, J. R. Poulsen, L. Qie, J. Reitsma, F. Rovero, M. D. Swaine, J. Talbot, J. Taplin, D. M. Taylor, D. W. Thomas, B. Toirambe, J. T. Mukendi, D. Tuagben, P. M. Umunay, G. M. F. van der Heijden, H. Verbeeck, J. Vleminckx, S. Willcock, H. Wöll, J. T. Woods, and L. Zemagho. 2020. Asynchronous carbon sink saturation in African and Amazonian tropical forests. Nature **579**:80-87.

Ibrahim, F., S. Adu-Bredu, S. D. Addo-Danso, A. Duah-Gyamfi, E. A. Manu, and Y. Malhi. 2020. Patterns and controls on fine-root dynamics along a rainfall gradient in Ghana. Trees-Structure and Function.

Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia **108**:389-411.

Johnson, M. O., D. Galbraith, M. Gloor, H. De Deurwaerder, M. Guimberteau, A. Rammig, K. Thonicke, H. Verbeeck, C. von Randow, A. Monteagudo, O. L. Phillips, R. J. W. Brienen, T. R. Feldpausch, G. L. Gonzalez, S. Fauset, C. A. Quesada, B. Christoffersen, P. Ciais, G. Sampaio, B. Kruijt, P. Meir, P. Moorcroft, K. Zhang, E. Alvarez-Davila, A. A. de Oliveira, I. Amaral, A. Andrade, L. Aragao, A. Araujo-Murakami, E. Arets, L. Arroyo, G. A. Aymard, C. Baraloto, J. Barroso, D. Bonal, R. Boot, J. Camargo, J. Chave, A. Cogollo, F. C. Valverde, A. C. L. da Costa, A. Di Fiore, L. Ferreira, N. Higuchi, E. N. Honorio, T. J. Killeen, S. G. Laurance, W. F. Laurance, J. Licona, T. Lovejoy, Y. Malhi, B. Marimon, B. Marimon, D. C. L. Matos, C. Mendoza, D. A. Neill, G. Pardo, M. Pena-Claros, N. C. A. Pitman, L. Poorter, A. Prieto, H. Ramirez-Angulo, A. Roopsind, A. Rudas, R. P. Salomao, M. Silveira, J. Stropp, H. ter Steege, J. Terborgh, R. Thomas, M. Toledo, A. Torres-Lezama, G. M. F. van der Heijden, R. Vasquez, I. C. G. Vieira, E. Vilanova, V. A. Vos, and T. R. Baker. 2016. Variation in stem mortality rates determines patterns of above-ground biomass in Amazonian forests: implications for dynamic global vegetation models. Global Change Biology **22**:3996-4013.

Kho, L. K., Y. Malhi, and S. K. S. Tan. 2013. Annual budget and seasonal variation of aboveground and belowground net primary productivity in a lowland dipterocarp forest in Borneo. Journal of Geophysical Research-Biogeosciences **118**:1282-1296.

Kira, T. 1967. Comparative ecological studies on three main types of forest vegetation in Thailand. IV. Dry matter production, with special reference to the Khao Chong rain forest. Nature and Life in Southeast Asia.

Kira, T. 1978. Community architecture and organic matter dynamics in tropical lowland rain forest of Southwest Asia with special reference to Pasoh Forest, West Malaysia. Tropical Trees as Living System.

Lewis, S. L., G. Lopez-Gonzalez, B. Sonke, K. Affum-Baffoe, T. R. Baker, L. O. Ojo, O. L. Phillips, J. M. Reitsma, L. White, J. A. Comiskey, M. N. Djuikouo, C. E. N. Ewango, T. R. Feldpausch, A. C. Hamilton, M. Gloor, T. Hart, A. Hladik, J. Lloyd, J. C. Lovett, J. R. Makana, Y. Malhi, F. M. Mbago, H. J. Ndangalasi, J. Peacock, K. S. H. Peh, D. Sheil, T. Sunderland, M. D. Swaine, J. Taplin, D. Taylor, S. C. Thomas, R. Votere, and H. Woll. 2009. Increasing carbon storage in intact African tropical forests. Nature **457**:1003-U1003.

Malhi, Y. 2012. The productivity, metabolism and carbon cycle of tropical forest vegetation. Journal of Ecology **100**:65-75.

