

# RECENT CHANGES IN AMAZON FOREST BIOMASS AND DYNAMICS

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**Abstract:** RAINFOR has led field-based monitoring of forests across Amazonia since the turn of the millenium, and incorporated colleagues work since 1980. This unique long-term, large-scale perspective has yielded many surprising findings. Even far from the impacts of deforestation and degradation, the remote Amazon forests are changing. They have gained biomass, trees are growing faster, and they are dying faster. These changes are affected by climate change, and the accelerating carbon fluxes are themselves feeding back on the rate of global climate change. Neither has biodiversity been untouched by these changes. As an Amazon nation, Peru is a key part of this fascinating story which shows the unique ability of long-term, science-based monitoring to reveal how our world is changing.

## 1.1 Overview

There is a major planet-wide experiment underway. Changes to the atmosphere-biosphere system mean that all ecosystems on Earth are now affected by human activities. While outright deforestation is physically obvious, other subtler processes, such as hunting and surface fires, impact forests in ways less evident to the casual observer. Anthropogenic atmospheric change is intensifying: by the end of our century carbon dioxide concentrations may reach levels unprecedented for at least 20 million years, inducing rapid climate change. Further, these atmospheric changes are coinciding with probably the greatest changes in land cover and species' distributions since at least the last mass extinction at ~65 million years ago. The collective evidence points to conditions with no clear past analogue. We have entered the Anthropocene, a new geological epoch dominated by human action.

In this chapter I focus on the changes occurring within remaining tropical forests, with an emphasis on Amazonia. Most forest vegetation carbon stocks lie within the tropics. Tropical forest ecosystems store 460 billion tonnes of carbon in their biomass and soil (Pan et al. 2011). They have other planetary influences via the hydrological cycle, and emit aerosols and trace gases, and are also characterised by their exceptional variety and diversity of life. Changes here therefore matter for several key reasons. First, the critical role that tropical forests play in the global carbon and hydrological cycles affects the rate and nature of climate change. Second, as tropical forests are home to at least half of all Earth's species, changes affect global biodiversity and the cultures, societies, and economies that are bound to this diversity. Finally, as different plant species vary in their ability to store and process carbon, climate and biodiversity changes are linked by feedback mechanisms. The identities of the 'winner' species under environmental changes might exacerbate, or perhaps mitigate, human-driven climate change.

That remaining forests globally are now changing fast there is no doubt. Simple 'top-down' analysis of the global carbon cycle shows that after accounting for known atmospheric and oceanic fluxes there is a large carbon sink in the terrestrial biosphere, reaching >3 Gt carbon a year now. An independent ground-up analysis by foresters suggests that forests in every vegetated continent are implicated in this terrestrial sink, even after accounting for the separate dynamics of deforestation and secondary forest recovery (Pan et al. 2011). One critical question is therefore: how should scientists go about documenting and monitoring the changing behaviour of tropical forests?

Of the many approaches and technologies available it is careful, persistent, on-the-ground monitoring at fixed locations on Earth that can provide reliable long-term evidence of ecosystem behaviour, and this is the focus of this chapter. On-the-ground measurements provide information on subtle changes in species composition, biomass and carbon storage – none of which has been successfully done using satellites in mature lowland tropical forests, as signals saturate at high biomass and cannot currently detect the density of each tree's wood, which substantially drives forest biomass. Yet, permanent sample plot work in the tropics has until quite recently been very sparse and mostly focussed on a few well-known locations, leaving most of the ~10 million km<sup>2</sup> expanse of the world's richest ecosystems unstudied.

## 1.2 A Networked Approach

A robust approach to monitoring change needs to more synoptic, and integrated hundreds of sample sites. The first attempts to do this (Phillips and Gentry 1994; Phillips et al. 1994, 1998) were inspired by the macroecological work of Gentry. Gentry had used intensive floristic inventories across hundreds of forest locations to reveal the major geographic gradients in diversity and composition. But, unlike Gentry's floristic work, these first macroecological analyses of tropical forest dynamics lacked methodological standardisation. We relied heavily on published data from different teams worldwide, and had limited sample sizes. To try to eliminate these weaknesses, since 2000 with many colleagues I have focussed on developing standardised, international, long-term networks of permanent plots in mature forests across Amazonia and elsewhere. These first draw together the existing efforts of local foresters and ecologists, who had often worked hitherto largely in isolation. Then, by analysing the gaps in geographical and environmental space, we have extended the network to fill the gaps, and built support for long-term spatially-extensive monitoring. The network of Amazonian-forest researchers, known as RAINFOR (*Red Amazónica de Inventarios Forestales*, [www.geog.leeds.ac.uk/projects/rainfor/](http://www.geog.leeds.ac.uk/projects/rainfor/)), now represents the long-term ecological monitoring efforts of 43 institutions worldwide including many from Amazonia. Here I synthesise some published results from RAINFOR to assess how mature Amazon forests have changed recently.

