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The response of South American tropical forests to contemporary atmospheric change

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12.1 INTRODUCTION

Ecosystems worldwide are changing as a result of anthropogenic activities. Processes such as deforestation are physically obvious, but others, such as hunting and surface fires, are subtler but affect biodiversity in insidious ways (cf. Lewis *et al.*, 2004a; Laurance, 2004). Increased rates of nitrogen deposition and increases in air temperatures and atmospheric CO₂ concentrations are altering the environment of even the largest and most well-protected areas (e.g., Prentice *et al.*, 2001; Galloway and Cowling, 2002; Malhi and Wright, 2004). Anthropogenic atmospheric change will become more significant during this century, as CO₂ concentrations reach levels unprecedented for the last 20 million or perhaps even 40 million years (Retallack, 2001; Royer *et al.*, 2001). Nitrogen-deposition rates and climates are predicted to move far beyond Quaternary envelopes (Prentice *et al.*, 2001; Galloway and Cowling, 2002). Moreover, the rate of change in all these basic ecological drivers is likely to be without precedent in the evolutionary span of most species on Earth today (Lewis *et al.*, 2004a). This then is the Anthropocene: we are living through truly epoch-making times (Crutzen, 2002).

Given the scale of the anthropogenic experiment with the atmosphere–biosphere system, it is now self-evident that all ecosystems on Earth are affected by human activities in some sense. Recent research (Malhi and Phillips, 2005) suggests that tropical forests far from areas of deforestation are indeed undergoing profound shifts in structure, dynamics, productivity, and function. Here we synthesize recent results from a network of long-term monitoring plots across tropical South America that indicate how these forests are changing.

Changes in tropical forests are of societal importance for three reasons. First, tropical forests play an important role in the global carbon cycle and hence the rate of climate change, as ~40% of terrestrial vegetation carbon stocks lie within tropical forests (Malhi and Grace, 2000). Second, as tropical forests house at least half of all

Earth's species, changes will have a large impact on global biodiversity (Groombridge and Jenkins, 2003). Finally, as different plant species vary in their ability to store and process carbon, both climate and biodiversity changes are potentially linked by feedback mechanisms (e.g., Cox *et al.*, 2000).

Evidence suggests that the remaining Amazonian rainforest is currently a global carbon sink (Malhi and Grace, 2000). The evidence is from long-term monitoring plots which show that forest stands are increasing in above-ground biomass (Phillips *et al.*, 1998, 2002a; Baker *et al.*, 2004a), and from inverse modeling of atmospheric CO₂ concentrations that indicate tropical ecosystems may contribute a carbon sink of 1–3 Gt (1 gigatonne = 1 billion metric tonnes) per year (e.g., Rayner *et al.*, 1999; Rodenbeck *et al.*, 2003). The existence of a substantial tropical carbon sink is consistent with modeling and laboratory studies that imply changes in the productivity of tropical forests in response to increasing CO₂ (e.g., Lloyd and Farquhar, 1996; Norby *et al.*, 1999; Lewis *et al.*, 2004a). Although these interpretations are still being debated (see Lewis *et al.*, 2004a), efforts to overcome limitations in each line of evidence have generally confirmed the presence of a sink. Thus, it is reasonable to suggest that tropical forests are providing a substantial buffer against global climate change. Indeed, the results from long-term forest-monitoring plots suggest that intact Amazonian forests have increased in biomass by ~0.3–0.5% per year, and hence sequester carbon at approximately the same rate that the European Union (in January 2004) emits it by burning fossil fuels (Phillips *et al.*, 1998; Malhi and Grace, 2000; Baker *et al.*, 2004a).

