PHILOSOPHICAL
TRANSACTIONS
OF
THE ROYAL
SOCIETY B

FirstCite®
e-publishing

Phil. Trans. R. Soc. B
doi:10.1098/rstb.2005.1711

Review

Tropical forests and the changing earth system

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Tropical forests are global epicentres of biodiversity and important modulators of the rate of climate change. Recent research on deforestation rates and ecological changes within intact forests, both areas of recent research and debate, are reviewed, and the implications for biodiversity (species loss) and climate change (via the global carbon cycle) addressed. Recent impacts have most likely been: (i) a large source of carbon to the atmosphere, and major loss of species, from deforestation and (ii) a large carbon sink within remaining intact forest, accompanied by accelerating forest dynamism and widespread biodiversity changes. Finally, I look to the future, suggesting that the current carbon sink in intact forests is unlikely to continue, and that the tropical forest biome may even become a large net source of carbon, via one or more of four plausible routes: changing photosynthesis and respiration rates, biodiversity changes in intact forest, widespread forest collapse via drought, and widespread forest collapse via fire. Each of these scenarios risks potentially dangerous positive feedbacks with the climate system that could dramatically accelerate and intensify climate change. Given that continued land-use change alone is already thought to be causing the sixth mass extinction event in Earth's history, should such feedbacks occur, the resulting biodiversity and societal consequences would be even more severe.

Keywords: review; deforestation; carbon cycle; biodiversity; fire; climate change

1. INTRODUCTION

Human-induced changes to the atmosphere and biosphere have reached the point where scientists now refer to a new geological epoch: *the Anthropocene* (Crutzen 2002). The twentieth century saw fossil fuel use and land-use changes increase atmospheric carbon dioxide concentrations by 25%, while global average air temperatures increased by 0.6 °C (IPCC 2001). Humans moved more rock, sediment and soil than all natural processes combined, by an order of magnitude (Wilkinson 2005). Between a third and half of all land was appropriated for human use (Vitousek *et al.* 1997; Rojstaczer *et al.* 2001). By the century's end three to six times as much water was held in reservoirs as in natural rivers (Reid *et al.* 2005). Global-scale biological responses proceeded apace, with shifts in phenology, composition, productivity and evolutionary processes (Thomas *et al.* 2001; Parmesan & Yohe 2003; Lewis *et al.* 2004*a*; Stuart *et al.* 2004; Reid *et al.* 2005). The diversity of life was reduced (Myers *et al.* 2000; Gaston *et al.* 2003; Reid *et al.* 2005). Without a doubt these were epoch-making times.

The twenty-first century is likely to witness many of these changes accelerating and intensifying, potentially rivalling the major perturbations in Earth's history. Two predictions stand out: changes in land-use will cause the sixth mass extinction in evolutionary history (Myers *et al.* 2000; Pimm & Raven 2000), while atmospheric CO_2 concentrations will reach their highest levels for 60 million years (Royer *et al.* 2001), causing further temperature rises (IPCC 2001), and possibly abrupt climatic shifts (Alley *et al.* 2003). This is illustrated by considering atmospheric carbon dioxide concentrations over the past 400 thousand years, current levels, and projected future levels (figure 1).

Given that everyone, without exception, ultimately depends on Earth's ecosystems and services for food, water and the physical basis of their cultures, understanding these diverse phenomena and their interactions—understanding the complete Earth system as an integrated whole—is essential if policy-makers and civil society are to have the opportunity to politically address these major environmental and societal challenges.

The atmosphere, oceans, terrestrial ecosystems and the dominant mammal—*Homo sapiens*—all interact in highly complex ways. Changes in one component affect the behaviour of the others. These changes are often characterized by nonlinear responses, complex feedback mechanisms and threshold changes. Understanding the links between components is, therefore, critical. For example, the rise in atmospheric carbon dioxide concentrations from fossil fuel use, and the resulting increases in air temperatures, and their impacts on the Earth system and human welfare, can only be understood by understanding the complete global carbon cycle, including the oceanic, atmospheric and terrestrial components and how carbon moves between them.

This paper synthesizes recent research on one key component of the changing Earth system: tropical

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Received 14 April 2005
Accepted 7 July 2005

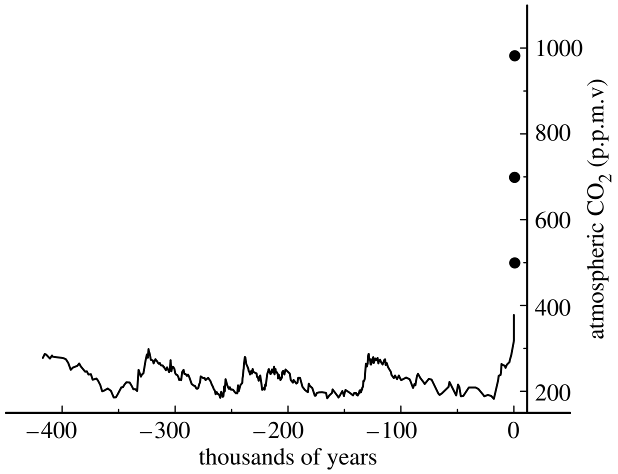

Figure 1. Atmospheric carbon dioxide concentrations from the Vostok ice core, East Antarctica (Petit *et al.* 1999), and present day direct measurements from Mauna Loa, Hawai'i (Keeling & Whorf 2004). The three dots represent double pre-industrial CO_2 concentrations, estimated concentrations in 2100 from the HAD3 global circulation model, both uncoupled and coupled versions, in ascending order. 'Coupling' describes the inclusion of dynamic vegetation that is responsive to climatic changes. Part of the difference between the models is due to differences in the future behaviour of tropical forests (Cox *et al.* 2000, 2004).

forests. Tropical forests cover only *ca* 10% of the Earth's land surface, but are of global importance, as they store and process large quantities of carbon—processing, via photosynthesis and respiration, approximately six times as much carbon as humans release into the atmosphere through fossil fuel use—and house between one-half and two-thirds of the world's species (Malhi & Grace 2000; Groombridge & Jenkins 2003). Thus, small changes within the tropical forest biome can potentially lead to major global impacts on both the rate and magnitude of climate change and the conservation of biodiversity.

The paper proceeds in three parts. Following a brief introduction to tropical forests, I firstly, review recent research on changes across the tropical forest biome focusing on two key aspects, land-use change (deforestation) and changes within remaining intact forest. Secondly, I look at the impacts of these changes on biodiversity and on the global carbon cycle, and hence the rate and magnitude of climate change. Finally, I consider some plausible future scenarios for tropical forests in a globally changing world, with potentially important societal impacts.

2. TROPICAL FORESTS: A BRIEF INTRODUCTION

Tropical forests circle the Earth around the equator. A consistent, precise and universal definition of 'tropical forest' is difficult to arrive at, as there are continua, both physical and biological, to sub-tropical, savanna and woodland systems, which are open to interpretation. A simple definition, used by the United Nations Food and Agriculture Organisation (FAO), is to couple the definition of 'forest': 'land with a tree canopy cover of more than 10%, >5 m (metres) tall, covering an area of more than 0.5 ha (100×100 m)', with the definition of 'tropical', i.e. between the tropics of Cancer and Capricorn. This includes a very diverse array of forests, including moist or rain forests, mangroves, montane forests, dry forests and wooded savanna systems. Recent FAO estimates are that there were 1803 million ha of tropical forest in 2000, 49% in tropical America, 34% in tropical Africa and 16% in tropical Asia (from country estimates; FAO 2001; also see figure 2).

Many studies refer to tropical rain forests, or moist, or humid tropical forests, often used interchangeably to refer to natural forests characterized by relatively dense stands of relatively tall mostly evergreen broadleaf trees, with a closed canopy usually composed of a high diversity of tree species. The climate is usually wet, with >1.5 m of rainfall annually, but with not more than 6 months with <0.1 m rainfall per month. There are usually 300–700 trees >0.1 m diameter (at 1.3 m height) in 1 ha, with a canopy 20–50 m tall, and 50–300 species >0.1 m diameter in 1 ha (Malhi *et al.* 2002; Ter Steege *et al.* 2003). Other characteristics include many trees with relatively large leaves and often with large buttresses, alongside abundant palms, climbing plants, epiphytes and hemi-epiphytes. Animal diversity, particularly insects, is also high (Odegaard 2000), although little is known about many organisms and processes (e.g. Ellwood & Foster 2004). Recent FAO estimates are that there were 1172 million ha of tropical humid forest in 2000, 56% in tropical America, 19% in tropical Africa and 26% in tropical Asia (from country estimates; FAO 2001; also see figure 2).

