

## CHAPTER FOUR

# Recent changes in tropical forest biomass and dynamics

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### 4.1 Introduction

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 our activities. While outright deforestation is physically obvious, other subtler processes, such as hunting and surface fires, also affect forests in ways that are less evident to the casual observer (*cf.* Estes *et al.* 2011; Lewis, Malhi & Phillips 2004a; Malhi & Phillips 2004). Similarly, anthropogenic atmospheric change is intensifying. By the end of the 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 the greatest global upheaval in vegetation cover and species' distributions since at least the last mass extinction at ~65 million years ago (Ellis *et al.* 2011). Collectively, the evidence points to conditions 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. Most forest vegetation carbon stocks lie within the tropics. Tropical forests store 460 billion tonnes of carbon in their biomass and soil (Pan *et al.* 2011), equivalent to more than half the total atmospheric stock, and annually process 40 billion tonnes (Beer *et al.* 2010). They have other planetary influences via the hydrological cycle, and emit aerosols and trace gases, and they are also characterised by their exceptional variety and diversity of life.

Changes to tropical forests 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 to these forests have an impact on global biodiversity and the cultures, societies and economies that are bound to this diversity (Groombridge & 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 enhance, or perhaps mitigate, human-driven climate change.

There is no doubt that remaining forests globally are now changing fast. 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 nearly 3 Gt by the middle part of the last decade (Le Queré *et al.* 2009). Independent analyses of data on atmospheric CO<sub>2</sub> concentration 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 bottom-up, independent analysis by foresters confirms that forests on every vegetated continent are implicated in this terrestrial sink (Pan *et al.* 2011). This leaves us with a critical question: 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. This is the focus of the current chapter. Most notably, on-the-ground measurements can provide information on subtle changes in species composition, biomass and carbon storage. Assessment of modest, long-term ecological change can be difficult using satellites, as signals often saturate at high biomass (e.g. Mitchard *et al.* 2009), technologies change, and sensors degrade. Yet, permanent sample plot work in the tropics has been very sparse and mostly focused on a few well-known locations, leaving most of the ~10 million square kilometre expanse of the world's richest ecosystems unstudied. This is particularly risky given that no one tropical forest, or small number of studied forests, can be taken as the mean state of all forests. Site-centric ecology is invariably skewed, since peculiar local features – such as fragmentation, unusual soil conditions, cyclones or fires – 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 in ecological science attempts are still sometimes made to scale results from a few selected locations to draw conclusions about what the behaviour of the whole biome might be.

## 4.2 A networked approach

Evidently, a more robust, synoptic approach is needed. The first attempts at such were inspired by the tropical macroecological approach of Gentry, in

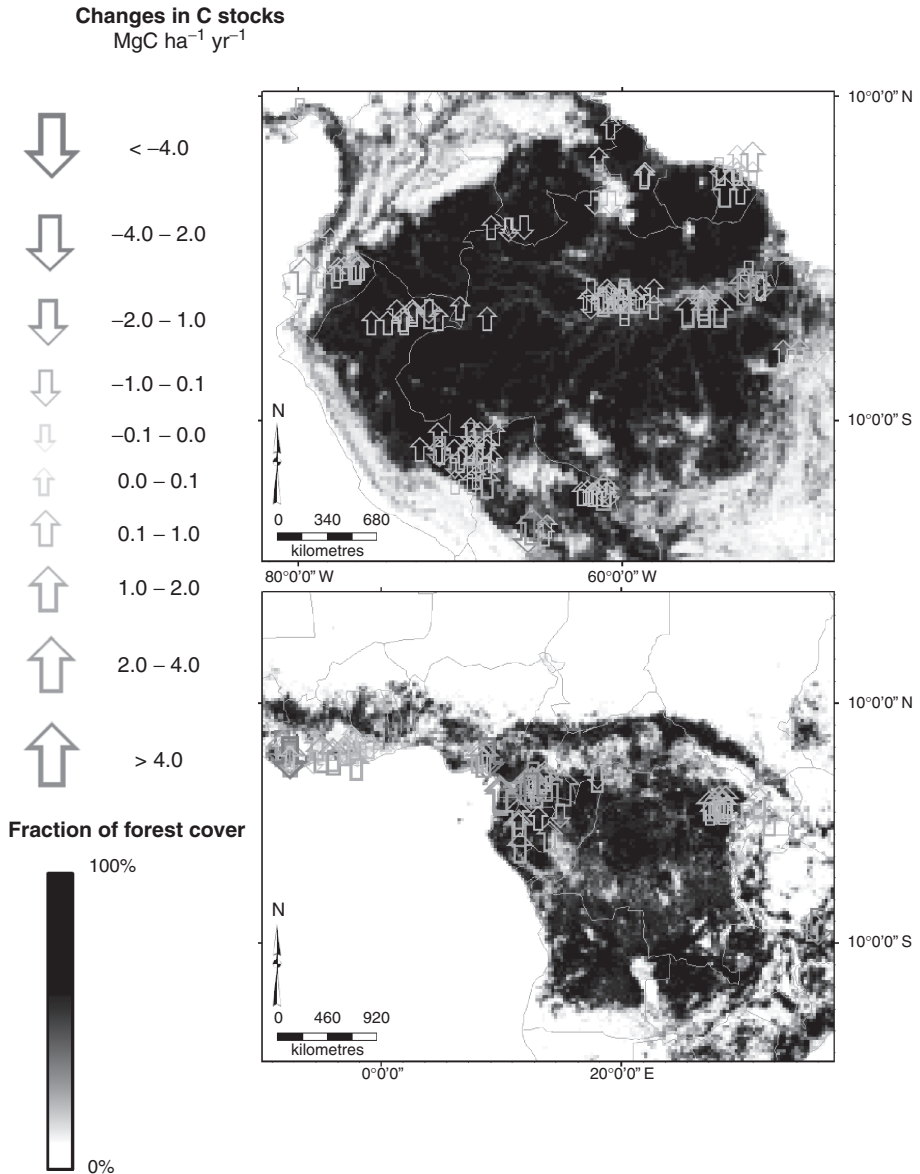
which he used intensive floristic inventories across hundreds of forest locations to reveal the major geographic gradients in diversity and composition (e.g. Gentry 1988a, b). The first macroecological analyses of tropical forest dynamics (Phillips & Gentry 1994; Phillips *et al.* 1994, 1998) also made significant claims, but – unlike Gentry’s floristic work – lacked complete methodological standardisation. They relied heavily on published data from different teams worldwide, and had more limited sample sizes. In response, since 2000 and in conjunction 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 botanists and foresters, hitherto often working 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, [www.rainfor.org](http://www.rainfor.org)), now represents the long-term ecological monitoring efforts on the ground of 43 institutions worldwide including from all Amazonian countries except Suriname. A parallel initiative in Africa, AfriTRON (African Tropical Rainforests Observation Network, [www.afritron.org](http://www.afritron.org)), spans researchers working in 10 countries across the African wet tropics. Collectively, and with known long-term plots in Asia and elsewhere (e.g. CTFS network, Chave *et al.* 2008a), there are several hundred long-term monitoring plots across structurally intact forest. In this chapter our aim is to synthesise published results from the networks to assess how forests have generally changed. Our main focus is Amazonia as the network here is most extensive and mature. Where appropriate, we also discuss results from additional, individual sites where these may shed further light on the processes involved. Needless to say, an endeavour such as this, realised across two continents, is only possible with the dedication and perseverance of many people – botanists, field leaders and assistants – who share the vision of discovery through widespread, repeated and careful measurement. The contributions of many of these colleagues are acknowledged at the end of the chapter.