Malhi, Y., F. F. Amezquita, C. E. Doughty, J. E. Silva-Espejo, C. A. J. Girardin, D. B. Metcalfe, L. Aragao, L. P. Huaraca-Quispe, I. Alzamora-Taype, L. Eguiluz-Mora, T. R. Marthews, K. Halladay, C. A. Quesada, A. L. Robertson, J. B. Fisher, J. Zaragoza-Castells, C. M. Rojas-Villagra, Y. Pelaez-Tapia, N. Salinas, P. Meir, and O. L. Phillips. 2014. The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru. Plant Ecology & Diversity **7**:85-105.

Malhi, Y., L. Aragao, D. B. Metcalfe, R. Paiva, C. A. Quesada, S. Almeida, L. Anderson, P. Brando, J. Q. Chambers, A. C. L. da Costa, L. R. Hutyra, P. Oliveira, S. Patino, E. H. Pyle, A. L. Robertson, and L. M. Teixeira. 2009. Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. Global Change Biology **15**:1255-1274.

Malhi, Y., T. R. Baker, O. L. Phillips, S. Almeida, E. Alvarez, L. Arroyo, J. Chave, C. I. Czimczik, A. Di Fiore, N. Higuchi, T. J. Killeen, S. G. Laurance, W. F. Laurance, S. L. Lewis, L. M. M. Montoya, A. Monteagudo, D. A. Neill, P. N. Vargas, S. Patino, N. C. A. Pitman, C. A. Quesada, R. Salomao, J. N. M. Silva, A. T. Lezama, R. V. Martinez, J. Terborgh, B. Vinceti, and J. Lloyd. 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. Global Change Biology **10**:563-591.

Malhi, Y., C. E. Doughty, G. R. Goldsmith, D. B. Metcalfe, C. A. J. Girardin, T. R. Marthews, J. del Aguila-Pasquel, L. Aragao, A. Araujo-Murakami, P. Brando, A. C. L. da Costa, J. E. Silva-Espejo, F. F. Amezquita, D. R. Galbraith, C. A. Quesada, W. Rocha, N. Salinas-Revilla, D. Silverio, P. Meir, and O. L. Phillips. 2015. The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. Global Change Biology **21**:2283-2295.

Malhi, Y., C. A. J. Girardin, G. R. Goldsmith, C. E. Doughty, N. Salinas, D. B. Metcalfe, W. H. Huasco, J. E. Silva-Espejo, J. del Aguilla-Pasquell, F. F. Amezquita, L. Aragao, R. Guerrieri, F. Y. Ishida, N. H. A. Bahar, W. Farfan-Rios, O. L. Phillips, P. Meir, and M. Silman. 2017. The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. New Phytologist **214**:1019-1032.

Malhi, Y., T. Jackson, L. P. Bentley, A. Lau, A. Shenkin, M. Herold, K. Calders, H. Bartholomeus, and M. I. Disney. 2018a. New perspectives on the ecology of tree structure and tree communities through terrestrial laser scanning. Interface Focus **8**.

Malhi, Y., A. D. Nobre, J. Grace, B. Kruijt, M. G. P. Pereira, A. Culf, and S. Scott. 1998. Carbon dioxide transfer over a Central Amazonian rain forest. Journal of Geophysical Research-Atmospheres **103**:31593-31612.

Malhi, Y., O. L. Phillips, J. Lloyd, T. Baker, J. Wright, S. Almeida, L. Arroyo, T. Frederiksen, J. Grace, N. Higuchi, T. Killeen, W. F. Laurance, C. Leano, S. Lewis, P. Meir, A. Monteagudo, D. Neill, P. N. Vargas, S. N. Panfil, S. Patino, N. Pitman, C. A. Quesada, A. Rudas-Ll, R. Salomao, S. Saleska, N. Silva, M. Silveira, W. G. Sombroek, R. Valencia, R. V. Martinez, I. C. G. Vieira, and B. Vinceti. 2002. An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). Journal of Vegetation Science **13**:439-450.

Malhi, Y., L. Rowland, L. E. Aragao, and R. A. Fisher. 2018b. New insights into the variability of the tropical land carbon cycle from the El Niño of 2015/2016. The Royal Society.

Malhi, Y., M. Silman, N. Salinas, M. Bush, P. Meir, and S. Saatchi. 2010. Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. Global Change Biology **16**:3171-3175.

Marthews, T., T. Riutta, I. Oliveras Menor, R. Urrutia, S. Moore, D. Metcalfe, Y. Malhi, O. Phillips, W. Huaraca Huasco, M. Ruiz Jaén, C. Girardin, N. Butt, R. Cain, and Colleagues from the RAINFOR and GEM networks. 2014. Measuring tropical forest carbon allocation and cycling: a RAINFOR-GEM field manual for intensive census plots. Version 3.0. Manual. Global Ecosystems Monitoring Network.

