Changing Ecology of Tropical Forests: Evidence and Drivers

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Abstract

Global environmental changes may be altering the ecology of tropical forests. Long-term monitoring plots have provided much of the evidence for large-scale, directional changes in tropical forests, but the results have been controversial. Here we review evidence from six complementary approaches to understanding possible changes: plant physiology experiments, long-term monitoring plots, ecosystem flux techniques, atmospheric measurements, Earth observations, and global-scale vegetation models. Evidence from four of these approaches suggests that large-scale, directional changes are occurring in the ecology of tropical forests, with the other two approaches providing inconclusive results. Collectively, the evidence indicates that both gross and net primary productivity has likely increased over recent decades, as have tree growth, recruitment, and mortality rates, and forest biomass. These results suggest a profound reorganization of tropical forest ecosystems. We evaluate the most likely drivers of the suite of changes, and suggest increasing resource availability, potentially from rising atmospheric CO_2 concentrations, is the most likely cause.

INTRODUCTION

The Earth's physical, chemical, and biological environment is changing in response to human activities. Some alterations such as rapid land-use change are obvious, whereas others such as increasing air temperatures, nitrogen deposition, and changes in atmospheric composition are not but can have subtle and insidious effects on ecosystems (Laurance & Peres 2006). It is the consequences for tropical forests of these latter effects—long-term anthropogenic changes that are predominantly global or regional in scale—that are the focus of this synthesis.

Tropical forests are the most biologically diverse ecosystems on Earth, performing ecosystem services with far-reaching consequences. They process and store globally significant quantities of carbon (Denman et al. 2007), and play important roles in promoting cloud formation and regional rainfall (Bala et al. 2007). Biome-wide changes in such functions could have profound consequences for biogeochemical cycles and biodiversity, some of which may have major societal repercussions such as buffering or accelerating the rate of global climate change (Denman et al. 2007, Lewis 2006).

The nature of contemporary longer-term, large-scale changes to the tropical environment is far from completely understood (Lewis et al. 2004a), and their implications for tropical forest ecology are controversial (Clark 2004, Fearnside 2004). Therefore, we assess, from disparate lines of evidence, whether tropical forests—especially tropical tree communities—are changing systematically in their ecology. We also assess whether we can begin to attribute any such changes to particular underlying drivers, akin to similar efforts in climate-change science (Hegerl et al. 2007).

To date, much attention has focused on interpreting data from the long-term monitoring of relatively small tropical forest plots, where individual trees above a certain size are monitored over time (Lewis et al. 2004b, 2009; Phillips et al. 2009; Wright 2005). Results have been contentious since the first studies suggested that tropical forests were not in long-term equilibrium (Phillips & Gentry 1994, Phillips et al. 1998), with criticisms focusing on perceived methodological problems (Clark 2002) and statistical ambiguities (Sheil 1995). Although many of the potential statistical and methodological flaws have since been investigated and resolved (Baker et al. 2004; Chave et al. 2008; Lewis et al. 2004c, 2009; Phillips et al. 2002a, 2009), the "changing ecology of tropical forests" hypothesis is still hotly debated (Muller-Landau 2009, Wright 2005). This debate arises, in part, because of inherent limitations in the use of forest plots to detect and understand widespread changes in the functioning of tropical forests, particularly the limited number and length of time such plots have been monitored, and constraints on understanding the drivers of trends given the limited monitoring of the tropical environment.

To help overcome such deficiencies, we evaluate here forest inventory data, alongside plant physiology experiments and modeling, ecosystem flux observations, Earth observations, atmospheric measurements, and dynamic global vegetation models. Individually each of these techniques has particular advantages and limitations, but taken together may provide new opportunities to cross-validate results, and perhaps new insights into recent changes in forest ecology. For example, our interpretations of changes in tree-growth rates and hence Net Primary Productivity (NPP) may be constrained by experiments on how plants respond physiologically to rising atmospheric CO_2 concentrations and air temperature. Likewise, measured large-scale increases or declines in forest productivity or changes in structure should be detectable with remote-sensing data, providing independent verification of key changes. This integrated approach is analogous to that being used to reconcile apparently conflicting evidence when attempting to balance the global carbon cycle (House et al. 2003).

We have three main goals in this review. First, we briefly highlight known potential drivers of changes in tropical forest ecology. Second, we critically evaluate evidence suggesting that the ecology of tropical forests is changing. We consider only evidence for or against directional changes in

intact tropical forests, ignoring studies of interannual variation. Finally, we integrate findings from the different research techniques to identify the most plausible drivers of change in tropical forests.

POTENTIAL DRIVERS OF CHANGE

Lewis et al. (2004a) provided a general framework to (*i*) systematically identify possible changes in the environment that may cause changes in tropical tree growth, recruitment, or mortality; (*ii*) determine how much each potential driver has changed over recent decades; and (*iii*) assess whether the level of change in each driver is sufficient to be ecologically meaningful. Nine potential drivers were identified: (*a*) increasing air temperatures, (*b*) changes in rainfall, (*c*) changes in incoming solar radiation, (*d*) changes in the frequency and/or intensity of extreme climatic (including El Niño Southern Oscillation) events, (*e*) rising atmospheric CO_2 concentrations, (*f*) increasing nutrient deposition (N and P), (*g*) ozone and acid deposition, (*h*) hunting pressure, (*i*) land-use change, and (*j*) secondary biological changes such as the abundance of lianas.

Three of these drivers could potentially alter multiple mechanisms that may affect forest functioning: Rising atmospheric CO_2 concentrations can affect light-use, water-use, and nutrient-use efficiency of plants; increasing air temperatures can affect photosynthetic and respiration rates and may alter soil nutrient availability via increasing soil temperatures; and land-use changes can affect plant mortality rates via edge effects or by an elevated seed rain of disturbance-adapted plants from nearby degraded lands. Collectively, this gives 17 potential mechanisms of change, plus disturbance effects (Lewis et al. 2004a). These are conveniently grouped into those that are expected to initially affect tree growth (air temperature, rainfall, solar radiation, carbon dioxide, nutrient deposition, ozone/acid deposition), mortality (climatic extremes, land-use changes creating edge effects), and recruitment (hunting, land-use change increasing the seed rain from disturbance-adapted species).

For seven of the nine drivers, the sign of temporal trend over the tropics is clearly positive, indicating that the driver has increased in importance in recent decades. The trend in tropical rainfall is negative (Malhi & Wright 2004), but varies among regions, whereas trends in tropical solar radiation are difficult to characterize (Lewis et al. 2004a). Changes in solar radiation are complex and poorly understood. Ground-based thermopile pyranometers suggest a reduction in solar radiation reaching large areas of the Earth's surface, from the 1950s to 1980s, followed by a subsequent brightening, although many tropical areas have not shown a brightening (Gilgen et al. 2009, Ohmura 2009, Wild et al. 2005). Any dimming would have been coupled with an increasing fraction of diffuse radiation, which itself would increase whole-canopy photosynthesis, NPP, and biomass, countering the impact of any dimming (Mercado et al. 2009). In contrast, satellite-derived top-of-atmosphere measurements show an increase in long wave radiation of 0.7 W m^{-2} a^{-1}, suggesting the tropics became less cloudy and sunnier in the 1990s compared to the 1980s (Wong et al. 2006). Note that this is a fourfold reduction in the increase compared to previous estimates (Wielicki et al. 2002). Overall, it is uncertain whether trees in tropical forests, on average, have experienced increased or decreased photosynthetically active radiation over recent decades or whether the direct:diffuse ratio has changed significantly.