## 2 METHODOLOGY

For these analyses, I define a monitoring plot as an area of old-growth, physiognomically mature forest where all trees  $\geq 10$  cm diameter at breast height (dbh, measured at 1.3m height or above any deformity) are tracked over time. All trees are marked with a unique number, measured, mapped, and identified. Periodically (generally every 1-5 years) the plot is revisited, all surviving trees are re-measured, dead trees are noted, and trees recruited to 10 cm dbh are numbered, measured, mapped, and identified. This allows calculation of (i) the cross-sectional area that tree trunks occupy (basal area), which can be used with allometric equations to estimate tree biomass; (ii) tree growth (the sum of all basal-area increments for surviving and newly recruited stems over a census interval); (iii) the total number of stems present; (iv) stem recruitment (number of stems added to a plot over time); and (v) mortality (either the number or basal area of stems lost from a plot over time).

Most plots are 1 ha in size and comprise  $\sim 500$  trees of  $\geq 10$  cm dbh. Most plots were established using randomised or systematic sampling protocols to locate plots in apparently old-growth forest landscape. Many have been monitored for more than a decade, although they range in age from 2 to 35 years (mean  $\sim 12$  yrs). Here I analyse results of censuses completed up to 2007, but for Amazonia I first report results prior to the intense drought of 2005, and then also summarize the impact of the drought and briefly review the latest findings from RAINFOR (Brienen et al 2015). Details of exact plot locations, inventory and monitoring methods, and the challenges involved in collating and analysing plot data are discussed elsewhere (e.g., Phillips et al. 2009; Baker et al. 2004; Lewis et al. 2004; Lopez-Gonzalez et al. 2011). It is important to point out that the samples are not evenly distributed over Amazonia because they use historical plot data, where possible, and also because considerations of access can limit where it is practical to work, nor are census intervals always regular, because of uneven funding, yet a wide range of environmental space is captured by the samples. The general distribution and sampling density of plots is indicated in Figure 1.

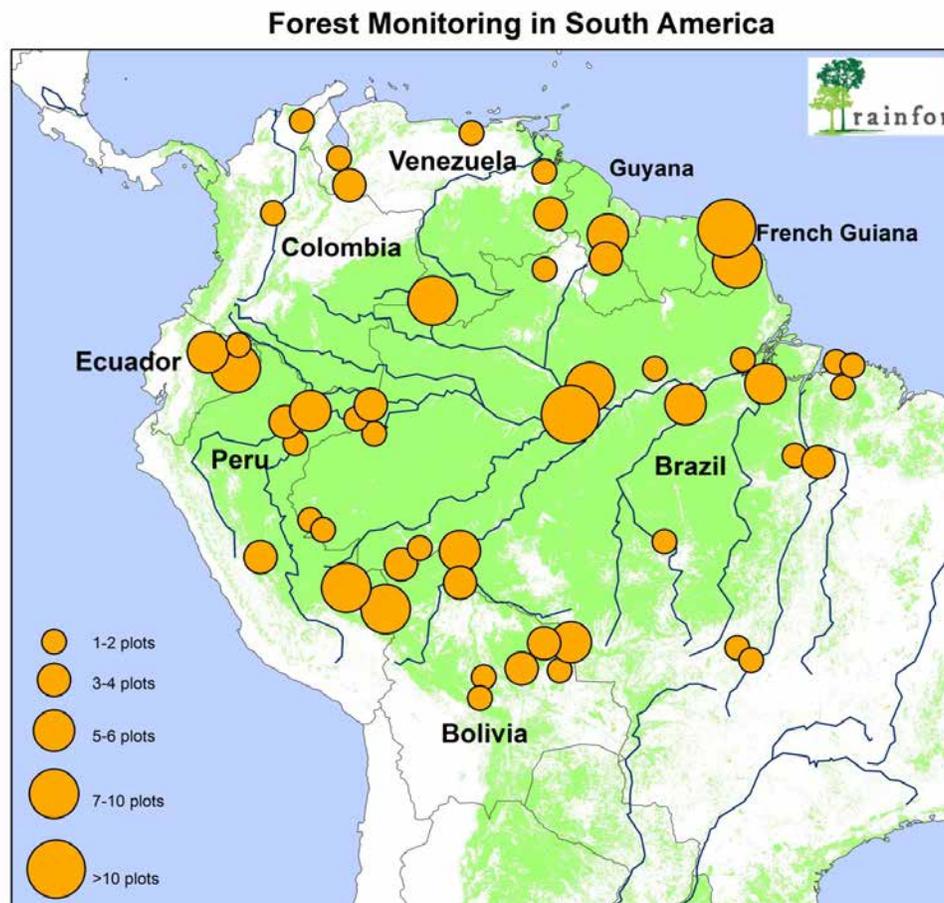
Scaling from individual tree to Amazon plot biomass is based on the diameter-based allometric equations detailed in Baker et al. 2004. I summarize findings from mature forests in terms of (a) structural change, (b) dynamic-process change, and (c) functional and compositional change, over the past two to three decades, including taking account of recent droughts in Amazonia.