Tropical forests occur on a variety of different soil types (Malhi *et al.* 2004), but infertile soils, from an agricultural point of view, predominate (Vitousek & Sandford 1986). Despite the often infertile soils, tropical forests are highly productive systems, with above-ground net primary productivity (NPP) estimated to be *ca* 9 Mg C ha^{-1} a^{-1}, on average, for Amazonian humid forests (1 Mg = 1 metric tonne; C, carbon; a, annum; Malhi *et al.* 2004). Nutrient limitation is often not what might be expected as there is often a virtually closed cycling system, where nutrients are stored in tree biomass and move from fallen leaves back to the biomass extremely quickly via a host of adaptations (Jordan 1985).

Tropical forests are of great importance to people. They provide the homes, sustenance and cultural basis for many of the world's remaining semi-nomadic hunter-gather groups, such as the Yanomami of Amazonia and the Baka (one of the so-called 'pygmy' groups) of central Africa. Furthermore, they provide food, building materials, medicines and other products for millions of people across the tropics (Prance 2002; Lawrence *et al.* 2005; Reid *et al.* 2005). Beyond this, evapotranspiration from forests contributes to rainfall, and alters cloud cover and soil moisture (Betts 2004; Chagnon *et al.* 2004). This is of benefit not only to the forest, but also to crop growth in small forest clearings. At a larger scale, tropical forests affect climate and vice versa, thus this broad vegetation class, or biome, affects global climate (Betts 2004; Delire *et al.* 2004).

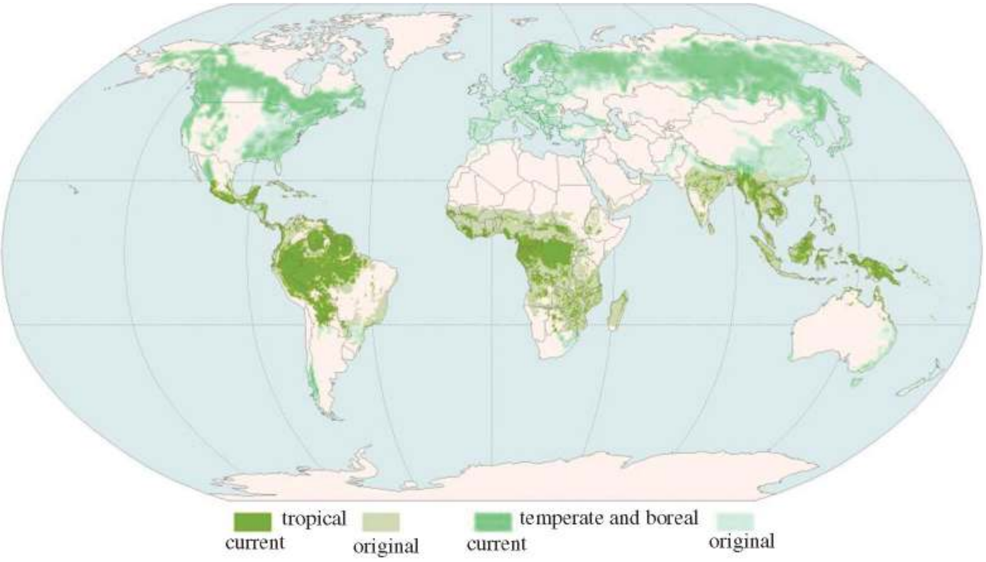

Figure 2. Distribution of tropical forests *ca* 8000 years ago and in the late twentieth century.

3. TROPICAL FORESTS: CHANGES OVER RECENT DECADES

The most dramatic change to occur to a tropical forest is conversion to some other land-use. The most common changes are to subsistence farming, or to cattle ranches, soya farms or palm oil plantations for capital gains. While other changes are common, such as timber extraction, increasing hunting pressures and habitat fragmentation, I focus here on changes in land-use across the tropics—specifically deforestation—and ecological changes in remaining intact forest. This is because the high diversity and carbon-dense nature of tropical forests means that deforestation of relatively small areas *on a global scale* may have important global impacts, while much more subtle changes over much larger areas of forest that remain intact may have equally important global impacts. I omit reviewing the effects of logging, as while it is a major feature—58, 19 and 28% of Asian, African and Latin American tropical forest, respectively, are estimated to have already been commercially logged by the mid-1990s (Johns 1997)—the new access to the forest that logging provides usually means other land-use changes follow in time (Laurance & Cochrane 2001). Thus, logged-forest is often a transitional state to further degradation and eventual forest loss.

(a) *Land-use change*

It is remarkable how little is known about the rate of tropical deforestation, the conversion of natural forest to other land-uses. Over a long timeframe, since the emergence and spread of agriculture, it is often quoted that between 25 and 50% of the world's tropical forest has been converted to other uses, although studies are scarce (figure 2; Pimm & Raven 2000; Ball 2001; Houghton 2003*a*; Reid *et al.* 2005). Over a much shorter timeframe, the UN Food and Agriculture Organisation provides what have been considered the bench-mark figures, stating that 14.2 million ha a^{-1} was lost over the 1990s (FAO 2001). Recently, two studies have given substantially lower figures, of 8.4 million ha a^{-1} (Achard *et al.* 2002, 2004) and 5.6 million ha a^{-1} (DeFries *et al.* 2002), for similar definitions of 'tropical forest'. There is no consensus as to which is the most accurate figure.

All three studies are very different from one another, both in terms of methods and results. The FAO estimates are from countries' governments, and expert opinion where official figures are unavailable. The FAO estimates seem unlikely to be systematically biased upwards, as it is unclear why some governments would inflate deforestation figures. Any bias is likely to be in the opposite direction as low deforestation rates play well with the international community. However, the use of secondary information, expert opinions and sometimes outdated data, given the lack of monitoring in many countries with tropical forest, all contribute to uncertain estimates (FAO 2001).

The Achard *et al.* (2002, 2004) studies are based on high-resolution satellite images covering 6.5% of the tropics, stratified towards deforestation 'hotspots' as defined by experts. Satellites measure visible and infrared light which can be converted into data on forest cover, as different vegetation gives different imagery. Thus, comparing the same location a few years later it is possible to make an estimate of how much less primary forest there is in the second image. It is possible that there is some underestimation of deforestation rates as: (i) the sampling may not adequately capture the highly spatially aggregated distribution of deforestation. Tucker & Townshend (2000) show sampling issues are critical: sampling 90% of an area may be required to estimate deforestation rates within ±20% of the actual rate; (ii) satellite images present difficulties in detecting forest loss when new vegetation rapidly replaces deforested areas, which may then be difficult to distinguish from forest in the later image and (iii) small clearings, where the largest trees remain, can be difficult to classify (in areas where farmers lack capital to access chainsaws and, therefore, leave the biggest trees when converting forest to subsistence agriculture). Thus, studies based on satellite images are likely to underestimate the rate of loss of primary forest (but estimate *net* changes in forest *cover* well). The Achard *et al.* (2002) results are consistently 0.5 million ha a^{-1} lower than the comparable FAO figures for each continent.

The Achard *et al.* satellite studies do not include the forest loss from the massive fires associated with the 1997–1998 El Niño southern oscillation (ENSO) event, as they compare 1990 with 1997. Cochrane (2003) estimated that >20 million ha of tropical forest burned during the 1997/1998 ENSO event. Thus if (i) most of these fires were established deliberately to clear land and (ii) many FAO country reports and expert opinions included these ENSO-associated fires, where Achard *et al.* (2002) did not, then these fires may explain some of the difference between the Achard and FAO figures. Unfortunately it is unclear how the 20 million ha of burnt tropical forest estimate was derived, or which FAO country reports include which year, or exact protocols for estimating deforestation rates when country reports did not span 1990–1999. Overall, the Achard *et al.* (2002) figures for the humid tropics are 1.5 million ha a^{-1} less than the FAO figures. If the 1997–1998 ENSO fires destroyed 15 million ha^{-1} of forest within the humid tropics, then there is no discrepancy between the FAO and Achard *et al.* figures. Given that 1.2 million ha burnt in a single Brazilian state, Roraima (Barbosa & Fearnside 1999), in addition to the well-known widespread South East Asian fires (Siegert *et al.* 2001; Page *et al.* 2002), this appears a plausible explanation of the differences.