Increasing atmospheric CO₂ concentrations and rising air temperatures will alter fundamental ecological processes and in turn will likely effect changes in tropical biodiversity. Changes in biodiversity as a consequence of anthropogenic climate change have in fact already been noted in better-studied temperate areas (e.g., Parmesan and Yohe, 2003) and in a well-studied old-growth tropical forest landscape in Brazil (Laurance *et al.*, 2004). The interactive “balance” among tens of thousands of tropical plant species and millions of tropical animal species is certain to shift, even within the largest and best-protected forest ecosystems, which are traditionally thought of as “pristine” wilderness. These areas are vital refugia—where global biodiversity may most easily escape the current extinction crisis—as they are large enough to allow some shifts in the geographic ranges of species in response to global changes, and are afforded some protection from industrial development, such as logging and agriculture. However, how most tropical forest taxa will respond to rising temperatures and CO₂ concentrations, among other global changes, is currently unknown (Thomas *et al.*, 2004).

Biodiversity change has inevitable consequences for climate change because different plant species vary in their ability to store and process carbon. One example of this is how shifts in the proportion of faster-growing light-demanding species may alter the carbon balance of tropical forests. Long-term plots suggest that mature humid Neotropical forests are a net carbon sink of ~0.6 gigatonnes per year (Phillips *et al.*, 1998; Baker *et al.*, 2004a). However, tree mortality rates have increased substantially in recent decades, so causing a likely increase in the frequency of tree-fall gap formation (Phillips and Gentry, 1994; Phillips *et al.*, 2004). A shift in

forests towards gap-favoring, light-demanding species with high growth rates, at the expense of more shade-tolerant species, is plausible (Körner, 2004). Such fast-growing species generally have lower wood-specific gravity, and hence lower carbon content (West *et al.*, 1999), than do shade-tolerant trees. An Amazon-wide decrease in mean wood specific gravity of just 0.4% would cancel out the carbon sink effect apparently caused by accelerated plant productivity. Whether such changes are occurring is currently poorly understood, but it is clear that the biodiversity and climate-change issues are closely linked and merit further study.

In this chapter we present a summary of the latest findings from permanent plots monitored by a large network of Amazon forest researchers, known as “RAINFOR” (*Red Amazónica de Inventarios Forestales*, or Amazon Forest Inventory Network; <http://www.geog.leeds.ac.uk/projects/rainfor/>). Here we summarize findings from old-growth forests in terms of (a) structural change, (b) dynamic-process change, and (c) functional change, over the past two decades.

12.2 THE PLOT NETWORK

For these analyses, we define a plot as an area of forest where all trees above 10-cm diameter at breast height (d.b.h., 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 5 years), the plot is revisited, and all surviving trees are re-measured, dead trees are noted, and trees recruited to 10-cm d.b.h. are uniquely numbered, measured, mapped, and identified. This allows calculation of: (i) the cross-sectional area that tree trunks occupy (termed “basal area”), which can be used with allometric equations to estimate tree biomass (Baker *et al.*, 2004a); (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 91 plots, depending upon selection criteria for different analyses (most critically, the number of census intervals from a plot and whether only stem-count data or the full tree-by-tree data set is available). The number of plots used for stem-density changes is more than that used in the biomass study because full tree-by-tree data are required to calculate biomass (using Baker *et al.*'s, 2004a methods), whereas stem-change data can often be obtained from published studies. The plots span the Amazonian forests of northern South America (Figure 12.1), including Bolivia, Brazil, Ecuador, French Guiana, Peru, and Venezuela. Most are 1 ha in size and comprise ~600 trees of ≥ 10 -cm d.b.h. The smallest are 0.4 ha and the largest is 9 ha, all large enough to avoid undue influence by the behavior of an individual tree (Chave *et al.*, 2003). Many plots have been monitored for more than a decade, although they range in age from 2 to 25 years. The earliest plot inventory was started in 1971, the latest in 2002. 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

