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Recent Changes in Amazon Forest Biomass and Dynamics

Oliver L. Phillips

Palabras clave. Amazonia, carbono, dinámica, sumidero, sequía

Abstract: RAINFOR is a continent-wide network of researchers dedicated to tracking the biodiversity, carbon balance, and long-term dynamics of South American tropical forests. By applying internationally standardised field-based monitoring techniques, this unique, long-term, large-scale collaboration is yielding many surprising findings. We have discovered that remote Amazon and adjacent lowland forests are changing, even far from the impacts of deforestation and degradation. Compared to the late twentieth century they have gained biomass, trees are growing faster, and trees are dying faster. These changes are linked to climate change, and the accelerating carbon fluxes are feeding back on the rate of global climate change. Neither has biodiversity been untouched by these changes. Together, these findings show the unique ability of collaborative, long-term, science-based monitoring across multiple field sites to reveal how our world is changing.

1.1.1 Introduction

All ecosystems on Earth are being affected by human activities, and by the end of our century carbon dioxide concentrations may reach levels unprecedented for at least 20 million years, inducing rapid climate change. These changes coincide with one of the greatest changes in land cover and species' distributions in life's 4 billion year history. Conditions now have no past analogue. We have entered the Anthropocene (Maslin and Lewis 2015), a new geological epoch dominated by human action. In this chapter I focus on changes occurring within remaining tropical forests, especially Amazonia.

Most forest vegetation carbon is tropical. Tropical forest ecosystems store 460 billion tonnes of carbon in 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 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 of climate change. Second, tropical forests are home to at least half of Earth's species, so changes affect global biodiversity and the cultures, societies, and economies bound to this diversity. Finally, because plant species vary in their ability to store and process carbon, climate and biodiversity changes are linked by feedback mechanisms. The identities of which species 'win' under environmental changes can also affect climate change. Remaining forests are now changing fast. For example, analysis by foresters suggests that forests across the world contribute a huge terrestrial sink of carbon from the atmosphere into trees, more than offsetting carbon losses from deforestation (Pan et al. 2011).

How should scientists go about documenting and monitoring the changing behaviour of tropical forests? The focus of this chapter is on careful on-the-ground monitoring at fixed locations on Earth, to provide long-term evidence of ecosystem behaviour. Only on-the-ground measurements have proven capable of revealing subtle changes in species composition, biomass and carbon storage. Yet permanent sample plot work in the tropics is challenging because of obvious issues of scale (tropical forests cover ~10 million km² worldwide) and access (much of Amazonia for example is extremely remote). A robust approach to monitoring change needs hundreds of sample sites. The first attempts (Phillips and Gentry 1994; Phillips et al. 1994, 1998) were inspired by Gentry's pioneering macroecology - Gentry used intensive floristic inventories across hundreds of forest locations to reveal key geographic gradients in diversity and composition, especially in Colombia and other Andean nations. But, unlike Gentry's floristic work, the first large-scale analyses of tropical forest dynamics lacked methodological standardisation. We relied heavily on published data from different teams worldwide and had limited sample sizes. To tackle this, the RAINFOR collaboration has developed standardised, international, long-term networks of permanent plots across Amazonia and beyond. These draw together existing efforts of local foresters and ecologists, who had often worked hitherto in isolation. By analysing the

gaps in geographical and environmental space, we then extended the network to fill gaps and support 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/) now combines long-term ecological monitoring efforts of 43 institutions worldwide. Here, given space limitations, I briefly synthesise some published results to review how mature lowland South American moist and wet forests have changed recently.

1.2 The Amazon Forest Inventory Network

In our monitoring plots, trees ≥ 10 cm diameter at breast height (dbh, measured at 1.3m height or above any deformity) are tracked over time. Each tree is marked with a unique number, measured, mapped, and identified. Periodically (generally every 1-5 years) the plot is revisited, surviving trees re-measured, dead trees noted, and trees recruited to 10 cm dbh 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 (the number or basal area of stems lost from a plot over time).

Most plots are 1 ha in size and comprise ~ 500 trees of ≥ 10 cm dbh, established using randomised or systematic sampling protocols to locate plots in old-growth forest landscape. Many have been monitored for more than a decade, although they range in age from 2 to 38 years (mean ~ 13). Here I analyse results of censuses completed up to 2007, but I first discuss results prior to the intense Amazon drought of 2005, and then also summarize the impact of the drought and briefly review more recent findings from RAINFOR (Brienen et al 2015). Details of exact plot locations, inventory and monitoring methods, and the challenges involved in analysing plot data are discussed elsewhere (e.g., Phillips et al. 2009; Baker et al. 2004; Lopez-Gonzalez et al. 2011). It is important to point out that the samples are not evenly distributed because they use historical plot data, and because of practical access issues. And yet a wide range of environmental space is captured by the samples. The general distribution and sampling density of plots is indicated in Fig. 1.

