Chapter 10
Recent Changes in Amazon Forest Biomass and Dynamics

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10.1 Introduction

10.1.1 Overview

There is a major planet-wide experiment under way. Anthropogenic 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 faunal imbalances and surface fires, impact forests in ways less evident to the casual observer (cf. Lewis et al. 2004a; Malhi and Phillips 2004; Estes et al. 2011). Similarly, anthropogenic atmospheric change is intensifying (Friedlingstein et al. 2006). By the end of the twenty-first century, carbon dioxide concentrations may reach levels unprecedented for at least 20 million years (e.g. Retallack 2001) and climates may move beyond Quaternary envelopes (Meehl et al. 2007). Moreover, the rate of change in these basic ecological drivers may be unprecedented in the evolutionary span of most species on Earth today. Additionally, these atmospheric changes are coinciding with probably the greatest changes in land cover and species' distributions since at least the last mass extinction at c. 65 million years ago (Ellis et al. 2011). The collective evidence points to conditions

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with no clear past analogue. We have entered the Anthropocene, a new geological epoch dominated by human action (Crutzen 2002; Steffen et al. 2011).

In this chapter, we 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 (Pg) of carbon in their biomass and soil (Pan et al. 2011), equivalent to more than half the total atmospheric stock, and annually process 40 Pg (Beer et al. 2010). 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 here impact on global biodiversity and the cultures, societies, and economies that are bound to this diversity (Groombridge and Jenkins 2003). Finally, as different plant species vary in their ability to store and process carbon, climate and biodiversity changes are linked by feedback mechanisms (e.g. Lewis 2006). 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. Analysis of the global carbon cycle shows that after accounting for known atmospheric and oceanic fluxes there is a large, and increasing, carbon sink in the terrestrial biosphere, reaching >3 Pg by the middle part of the last decade (Le Quéré et al. 2009); independent analyses of atmospheric carbon dioxide concentration data to infer sources and sinks of carbon imply carbon uptake over the terrestrial land mass in both tropical and extra-tropical latitudes (Stephens et al. 2007); a ground-up, independent analysis by foresters suggests that forests in every vegetated continent are implicated in this terrestrial sink (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 can 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 (e.g. Mitchard et al. 2009) and cannot yet detect species composition and hence the density of each tree's wood, which substantially drives forest biomass (Mitchard et al. 2014). Yet, permanent sample plot work in the tropics has until quite recently been very sparse and mostly focused on a few well-known locations, leaving most of the ~10 million km^2 expanse of the world's richest ecosystems unstudied. This is particularly risky given that no one location, or small number of studied forests, can be taken as the mean conditions of all forests. Site-centric ecology is invariably skewed, since peculiar local features—such as fragmentation, unusual soil conditions, cyclones, or fires—strongly colour interpretations. In most

fields, such as climate change, it would be an obvious folly to infer the presence or absence of global effects from records at a few sites, but long-term ecological monitoring is difficult and under-funded. As a result, attempts are still made to scale results from a few selected locations to draw conclusions about what the behaviour of the whole biome might be.

10.1.2   A Networked Approach

A robust approach to monitoring change needs to be much more synoptic. The first attempts to do this (Phillips and Gentry 1994; Phillips et al. 1994, 1998; Phillips 1996) drew inspiration from the macroecological work of Gentry, who had used intensive floristic inventories across hundreds of forest locations to reveal the major geographic gradients in diversity and composition (e.g. Gentry 1998a, b). But, unlike Gentry's floristic work, these first macroecological analyses of tropical forest dynamics lacked methodological standardisation. They 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 we have focused on developing standardised, international, long-term networks of permanent plots in mature forests across Amazonia and Africa. These first draw together the existing efforts of local foresters and ecologists, often working hitherto largely in isolation. Then, by analysing the gaps in geographical and environmental space, efforts can be made to extend the site network to fill the gaps and build support for long-term spatially extensive monitoring. The network of Amazonian-forest researchers, known as RAINFOR (*Red Amazónica de Inventarios Forestales*, http://www. geog.leeds.ac.uk/projects/rainfor/), now represents the long-term ecological monitoring efforts of 43 institutions worldwide including many from Amazonia itself. A parallel initiative in Africa, AfriTRON (*African Tropical Rainforests Observation Network*, http://www.geog.leeds.ac.uk/projects/afritron/), spans 11 countries across the African wet tropics. Here our aim is to synthesise some published results from RAINFOR to assess how Amazon forests have, on average, changed recently. Where appropriate, we also discuss results from the African network and from additional, individual sites where these shed light on the processes involved.

10.2   Methods

For these analyses, we define a monitoring plot as an area of old-growth, physiognomically mature forest where all trees ≥ 10 cm diameter at breast height (dbh, measured at 1.3 m height or above any buttress or other deformity) are tracked individually over time. 'Maturity' is inferred by the existence of a complex multi-age structure, multiple canopy tree species, large lianas, and large dead trees, together implying forests at least several centuries old. 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 remeasured, dead trees are noted, and trees recruited to 10 cm dbh are uniquely 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 (Higuchi et al. 1998; Baker et al. 2004a; Chave et al. 2005); (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). We present results from 50 to 123 plots, depending upon selection criteria for different analyses. The 'Amazon' plots span the forests of northern South America (Fig. 10.1), including Bolivia,
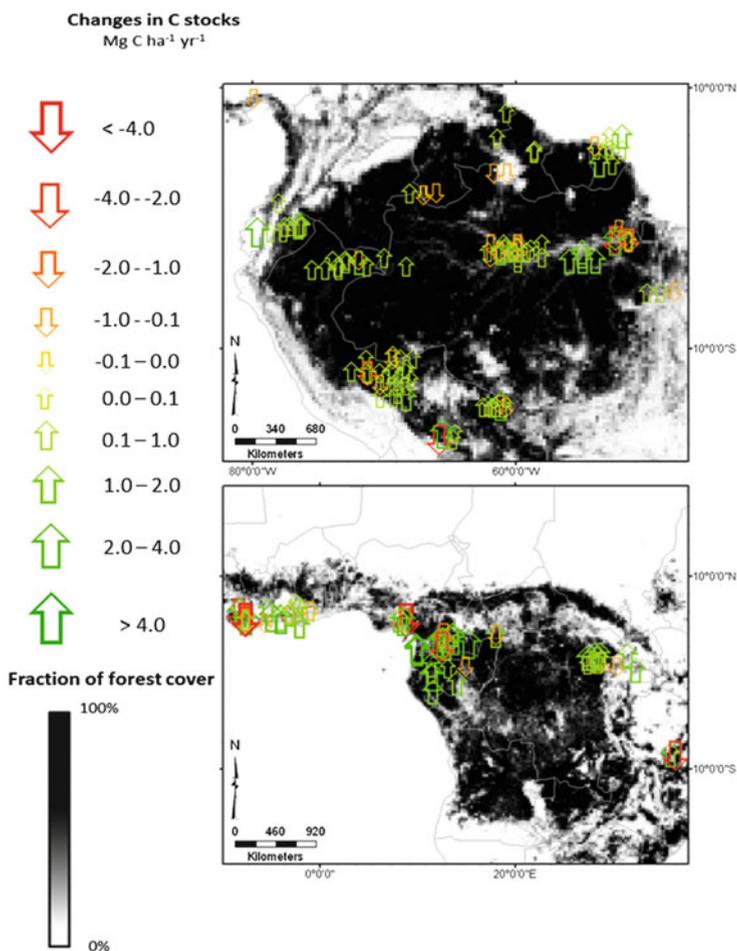