## 3 RESULTS AND DISCUSSION

### 3.1 Structural Change

For 123 long-term mature forest Amazonian plots with tree-by-tree data there was a significant increase in above-ground biomass between the first measurement (median date 1991) and the last measurement before the 2005 drought (median

date 2003). For trees  $\geq 10$  cm diameter the increase has been  $0.45$  ( $0.33, 0.56$ )  $\text{t C ha}^{-1} \text{ yr}^{-1}$  (mean and 2.5%, 97.5% confidence limits; Phillips et al. 2009). Using the same approach we also discovered a similar phenomenon in African forests (Lewis et al. 2009).



**Figure 1:** Distribution of long-term RAINFOR plots used for monitoring forest changes in Amazonia. With vital contributions from more than 100 botanists, ecologists and foresters working in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, and Venezuela, more than 300 plots help to build a long-term picture of the changing dynamics of Amazon forests since the late twentieth century to now. Within each plot almost every tree has had its species identified, diameter measured, and its life followed.

There are various ways by which these plot-based measures can be scaled to tropical forests across Amazonia and Africa. We used a simple approach given the various uncertainties, not all quantifiable, for example in terms of below-ground (root) biomass carbon, carbon in dead trees, area of each forest type, and degree of human disturbance. Thus we assumed that measurements were on average representative of the old-growth forest landscape, and that other components were also increasing proportionally but that soil carbon stocks were static, and estimated the magnitude of the sink in each continent by multiplying the plot-based net carbon gain rate by correction factors to account for these. For the 1990s this yielded a total estimated South American forest sink of  $0.65 \pm 0.17 \text{ Pg C yr}^{-1}$  (and in African forests  $0.53 \pm 0.30 \text{ Pg C yr}^{-1}$  and  $0.14 \pm 0.04 \text{ Pg C yr}^{-1}$  in mature undisturbed Asian forests (Pan et al 2011)). Thus the combined mature tropical forest sink in the 1990s is estimated to have been  $1.3 \pm 0.35 \text{ Pg C yr}^{-1}$  before allowing for any change in soil carbon stock. In the decade of the 2000's the American tropical sink has declined by about a third (Brienen et al. 2015).

The validity of these estimates depend on (i) measurement techniques; (ii) how representative the plots are of mature forests; and (iii) assumptions about the extent of mature forest remaining. However, they are consistent with independent evidence from recent inversion-based studies, showing the tropics are either carbon neutral or sink regions, despite widespread deforestation (Denman et al. 2007), and the large net sink in the terrestrial biosphere after accounting for other sources and sinks. Potentially unobserved large disturbances are much too rare to affect the inference from the plot network of a sustained, widespread biomass carbon sink into mature Amazon forests (Espirito-Santo et al. 2014).