In addition, some have suggested that inventory plot results may merely reflect recovery from past disturbance if entire regions, such as the Amazon, are recovering from a past continental-scale disturbance (e.g., Wright 2005). Such regional-to-continental scale disturbance events may conceivably have occurred in the recent-enough past to drive large-scale changes in tropical forests, but indicative evidence has not been found to date (Baker et al. 2004, Lewis et al. 2009, Wright 2005). For example, the arrival of Europeans in South America five centuries ago led to widespread forest regeneration following the reduction in the numbers of indigenous Americans;

however, paleoclimatological and paleoecological analyses show that these events are unlikely to be affecting any discovered changes in the biomass of Amazonian forests today (Nevle & Bird 2008). Similarly, the most severe more recent disturbance is considered to be the 1926 ENSO drought (Wright 2005). Working backward from today, increased carbon storage of ∼0.5 Pg a^{-1} over at least 20 years across Amazonia (Phillips et al. 2008) suggests a total uptake of >40 Pg C since 1926, if an ongoing recovery from disturbance is the cause. Hence losses in 1926 are presumably of a similar magnitude and would therefore be expected to appear as an anomalous increase in atmospheric CO_2 data. There is no evidence that 40 Pg C (∼19 ppm, and four times the impact of the arrival of Europeans in the Amazon) of "extra" CO_2 was added to the atmosphere in years following the 1926 drought (Etheridge et al. 1996). To put these hypothesized past events in context, the anomalous extreme 2005 drought across Amazonia had a carbon impact of 1.2–1.6 Pg C (Phillips et al. 2009). Based on the limited evidence, large-scale disturbance is unlikely to be a major driver of directional changes over large areas of the tropics.

PLANT PHYSIOLOGY EXPERIMENTS AND THEORY

Over recent decades the two most ubiquitous and clear directional environmental changes that tropical forest trees have experienced are an increase in temperature of 0.026 ± 0.005°C a^{-1} from 1976 to 1998 (Malhi & Wright 2004) and an increase in atmospheric CO_2 concentrations of 1.66 ppm a^{-1} or 0.46% a^{-1} from 1980 to 2007 (Keeling & Whorf 2008). Yet the influence of these changes on two key processes that determine net primary productivity, photosynthesis and respiration, has been controversial among some tropical ecologists (Clark 2004, Wright 2005). Hence we consider each in turn.

Photosynthesis

Tropical forest productivity increases with increasing light availability (Graham et al. 2003), and very likely the ratio of diffuse:direct radiation (Gu et al. 2003, Mercado et al. 2009). However, do plants also respond to increasing atmospheric CO_2 concentrations? The answer depends on whether tropical tree growth is limited by photosynthetic carbon supply (Lloyd & Farquhar 2008). Formal meta-analyses of CO_2-enhancement experiments show increases in carbon gains and plant growth using open-topped chambers (Curtis & Wang 1998, Curtis et al. 2003, Kimball et al. 2007), free-air CO_2 enrichment (FACE) approaches (Ainsworth & Long 2005, Nowak et al. 2004), and plants growing near natural CO_2 vents (Bartak et al. 1999, Idso 1999), and include experiments on in situ tropical trees (Wurth et al. 1998) with the longest studies spanning 30 years. This is because, along with light availability, CO_2 is a limiting factor for photosynthesis, with plant growth being especially responsive to CO_2 at low light levels, in line with theoretical predictions (Lloyd & Farquhar 1996). In addition, stomatal conductance decreases with increasing CO_2 (Ainsworth & Long 2005), which increases water-use efficiency, again in line with theoretical predictions (Lloyd & Farquhar 1996).

However, some have argued that CO_2 is unlikely to be limiting to tropical plants. For example, it has been argued that, because carbohydrate concentrations in tropical trees are considerable, this indicates that carbon is in plentiful supply and therefore increasing atmospheric CO_2 is unlikely to stimulate plant growth (Korner 2003, Wurth et al. 2005). Yet such carbohydrates may actually be accumulated as "insurance" against future plant damage, such as leaf or crown loss, indicating that high carbohydrate concentrations are evolutionary adaptations to environmental stochasticity, rather than carbon limitation (Lewis et al. 2004a, Lloyd & Farquhar 2008). The insurance hypothesis is supported by experiments that increase light to in situ tropical trees, which showed an increase in both growth and carbohydrate concentrations (Graham et al. 2003).

However, the tendency for many lowland tropical forests to occur on soils low in phosphorus (Quesada et al. 2009) could limit their responses to increasing CO_2 (Friedlingstein et al. 1995, McKane et al. 1995), although plausible mechanisms exist that may allow plants to obtain more phosphorus in a CO_2-rich environment (Lloyd et al. 2001).

Temperature affects photosynthesis. Air temperature changes change the activity rates of photosynthetic enzymes and the electron transport chain (Sage & Kubien 2007) and alter the leaf-to-air vapor pressure difference, which influences stomatal conductance (Doughty & Goulden 2008, Lloyd & Farquhar 2008). With rising temperatures Rubisco (the key photosynthetic enzyme) kinetics increase to a point of inflection followed by a rapid irreversible decrease as the enzyme denatures. This is thought to occur at ∼45°C (Lloyd & Farquhar 2008, Sung et al. 2003). In contrast, electron transport increases to a reversible point of inflection at ∼37°C, likely with a similar irreversible decline at very high temperatures (Lloyd & Farquhar 2008, Sung et al. 2003). As leaf temperatures rise, evaporative demand increases, causing stomata to close to reduce water loss and thereby decrease photosynthetic rates (Doughty & Goulden 2008, Lloyd & Farquhar 2008). Experiments and eddy-covariance flux measurements suggest that photosynthesis in present-day lowland tropical forests may be approaching, but has not passed, its high-temperature threshold on the warmest days (Doughty & Goulden 2008, Goulden et al. 2004, Graham et al. 2003, Ishida et al. 1999, Loescher et al. 2003).