Fig. 10.1 Locations of RAINFOR and AfriTRON network plots used in this study. For each we indicate whether they individually increased in biomass or decreased in biomass over the period monitored (ending prior to the 2005 drought for Amazonia)

Brazil, Colombia, Ecuador, French Guiana, Peru, and Venezuela, from the driest to the wettest and the least to the most fertile soils. Most plots are 1 ha in size and comprise ~400–600 trees of $\geq$10 cm dbh, but the smallest is 0.25 ha and the largest 10 ha. The large majority result from applying locally randomised or systematic sampling protocols to locate plots in apparently old-growth forest landscape and then tracking their subsequent dynamics. Many plots have been monitored for more than a decade, although they range in age from 2 to 30 years (mean ~10 years). Here we analyse results of censuses completed up to 2007, but for Amazonia we first report results prior to the intense drought of 2005 (Aragão et al. 2007) and then also summarise the impact of the drought and briefly review the latest findings from RAINFOR (Brienen et al. 2015). Details of the exact plot locations, inventory and monitoring methods, and issues relating to collating and analysing plot data are discussed elsewhere in detail (Phillips et al. 2002a, b, 2004, 2009; Baker et al. 2004a, b; Malhi et al. 2002, 2004; Lewis et al. 2004b, 2009a; 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 limit where it is practical to work; nevertheless, a wide range of environmental space is captured by the samples (c.f. Fig. 10.2).

   Scaling from individual tree to Amazon plot biomass is based on the diameter-based allometric equations detailed in Baker et al. (2004a). Thus, we used an equation developed for the Manaus area (Chambers et al. 2001a), modified by taking account of the taxon-specific wood density of each tree relative to the mean wood density of trees in the Manaus region. Alternatively, biomass can be estimated by universal, tropical forest equations such as those of Chave et al. (2005). The Manaus equation is based on a smaller sample size but has the advantage of being local. More allometric equations have been developed by the research community. For simplicity, we only show results using the Baker et al. (2004a) equation here, but note that while different methods certainly result in systematic differences in biomass estimates (e.g. Chave et al. 2003; Peacock et al. 2007; Feldpausch et al. 2012), the rates of net biomass change calculated across Amazonia are largely insensitive to the equation used (Baker et al. 2004a). For Africa, we use the Chave et al.'s (2005) moist forest equation including tree height and propagate the uncertainty in both the diameter and height parameters to obtain final biomass estimates (Lewis et al. 2009a). We summarise findings from mature forests in terms of (a) structural change, (b) dynamic-process change, and (c) functional and compositional change, over the past two–three decades, including taking account of recent droughts in Amazonia.

Fig. 10.2 Sampling in environmental space across Amazonia. Most plots sampled are on acid soils in weakly seasonal rainforest climates, reflecting the dominant conditions of the region, but span a broad environmental range that includes more than two orders of magnitude in soil acidity for example. Figure depicts the location of 87 Amazon plots whose soil has been characterised by the time of the post-2005 drought analysis
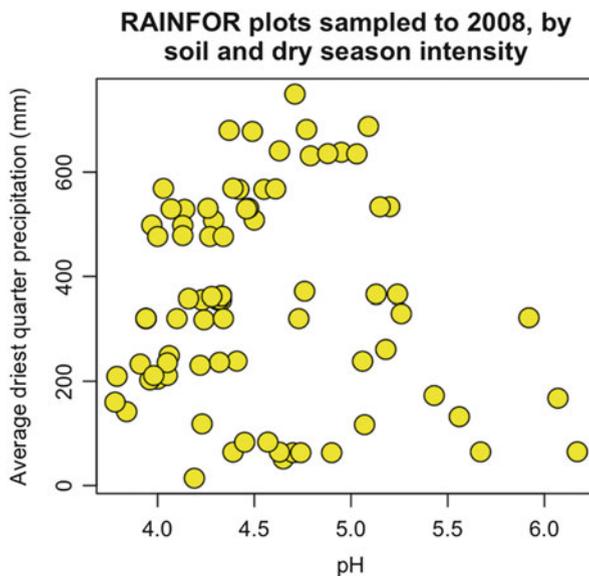
10.3 Results and Discussion

10.3.1 Structural Change

Among 123 long-term mature forest Amazonian plots with full tree-by-tree data, there was a significant increase in above-ground biomass between the first measurement (late twentieth century, 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) Mg C ha^{-1} $year^{-1}$ (mean and 2.5, 97.5 % confidence limits; Phillips et al. 2009). Across all 123 plots, the above-ground change was approximately normally distributed and shifted to the right of zero (Fig. 10.3a). The overall net increase estimated is slightly lower than but statistically indistinguishable from the 0.54 ± 0.29 Mg C ha^{-1} $year^{-1}$ estimated by Phillips et al. (1998) for the lowland Neotropics using 50 sites up to 1996, and the Baker et al.'s (2004a) estimate of 0.62 ± 0.23 Mg C ha^{-1} $year^{-1}$ for 59 core RAINFOR Amazon plots up to 2000. In the large dataset now available, estimates of biomass carbon change are also rather insensitive to different weightings based on measurement interval and plot area (supplementary information in Phillips et al. 2009). Using the same approach, we also discovered a similar phenomenon in African forests (see Box: 'Changing African Forests').
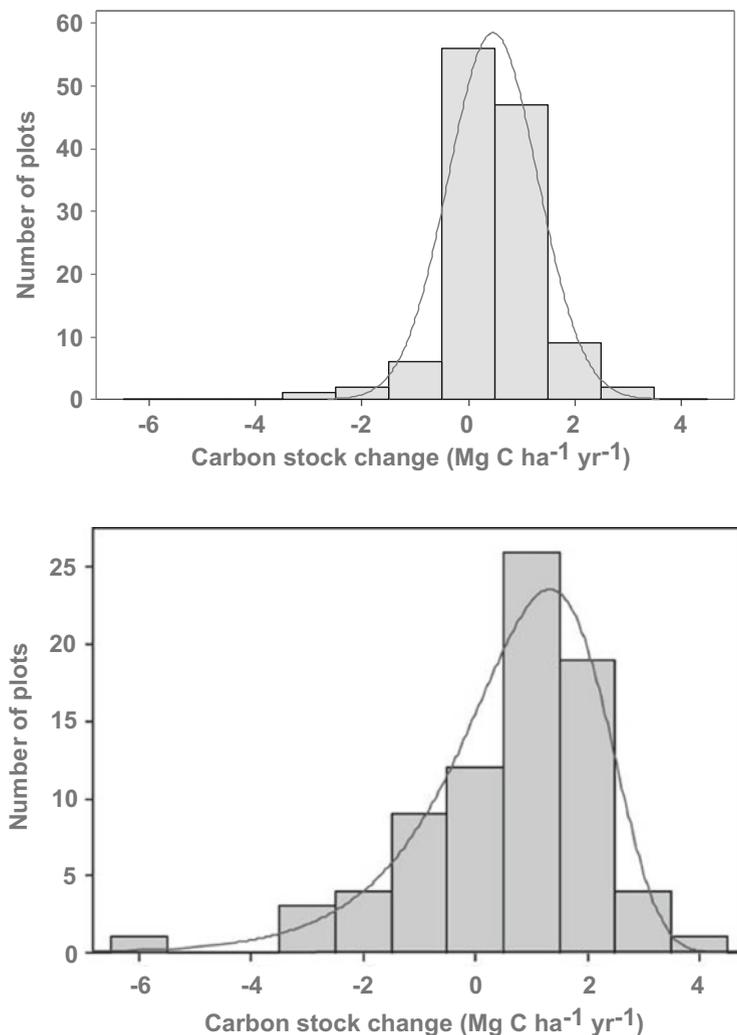
Fig. 10.3 Above-ground biomass carbon change of trees >10 cm diameter. (**a**) Across 123 Ama-zonian plots, based on initial and final stand-biomass estimates calculated using an allometric equation relating individual tree diameter and wood density to carbon. (**b**) Across 79 plots from Africa, but including estimated tree height for each stem, in addition to diameter and wood density, to estimate carbon, with uncertainty in the height and diameter measurement both propagated to final biomass carbon change estimates. As would be expected in a random sample of small plots measured for a finite period, some sites show a decline in biomass carbon during that period indicating that at that particular point in space and time tree mortality has exceeded tree growth. However, the mean and median are shifted significantly to the right for both datasets ($P < 0.001$)