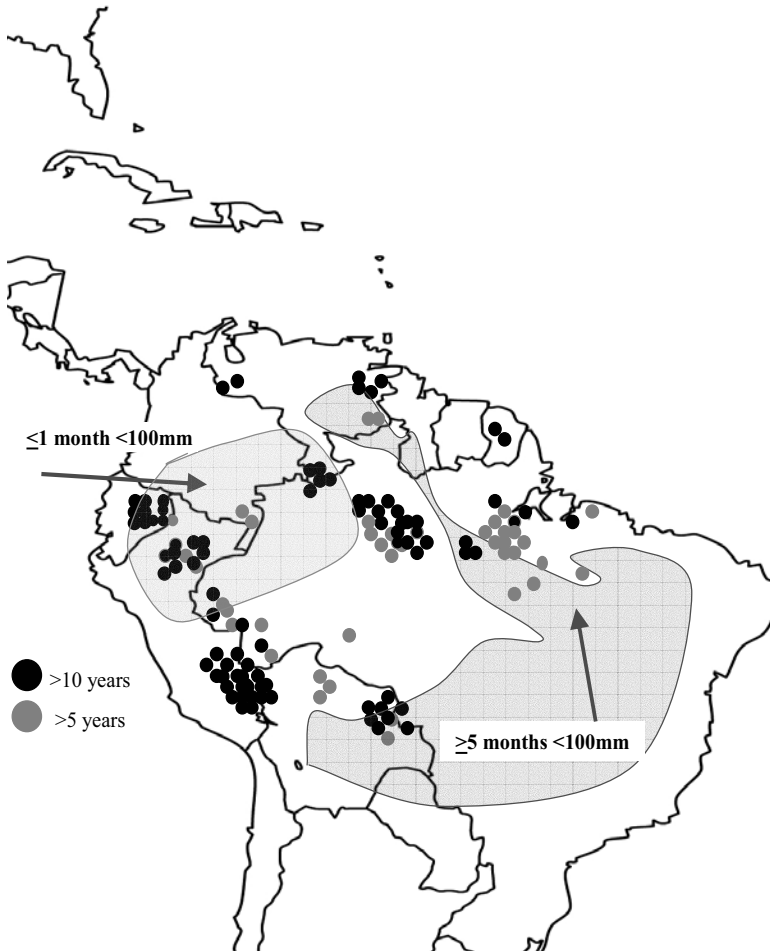


Figure 12.1. Plot locations used in this study. Symbols represent approximate locations of each plot; grey circle for plots monitored for 5–10 years, black for those with >10 years of monitoring. The approximate extent of seasonal and highly seasonal areas of tropical South America are indicated.

elsewhere (Phillips *et al.*, 2002a, b, 2004; Baker *et al.*, 2004a, b; Malhi *et al.*, 2002, 2004; Lewis *et al.*, 2004b).

12.3 STRUCTURAL CHANGES

Among 59 plots monitored in old-growth Amazon forests with full tree-by-tree data, there has been a significant increase in above-ground biomass between the first and last time they were measured. Over approximately the last 20 years, the increase

has been 0.61 ± 0.22 tonnes of carbon per hectare per year, or a relative increase of $0.50 \pm 0.17\%$ per year (mean \pm 95% confidence interval; Baker *et al.*, 2004a). Across all 59 plots, the above-ground biomass change is normally distributed and shifted to the right of 0 (Figure 12.2a). The estimate of a net increase of $0.61 \pm 0.22 \text{ t C ha}^{-1} \text{ yr}^{-1}$ is slightly higher than the $0.54 \pm 0.29 \text{ t C ha}^{-1} \text{ yr}^{-1}$ estimated earlier for the lowland Neotropics by Phillips *et al.* (1998) using 50 sites up to 1996.

