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

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## **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;

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

90

## 91 **2. Background and History**

92

### 93 *2.1 Context*

94 Attempts to describe the full carbon and energy budgets of ecosystems have  
95 been a feature of ecosystem ecology since the 1960s. Much effort has focused on  
96 northern temperate and boreal systems, which tended to have more convenient  
97 access for better-funded institutions. The first attempts to describe the carbon  
98 cycle of a tropical forest was conducted in Puerto Rico by Odum and Pigeon  
99 (1970) and in Thailand by Kira (1967). International programmes in the 1970s  
100 fuelled attempts at similar descriptions of ecosystems around the world,  
101 including a tropical forest site in Malaysia (Kira 1978). In parallel, the first  
102 attempts emerged to quantify the primary productivity of the biosphere, by  
103 scaling up from site-based estimates in a range of biomes {Lieth, 1975 #635}.  
104 These early attempts were constrained by limited tools for measuring carbon  
105 dioxide gas exchange (*e.g.*, absorbing chemicals were used at the time, rather  
106 than portable infrared gas analysers). Such activities fell into a lull in the late  
107 1970s and early 1980s, but resurfaced in the 1990s with increased scientific  
108 interest in the global carbon cycle and its links with climate change, specifically  
109 to pinpoint the role of the terrestrial biosphere as either a source or a sink of  
110 carbon. This renewed interest was coupled with the development of  
111 micrometeorological tools and techniques, such as eddy covariance, to measure  
112 the net flux of carbon dioxide above vegetation canopies. At the same time,  
113 global biosphere models were advancing substantially, and there was increased  
114 demand for empirical ecosystem-level quantification of key aspects and  
115 processes of the biosphere carbon cycle to develop and test these models.  
116 Comprehensive measurements of the components of the carbon budgets  
117 provided a source of validation for models and micrometeorological studies, but  
118 also enabled a deeper process-level understanding of how different components  
119 of the system contributed to the magnitude and variability of the carbon budget.

120

121 Ecosystem flux measurements in the tropics tended to lag behind better-funded  
122 studies in North America and Europe. The first eddy covariance studies in the  
123 tropics were in Brazilian Amazonia in the late 1980s and early 1990s (Fan et al.  
124 1990, Grace et al. 1995, Malhi et al. 1998), from where they substantially  
125 expanded through the LBA (Large Scale Biosphere-Atmosphere study in  
126 Amazonia) programme. However, eddy covariance approaches remained limited  
127 in coverage in the tropics because of the specialised equipment required, and, on  
128 their own, only described the net exchange of carbon, water and energy between  
129 ecosystems and the atmosphere. Their large footprint (100s-1000s m<sup>2</sup>), while an  
130 advantage in some aspects, also limit their utility in fragmented and patchy  
131 landscapes, or in sites with extreme topography.

132

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

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

160

## 161 *2.2. Motivation for development of the GEM network*

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

176

177 Another key tool in biosphere-focussed ESS has been the development of field  
178 observation networks. The macrosopes need testing and ground-truthing  
179 against field observations that are embedded in a rich understanding of local  
180 ecosystem processes dynamics. Some networks such as the FLUXNET network of  
181 eddy covariance flux towers have tended to be focused on resource-rich regions  
182 such as North America, Europe, East Asia and Australia. Others, such as the  
183 Forest Plots and CTFS/ForestGEO networks mentioned above have developed  
184 impressive coverage of the old-growth tropical rainforest zones, while others  
185 (2ndFor and the Tropical Managed Forests Observatory) have focused on

186 secondary and logged forests (Sist et al. 2015, Poorter et al. 2016). These  
187 networks have focused on forest inventories and yielded important insights into  
188 forest properties such as the net tropical forest carbon sink, continental  
189 variation in biodiversity and biomass dynamics, and rates of recovery from  
190 disturbance. However, integrating these results with the ESS macroscopes of  
191 modelling and remote sensing presents some challenges. Optical remote sensing  
192 focuses on canopy surface reflectance and fluorescence, often to infer fraction of  
193 absorbed photosynthetic radiation and hence GPP. Radar- or lidar-based remote  
194 sensing provides insights into structure and biomass, but does not directly  
195 capture the processes that generate that structure. Modelling of the carbon cycle  
196 has required representation of processes such as allocation, autotrophic  
197 respiration and soil carbon dynamics, aspects that are not immediately  
198 deducible from forest inventories alone. *GEM seeks to provide a bridge between*  
199 *the forest inventory networks and Earth system macroscopes*: it emerged out of  
200 the RAINFOR Amazonian forest plots network, but by focusing on a more holistic  
201 view of carbon cycling, it seeks to speak the “language” of biosphere carbon  
202 cycling models. Similarly, the recent focus on canopy functional traits under  
203 GEM-TRAITS (see below) seeks to act as a bridge between environment, tree  
204 community composition, ecosystem carbon cycling and remote sensing.

205  
206

### 207 *2.3 Network Development*

208 The GEM network emerged gradually from the RAINFOR network, starting in  
209 2005 with the introduction of detailed carbon budget studies at two relatively  
210 fertile RAINFOR plots in Tambopata, Peru, compared with two relatively infertile  
211 plots in Caxiuanã, Brazil. The impetus for this study was the discovery that the  
212 woody productivity of forests in western Amazonia appeared to be generally  
213 greater than that of eastern Amazonia (Malhi et al. 2004), a feature that  
214 appeared related to soil properties (Quesada et al. 2012). It was unclear whether  
215 this difference in woody growth rates reflected a difference in GPP (i.e. forests in  
216 lowland Peru were intrinsically more productive, perhaps because the leaves  
217 had higher nutrient concentrations), or whether there were differences in the  
218 allocation of captured carbon (*e.g.* a larger fraction of NPP goes to wood, or there  
219 is lower expenditure in autotrophic respiration). The results from this study  
220 were presented by Aragão et al. (2009) and Malhi et al. (2015), showing that the  
221 difference was mainly driven by lower autotrophic respiration in the Peruvian  
222 sites, with smaller influences from differences in allocation to wood and in  
223 overall GPP. This work highlighted the importance of understudied components  
224 of the carbon cycle, such as Carbon Use Efficiency (the ratio of NPP to GPP), or  
225 fractional allocation of NPP to canopy, wood and root tissue.

226

227 In parallel, the LBA (Large-Scale Biosphere-Atmosphere Programme in  
228 Amazonia) was collecting detailed carbon cycle measurements at a number of  
229 locations in Brazilian Amazonia, but the work was dispersed across multiple  
230 research organisations. Malhi et al. (2009) presented a compilation of data for  
231 three forest sites in Brazilian Amazonia, including Caxiuanã, gathered through  
232 LBA that helped provide an overall framework for providing a holistic carbon  
233 cycle description of forest ecosystems. This showed both the potential for  
234 detailed carbon cycle descriptions, how they cross-checked well with eddy  
235 covariance measurements, and the relatively small magnitude (in carbon budget  
236 terms) of some harder-to measure terms such as lateral dissolved inorganic

237 carbon flows and methane and volatile organic carbon emissions. In addition,  
238 Metcalfe et al. (2010) presented a detailed carbon budget analysis for the drought  
239 and control forest plots in Caxiuanã, showing that long-term drought resulting in  
240 increased autotrophic respiration and hence a reduced proportion of GPP being  
241 allocated to biomass production.