Changing African Forests

African plots have been monitored in Liberia, Ivory Coast, Ghana, Nigeria, Cameroon, Central African Republic, Gabon, Democratic Republic of Congo, Uganda, and Tanzania and span West, Central, and East Africa biogeographic regions and from wet (~3000 mm rainfall per year) to dry (those adjacent to the savanna boundary) climates and a range of soil types (Lewis et al. 2009a).

Here, we measured a similar net sink in trees >10 cm diameter with a mean of +0.63 (bootstrapped 95 % CI 0.22–0.94) tonnes of carbon per hectare per year ($n = 79$ plots, mean start date 1987 and mean end date 1996; Lewis et al. 2009a). The distribution is left skewed and shifted to the right of zero (see Fig 10.3b). Resampling shows that obtaining such a sample of increasing biomass from a domain that was not increasing in biomass is highly unlikely ($P < 0.001$; Lewis et al. 2009a). African forests have greater biomass per unit area than Amazon forests (202 versus 154 Mg C ha^{-1}); once this difference is accounted for, both forest blocks have been gaining net biomass at the same relative rate (0.30 % per year for Amazonia, 0.29 % per year for Africa).

In Africa, Lewis et al. (2009a) also reported the relative change in biomass for 916 species from 79 plots across the tropical region, showing that there was no relationship between the wood density of a species and its change in biomass, relative to the stand. Similarly, there was no relationship between relative change in biomass and mean wood density when 200 common genera rather than species were analysed. Taken together with the results from Amazonia, this runs counter to expectations if tropical forest plots were mostly in late successional recovery from past disturbances.

There are various ways by which these plot-based measures can be scaled to tropical forests across Amazonia and Africa. We adopted a relatively simple approach given the various uncertainties, not all quantifiable, for example in terms of smaller stems, below-ground (root) biomass carbon, carbon in dead trees and litter, area of each forest type, and degree of human disturbance. Thus, we assumed that our measurements were, on average, representative of the wider forest landscape, and that other biomass and necromass 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 a series of correction factors to account for biomass of lianas, trees <10 cm diameter, necromass, and below-ground carbon, and a mid-range estimate of the surviving forest area for the year 2000 (Table 10.1). For the 1990s, this yielded a total estimated South American forest sink of 0.65 ± 0.17 Pg C year^{-1} and a corresponding sink in African forests of 0.53 ± 0.30 and 0.14 ± 0.04 Pg C year^{-1} in mature undisturbed Asian forests if these responded as other tropical forests did (Pan et al. 2011). Thus, the combined mature tropical forest sink in the 1990s is

Table 10.1 Estimated annual change in carbon stock (Tg C year^{-1}) in tropical intact forests by region for the periods of 1990–1999 and 2000–2007

	1990–1999								2000–2007							
	Estimated annual change in C stock (Tg C year^{-1})							Change per area	Estimated annual change in C stock (Tg C year^{-1})							Change per unit area
	Biomass	Dead wood	Litter	Soil	Wood product	Total change	Uncertainty	Mg C ha^{-1} year^{-1}	Biomass	Dead wood	Litter	Soil	Wood product	Total change	Uncertainty	Mg C ha^{-1} year^{-1}
Asia	125	13	2	ND	5	144	38	0.88	100	10	1	ND	6	117	30	0.90
Africa	469	48	7	ND	9	532	302	0.94	425	43	6	ND	8	482	274	0.94
Americas	573	48	9	ND	22	652	166	0.77	345	45	5	ND	23	418	386	0.53
Total	1167	108	17	ND	35	1328	347	0.84	870	98	13	0	36	1017	474	0.71

Table adapted from Pan et al. (2011), see that paper for details of calculations

ND data are not available

estimated to have been 1.3 ± 0.35 Pg C year^{-1}, before allowing for any possible net change in soil carbon stock. This is similar to the figure given by Lewis et al. (2009a), of 1.3 Pg C year^{-1} (bootstrapped CI 0.8–1.6) using plots with a mean interval of 1987–1997 and slightly differing methodology (Tropical America, 0.62; Tropical Africa, 0.44; and Tropical Asia 0.25 Pg C year^{-1}). In the decade of the 2000s, the American tropical sink apparently declined partly as a result of the 2005 Amazon drought; we discuss this later below.

The validity of these estimates depends on (i) measurement techniques; (ii) how representative the plots are of mature forests in South America, and the rest of the tropics; (iii) assumptions about the extent of mature forest remaining; and (iv) the extent to which we have sampled the regional-scale matrix of natural disturbance and recovery. Moreover, they represent average annual estimates for the period around the turn of the twenty-first century—forest plots are rarely measured sufficiently frequently in enough places to estimate biome carbon balance on a year-by-year basis. 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, p. 522; Stephens et al. 2007), and the large net sink in the terrestrial biosphere after accounting for other sources and sinks (e.g. Le Quéré et al. 2009).

10.3.2 Recovery from Large Disturbances?

The finding of increasing forest biomass over recent decades has been remarkably controversial (cf. for example Clark 2002; Phillips et al. 2002a; Wright 2005; Lewis et al. 2006, 2009b), despite the fact that an uptake of >2 Pg C year^{-1} somewhere on Earth's land surface is evident from independent mass-balance observations of the global carbon cycle. The most persistent area of controversy has been prompted by the statement 'Slow in, rapid out' (Körner 2003). The 'Slow in, rapid out' argument stresses that forest growth is a slow process while mortality can potentially be singular in time, thereby causing rapid biomass loss and sometimes resetting forest stand structure. Consequently, limited sampling or sampling over short observation periods may tend to miss severe perturbation events over large scales. Inferences based on such sampling could therefore result in positively biased estimates of above-ground biomass trends in mature forests when results from plot networks are extrapolated to a large area. Given the still relatively small number of tropical plots—relative to the total biome area—this concern is understandable. However, it is unlikely to be a major source of uncertainty or bias in our calculations for three reasons.