The second recent study, showing substantially lower deforestation rates of 5.6 million ha a^{-1}, is DeFries *et al.* (2002). This is based on coarse-resolution (8 km^2) satellite data, calibrated with high-resolution satellite data to identify the small clearings not detectable with the coarse-resolution data. Thus, this is likely to be less reliable than the estimates of Achard *et al.* (2002, 2004). The problems with this method appear greatest in tropical Africa, where according to DeFries *et al.* (2002) there is little deforestation (0.4 million ha a^{-1}; <0.1% a^{-1} forest loss). This is unlikely to be the case: it would not have escaped peoples' attention if deforestation almost ceased for a decade! The predominantly drier African forests, mixed with areas of savanna, and the dominance of minimal capital-investment subsistence agriculture, not major clearing for industrial farming or plantations, are probably causing the major differences in the DeFries *et al.* (2002) study compared to others. Three other independent satellite studies report African deforestation figures for the 1990s of an order of magnitude higher and very similar at 0.4% a^{-1} forest loss (FAO 2001; Achard *et al.* 2002, 2004; Zhang *et al.* 2005).

Overall, despite the 'headline news' of much lower than thought deforestation rates, the DeFries *et al.* (2002) paper does not seem robust, as the claims for Africa, at least, are difficult to reconcile with other studies or my own views from planes flying over West and Central Africa. The Achard *et al.* (2002) paper compares a portion of a decade of deforestation (1990–1997), but is often erroneously compared to FAO (2001) figures from the entire decade. Achard *et al.* (2002) missed *the* major deforestation event of the decade, the 1997–1998 ENSO event. Inclusion of the ENSO years may remove some of the differences between the FAO and Achard *et al.* (2002, 2004) figures. This appears plausible as the loss of 15 million ha of forest each releasing an average of 150 Mg C ha^{-1}, would add 2.3 Pg C to the atmosphere, meanwhile atmospheric CO_2 concentrations increased by ~3 Pg in 1998 over-and-above the ~2.5 Pg increases immediately before and after the ENSO event, consistent with major forest loss during the 1997/1998 ENSO event. However, given the lack of details regarding the relationship between ENSO fires and land clearance this is open to interpretation. Thus, careful interpretation of deforestation figures, not just the headline figures, is necessary, especially for such policy-relevant parameters. The higher FAO figures, on closer inspection, may be reasonably consistent with the Achard *et al.* (2002) satellite data. However, there is a clear need for major investment in monitoring African tropical forests and the role of fire, particularly those of anthropogenic origin, in tropical forest systems.

(**b**) ***Intact forest***

Tropical ecologists have tended to view remote tropical forests, far from areas of deforestation and direct human contact, as pristine, 'virgin' forests. Recent research over the past decade has profoundly altered that perception. Remaining tropical forests are almost certainly undergoing major shifts in structure, dynamics, productivity and function, as the physical, chemical and biological environment that forest species occur in has altered appreciably over recent decades (Lewis *et al.* 2004*a*,*b*).

Most information on changes in tropical forest structure, dynamics, productivity and function has come from the long-term monitoring of tropical tree populations, within permanent sample plots (e.g. Lewis *et al.* 2004*a*). However, satellite data (Weishampel *et al.* 2001), micrometerological measurements (Grace *et al.* 1996) and direct measurements of atmospheric carbon dioxide concentrations and atmospheric transport models (Rodenbeck *et al.* 2003) also suggest that the ecology of remaining intact tropical forests has altered.

Long-term monitoring allows changes in forest stand growth, recruitment and mortality rates to be calculated. Furthermore, by using allometric equations tree diameter measurements can be converted to biomass, and carbon content, to ascertain if intact tropical forests are currently a carbon sink, source, or are neutral, and hence how they modulate the rate and magnitude of climate change.

Amazonian forests are showing structural changes. Over approximately the last 20 years, long-term monitoring of 59 plots showed that above-ground biomass increased by 0.6 ± 0.2 tonnes C ha^{-1} a^{-1}, or a relative increase of $0.50 \pm 0.17\%$ a^{-1} (mean ± 95% confidence interval; Baker *et al.* 2004*a*). Across all plots, the above-ground biomass change is normally distributed and shifted to the right of zero (figure 3). This estimate is slightly higher than that documented by Phillips *et al.* (1998) using a smaller and earlier dataset, which provoked much debate at the time.

The original increasing biomass result was initially challenged as being an artefact of poor quality tree measurements, and the location of some plots in areas

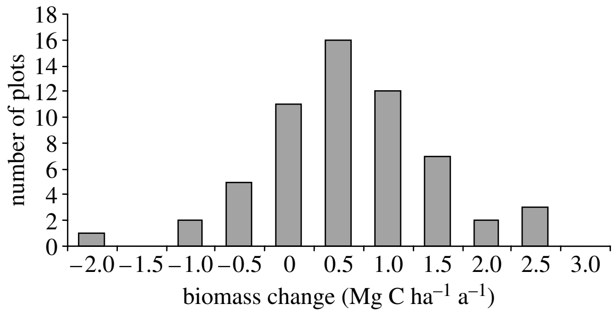

Figure 3. Frequency distribution of biomass change, from 59×1 ha plots from across Amazonia. Includes corrections for wood density, lianas and plants <100 mm diameter (from Baker *et al.* 2004*a*,*b*). 1 Mg = 1 metric tonne.

some considered to be still undergoing primary succession. A reanalysis by Clark (2002) of the original dataset (Phillips *et al.* 1998) showed no increase in biomass. Various additional analyses asserted that Clark's claims were either incorrect or led to minor adjustments (Phillips *et al.* 2002*a*). The wider community appeared unconvinced by either set of propositions (e.g. Houghton 2003*b*). In response, the individual measurements of >60 000 trees were manually checked, the dataset of plots across Amazonia extended through the development of new collaborations and extensive field campaigns (Malhi *et al.* 2002), and the plots that Clark (2002) viewed as problematic removed from certain analyses. The original increasing biomass results were confirmed (Baker *et al.* 2004*a*, cf. Phillips *et al.* 1998).

Amazonian forests are also showing changes in dynamics. Trees are recruited into a population, grow, and eventually die. Thus, how dynamic a forest is can be calculated from the rate at which stems are added (stem recruitment), and are lost (stem mortality), over time. However, most surviving trees grow, thus gaining biomass, and eventually die. Therefore, the stand-level rate of 'biomass growth' and 'biomass loss' can also be calculated. Among 50 old-growth plots across tropical South America with at least three repeated tree measurement censuses (and, therefore, at least two consecutive monitoring periods that can be compared), stem recruitment, stem mortality, and biomass growth, and loss, *all* increased significantly (figure 4; Lewis *et al.* 2004*a*). Thus, over the past two decades, these forests have shown concerted changes in their ecology, becoming, on average, faster growing—more productive—and more dynamic, and showing a net increase in above-ground biomass.

While concerted changes across forests in South America have been shown, the picture from the rest of the tropics is less clear because of a lack of analyses. However, across the paleotropics forest dynamism has been steadily increasing for five decades (Phillips & Gentry 1994). Preliminary analyses also suggest the African and Australian forests are showing structural changes similar to South American forests (Lewis *et al.* in preparation).

What is causing this suite of concerted changes across, at least, South American tropical forests? The results appear to show a coherent fingerprint of increasing NPP across tropical South America, caused by a long-term increase in resource availability (Lewis *et al.* 2004*a*,*b*). It has been suggested that increasing resource availability increases NPP which then increases stem growth rates. This accounts for the increase in stand-level biomass growth and stem recruitment rates, and the fact that these show the 'clearest' signals (statistically most significant) in the analyses (Lewis *et al.* 2004*a*). 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. Thus, the system gains biomass and stems while the losses lag some years behind, causing the increase in above-ground biomass and stems. Overall, this suite of changes documented may be qualitatively explained by a long-term increase in a limiting resource.