Scaling from individual tree to plot biomass is based on diameter-based allometric equations (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.

1.3 Key Findings

1.3.1 Structural Change. For 123 long-term mature forest plots with tree-by-tree data, biomass increased substantially between the first measurement (median date 1991) and the last measurement before the 2005 drought (median date 2003). For trees 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 discovered that African forests are also gaining biomass (Lewis et al. 2009).

There are various ways by which these plot-based measures can be scaled to tropical forests across Amazonia, and beyond. We used a simple approach given the various uncertainties. Thus we assumed that measurements were on average representative of the forest landscape, and that other components increased proportionally but that soil carbon stocks were static. We estimated the carbon 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 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, including those reported in plots of the CTFS network (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 and degradation, and the large net sink in the terrestrial biosphere after accounting for other sources and sinks. Also, unobserved large disturbances are 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).

1.3.2 Dynamic Changes. An alternative way to examine forest change is to look for changes in the processes (growth, recruitment, death) as well as the structure. For Amazonia we have measured these

forest dynamic processes in two ways. First, we examined changes in stem population dynamics. We estimated turnover between any two censuses as the mean of annual mortality and recruitment rates for the population of trees ≥ 10 cm diameter (Phillips and Gentry 1994, Phillips et al. 1994, Phillips 1996). Second, 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 (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 (Lewis et al. 2004). Thus, over the 1980s and 1990s these forests on average became faster-growing and more dynamic, as well as bigger.

We could also separate these plots into two distinct groups, one fast-growing and more dynamic (mostly in western Amazonia), and one slow-growing and much less dynamic (mostly in eastern Amazonia). Both groups showed increased stem recruitment, stem mortality, and biomass growth and loss rates, with greater absolute increases in rates in the faster-growing and more dynamic sites (Lewis et al. 2004), but with proportional increases in rates similar among forest types. It should be stressed that these results represent average responses of all forests measured. Within the dataset individual plots show a range of individual behaviour. But when viewed as whole the permanent plot record from neotropical mature forests is clear: there has been increasing growth, recruitment, and mortality for at least two decades across different forest types and geographically widespread areas.

1.3.3 Compositional Changes. Such structural and dynamic change is likely to affect other parts of the forest ecosystem too. Woody climbers (lianas), contribute 10-30% of forest leaf productivity, but are ignored in most stem monitoring studies. In RAINFOR plots of western Amazonia there was a concerted increase in the density and size of lianas (Phillips et al. 2002). 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 lowland forests. 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 sub-canopy and understory declined. Further studies are needed to determine whether comparable shifts in tree communities are occurring throughout Amazonia, and to update the Amazon liana trajectory over the early 21st century.

1.3.4 Recent Drought Impacts in Amazonia. The results discussed so far reflect forest changes up to the early part of the first decade of the twenty-first century. In 2005 parts of the Amazon region was struck by a major drought. With the RAINFOR network 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 recensusing plots to create 'drought census intervals' of typically 1 to 2 years per plot. In plots that were droughted the above-ground biomass change rate was clearly negative (-1.62 (- 3.16, -0.54) Mg ha⁻¹) (Phillips et al. 2009), and the size of the biomass change anomaly was closely correlated to the moisture deficit anomaly experienced. This implies that it was the drought that was responsible for the biomass loss, by contributing to extra mortality. We estimated the Amazon-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 Pg C. This large regional impact is now confirmed 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 requires monitoring of forests through post-drought recovery and repeated droughts, such as the 2015-16 El Niño event.

1.3.5 What is Driving these Increases in Growth, Recruitment, Mortality, and Biomass? Overall, the results show a clear fingerprint of increasing growth across tropical South America caused by a long-term increase in resource availability. 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 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 (Lewis et al. 2004).

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 CO₂ is the leading candidate, because of the long-term increase in CO₂ concentrations, the key role of CO₂ in photosynthesis, and its positive effects on plant growth. The carbon dioxide explanation is somewhat controversial still (cf. Phillips and Lewis 2014), in part because of the great challenge in conducting ecosystem experiments of the impacts of CO₂ fertilization at sufficient spatial and temporal scale. –Of course, given the global nature of the CO₂ increase and ubiquitous biochemistry of the plant response involved, we expect to see the same phenomenon in other biomes. In spite of important local variations and differences, increases in biomass and growth have now been reported from every continent where foresters measure trees (Pan et al. 2011).