Models of leaf-scale photosynthesis (Farquhar et al. 1980) applied to tropical forest canopies suggest (*i*) the indirect effect of rising temperature in recent decades on stomatal closure is likely to be much more important than the direct impacts of exceeding thresholds for Rubisco function or the electron transport chain, and (*ii*) the positive effect of rising atmospheric CO_2 likely exceeds the negative effect of rising temperature on photosynthetic carbon gains over recent decades (Lloyd & Farquhar 2008). Thus, average gross primary productivity of tropical forests should have increased from ∼19.4 Mg ha^{-1} a^{-1} in 1730 to ∼24.4 Mg ha^{-1} a^{-1} in 1985 in response to rising atmospheric CO_2 (Lloyd & Farquhar 1996). Although the evidence is limited (there are no long-term FACE experiments in tropical forests), tropical trees are expected to have increased photosynthetic carbon gains and biomass growth in response to the effect of increasing atmospheric CO_2 concentrations, with a smaller effect of increasing air temperatures over recent decades partially offsetting those increases (Lloyd & Farquhar 2008).

Respiration

Respiration increases with rising temperature (Amthor 2000, King et al. 2006). This relationship is commonly described as an exponential function, known as Q_{10}, with a value of ∼2 in many systems (that is, a 10°C increase in air temperature doubles respiration rates), including tropical forests (Meir et al. 2008, Wright et al. 2006). However, some evidence suggests that plants can acclimate to higher temperatures, with Q_{10} functions overestimating the effect of temperature on respiration (Atkin et al. 2005, Wright et al. 2006). If tropical trees are carbon limited, however, then rising temperatures would lead to an increase in carbon allocated to respiration with growth rates and productivity decreasing, if other factors remain equal. This mechanism has been invoked in two studies that have shown decreases in tropical tree growth during warmer years (Clark et al. 2003, Feeley et al. 2007). However, for temperature to cause the magnitude of effect shown in these studies, Q_{10} values would need to exceed 5 (Lloyd & Farquhar 2008), which is unlikely (Atkin et al. 2005, Wright et al. 2006). Models suggest that the increase in air temperature and resulting decrease in productivity over recent decades have not been of sufficient magnitude to fully offset the increase in photosynthetic carbon gains from rising atmospheric CO_2 concentrations (Lloyd & Farquhar 2008).

LONG-TERM FOREST PLOTS

Forest monitoring plots usually range from 0.5–50 ha in area. Within them, every individual tree over a certain threshold size (usually ≥100 mm diameter-at-breast-height, defined as 1.3 m along the stem or above all buttresses or stem deformities) is identified, measured, and monitored over time. We consider the forest as a pool of biomass to which new biomass is continually being added through the growth of existing trees and recruitment of new trees. Such increases are to varying degrees balanced by ongoing biomass losses from tree mortality, breakage, and litterfall. We discuss apparent changes to these pools and fluxes using the available evidence.

Changes in Pools: Basal Area, Biomass, and Carbon

A key use of tropical forest plots has been to estimate the changes in basal area, biomass and carbon balance. Three major networks of plots have recently published estimates of temporal changes in forest carbon stocks:

1. The RAINFOR network of plots across South America reported a significant increase of 0.45 Mg C ha^{-1} a^{-1} (95% CI = 0.33–0.56) between 1975 and 2005 (**Figure 1**). In this network of 123 plots, 76% showed increasing biomass over time (mean interval 1990–2002). The average increase declined to 0.36 Mg C ha^{-1} a^{-1} when results from the 2005 Amazon drought were included (Phillips et al. 2009). This new estimate is smaller than an earlier estimate (0.62 ± 0.23 Mg C ha^{-1} a^{-1}) based on 59 plots (Baker et al. 2004), most likely because Phillips et al. (2009) weighted plot results by sampling effort and included more plots from slower-growing forests in Central and Eastern Amazonia.

2. Results from the AfriTRON network of plots across Africa showed a significant increase of 0.63 Mg C ha^{-1} a^{-1} (CI = 0.22–0.94) between 1968 and 2007 (**Figure 1**). In this network of 79 plots, 73% had increasing biomass over a mean interval from 1987–1996 (Lewis et al. 2009).

3. The Centre for Tropical Forest Science (CTFS) pan-tropical network of large monitoring plots (each from 10–52 ha in area) estimated a significant increase of 0.24 Mg C ha^{-1} a^{-1} from 1982 to 2006 (CI = 0.07–0.39; **Figure 1**) for 10 intact forest plots (**Figure 1**). Seven of these plots showed increasing biomass over a mean interval of 1992–2001 (Chave et al. 2008). The increase is smaller than the AfriTRON and RAINFOR network results, but is sensitive to the small number of plots sampled (e.g., excluding the site with the largest biomass decline would increase the mean change in carbon stocks by 34%, compared to just 6% for the Phillips et al. 2009 study).

To help synthesize these studies, Lewis et al. (2009) combined all standardized inventory data from the RAINFOR (Baker et al. 2004), AfriTRON (Lewis et al. 2009) and CTFS networks (Chave et al. 2008), along with data from other Asian plots (Phillips et al. 1998). Results from these 156 plots (562 ha in area, overall combined census length 1649 years, mean interval 1987–1997) were weighted by sampling effort (square root of census length and cube root of plot area). This combined analysis suggested an overall increase of 0.49 Mg C ha^{-1} a^{-1} (CI = 0.29–0.66) in tropical forest plots globally. For visual comparison we replotted the RAINFOR, AfriTRON, and CTFS data alongside Asian data from Phillips et al. (1998) in **Figure 1**.

Across the RAINFOR, AfriTRON, and CTFS networks, the most plausible causes of increasing biomass were identified as increasing resource availability (Baker et al. 2004, Phillips et al. 2009), increasing resource availability with some influence of recovery from past disturbance (Lewis et al. 2009) and recovery from past disturbance with some influence of increasing resource availability (Chave et al. 2008), respectively.
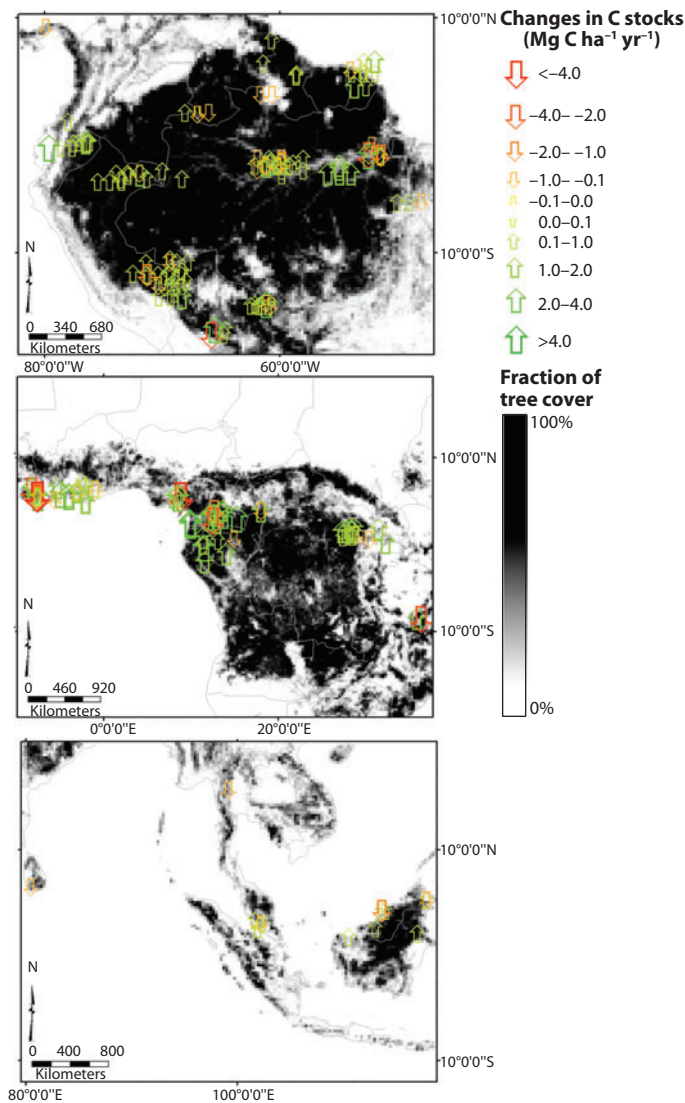
Figure 1