242  
243 In 2007, similar plots to those in Tambopata and Caxiuanã were established at  
244 multiple sites along a ~3500 m elevation gradient in south-eastern Peru  
245 (Girardin et al. 2010, Malhi et al. 2010), stretching upwards from the lowland  
246 rainforest site at Tambopata. The elevation transect had already been  
247 established by the Andes Biodiversity and Ecosystems Research Group (ABERG)  
248 in the early 2000s (Malhi et al. 2017) and has since become a major focus of  
249 interdisciplinary research into how elevation and temperature control  
250 ecosystem composition and function, and how these are changing under global  
251 warming.

252  
253 A large boost to the nascent GEM network came with funding from the Gordon  
254 and Betty Moore Foundation over 2008-2014, which enabled establishment and  
255 monitoring of 16 plots across Amazonia and the Andes (Malhi et al. 2015, Malhi  
256 et al. 2017). This period of funding also enabled formalisation of this network,  
257 including development of a detailed protocol available online, training courses in  
258 South America, a website <http://gem.tropicalforests.ox.ac.uk/> and the  
259 establishment and use of the name GEM. A key output from this period was the  
260 publication of eight site-based papers describing the carbon budget of each site  
261 in South America, in a special issue of *Plant Ecology and Diversity* in 2014  
262 (Araujo-Murakami et al. 2014, da Costa et al. 2014, del Aguila-Pasquel et al.  
263 2014, Doughty et al. 2014b, Galbraith et al. 2014, Girardin et al. 2014, Huasco et  
264 al. 2014, Malhi et al. 2014, Rocha et al. 2014). Many of these papers were led by  
265 local students and researchers, and provided a model for building local capacity  
266 in analysis and paper writing. For the first time, a library of detailed carbon cycle  
267 assessments was being assembled, each addressing locale-specific questions, but  
268 ultimately contribute to broader, biome-wide analyses (Doughty et al. 2015b,  
269 Malhi et al. 2015, Malhi et al. 2017).

270  
271 The success of this model for an intensive carbon cycle plots network in South  
272 America led to similar project development in SE Asia and in Africa. A series of  
273 plots were established in Malaysian Borneo; first with two plots at Lambir,  
274 Sarawak in 2007 as part of a PhD project (Kho et al. 2013), then 7 plots were  
275 established in Sabah in 2010-11 in old-growth and logged forest under the  
276 auspices of the SAFE (Stability of Altered Forest Ecosystems) programme (Ewers  
277 et al. 2011, Riutta et al. 2018). In Africa, a NERC research grant enabled  
278 establishment in 2011 of 14 plots along a wet-dry gradient in Ghana and 6 plots  
279 in Gabon, providing the first measured NPP values for African lowland forests  
280 (Moore et al. 2018).

281  
282 In addition to this pantropical coverage in old-growth systems, other trends in  
283 recent years have been increased coverage of human-modified forests (e.g.  
284 logged forests, burned forests and tree crops), and the beginnings of coverage in  
285 savanna and grassy ecosystems (Figure 1). For example, recent plots have been  
286 established in natural forest-cocoa agroforest gradients in Ghana (Morel et al.  
287 2019), in natural forest-coffee agroforest gradients in Ethiopia (Morel et al,

288 unpublished), in savannas in Brazil (Peixoto et al. 2017), Gabon and South Africa,  
289 and along gradient of human-disturbance in Brazilian Amazonia, including  
290 selectively-logged forests, burned forests, and secondary forests (Berenguer et  
291 al. 2018). A number of GEM sites also span control and treatment plots in  
292 experimental treatments, including the 20-year old drought experiment in the  
293 Caxiuana, Brazil (Rowland et al. 2015), the fire experiment in Tanguro, Brazil  
294 (Brando et al. 2016) and the Free Air Carbon Dioxide Enrichment experiment in  
295 Australia {Jiang, 2020 #637}.

296  
297 Separate from the GEM network, there has been a surge of detailed NPP (and, to  
298 a lesser extent, GPP) measurements in tropical forests, particularly in SE Asia  
299 and in China and more recently in Central Africa (Rwanda and the Congos).  
300 Anderson-Teixeira et al. (2016) provide a summary of these data across the  
301 tropics, incorporated in the Global Forest Carbon (ForC) database ([https://forc-  
302 db.github.io](https://forc-db.github.io)). In recent years GEM has also sought to be a convening hub for this  
303 wider tropical network of carbon cycling and productivity data, bringing in self-  
304 funded partners who wish to standardise data collection protocols, take  
305 advantage of the data management within the GEM network, and contribute to  
306 regional or global analyses.

307  
308  
309 Although the focus of core GEM activities has been predominantly tropical, there  
310 have been occasional forays into temperate forests while employing the same  
311 protocol. Fenn et al. (2015) applied this protocol in Wytham Woods, a long-  
312 established maritime broadleaf woodland near Oxford, UK. Urrutia-Jalabert et al.  
313 (2015) reported on the productivity and carbon dynamics of *Fitzroya*-dominated  
314 temperate rainforests in Chile (“the oldest, slowest rainforests on Earth”) and  
315 more recently similar plots have been established in Ponderosa pine forests in  
316 Arizona (Doughty et al. 2020) and *Populus tremuloides* stands in Colorado (B.  
317 Blonder, *pers. comm.*).

318  
319 In terms of climate space, the GEM network now covers substantial elevation  
320 gradients in the tropics, as well as spanning the lowlands of these regions  
321 (Figure 2a). Water stress gradients are also spanned, ranging from dry savannas  
322 in Ghana and South Africa, through mesic savannas, seasonally dry forests and  
323 aseasonal rainforests (Figure 2c). The coverage of some seasonal temperate sites  
324 provides some useful contrasts with high elevation tropical sites (Figure 2c),  
325 enabling exploration of the role of seasonality in shaping ecosystem carbon  
326 cycling and function. A selection of GEM sites are shown in Figure 3.

327  
328  
329 **3. Features of the GEM Network**

330  
331 The core framework which defines the GEM network is the estimation of the key  
332 components of ecosystem productivity, through routine measurements at  
333 relatively high frequency (biweekly/monthly/trimonthly, depending on site and  
334 measurement type). A minimum requirement would be measurement of the  
335 main components of NPP (canopy litterfall, woody growth and fine root  
336 productivity). Many GEM sites also cover the main components of ecosystem  
337 respiration (woody stem respiration, leaf respiration and soil respiration  
338 partitioning into heterotrophic and autotrophic components), which enable

339 estimations of total autotrophic respiration. The summation of autotrophic  
340 respiration and NPP gives an estimation of GPP (on annual or longer timescales,  
341 when the balance between photosynthesis and vegetation use of photosynthate  
342 can be assumed to be close to equilibrium).

343  
344 An important attribute of the GEM protocol is the standardisation of sampling  
345 protocols. There is potential of much variation in protocols, and this  
346 standardisation facilitates comparisons across regions and ecosystems. Soils  
347 collected by the central GEM project are collected using the RAINFOR soil  
348 sampling protocol (Quesada et al. 2011). Such samples have largely been  
349 analysed in the cross-referenced soil laboratories of INPA in Manaus, Brazil (for  
350 most sites in Amazonia) or at the University of Leeds, UK (for most other sites).