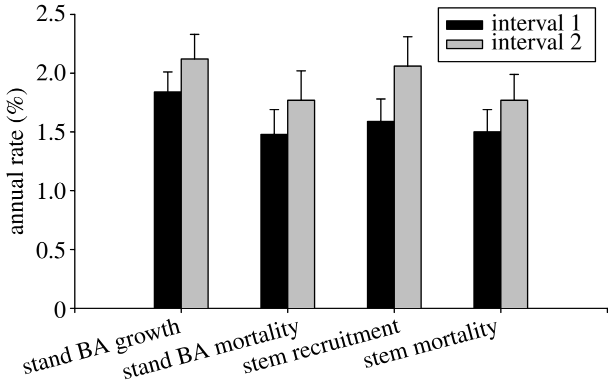

Figure 4. Annualized mean rates of stand-level basal area growth, stand-level basal area mortality, stem recruitment and stem mortality from two consecutive census intervals, from 50 plots from across South America, with 95% confidence intervals (from Lewis *et al.* 2004*a*). The average mid-year of the first and second censuses was 1989 and 1996, respectively. All four parameters show significant increases ($p<0.05$).

Which plant resource(s) are increasing in availability across South America? While there have been widespread changes in the physical, chemical and biological environment that tropical trees grow in (Lewis *et al.* 2004*b*), only increasing atmospheric CO_2 concentrations (IPCC 2001; Keeling & Whorf 2004), increasing solar radiation inputs (Wielicki *et al.* 2002), rising air temperatures (IPCC 2001; Malhi & Wright 2004), and nutrient depositions (Artaxo *et al.* 2002; Galloway *et al.* 2002) have been documented across South America and could conceivably increase resource supply rates. However, for none of these environmental changes do we have good evidence that the driver has actually changed *and* that such a change will increase forest NPP, growth and dynamism (Lewis *et al.* 2004*b*).

The most parsimonious explanation is the increase in atmospheric CO_2, because of the undisputed long-term historical increase in CO_2 concentrations, the key role of CO_2 in photosynthesis, and the demonstrated positive effects of CO_2 fertilization on plant growth rates including experiments on whole temperate-forest stands (Ainsworth & Long 2005). At present, however, no experiments have assessed the effects of increasing CO_2 availability on intact, mature tropical forest stands, and thus this interpretation is still open to debate (e.g. Chambers & Silver 2004; Clark 2004; Lewis *et al.* 2004*b*).

Air-temperature increases are also undisputed, and could conceivably be causing the changes we document. However, many authors expect that the *ca* 0.5 °C air-temperature increase over the study period (Malhi & Wright 2004) would actually reduce, not increase, forest growth, as respiration costs are likely to increase with temperature (Amthor 2000). However, air temperatures will also increase soil temperatures, which could in turn increase soil mineralization rates and thus nutrient availability (Lewis *et al.* 2004*b*). Whether recent rises in air temperature have increased or decreased tropical forest NPP, therefore, 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, thought to be a decadal-scale natural variation, and not of anthropogenic origin (Wielicki *et al.* 2002). However, this data appears to contradict land-based sensors that show a decrease in incoming solar radiation over the past three decades (termed 'global dimming', Stanhill & Cohen 2001, see Lewis *et al.* 2004*b* for discussion). Three lines of evidence suggest that this is not the sole cause of the changes documented. (i) Losses from mortality lag *ca* 10–15 years behind gains from growth and recruitment (Phillips *et al.* 2004), hence as the *difference* between stand-level biomass growth and mortality was similar at the start (1980s) and end (1990s) of the study by Lewis *et al.* (2004*a*), the factor(s) causing changes in growth, recruitment and mortality were probably operating well before the onset of the study, and hence before the observed increase in incoming solar radiation. (ii) The *relative* rates of change in stand-level basal-area growth and loss, and stem recruitment and mortality are invariant across the continent (Lewis *et al.* 2004*a*). This suggests a relatively uniform increase in resource supply rates across the continent, without a strong spatial pattern (unlike the cloudiness data), as plants are thought to show similar relative increases in growth with similar increases in available resource levels (Lloyd & Farquhar 2000). (iii) Stem turnover has increased steadily across the tropics since the 1950s (Phillips & Gentry 1994; Phillips 1996), thus 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 altered dynamics. Nevertheless, the temporary increase in incoming solar radiation, coupled with rising CO_2 concentrations, and their interaction, may account for the very large increases in growth (*ca* 2% yr^{-1}) observed across South America in the 1980s and 1990s (Lewis *et al.* 2004*a*).

Nutrient deposition, either nitrogen from industry, or phosphorus and other nutrients from aerosols from burning forests is an unlikely candidate, as deposition should show a strong spatial signal, most likely downwind of forest clearance and industry, but the relative increases in growth, recruitment and mortality are similar across the continent (Lewis *et al.* 2004*b*). Furthermore, most tropical forests may not be nitrogen-limited (Vitousek & Farrington 1997; Tanner *et al.* 1998), thus increasing nitrogen depositions may not cause increases in forest productivity and dynamism. Indeed, increasing nitrogen deposition may lead to soil acidification, and the depletion of base cations, leading to a decrease in plant-available soil nutrients, and a decrease in forest growth (Asner *et al.* 2001).

The determination of which environmental change(s) have caused the suite of changes documented across South American tropical forests is difficult and open to debate. 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 (for example, depending upon soil fertility). Analyses of forest plot data from Africa, Asia and Australia, all underway, should allow a further narrowing of potential causes underlying rising productivity across South American and possibly other tropical forests (Lewis *et al.* 2004*a*). However, at present the most parsimonious explanation for the changes documented to date is the anthropogenic increase in atmospheric carbon dioxide concentrations, increasing forest NPP leading to accelerated forest growth and dynamics.

4. IMPLICATIONS OF CHANGE

There are numerous implications of the annual loss of millions of hectares of tropical forest and changes within intact forests over recent decades, such as deforestation affecting local climate (Chagnon *et al.* 2004), hunting for wild meat (bushmeat) altering forest regeneration (Wright *et al.* 2000), and habitat fragmentation affecting biodiversity and fire risk (Terborgh *et al.* 2001; Laurance 2004). Here I review two effects of global significance: how has deforestation, and changes in remaining forest, affected biodiversity and the evolution of climate change, via the impacts on the global carbon cycle?

(a) ***Biodiversity implications***

The majority of the world's species reside in tropical forests. Tropical deforestation is, therefore, likely to cause population changes for many species, including driving some to extinction. Two major problems arise when attempting to determine how many species become extinct annually because their habitat is destroyed by tropical deforestation. Firstly, it is unknown, even to within an order of magnitude, how many species there are within tropical forests. Secondly, how many resources should one expend looking for a particular species before it can be confidently predicted to not be anywhere? Given that the number of species is unknown for a given forest and proving something is not there is practically impossible, the numbers of species lost via deforestation is extremely difficult to determine.

Recent refinements of estimates of the total number of species on Earth have reduced the 3–100 million range commonly cited in the past to 5–30 million

(Dirzo & Raven 2003; Reid *et al.* 2005). Revisions of the global number of arthropods, to 5–10 million species (from >30 million, Odegaard 2000), and other poorly studied groups, such as fungi (Hawksworth 2001), and the question of specimens being given recognized names (Alroy 2002) have all helped to reduce the range. However, many groups such as micro-organisms are very poorly studied, thus estimates may still undergo major revisions in the future. If two-thirds of species occur in the tropics (Groombridge & Jenkins 2003), then current estimates are that 3.3–20 million species reside there, the overwhelming majority in tropical forests.

If 25–50% of Earth's tropical forests have already been lost, and current loss rates are *ca* 1% per annum (see §3), how many species have been lost? A crude answer can be given from island biogeography theory, which provides a formula to relate the area of an island, or area of habitat, and the number of species expected to be present (McArthur & Wilson 1967). As the size of remaining forest 'islands' decreases in a 'sea' of land converted to other uses, the number of species should decrease predictably. The relationship is nonlinear (and possibly not as McArthur & Wilson (1967) stated, see Lomolino 2000). Thus the loss to date of around half of all tropical forests is expected to equal *ca* 15% of the species that inhabit tropical forests (Pimm & Raven 2000). Of course not all species become immediately extinct. Some will persist in remnant populations, but are 'committed to extinction'. Thus it is unsurprising that globally 10–30% of plants, birds, amphibians and mammals are threatened with extinction (IUCN red lists, summarized in Reid *et al.* 2005), but the number of documented extinctions is much lower, at only 844 species (IUCN online searchable database). The extinction of 15% of all species in tropical forests would equal at least 500 000 species, and possibly 3 million. Most of these are not extinct now, but will disappear over the coming decades.