Changes in carbon storage in Mg C ha^{-1} a^{-1}, from the RAINFOR network before the 2005 Amazon drought (Phillips et al. 2009; *top panel*); the AfriTRON network (Lewis et al. 2009; *middle panel*); plots across Asia (Phillips et al. 1998; *bottom panel*); and the pan-tropical CTFS network (*across all three panels*). Forest cover is from the Global Land Cover 2000 map (Bartholome et al. 2002) and is the percentage tree cover (all tropical forest types, including degraded forest, combined) in a 0.25° grid cell. Arrows have been displaced slightly if many plots occur in a given area and represent mean changes unweighted by differing plot sizes or census interval lengths.

Changes in Pools: Stem Density

Significant increases in stem density (stems ≥100 mm diameter) were documented for 50 plots across South America from 1971–2002 (Lewis et al. 2004b), and later expanded to 91 plots (Lewis et al. 2006b). These results showed that statistically significant increases in stem density have occurred, but to a lesser degree than the increasing biomass results. Stem-density changes have

not been published for the CTFS or AfriTRON networks, but data from four CTFS plots show a similar though nonsignificant increase for stems $\geq$100 mm in diameter (Losos & Leigh 2004). Using the same weighting by sampling effort as used for biomass change (Lewis et al. 2009, Phillips et al. 2009), we estimate that stem density has risen significantly across all available plots, by an average of 0.73 ± 0.61 stems ha^{-1} a^{-1} ($0.13 \pm 0.12\%$; $n = 95$). An increase in resource availability was identified as the most plausible cause of rising stem density (Lewis et al. 2004b, 2006b).

Changes in Fluxes: Tree Growth and Productivity

Estimating temporal changes in tree growth or productivity is challenging because it requires at least three consecutive censuses of forest plots, thereby limiting available sample sizes. At the stand level, Phillips (1996) estimated growth as the sum of tree basal-area increments plus the basal areas of newly recruited trees, across each of at least two census intervals, reporting a significant acceleration in tree growth in 11 of 14 sites from across the tropics. Similarly, an increase in stand-level basal-area growth of 0.08 ± 0.04 m^2 ha^{-1} a^{-1} was reported for 50 plots across South America, with 68% of plots increasing over a mean interval from 1985–1999 (Lewis et al. 2004b). Chave et al. (2008), however, found varying results for three large inventory plots: Barro Colorado Island (BCI) in Panama showed marginally increased stand-level growth over time (+0.04 Mg ha^{-1} a^{-1} dry mass, from 1982–2005), whereas two other plots, Pasoh in Peninsular Malaysia and Lambir in Borneo, both exhibited declining growth (−0.2 and −0.1 Mg ha^{-1} a^{-1} dry mass, over 1986–2000 and 1992–2002, respectively). The only available study of basal-area growth rates from Africa is that of Taylor et al. (2008) who, working in Uganda, reported a small decline over time.

Two other types of measurement have been made to assess changes in tree growth or productivity over time: changes in the growth rates of cohorts of trees over time, and leaf production (litterfall) measurements. Feeley et al. (2007) reported declining growth of tree cohorts from BCI and a dramatic decline at Pasoh (in contrast to the increase and more modest declines reported for BCI and Pasoh, respectively, by Chave et al. 2008). Similarly, declines were found in a cohort of 164 large trees monitored for 16 years at La Selva, Costa Rica (Clark et al. 2003). Total litterfall production increased marginally at BCI over 17 years, by ∼0.07 Mg ha^{-1} a^{-1} (Wright et al. 2004). Interestingly, this value is similar to that estimated for stem-biomass growth at the same site (Chave et al. 2008).

Overall, among the various studies, we encountered 47 different published accounts of plots showing growth increases over time and 25 showing decreases over time. This represents a significant departure from a 1:1 ratio ($\chi^2 = 6.12$, $P = 0.013$, including Yate's correction for 1 d.f.), suggesting an overall increase in recent decades in tree growth and productivity across the tropics.

The authors of the various studies have suggested the following causes of the changes in tree growth: increasing growth across the Amazon caused by increasing resource availability (Lewis et al. 2004b); declines in growth at BCI, Pasoh, and La Selva caused by temperature increases (Feeley et al. 2007, Clark et al. 2003); decreases at Pasoh and Lambir caused by drought (the 1997–1998 El Niño event; Chave et al. 2008); and increases in leaf production at BCI by increases in solar radiation (Wright et al. 2004). The declines in growth were disproportionately detected when monitoring changes in the diameter of stems of cohorts of trees (Clark et al. 2003, Feeley et al. 2007). This may in part be driven by (*a*) nonconstant recruitment and mortality, (*b*) the fact that cohort studies reflect a mix of temporal environmental changes, ontogenetic shifts in allocation as the cohort ages, and switches in allocation from wood production to reproduction, which may tend to bias results toward declines, and (*c*) differences in measurement, as species composition changes may cause apparent declines in stem diameter growth where biomass and NPP may not have actually declined (see differences between results of Feeley et al. 2007 and

Chave et al. 2008). Changes in recruitment and mortality were not the main cause of the increase in stand-level growth across Amazonia, as the net number of trees increased by $\sim$1 tree ha^{-1} a^{-1}, equivalent to $\sim$10% of the observed increase in stand-level basal-area growth (Lewis et al. 2004b).