351  
352 An additional key feature of the GEM protocol is its emphasis on relatively low  
353 technology and low-cost approaches. Conversely, it is fairly heavy in human  
354 labour inputs, typically requiring field teams to spend a week every month at a  
355 cluster of field plots, and longer periods every three months. These features (low  
356 capital inputs and high labour inputs) have made it well-suited to many  
357 developing region contexts. This has facilitated its spread across multiple sites in  
358 low- and middle-income countries, where students and technicians are often  
359 available to conduct research but capital and equipment resources are low. Its  
360 application has been more challenged in high-income countries, where labour  
361 costs are higher (including tropical countries such as northern Australia). As a  
362 result, the GEM network has expanded well across the tropics, to the extent that  
363 there are currently more site-level NPP data available from tropical regions than  
364 from temperate regions. This is a remarkable reversal of the normal pattern of  
365 ecological data availability, where the tropics tend to have the strongest data  
366 deficits.

### 367 368 *3.1 Plot location and size*

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

### 383 384 *3.2 GEM field methodologies*

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

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

396

### 397 3.2.1 Components of Net Primary Productivity

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

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

406

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

412

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

419

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

432

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

437

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

### 445 3.2.2 Components of Ecosystem Respiration

446 The more complete GEM sites also measure the main components of ecosystem  
447 respiration. Summation of NPP and the autotrophic component of respiration  
448 enable the estimation of GPP, and the difference between above-ground NPP and  
449 total soil CO<sub>2</sub> efflux provides an estimate of net carbon balance.

450  
451 Total soil CO<sub>2</sub> efflux is measured at monthly frequency in a grid across the plot,  
452 at fixed collar locations. Many GEM sites attempt to partition this efflux into  
453 components (litter layer, soil organic matter and fine roots) by installing a  
454 separate partitioning experiment (Metcalf et al. 2018). Furthermore, at some  
455 sites a fine mesh treatment is employed, which enables passage of fungal hyphae  
456 but acts as a barrier to fine roots. This enables an estimation of the respiration  
457 associated with mycorrhizal fungi – as this respiration is derived from recent  
458 photosynthate transferred directly via plant roots, it can be considered an  
459 additional component of NPP.

460  
461 Above ground, *woody tissue respiration* is measured at monthly frequency by  
462 installing similar collars on a subset of tree stems, scaling to the whole tree using  
463 tree surface area allometries, and then scaling to the full plot tree census.

464  
465 *Canopy foliar dark respiration* is not measured regularly, but estimated in canopy  
466 sampling campaigns (either seasonally or in a one-off campaign associated with  
467 leaf traits collection, see below) by applying gas exchange measurements to  
468 leaves on cut branches. Frequently, *leaf photosynthetic parameters* are also  
469 measured in the same campaigns (photosynthesis under high light and/or high  
470 carbon dioxide), which can be employed in a canopy modelling framework to  
471 provide an independent estimate of GPP.

472  
473 *Respiration from dead wood* is a term that is measured at a few GEM plots by  
474 attaching collars to dead trunks or placing small dead wood material in closed  
475 chambers. It can be a significant component of ecosystem heterotrophic  
476 respiration (Gurdak et al. 2014), especially so in logged forests.

### 477 3.2.3 Missing terms

478  
479 There are a number of components of NPP that are challenging to quantify and  
480 are non-standard in NPP or carbon cycle assessments. These include, in likely  
481 declining order of importance: production of root exudates and transfer of  
482 photosynthate to mycorrhizae (although at some sites GEM estimates these  
483 through the soil respiration partitioning experiment, as described above),  
484 canopy productivity by epiphytes that senesce and decay *in situ* in the canopy,  
485 productivity of the herbaceous understory (not routinely measured in forest  
486 plots), release of volatile organic compounds such as isoprene or monoterpenes,  
487 methane fluxes from the soil, and lateral export of material as particulate or  
488 dissolved organic carbon. One cross check of whether these extra terms are

489 significant is through constructing more complete carbon budgets where rich  
490 data streams enable this and cross-comparisons with independent eddy-  
491 covariance estimates of GPP (see below). Malhi et al. (2009) took advantage of  
492 the comprehensive range of research conducted in Brazilian Amazonia under the  
493 auspices of the LBA programme to quantify many of these terms for three old-  
494 growth *terra firme* Amazonian forests. VOC, methane and lateral carbon effluxes  
495 were found to be small in relation to the main carbon flux components above.

496

### 497 *3.2.4 Functional traits collection*

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

504

505 Use of a plant functional traits framework has provided rich ground for  
506 theoretical and empirical analyses, particularly in high biodiversity tropical  
507 ecosystems where use of a few key functional traits is more tractable than  
508 engaging with thousands of plant species. To address this challenge, the GEM-  
509 TRAITS programme has been collecting leaf and wood functional traits for  
510 dominant canopy species in GEM sites across the tropics. The collection protocol  
511 is stratified according to basal area dominance, with tree species that contribute  
512 most of plot basal area (a proxy for canopy area) being prioritised. A goal of  
513 sampling the fewest species that contribute to 80% of the basal area is the target,  
514 although this is not always achieved in diverse lowland rainforest sites.

515 Traits collected include leaf morphological, chemical and photosynthetic traits,  
516 and in some cases wood and leaf hydraulic traits. As with many features of GEM,  
517 the traits programme and methodology were initially developed along the  
518 Amazon-Andes transect in Peru, before being deployed across all tropical  
519 continents. These traits data have a variety of applications, including  
520 understanding the link between leaf and wood traits and ecosystem dynamics,  
521 parametrizing canopy parameters in biosphere models, and linking canopy traits  
522 to remote sensing data.

523

## 524 **4 Challenges for the GEM approach**

525

### 526 *4.1 Uncertainty and Error Propagation*

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

535

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

540 Each of these uncertainties can be accounted for by rigorous error propagation  
541 during summation. Random sampling errors can be estimated from the variance  
542 of observations (Metcalf et al. 2008), but systematic errors are assigned  
543 (usually conservatively) from expert judgement.  
544

545 Given the inherent uncertainty in each type of measurement, one remarkable  
546 feature is that overall uncertainty in estimated NPP or GPP can be fairly  
547 constrained, typically around  $\pm 10\%$  (Malhi et al. 2016, 2017). This under-  
548 appreciated feature comes from the nature of error propagation: as each  
549 component measurement is independent, uncertainties propagate in quadrature,  
550 and hence relatively slowly compared to the summation. Hence, the biometric  
551 GEM approach can compare favourably against, for example, an eddy covariance  
552 approach to estimating GPP. The latter relies essentially only on one variable  
553 being measured (net carbon flux), and hence is more vulnerable to any  
554 systematic biases associated with that single measurement type.  
555

#### 556 *4.2 Cross-checks with eddy covariance measurements*

557 One useful cross-check for the GEM approach has been cross-checks with the  
558 independent “top-down” eddy-covariance approaches to estimate GPP. Eddy  
559 covariance is a tower-based approach that continuously measures the net  
560 turbulent exchange of carbon dioxide between the vegetation canopy and the  
561 atmosphere. Once suitable corrections are applied for estimating daytime  
562 ecosystem respiration (based on night-time ecosystem respiration rates), the  
563 total ecosystem photosynthesis (GPP) can be estimated. Eddy covariance comes  
564 with its own challenges, particularly under low turbulence night-time conditions.  
565 Nevertheless, good agreement between eddy covariance and GEM approaches  
566 provides some reassurance that no major carbon cycle components are being  
567 missed, and that measurement and scaling uncertainties are well-constrained.  
568

569 At three sites in Brazilian Amazonia (Malhi et al. 2009), agreement between the  
570 two approaches has been good. Campioli et al. (2016) conducted a systematic  
571 cross-comparison of eddy covariance and biometric approaches across 18 forest  
572 sites (spanning boreal, temperate and the same three Brazilian tropical forests),  
573 and found no significant difference in estimation of annual mean GPP and total  
574 ecosystem respiration between the two approaches.  
575