Firstly, large and intense natural disturbances are rare in the lowland humid tropics, and probably much rarer than in temperate and boreal forests. Thus, even when accounting for Landsat-based measurements of large disturbances and conservatively using a disturbance frequency/magnitude model fit that overestimates the frequency of large magnitude disturbances, it is clear that disturbances capable

of removing 100 Mg above-ground biomass at the 1-ha scale (i.e. about one-third of total standing biomass) have return times of 1000 years or more in Amazonia (Gloor et al. 2009: Table 1). Furthermore, Gloor et al. (2009) used a stochastic simulator to show for South American forests that any sampling biases resulting from such a disturbance regime, given the sample sizes available in the RAINFOR network, are too small to explain the gains detected by the plot network. Recent, independent analyses using satellite data from across the Amazon basin (Espírito-Santo et al. 2010, 2014) show just how rare large, intense disturbances in fact are. Thus, the return time of stand-initiating scale disturbances in western Amazonia is c. 27,000 years, while in eastern Amazonia it is ≈90,000 years. The basin-wide mean, c. 39,000 years, is so large that any impacts on our Amazon dataset are negligible (and in light of these values it is hardly surprising that RAINFOR plots have yet to sample a single stand-resetting disturbance). This accords with the first pioneering large-scale analysis, which also showed the rarity of large-scale disturbance events in the Amazon basin (Nelson et al. 1994). The 'Slow-in, rapid-out' debate was magnified by a theoretical paper which attempted to simulate its impacts (Fisher et al. 2008), but which parameterised the size-frequency distribution of disturbance events incorrectly—thus overestimating the frequency of large disturbance events (c.f. Lloyd et al. 2009)—, and then managed to compare single-year time-step simulations with actual RAINFOR results which averaged intervals of 10 years. These large errors both exaggerated the apparent magnitude of the 'Slow-in, rapid-out' effect. A recent analysis of the entire Amazon disturbance intensity/frequency spectrum using LiDAR, Landsat, and multiple on-the-ground measurements has shown quite clearly that the large majority of tree death in Amazonia occurs in very small events (one, two, or three trees) and that 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 (Espírito-Santo et al. 2014).

Secondly, the RAINFOR network was successfully utilised to detect the impact of a major disturbance (the 2005 Amazon drought; see below) and to differentiate its dynamic and floristic effects from the background state of long-term biomass accumulation. This biomass decline was in fact dominated by a clearly detectable increase in mortality (Phillips et al. 2009). Thus, if there was a dominating impact of very large, late-twentieth century disturbance events on Amazon forests, for example associated with intense El Niño or La Niña years, these should have been detected. It has been suggested that Amazonia may still be recovering from earlier potentially greater 'mega-disturbances', such as the 1926 drought, or even widespread deforestation pre-1492. While such ideas can be appealing, simple back-of-the-envelope calculations show that for the forest to still be recovering at the end of the twentieth century at the rate of hundreds of millions Mg C year^{-1}, then the carbon lost to the atmosphere at the time needs to be in the order of tens of billions of tonnes—or more—well beyond anything recorded in the global atmospheric record of CO_2. We note that while the 2005 impact was large in magnitude at the scale of 1–2 years, its impacts were in the order of one to two billion tonnes of carbon, much too weak to shut down the sink even for a decade.

Thirdly, our plots lack the basic ecological signatures of forests recovering from large disturbances. Thus, the biomass increase has been only one of several changes recorded in Amazonian forest plots. Across 91 RAINFOR plots where we tracked populations to 2002, there was also a small increase in the stand density between the first and last measurements, of 0.84 ± 0.77 stems ha^{-1} year^{-1}, an annual increase of $0.15 \pm 0.13\%$ (Phillips et al. 2004). The same test using a longer-term subset of plots (50 plots from Lewis et al. 2004b) showed a slightly larger increase ($0.18 \pm 0.12\%$ per year). These increases in stand density, while proportionally smaller than the biomass changes, are counter to expectations if the plots were in an advanced state of secondary succession (e.g. Coomes and Allen 2007), as do the simultaneous increases in tree growth rates (see below). In Africa stand density changes have yet to be evaluated, but in both Africa and Amazonia there has been no shift in species composition towards more shade-tolerant taxa that would occur in a domain that was recovering from past disturbance events (e.g. Lewis et al. 2009a; Phillips et al. 2009), nor has there been on average over the networks the clear decline in growth and slowing stem dynamics that late-recovery tropical forests exhibit (Chambers et al. 2004). In sum, analysis of other structural, dynamic, and floristic change in the same plots is not consistent with a widespread disturbance-recovery signature. These results argue against the notion that the generalised biomass increase observed across Amazon and African plots can be explained as a result of a combination of disturbance recovery and small sample sizes.

Lastly, independent evidence from a network of large plots (Chave et al. 2008a), from atmospheric CO_2 data (Denman et al. 2007; Stephens et al. 2007), and from carbon mass-balance approaches (Le Quéré et al. 2009) all imply a carbon sink in tropical forests (c.f. Phillips and Lewis 2014). Parsimony therefore suggests that the increase in biomass is not the result of a statistical artefact based on frequent forest disturbance episodes that have been poorly sampled.

The plots in the long-term monitoring networks are, however, not randomly distributed. It is possible to test whether this spatial bias might be driving the result by assessing whether we have oversampled unusually heavily in regions that happened to be gaining biomass, and under-sampled those that happened to lose biomass. At smaller scales this is unlikely, since the long-term mean net gain in Amazonia is almost identical whether the sampling unit is taken to be the 'plot' (as here), or a larger unit such as a 'landscape cluster of plots' in both Amazonia and Africa (Phillips et al. 2009; Lewis et al. 2004b, 2009a). At larger scales while the networks still leave large expanses of Brazilian Amazonia and the Central Congo Basin unmonitored (Fig. 10.1), the climate- and soil-environmental space is well covered (Fig. 10.2).

Looking forward, much greater monitoring efforts in the vast still difficult-to-access regions of Amazonia are clearly needed in the future to reduce the uncertainty due to incomplete spatial coverage. One strategy would be to purposefully try to fill the large spatial gaps. Alternatively/additionally, a systematic grid-based approach is also appealing and is being planned by some national-level inventory programmes. The access challenges in many tropical forests for once-off inventory, let alone for sustaining multiple high-quality remeasurements in remote locations,

can hardly be overstated however. We expect that the most cost-effective strategy for monitoring the more remote remaining tropical forests would combine (1) - gap-filling the monitoring networks where possible—with locally randomised plots—with (2) extensive remote sensing (viz. LiDAR, radar). The potential power of remote sensing techniques for scaling-up is abundantly clear. The need for careful ground-based assessments to permit calibrating and validating forests' electromagnetic reflectance in terms of productivity, biomass, and biodiversity is equally obvious.

10.3.3   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 ≥10 cm diameter (Phillips and Gentry 1994). Secondly, we examined changes in biomass fluxes of the forest—in terms of growth of trees and the biomass lost with mortality events. These stand-level rates of biomass growth and biomass loss should be approximately proportional to the rate at which surviving and recruiting trees gain basal area and the rate at which basal area is lost from the stand through tree death (Phillips et al. 1994).

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 all of these key ecosystem processes—stem recruitment, mortality, and turnover, and biomass growth, loss, and turnover—increased significantly (Fig. 10.4) when the first monitoring period is compared with the second (Lewis et al. 2004b). 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, and mortality) were about an order of magnitude greater than the increases in the structural pools (above-ground biomass and stem density; Lewis et al. 2004b).

These and similar results can be demonstrated graphically in a number of ways. In Fig. 10.5, we plot the across-site mean values for stem recruitment and mortality as a function of calendar year. The increase is evidently not the short-term result of a year with unusual weather: recruitment rates on average consistently exceeded mortality rates, and mortality appears to have lagged recruitment (Phillips et al. 2004; Lewis et al. 2004b).