Changes in Fluxes: Tree Mortality

Temporal changes in tree mortality, on a basal-area or biomass basis, have only been assessed in three studies. Phillips (1996) documented a significant pan-tropical increase in mortality (calculated as the basal area of all trees lost over at least two census intervals), finding that mortality rose over time in 12 of 14 plots examined. Using a similar approach, Lewis et al. (2004b) found 28 out of 50 plots across South America showing increased mortality (0.08 ± 0.07 m^2 ha^{-1} a^{-1}; mean census interval, 1985–1999). Finally, Chave et al. (2008) calculated tree biomass lost at BCI, Lambir and Pasoh, with all three showing increases in mortality over time. Overall, these studies showed mortality increasing over time in 43 published accounts of forest plots and declining over time in 24 plots. This difference is significant when compared to a 1:1 ratio ($\chi^2 = 4.84$, $P = 0.028$). The authors identified the potential causes of the increase in mortality as drought (Chave et al. 2008) and growth increases due increasing resource availability in turn leading to increased mortality (Lewis et al. 2004b).

Changes in Fluxes: Stem Dynamics

An increase in stem turnover (mean of stem recruitment and stem mortality, a measure of forest dynamism) was first documented based on 40 plots from across the tropics, suggesting a doubling in rates from the 1950s to 1990s (Phillips & Gentry 1994). This result was reconfirmed with data for 67 plots (Phillips 1996), including when differing census-interval lengths in the data set were accounted for (Lewis et al. 2004c). For South America, Phillips et al. (2004) showed that average stem recruitment and stem mortality have increased over time. Moreover, turnover, recruitment, and mortality all increased significantly over time when the data set was disaggregated into plots on richer soils, poorer soils, aseasonal climates, seasonal climates, and western-southern versus central-eastern Amazonia (Phillips et al. 2004). In addition, mortality increases lagged behind recruitment increases (Lewis et al. 2004b, Phillips et al. 2004). Overall, these studies reveal 56 different plots where stem recruitment increased over time and 16 cases where it declined, a significant departure from a 1:1 ratio ($\chi^2 = 21.12$, $P < 0.0001$). Tree mortality also accelerated significantly (55 of 77 plots increasing, $\chi^2 = 13.3$, $P = 0.003$). The authors of the studies all suggested the increases resulted from increasing resource availability.

Within-Stand and Functional Changes

Four studies have assessed larger-scale, within-stand patterns over time. Laurance et al. (2004) showed an increase in absolute basal-area growth for most (87%) tree genera across a wide range of ecological habits in Central Amazonia. Of the 115 commonest genera, 14 significantly increased in net basal area, whereas one decreased. On a stem-density basis, 14 genera significantly decreased in density, whereas two increased. Changes on a basis relative to the changes in the stand as a whole were not reported because overall density and basal area did not alter significantly over time (Laurance et al. 2004).

Chave et al. (2008) reported functional changes across 10 large forest plots by grouping species into quartiles based on growth rate, wood density, seed size, and maximum plant size. On an absolute basis, there were significant increases in biomass of the fastest- and slowest-growing quartiles of species, no significant change in biomass of the highest and lowest quartiles based

on wood density, a significant increase in absolute biomass of the quartile with the smallest seed size, and no changes in biomass of quartiles based on maximum tree size. However, if these shifts are calculated relative to the changes in biomass of the stand, one result is significant: Assigning quartiles based on maximum tree size, the largest trees significantly decreased in biomass relative to the stand, whereas the smallest trees showed no relative change.

Lewis et al. (2009) 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 analyzed (Lewis et al. 2009). Feeley et al. (2007) similarly show widespread within-stand changes across widely differing species, showing pervasive declines in absolute diameter growth for two plots. Collectively, results from these studies, which span the tropics, suggest that the average increase in forest stand biomass is being caused by concurrent increases of many species with differing ecological habits.

Changes in Plant Reproduction

Only two studies have assessed changes in tree reproduction over time. At Kibale, Uganda, a 32-year record of change was compiled, but the methods and sampling differed over time, making robust conclusions difficult (Chapman et al. 2005). Combining the data showed that over the 1990s the proportion of trees fruiting increased dramatically (Chapman et al. 2005). This coincided with an increase in rainfall, decrease in mean monthly minimum temperatures, and an increase in mean monthly maximum temperatures. In a separate study, flower production for 81 species was monitored at BCI from 1987–2003 using consistent methods, also showing a large increase over time of both tree and liana species, which was suggested to be driven by increasing solar radiation associated with ENSO events (Wright & Calderon 2006). In contrast, there was no change in seed production over the same time period.

Change in Lianas

Two studies have assessed changes over time in lianas (structural parasites on trees). In Western Amazonia an increase was observed in the density of large lianas ≥ 100 mm in diameter (0.22 ± 0.11 lianas ha^{-1} a^{-1}), their basal area (0.0037 m^2 ha^{-1} a^{-1}), and their rates of recruitment and mortality, from a network of 28 plots spanning 1979–2002 (Phillips et al. 2002b). In addition, at BCI, litterfall records over 18 years show that the production of liana leaves has increased (Wright et al. 2004), as did liana flower production but not seed production (Wright & Calderon 2006). Both the Western Amazonian and BCI studies showed an increase in the relative dominance of lianas compared to trees. In contrast, the only study in African forest to document changes in liana density and basal area over time showed a significant decrease at Makouko, Gabon (Caballe & Martin 2001).

Interpreting the Plot-Based Studies

Analyses of the combined plot data reveal significant increases in carbon storage (biomass) and stem density, and an acceleration of tree growth, recruitment, and mortality—that is, forests are becoming bigger and more dynamic over time. This is consistent with results from the first studies of networks of forest plots (Phillips & Gentry 1994, Phillips et al. 1998). Of course, some individual plots do not exhibit these patterns, but the majority do. Furthermore, among 10 widely separated locations across the tropics where all these parameters have been measured simultaneously, aboveground biomass, growth, mortality, stem density, and stem turnover rose in 70%, 70%, 90%, 80%, and 80% of all plots, respectively (**Table 1**). In addition, the gains of biomass to forest plots (growth

Table 1 All long-term forest plots with simultaneously reported above-ground biomass, tree growth (basal area or biomass), tree mortality (basal area or biomass), stem density, and stem turnover changes over time, each reported for trees ≥100 mm in diameter reported, and below a priori predictions or "fingerprints" from three potential drivers of change[a]. Different reporting of units in original publications means only directional signs of change are given.