#### 576 *4.3 Logistics and management*

577 The creation and management of a global observation network inevitably  
578 generates a number of management and logistical challenges. There has been a  
579 need to support central coordination, management and data cleaning, in addition  
580 to field data collection. The central coordination activities of GEM were  
581 supported by a number of funding initiatives, notably from the Gordon and Betty  
582 Moore Foundation (2008-2012) over the initial phase of developing a  
583 standardised network over the Amazon-Andes, from the European Research  
584 Council (2013-2018) that supported development and integration into a global  
585 network and the advance of the traits data collection, and from the Natural  
586 Environment Research Council (2016-2020) to continue this collection, analysis  
587 and databasing in the wake of the 2015/16 El Niño event. Both carbon cycle and  
588 traits data are stored in a dedicated GEM database {Shenkin, 2017 #640}, and  
589 made freely available to all users, subject to fair use agreements that

590 acknowledge and protect the prior publication rights of data collectors and data  
591 providers ([DOI to be inserted in final proof])  
592

593 One key advantage of GEM is the standardisation of data collection protocols  
594 across the global network, though inevitably there are some small local  
595 variations in protocols (sometimes inadvertent, sometimes deliberate because of  
596 locale-specific challenges or questions). For example, in sites with high elephant  
597 abundance such as in Gabon or Sabah, litter traps are frequently deliberately  
598 destroyed by elephants and an alternative or additional protocol of marking out  
599 discrete quadrants on the ground is employed, even though this risks higher  
600 rates of *in situ* decomposition prior to collection because of the activities of litter  
601 layer fauna. Small variations in protocols can also lead to substantial additional  
602 challenges in incorporation into the database.  
603

#### 604 *4.4 Capacity-strengthening and training*

605 The development of local research capacity is an essential feature of GEM. The  
606 basic research model is dependent on autonomous and long-term local collection  
607 of data, which requires the training of local students or technicians in both data  
608 collection and analysis. This is achieved through workshops and hands-on  
609 training *in situ* and online. A number of GEM students have gone on to Masters  
610 and PhD qualifications, in many cases using the GEM data they collected in the  
611 field. Local students are strongly encouraged and supported to lead scientific  
612 papers based on their local site data (e.g. Huasco et al. 2014, Peixoto et al. 2017,  
613 Addo-Danso et al. 2018, Ibrahim et al. 2020), though the challenges of writing a  
614 paper to international scientific journal standards are not to be underestimated.  
615

616 A particularly exciting feature of GEM has been South-South training, where  
617 experienced field data collectors in one region have the opportunity to travel to  
618 other regions to train in plot installation and data collection. As an example,  
619 students and data technicians from Cusco, Peru (as the base for the Andes-  
620 Amazon transect, the oldest and most advanced of our GEM focal regions) have  
621 led training events and plot installation in Brazil, Belize, Chile, Gabon and  
622 Malaysia. Similarly, students from Ghana have collected traits data in Gabon, and  
623 students from Gabon have helped establish plots in South Africa. Such exchange  
624 enables flourishing cross-tropics relationships and collaborations amongst an  
625 emerging generation of tropical ecosystem ecologists.  
626

#### 627 *4.5 Long term funding and prioritisation*

628 A key challenge, as with all long-term observation networks, is maintaining long-  
629 term funding. In GEM the funding model to date has been dominated by a  
630 number of locale-focused grants centered on specific questions (e.g. temperature  
631 in the Andes, logging in Malaysia, fire in Amazonia), coupled with some large  
632 central grants that support network expansion, management and coordination.  
633 In some cases, notably in more prosperous tropical countries such as Brazil and  
634 Malaysia, this has led to locally sourced funding that enables continuation of  
635 measurements for the long-term. In most countries, however, continued data  
636 collection is dependent on centralised international funding. As the network has  
637 matured, additional partners have been brought into the network, who bring  
638 their own funding but would like their data to fit within the wider standardised  
639 network and contribute to large-scale analyses.  
640

641 Dependency on centralised funding leads to a trade-off between supporting long-  
642 term time series, vs. expanding coverage of sites. How much information is  
643 gained from maintaining a site with monthly data collection for over a decade  
644 (e.g. the Tambopata, Peru plots were run over the period 2005-2017 (Malhi et al.  
645 2014)) vs. investing in new collection of a few years of data from additional sites  
646 that enable better coverage of the heterogeneity of the tropical forest biome?  
647 The answer to this depends of course on the question being asked, and on the  
648 temporal and spatial variability being observed. Long-term time series have, for  
649 example, been immensely valuable in understanding the impacts of the 2015/6  
650 El Niño (Rifai et al. 2018), and, in conjunction with forest inventories, may be the  
651 most cost-effective and practical way to collect long-term carbon flux time series  
652 and understanding global change impacts on forests. Broadly however, the focus  
653 in recent years has been to expand spatial coverage (either through setting up  
654 new plots or by bringing on board partners with new data collections), at the  
655 expense of long-term continuation of existing sites. However, it typically takes a  
656 few months to set up a new cluster of sites, and several months before all data  
657 collection protocols are properly underway and producing anything useful.  
658 Hence very short-term projects have a poor ratio between set-up phase and  
659 productive data output.

660

## 661 **5. Key Discoveries**

662

### 663 *5.1 Variation of productivity and allocation across regions*

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

678

679 Carbon use efficiency (CUE), the ratio of NPP to GPP, is a highly uncertain term in  
680 global biosphere modelling, yet has received much less attention than GPP. GEM  
681 has greatly increased the number of direct estimates of tropical CUE but found  
682 great site-to-site variability across lowland tropical forest sites. For example,  
683 CUE in lowland Amazonia averages 0.37 but ranges between ~0.25 and ~0.45  
684 across Amazonian GEM sites. Overall, Amazonian forests have lower CUE in  
685 forest stands with slow growing trees and with lower fertility (Doughty et al.  
686 2018a).

687

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

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

697  
698 The GEM network has also revealed striking regional differences. Until around  
699 2010, most understanding of tropical forest productivity and carbon cycling has  
700 emerged from the Neotropics, and in particular from eastern Amazonia, which  
701 was the focus of the LBA programme in Brazil. The wider GEM network has  
702 revealed that eastern Amazonia has amongst the lowest net primary  
703 productivity observed in the humid lowland tropics, probably because of its  
704 highly weathered soils. Higher values of productivity are observed in western  
705 Amazonia (Aragão et al. 2009, Malhi et al. 2015), Borneo (Kho et al. 2013, Riutta  
706 et al. 2018) and most remarkably in West Africa (Moore et al. 2018), which has  
707 the highest recorded values for mature forests. The reasons for these contrasts is  
708 unclear, and are under investigation in an ongoing synthesis study across the  
709 network.

710  
711 In old growth forests, GEM has also highlighted the relative importance of  
712 turnover time (mortality rates) in determining forest biomass and vegetation  
713 carbon stocks. Spatial gradients in biomass across the tropics are only weakly  
714 shaped by gradients in woody productivity, and much more strongly determined  
715 by gradients in mortality and turnover time (Galbraith et al. 2013, Malhi et al.  
716 2015, Johnson et al. 2016). This presents a major challenge for terrestrial  
717 biosphere models, which have tended to prioritise the modelling of  
718 photosynthesis and productivity over the far less well-understood process of  
719 tree mortality (Friend et al. 2014).