These figures do not tell the whole story, as species are not evenly distributed. Some 40% of all vascular plant, mammal, bird, amphibian and reptile species occur in 25 areas identified as global biodiversity 'hotspots', which collectively cover $<2\%$ of Earth's land surface (Myers *et al.* 2000). Seventeen of these hotspots are in tropical forests. On average, only 12% of the original primary forest remains of these hotspot areas, compared to the tropical forest average of $\geq 50\%$. According to McArthur & Wilson (1967), a 90% reduction in area leads to a 50% loss of species. Thus if the minimum number of species in the tropics is correct, at 3.3 million, then in the 'hotspots' there are a minimum of 40% of 3.3 million species residing there, of which half are estimated to be 'committed to extinction', while of the remaining species outside the hotspots, 15% are committed to extinction. The total number of species from tropical forests 'committed to extinction' is, therefore, 1 million species. If 20 million species reside in the tropics then the figures are a staggering 5.8 million species. It is entirely plausible that, without major societal changes, we have already committed in excess of 1 million species to extinction this century from land-use change alone.

The rapid changes in the structure and dynamics of remaining tropical forest, described in §3*b*, are likely to be accompanied by changes in species composition. Such changes appear to be occurring: in forest plots across western Amazonia the density, size, basal area and mean size of lianas, woody vines that are structural parasites on trees, have increased over the past two decades (Phillips *et al.* 2002*b*). In addition, analyses of a cluster of plots in central Amazonia have shown 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 many slower-growing genera of subcanopy 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, with faster-growing genera showing much larger absolute and relative increases in growth relative to slower-growing genera.

Overall, the widespread increase in forest productivity and acceleration of forest dynamics is likely to be altering the interactive balance of millions of plant and animal species in unstudied and unknown ways. One prediction is that such changes are likely to be benefiting disturbance-adapted taxa, as faster growing taxa benefit absolutely more from an increase in resource supply rates (Coomes & Grubb 2000; Lewis *et al.* 2004*b*). A second prediction is that faster-growing, disturbance-adapted taxa will benefit because rates of tree mortality are increasing, causing an increase in the frequency of openings in the forest canopy, further increasing resource supply rates (Körner 2004; Lewis *et al.* 2004*a*,*b*). Unfortunately these species are not usually those most in need of conservation measures, as it is the slow-growing, limited-dispersal, disturbance-averse species that are usually more vulnerable to extinction. However, the long-term implications of such compositional shifts in tropical forests on species loss are unknown.

(b) *Climate change implications*

The positive radiative forcing of CO_2 means that changes in atmospheric CO_2 concentrations largely determine the rate of increase in air temperatures and other features of climate change (IPCC 2001). The increase in atmospheric CO_2 is governed by four major fluxes, the carbon flux from fossil fuel use, the flux from land-use change, and the net fluxes to the oceans and terrestrial ecosystems (figure 5). This simple cycle must balance: the net increase in atmospheric CO_2 must equal the source terms minus the sink terms, and importantly an under- or over-estimate of one parameter implies a corresponding error in one or more other parameters. As figure 5 shows, in the 1990s half of all carbon emitted from fossil fuel use did not stay in the atmosphere, due to uptake by the oceans and terrestrial ecosystems. Thus, the rate of climate change is currently modest compared to that expected from fossil fuel emissions, because of this free 'subsidy' from nature (IPCC 2001). By far the most uncertain fluxes are the carbon emissions from land-use change, which over recent decades have overwhelmingly been caused

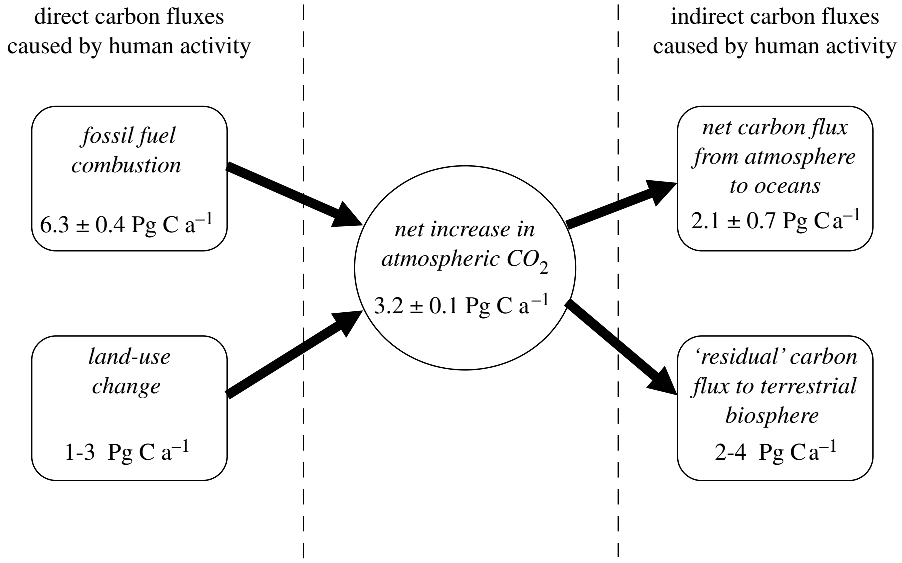

Figure 5. Annual carbon fluxes over the 1990s. 1 Pg$=1\times10^{15}$ g$=1$ Giga-tonne$=1$ billion metric tonnes (after Royal Society 2001 & Lewis *et al.* in press).

by tropical deforestation, and the residual terrestrial sink, part of which may be in tropical forests (figure 5).

Recent estimates of carbon fluxes from land-use change in the tropics range from 0.9 Pg C a^{-1} (DeFries *et al.* 2002) to 1.1 Pg C a^{-1} (Achard *et al.* 2004), to 1.7 Pg C a^{-1} (IPCC 2001), to between 1.4 and 3.0 Pg C a^{-1} (House *et al.* 2003), *ca* 2 Pg C a^{-1} (Malhi & Grace 2000; Fearnside & Laurance 2004) and 2.2 Pg C a^{-1} (Houghton 2003*a*) for the 1990s (1 Pg$=1\times10^{15}$ g$=1$ Giga-tonne$=1$ billion metric tonnes). There is no consensus as to the most accurate figure (e.g. see Achard *et al.* 2002 and responses Eva *et al.* 2003; Fearnside & Laurance 2003, 2004; Achard *et al.* 2004). To put this in context, in the 1990s humans emitted 6.3 Pg C a^{-1} from fossil fuel combustion, while atmospheric CO$_2$ concentrations increase by 3.2 Pg C a^{-1} in the 1990s (IPCC 2001). Thus, the poor understanding of carbon fluxes from deforestation is a major limitation on understanding the global carbon cycle and climate change (IPCC 2001; Houghton 2003*b*; House *et al.* 2003).

These estimates differ threefold, largely due to: (i) The use of very different deforestation rates. (ii) Assumptions as to what occurs to the land post-deforestation. Is forest replaced by bare ground, or some other vegetation type, and how does this change over time? (iii) Assumptions on what happens to soil carbon post-deforestation. (iv) The use of differing estimates of forest biomass (carbon) per unit area. This is especially problematic as different forests have different biomass, complex spatial distributions, and measuring the mass of an entire tropical forest is an expensive, laborious and time-consuming process, so is rarely done (Baker *et al.* 2004*a*,*b*; Malhi *et al.* 2004). Thus tropical deforestation is a significant source of carbon to the atmosphere, but of very uncertain magnitude.

In §3*a*, above, I suggest that the new 'low' deforestation rates may be underestimates. If this is the case then the carbon flux will also be correspondingly underestimated, because the area of forest loss would be underestimated. Of note is the analysis by House *et al.* (2003), which reviews a variety of techniques with which to study terrestrial carbon budgets, which taken together provide complementary information on processes and add constraints on possible flux values. Their range of flux values from tropical deforestation is 1.4–3.0 Pg C a^{-1}, and does not overlap either the Achard *et al.* (2004) or DeFries *et al.* (2002) estimates of carbon fluxes to the atmosphere. This suggests that either the 'new' deforestation estimates are too low, and/or conversions of deforestation to carbon fluxes are too low, as suggested by Fearnside & Laurance (2004).