For the 50 Amazon 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
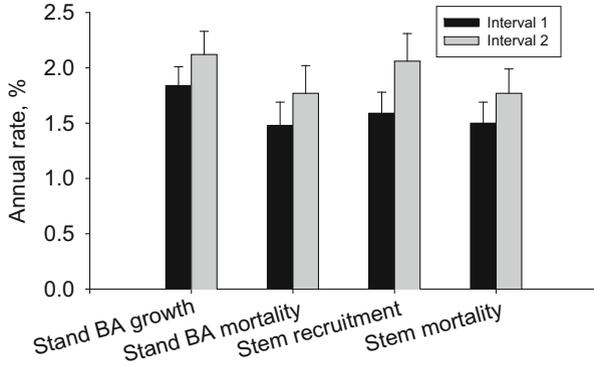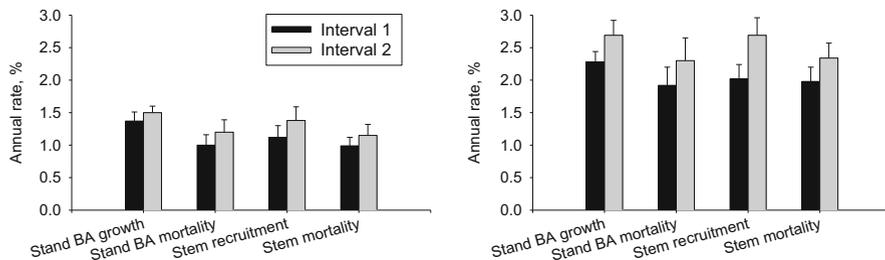
Fig. 10.4 Annualised rates of stand-level basal-area growth, basal-area mortality, stem recruit-ment, and stem mortality from plots with two consecutive census intervals, each giving the mean from 50 plots with 95 % confidence intervals. Paired *t*-tests show that all of the increases are significant. The average mid-year of the first and second censuses was 1989 and 1996, respectively (from Lewis et al. 2004b)
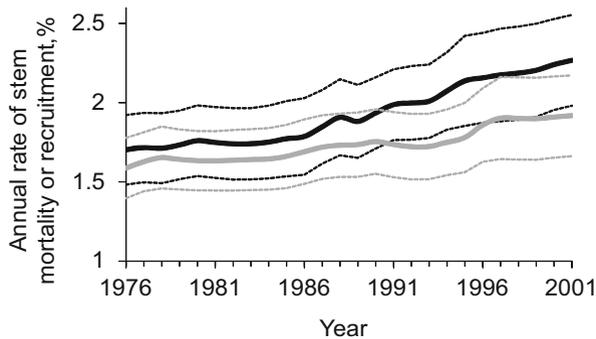
Fig. 10.5 Mean and 95 % confidence intervals for stem recruitment and mortality rates against calendar year, for plots arrayed across Amazonia. Rates for each plot were corrected for the effects of differing census-interval lengths, for 'site-switching' (changes through time in the plots being measured), and for 'majestic-forest bias' (potential avoiding of gaps when establishing plots). A detailed justification methodology for these corrections is given in Phillips et al. (2004); all trends hold if these corrections are not applied; *black* indicates recruitment, *grey* indicates mortality, *solid lines* are means, and *dots* are 95 % confidence intervals (from Phillips et al. 2004)

gradient across Amazonia (Phillips et al. 2004; ter Steege et al. 2006; Quesada et al. 2012). 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 (Fig. 10.6; Lewis et al. 2004b), but proportional increases in rates that were similar and statistically indistinguishable among forest types (Lewis et al. 2004b). It should be stressed that these results represent the mean response of all mature forests measured. Within the dataset naturally there are many

Fig. 10.6 Annualised rates of stand-level basal-area growth, basal-area mortality, stem recruitment, and stem mortality over consecutive census intervals for plots grouped into 'slower-growing less-dynamic' (*left*) and 'faster-growing more-dynamic' (*right*) forests. Of the slower-dynamics group, 20 of 24 plots are from eastern and central Amazonia, whereas just two are from western Amazonia. Of the faster-dynamics group, 24 of 26 plots are from western Amazonia, with just one from central Amazonia. The remaining three plots are from Venezuela and outside the Amazon basin. Changes have occurred across the South American continent and in both slower- and faster-dynamic forests (from Lewis et al. 2004b)

individual plots showing different, individual responses, just as within the whole literature there are some reports of individual sites showing similar or different patterns (e.g. Chave et al. 2008b; Feeley et al. 2007). Nevertheless, when viewed as whole the permanent plot record from Amazon and neotropical mature forests indicates that increasing growth, recruitment, and mortality occurred for at least two decades across different forest types and geographically widespread areas.

The simultaneous recent increases in plot dynamic rates, biomass, and stand density raise the question—for how long has this been going on? Only a handful of Amazon plots were monitored before the 1980s. To go further back in time requires alternative methods, for example annual dating of growth rates of a large sample of individual trees from different species, such as has been done in two locations in non-flooded mature forest (Vieira et al. 2005), using radiocarbon dating. Although the majority of trees tested did grow faster since 1960 than before 1960, the null hypothesis of no change in growth rate could not be rejected. This technique is complicated by potential ontogenetic variation in growth rates, partly related to changing light environments (e.g. Worbes 1999), and could overestimate stand-level growth rates in the past because individual trees with slow and declining growth are more susceptible to mortality (Chao et al. 2008) and therefore less likely to survive to the point at which they are dated. Similarly, as trees mature and increasingly allocate resources to flower, fruit, and seed production, ageing cohorts can exhibit slowing growth over time.

An alternative approach has been to analyse multiple dated herbarium samples stretching back to the nineteenth century for $\delta^{13}C$, ^{18}O, and stomatal density to assess possible changes in photosynthesis (and by implication, growth). For two species from the Guiana Shield, both showed implied increased photosynthesis over the past century (Bonal et al. 2011). A third approach—using tree rings to project growth of some tree species back in time—suffers from similar biases as the radiocarbon studies.

10.3.4   Functional Compositional Changes

Changes in the structure and dynamics of tropical forests can be expected to be accompanied by changes in species and functional composition. Phillips et al. (2002a) 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 (Fig. 10.7; Phillips et al. 2002b). Over the last two decades of the twentieth century, the density of large lianas relative to trees increased here by 1.7–4.6 % per year—i.e. roughly doubling 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. Other scattered reports since have suggested that the phenomenon of increasing lianas extended across other neotropical forests too (reviewed by Schnitzer and Bongers 2011). There is some limited experimental evidence (Granados and Körner 2002) for growth responses in tropical lianas to elevated atmospheric CO_2 concentrations to be stronger than those of trees.

Finally, a handful of studies have considered whether there have been consistent changes in tree species composition in forests over the past two decades (Laurance et al. 2004; Chave et al. 2008a; Lewis et al. 2009a; Butt et al. 2012). In the first, on a large cluster of plots in north of Manaus, many faster-growing genera of canopy and emergent stature trees increased in basal area or density, whereas some slower-growing genera of subcanopy or understory trees declined. Laurance et al. (2004) provided evidence of pervasive changes in this locality: growth, mortality, and recruitment all increased significantly over two decades (total basal area also increased, but not significantly so), with faster-growing genera showing larger increases in growth, relative to slower-growing genera. Further studies are needed to determine whether comparable shifts in tree communities are occurring throughout Amazonia.