### 4.3 Methodology

For these analyses, we define a monitoring plot as an area of old-growth forest where all trees  $\geq 10$  cm diameter at breast height (dbh, measured at 1.3 m height or above any buttress or other deformity) are tracked individually over time. All trees are marked with a unique number, measured, mapped and identified. Periodically (generally every 1–5 years) the plot is revisited, and all surviving trees are re-measured, dead trees are noted, and trees recruited to 10 cm dbh are uniquely numbered, measured, mapped and

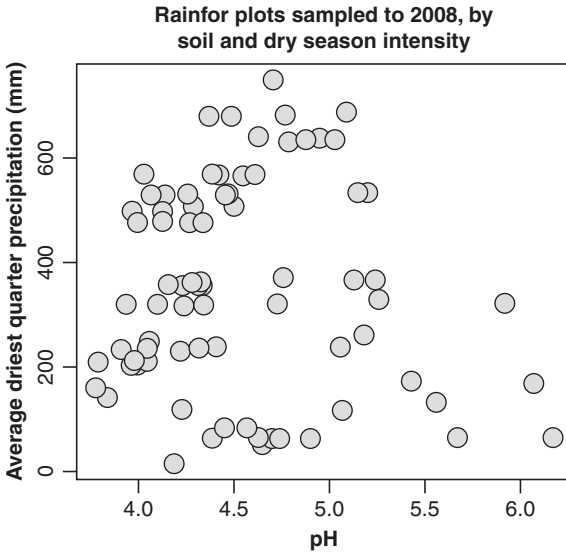
identified. This allows calculation of: (i) the cross-sectional area that tree trunks occupy (basal area), which can be used with allometric equations to estimate tree biomass (Baker *et al.* 2004a; Chave *et al.* 2005; Higuchi *et al.* 1998); (ii) tree growth (the sum of all basal-area increments for 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 on selection criteria for different analyses. The 'Amazon' plots span the forests of northern South America (Figure 4.1), including Bolivia, Brazil, Colombia, Ecuador, French Guiana, Peru and Venezuela, from the driest to the wettest and the least to the most fertile Amazonian 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, as well as a range of soil types (Lewis *et al.* 2009a). Most 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. Many plots have been monitored for more than a decade, although they range in age from 2 to 30 years (mean ~11 years). The earliest plot inventory was in 1968, the latest in 2007. Here we analyse results of censuses completed up to 2007, but for Amazonia we first report results prior to the intense drought of 2005 (Aragao *et al.* 2007) before summarising the impact of the drought. Details of the exact plot locations, inventory and monitoring methods, and issues relating to collating and analysing plot data, are omitted from this chapter for reasons of space but are discussed in detail elsewhere (Baker *et al.* 2004a,b; Lewis *et al.* 2004b, 2009a; Lopez-Gonzalez *et al.* 2011; Malhi *et al.* 2002, 2004; Phillips *et al.* 2002a,b, 2004, 2008, 2009). It is important to point out that the samples are not randomly distributed across each rainforest region; historical plot data have been used, where possible, and considerations of access limit where it is practical to monitor forests. Nevertheless, a wide range of environmental space is captured by the whole sample (*cf.* Figure 4.2 for Amazonia).

For Amazonia, diameter-based allometric equations detailed in Baker *et al.* (2004a) are used to scale individual tree measurements to biomass. In brief, 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 derived from trees from Amazonia but has the advantage of being local. More allometric equations have been developed by the research community. For



**Figure 4.1** 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). See plate section for colour version.

simplicity, we do not show results using equations other than Baker *et al.* (2004a) here, but note that while different methods certainly result in systematic differences in biomass estimates (e.g. Chave *et al.* 2003; Feldpausch *et al.* 2012; Peacock *et al.* 2007), the rates of *net* biomass change calculated across



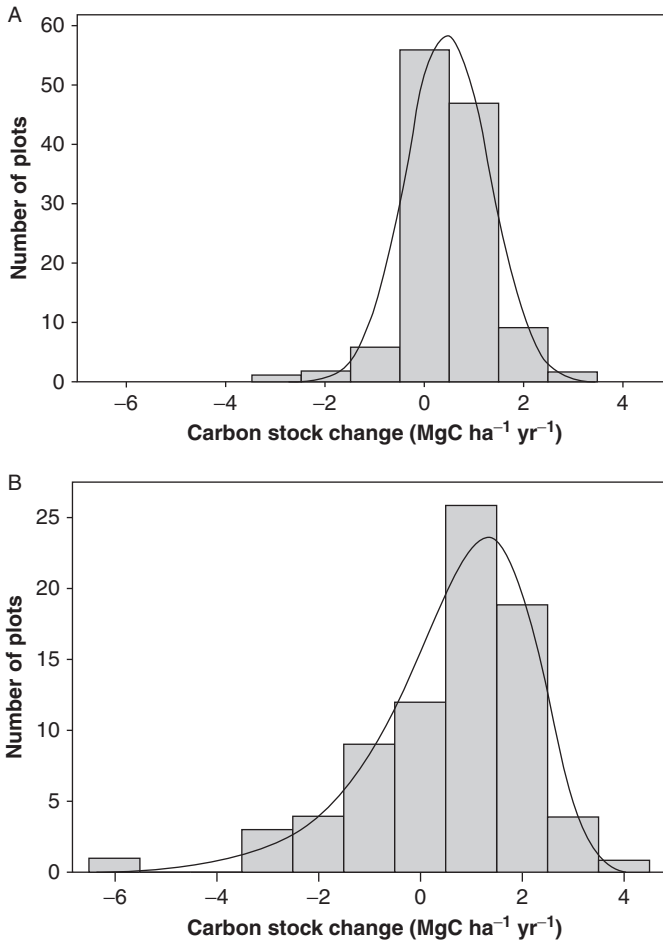
**Figure 4.2** Sampling in environmental space across Amazonia. Most plots sampled are on acid soils in weakly seasonal rain-forest climates, reflecting the dominant conditions of the region, but span a broad environmental range that includes more than two orders of magnitude in soil acidity for example.