It is known from atmospheric CO$_2$ measurements and the use of atmospheric transport models that the terrestrial tropics as a whole are either neutral or a modest source of carbon, with clear inter-annual variability (Gurney *et al.* 2002; House *et al.* 2003; Rodenbeck *et al.* 2003). Thus, two options emerge regarding the land-use change fluxes: either carbon sources from deforestation are relatively high (*ca* 2 Pg C a^{-1}), but these are balanced by a relatively large sink in the terrestrial tropics (1–2 Pg C a^{-1}), or carbon sources are relatively low (*ca* 1 Pg C a^{-1}), with little, if any, sink in the terrestrial tropics (Houghton 2003*b*). Thus the presence or absence of sinks in the tropics can provide an additional constraint on the land-use change flux.

Data from long-term forest monitoring plots suggests that South American forests are gaining above-ground biomass, and are a sink of *ca* 0.6 Pg C a^{-1} (Phillips *et al.* 1998; Baker *et al.* 2004*a*). If African forests are increasing in biomass similarly, as preliminary analyses suggest (Lewis *et al.* in preparation), then the sink increases to *ca* 1 Pg C a^{-1}, and may be 1.2 Pg C a^{-1}, if Asian forests are also responding similarly. Increasing tropical forest biomass is consistent with theoretical predictions and models of plant growth under increasing CO$_2$ concentrations, and experiments in temperate forest stands (e.g. Lloyd & Farquhar 1996; Norby *et al.* 1999, 2002; Cramer *et al.* 2004; Lewis *et al.* 2004*b*; Ainsworth & Long 2005). However, the sink may be much larger than monitoring plots suggest, as fluxes measured from forest inventories do not include changes in soil carbon, which may also contribute to a net carbon sink in the terrestrial tropics. This is the case in the northern extra-tropical zone: detailed work shows that approximately half the temperate sink is in forests, while the other half is in soils and non-forest vegetation (House *et al.* 2003). Thus, carbon uptake by soils and the woody encroachment of savannas, both neglected areas of study, could plausibly give a total tropical sink of >2 Pg C a^{-1}.

Overall, of the two options for the tropics—big source, big sink, or small source, small sink—evidence suggests that they are a 'big source, big sink', and hence a highly dynamic component of the global carbon cycle. On balance, deforestation in the tropics most likely adds carbon to the atmosphere towards the higher end of the 1–2 Pg C a^{-1} estimated from recent studies, while remaining forests are a sink of *ca* 1 Pg C a^{-1}, possibly double that when including soils and the terrestrial tropics as a whole. Regardless of the exact magnitudes it is clear that human-induced changes across the tropics are playing a key role in modulating the rise of atmospheric CO_2, and hence the rate and magnitude of climate change.

Finally, carbon dioxide is not the only product of deforestation that exhibits radiative forcing. Biomass burning also leads to the production of various trace gases, including nitrous oxides and methane. Such gasses may increase radiative forcing by 6–25%, compared to merely accounting for the carbon emissions (Fearnside 2000). However, by contrast, the production of aerosols provides some negative radiative forcing from biomass burning (Ramanathan *et al.* 2001). Complete accounting of the differing processes associated with biomass burning is necessary to understand the total effects of deforestation on the climate system.

5. FUTURE SCENARIOS

To make predictions about the future, we must understand the drivers of change and how these then percolate through and alter the Earth system (often affecting the drivers themselves). There is great uncertainty at all stages of this predictive process. Below I focus solely on interactions and potential positive feedbacks between the tropics and changes expected from climate change that may have important Earth system and societal impacts. Four plausible positive feedback scenarios are presented below: changes in photosynthesis/respiration rates, biodiversity changes in intact forests, widespread forest collapse via drought, and widespread forest collapse via fire. Each risk 'runaway carbon dynamics' that may accelerate the rate and increase the magnitude of climate change, making the 'extreme' predictions of some models plausible possibilities (Betts *et al.* 2004; Cox *et al.* 2004; Stainforth *et al.* 2005). These feedbacks risk causing the climate to shift abruptly, as it has in the past (Alley *et al.* 2003). Such abrupt changes would likely have serious human welfare and biodiversity implications. In addition such threshold changes in tropical forests have, to my knowledge, not been systematically addressed and are poorly understood. Here I make a first attempt to sketch the various physically plausible tropical forest-climate positive feedback scenarios.

(a) *Photosynthesis/respiration changes*

Currently old-growth tropical forests, in South America at least, appear to be increasing in biomass (Baker *et al.* 2004*a*,*b*). This sink is ultimately caused by the gain of carbon by stands of forest trees from photosynthesis exceeding the losses of carbon from respiration. Under the simplest scenario of a steady rise in forest productivity over time, some models predict that forests may remain a carbon sink for decades (Chambers *et al.* 2001; Cramer *et al.* 2001). However, this situation is not expected to persist through the twenty-first century. Firstly, while the cause(s) of increasing photosynthetic rates are debated (see §3*b* above), the most parsimonious explanation is the increase in carbon availability, as atmospheric CO_2 concentrations are rising. However, whatever the cause, the increase in photosynthetic rates, apparently caused by year-on-year better conditions for growth, will saturate as trees become limited by other resources, such as soil nutrients, at some point in the future. Thus, the recent carbon sink contribution of tropical forests should decline over the coming decades.

Secondly, warmer temperatures increase the rates of virtually all chemical and biological processes in plants and soils, until temperatures reach points where enzymes and membranes cannot perform their usual functions. Thus, respiration costs will generally increase with temperature (Amthor 2000). As air temperatures continue to rise, at some point in the future increasing respiration costs will exceed photosynthetic rates, especially as photosynthetic rates cease to increase at current rates. Remaining tropical forests should then become a source of carbon to the atmosphere.

Simple models, therefore, show that there are likely to be thresholds, where terrestrial ecosystems will move from sinks to sources of carbon (Cox *et al.* in press). This threshold depends on four inter-related relationships, that between atmospheric CO_2 concentrations and air temperatures ('climate sensitivity'), between photosynthesis and CO_2, between photosynthesis and temperature, and between respiration and temperature. The HAD3 coupled global circulation model (GCM) suggests that the threshold is around 550 p.p.m.v. (parts per million by volume) CO_2 in the atmosphere (Cox *et al.* 2004, in review; Betts *et al.* 2004). However, this is highly dependent upon the climate sensitivity to CO_2 (the equilibrium increase in temperature caused by a doubling of atmospheric CO_2 from pre-industrial levels) which is highly uncertain (Stainforth *et al.* 2005) and the response of respiration to temperature, also highly uncertain (Amthor 2000; Betts *et al.* 2004; Lewis *et al.* 2004*b*).

Such changes may have considerable impacts. An increase of carbon stocks of just 0.5% a^{-1} gives a tropical forest carbon sink of *ca* 1.2 Pg C a^{-1}. The current increase in atmospheric CO_2 is 3.2 Pg C a^{-1}. A shutdown of the tropical forest carbon sink *alone*, all other things being equal, would see the annual increase of atmospheric CO_2 increase dramatically. A shift to a modest source of only a few tenths of a percent could greatly increase atmospheric CO_2, and hence increase air temperature warming. This in turn may create a dangerous feedback, as respiration costs continue to rise with the rising temperatures further causing forests to release carbon. However, oceanic CO_2 uptake may increase if atmospheric CO_2 concentrations increased, potentially mitigating such a feedback.

Temperature increases in the world's warmest regions may pass other thresholds: temperatures may increase such that the enzyme and membrane integrity of organisms is impaired. These are poorly researched areas at present. However, such questions are especially pertinent given recent evidence that the 'climate sensitivity' of GCMs used to make predictions of future climate range from 2 to 11 °C (Stainforth *et al.* 2005), and under 'business as usual' scenarios doubling CO_2 will occur in the coming decades.