1.3.6 The Future: How Vulnerable is Amazonia to Environmental Stress and Compositional Changes? Our long-term observations show that mature forests in the world's largest tract of tropical forest have changed. Such rapid alterations - regardless of the cause - were not anticipated by ecologists. This raises 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 lowland South American tropical forests have helped to slow the rate at which CO₂ has accumulated in the atmosphere, so acting as a buffer to global climate change. The concentration of atmospheric CO₂ 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 the African sink of 0.3-0.5 Pg C per year. This subsidy from nature could be a relatively short-lived phenomenon. A switch of mature tropical forests from this moderate carbon sink to even a small carbon source would impact on global climate and human welfare. 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. These thresholds will respond to rising temperatures which increase evaporation. The 2005 drought provides direct evidence of the potential for intense dry periods to impact rainforest vegetation. But it remains to be seen whether droughts are powerful and frequent enough to permanently shift the dominant pattern of biomass gains witnessed across mature tropical forests wherever they have been extensively monitored. We expect that only frequent 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 a larger 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 including its record warm temperatures are yet to be analysed.

Photosynthesis/ respiration changes: Forests are sinks as long as carbon uptake associated with photosynthesis exceeds losses from respiration. Under the simplest scenario of a steady rise in productivity over time, it is predicted that even mature forests will be carbon sinks for decades (e.g. Lloyd and Farquhar 1996). However the recent increases in productivity cannot continue indefinitely: if CO₂ is the cause, trees will become CO₂-saturated (limited by another resource) sooner or later.

Rising temperatures could also reduce the sink. Warmer temperatures increase the rates of 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, already reach such inflection-points. Canopy-to-air vapour deficits and stomatal feedback effects may also be paramount in any response of tropical forest photosynthesis to future climate change. The indirect effect of rising temperatures on photosynthesis via stomatal closure is probably the dominant negative impact on tropical forest growth (Lloyd & Farquhar 2008), but this is currently offset by increases in photosynthesis from increasing atmospheric CO₂. 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 CO₂ on tree growth is critical, and are areas of very active research and debate.

Carbon losses from respiration will 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 are unlikely, but cannot be ruled out.

Compositional change: Most models that project the future carbon balance in Amazonia (and future climate-change scenarios) still ignore the possibility that the forest species composition will change. Representing biodiversity is challenging, because of the computational complexities in integrating ecological processes into ecophysiology-driven models. But representing it better is important. Large changes in tree communities could lead to net losses of carbon from tropical forests. 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 (e.g., Baker et al. 2009). In Amazonia, compositional changes driven by greater resource supply, increased mortality rates, and gains in the fast-growing, light-wooded trees which escape lianas, and potentially which may benefit from a world largely stripped of its mega- and mesofaunal seed dispersers (e.g. Peres et al. 2016) could shut down the carbon sink function of tropical forests much earlier than ecophysiological models predict.

1.4 Conclusions

Long-term, high-quality monitoring is critical for any nation wanting to understand the behaviour of forests, and to respond to it with actions including in terms of protected area strategy. The big 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 (e.g. more montane species will decline, as is already being witnessed to some extent in Colombia (Duque et al. 2015)), but many surprises are likely.

What then would a nation-wide forest monitoring system look like in Colombia, a hyperdiverse, carbon-rich country with a major share of the Amazon? Such a network has to embrace science-led monitoring. This requires a collaborative vision and a national long-term funding commitment to match. Data must be 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 (exchanges with Amazon countries, exchanges with Europe). 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 so herbaria have to be involved too, and young taxonomists trained. Some plots can 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 validation, plant and animal DNA sampling, invertebrate surveys, training sites for students, etc.

Colombia can benefit directly from involvement in international collaborations like RAINFOR, but current efforts are insufficient. Much greater sampling in the vast regions of Amazonia is needed to reduce uncertainty due to incomplete spatial coverage, with a major effort to fill the large spatial gaps. Additionally, better integration with LiDAR approaches (which measure forest height) is 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, with (2) extensive remote sensing (LiDAR, radar), using the potential power of remote sensing techniques for scaling-up. Careful ground-based assessments to calibrate and validate forests' remotely-sensed canopy properties in terms of productivity, biomass, and biodiversity, and change, remain critical. Establishing quality, repeat census plots along the key geographic gradients is essential – in Colombia this means replicated sampling across elevation gradients from the Andean cordilleras to lowland Amazonia. These need to be tied to protected areas – thus the monitoring network helps nations fulfil CBD obligations of assessing the effectiveness of its protected areas. Finally, researchers need to co-ordinate efforts monitoring disturbed forests too, and of key resources for livelihoods. A skeleton framework for some of this already exists with RAINFOR and colleagues (eg PN Amacayacu, and sites in Chocó and Magdalena) as well as larger plots in PN Amacayacu and La Planada in the CTFS network. But many new plots are needed 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, the accelerated growth, mortality, and generally increasing biomass of tropical forests is a response to large-scale and slow-acting drivers such as increased carbon dioxide concentrations. 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.