We estimate the magnitude of the South American carbon sink by multiplying 0.61 tonnes per hectare per year by the estimated area of mature Neotropical humid-forest cover (c. 8,705,100 km²; FAO, 1990), which yields a value of about 0.5 gigatonnes of carbon per year. If we further assume that the ratio of above-ground to below-ground biomass is 3 : 1 (cf. Phillips *et al.*, 1998), and that below-ground biomass is increasing in proportion to above-ground biomass, then the sink increases to 0.71 ± 0.26 gigatonnes of carbon per year. If other biomass components—such as small trees, lianas, and coarse woody debris—are also increasing in biomass, then the sink will be fractionally larger still. However, these estimates depend critically on (i) how representative the 59 tree-by-tree plots are of South American forests; (ii) assumptions about the extent of mature, intact forest remaining in South America; (iii) the extent to which we have sampled the regional-scale matrix of natural disturbance and recovery.

Clark (2002) raised two concerns about the original findings of Phillips *et al.* (1998) that Amazon biomass was increasing, suggesting that (i) some floodplain plots that Phillips *et al.* considered mature may still be affected by primary succession, and that (ii) large buttress trees in some plots may have been measured in error—that is, not above the buttress, as protocols dictate, but around them. However, Baker *et al.* (2004a) showed that the carbon sink remains when plots on old floodplain substrates and those that may have buttress problems are removed from the analysis.

Consideration of all 91 RAINFOR plots shows a small increase in stem density between the first and last time they were measured, of 0.84 ± 0.77 stems per hectare per year (Figure 12.2b; paired *t*-test, $t = 2.12$, $P = 0.037$), or a $0.15 \pm 0.13\%$ per year increase (Phillips *et al.*, 2004). Across all plots, stem-change rates are approximately normally distributed and slightly shifted to the right of 0 (Figure 12.2b). The same test using 59 plots (from the Baker *et al.* 2004a study) shows a similar increase in stem density ($0.16 \pm 0.15\%$ per year), while a smaller but longer-term data set (50 plots from Lewis *et al.*, 2004b) shows a slightly larger increase ($0.18 \pm 0.12\%$ per year). While still significant, these changes in stem density are proportionally not as great as the biomass changes.

12.4 DYNAMIC CHANGES

An alternative way of examining forest change is to look for changes in processes (growth, recruitment, death), as well as in structure (biomass, stem density). Are these forests getting more active or simply gaining mass? We measure the dynamics of forests in two ways. First, we can examine changes in stem population dynamics. By