Plot name(s)	Country	No. ha monitored	Dates monitored	Above-ground biomass	Tree growth	Tree mortality	Stem density	Stem turnover	Compositional changes
Jatun Sacha[b]	Ecuador	2.92	1988–2002	←	←	←	←	←	↑ Lianas
N. Peru[b] (Allpahuayo, Yanomono, Sucusari)	Peru	4.76	1989–2001	→	←	←	←	←	↑ Lianas
S. Peru[b] (Tambopata, Cuzco Amazonica)	Peru	9.38	1985–1999	←	←	→	←	←	↑ Lianas
Tapajos[b]	Brazil	3	1983–1995	←	→	←	→	→	Unknown
Jari[b]	Brazil	1	1985–1996	→	←	←	←	←	Unknown
Caixuana[b]	Brazil	1	1994–2002	←	←	←	←	←	Unknown
N. Manaus[b] (BDFFP, Bionte, Jacaranda)	Brazil	37	1985–1999	←	←	←	→	←	Faster-growing species ↑, canopy trees↑, understorey species ↓
Barro Colorado Island (BCI)[c]	Panama	50	1982–2005	→	←	←	↑[e]	↑[e]	Wetter-adapted species↓, lianas↑
Pasoh[c]	Malaysia	50	1987–2000	←	→	←	←	→	Relative ↑ slower-growing species
Mpanga[d]	Uganda	0.64	1968–1993	←	→	←	←	←	↓ Seral and understorey species ↓, canopy species↑
Mean		15.97	1985–1999	70%↑	70%↑	90%↑	80%↓	80%↑	
Disturbance hypothesis				>50%↑	~50%↑	>50%↑?	>50%↓	>50%↓	Slower growing, harder wooded, larger seeded species ↑
Increased resource availability hypothesis				>50%↑	>50%↑	>50%↑	>50%↑	>50%↑	Unclear, all species similarly affected, or faster-growing species ↑? Disturbance-adapted taxa ↑?
Temperature increases increasing respiration costs hypothesis				>50%↓	>50%↓	>50%↑	>50%↓	>50%↑	Unclear, all species similarly affected?

[a]Plots <50 km apart are grouped together.
[b]Biomass change data from Baker et al. (2004); growth, recruitment, mortality, and turnover data from Lewis et al. (2004b); and liana data from Phillips et al. (2002b).
[c]Biomass change, growth, and mortality data from Chave et al. (2008); and stem turnover data from Losos & Leigh (2004).
[d]From Taylor et al. (2008).
[e]From 1982–1995 only.

and recruitment) are much more statistically significant than are losses (mortality), with mortality apparently lagging behind recruitment.

Do these patterns imply a large-scale shift in the ecology of tropical forests? The answer depends on assessing two potential artifacts of long-term plot data. First, in terms of biomass stocks, most forest plots will be accumulating biomass most of the time, as they are at some stage of recovery following a previous disturbance. Thus, to obtain unbiased estimates of biomass and other parameters, sample sizes need to be large enough and of long-enough duration to capture occasional mortality events that cause infrequent (but sometimes large) decreases in biomass (Fisher et al. 2008). In general, available plot networks seem adequate to obtain unbiased estimates of biomass change. The critical parameter is the clustering of mortality events, which is often assumed to follow a power-law distribution (Fisher et al. 2008, Kellner & Asner 2009). Power-law exponents of about -1.6 to -1.1 may lead to an overestimation of biomass change derived from low sample sizes and one-year census intervals (Fisher et al. 2008). However, power-law exponents from forests across the Amazon, Africa, and Central America range from approximately -1.8 to -3.1 (Gloor et al. 2009, Kellner et al. 2009, Kellner & Asner 2009, Lewis et al. 2009, Lloyd et al. 2009), which suggests, according to simulations, that large, rare mortality events do not cause biases in biomass estimate given reasonable sample sizes, and therefore such events do not dominate the dynamics of these regions. Indeed, for these regions $\sim$20 small plots (0.25 ha each) monitored for just one year should produce unbiased biomass change estimates (Fisher et al. 2008).

In reality, far larger sample sizes are available. For example, **Table 1** reports results from 10 areas from across the tropics, each monitoring an average of 16 ha for 14 years each, and Lewis et al. (2009) presented biomass data from 156 plots (562 ha total area, total monitoring period 1649 years). Thus, the conclusion that a large-scale shift in the ecology of tropical forests is occurring appears robust, regarding this potential sampling bias. Moreover, the observed increase in forest biomass has arisen from biomass additions from species with a range of differing ecological habits, which is not a pattern one would expect if forests were exclusively recovering from past disturbances. Likewise, the increases in tree growth and stem density documented are not expected as signatures in the data that would be anticipated if recovery from disturbance were the cause of the changes documented.

A second concern is that some plots might not have been placed at random within landscapes. Instead, it has been suggested that some researchers may have had specific criteria, such as avoiding large gaps or regenerating areas or placing plots in "representative" areas of forest. Both strategies could cause biases. For example, avoiding large gaps can lead to underestimates of average biomass increase across plots, because parts of a forest that are accruing biomass most rapidly are omitted. Alternatively, placing plots in "representative" forest can mean choosing attractive forest areas with many large trees, the so-called majestic forest bias, that may tend to lose biomass over time, as large, high-biomass trees die and are replaced by smaller trees. Explicit tests that have excluded plots from analyses that were not placed at random within landscapes show that this potential bias is not the cause of the observed trends in forest biomass or other parameters published to date (Lewis et al. 2009, Phillips et al. 2004). Thus, in summary, neither limited sample sizes nor nonrandom plot placement appears to have seriously biased current plot networks, and the general conclusion of concerted, widespread, and directional shifts in the ecology of tropical forests appears robust to these potential biases.

ECOSYSTEM FLUX STUDIES

Towers built above the forest canopy with sensors to measure the movement of CO_2, known as eddy-covariance or micrometeorological techniques, can help to determine the carbon balance of 50–100 ha of forest, the "footprint" of the sensor. Observations using these techniques have

suggested that tropical forests are either a moderate carbon sink of 1.0 Mg C ha^{-1} a^{-1} (Grace et al. 1995, 1996); a much larger sink, of up to 5.7 C Mg ha^{-1} a^{-1} (Araujo et al. 2002, Carswell et al. 2002, Malhi et al. 1998); or a source of 1.3 Mg C ha^{-1} a^{-1} (Saleska et al. 2003). Large budget discrepancies have even been documented over time within the same site: Loescher et al. (2003) showed that the forest at La Selva was neutral in 1998 (-0.05 Mg ha^{-1} a^{-1}), a moderate sink in 1999 (1.5 Mg ha^{-1} a^{-1}), and a very large sink (6.0 Mg ha^{-1} a^{-1}) in 2000. This is striking as the growth rates of trees within the same forest in the same years contrast sharply with these results (Clark et al. 2003). The potentially serious problem with this technique is the apparent failure of measurement systems to capture CO_2 efflux on calm nights, with no community agreement on when this creates a problem or how to correct it (Houghton et al. 2009, Lloyd et al. 2007, Loescher et al. 2006). Therefore, although useful for tackling many ecological questions, eddy-covariance studies do not yet provide sufficiently robust evidence to assess whether systematic changes in the ecology of tropical forests have occurred.

EARTH OBSERVATION

Satellite remote sensing can be used to detect many changes in tropical forests, because the spectral characteristics, backscatter, and texture of optical, lidar (LIght Detection And Ranging) and radar remote sensing images can indicate changes in forest productivity, structure, and dynamics (Chambers et al. 2007). However, few studies have attempted to detect widespread temporal changes in tropical forests.