### 3.2 Dynamic Changes

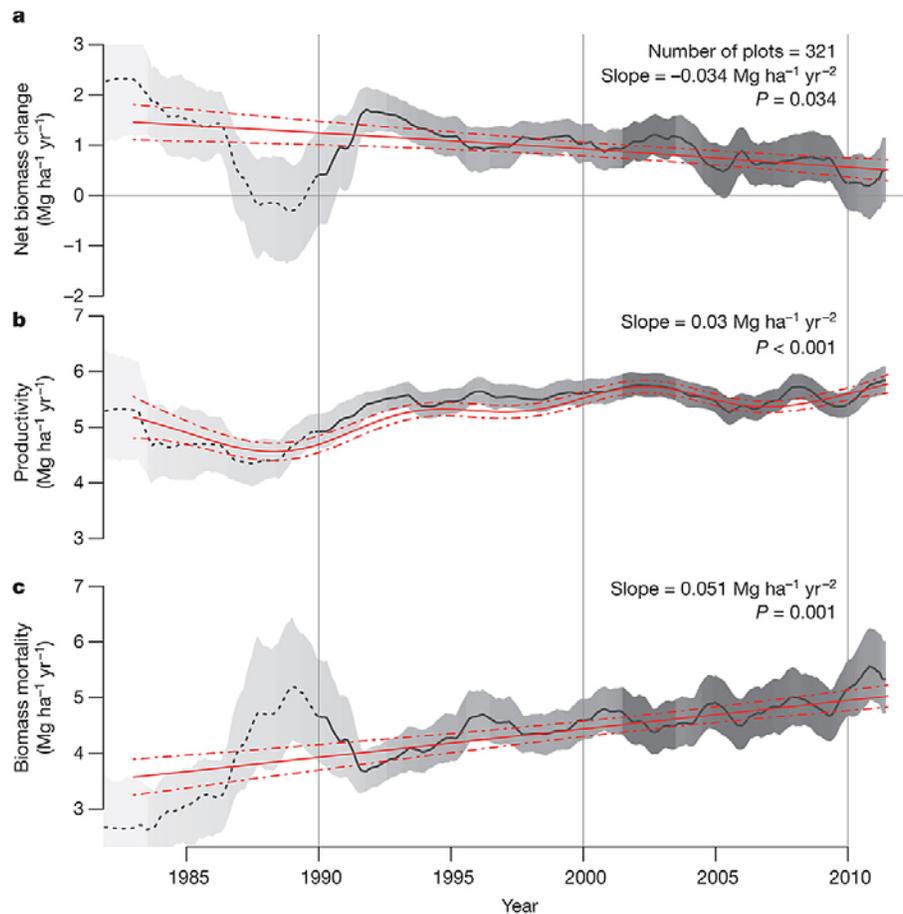
An alternative way of examining forest change is to look for changes in the processes (growth, recruitment, death), as well as the structure: have these forests simply gained mass, or have they become more or less dynamic too? For Amazonia we have measured the dynamics of forests in two ways. Firstly, we examined changes in stem population dynamics. By convention we estimated stem turnover between any two censuses as the mean of annual mortality and recruitment rates for the population of trees  $\geq 10$  cm diameter (Phillips and Gentry 1994, Phillips et al. 1994, Phillips 1996). Secondly, we examined changes in biomass fluxes of the forest – in terms of growth of trees and the biomass lost with mortality events.

Among 50 mature forest plots across tropical South America with at least three censuses to 2002 (and therefore at least two consecutive monitoring periods that can be compared), we found that these key ecosystem processes - stem recruitment, mortality, and turnover, and biomass growth, loss, and turnover – all increased significantly when the first monitoring period is compared with the second (Lewis et al. 2004). Thus, over the 1980s and 1990s these forests on average became faster-growing and more dynamic, as well as bigger. The increases in the rate of the dynamic stem fluxes (growth, recruitment, mortality) were about an order of magnitude greater than the increases in the structural pools (above-ground biomass and stem density).

For the plots which have two consecutive census intervals we can separate them into two groups, one fast-growing and more dynamic (mostly in western Amazonia), and one slow-growing and much less dynamic (mostly in eastern and central Amazonia), which reflects the dominant macroecological gradient across Amazonia. Both groups showed increased stem recruitment, stem mortality, stand basal-area growth, and stand basal-area mortality, with greater absolute increases in rates in the faster-growing and more dynamic sites than in the slower-growing and less dynamic sites (Lewis et al. 2004), but proportional increases in rates were similar among forest types. It should be stressed that these results represent the mean response of all mature forests measured. Within the dataset naturally there are many individual plots showing different, individual responses. But when viewed as whole the permanent plot record from Neotropical mature forests shows increasing growth, recruitment, and mortality for at least two decades across different forest types and geographically widespread areas.

### 3.3 Biodiversity Compositional Changes

Changes in the structure and dynamics of tropical forests are unlikely to leave species and functional composition unchanged. Phillips et al. (2002) studied woody climbers (structural parasites on trees, also called lianas), which typically contribute 10-30% of forest leaf productivity, but are ignored in most stem monitoring studies. Across the RAINFOR plots of western Amazonia there was a concerted increase in the density, basal area, and mean size of lianas. Over the last two decades of the twentieth century, the density of large lianas relative to trees roughly doubled over the period, albeit from a low base. This was the first direct evidence that mature tropical forests are changing in terms of their life form composition. A few other studies have also considered whether there have been consistent changes in tree species composition in forests over the past two decades. Laurance et al. (2004) for example, working with a large cluster of plots north of Manaus, found that many faster-growing genera of canopy and emergent stature trees increased in basal area or density, and some slow-growing trees of the subcanopy and understory declined. Further studies are needed to determine whether comparable shifts in tree communities are occurring throughout Amazonia, and indeed to update the Amazon liana trajectory over the early 21<sup>st</sup> century.



**Figure 2:** Trends in net above-ground biomass change, productivity and mortality across all RANFOR Sites, analysed up to 2011. Black lines show the overall mean change for 321 plots weighted by plot size, and its bootstrapped confidence interval (shaded area). The red lines indicate the best model fit for the long-term trends since 1983 using general additive mixed models (GAMM), accounting for differences in dynamics between plots (red lines denote overall mean, broken lines denote standard errors of the mean). Estimated long-term (linear) mean slopes and significance levels are indicated, and are robust regardless of whether parametric or non-parametric analyses are used. Shading corresponds to the number of plots that are included in the calculation of the mean, varying from 25 plots in 1983 (light grey) to a maximum of 204 plots in 2003 (dark grey). The uncertainty and variation is greater in the early part of the record owing to relatively low sample size. (Reproduced from Brienen et al. 2015).