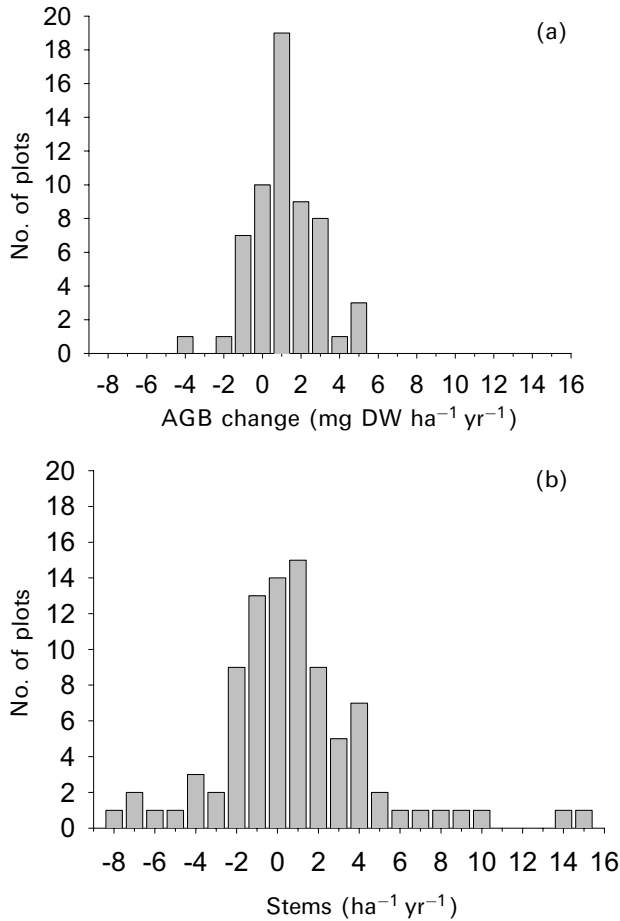


Figure 12.2. (a) Above-ground biomass change (dry weight) of trees greater than 10-cm diameter in 59 Amazon plots, based on initial and final stand-biomass estimates calculated using an allometric equation relating individual tree diameter to biomass, and incorporating a correction factor to account for variation in wood density among species (from Baker *et al.*, 2004a). 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 ($P < 0.01$). (b) Stem number change in 91 plots from across South American tropical forests. Stems were counted during the first and final censuses of each plot (plots are the same as those used by Phillips *et al.*, 2004). The mean and median are shifted significantly to the right ($P < 0.05$).

convention (Phillips and Gentry, 1994) we estimate stem turnover between any two censuses as the mean of annual mortality and recruitment rates for the population of trees ≥ 10 -cm diameter. Second, we examine changes in biomass fluxes of the forest—in terms of growth of trees and the biomass lost with mortality events. These stand-

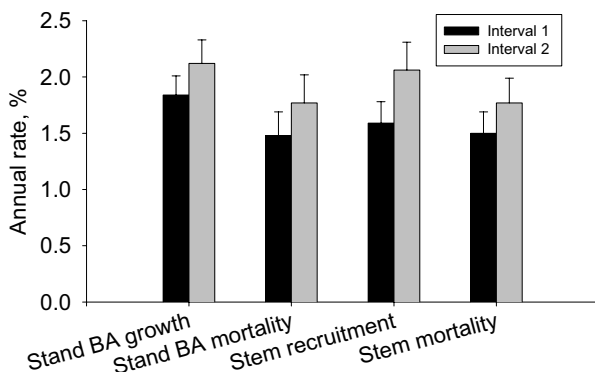


Figure 12.3. Annualized rates of stand-level basal-area growth, basal-area mortality, stem recruitment, and stem mortality from plots with two consecutive census intervals (i.e., the subset of RAINFOR sites that have been inventoried on at least three successive occasions), each giving the mean from 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).

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 old-growth plots across tropical South America with at least three censuses (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—are increasing significantly (Figure 12.3), between the first and second halves of the monitoring period (Lewis *et al.*, 2004b). Thus, over the past two decades, these forests have become, on average, faster growing and more dynamic. Notably, the increases in the rate of dynamic fluxes (growth, recruitment, and mortality) are about an order of magnitude larger than are 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 Figure 12.4, we plot the across-site mean values for stem recruitment and mortality as a function of calendar year. This shows that the increase has not been short-term (e.g., the result of a spike around a year with unusual weather), that recruitment rates have on average consistently exceeded mortality rates, and that mortality appears to lag recruitment (Phillips *et al.*, 2004).

Using data for the 50 plots with two consecutive census intervals, we can also separate them into two groups: one faster growing and more dynamic (mostly western Amazonian), and one slower growing and less dynamic (mostly eastern and central Amazonian). Both groups showed increased stem recruitment, stem mortality, stand basal-area growth, and stand basal-area mortality, with larger absolute increases in rates in the faster growing and more dynamic sites than in the slower-growing and less dynamic sites (Figure 12.5; Lewis *et al.*, 2004b). However, the proportional increases

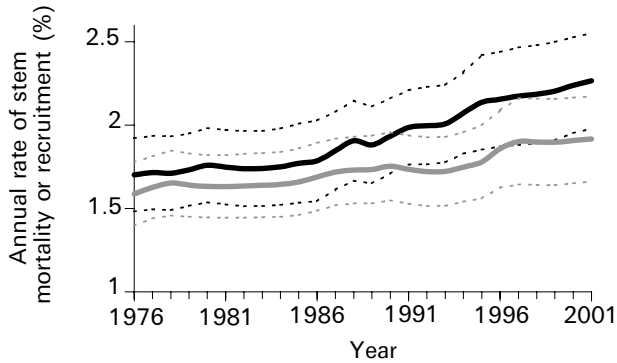


Figure 12.4. Mean and 95% confidence intervals for stem recruitment and mortality rates against calendar year, for plots arrayed across Amazonia. Rates for each plot were corrected for the effects of differing census-interval lengths, for “site-switching”, and for “majestic-forest bias”. A detailed justification methodology for these corrections is given in Phillips *et al.* (2004); all trends are robust and hold equally 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).