Amazonia appear largely insensitive to the equation used (Baker *et al.* 2004a, and unpublished RAINFOR analyses). For Africa, we use the Chave *et al.* (2005) moist forest equation including tree height. We then propagate the uncertainty in both the diameter and height parameters to obtain final biomass estimates (Lewis *et al.* 2009a). We summarise findings from old-growth forests in terms of (i) structural change, (ii) dynamic-process change and (iii) functional and compositional change, over the past two to three decades, including consideration of recent droughts in Amazonia.

## 4.4 Results and discussion

### 4.4.1 Structural change

Among 123 long-term old-growth Amazonian plots with full tree-by-tree data, there was a significant increase in aboveground 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) tonnes of carbon per hectare per year (mean, 2.5% and 97.5% confidence limits; Phillips *et al.* 2009). Across all 123 Amazon plots, the aboveground biomass change is approximately normally distributed and shifted to the right of zero (Figure 4.3A). The overall net increase estimated is slightly lower than but statistically indistinguishable from the  $0.54 \pm 0.29$  tC ha<sup>-1</sup> yr<sup>-1</sup> estimated by Phillips *et al.* (1998) for the lowland Neotropics using 50 sites up to 1996, and the Baker *et al.* (2004a) estimate of  $0.62 \pm 0.23$  tC ha<sup>-1</sup> yr<sup>-1</sup> for 59 core RAINFOR Amazon plots up to 2000. In the larger dataset that is now available, estimates of biomass carbon change always give a positive carbon uptake and are also rather



**Figure 4.3** Aboveground biomass change (dry weight) of trees greater than 10 cm diameter. (A) Across 123 Amazonian plots, based on initial and final stand-biomass estimates calculated using an allometric equation relating individual tree diameter and wood density to biomass. (B) Across 79 plots from Africa, but including estimated tree height for each stem, in addition to diameter and wood density, to estimate biomass, with uncertainty in the height and diameter measurement both propagated to final biomass 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 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 ( $P < 0.01$ ).

insensitive to different weightings based on measurement interval and plot area (supplementary information in Phillips *et al.* 2009). Using the same approach, we recently discovered a comparable phenomenon in African forests. Here, we measured a similar net sink in trees  $\geq 10$  cm diameter with a mean

of 0.63 (bootstrapped 95% confidence interval, 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 (Figure 4.3B). Re-sampling 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 vs. 154 MgC ha<sup>-1</sup>); 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).

There are various possible ways by which these plot-based measures can be scaled to tropical forests across Amazonia, South America and Africa. Here, we adopt a relatively simple approach, given the various and not always quantifiable uncertainties, for example in terms of stems smaller than those we measure, belowground (root) biomass carbon, carbon in dead trees and litter, area of each forest type and degree of human disturbance. Thus, we assume that our measurements are representative of the wider forest landscape, and that other biomass and necromass components also increase proportionally, but that soil carbon stocks are static. We estimate 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 belowground carbon, and a mid-range estimate of the surviving forest area for year 2000 (Table 4.1). For the 1990s this yields a total estimated South American forest sink of  $0.65 \pm 0.17$  PgC yr<sup>-1</sup> and a corresponding sink in African forests of  $0.53 \pm 0.30$  PgC yr<sup>-1</sup>. Meanwhile,  $0.14 \pm 0.04$  PgC yr<sup>-1</sup> in mature undisturbed Asian forests may be assumed if these responded as African and South American forests did (Pan *et al.* 2011). Thus the combined old-growth tropical forest sink in the 1990s is estimated to have been  $1.3 \pm 0.35$  PgC yr<sup>-1</sup>, before allowing for any possible net change in soil carbon stock. This is very similar to the figure given by Lewis *et al.* (2009), of 1.3 PgC yr<sup>-1</sup> (bootstrapped CI, 0.8–1.6) using plots with a mean time interval of 1987–97 and slightly differing methodology (Tropical America, 0.62; Tropical Africa, 0.44; and Tropical Asia 0.25 PgC yr<sup>-1</sup>). In the subsequent decade the American tropical sink declined as a result of the 2005 Amazon drought; we discuss this below.

Clearly these estimates depend on: (i) measurement techniques; (ii) how representative the plots are of 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 late twentieth century – forest plots are not 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 that the tropics are either carbon



**Table 4.1** Estimated annual change in carbon stock (TgC yr<sup>-1</sup>) in tropical intact forests by region for the periods of 1990 to 1999, and 2000 to 2007. Table adapted from Pan et al. (2011); see that paper for details of calculations. ND, data are not available.

	1990–1999						2000–2007								
	Estimated annual change in C stock (TgC yr <sup>-1</sup> )						Estimated annual change in C stock (TgC yr <sup>-1</sup> )								
	Dead wood		Litter		Soil		Dead wood		Litter		Soil				
Asia	125	13	2	ND	5	144	38	100	10	1	ND	6	117	30	0.90
Africa	469	48	7	ND	9	532	302	425	43	6	ND	8	482	274	0.94
Americas	573	48	9	ND	22	652	166	345	45	5	ND	23	418	386	0.53
Total	1167	109	17	ND	35	1328	347	870	98	13	0	36	1017	474	0.71

neutral or carbon sink regions, despite widespread deforestation (Denman *et al.* 2007, p. 522; Stephens *et al.* 2007), and the fact that the terrestrial biosphere as a whole has been acting as a very large net sink for decades now (e.g. Le Quéré *et al.* 2009).