(b) *Biodiversity changes*

Remaining tropical forests, in South America, at least, are growing faster (Lewis *et al.* 2004*a*), and increasing in dynamism (Phillips & Gentry 1994; Phillips 1996; Weishampel *et al.* 2001; Phillips *et al.* 2004). Such changes will lead to some species doing relatively better than others. How will these compositional changes themselves alter the carbon balance of tropical forests? Firstly, increased resource availability and the increasing frequency of tree-fall gaps (openings in the canopy), from increasing tree mortality rates, will likely benefit faster growing disturbance-adapted species. This suggests a shift towards light-demanding species with high growth rates at the expense of more shade-tolerant species (Körner 2004; Laurance *et al.* 2004; Lewis *et al.* 2004*b*). Such fast-growing species are associated with lower wood specific gravity, and hence lower volumetric carbon content (West *et al.* 1999). A decrease in mean wood specific gravity across Amazonia of just 0.4% a^{-1} would be enough remove the carbon sink effect of 0.6 Mg C a^{-1} ha^{-1} (Lewis & Baker, unpublished data). As mean stand-level wood specific gravity values differ by >20% among Amazonian forests and species values vary fivefold (Baker *et al.* 2004*b*), it is possible that changes in species composition alone could remove or reverse the current sink contribution of tropical forests (Körner 2004). It is known that high-productivity and high-dynamism forests are composed of, on average, trees with lower volumetric carbon content (have 'lighter' woods), and thus store much less carbon than low-dynamism forests (figure 6; Baker *et al.* 2004*b*). Whether the lower carbon storage associated with higher dynamism shown in different locations within Amazonia will occur over time, as forests increase in dynamism, are unknown, but is a plausible scenario with serious implications (figure 6).

Secondly, lianas are structural parasites that decrease tree growth and increase mortality, and are disturbance-adapted (Schnitzer & Bongers 2002). Thus the rapid increase in abundance and size of large lianas across Western Amazonia over the past two decades could also turn surviving forests into a carbon source over the coming decades, if current trends continue (Phillips *et al.* 2002*b*).

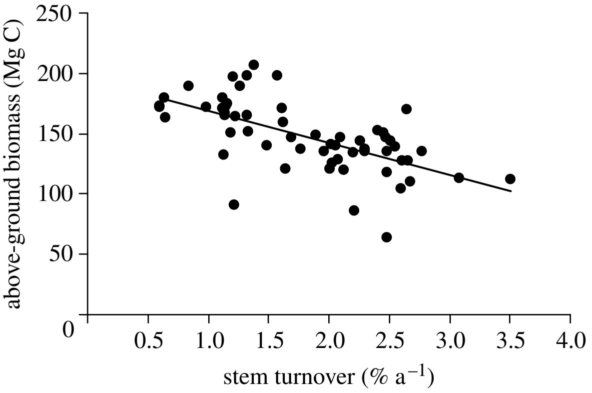

Figure 6. Relationship between forest dynamism (stem turnover), and carbon storage (above-ground biomass), for 59 plots from across Amazonia (biomass data from Baker *et al.* (2004*a*,*b*), stem turnover data from Phillips *et al.* 2004). 1 Mg = 1 metric tonne.

(c) *Tropical forest collapse: drought*

Climate change will alter precipitation patterns (IPCC 2001). There are critical thresholds of water availability below which tropical forests cannot persist and are replaced by savanna systems (Salzmann & Hoelzmann 2005). They are often around 1200–1500 mm rainfall per annum. Rainfall has reduced dramatically over the Northern Congo basin over the past two decades (Malhi & Wright 2004). This current drying trend is of unknown cause. These forests are already relatively dry for tropical forests (*ca* 1500 mm a^{-1}), and may become savanna if current trends continue, leading to large carbon fluxes to the atmosphere. If the current drying trend is caused by climate change, this could lead to a positive feedback with the climate system exacerbating forest losses and carbon fluxes to the atmosphere.

The first GCM used to predict the evolution of climate change that included dynamic vegetation and a carbon cycle that is responsive to these dynamic changes showed large differences in atmospheric CO_2 concentrations over the twenty-first century compared to previous models (Cox *et al.* 2000). Under the 'business as usual' scenarios of emissions, IS92a, previous GCMs predicted that atmospheric CO_2 concentrations would be ~700 p.p.m.v. in 2100, while the Cox *et al.* (2000) predictions were 980 p.p.m.v., or an extra 1.5 °C air temperature increase, on top of the warming by 2100 without the vegetation–climate feedbacks. These higher CO_2 concentrations depend critically on: (i) the dieback of the Eastern Amazon rainforests, caused by climate change induced drought and (ii) the subsequent release of C from soils. The initial drying of the Amazon was driven by two processes, the closure of stomata caused by increasing atmospheric CO_2 concentrations, leading to reduced evapotranspiration and hence precipitation, and the radiative forcing of increasing CO_2 on precipitation patterns (Betts *et al.* 2004). The initial dieback of forest then exerts two positive feedbacks: reduced forest cover further reduces local evapotranspiration, and hence rainfall, and the release of CO_2, which further accelerates air temperature increases and precipitation reductions (Betts *et al.* 2004). The reduced forest cover is a much stronger feedback than

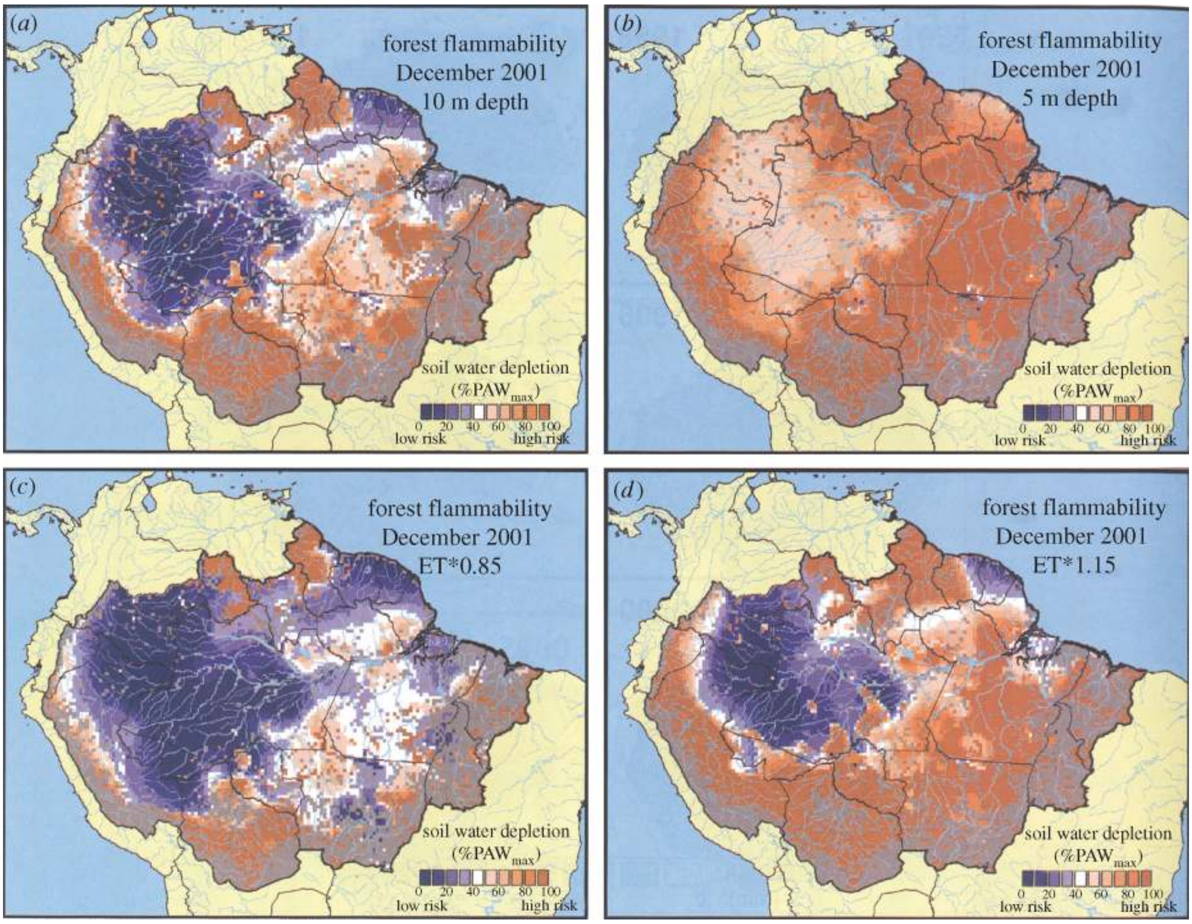

Figure 7. Many tropical forests are susceptible to burning during periodic droughts. Model output of potential available water for December 2001 across Amazonia, showing the effect of manipulating soil depth and evapotranspiration parameters. (*a*) Soil depth set at 10 m, evapotranspiration unaltered; (*b*) soil depth of 5 m, evapotranspiration unaltered; (*c*) soil depth of 10 m with 15% depression in evapotranspiration; (*d*) soil depth of 10 m with 15% increase in evapotranspiration (from Nepstad *et al.* 2004). Under scenario (*a*) one-third of Amazonia was susceptible to fire. The large effects of small changes in evapotranspiration show the sensitivity of these forests to increasing temperatures and possible reductions in precipitation.

the release of CO_2 (which has alarming implications given continuing deforestation rates).