Second, in Africa (see Box) wood density of a taxon has no predictive value of its change through time (Lewis et al. 2009a). Thirdly, Chave et al. (2008a) reported functional changes across ten forest plots across the tropics, by grouping species into quartiles based on growth rate, wood density, seed size, and maximum plant size. On an absolute basis, there were significant increases in biomass of the fastest- and slowest-growing quartiles of species, no significant change in biomass of the highest and lowest quartiles based on wood density, a significant increase in absolute biomass of the quartile with the smallest seed size, and no changes in biomass of quartiles based on maximum tree size. However, if these shifts are calculated relative to the changes in biomass of the stand, only one result is significant: the largest trees significantly decreased in biomass relative to the stand, whereas the smallest trees showed no relative change. Collectively, results from these three studies suggest that the increase in forest stand biomass is being caused by concurrent increases of many species with differing ecological habits.
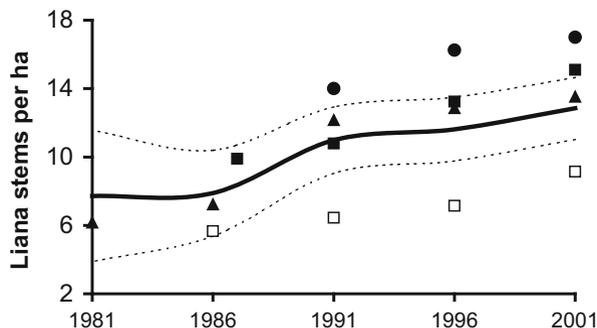
Fig. 10.7 Five-year running means (*solid line*) with 95 % confidence intervals (*dashed lines*) of liana stem density per hectare ($\geq$10 cm diameter at breast height), with values plotted separately for northern Peru (*filled squares*), southern Peru (*filled triangles*), Bolivia (*filled circle*), and Ecuador (*unfilled squares*) (adapted from Phillips et al. 2002b; see that paper for full details of field and analytical methodology)

10.3.5   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 unusual characteristic of being driven by strong warming in the tropical north Atlantic, a feature that appears in some global circulation model outcomes of projected climate change (e.g. Cox et al. 2004). With the RAINFOR network largely in place and a good forest dynamics baseline established, we had an opportunity to use this 'natural experiment' to assay the sensitivity of the largest tropical forest to an intense, short-term drought, by rapidly re-censusing plots across the basin. Of 55 plots which we surveyed in 2005, the mean annual above-ground biomass change was -0.59 (-1.66, $+0.35$) 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) Mg ha^{-1}]. Moreover, across the measured plots the magnitude of the biomass change anomaly was closely correlated to the magnitude of the moisture deficit anomaly experienced in the same period, with most of the difference being related to increased mortality, implying 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 (-2.01, -0.57) Pg C and -1.60 Pg C (-2.63, -0.83) (Tables 10.2 and 10.3). The first value is based on scaling the per-plot impact by the total area impacted by drought; the second greater value is based on using remotely sensed rainfall data to scale from the relationship of biomass change data with relative drought intensity. The biomass dynamics/climate approach makes use of more of the information on forest response to drought than the simple scaling-up of the mean drought-impacted plot effect, but requires additional assumptions

Table 10.2 Estimated 2005 Amazon drought impact, from plot data, using two different approaches. (A) Scaling from the statistical distribution of plot biomass change data (sampling effort-corrected AGB change relative to pre-2005 for each plot) to the whole area of Amazon forest affected in 2005

			Mean	2.5 % CI	97.5 % CI
		Mg AGB $ha^{-1} a^{-1}$	*−2.39*	*−1.12*	*−3.97*
	Expansion factor				
Mean 2005 interval length, years	*1.97*				
Smaller trees and lianas	*1.099*				
Droughted forest area, ha (TRMM data)	3.31×10^8				
Additional fraction of Amazonia with unreliable TRMM data	*1.031*				
Sum AGB impact, Mg			-1.76×10^9	-8.25×10^8	-2.93×10^9
Below ground	*1.37*		-6.52×10^8	-3.05×10^8	-1.08×10^9
Sum biomass impact, Mg			-2.41×10^9	-1.13×10^9	-4.01×10^9
Sum carbon impact, Mg	***0.5***		$\mathbf{-1.21 \times 10^9}$	$\mathbf{-0.57 \times 10^9}$	$\mathbf{-2.01 \times 10^9}$

For details of the methodology, see online supplementary information published with Phillips et al. (2009)
[*]The text in italics and bold italics signify 95% confidence intervals

Table 10.3 Estimated 2005 Amazon drought impact, from plot data, using two different approaches. (B) Scaling from the plot biomass dynamics versus climate relationship to the whole Amazon forest area affected in 2005, using the relationship between change in mean annual maximum cumulative water deficit values and change in biomass dynamics

			Mean	2.5 % CI	97.5 % CI
		Mg AGB	*−1.05 × 10⁻⁹* (-1.05×10^{-9})	*−5.46 × 10⁻⁸* (-5.46×10^{-8})	*−1.72 × 10⁻⁹* (-1.72×10^{-9})
	Expansion factor				
Mean 2005 interval length, years	*1.97*				
Additional proportion of Amazonia with unreliable TRMM data	*1.031*				
Smaller trees and lianas	*1.099*				
Sum AGB impact, Mg			-2.33×10^{-9}	-1.22×10^{-9}	-3.83×10^{-9}
Below ground, Mg	*1.37*		-8.63×10^{-8}	-4.51×10^{-8}	-1.42×10^{-9}
Sum biomass impact, Mg			-3.20×10^{-9}	-1.67×10^{-9}	-5.25×10^{-9}
Sum carbon impact, Mg	***0.5***		$\mathbf{-1.60 \times 10^{-9}}$	$\mathbf{-0.83 \times 10^{-8}}$	$\mathbf{-2.63 \times 10^{-9}}$

For details of the methodology, see online supplementary information published with Phillips et al. (2009)
[*]The text in italics and bold italics signify 95% confidence intervals

which may introduce error. The consistency of the results from the different analyses indicated a significant regional impact (confirmed now by new, independent analyses, e.g. Gatti et al. 2014; Grace et al. 2014), but much of this might not be 'seen' by the atmosphere until future years. Thus, the main impact was a temporary increase in dead wood production, implying losses to the atmosphere over future years as these dead trees decompose. In the drought year itself the sink may decline (reduction in growth) but not halt (as the new necromass only begins to decompose). Potentially, the sink could even increase temporarily if potential short-term reductions in soil respiration are allowed for, although aircraft measurements of atmospheric CO_2 concentrations show that in the 2010 drought the overall effect was indeed to completely suppress the long-term biomass sink for a year (Gatti et al. 2014).

Regardless of these details, the total committed 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, Figure 1). By combining results from 2005 with published and unpublished information on tropical tree mortality from elsewhere, we have been able to extend the drought–mortality response relationship further. This second analysis (Phillips et al. 2010) suggested that across the biome, forest sensitivity to moisture anomalies may be predictable, and that even relatively weak drying compared to normal climatology can cause excess deaths once adequate sampling is in place to detect them. However, it should be noted that these are the impacts of short-term intense drought events. Recent analyses of 19 long-term plots from West Africa, which has seen a decades-long drying, saw a net increase in biomass coupled with strong increase in dry-adapted species over a c. 20-year period of monitoring (Fauset et al. 2012), similar to preliminary findings from western Amazonia (Butt et al. 2012). This might reflect the fact that the more marginal forest climate in West Africa and Pleistocene history of dry episodes may have already reduced the diversity and importance of wet forest taxa (Parmentier et al. 2007). Fuller understanding of the impacts of drought will require monitoring of forests through post-drought recovery and repeated droughts (such as occurred also in Amazonia in 2010) over the long term.