The finding of increasing forest biomass over recent decades has proved remarkably controversial (*cf.* for example Clark 2002; Lewis, Phillips & Baker 2006, 2009b; Phillips *et al.* 2002a; Wright 2005), despite the fact that an uptake of  $>2 \text{ PgC yr}^{-1}$  somewhere on Earth's land surface is evident from independent mass-balance observations of the global carbon cycle. While there is not space here to review the many early debates, the most persistent area of controversy can be characterised by the phrase 'slow in, rapid out' (Körner 2003). This 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 such more severe events. Inferences based on such sampling could therefore result in positively biased estimates of aboveground biomass trends in old-growth forests when results from plot networks are extrapolated to a large area. Given the still small number of tropical plots relative to the total biome area, this concern is understandable. However, we suggest it is unlikely to be a major source of uncertainty or bias in our calculations for four reasons.

First, large and intense natural disturbances are rare in the lowland tropics, certainly compared with boreal forests and probably compared with temperate ones too. Thus, even when accounting for Landsat-based measurements of large disturbances and conservatively using a disturbance frequency/magnitude model fit that is likely to over-estimate the frequency of large-magnitude disturbances, it is clear that disturbances capable of removing 100 Mg aboveground biomass (AGB) at the 1 ha scale (i.e. about 1/3 total standing biomass) have return times of 1000 years or more in Amazonia (Gloor *et al.* 2009: Table 4.1). 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. More recent independent analyses using satellite data from across the Amazon basin (Espírito-Santo *et al.* 2010) show that the return time of stand-initiating scale disturbances in western Amazonia is  $\sim 27\,000$  years, while in eastern Amazonia it is  $\sim 90\,000$  years. The basin-wide mean,  $\sim 39\,000$  years, is so large that any impacts on our Amazon dataset are negligible, and it explains why we have not sampled a stand-resetting disturbance. This accords with the first pioneering large-scale analysis, which showed the rarity of large-scale disturbance events in the Amazon Basin (Nelson *et al.* 1994). For Africa, analysis of a single available dataset from large-scale

ground-based surveys of forest gaps, alongside mortality rates in the AfriTRON plots, both showed a similar pattern: the size frequency-distribution of disturbance events contain too few large-scale events to cause the increase in biomass shown in the presented results (Lewis *et al.* 2009b). This accords with the high biomass and large number of large diameter trees in African forests, which most closely match theoretical 'disturbance-free' forests (Enquist & Niklas 2001), implying that large-scale mortality events are rare. The 'slow-in, rapid-out' debate was magnified by a theoretical paper that unfortunately compared single-year time-step simulations with actual RAINFOR results, which are averaged at intervals of 10 years (Fisher *et al.* 2008). Furthermore, the size-frequency distribution of disturbance events was also parameterised incorrectly, thus overestimating the frequency of large disturbance events (*cf.* Lloyd, Gloor & Lewis 2009). These two errors greatly exaggerated the apparent magnitude of the 'slow-in, rapid-out' effect, by more than an order of magnitude.

Second, the RAINFOR network was successfully used 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 past disturbance events on Amazon forests these would have been detected, as the network is proven to be large enough to detect much more modest disturbance events.

Third, the plot network lacks the basic signatures of forests recovering from large disturbances. Biomass increase is not the only structural change recorded in Amazonian forest plots. Across 91 RAINFOR plots where we tracked populations back to 2002 there has been a small increase in the stand density between the first and last measurements of  $0.84 \pm 0.77$  stems per hectare per year, 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) shows a slightly larger increase ( $0.18 \pm 0.12\%$  per year). These increases in stand density, while proportionally smaller than the biomass changes, run counter to expectations of declines if the plots were in an advanced state of secondary succession (e.g. Coomes & Allen 2007), as do simultaneous increases in 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 2009a; Phillips *et al.* 2009). In summary, 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.

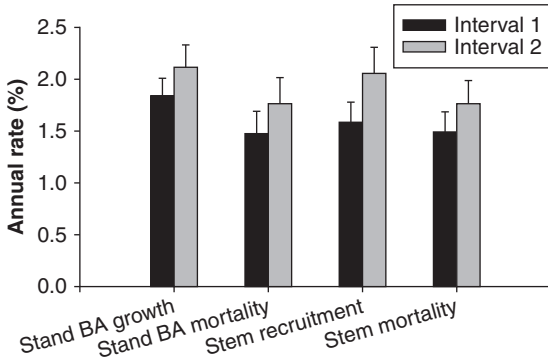
Lastly, a network of fewer larger plots (Chave *et al.* 2008a), atmospheric CO<sub>2</sub> data (Denning *et al.* 2007; Stephens *et al.* 2007) and carbon mass-balance approaches (Le Queré *et al.* 2009) – evidence independent from the plot networks reported here – each imply that there is a carbon sink in tropical forests (summarised in Lewis *et al.* 2009a). Parsimony therefore suggests that the increase in biomass is not the result of a statistical artefact based on forest disturbance episodes that have been poorly sampled.

Nevertheless, our Amazon and African samples are non-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 unsampled (Figure 4.1), the climate- and soil-environmental space is well covered (Figure 4.2). Greater monitoring efforts in the difficult-to-access regions are of course needed to reduce the uncertainty due to incomplete spatial coverage.