### 3.4 Recent Drought Impacts in Amazonia

The Amazon results discussed so far reflect forest changes up to the early part of the first decade of the twenty-first century. In 2005 the region was struck by a major drought. With the RAINFOR network largely in place and a forest dynamics baseline established, we had an opportunity to use this ‘natural experiment’ to explore the sensitivity of the largest tropical forest to an intense, short-term drought, by rapidly re-censusing plots across the Basin to create ‘drought census intervals’ of typically 1 to 2 years per plot. Of 55 plots surveyed across 2005, the mean annual above-ground biomass change was  $-0.59$  ( $-1.66, +0.35$ )  $\text{Mg ha}^{-1}$ , and among those plots that were actually impacted by drought the above-ground biomass change rate was clearly negative ( $-1.62$  ( $-3.16, -0.54$ )  $\text{Mg ha}^{-1}$ ). Moreover, the size of the biomass change anomaly was closely correlated to the moisture deficit anomaly experienced in the period. This implies that it was the unusual moisture deficits that were responsible for the biomass loss by contributing to an enhanced mortality. We estimated the Basin-wide impact of the drought on biomass carbon, as compared to the baseline of a net biomass sink in pre-drought measurement period, as between  $-1.21$  and  $-1.60$   $\text{Pg C}$ , using remotely-sensed rainfall data to scale from

the relationship of biomass change data with relative drought intensity. This suggests a large regional impact (confirmed now by new, independent analyses, Gatti et al. 2014). The total carbon impact of the 2005 drought exceeds the annual net C emissions due to land-use change across the neotropics (0.5-0.7 Pg C) (Pan et al. 2011). Fuller understanding of the impacts of drought will require monitoring of forests through post-drought recovery and repeated droughts, such as the strong 2015-16 El Niño event.

### 3.5 What is Driving these Changes?

What could have caused the continent-wide increases in tree growth, recruitment, mortality, and biomass? Many factors could be invoked but overall the results show a clear fingerprint of increasing growth across tropical South America, probably caused by a long-term increase in resource availability (Lewis et al. 2004). According to this explanation, increasing resource availability stimulates growth. This accounts for the increase in stand basal-area growth. Because of increased growth, competition for limiting resources, such as light, water, and nutrients, increases. Over time some of the faster-growing, larger trees die, as do some of the 'extra' recruits, as the accelerated growth percolates through the system. This accounts for the increased losses from the system: mortality rates increase. Thus, the system gains biomass, while the losses lag some years behind, causing an increase in carbon storage.

The changes in biodiversity composition may also be related to increasing resource availability, as the rise in liana density may be either a direct response to rising resource supply rates, or a response to greater disturbance caused by higher tree-mortality rates. The changing tree composition in central-Amazonian plots (Laurance et al. 2004) is also consistent with increasing resource supply rates, as experiments show that faster-growing species are often the most responsive, in absolute terms, to increases in resource levels.

What environmental changes could increase the productivity of tropical forests? While there have been many changes in the tropical environment, the increase in atmospheric CO<sub>2</sub> is the leading candidate, because of the clear long-term increase in CO<sub>2</sub> concentrations, the key role of CO<sub>2</sub> in photosynthesis, and the positive effects of CO<sub>2</sub> fertilization on plant growth. However, some role for increased insolation, or aerosol-induced increased diffuse fraction of radiation, or rising temperatures increasing soil nutrient mineralization rates, cannot be ruled out (Malhi and Phillips 2004). The carbon dioxide explanation remains somewhat controversial still (c.f. discussion in Phillips and Lewis 2014), in part because of the great challenge in conducting ecosystem experiments of the impacts of CO<sub>2</sub> fertilization at sufficient spatial and temporal scale. This process should not be confined to tropical forests - given the global nature of the CO<sub>2</sub> increase and ubiquitous biochemistry of the plant response involved, we may expect to see the same phenomenon in other biomes. Indeed, increases in biomass and growth have indeed now been reported from every continent where foresters make measurements in enough sites (Pan et al. 2011).

### 3.6 The Future: How Vulnerable is Amazonia to Environmental Stress and Compositional Changes?

Our long-term observations show that mature forests in Amazonia, the world's largest tract of tropical forest, experienced concerted changes in dynamics in recent decades. Such rapid alterations - regardless of the cause - were not anticipated by ecologists and raise concerns about other possible surprises that might arise as global changes accelerate in coming decades. On current evidence tropical forests are sensitive to changes in resource levels and will show further structural and dynamic changes in the future, as resource levels alter further, temperatures continue to rise, and precipitation patterns shift. The implications of such rapid changes for the world's most biodiverse region could be substantial.