10.3.6   What is Driving these Changes?

What could have caused the continent-wide increases in tree growth, recruitment, mortality, stem density, and biomass? Many factors could be invoked, but there is only one parsimonious explanation for the pre-2005 pattern. The results appear to show a coherent fingerprint of increasing growth [i.e. increasing net primary productivity (NPP)] across tropical South America, probably caused by a long-term increase in resource availability (Lewis et al. 2004a, b; 2009a, b). According to this explanation, increasing resource availability increases NPP, which then increases stem growth rates. This accounts for the increase in stand basal-area growth and stem recruitment rates and the fact that these show the clearest, most

highly significant changes (Lewis et al. 2004b). 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: biomass mortality and stem mortality rates increase. Thus, the system gains biomass and stems, while the losses lag some years behind, causing an increase in above-ground biomass and stems. Overall, this suite of changes may be qualitatively explained by a long-term increase in a limiting resource.

The changes in 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 (Coomes and Grubb 2000). Others, however, have argued (e.g. Körner 2004; Lloyd pers. comm.) that the greatest proportional response should be in understory seedlings and saplings for whom a small increase in photosynthetic rate here could have a great proportional impact on carbon balance—and there is some experimental evidence to support this view (e.g. Kerstiens 2001; Aidar et al. 2002).

What environmental changes could increase the growth and productivity of tropical forests? While there have been widespread changes in the physical, chemical, and biological environment of tropical trees (Lewis et al. 2004a), only increasing atmospheric CO_2 concentrations, increasing solar radiation inputs (Wong et al. 2006), rising air temperatures, and changing precipitation patterns (Trenberth et al. 2007) have been documented across most or all of Amazonia over the relevant time period and could be responsible for increased growth and productivity. Additionally, it is conceivable that nutrient inputs have increased, first, from biomass burning that is occurring closer to once-remote tropical forest plots that are increasingly encroached upon by deforestation (Laurance 2004), and second, long-range inputs of Saharan dust to Amazonia (and west African forests) have increased over recent decades, possibly in response to climate change.

Yet for only one of these changes do we have clear evidence that the driver has both certainly changed over a large enough area and that such a change is likely to accelerate forest growth (Lewis et al. 2004a, 2009b). The increase in atmospheric CO_2 is the primary candidate, because of the undisputed long-term increase in CO_2 concentrations, the key role of CO_2 in photosynthesis, and the demonstrated positive effects of CO_2 fertilisation on plant growth rates, including experiments on forest stands, although not yet in the tropics (Norby et al. 2002; Hamilton et al. 2002; Lewis et al. 2004a, 2009b; Norby and Zak 2011). However, some role for increased insolation (e.g. Nemani et al. 2003; Ichii et al. 2005), or aerosol-induced increased diffuse fraction of radiation (e.g. Oliveira et al. 2007), or nutrient inputs, or rising temperatures increasing soil nutrient mineralisation rates, cannot be ruled out (Lewis et al. 2004a, 2006; 2009b; Malhi and Phillips 2004, 2005). Lastly,

given the global nature of the CO_2 increase and ubiquitous biochemistry of the plant response involved, we may expect to see the same phenomenon in other biomes. Similarly to the tropics, increases in biomass and/or growth have recently been reported in maritime forests of western Canada (Hember et al. 2012), and across the temperate forests of the northern hemisphere (Luyssaert et al. 2008), and indeed on every continent where foresters are making measurements in multiple sites (Pan et al. 2011).

10.3.7   The Future: Potential Susceptibility of Amazon Forest to Environmental Stress and Compositional Changes

Long-term observations indicate that Amazonia, the world's largest tract of tropical forest, has shown concerted changes in forest dynamics over recent decades. Such unexpected and 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 may 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_2 has accumulated in the atmosphere, thereby acting as buffer to global climate change. The concentration of atmospheric CO_2 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 $year^{-1}$ (and an African sink of 0.3–0.5 Pg C $year^{-1}$). This subsidy from nature could be a relatively short-lived phenomenon. Mature Amazonian forests may (i) continue to be a carbon sink for decades (e.g. Chambers et al. 2001b; Cramer et al. 2001; Rammig et al. 2010), (ii) soon become neutral or a small carbon source (Cramer et al. 2001; Phillips et al. 2002b; Körner 2004; Laurance et al. 2004; Lewis et al. 2011), or (iii) become a mega-carbon source (Cox et al. 2000; Cramer et al. 2001; Rammig et al. 2010; Galbraith et al. 2010), with modelling results reporting all three responses following a major model-inter-comparison project (Friedlingstein et al. 2006). 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 be enough to 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, which we discuss below.

10.3.7.1 Moisture Stress

Anthropogenic climate change will include altered precipitation patterns. There are critical thresholds of water availability below which tropical forests cannot persist and are replaced by savanna systems; currently, as long as soil conditions are adequate, the threshold lies around 1000–1500 mm rainfall per annum (Salzmann and Hoelzmann 2005; Staver et al. 2011), but this level could increase with rising temperatures which increase evaporation, or it could decrease if rising atmospheric CO_2 concentrations reduce transpiration. The outcome of the interplay between these factors is therefore critical to determining transitions between carbon-dense tropical forests and carbon-light savanna systems. The degree to which tropical forests may be ecophysiologically resilient to extreme temperatures, particularly in the context of rising atmospheric CO_2 concentration, is a subject of active research, reviewed elsewhere (Lloyd and Farquhar 2008; Lewis et al. 2009b), and explored on a biome-wide scale by Zelazowski et al. (2011).

The 2005 drought provides direct evidence of the potential for intense dry periods to impact rainforest vegetation. However, while events such as the 2005 Amazon drought are clearly capable of at least temporarily disrupting some of the long-term trends in forest biomass, it remains to be seen whether they 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 c. 5-year mean interval length available for plots at that time (fig. 1 in Phillips et al. 2009), implying a rapid recovery. We expect therefore that only frequent, multiple droughts would cause the sustained increases in necromass production needed to turn the long-term carbon sink in mature forest into a sustained source.

In 2010, a new drought affected the Amazon forest, again dropping some rivers to record lows. If the water deficit intensity–forest carbon loss relationship that we measured during 2005 also holds for the 2010 drought, then a total impact on mature forest biomass carbon in the region of c. 2 Pg can be anticipated (Lewis et al. 2011). It remains an open question as to how much the forest had recovered from the 2005 drought before the 2010 drought impacted the forest plots. Only coordinated monitoring with distributed networks of plots can determine whether the recent events represent one-off perturbations for forest carbon stocks from which a full recovery is made within 5 years, or the start of a longer-term climate-induced phase shift in which mature Amazonia becomes carbon neutral or a carbon source. A more recent, long-term analysis from a larger RAINFOR plot dataset (Brienen et al. 2015) has found evidence of a progressive decline in the net Amazon sink, in spite of the long-term growth gains. Recent droughts have played a part, but this enhanced dataset also indicates clearly that mortality has been

increasing over a longer period, suggesting that other mechanisms are also constraining the carbon density of Amazon forests.