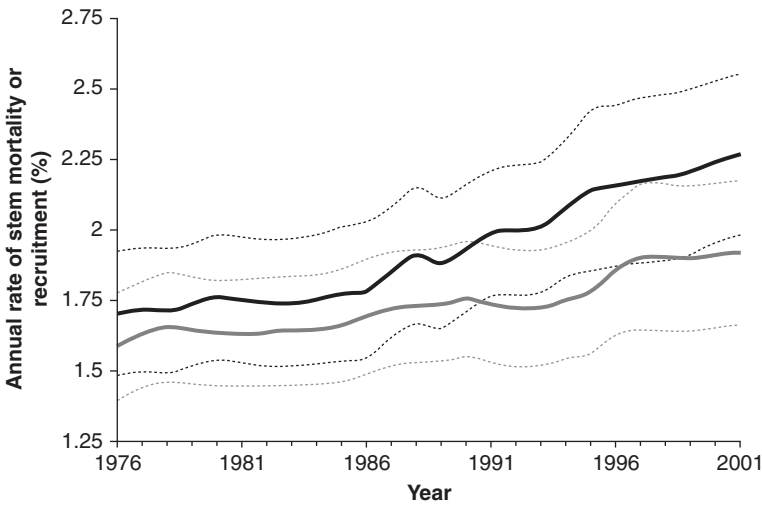
#### 4.4.2 Dynamic changes

A complementary way of examining forest change is to look for changes in the processes (growth, recruitment, death): have these forests simply gained mass, or have they become more or less dynamic too? For the Amazon Basin, we have measured the dynamics of forests until 2002 in two ways. First, we examined changes in stem population dynamics, by convention estimating stem turnover between any two censuses as the mean of annual mortality and recruitment rates for the population of trees  $\geq 10$  cm diameter (Phillips & Gentry 1994). Second, we examined changes in biomass fluxes of the forest in terms of growth of trees and the biomass lost from mortality events. These stand-level rates of biomass gain and 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 old-growth 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 find that *all* of these key ecosystem processes – stem recruitment, mortality and turnover, and biomass growth, loss and turnover – increased significantly (Figure 4.4) between the first and second monitoring periods (Lewis *et al.* 2004b). Thus, over the 1980s and 1990s these forests became, on average, faster-growing and more dynamic,



**Figure 4.4** Annualised rates of stand-level basal-area (BA) growth, basal-area mortality, stem recruitment 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).



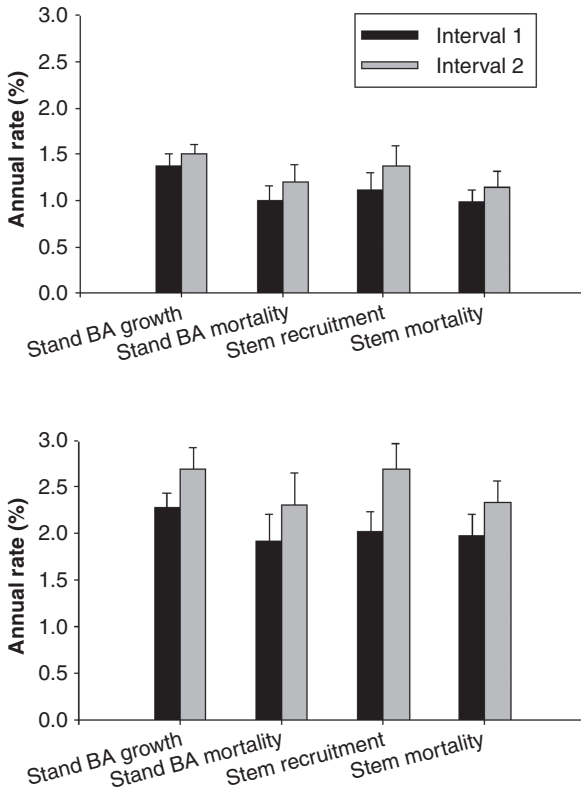
**Figure 4.5** Mean and 95% confidence intervals for stem recruitment and mortality rates against calendar year, for plots arrayed across Amazonia. Rates for each plot were corrected for the effects of differing census-interval lengths, for ‘site-switching’ (changes through time in the plots being measured) 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).

as well as bigger. The increases in the rate of the dynamic fluxes (growth, recruitment and mortality) were about an order of magnitude greater than the increases in the structural pools (aboveground biomass and stem density; Lewis *et al.* 2004b).

These and similar results can be demonstrated graphically in a number of ways. In Figure 4.5, 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).

The 50 plots that have two consecutive census intervals can be separated into two groups, one fast-growing and more dynamic (mostly in western Amazonia), and one slow-growing and much less dynamic (mostly in eastern and central Amazonia), which reflects the dominant macroecological gradient across Amazonia (Phillips *et al.* 2004; Quesada *et al.* 2012; ter Steege *et al.* 2006). 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 (Figure 4.6; Lewis *et al.* 2004b), but similar and statistically indistinguishable *proportional* increases in rates among forest types (Lewis *et al.* 2004b). It should be stressed that these results represent the mean response of all mature forests measured. Within our dataset, there are many individual plots showing different, individual responses, just as within the whole literature there are some reports of individual sites showing



**Figure 4.6** Annualised rates of stand-level basal-area (BA) growth, basal-area mortality, stem recruitment and stem mortality over consecutive census intervals for plots grouped into ‘slower growing less-dynamic’ (top) and ‘faster growing more-dynamic’ (bottom) 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 drainage basin. Changes have occurred across the South American continent, and in both slower- and faster-dynamic forests (from Lewis *et al.* 2004b).

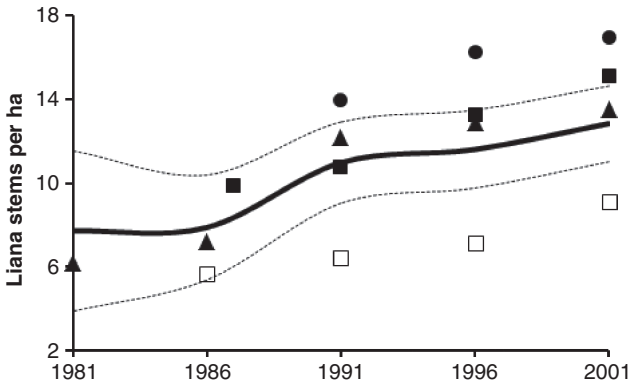
similar or different patterns (e.g. Chave *et al.* 2008b; Feeley *et al.* 2007). Nevertheless, when viewed as whole, the permanent plot record from Amazonian and neotropical old-growth forests indicates that increasing growth, recruitment and mortality occurred for at least two decades across different 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 Amazonian 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 old-growth 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  $\delta^{13}\text{C}$ ,  $^{18}\text{O}$  and stomatal density to assess possible changes in photosynthesis (and by implication, growth). By this method, results for two species from the Guiana Shield indicated 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 to the radiocarbon studies, but holds promise if effective techniques are developed to overcome them.

