# Tropical forests in a changing environment

## S. Joseph Wright

Smithsonian Tropical Research Institute, Apartado 0843 – 03092, Balboa, Ancón, Panamá, República de Panamá

**Understanding and mitigating the impact of an ever-increasing population and global economic activity on tropical forests is one of the great challenges currently facing biologists, conservationists and policy makers. Tropical forests currently face obvious regional changes, both negative and positive, and uncertain global changes. Although deforestation rates have increased to unprecedented levels, natural secondary succession has reclaimed approximately 15% of the area deforested during the 1990s. Governments have also protected 18% of the remaining tropical moist forest; however, unsustainable hunting continues to threaten many keystone mammal and bird species. The structure and dynamics of old-growth forests appear to be rapidly changing, suggesting that there is a pantropical response to global anthropogenic forcing, although the evidence comes almost exclusively from censuses of tree plots and is controversial. Here, I address ongoing anthropogenic change in tropical forests and suggest how these forests might respond to increasing anthropogenic pressure.**

## Introduction

Tropical forest landscapes are changing rapidly as human populations and economies grow. Tropical forests also have a disproportionate role in global carbon and energy cycles [1] and support ~50% of described species and an even larger number of undescribed species [2]. An understanding of anthropogenic change in tropical forests is thus crucial to understanding global climate change and the conservation of nature.

Anthropogenic effects on tropical forests can be grouped into two broad categories. Local effects include local land-cover change, invasive species, and timber and bush meat extraction. Global effects include changes to the atmosphere and climate caused largely by fossil-fuel consumption and remote land-cover change. The challenge is to understand the overall impact of this mix of anthropogenic drivers, particularly because anthropogenic forcing is likely to only intensify. The population of tropical countries increased from 1.8 billion in 1950 to 4.9 billion in 2000 and is projected to grow by a further 2 billion before 2030 [3]. Tropical and global economies are both projected to grow even more rapidly.

Here, I address ongoing anthropogenic change in tropical forests with an eye toward understanding how these forests might respond to increasing anthropogenic pressure. I evaluate local effects first because they are unequivocally detectable, vary widely among countries, and set the stage for potential synergisms with global effects. The evidence for global effects suggests that a massive reorganization of the structure and dynamics of tropical forests is already underway. The evidence comes almost exclusively from repeated censuses of tree plots; however, and additional independent evidence is needed.

## Local anthropogenic influences on tropical forests
### Deforestation

Land use and forest cover are changing throughout the tropics (Box 1). Approximately half of the potential tropical closed-canopy forest has already been removed and the land converted to other uses (Table 1). For comparison, the extant forest cover of the eastern USA has never fallen below ~40% of its potential area [4], a threshold that has already been passed in tropical Asia and Africa (Table 1). The highest rates of tropical deforestation yet recorded occurred during the 1980s and 1990s [5], and have continued to increase in some areas. Across tropical Asia, deforestation rates increased significantly from $1.8 \times 10^6$ ha y$^{-1}$ during the 1980s to $2.6 \times 10^6$ ha y$^{-1}$ during the 1990s [6]. In the Brazilian Amazon, deforestation rates increased from $1.7 \times 10^6$ ha y$^{-1}$ during the 1990s to 1.8, 2.3 and $2.4 \times 10^6$ ha y$^{-1}$ in 2001, 2002, and 2003, respectively [7]. The immense deforested area, larger than the combined areas of Canada and France, is just part of the story.

Deforestation creates a patchwork landscape, with forest fragments scattered among towns, pastures and fields and abrupt edges separating forests from other land uses. Each year, deforestation results in 20 000 km of new forest edge in the Brazilian Amazon alone [8], and the area of forest in fragments of $<100$ km$^2$ or within 1 km of the nearest forest edge is greater than the area deforested [9]. Globally, there was $45.3 \times 10^6$ ha of fragmented tropical forest in 1997 [10]. Active deforestation is underway in close proximity (defined as 1% clearing in $10^6$ ha) to 15%, 12%, and 8% of the remaining closed-canopy forest in tropical Asia, America, and Africa, respectively [6]. This brings loggers and colonists closer to previously remote forests and contributed to the degradation of an additional $2.3 \times 10^6$ ha of forest each year during the 1990s [10]. Thus, deforestation fragments and facilitates the degradation of remaining forests.