in rates were similar, and statistically indistinguishable, across both forest types (Lewis *et al.*, 2004b). This shows that increasing growth, recruitment, and mortality rates are occurring proportionately similarly across different forest types and geographically widespread areas.

12.5 FUNCTIONAL CHANGES

Changes in the structure and dynamics of tropical forests are likely to be accompanied by changes in species composition and function. There is, moreover, no *a priori* reason to expect that large changes in Amazon forests should be restricted to trees. Phillips *et al.* (2002b) studied woody climbers (structural parasites on trees, also called “lianas”), which typically contribute 10–30% of forest leaf productivity but are ignored in almost all monitoring studies except in most of our western Amazonian sites. Across the RAINFOR plots of western Amazonia there has been a concerted increase in the density, basal area, and mean size of lianas (Figure 12.6; Phillips *et al.*, 2002b). Over the last two decades of the 20th 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 intact tropical forests are changing in terms of their composition and function. A long-term monitoring study from beyond Amazonia (Barro Colorado Island in Panama) has since reported a substantial increase in absolute and relative liana leaf-fall rates since the 1980s, indicating that lianas are both increasing and becoming more dominant there (Wright *et al.*, 2004). There is some experimental evidence (Granados and Körner, 2002) for a very strong response of tropical lianas to elevated atmospheric CO₂ concentrations, much stronger than the normal experimental response of trees.

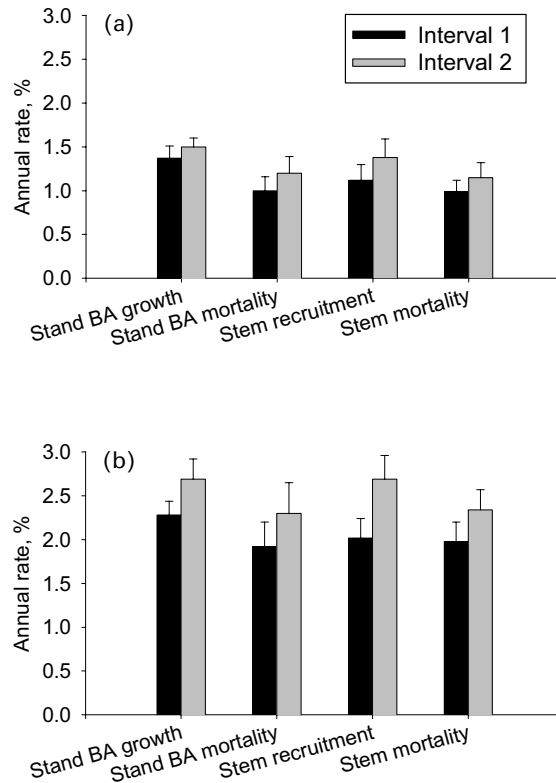


Figure 12.5. Annualized rates of stand-level basal-area growth, basal-area mortality, stem recruitment, and stem mortality over consecutive census intervals for plots grouped into “slower growing less-dynamic” (a) and “faster growing more-dynamic” (b) forests. Of the slower-dynamics group, 20 of 24 plots 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).

Finally, a recent paper from a cluster of plots in central Amazonia has shown consistent changes in tree species composition over the past two decades (Laurance *et al.*, 2004). Many faster-growing genera of canopy and emergent stature trees increased in basal area or density, whereas some slower-growing genera of sub-canopy or understory trees decreased in density. Laurance *et al.* (2004) provide evidence of pervasive changes in central Amazonian forests: growth, mortality, and recruitment all increased significantly over two decades (basal area also increased, but not significantly so), with faster-growing genera showing much larger absolute and relative increases in growth, relative to slower-growing genera. Further studies are urgently needed to determine whether comparably large shifts in tree communities are occurring throughout the tropics.