#### 4.4.3 Functional composition changes

Changes in the structure and dynamics of tropical forests are likely to be accompanied by changes in species composition and forest function. Phillips *et al.* (2002) studied woody climbers (structural parasites on trees, also called lianas), which typically contribute 10–30% of forest leaf productivity, but are ignored in most monitoring studies. Across the RAINFOR plots of western Amazonia there was a concerted increase in the density, basal area and mean size of lianas (Figure 4.7; 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. This was the first direct evidence that mature tropical forests are changing in terms of their functional composition. A number of subsequent studies suggest that the phenomenon of increasing lianas extends



**Figure 4.7** 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 circles) and Ecuador (unfilled squares) (adapted from Phillips *et al.* 2002b; see that paper for full details of field and analytical methodology).

across other neotropical forests too (reviewed by Schnitzer & Bongers 2011). There is some limited experimental evidence (Granados & Körner 2002) for growth responses in tropical lianas to elevated atmospheric  $\text{CO}_2$  concentrations being stronger than those of trees.

Finally, three large-area studies have considered whether there have been consistent changes in tree species composition in non-droughted forests over the past two decades (Chave *et al.* 2008a; Laurance *et al.* 2004; Lewis *et al.* 2009a). In the first, in a large cluster of plots from one Amazon locality, many faster-growing genera of canopy and emergent-stature trees increased in basal area or density, whereas some slower-growing genera of subcanopy or understorey trees declined. Laurance *et al.* (2004) provide evidence of pervasive changes in this locality: growth, mortality and recruitment all increased significantly over two decades (basal area also increased, but not significantly), 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, Lewis *et al.* (2009a) reported the relative change in biomass for 916 species from 79 plots across Africa, 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. Third, Chave *et al.* (2008a) reported functional changes across 10 large 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 lowest and highest quartiles of species based on growth rate, 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. While it is difficult to draw conclusions, results from these three studies suggest that the pervasive increase in forest stand biomass is being caused by concurrent increases in biomass of many species with differing ecological habits.

#### 4.5 Recent findings on drought impacts in Amazonia

The results from the Amazon discussed so far reflect forest changes before 2005. In that year 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 projections of climate change from some global circulation models (e.g. Cox *et al.* 2008). The drought caused substantial economic dislocation by its effect on river transport and resultant fires leading to the disruption of air transport. 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 recensusing plots across the Basin. Of 55 plots which we monitored through 2005, the mean annual aboveground biomass change was  $-0.59$  ( $-1.66$ ,  $+0.35$ )  $\text{Mg ha}^{-1}$ , and among those plots that were actually droughted the AGB change rate was clearly negative ( $-1.62$  ( $-3.16$ ,  $-0.54$ )  $\text{Mg ha}^{-1}$ ). 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 driven by increased mortality, implying that it was the unusual moisture deficits that were responsible for the biomass loss by contributing to an enhanced mortality risk.

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  $-1.21$  ( $-2.01$ ,  $-0.57$ )  $\text{PgC}$  and  $-1.60$   $\text{PgC}$  ( $-2.63$ ,  $-0.83$ ) (Table 4.2). The first value is based on simply scaling the per-plot impact by the total area droughted; the second, greater value is based on using remotely sensed rainfall data to model the relationship between biomass change and relative drought intensity. The latter biomass dynamics/climate approach makes use of more of the information on forest response to drought than the simple scaling-up of the mean droughted plot impact, but requires additional assumptions that may introduce error. The consistency of the results from the different analyses indicates a significant regional impact, but much of this might not be 'seen' by the atmosphere until future years. Thus, the main impact is a temporary increase in dead wood production, implying losses to the atmosphere over future years as these dead trees decompose. During the

**Table 4.2** *Estimated 2005 Amazon drought impact, from plot data, using two different approaches. For details of the methodology see online supplementary information published with Phillips et al. (2009).*

**Table 4.2a** *Scaling from the statistical distribution of data for per-hectare plot biomass change (sampling effort-corrected AGB change relative to pre-2005 for each plot), to the whole area of Amazon forest affected in 2005. The method thus applies the mean plot-level biomass impact of the 2005 event (result shown in top line) and scales this by the stated expansion factors, including the simplified assumption of uniform impact across the entire area of Amazon forest suffering drought in 2005.*

		Mean	2.5% CI	97.5% CI	
		Mg AGB ha <sup>-1</sup> yr <sup>-1</sup>	-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 <sup>8</sup>				
Additional fraction of Amazonia with unreliable TRMM data	1.031				
Sum AGB impact (Mg)		-1.76 × 10 <sup>9</sup>	-8.25 × 10 <sup>8</sup>	-2.93 × 10 <sup>9</sup>	
Belowground	1.37	-6.52 × 10 <sup>8</sup>	-3.05 × 10 <sup>8</sup>	-1.08 × 10 <sup>9</sup>	
Sum biomass impact (Mg)		-2.41 × 10 <sup>9</sup>	-1.13 × 10 <sup>9</sup>	-4.01 × 10 <sup>9</sup>	
<b>Sum carbon impact (Mg)</b>	<b>0.5</b>	<b>-1.21 × 10<sup>9</sup></b>	<b>-0.57 × 10<sup>9</sup></b>	<b>-2.01 × 10<sup>9</sup></b>	

**Table 4.2b** *Scaling from the plot biomass dynamics vs climate relationship having applied this relationship individually to each TRMM grid cell in the Amazon forest area affected in 2005. The method thus uses the measured plot-level relationship between change in mean annual maximum cumulative water deficit values and change in biomass dynamics, applies this to a spatially explicit pixel-by-pixel measure of the Amazon 2005 climate, to estimate the whole Amazon impact (result in top line) and scales by the stated expansion factors.*

		Mean	2.5% CI	97.5% CI	
		Mg AGB	-1.05 × 10 <sup>9</sup>	-5.46 × 10 <sup>8</sup>	-1.72 × 10 <sup>9</sup>
		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 <sup>-9</sup>	-1.22 × 10 <sup>-9</sup>	-3.83 × 10 <sup>-9</sup>	
Belowground (Mg)	1.37	-8.63 × 10 <sup>-8</sup>	-4.51 × 10 <sup>-8</sup>	-1.42 × 10 <sup>-9</sup>	
Sum biomass impact (Mg)		-3.20 × 10 <sup>-9</sup>	-1.67 × 10 <sup>-9</sup>	-5.25 × 10 <sup>-9</sup>	
<b>Sum carbon impact (Mg)</b>	<b>0.5</b>	<b>-1.60 × 10<sup>-9</sup></b>	<b>-0.83 × 10<sup>-8</sup></b>	<b>-2.63 × 10<sup>-9</sup></b>	

drought year itself the sink may decline (reduction in growth), but not halt (as the new necromass only begins to decompose); the sink could even increase temporarily if potential short-term reductions in soil respiration occur.