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Figure Legends

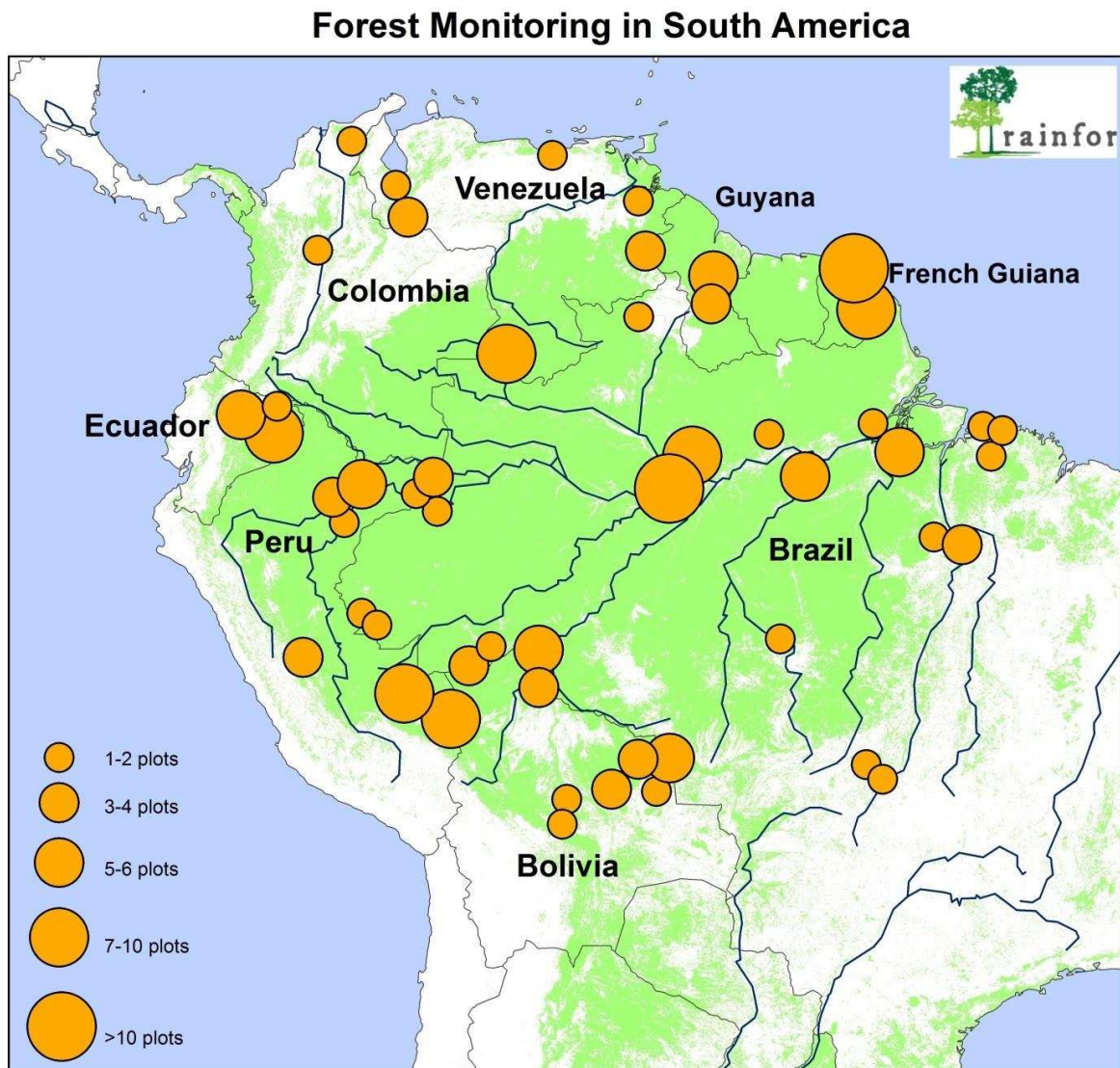


Figure 1. Distribution of long-term RAINFOR plots used for monitoring forest changes across northern lowland South America. With vital contributions from more than 100 botanists, ecologists and foresters working in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, and Venezuela, more than 300 plots help to build a long-term picture of the changing dynamics of Amazon and adjacent lowland 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.