Mature Amazonian forests have evidently helped to slow the rate at which CO<sub>2</sub> has accumulated in the atmosphere, so acting as a buffer to global climate change. The concentration of atmospheric CO<sub>2</sub> has risen recently at an annual rate equivalent to ~4 Pg C; this would have been significantly greater without the tropical South American biomass carbon sink of 0.4-0.7 Pg C per year (and an African sink of 0.3-0.5 Pg C per year). This subsidy from nature could be a relatively short-lived phenomenon. Given that a 0.3% annual increase in Amazonian forest biomass roughly compensates for the entire fossil-fuel emissions of western Europe (or the deforestation in Amazonia), a switch of mature tropical forests from a moderate carbon sink to even a moderate carbon source would impact on global climate and human welfare. The ~0.3% annual increase in carbon storage represents the difference between two much larger values: stand-level growth (averaging ~2%) and mortality (averaging ~1.7%), so a small decrease in growth or a sustained increase in mortality

would shut the sink down. There are several mechanisms by which such a switch could occur, apart from the obvious and immediate threats posed by land use change and associated disturbances by fragmentation and fire. I discuss these briefly.

**Moisture Stress:** Climate change alters rainfall patterns. There are critical thresholds of water availability below which tropical forests cannot persist and are replaced by savanna systems, and these thresholds will respond to rising temperatures which increase evaporation. How sensitive tropical forests are to extreme temperatures, particularly in the context of rising atmospheric CO<sub>2</sub> concentration, is a subject of active research, reviewed elsewhere (Lloyd and Farquhar 2008).

The 2005 drought provides direct evidence of the potential for intense dry periods to impact rainforest vegetation. However, it remains to be seen whether droughts are powerful and frequent enough to permanently shift the dominant regime of biomass gains witnessed across mature tropical forests wherever they have been extensively monitored. The 1998 El Niño drought was equally strong in parts of Amazonia, but its impacts are not distinguishable from the signal of increased biomass and growth over the ~5 year mean interval length available for plots at that time (Fig. 2), implying a rapid recovery. We expect therefore that only frequent, multiple droughts would cause the sustained increases in mortality needed to turn the long-term carbon sink in mature forest into a source. This may now be happening.

In 2010 a new drought affected the Amazon forest, again dropping some rivers to record lows. Our recent, long-term analysis from an even larger RAINFOR plot dataset (Brienen et al. 2015) found evidence of a progressive decline in the net Amazon sink (Fig. 2), in spite of the long-term growth gains. The impacts of the 2015-16 El Niño event are yet to be measured.

**Photosynthesis/ respiration changes:** Forests remain sinks as long as carbon uptake associated with photosynthesis exceeds the losses from respiration. Under the simplest scenario of a steady rise in forest productivity over time, it is predicted that even mature forests would remain a carbon sink for decades (e.g. Lloyd and Farquhar 1996). However, the recent increases in productivity, apparently caused by continuously improving conditions for tree growth, cannot continue indefinitely: if CO<sub>2</sub> is the cause, trees will become CO<sub>2</sub>-saturated (limited by another resource) sooner or later.

Rising temperatures could also reduce the sink, or cause forests to become a source. Warmer temperatures increase the rates of virtually all chemical and biological processes in plants and soils, until temperatures reach inflection-points where enzymes and membranes lose functionality. There is some evidence that the temperatures of leaves at the top of the canopy, on hot days, may be reaching such inflection-points around midday at some locations. Canopy-to-air vapour deficits and stomatal feedback effects may also be paramount in any response of tropical forest photosynthesis to future climate change (Lloyd et al. 1996). Simulations suggest that the indirect effect of rising temperatures on photosynthesis via stomatal closure is the dominant negative impact on tropical forest growth (Lloyd & Farquhar 2008), but that this is currently more than offset by increases in photosynthesis from increasing atmospheric CO<sub>2</sub>. Warmer temperatures also mean higher respiration costs, which will also impact on the ability of plants to maintain a positive carbon balance in the future. Understanding these complex relationships between temperature changes and their impacts on respiration and photosynthesis, plus the impact of rising atmospheric CO<sub>2</sub> on tree growth is critical, and are areas of very active research (and debate).

Carbon losses from respiration will almost certainly increase as air temperatures continue to increase. The key question is what form this relationship takes. Carbon gains from photosynthesis cannot rise indefinitely, and will almost certainly reach an asymptote. Thus, I conclude that the sink in mature tropical forests is bound to diminish, and possibly even reverse. The more catastrophic outcomes of large-scale biomass collapse indicated in some models appear very unlikely, but cannot be ruled out.