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 PgC) (Pan *et al.* 2011, Figure 4.1). 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) suggests that across the biome, forest sensitivity to moisture anomalies may be largely predictable, and that even relatively weak drying compared with 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 a strong increase in dry-adapted species over a *c.* 20 year period of monitoring (Fauset *et al.* 2012). A fuller understanding of the impacts of drought will require monitoring of forests through post-drought recovery and repeated droughts (such as in Amazonia in 2010) over the long term.

#### 4.6 What is driving the 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, Malhi & Phillips 2004a; Lewis *et al.* 2004b, 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 (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 aboveground 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 & Grubb 2000). However, it has been proposed by others (e.g. Körner 2004; J. Lloyd pers. comm.) that the greatest proportional response should be in understory seedlings and saplings, which are likely to be close to carbon deficit owing to shading: a small increase in photosynthetic rate here could therefore have a great proportional impact on carbon balance. There is some experimental evidence to support this view (e.g. Aidar *et al.* 2002; Kerstiens 2001).

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, Malhi & Phillips 2004a), only increasing atmospheric CO<sub>2</sub> concentrations (Prentice *et al.* 2001), 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: from biomass burning near to once-remote tropical forest plots that are increasingly encroached upon by deforestation (Laurance 2004), and from long-range inputs of Saharan dust to South American (and African) forests, which have increased over recent decades, possibly in response to climate change (Engelstaedter *et al.* 2006).

For only one of these changes, however, do we have clear evidence that the driver has changed over a large enough area *and* that such a change is likely to accelerate forest growth (Lewis, Malhi & Phillips 2004a; Lewis *et al.* 2009b). The increase in atmospheric CO<sub>2</sub> is the primary candidate, because of the undisputed long-term increase in CO<sub>2</sub> concentrations, the key role of CO<sub>2</sub> in photosynthesis, and the demonstrated positive effects of CO<sub>2</sub> fertilisation on plant growth rates, including experiments on whole temperate-forest stands (Norby *et al.* 2002; Hamilton *et al.* 2002; Lewis, Malhi & Phillips 2004a; Lewis *et al.* 2009b; Norby & 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. Elsewhere we have discussed the candidate tropical drivers in more detail (Lewis, Malhi & Phillips 2004a; Lewis *et al.* 2006, 2009b; Malhi & Phillips 2004, 2005). Lastly, given the global nature of the CO<sub>2</sub> increase and ubiquitous biochemistry of the plant response involved, we may expect to see the same phenomenon in other biomes. 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 have measured sufficient sites and land area (Pan *et al.* 2011).

#### 4.7 The future: potential susceptibility of Amazonian forests to environmental stress and compositional changes

In summary, 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 advance in coming decades. On current evidence, tropical forests are sensitive to changes in incoming 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.

##### 4.7.1 Carbon sinks to carbon sources?

Old-growth Amazonian forests have evidently helped to slow the rate at which CO<sub>2</sub> has accumulated in the atmosphere, thereby acting as a buffer to global climate change. The concentration of atmospheric CO<sub>2</sub> has risen recently at an annual rate equivalent to ~4 PgC; this would have been significantly greater without the tropical South American biomass carbon sink of 0.4–0.7 PgC per year (and an African sink of 0.3–0.5 PgC per year). This subsidy from nature could be a relatively short-lived phenomenon. Mature Amazonian forests may either (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; Körner 2004; Laurance *et al.* 2004; Lewis *et al.* 2011; Malhi *et al.* 2009; Phillips *et al.* 2002b), or (iii) become a *mega-carbon source* (Cox *et al.* 2000; Cramer *et al.* 2001; Galbraith *et al.* 2010; Rammig *et al.* 2010), with all three responses being reported from a major model-intercomparison project (Friedlingstein *et al.* 2006). For Africa similar scenarios exist: a continued sink, becoming neutral or a small source (Friedlingstein *et al.* 2006), or becoming a large source (Paeth *et al.* 2009). 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.

#### 4.7.2 Moisture stress

Climate change will alter precipitation patterns. There are critical thresholds of water availability below which tropical forests cannot persist and are replaced by savanna systems. Currently the threshold lies at around 1000–1500 mm rainfall per annum (Salzmann & Hoelzmann 2005; Staver, Archibald & Levin 2011) but this level could increase with rising temperatures which increase evaporation, or this level could decrease if rising atmospheric CO<sub>2</sub> concentration decreases 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 ecophysiologicaly resilient to extreme temperatures, particularly in the context of rising atmospheric CO<sub>2</sub> concentration, is a subject of active research, reviewed elsewhere (Lewis *et al.* 2009b; Lloyd & Farquhar 2008), 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 damage rain-forest vegetation. However, whilst strong events such as the 2005 Amazonian 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 old-growth tropical forests wherever they have been extensively monitored. The 1998 El Niño drought was equally strong to 2005 in parts of Amazonia, but its impacts are not distinguishable from the signal of increased biomass and growth over the ~5 year mean interval length available for plots at that time (*cf.* Figure 4.1 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 further drought affected the Amazon forest, again dropping some rivers to record lows. If the relationship between water deficit intensity and forest carbon loss that we measured during 2005 also holds for the 2010 drought, then a total impact on old-growth forest biomass carbon in the region of ~2 gigatonnes 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 affected the forest plots. Coordinated monitoring with distributed networks of plots is needed to 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 old-growth Amazonia becomes carbon-neutral or a carbon-source.