Relatively coarse-scaled AVHRR data (1 km^2 resolution) have, however, been used to parameterize models of changes in forest productivity, though their reliability is questionable given their limited ground-truthing. The absolute magnitude of predicted changes in the tropics (20°N to 20°S) is consistent between two major global studies, with estimates of NPP increasing by 0.41% a^{-1} (Nemani et al. 2003) from 1982–1999 and 0.48% a^{-1} (Cao et al. 2004) from 1981–2000. However, these studies differed in what they viewed as the most important driver: increases in the concentration of atmospheric CO_2 (Cao et al. 2004), or increased solar radiation caused by a reduction in cloud cover (Nemani et al. 2003).

Weishampel et al. (2001) compared textural metrics derived from Landsat images in the mid-1970s and mid-1980s across Africa, South America, and South-East Asia, reporting a highly significant increase in the average size of aggregations and entropy (the degree of inverse correlation between neighboring pixels) in the later time period. The authors interpret this as a result of forests becoming more dynamic and increasing in biomass, with more emergent trees and thus more shadows, and more large canopy gaps (Weishampel et al. 2001). This paper was criticized because data had been compared from different sensors (Wright 2006), although, in fact, the sensors on the differing Landsat missions were identical (Cohen & Goward 2004). Nonetheless, caution is required in interpreting these data as the dominant aggregations identified were considerably larger than most canopy gaps. Thus, although it seems likely that forest structure has changed over time, it is impossible to know exactly how (Malhi & Roman-Cuesta 2008). At a much smaller scale (444 ha), in La Selva, lidar was used to assess changes in canopy height over an 8.5-year period, but with little change detected (Kellner et al. 2009). Overall, the limited Earth observation studies are consistent with the plant physiological and forest inventory approaches, suggesting that large-scale directional changes are occuring in the ecology of tropical forests.

ATMOSPHERIC OBSERVATIONS

Surface fluxes of CO_2 result in the accumulation or depletion of this gas in the overlying air. Thus, if air movement can be understood then a combination of atmospheric CO_2 concentration data

and models of atmospheric transport can, in principle, be used to estimate surface fluxes and how they change over time. Such approaches, known as inverse methods, have been used to estimate fluxes at coarse resolutions such as the terrestrial tropics. The net flux of CO_2 over the terrestrial tropics can then be estimated by subtracting the carbon flux from land-use change (1.6 Pg C a^{-1}; Denman et al. 2007) to assess the carbon balance of tropical land and potential directional changes.

Unfortunately, results from inverse methods vary significantly and are inconclusive. For example, inversions over the period 1992 to 1996 have shown, after accounting for fluxes from land-use change, three distinct patterns: (*a*) no appreciable net carbon uptake in the terrestrial tropics (Gurney et al. 2002), (*b*) a globally significant net carbon uptake in the terrestrial tropics of >1 Pg C a^{-1} (Rodenbeck et al. 2003, Stephens et al. 2007), and (*c*) a globally significant net carbon source to the atmosphere of >1 Pg C a^{-1} (Jacobson et al. 2007).

These results are highly uncertain because (*a*) the atmosphere is poorly sampled, especially in the main tropical forest areas; (*b*) models of atmospheric transport are uncertain; (*c*) flux estimates are sensitive to biases and uncertainties in both data and modeled transport; and (*d*) data to calibrate air transport in models are sparse (Houghton et al. 2009). Although it is encouraging that new sampling programs in the tropics are currently being initiated, the atmospheric approach has yet to yield conclusive results regarding the tropical land-carbon balance, and therefore any changes in the ecology of tropical forests.

MODELS OF VEGETATION RESPONES TO GLOBAL CHANGE

Dynamic Global Vegetation Models (DGVMs) are representations of terrestrial vegetation designed to produce spatially explicit stores and fluxes of carbon and water inside global circulation models. They also predict the distribution of different vegetation types and how they change in a changing environment. Typically, DGVMs aggregate plant species into a small set of plant functional types, but differ in the processes they include and how they are represented (Prentice et al. 2007, Sitch et al. 2008). As an aid to understanding the differences among the main models and how they represent tropical plant communities, we summarize their characteristics in **Supplemental Table S1**. (Follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org.**)

A recent DGVM model intercomparison project used monthly twentieth-century climate and annual global atmospheric CO_2 concentration data to drive five DGVMs over the late-twentieth century to compare predictions in terms of carbon storage and vegetation change caused by light, water, CO_2, and air-temperature changes for the world's terrestrial land surface (Sitch et al. 2008). The results suggest a global carbon uptake of 1.3 to 1.7 Pg C a^{-1}, depending upon the model (mean = 1.6 Pg C a^{-1}) in the 1980s, and 1.5 to 2.8 Pg C a^{-1} (mean = 2.3 Pg C a^{-1}) in the 1990s in vegetation. This is in good agreement with estimates from the IPCC based on measurements of 1.7 and 2.6 Pg C a^{-1} in the 1980s and 1990s, respectively, for the residual terrestrial carbon sink (Denman et al. 2007). These findings suggest a directional shift toward increasing carbon storage in at least some of the world's vegetation.

Sitch et al. (2008) published all the DGVM model runs (available at **http://www.dgvm. ceh.ac.uk/**), allowing us to assess whether predicted trends are similar to those found in the long-term forest plots. We selected only the grid cells where both the individual DGVM simulates, and the Global Land Cover 2000 classification (Bartholome et al. 2002) indicates, >75% woody coverage within 15°S–15°N latitude. The DGVM results show an average increase in vegetation carbon of 0.35 Mg ha^{-1} a^{-1} (range 0.22–0.62) for the pan-tropics over the period 1980–2000 (**Figure 2**). This is smaller, but of similar magnitude to the 0.49 Mg C ha^{-1} a^{-1} pan-tropical average increase documented from forest inventory data (Lewis et al. 2009). This
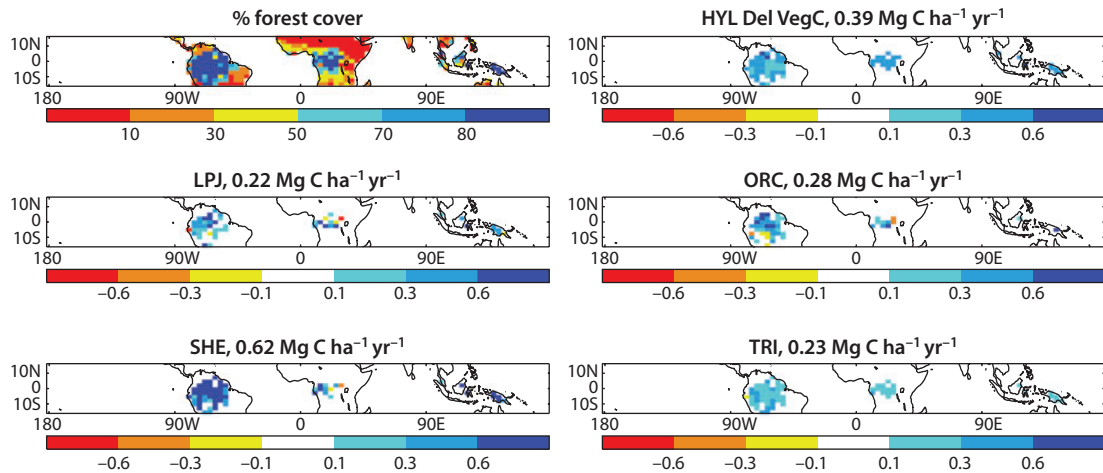
Figure 2