10.3.7.2   Photosynthesis/Respiration Changes

Forests remain a sink 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 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_2 is the cause, trees are likely to become CO_2 saturated (i.e. limited by another resource) at some point in the future. More generally, whatever the driver for recently accelerated growth, forest productivity will not increase indefinitely, as other factors, such as soil nutrients, will limit productivity.

Rising temperatures could also reduce the forest sink or cause forests to become a source in the future. 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 (Lewis et al. 2004a; Doughty and Goulden 2008). 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 and Farquhar 2008), which is currently more than offset by increases in photosynthesis from increasing atmospheric CO_2. Alternatively, there is evidence that electron transport is the critical step in maximising photosynthesis at a given light level (Haxeltine and Prentice 1996), and the electron transport chain undergoes a reversible point of inflection as low as c. 37 °C (Lloyd and Farquhar 2008), thereby reducing photosynthesis at higher temperatures. Additionally, higher air temperature also means higher respiration costs which will also impact on the ability of plants to maintain a positive carbon balance in the future, which has been argued to be already affecting one forest in Costa Rica (Clark et al. 2010).

Understanding this complex relationship between temperature changes and their impacts on respiration and photosynthesis, plus the impact of rising atmospheric CO_2 on tree growth, is critical. The first global circulation model (GCM) to include dynamic vegetation and a carbon cycle that is responsive to these dynamic changes suggested that under the 'business as usual' scenario of emissions, IS92a, atmospheric CO_2 concentrations reach >900 ppmv (parts per million by volume) in 2100, compared to ~700 ppmv from previous GCMs (Cox et al. 2000, 2004). These concentrations depend on (1) dieback of the eastern Amazonian forests, caused by climate change-induced drought, and (2) the subsequent release of C from soils. The release of C from soils is critically dependent on the assumed response of
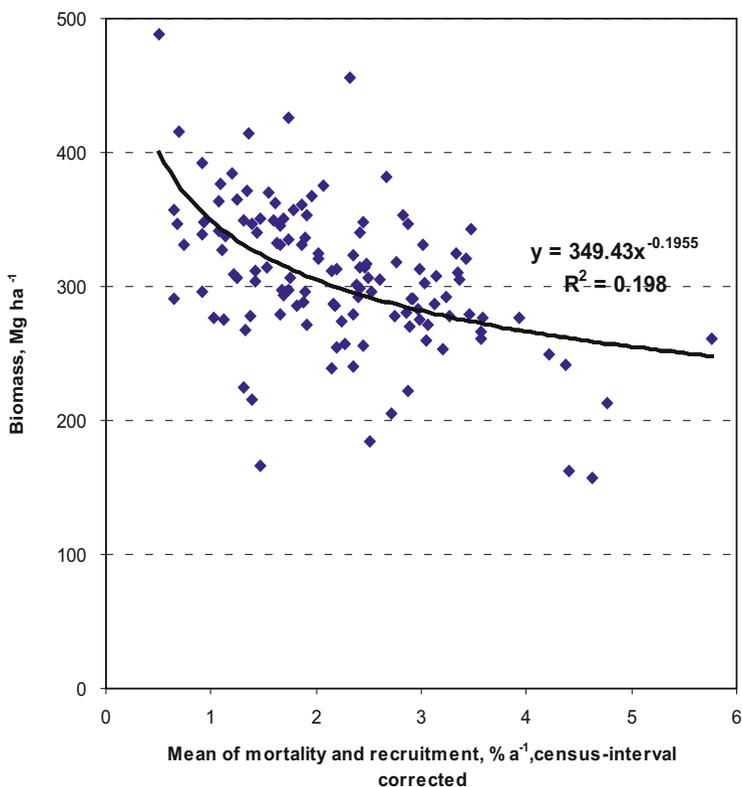
respiration to temperature, coupled with the simplified representation of soil moisture and soil carbon. A decade on, both Galbraith et al. (2010) and Rammig et al. (2010) reanalysed the climate and dynamic vegetation models and found that rising air temperature was an important cause of dieback in most models. However, the dominant temperature-related mechanism differed among models, with, variously, increases in plant respiration, reduced photosynthesis, and increased vapour pressure deficit all resulting in loss of carbon. Yet, the level of the positive impact of CO_2 fertilisation had the largest single impact within the models, larger than the negative temperature and negative rainfall reduction impacts. In a recent review of free-air carbon dioxide enrichment (FACE) experiments, Norby and Zak (2011) conclude that photosynthetic C uptake increases in response to CO_2 under field conditions and that the enhancement is sustained over time. But they point out that it remains to be seen whether these growth-related responses also apply to tropical forests. Thus, overall, the uncertainties about (1) how much tropical plants will respond to CO_2, (2) how they will respond to long-term increases in high air temperatures, (3) how much rainfall may decline by in the dry season, and (4) how much plants will respond to the decline in rainfall still preclude robust statements about the timing and magnitude of any reversal of the tropical forest carbon sink.

To conclude, 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, we conclude 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.

10.3.7.3   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. Representation of composition is challenging, both 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. Lianas, for example, ignored in all forest models, often contribute little to forest biomass but heavily affect productivity (Schnitzer and Bongers 2002), while killing trees (Phillips et al. 2005) and preferentially infesting denser-wooded species (van der Heijden et al. 2008); their recent increase suggests that the tropical carbon sink might shut down sooner than models suggest. Large changes in tree communities could also lead to net losses of carbon from tropical forests (Phillips and Gentry 1994; Körner 2004). One way this could happen is a shift to faster-growing species, driven by increasing tree mortality

rates and frequency of gap formation (Phillips and Gentry 1994; Phillips et al. 2004; Lewis 2006). Such fast-growing species generally have lower wood specific gravity, and hence less carbon (West et al. 1999), than shade-tolerant trees. 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 c. 20 % less dense wood than the slower-growing forests of the east (Baker et al. 2004b); because these faster-growing western forests also have lower basal area, the differences in terms of biomass carbon stored are somewhat greater still (Fig. 10.8). Concerted compositional changes driven by greater resource supply, increased mortality rates, and possible increases in the proportion

Plot showing biomass vs mean of mortality and recruitment. Fitted curve labelled:

$$y = 349.43x^{-0.1955}$$
$$R^2 = 0.198$$

x-axis: **Mean of mortality and recruitment, % a^{-1}, census-interval corrected**

y-axis: **Biomass, Mg ha^{-1}**

Fig. 10.8 Tree biomass as a function of mean stem turnover rates, for 127 lowland forest plots across South America monitored in the 1980s and 1990s. Note that the faster forests, typically in western Amazonia, have lower wood density and much lower biomass

of faster-growing trees which escape lianas could therefore shut down the carbon sink function of tropical forests earlier than ecophysiological analyses predict. While the initial moves towards individual-based models within Global Circulation Models provide a framework within which to evaluate these types of interaction and changing composition (Purves and Pacala 2008), any such analyses will need to be data driven.

10.4   Conclusion

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 and, perhaps for some, not so unexpected. Thus, in experiencing accelerated growth, mortality, and generally increasing biomass, the tropical biome appears to have been responding for many years to the kind of large-scale but slow-acting drivers that until recently have been unfamiliar to ecologists. New technologies are now helping us to see tropical landscapes with fresh perspectives, but gaining an authoritative understanding of how forest biodiversity and carbon may be changing in the Anthropocene remains a huge challenge. Repeated, standardised, careful, and adequately replicated on-the-ground measurements will be key to making significant progress towards this goal.

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