## 720 721 *5.2 Seasonal variation of productivity, allocation and phenology*

722  
723 Understanding the processes that govern seasonal carbon allocation strategies of  
724 humid and dry forests help provide a carbon and nutrient budget perspective on  
725 phenology. Many GEM sites collect bi-weekly data on fruit and flower fall.  
726 Focussing on tropical South American plots, Girardin et al. (2016) provided  
727 evidence that suggests solar irradiance may be a cue for flowering events  
728 governed by phylogeny. The energetic cost of reproduction was found to be  
729 trivial, suggesting that nutrient considerations are the predominant  
730 physiological constraint on timing and abundance of flowering and fruiting.  
731 In terms of the overall allocation of NPP, two main seasonal allocation strategies  
732 were identified in Amazonian forests: trade-offs between allocation to wood and  
733 canopy in dry sites, and trade-offs between allocation to roots and canopy in  
734 humid sites (Doughty et al. 2014a, Girardin et al. 2016). When considering the  
735 full GPP, NPP and respiration budget, the data suggested that there is a temporal  
736 decoupling between total photosynthesis from eddy covariance and total carbon  
737 usage (from GEM studies) that indicates that nonstructural carbohydrates could  
738 be serving as seasonal stores of energy reserves that have a strong influence on  
739 shaping patterns of seasonality and interannual variability (Doughty et al. 2015a,  
740 Doughty et al. 2015b).

## 741 742 *5.3 Logging, disturbance and the ecosystem carbon cycle*

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

#### 761 762 *5.4 Response of carbon cycle to droughts*

763 The rate of rise of atmospheric CO<sub>2</sub> shows strong interannual variability, and it is  
764 known that this variability is largely determined by the variability of the net  
765 carbon balance of the tropical terrestrial biosphere (Malhi et al. 2018b).

766 Monitoring in the GEM network has now spanned a number of major drought  
767 events in the tropics, most notably the 2010 drought in Amazonia (Doughty et al.  
768 2015a, Doughty et al. 2015b) and the 2015/16 El Niño, which was the strongest  
769 such event in decades. Moreover, these drought events sit on top of a long-term  
770 anthropogenic warming trend (Rifai et al. 2019), which means that every major  
771 drought event occurs under conditions of increasing peak temperature and  
772 atmospheric water stress.

773  
774 Doughty et al. (2015a) examined impacts of the 2010 drought in 13 GEM sites  
775 across Amazonia. They found that, as expected, the drought caused a reduction  
776 in GPP but that, remarkably, there was no corresponding reduction in NPP and  
777 or woody growth; instead, there was a decline in autotrophic respiration. The  
778 study proposed that this indicated a decreased investment in plant maintenance  
779 and defence in favour of continued biomass growth, but that such a strategy may  
780 contribute to increased mortality in the years following drought. A worldwide  
781 analysis of GEM plots in the 2015/16 El Niño shows a similar pattern of little  
782 shift in NPP, but offers an additional insight in showing a strong pulse of  
783 increased soil respiration, suggesting that the interannual variability of the  
784 tropical forest carbon cycle is driven mainly by soil processes rather than plant  
785 processes (Malhi et al., unpublished analysis). Coupling traits data with the  
786 longer term forest inventories also enables an improved description of potential  
787 shifts in ecosystem function traits over time, as has been demonstrated by the  
788 Ghana rainfall gradient study (Aguirre-Gutierrez et al. 2019).

#### 789 790 *5.5 Linking canopy traits to ecosystem productivity and resilience through theory 791 and models*

792 A key goal of the traits-based research in GEM has been to link canopy functional  
793 traits to ecosystem productivity and resilience under climate change. Both

794 theory and modelling approaches have been applied to this challenge, with an  
795 initial focus being the Andes-Amazon elevation gradient (Marthews et al. 2012,  
796 Enquist et al. 2017, Fyllas et al. 2017, Peng et al. 2020). Fyllas et al. (2017)  
797 showed that a traits-based model could accurately predict the magnitude and  
798 trends in forest productivity with elevation, with solar radiation and plant  
799 functional traits being sufficient to describe productivity variation. Remarkably,  
800 there was no need to explicitly represent temperature variation with elevation,  
801 as trait variation driven by species turnover appears to capture the effect of  
802 temperature. Enquist et al. (2017) applied a metabolic-theory-based approach to  
803 the same (Aguirre-Gutierrez et al. 2019) dataset, and arrived at a broadly similar  
804 conclusion, that the turnover in species results in an adaptive compensation for  
805 the effects of temperature on ecosystem productivity, a feature that current  
806 biosphere models struggle to represent. Peng et al. (2020) analysed the same  
807 rich dataset through a framework of optimisation of photosynthesis to  
808 temperature, and argued that an adjustment in leaf-level photosynthetic capacity  
809 was sufficient to explain ecosystem-level trends in nutrient stocks and  
810 productivity. While these interpretations differ in details, they all agree that the  
811 widely presumed sensitivity of ecosystem function to temperature is much less  
812 than expected, and demonstrated fundamental new insights into how  
813 temperature influences ecosystem function. Similar approaches and analyses are  
814 currently being applied to the very different context of the GEM rainforest-  
815 savanna gradient in Ghana (e.g. Aguirre-Gutierrez et al. 2019, Oliveras et al.  
816 2020), and this is a fruitful direction where GEM can contribute to both theory  
817 and modelling. Previous studies using the GEM-trait database from the Peruvian  
818 elevation gradient suggest that leaf traits such as LMA may be changing in  
819 response to climate change (Enquist et al. 2017) and other studies have found  
820 that this could impact leaf reflectance by essentially darkening tropical leaves  
821 and changing the albedo of the tropical biosphere (Doughty et al. 2018b).

822  
823 In a further model application, Fauset et al. (2019) applied a more advanced  
824 dynamic model that incorporated diverse tree strategies, realistic physiology  
825 and detailed forest structure. They explored the links between traits,  
826 demography (recruitment and mortality) forest structure and NPP and GPP, in  
827 the context of seasonal and aseasonal lowland forest GEM sites in Peru. The  
828 study found that in this case the differences in productivity between the two  
829 sites could be explained by climate alone and not by traits differences, but  
830 modelling the allocation of NPP to organs remained problematic. The rich  
831 allocation datasets now available from many GEM sites offer the opportunity for  
832 a better understanding of allocation strategies than can inform and test such  
833 models.

### 834 835 *5.6 Linking field data to remote sensing*

836 The link between ecosystem function and leaf traits opens the prospect for  
837 monitoring ecosystem function and health through airborne or satellite-based  
838 remote sensing. Long-established optical earth observation approaches are  
839 limited in the amount of information potentially contained in their few optical  
840 bands, and the tropical forest canopy is reduced to a largely uninformative green  
841 surface. However, new richer multispectral (> 5 bands) and hyperspectral  
842 (hundreds of distinct bands) approaches, coupled with information on  
843 ecosystem structure through Lidar and textural analysis, offer the promise of  
844 elucidating key canopy traits and structural features. Thereby, through the

845 theoretical and modelling approaches outlined in the previous section, this  
846 opens up the potential of providing richly detailed maps and monitoring of  
847 tropical ecosystem function. Flights in 2011 and 2013 using hyperspectral and  
848 lidar sensors on board the Carnegie Airborne Observatory over much of the  
849 Andes-Amazon transect demonstrated the potential of linking canopy function to  
850 airborne remote sensing (Asner et al. 2014, Asner et al. 2017), thereby  
851 successfully predicting ecosystem productivity from remotely sensed functional  
852 diversity (Duran et al. 2019). Swinfield et al. (2020) used a similar combination  
853 of Lidar and imaging spectroscopy coupled with traits sampling in the GEM plots,  
854 to map nutrients in the matrix of intact and logged forests in Sabah, Malaysian  
855 Borneo. They showed that canopy foliar nitrogen and phosphorus  
856 concentrations decreased with elevation, a feature not detectable from the  
857 ground surveys alone. Once topography was controlled for, logged forests were  
858 found to have relatively depleted phosphorus concentrations as this limiting  
859 nutrient was extracted through harvest, highlighting long-term sustainability  
860 issues in repeated logging.