**Compositional change:** Biodiversity change has inevitable consequences for climate change because different plant species vary in their ability to store and process carbon and different plant species will benefit and decline as global environmental changes unfold. Yet most models that project the future carbon balance in Amazonia (and future climate-change scenarios) make no allowance for changing forest composition. Representing biodiversity is challenging, because of the computational complexities in integrating ecological processes into ecophysiology-driven models, and because the ecological data themselves are sparse. Representing composition better, and its potential for change, is important. Large changes in tree communities could lead to net losses of carbon from tropical forests (Phillips & Gentry 1994). One way this could happen is a shift to faster-growing species, driven by increasing tree mortality rates and gap formation

(Phillips & Gentry 1994). Fast-growing species have less dense wood, and hence less carbon. The potential scope for such impacts of biodiversity changes on carbon storage is highlighted by Bunker et al. (2005), who explored various biodiversity scenarios based on the tree species at Barro Colorado Island: if slower-growing tree taxa were lost from an accelerated, liana-dominated forest, as much as one-third of the carbon storage capacity of the forest could be lost. In Amazonia a small and sustained basin-wide annual decrease in mean wood specific gravity could potentially cancel out the carbon sink effect. Currently, the more dynamic forests in the west of Amazonia have ~20% less dense wood than the slower-growing forests of the east; because these faster-growing western forests also have lower basal area, the differences in terms of biomass carbon stored are somewhat greater still. Concerted compositional changes driven by greater resource supply, increased mortality rates, and gains in the proportion of faster-growing trees which escape lianas, could therefore shut down the carbon sink function of tropical forests earlier than ecophysiological analyses predict.

#### 4 CONCLUSION

Long-term, high-quality, tree-centred monitoring is critical for any nation wanting to understand the behaviour of forests, to report it to the wider world, and to respond to it with actions including in terms of protected area strategy. The dominant monitoring challenge now is to understand how biodiversity and ecosystem processes are responding to climate change. Some changes may be slow and gradual, some will be rapid. We may predict some with high confidence (eg more montane species will become progressively reduced and restricted), but many surprises are likely. *What then would a nation-wide forest monitoring system look like fit for purpose in a hyper-diverse, carbon-rich country with a major share of the Amazon, such as Peru?*

**How to work?** Such a network needs to embrace science-led monitoring to work. This requires a long-term funding commitment, fully open-access with data-sharing built in from the start, and an emphasis on hands-on training in field and lab and international exchanges (into Peru, out of Peru, exchanges with Amazon countries, exchanges with Europe). International help can be intense at first, but a growing level of scientific leadership by the country should be built-in to the plan. Rigorous data quality is essential. Standard botanical and forestry approaches are needed, always well integrated, as are careful soil inventory and analysis. The single biggest challenge is timely, accurate species identification of trees, and thus herbaria need to be involved too, and young taxonomists trained. Selected plots should become 'long-term living laboratories' – many other exciting and important work can be added on, such as ethnobotanical surveys, intensive carbon cycle studies, soil mycorrhizae, remote sensing calibration/validation, plant and animal DNA sampling, invertebrate surveys, training sites for students, etc.

Nations like Peru can benefit directly from involvement in international collaborations like RAINFOR, but current efforts are insufficient. Much greater sampling in the vast difficult-to-access regions of Amazonia is clearly needed in the future to reduce uncertainty due to incomplete spatial coverage, with a purposeful effort to fill the large spatial gaps. Additionally, better integration with LiDAR approaches (which measure forest height) is clearly also desirable. I expect that the most cost-effective strategy for monitoring the more remote remaining tropical forests will combine (1) gap-filling the monitoring networks where possible - with locally randomised plots -, with (2) extensive remote sensing (viz LiDAR, radar), with the potential power of remote sensing techniques for scaling-up very clear. The need for careful ground-based assessments to permit calibrating and validating forests' remotely-sensed canopy properties in terms of productivity, biomass, and biodiversity, and change, is equally obvious.

**Where to work?** Establishing quality, repeat census plots along the key geographic gradients is essential – thus in Peru, replicated sampling of the elevation gradients from high Andes to low Amazon, and the precipitation seasonality gradient from North to South. These need to be tied to protected areas – thus the monitoring network helps Peru fulfil CBD obligations of assessing the effectiveness of its protected areas. Finally, researchers need to co-ordinate efforts too for long-term monitoring of directly impacted forests, and of key resources for livelihoods – e.g. swamps of aguaje (*Mauritia flexuosa*), and stands of castaña (*Bertholletia excelsa*). A skeleton framework for much of this already exists with RAINFOR and colleagues (eg RC Sira, PN Yanachaga-Chemillen, PN Manu). But many new plots will need to be established to fill environmental and spatial gaps.