Marthews, T. R., Y. Malhi, C. A. J. Girardin, J. E. S. Espejo, L. Aragao, D. B. Metcalfe, J. M. Rapp, L. M. Mercado, R. A. Fisher, D. R. Galbraith, J. B. Fisher, N. Salinas-Revilla, A. D. Friend, N. Restrepo-Coupe, and R. J. Williams. 2012. Simulating forest productivity along a neotropical elevational transect: temperature variation and carbon use efficiency. Global Change Biology **18**:2882-2898.

Meir, P., A. Shenkin, M. Disney, L. Rowland, Y. Malhi, M. Herold, and A. C. L. da Costa. 2017. Plant Structure-Function Relationships and Woody Tissue Respiration: Upscaling to Forests from Laser-Derived Measurements. Pages 89-105 *in* G. Tcherkez and J. Ghashghaie, editors. Plant Respiration: Metabolic Fluxes and Carbon Balance.

Metcalfe, D., P. Meir, L. Aragao, A. da Costa, S. Almeida, A. Braga, P. Goncalves, J. Athaydes, Y. Malhi, and M. Williams. 2008. Sample sizes for estimating key ecosystem characteristics in a tropical terra firme rainforest. Forest Ecology and Management **255**:558-566.

Metcalfe, D. B., G. P. Asner, R. E. Martin, J. E. S. Espejo, W. H. Huasco, F. F. F. Amezquita, L. Carranza-Jimenez, D. F. G. Cabrera, L. D. Baca, F. Sinca, L. P. H. Quispe, I. A. Taype, L. E. Mora, A. R. Davila, M. M. Solorzano, B. L. P. Vilca, J. M. L. Roman, P. C. G. Bustios, N. S. Revilla, R. Tupayachi, C. A. J. Girardin, C. E. Doughty, and Y. Malhi. 2014. Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. Ecology Letters **17**:324-332.

Metcalfe, D. B., P. Meir, L. Aragao, R. Lobo-do-Vale, D. Galbraith, R. A. Fisher, M. M. Chaves, J. P. Maroco, A. C. L. da Costa, S. S. de Almeida, A. P. Braga, P. H. L. Goncalves, J. de Athaydes, M. da Costa, T. T. B. Portela, A. A. R. de Oliveira, Y. Malhi, and M. Williams. 2010. Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. New Phytologist **187**:608-621.

Metcalfe, D. B., W. Rocha, J. K. Balch, P. M. Brando, C. E. Doughty, and Y. Malhi. 2018. Impacts of fire on sources of soil CO2 efflux in a dry Amazon rain forest. Global Change Biology **24**:3629-3641.

Moore, S., S. Adu-Bredu, A. Duah-Gyamfi, S. D. Addo-Danso, F. Ibrahim, A. T. Mbou, A. de Grandcourt, R. Valentini, G. Nicolini, G. Djagbletey, K. Owusu-Afriyie, A. Gvozdevaite, I. Oliveras, M. C. Ruiz-Jaen, and Y. Malhi. 2018. Forest biomass, productivity and carbon cycling along a rainfall gradient in West Africa. Global Change Biology **24**:E496-E510.

Morel, A. C., M. A. Sasu, S. Adu-Bredu, M. Quaye, C. Moore, R. A. Asare, J. Mason, M. Hirons, C. L. McDermott, E. J. Z. Robinson, E. Boyd, K. Norris, and Y. Malhi. 2019. Carbon dynamics, net primary productivity and human-appropriated net primary productivity across a forest-cocoa farm landscape in West Africa. Global Change Biology **25**:2661-2677.

Odum, H. T., and R. F. Pigeon. 1970. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. US Atomic Energy Comm.

Oliveras, I., L. Bentley, N. M. Fyllas, A. Gvozdevaite, A. F. Shenkin, T. Prepah, P. Morandi, K. S. Peixoto, M. Boakye, and S. Adu-Bredu. 2020. The influence of taxonomy and environment on leaf trait variation along tropical abiotic gradients. Frontiers in Forests and Global Change **3**:18.

Oliveras, I., C. Girardin, C. E. Doughty, N. Cahuana, C. E. Arenas, V. Oliver, W. H. Huasco, and Y. Malhi. 2014. Andean grasslands are as productive as tropical cloud forests. Environmental Research Letters **9**.

Peacock, J., T. Baker, S. Lewis, G. Lopez-Gonzalez, and O. Phillips. 2007. The RAINFOR database: monitoring forest biomass and dynamics. Journal of Vegetation Science **18**:535-542.