861  
862 At a smaller scale, measurements of leaf spectroscopy along the Peruvian  
863 elevation gradient suggested that many new traits could be remotely sensed  
864 through correlations with other leaf traits, such as photosynthesis, leaf venation,  
865 wood density (Doughty et al. 2017). Another study, in Borneo, suggested that  
866 leaf spectroscopy has some potential in providing early warning of future tree  
867 mortality (Doughty et al., in review). Scaling up slightly more, drone-based  
868 hyperspectral remote sensing also showed potential in mapping canopy leaf  
869 nutrients and traits along the wet-dry ecosystem GEM gradient in Ghana  
870 (Thomson et al. 2018). An immediate goal of the GEM network is to exploit the  
871 latest generation of satellite-based sensors, such as the multispectral bands of  
872 the Sentinel-2 mission from the European Space Agency (ESA) or the Lidar on  
873 the GEDI mission, to develop the potential real-time remote sensing of canopy  
874 properties and ecosystem function (Aguirre-Gutierrez et al. 2020).

## 875 876 **6. New scientific directions**

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

### 882 883 *6.1 GEM-Nutrients*

884 The nutrient status of ecosystems is often described in static terms such as  
885 concentrations or stocks of nitrogen or phosphorus. However, the coupling of  
886 NPP (the signature feature of the GEM network) with the stoichiometry of leaves,  
887 wood and fine root tissue enables the quantification of ecosystem use and flows  
888 of nutrients, enabling direct assessment of ecosystem nutrient demand and use  
889 efficiency. This approach is currently being applied to GEM sites in Malaysia  
890 (Inagawa et al., in prep), Brazil (Scalon et al, in review), Ghana and South Africa,  
891 and offers the prospect of a network of standardised assessment of nutrient  
892 dynamics. In principle, the approach can be applied to any nutrient or organic  
893 compound: Feakins et al. (2016) applied such an approach to leaf wax *n*-alkane  
894 concentrations along the Andes-Amazon transect, and was thus able to uniquely  
895 quantify the variation of ecosystem wax production rates with elevation. They

896 showed that ecosystem n-alkane production rates increased with elevation by  
897 more than an order of magnitude, most likely as a defence mechanism for long-  
898 lived montane-forest leaves. Such waxes are promising and important  
899 paleoindicators of ecosystem composition and function. This result shows the  
900 potential of new insights into the dynamics of ecosystem nutrients and complex  
901 organic compounds made possible through a network of NPP measurements.  
902

### 903 *6.2 Tree architecture as a functional trait*

904 The consideration of plant functional traits has tended to focus on leaf or wood  
905 functional traits. However, consideration of tree architecture provides a series of  
906 traits that directly link species composition to ecosystem structure and biomass.  
907 It has been quite challenging to address architectural traits, as their collection  
908 has been laborious and often imprecise. This impediment has recently been  
909 largely removed with the advent of terrestrial laser scanning approaches (Malhi  
910 et al. 2018a) that enable digital extraction of detailed tree skeletons, from which  
911 a suite of architectural parameters can be derived. Recent field campaigns have  
912 collected such tree architectural data from a suite of GEM sites where NPP and  
913 traits data have been collected, including in Peru, Brazil, Ghana, South Africa,  
914 Malaysia and Australia. Immediate priorities are to understand the association  
915 between tree architecture and other plant functional traits, and the patterns of  
916 geographical and taxonomic variation in architecture. In addition, such data  
917 enable development of much more accurate descriptions and allometries of tree  
918 woody surface area, thereby enabling improved estimation of woody respiration,  
919 a key component of the GEM carbon cycle measurements (Meir et al. 2017).  
920

### 921 *6.3 GEM-Animals: a multitrophic view of ecosystems*

922 A new direction for GEM is to combine the vegetation-focused conventional GEM  
923 focus with a holistic view of energy and nutrient flows through the fauna and  
924 multiple trophic levels of an ecosystem. These efforts link back to the earliest  
925 attempts in ecosystem ecology to describe whole ecosystem energy flow through  
926 both flora and fauna {Lindeman, 1942}. Such an approach is possible where  
927 there are rich data on the composition and abundance of faunal populations,  
928 where metabolic mass-based scaling approaches can be used to estimate energy  
929 needs and food consumption by each animal species or functional group. This  
930 can be complemented by direct estimates of herbivory, such as measuring what  
931 fraction of leaf area is consumed by insect herbivores. The advantage of using  
932 GEM sites is that the NPP and productivity data are available, enabling framing in  
933 terms of the fraction of total productivity and photosynthesis that is flowing  
934 through different populations and trophic levels. This approach is only possible  
935 at the few sites where detailed studies of animal populations are available. It is at  
936 an advanced stage at Wytham Woods, the UK GEM site with a rich history of  
937 animal research, and is also being developed at intact and logged forests in  
938 Sabah, Malaysia, where rich faunal datasets have been collected in the SAFE  
939 project (Ewers et al. 2011, Riutta et al. 2018), and also at the Wits Rural savanna  
940 sites in South Africa, where termite and ant exclusion experiments have been  
941 implemented. A recent study used combined the GEM methodology and large  
942 mammal data data (dung count and camera trap) to find forest thinning in North  
943 America appeared to increase energy flow from primary producers to primary  
944 consumers (Doughty et al. 2020).  
945

## 946 **7. Conclusions**

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

958

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

964

965

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981 **Figures**

982

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

989

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

996

997 **Figure 3:** A selection of sites from the GEM network: (a) Fine root productivity measurements  
998 in Ivindo National Park, Gabon, Central Africa; (b) Measuring diameter of large trees with a  
999 ladder to reach above the buttress, Maliau Hills National park, Sabah, Malaysia; (c) Measuring  
1000 leaf traits in montane cloud forest, Wayqecha, Peruvian Andes. (d) Measuring Leaf area Index  
1001 in Bobiri Forest Reserve, Ghana; (e) Measuring herbaceous layer productivity in a savanna in  
1002 Wits Rural Facility, South Africa; (f) Plot locations in a coral atoll in Tetiaroa, French  
1003 Polynesia, looking at the impacts of invasive rat eradication on ecosystem functioning.

1004

1005 **Figure 2:** The key components of the GEM protocol. See main text for details.