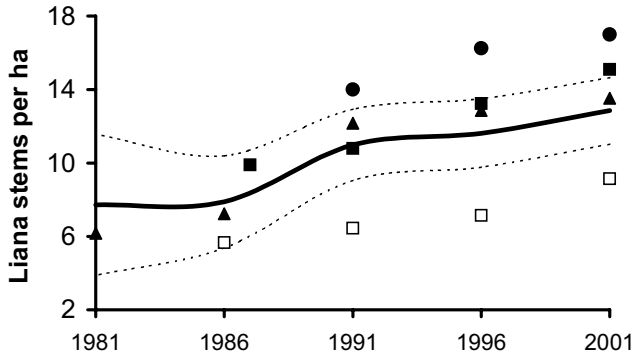


Figure 12.6. Five-year running means (*solid line*) with 95% confidence intervals (*dashed lines*) of liana stem density per hectare (>10-cm diameter at breast height), with values plotted separately for northern Peru (*filled squares*), southern Peru (*filled triangles*), Bolivia (*filled circle*), and Ecuador (*unfilled squares*) (adapted from Phillips *et al.*, 2002b; see that paper for full details of field and analytical methodology).

12.6 WHAT IS DRIVING THESE CHANGES?

What could be causing the continent-wide changes in tree growth, recruitment, mortality, stem density, and biomass? Many factors could be invoked, but there is only one parsimonious explanation. The results appear to show a coherent fingerprint of increasing growth—that is, increasing net primary productivity (NPP)—across tropical South America, probably caused by a long-term increase in resource availability (Lewis *et al.* 2004a, b). According to this explanation, increasing resource availability increases NPP, which then increases stem growth rates. Faster individual growth rates account for the increase in stand basal-area growth and stem recruitment rates, and the fact that these factors show the “clearest” signals (statistically most significant) in the analyses (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), resulting in increases in the rate of biomass mortality and stem mortality. 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 can also be explained by 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).

What environmental changes could be increasing 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 CO₂ concentrations (Prentice *et al.*, 2001), increasing solar radiation inputs (Wielicki *et al.*, 2002), and rising air temperatures (Malhi and Wright, 2004) have been documented across Amazonia and could be responsible for increased growth and productivity. For none of these three changes, however, do we have overwhelming evidence that the driver has both actually changed and that such a change must accelerate forest growth (Lewis *et al.*, 2004a).

The increase in atmospheric CO₂ is our leading candidate, because of the undisputed long-term increase in CO₂ concentrations, the key role of CO₂ in photosynthesis, and the demonstrated positive effects of CO₂ fertilization on plant growth rates, including experiments on whole temperate-forest stands (Hamilton *et al.*, 2002; Norby *et al.*, 2002; Lewis *et al.*, 2004a). At present, however, no experiments have assessed the effects of increasing CO₂ availability on intact, mature tropical-forest stands, and this interpretation is still contested by some (e.g., Chambers and Silver, 2004).

Air-temperature increases are also undisputed, and could conceivably be causing the changes we document. However, many authors expect that the 0.26°C per decade air-temperature increase (Malhi and Wright, 2004) would actually reduce, not increase, forest growth, as respiration costs are likely to increase with temperature. However, increased air temperatures will also increase soil temperatures, which could in turn increase soil mineralization rates and thus nutrient availability (see review by Lewis *et al.*, 2004a). Whether recent rises in air temperature have increased or decreased tropical forest NPP requires further study.