Peixoto, K. S., B. Marimon, B. S. Marimon, F. Elias, J. de Farias, R. Freitag, H. A. Mews, E. C. das Neves, N. Prestes, and Y. Malhi. 2017. Unravelling ecosystem functions at the Amazonia-Cerrado transition: II. Carbon stocks and CO2 soil efflux in cerradao forest undergoing ecological succession. Acta Oecologica-International Journal of Ecology **82**:23-31.

Peng, Y., K. J. Bloomfield, and I. C. Prentice. 2020. A theory of plant function helps to explain leaf-trait and productivity responses to elevation. New Phytol **226**:1274-1284.

Phillips, O. L., L. Aragao, S. L. Lewis, J. B. Fisher, J. Lloyd, G. Lopez-Gonzalez, Y. Malhi, A. Monteagudo, J. Peacock, C. A. Quesada, G. van der Heijden, S. Almeida, I. Amaral, L. Arroyo, G. Aymard, T. R. Baker, O. Banki, L. Blanc, D. Bonal, P. Brando, J. Chave, A. C. A. de Oliveira, N. D. Cardozo, C. I. Czimczik, T. R. Feldpausch, M. A. Freitas, E. Gloor, N. Higuchi, E. Jimenez, G. Lloyd, P. Meir, C. Mendoza, A. Morel, D. A. Neill, D. Nepstad, S.

Patino, M. C. Penuela, A. Prieto, F. Ramirez, M. Schwarz, J. Silva, M. Silveira, A. S. Thomas, H. ter Steege, J. Stropp, R. Vasquez, P. Zelazowski, E. A. Davila, S. Andelman, A. Andrade, K. J. Chao, T. Erwin, A. Di Fiore, E. Honorio, H. Keeling, T. J. Killeen, W. F. Laurance, A. P. Cruz, N. C. A. Pitman, P. N. Vargas, H. Ramirez-Angulo, A. Rudas, R. Salamao, N. Silva, J. Terborgh, and A. Torres-Lezama. 2009. Drought Sensitivity of the Amazon Rainforest. Science **323**:1344-1347.

Poorter, L., F. Bongers, T. M. Aide, A. M. Almeyda Zambrano, P. Balvanera, J. M. Becknell, V. Boukili, P. H. Brancalion, E. N. Broadbent, R. L. Chazdon, D. Craven, J. S. de Almeida-Cortez, G. A. Cabral, B. H. de Jong, J. S. Denslow, D. H. Dent, S. J. DeWalt, J. M. Dupuy, S. M. Duran, M. M. Espirito-Santo, M. C. Fandino, R. G. Cesar, J. S. Hall, J. L. Hernandez-Stefanoni, C. C. Jakovac, A. B. Junqueira, D. Kennard, S. G. Letcher, J. C. Licona, M. Lohbeck, E. Marin-Spiotta, M. Martinez-Ramos, P. Massoca, J. A. Meave, R. Mesquita, F. Mora, R. Munoz, R. Muscarella, Y. R. Nunes, S. Ochoa-Gaona, A. A. de Oliveira, E. Orihuela-Belmonte, M. Pena-Claros, E. A. Perez-Garcia, D. Piotto, J. S. Powers, J. Rodriguez-Velazquez, I. E. Romero-Perez, J. Ruiz, J. G. Saldarriaga, A. Sanchez-Azofeifa, N. B. Schwartz, M. K. Steininger, N. G. Swenson, M. Toledo, M. Uriarte, M. van Breugel, H. van der Wal, M. D. Veloso, H. F. Vester, A. Vicentini, I. C. Vieira, T. V. Bentos, G. B. Williamson, and D. M. Rozendaal. 2016. Biomass resilience of Neotropical secondary forests. Nature **530**:211-214.

Quesada, C., J. Lloyd, L. Anderson, N. Fyllas, M. Schwarz, and C. Czimczik. 2011. Soils of Amazonia with particular reference to the RAINFOR sites. Biogeosciences **8**:1415-1440.

Quesada, C. A., O. L. Phillips, M. Schwarz, C. I. Czimczik, T. R. Baker, S. Patino, N. M. Fyllas, M. G. Hodnett, R. Herrera, S. Almeida, E. A. Davila, A. Arneth, L. Arroyo, K. J. Chao, N. Dezzeo, T. Erwin, A. di Fiore, N. Higuchi, E. H. Coronado, E. M. Jimenez, T. Killeen, A. T. Lezama, G. Lloyd, G. Lopez-Gonzalez, F. J. Luizao, Y. Malhi, A. Monteagudo, D. A. Neill, P. N. Vargas, R. Paiva, J. Peacock, M. C. Penuela, A. P. Cruz, N. Pitman, N. Priante, A. Prieto, H. Ramirez, A. Rudas, R. Salomao, A. J. B. Santos, J. Schmerler, N. Silva, M. Silveira, R. Vasquez, I. Vieira, J. Terborgh, and J. Lloyd. 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences **9**:2203-2246.