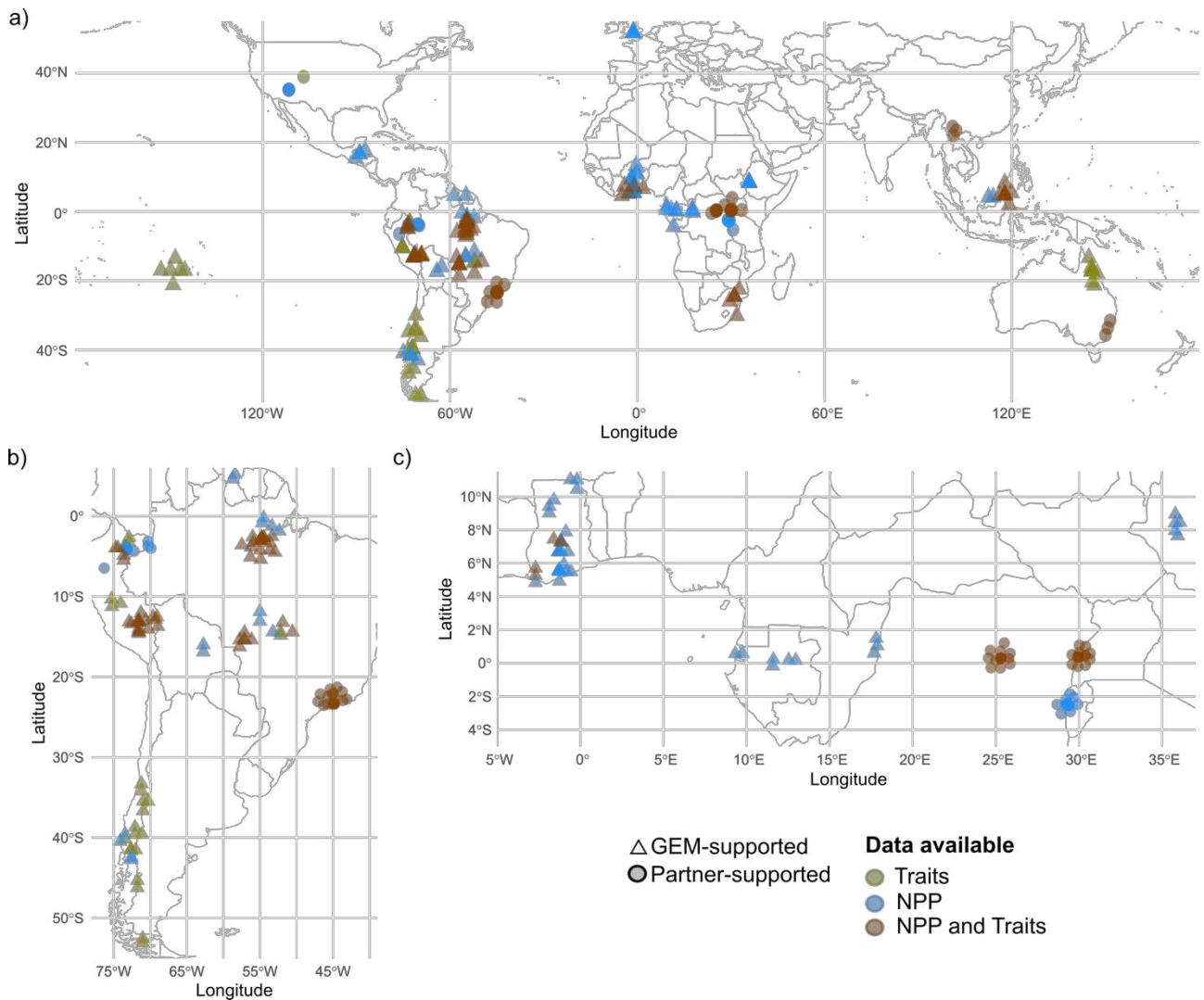
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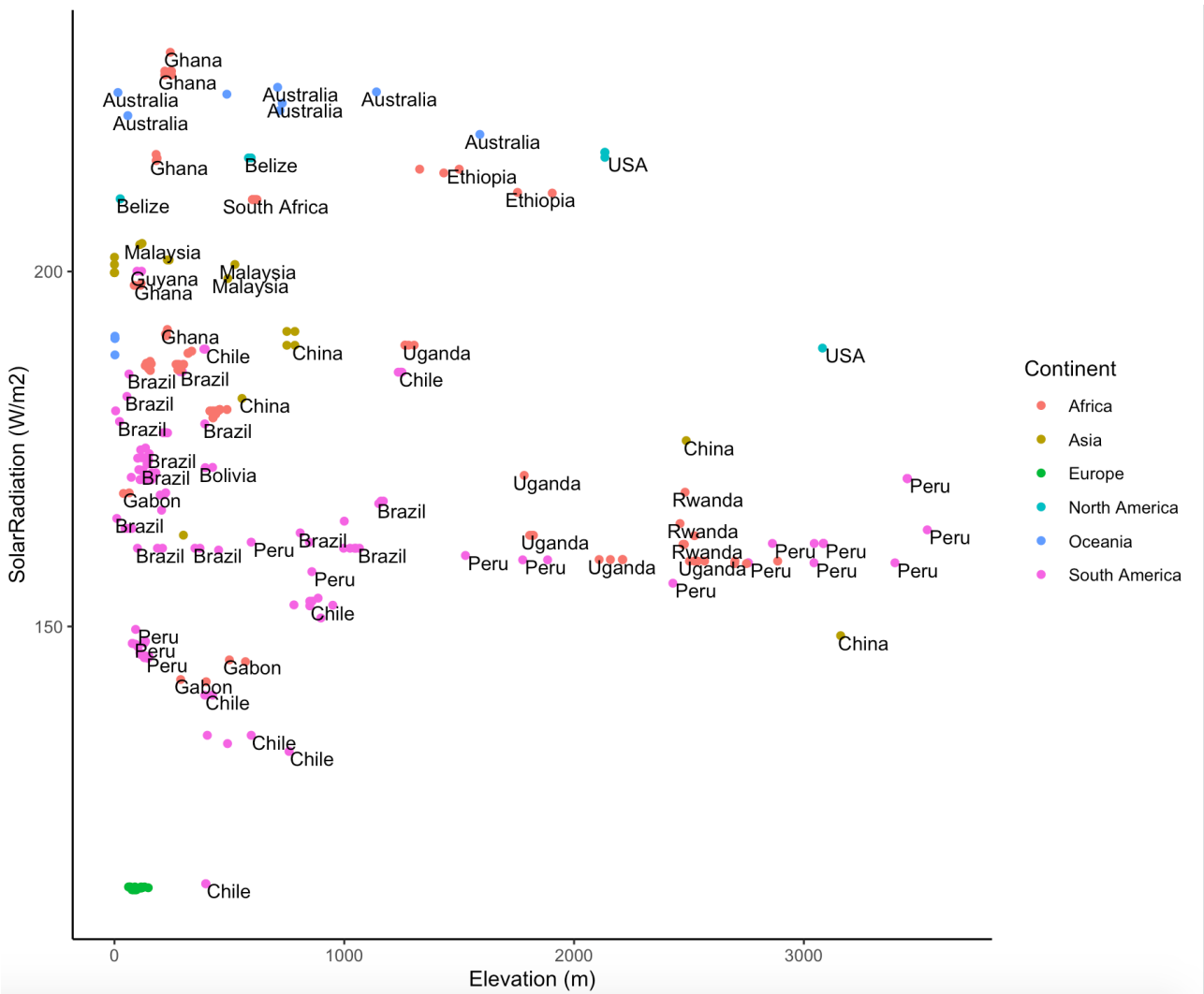
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**Figure 2(a)**