Change in tropical vegetation carbon over the period 1980–2000 for five Dynamics Global Vegetation Models, and reference Global Land Cover 2000 map (Bartholome et al. 2002). Units are in Mg C ha^{-1} a^{-1}.

is largely due to an average increase in simulated Gross Primary Productivity, due to improved growing conditions across the tropics, caused by increasing atmospheric CO_2, a moderate increase in temperature, a small increase in irradiance, and changes in rainfall in some areas (Sitch et al. 2008). The among-DGVM variability in simulated productivity is likely due to (*a*) their differential response to increasing atmospheric CO_2, as DGVMs that show the largest CO_2-fertilization effect (Sitch et al. 2008) also show the largest increases in plant productivity from 1980–2000 (Sitch et al. 2008; **Figure 2**); and (*b*) model differences in allocation and turnover rates, which affect the proportion of increased productivity that translates into vegetation carbon. Overall, each of the five DGVMs simulates large-scale changes in the ecology of tropical forests over 1980–2000 when driven by known twentieth-century increases in atmospheric CO_2 concentration and well-characterized meteorological data.

FINGERPRINTS OF DRIVERS OF CHANGE

From our literature review we draw four conclusions. First, experiments and theory suggest that plant photosynthesis should have increased in response to increasing CO_2 concentrations, causing increased plant growth and forest biomass, partially offset by decreases in growth from increasing air temperatures increasing the carbon required for respiration. Second, long-term plot data collectively indicate an increase in carbon storage, as well as significant increases in tree growth, mortality, recruitment, and forest dynamism (**Table 1**). Third, satellite measurements also indicate increases in productivity and forest dynamism, although the number of available studies is small. Finally, five DGVMs, incorporating plant physiology, competition, and dynamics, all predict increasing gross primary productivity, net primary productivity, and carbon storage when forced using late-twentieth century climate and atmospheric CO_2 concentration data. Notably, the predicted increases in carbon storage via the differing methods are all of similar magnitude (0.2% to 0.5% a^{-1}).

Collectively, these results point toward a widespread shift in the ecology of tropical forests, characterized by increased tree growth and accelerating forest dynamism, with forests, on average,

getting bigger (increasing biomass and carbon storage). The gain terms (growth, recruitment) show clearer increases (statistically more significant) than the loss terms (mortality), and the increase in the loss terms appears to be lagging behind the increase in the gain term. This suggests that, among potential environmental changes, those that could increase plant growth pan-tropically are the most likely drivers. These are increases in rainfall, increases in nutrient deposition, air-temperature increases, changes in incoming solar radiation, and increases in atmospheric CO_2 concentration.

The pan-tropical trend in rainfall is negative, not positive, so it is unlikely to be the main cause of the widespread increases in forest biomass and dynamism (Malhi & Wright 2004). Similarly, there is little evidence that nutrient deposition (N and P), largely from biomass burning, has increased, as biomass burning over the twentieth century may have even decreased (Marlon et al. 2008), and tropical deforestation rates have not changed markedly over recent decades (Achard et al. 2002, Ramankutty et al. 2007). However, it is conceivable that nutrient inputs into remaining forests from biomass burning are increasing as once-remote forests are increasingly encroached upon by deforestation (Laurance 2005). In addition, long-range inputs of Saharan dust to both African and the Latin American forests may have increased over recent decades, possibly in response to climate change (Engelstaedter et al. 2006). This provides an intriguing possibility as to why the increases in biomass appear larger in South America and Africa compared to SE Asia.

Average air temperatures have increased over the tropics, but such increases are usually hypothesized to decrease tree growth, not increase it (Clark et al. 2003, Feeley et al. 2007). Yet, if increasing soil temperatures increase soil-nutrient mineralization rates and other chemical reactions, then it is conceivable that air temperatures might actually increase tree growth and biomass, although most evidence points to lower growth with rising temperatures due to higher allocation of scarce carbon to respiration, all else being equal. However, African forests are cooler, on average, than South American forests, which could explain the larger increase in biomass per unit area in Africa compared to South America (Lewis et al. 2009, Phillips et al. 2009) as these cooler forests are presumably further from any high-temperature threshold affecting photosynthesis.

The remaining potential drivers are changes in incoming solar radiation, its direct:diffuse ratio, and increases in atmospheric CO_2 concentrations. It is difficult to separate these based on available data, particularly as CO_2 increases are relatively uniform and changes in solar radiation are poorly understood. It seems reasonable to conclude that the large-scale, consistent, and directional changes in tropical forests are most likely to have been caused by an increase in resource availability, with leading candidates being increasing atmospheric CO_2 concentrations, possibly in concert with increases in incoming solar radiation, the direct:diffuse ratio, and perhaps nutrient deposition rates.

Our interpretation of changes in tropical forest carbon storage and dynamism, and our conclusions regarding the most plausible drivers, differs conspicuously from some other recent studies. For example, Wright (2005) and Muller-Landau (2009) have suggested that biomass accumulation in forest plots might best be explained by recovery from recent past disturbances, whereas Clark et al. (2003), Clark (2004), and Feeley et al. (2007) have argued that forest carbon storage should likely decline, not increase, because rising air temperatures will increase plant respiration costs and thereby decrease plant growth. We compared predictions from these hypotheses with results from long-term forest plot data (**Table 1**) and the evidence from other techniques, but found little evidence in support of them.

Alternative explanations exist for individual results that contradict the increasing resource availability hypothesis. For example, Chave et al. (2008) plausibly believe that the declining tree growth observed at Pasoh, also documented by Feeley et al. (2007), was likely caused by the 1997–1998 ENSO drought. Alternatively, SE Asian forests may be affected by acid depositions from rapid regional industrialization, which may decrease tree growth rates (Lewis et al. 2004a). However,

respiration-driven tree growth declines at La Selva (Clark et al. 2003) are inconsistent with the finding that wood respiration did not covary with large seasonal temperature changes over a two-year period in the same forest (Cavaleri et al. 2006). Similarly, it is difficult to account for the observed widespread increases in wood production (stand-level basal-area growth) if the principal driver were forest succession following widespread past disturbance (Lewis et al. 2004b, 2006a). This is not to dismiss recovery from disturbance as an important process operating on small scales in certain areas, nor to suggest that plant respiration costs do not increase with rising temperatures; we merely note that these are unlikely drivers of the large-scale changes in tropical forests documented over recent decades using a variety of techniques.

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