Altering key sensitivities in the Cox *et al.* (2000, 2004) model causes the dieback to be either earlier or later than 2050, and under some scenarios the magnitude of forest loss is reduced, but no combination removes the dieback (Huntingford *et al.* 2004). However, in an alternative fully coupled model (UMD), while predicting higher atmospheric CO_2 (by 90 p.p.m.v.) and temperatures (by 0.6 °C) by 2100 compared to the uncoupled model, there is no Amazon-drought and subsequent dieback (Zeng *et al.* 2004). This is because of the poor agreement between the fully coupled models on changing precipitation patterns, in terms of locations, durations and magnitudes (Zeng *et al.* 2004).

GCMs generate predictions from a specific scenario for a given model. These models are far from perfect: the Cox *et al.* (2000, 2004) model fails to predict present day precipitation patterns, including over the Amazon, thus results from the model should be treated with caution. Furthermore, GCMs do not provide probabilities of the likelihood of a given scenario occurring. These models point to possible outcomes when combining physically plausible processes with state of the art parameterization under a variety of carbon emissions scenarios. A warming and drying world leading to the loss of half of the world's largest tract of tropical forest, and accelerated climate change is, therefore, a plausible scenario requiring urgent attention.

(**d**) ***Tropical forest collapse: fire***

If tropical forests get dry they are susceptible to burning, by lightening or human actions. While naturally occurring fires have been historically rare in tropical moist forests, those of anthropogenic origin, often used to clear forest for agriculture, have become much more frequent over recent decades (Cochrane 2003). The 1997–1998 ENSO event—the most intense in the twentieth century—is estimated to have led to *ca* 20 million ha of fires across the world's tropical forests (Barbosa & Fearnside 1999; Nepstad *et al.* 1999; Siegert *et al.* 2001; Cochrane 2003). If each hectare released 150 tonnes carbon to the atmosphere, then this is ~3 Pg in total. These fires coincided with 1998 being the warmest year since records began, and the highest annual increase in atmospheric CO_2 concentration ever recorded from direct atmospheric measurements, some 5.8 Pg C being added to the atmosphere, ~3 Pg more than that added in the years immediately before or following the ENSO event (Keeling & Whorf 2004).

As the world warms and periodically dries, more forest is likely to be susceptible to burning more frequently, increasing the number, size and severity of forest fires. As such fires increase carbon fluxes to the atmosphere, this would further increase air temperatures, hence increasing the likelihood that forests may burn, creating a potentially dangerous positive feedback.

The scale of the problem can be seen by looking at modelled plant available water across the Amazon basin during the 2001 ENSO drought: one third of the forests of the Amazon basin were susceptible to burning (figure 7; Nepstad *et al*. 2004). This model includes only a simple water balance model, using rainfall, soil profile data, evapotranspiration and incoming solar radiation data. It does not include human-induced factors that increase flammability, such as proximity to deforested areas or habitat fragmentation (Laurance 2004). Thus it is quite possible for simultaneous increases in average air temperatures, more severe and regular ENSO events, high rates of forest clearing, and resulting edge creation and habitat fragmentation, to significantly increase forest fires and hence carbon emissions. This could lead to precipitation reductions and increased temperatures via the loss of forest cover and reduced evapotranspiration, and increased flammability. Further, carbon fluxes to the atmosphere may risk creating a potentially dangerous positive feedback and widespread tropical forest collapse. The separate parts of this scenario are individually well known (e.g IPCC 2001; Laurance & Cochrane 2001; Cochrane 2003; Betts 2004; Laurance 2004). However, the impact of these changes on global temperatures and the evolution of climate change is almost entirely unknown, as human decisions on starting fires, the effects of such fire effects, and the resulting relevant feedbacks are not included in current coupled GCMs.

6. CONCLUDING REMARKS

Tropical forests and the Earth as an integrated system have recently moved well beyond the range of natural variability covering, at the very least, the past half-million years (Crutzen & Steffen 2003; Reid *et al.* 2005). These human-induced *and* simultaneous changes of many key environmental parameters are largely unprecedented in both magnitude and rate, from carbon dioxide concentrations in the atmosphere, to species extinction rates, as documented here (e.g. figure 1). While human-induced changes to the Earth system may have been discernable for several thousand years (Ruddiman 2003), and have been clear for hundreds of years (Crutzen 2002), the past 50 years have seen humans move from *influencing* the Earth system, to *dominating* it (Crutzen & Steffen 2003; Reid *et al.* 2005).

What caused the transformation of humans into a collective force of nature? While it is far beyond the scope of this paper to answer that question, such an answer is critical if scientists are to make robust predictions about the future and society to modify actions accordingly. Briefly, two common explanations prevail. Some emphasize the unprecedented expansion of the number of humans, while others emphasize the emergence and spread of particular forms of human social organization. Human numbers have increased at unprecedented rates: globally there has been a tenfold rise over 300 years and a fourfold increase in the twentieth century, to over 6 billion in 2005 (Lutz & Qiang 2002). Such increases are obviously important, but can only be proximate causes, as human fertility and survival rates are not deterministic, but are greatly influenced by social and economic factors (Collins *et al.* 2001; Lutz & Qiang 2002). Furthermore, the peak growth *rate* was in the 1960s, and has been declining since, while *absolute* population increments peaked in the mid-1980s, and have declined since (Lutz & Qiang 2002). Yet the late twentieth and early twenty-first centuries have witnessed the greatest impacts on the Earth system (Crutzen & Steffen 2003; Reid *et al.* 2005).

Different forms of social organization may, therefore, hold the key to understanding our impacts on the Earth system, and our ability to alter them. Two well-known new social systems have emerged historically that have led to major changes in human impacts on the Earth system. The first was the emergence of a social system based around agriculture and animal husbandry, in the Fertile Crescent of South West Asia, and its subsequent near-global spread over several thousand years (Diamond 1997). This led to the first discernibly human-induced global changes to the Earth system. Atmospheric carbon dioxide and methane concentrations were probably pushed beyond the variability expected from changes in the Earth's orbit over the past 350 000 years (Ruddiman 2003). However, the impacts were, relative to now, modest in terms of global environmental processes.

The second was the emergence in Europe, some 200–500 years ago, depending upon definitions, of a second new form of social organization, based around private property and the production of goods and services for sale in a competitive market in which the object is to realize the maximum profit, termed capitalism (Polanyi 1944; Wallerstein 1974; Brenner 1977). The internal logic and positive feedback of the pursuit of profits, of which some is used to generate more profits, has led to both the ever-increasing use of environmental resources, and an increasingly global search for exploitable resources—for use in an ever-expanding global economy. Thus over the past 50 years there has been a sixfold increase in the world economy, coupled with a step-change in the range and magnitude of impacts on global environmental processes, contrasting with a twofold increase in the human population (Crutzen & Steffen 2003). Thus, it is plausbile to suggest that the changing Earth system is caused in large part by a central goal of the current form of human social organization.

Perhaps *the* key question for the twenty-first century may well be 'Can a new form, or forms, of social organization be created that allow humans to prosper within the natural variability of the Earth system, or will such changes in human social systems be imposed by crossing critical Earth system thresholds?' It is a choice societies have faced in the past, sometimes unknowingly, but never on a global scale (Diamond 2005). I hope that this paper is one small contribution to the knowledge required to avoid the latter becoming reality.

Many thanks to Tim Baker, Oliver Phillips, Ben Trott, Tadzio Mueller and two anonymous reviewers for comments on the manuscript. Thanks to UNEP-WCMC for permission to reprint figure 2, and Daniel Nepstad and Blackwell Scientific Publishing for permission to reprint figure 7. This work was funded by a Royal Society University Research Fellowship.

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