Corresponding author: Wright, S.J. (wrightj@si.edu).

**Box 1. Estimates of tropical forest cover, deforestation and reforestation**

Table 1 (main text) compares estimates of potential forest cover, extant forest cover and recent change in forest cover for the tropics. These best available estimates must be compared cautiously because methods and forest definitions differ.

Potential forest cover was estimated from a 1-km resolution satellite-based land-cover data set supplemented by the BIOME3 vegetation model [5]. The vegetation model was used to identify the potential vegetation cover wherever crops or natural vegetation covered >50% or <20% of a 5-min, latitude-longitude grid cell, respectively [5]. Tropical forest included the 'tropical evergreen and tropical deciduous forest/woodland biomes'. The principal limitation is the use of 5-min latitude–longitude grid cells [5] and the difficulty of matching biomes with the definitions of forest used in the three estimates of extant forest cover [14].

The best known estimate of extant forest cover is compiled each decade from national forest inventories by the Forestry Department of the UN Food and Agricultural Organization (FAO) [64]. The FAO defines 'all forests' as land where > 10% of the area is covered by the crowns of trees >5-m tall [64]. This definition includes large areas of tropical savannah and is therefore not discussed here. The FAO also defines 'closed forest' as land where >40% of the area is covered by tree crowns and a continuous grass layer is absent. The FAO estimates extant 'closed forest' cover [64] but not changes in 'closed forest' cover. The principal limitations are that the working definition of forest, the dates and the quality of national inventories vary among countries.

The satellite-based Advanced Very High Resolution Radiometer (AVHRR) has also been used to estimate closed forest cover [6]. Closed forest was defined to include land where tree crown coverage exceeds 60% [6]. The principal advantage is annual, global coverage, and the principal limitation is the coarse 8-km spatial resolution of the AVHRR. Forest degradation is undetectable and deforestation and the small clearings made for shifting agriculture are difficult to detect [6]. Only the abrupt change when continuous forest is replaced by extensive agriculture is readily detected.

The third estimate of tropical forest cover comes from Landsat Thematic Mapper imagery [10]. Forest was defined to include the 'evergreen and seasonal forests of the tropical humid bioclimatic zone'. The principal advantage is a 30-m resolution, which enables the quantification of forest degradation, small clearings and the recovery of forests through natural secondary succession. The principal limitation is incomplete spatial and infrequent temporal coverage. Estimates of forest cover, deforestation and reforestation were based on a random 6.5% sample of the appropriate lands stratified by an independent assessment of previous deforestation [10].

Two robust results emerge in spite of differences in methods and forest definitions among the studies summarized in Table 1 (main text). First, secondary forest succession offset one of each six to seven hectares deforested during the 1990s, contributing to the widespread replacement of old-growth forest by secondary forest throughout the tropics. Second, cumulative deforestation is reaching critical levels at the scale of tropical Africa and Asia. In spite of ongoing secondary succession, extant forest is likely to be <40% of potential forest cover for the tropical portions of both continents. The situation varies widely among countries and biomes, and the local situation can be much better or much worse than suggested by these continental-scale compilations [14,19].

## Secondary forest succession

Natural secondary forest succession occurs where land is abandoned or temporarily fallowed [11,12], and this site-specific mix will determine the long-term prospects of secondary forests. Secondary forests reclaimed one hectare for every six to seven hectares deforested in the tropics during the 1990s (Box 1). Land might be abandoned because agricultural yields fall, government subsidies change, or greater economic opportunity lies elsewhere. In the Brazilian Amazon, for example, the rural:urban income ratio averages 0.6, the percentage of the population living in rural settings declined from 57% to 40% in 16 years, the number of rural establishments declined by 23% in 11 years, and secondary forest has reclaimed 31% of the once deforested land [12]. More generally, rural–urban migration is contributing to the intense urbanization of most tropical countries, former agricultural lands are being abandoned, and secondary forests are becoming more widespread [13,14].