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1049 **Figure 2(b)**  
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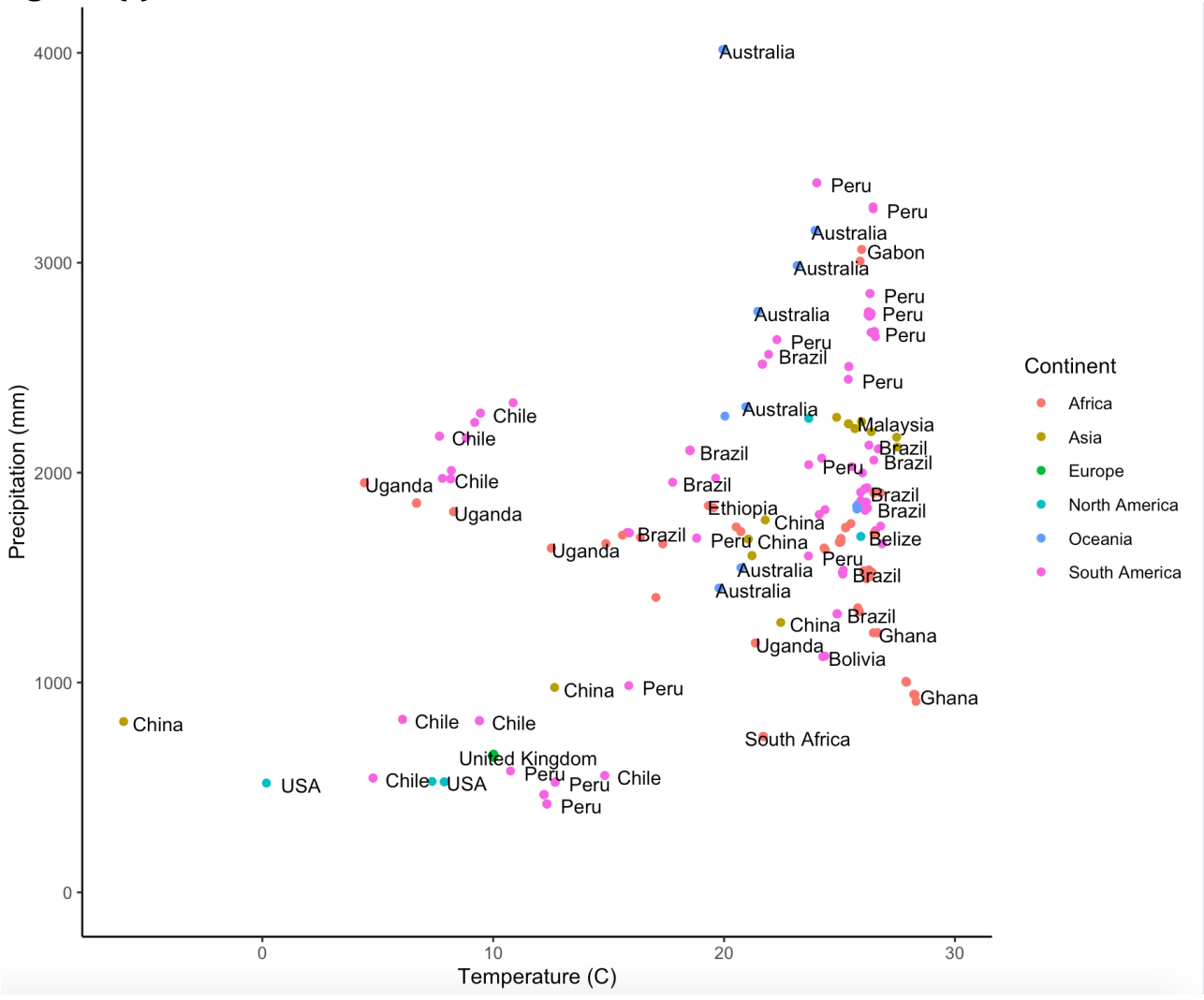


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Figure 2(c)



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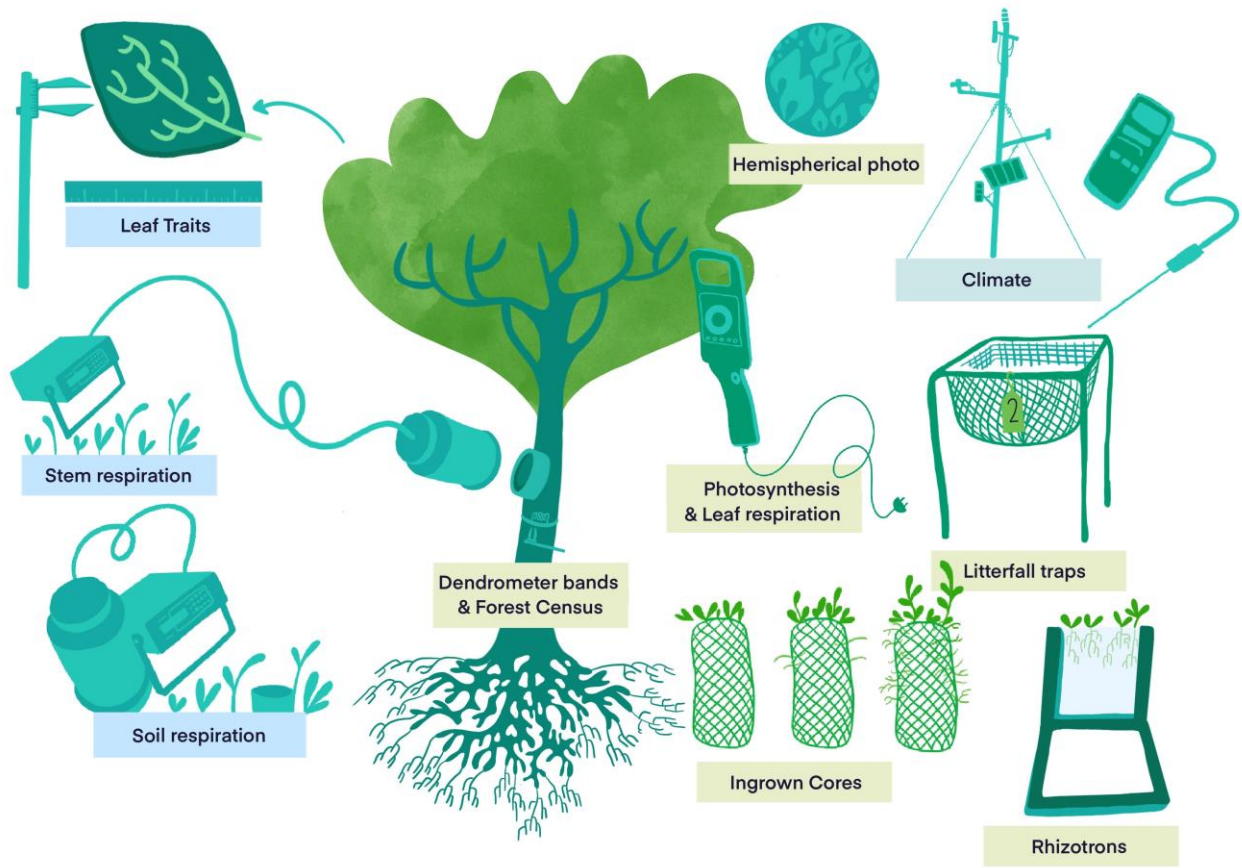
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1064

1065 **Figure 4:** The key components of the GEM protocol. See main text for details.



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### 1503 **Supplementary Information**

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1506 *Table S1. Field methods for intensive monitoring of NPP (see also RAINFOR-GEM*  
1507 *manual (Marthews et al. 2014))*  
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