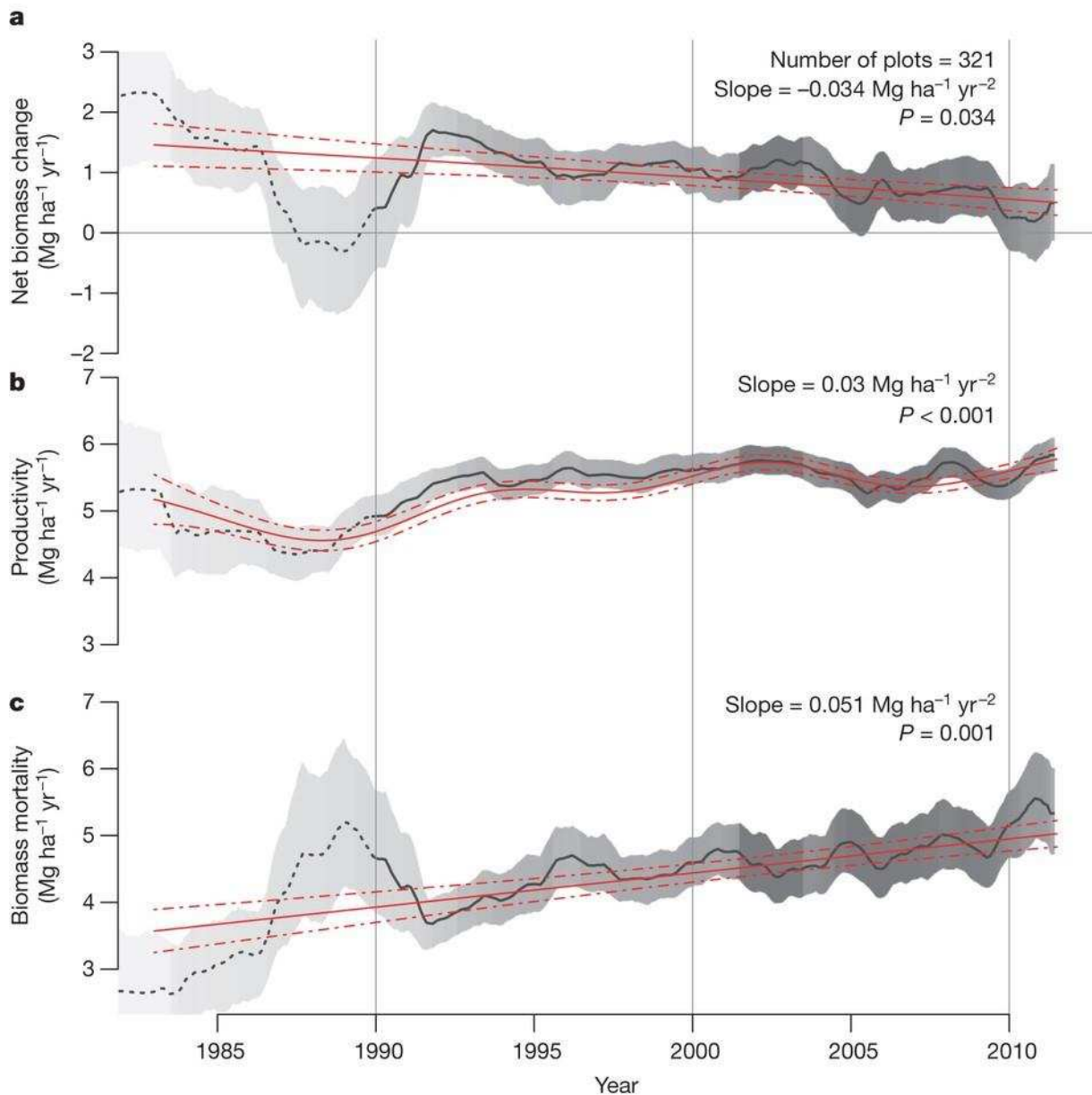


Figure 2. Trends in net above-ground biomass change, productivity and mortality across all RAINFOR sites, analysed up to 2011. Black lines show the overall mean change for 321 plots weighted by plot size, and its bootstrapped confidence interval (shaded area). The red lines indicate the best model fit 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).