**In Sum:** By carefully tracking the lives, deaths, and identities of trees at hundreds of plots it has been possible over the past three decades to build a preliminary understanding of how the world's mature tropical forests have been changing. The picture that emerges is at once both surprising but, with the benefit of hindsight perhaps not unexpected. Thus, in experiencing accelerated growth, mortality, and generally increasing biomass, the tropical biome has been responding for many years to the large-scale but slow-acting drivers that until recently were unfamiliar to ecologists. Gaining an authoritative understanding of how and why forest biodiversity and carbon are changing in the Anthropocene remains a huge challenge. Repeated, standardised, careful, and adequately replicated on-the-ground measurements will be a key contributor to making significant progress toward this goal.

## 5 ACKNOWLEDGMENTS

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## 6 REFERENCES

- Baker TR, OL Phillips, Y Malhi et al. (2004) Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society, Series B* 359: 353-365.
- Brienen T, OL Phillips et al. (2015) Long-term decline of the Amazon carbon sink. *Nature* 519: 344-8.
- Butt, N, Malhi, Y, New M, et al. (2012) Shifting dynamics of climate-functional groups in old-growth Amazonian forests. *Plant Ecology & Diversity* 7: 267-279
- Denman K, G Brasseur, A Chidthaisong et al. (2007) Couplings Between Changes in the Climate System and Biogeochemistry. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (S Solomon, D Qin, M Manning et al. (eds)). CUP, Cambridge, UK and New York, NY, USA
- Doughty C & Goulden M (2008) Are tropical forests near a high temperature threshold? *Journal of Geophysical Research-Biogeosciences*, 113, G00B07.
- Espírito-Santo F, M Gloor, M Keller et al. (2014) Size and frequency of natural forest disturbances and the Amazon forest carbon balance. *Nature Communications* 5.
- Fauset S, Baker T, Lewis S et al. (2013) Drought induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecology Letters* 15: 1120-1129.
- Gatti L, Gloor M, Miller J et al. (2014) Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* 506: 76-80.
- Laurance W (2004) Forest-climate interactions in fragmented tropical landscapes. *Philosophical Transactions of the Royal Society, Series B* 359: 345-352.
- Laurance W, A Oliveira, S Laurance et al. (2004) Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* 428: 171-174.
- Lewis SL, OL Phillips, T Baker et al. (2004) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Phil. Trans. Roy. Soc., Ser. B* 359: 421-436.
- Lewis SL, G Lopez-Gonzalez, B Sonké et al. (2009) Increasing carbon storage in intact African tropical forests. *Nature* 477: 1003-1006.

- Lloyd J, G Farquhar (1996) The CO<sub>2</sub> dependence of photosynthesis, plant growth responses to elevated atmospheric CO<sub>2</sub> concentrations & their interaction with plant nutrient status. *Functional Ecology* 10: 4-32.
- Lloyd J, J Grace, AC Miranda et al. (1996) A simple calibrated model of Amazon rainforest productivity based of leaf biochemical properties. *Plant Cell & Environment* 18: 1129-1145.
- Lloyd J, Farquhar GD (2008) Effects of rising temperatures and (CO<sub>2</sub>) on the physiology of tropical forest trees. *Phil. Trans. Roy. Soc., Ser. B* 363: 1811-1817.
- Lopez-Gonzalez G, Lewis S, Burkitt M, Phillips O (2011) ForestPlotsnet: a web application & research tool to manage and analyse tropical forest plot data. *Journal of Vegetation Science* 22: 610-3.
- Malhi Y & OL Phillips (2004) Tropical forests and global atmospheric change: a synthesis. *Philosophical Transactions of the Royal Society, Series B* 359: 549-55.
- Pan Y, R Birdsey, J Fang et al. (2011) A large and persistent carbon sink in the world's forests. *Science* 333: 988-93.
- Phillips OL (1996) Long-term environmental change in tropical forests: increasing tree turnover. *Environmental Conservation* 23: 235-48.
- Phillips OL, L Aragão et al (2009) Drought sensitivity of the Amazon rainforest. *Science* 323:1344-7.
- Phillips OL and AH Gentry (1994) Increasing turnover through time in tropical forests. *Science* 263: 954-8.
- Phillips OL, P Hall, AH Gentry et al. (1994) Dynamics and species richness of tropical forests. *Proceedings of the National Academy of Sciences (USA)* 91: 2805-9.
- Phillips OL & S Lewis (2014) Evaluating the tropical forest carbon sink. *Gl. Change Biol.* 7: 2039–41.
- Phillips OL, Y Malhi, N Higuchi et al. (1998) Changes in the carbon balance of tropical forest: evidence from long-term plots. *Science* 282: 439-42.
- Phillips OL, RV Martínez, L Arroyo et al. (2002) Increasing dominance of large lianas in Amazonian forests. *Nature* 418: 770-774.