Rifai, S. W., C. A. J. Girardin, E. Berenguer, J. del Aguila-Pasquel, C. A. L. Dahlsjo, C. E. Doughty, K. J. Jeffery, S. Moore, I. Oliveras, T. Riutta, L. M. Rowland, A. A. Murakami, S. D. Addo-Danso, P. Brando, C. Burton, F. E. Ondo, A. Duah-Gyamfi, F. F. Amezquita, R. Freitag, F. H. Pacha, W. H. Huasco, F. Ibrahim, A. T. Mbou, V. M. Mihindou, K. S. Peixoto, W. Rocha, L. C. Rossi, M. Seixas, J. E. Silva-Espejo, K. A. Abernethy, S. Adu-Bredu, J. Barlow, A. C. L. da Costa, B. S. Marimon, B. Marimon, P. Meir, D. B. Metcalfe, O. L. Phillips, L. J. T. White, and Y. Malhi. 2018. ENSO Drives interannual variation of forest woody growth across the tropics. Philosophical Transactions of the Royal Society B-Biological Sciences **373**.

Rifai, S. W., S. Li, and Y. Malhi. 2019. Coupling of El Niño events and long-term warming leads to pervasive climate extremes in the terrestrial tropics. Environmental Research Letters **14**:105002.

Riutta, T., Y. Malhi, L. K. Kho, T. R. Marthews, W. Huaraca Huasco, M. Khoo, S. Tan, E. Turner, G. Reynolds, S. Both, D. F. R. P. Burslem, Y. A. Teh, C. S. Vairappan, N. Majalap, and R. M. Ewers. 2018. Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests. Global Change Biology **24**:2913-2928.

Rocha, W., D. B. Metcalfe, C. E. Doughty, P. Brando, D. Silverio, K. Halladay, D. C. Nepstad, J. K. Balch, and Y. Malhi. 2014. Ecosystem productivity and carbon cycling in intact and annually burnt forest at the dry southern limit of the Amazon rainforest (Mato Grosso, Brazil). Plant Ecology & Diversity **7**:25-40.

Rowland, L., A. C. L. Da Costa, D. R. Galbraith, R. S. Oliveira, O. J. Binks, A. A. R. Oliveira, A. M. Pullen, C. E. Doughty, D. B. Metcalfe, S. S. Vasconcelos, L. V. Ferreira, Y. Malhi, J.

Grace, M. Mencuccini, and P. Meir. 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. Nature **528**:119-122.

Sist, P., E. Rutishauser, M. Peña-Claros, A. Shenkin, B. Hérault, L. Blanc, C. Baraloto, F. Baya, F. Benedet, and K. E. Da Silva. 2015. The Tropical managed Forests Observatory: a research network addressing the future of tropical logged forests. Applied Vegetation Science **18**:171-174.

Swinfield, T., S. Both, T. Riutta, B. Bongalov, D. Elias, N. Majalap-Lee, N. Ostle, M. Svatek, J. Kvasnica, D. Milodowski, T. Jucker, R. M. Ewers, Y. Zhang, D. Johnson, Y. A. Teh, D. Burslem, Y. Malhi, and D. Coomes. 2020. Imaging spectroscopy reveals the effects of topography and logging on the leaf chemistry of tropical forest canopy trees. Global Change Biology **26**:989-1002.

Thomson, E. R., Y. Malhi, H. Bartholomeus, I. Oliveras, A. Gvozdevaite, T. Peprah, J. Suomalainen, J. Quansah, J. Seidu, C. Adonteng, A. J. Abraham, M. Herold, S. Adu-Bredu, and C. E. Doughty. 2018. Mapping the Leaf Economic Spectrum across West African Tropical Forests Using UAV-Acquired Hyperspectral Imagery. Remote Sensing **10**.

Urrutia-Jalabert, R., Y. Malhi, and A. Lara. 2015. The Oldest, Slowest Rainforests in the World? Massive Biomass and Slow Carbon Dynamics of Fitzroya cupressoides Temperate Forests in Southern Chile. Plos One **10**.

Supplementary Information

Table S1. Field methods for intensive monitoring of NPP (see also RAINFOR-GEM manual (Marthews et al. 2014))