### 4.7.3 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 & Farquhar 1996). However, the recent increases in productivity, apparently caused by continuously improving conditions for tree growth, cannot continue indefinitely: if CO<sub>2</sub> is the cause, trees are likely to become CO<sub>2</sub>-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 warm days, may be reaching such inflection-points around midday at some locations (Doughty & Goulden 2008; Lewis, Malhi & Phillips 2004a). Canopy-to-air vapour deficits and stomatal feedback effects may also be paramount in any response of tropical forest photosynthesis to future climate change (Lloyd *et al.* 1996). Simulations suggest that the indirect effect of rising temperatures on photosynthesis via stomatal closure is the dominant negative impact on tropical forest growth (Lloyd & Farquhar 2008), which is currently more than offset by increases in photosynthesis from increasing atmospheric CO<sub>2</sub>. Alternatively, there is evidence that electron transport is the critical step in maximising photosynthesis at a given light level (Haxeltine & Prentice 1996), and the electron transport chain undergoes a reversible point of inflection at a low ~37 °C (Lloyd & Farquhar 2008), thereby reducing photosynthesis at higher temperatures. Additionally, higher air temperature also means higher respiration costs which will also impact on plants' ability to maintain a positive carbon balance in the future. This has been argued to be affecting a forest site in Costa Rica already (Clark & Clark 2010).

Understanding this complex relationship between temperature changes and their impacts on respiration and photosynthesis, plus the impact of rising atmospheric CO<sub>2</sub> on tree growth, is critical. 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<sub>2</sub> concentrations reach >900 ppmv (parts per million by volume) in 2100, compared with ~700 ppmv from previous GCMs (Cox *et al.* 2000, 2004). These concentrations depend on (i) dieback of the eastern Amazonian forests, caused by climate change-induced drought, and (ii) the subsequent release of carbon from soils. The latter process 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) re-analysed 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 amongst models with, variously, increases in plant respiration, reduced photosynthesis and increased vapour pressure deficit all resulting in loss of carbon. Yet, CO<sub>2</sub> 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 CO<sub>2</sub> enrichment ('FACE') experiments, Norby and Zak (2011) conclude that photosynthetic carbon uptake increases in response to CO<sub>2</sub> 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 (i) how much tropical plants will respond to CO<sub>2</sub>, (ii) how they will respond to long-term increases in high air temperatures, (iii) how much rainfall may decline by in the dry season, and (iv) how much plants will respond to the decline in rainfall, still preclude robust statements about the timing and magnitude of any slow down or 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 be asymptotic. Thus, the sink in old-growth tropical forests will diminish and potentially reverse. The more catastrophic scenarios indicated in some models seem unlikely but cannot be ruled out.

#### **4.7.4 Compositional change**

Biodiversity change has inevitable consequences for climate change because different plant species vary in their ability to store and process carbon. At the same time, 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

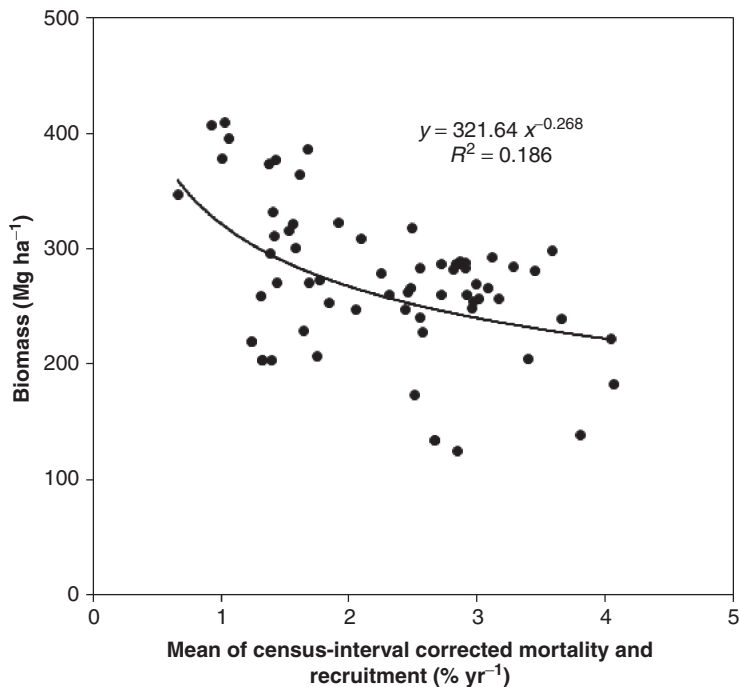


ecological data themselves are sparse. Representing composition better, and its potential for change, is important. Lianas, for example, ignored in all forest models, often contribute little to forest biomass but contribute heavily to productivity (Schnitzer & Bongor 2002), while killing trees (Phillips *et al.* 2005) and preferentially infesting denser-wooded species (Van der Heijden, Healey & Phillips 2008); their recent increase suggests that the tropical carbon sink might shut down sooner than current models suggest. Large changes in tree communities could also lead to net losses of carbon from tropical forests (Körner 2004; Phillips & Gentry 1994). One way this could happen is a shift to faster-growing species, driven by increasing tree mortality rates and frequency of gap formation (Lewis 2006; Phillips & Gentry 1994; Phillips *et al.* 2004). Such fast-growing species generally have lower wood specific gravity, and hence less carbon (West, Brown & Enquist 1999), than shade-tolerant trees. More effort to detect whether such changes are occurring is clearly a priority for future monitoring efforts. 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 are 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 basin-wide annual decrease in mean wood specific gravity would cancel out the carbon sink effect. Currently, the more dynamic forests in the west have ~20% less dense wood than the slower forests of the east (Baker *et al.* 2004b); because these faster western forests also have lower basal area, the differences in terms of biomass carbon stored are significantly greater still (Figure 4.8).

Concerted compositional changes driven by greater resource supply, increased mortality rates and possible increases in the proportion of faster-growing trees that 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 GCMs provides the framework within which to evaluate these types of interaction and changing composition (Purves & Pacala 2008), any such analyses will need to be data-driven. Therefore, there are unlikely to be short-cuts to gaining an authoritative understanding of how forest biodiversity and carbon may be changing in the Anthropocene. Repeated, standardised, careful and adequately replicated on-the-ground measurements, coupled with targeted experiments and physiological measurements, will remain key to making significant progress.

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**Figure 4.8** Tree biomass as a function of mean stem turnover rates, for 66 lowland forest plots across South America monitored for at least 5 years in the 1980s and 1990s. Note that faster forests, typically in western Amazonia, have lower wood density and much lower biomass.

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