Recent satellite data suggest an increase in incoming solar radiation across the tropics between the mid-1980s and late 1990s as a result of reduced cloudiness (Wielicki *et al.*, 2002). However, because stem turnover has increased across the tropics since the 1950s (Phillips and Gentry, 1994; Phillips, 1996), increasing solar radiation since the mid-1980s may not have occurred over a long enough period of time to explain the trends in forest-plot data, at least in terms of stem turnover. Furthermore, as the *difference* between stand-level basal-area growth and mortality was similar at the start (1980s) and end (1990s) of the study by Lewis *et al.* (2004b), the factor causing changes in growth, recruitment, and mortality was probably operating before the onset of the study, and hence before the observed increase in incoming solar radiation. Finally, the evidence for increased insolation in Amazonia is not strong and there is a possibility that forest NPP may be greater under cloudy conditions (e.g., Roderick *et al.*, 2001: cloudiness increases the fraction of radiation that is indirect, which penetrates further into the canopy and could thus have a positive impact on whole forest NPP since canopy leaves overheat in midday tropical sun and may already be saturated with respect to light).

Determining which environmental change, or changes, has caused the trends we document across South American tropical forest is very difficult. However, each environmental change is expected to leave a unique signature, or fingerprint, in forest data, as different environmental changes initially impact different processes, have different distributions in time and space, and may affect some forests more than others (e.g., depending upon soil fertility). Future analyses of forest-plot data at finer

spatially and temporally resolved scales should therefore allow a further narrowing of potential causes underlying rising productivity across South American tropical forests (Lewis *et al.*, 2004a).

12.7 THE FUTURE

For those concerned about future biodiversity losses and global climate change, our analyses suggest both worrying trends and some apparently “good news”. The Amazon, the world’s largest remaining tract of tropical forest, has shown concerted changes in forest dynamics over the past two decades. Such unexpected and rapid alterations—apparently in response to anthropogenic atmospheric change—raise concerns about other possible surprises that might arise as global changes accelerate in coming decades. Tropical forests are evidently very sensitive to changes in incoming resource levels and may show large structural and dynamic changes in the future, as resource levels alter further and temperatures continue to rise (Lewis *et al.*, 2004a). The implication of such rapid changes for the world’s most biodiverse region is unknown, but could be substantial.

Moreover, old-growth Amazonian forests are evidently helping to slow the rate at which CO₂ is accumulating in the atmosphere, thereby acting as a buffer to global climate change—certainly “good news” for the moment. The concentration of atmospheric CO₂ is rising at a rate equivalent to 3.2 gigatonnes of carbon per year; this would be significantly greater without the tropical South American carbon sink of 0.5 to 0.8 gigatonnes of carbon per year. However, 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 (Chambers *et al.*, 2001, Cramer *et al.*, 2001), or (ii) soon become a *small carbon source* because of changes in functional and species composition (Cramer *et al.*, 2001; Phillips *et al.*, 2002b; Körner, 2004; Laurance *et al.*, 2004), or (iii) become a *mega-carbon source*, possibly in response to climate change (Cox *et al.*, 2000; Cramer *et al.*, 2001). Given that a 0.3% annual increase in Amazon forest biomass is roughly equivalent to the entire fossil-fuel emissions of the European Union (in January 2004), a switch of tropical forests from a moderate carbon sink to even a moderate carbon source would have profound implications for global climate, biodiversity, and human welfare.

Finally, it is important to emphasize that climate-based models that project the future carbon balance in Amazonia (and future climate-change scenarios) have made no allowance for changing forest composition. This omission is likely to lead to erroneous conclusions. For example, lianas contribute little to forest biomass but kill trees and suppress tree growth (Schnitzer and Bongers, 2002), and their rapid increase suggests that the tropical carbon sink might shut down sooner than current models suggest. Large changes in tree communities could undoubtedly lead to net losses of carbon from tropical forests (Phillips and Gentry, 1994; Körner, 2004). 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. When 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. Clearly, projections of future carbon fluxes will need to account for the changing composition and dynamics of tropical forests.

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