Secondary forests are important for global carbon cycles [10] and could have great conservation value. Tropical secondary forests recover animal species diversity in 20–40 years [15], but support fewer tree species than do old-growth forests [16,17]. The species composition of plant and animal communities often differs between secondary and old-growth forests [15–17]. In particular, weedy species can become more widespread as secondary forests become more important, homogenizing species composition over large areas. The long-term conservation value of secondary forest will vary with the proportion of species whose distributions are restricted to old-growth forest.

## Table 1. Potential and extant forest cover and recent rates of deforestation, reforestation and forest degradation in the tropics

| Source / Region | Forest area ($10^6$ ha) | | | | Rate of change in area ($10^6$ ha y$^{-1}$) [e] | | | | |
| | Potential forest area | Extant forest area | | | Deforested area | | Secondary forest area | | Degraded area |
| | DISCover satellite imagery [a] | National inventories [b] | AVHRR satellite imagery [c] | Landsat satellite imagery [d] | AVHRR satellite imagery [c] | Landsat satellite imagery [d] | AVHRR satellite imagery [c] | Landsat satellite imagery [d] | Landsat satellite imagery [d] |
|---|---|---|---|---|---|---|---|---|---|
| Africa | 539 | 345 | 172 | 193 | 0.37 | 0.85 | 0.43 | 0.14 | 0.39 |
| Americas | 1047 | 891 | 701 | 653 | 4.3 | 2.5 | 0.37 | 0.28 | 0.83 |
| Asia | 564 | 255 | 199 | 270 | 2.6 | 2.5 | 0.26 | 0.53 | 1.10 |
| Pantropical | 2150 | 1491 | 1072 | 1116 | 7.3 | 5.9 | 1.06 | 0.95 | 2.32 |

[a]DISCover 1-km resolution satellite imagery supplemented by the BIOME3 vegetation model [5] for countries whose geographical centers fall within the tropics [14].
[b]National forest inventories compiled by the FAO [64] for countries whose geographical centers fall within the tropics [14].
[c]Advanced Very High Resolution Radiometer 8-km resolution satellite imagery for all lands between the tropics [6].
[d]LandSat 30-m resolution satellite imagery for the 'evergreen and seasonal forest of the tropical humid bioclimatic zone' for all continents plus the 'dry biome of continental Southeast Asia' [10]. Excludes Mexico and the Atlantic coastal forest of Brazil.
[e]Rates of deforestation, secondary forest succession and forest degradation are for 1990–1997.

## Spatial variation in land-use change

The local loss of forest cover can be extreme. Myers *et al.* [18] identified 25 endemicity 'hotspots' that include the entire ranges of 44% and 35% of all vascular plants and terrestrial vertebrates, respectively. Of these, the 16 hotspots that support tropical forest have lost significant percentages of their original vegetation cover (Figure 1) [19]. Simple species–area projections incorporating this level of habitat loss indicate that extinction now threatens ~50% of the tropical hotspot endemics that require old-growth forest cover [19]. Tropical dry forests are the most endangered forests worldwide with, for example, <2% of the original tropical dry forest remaining in Central America [20].

By contrast, old-growth forests have largely survived where human population density is low. Rural population density explains 66–83% of the among-country variation in the percentage of potential closed-canopy forest remaining in tropical Africa, America and Indo-Malaya [14]. For example, Bangladesh (975 people $km^{-2}$) and Haiti (293 people $km^{-2}$) support <10% of their potential closed-canopy forest, whereas French Guiana (2.0 people $km^{-2}$), Gabon (4.6 people $km^{-2}$), Papua New Guinea (10.4 people $km^{-2}$) and Suriname (2.7 people $km^{-2}$) support >90%.

Old-growth forests also survive in protected areas. Globally, 18% of all tropical and subtropical moist forests and 9% of all tropical dry forests are nominally protected [21]. Thus, tropical moist forests are potentially among the best protected biomes; of 14 major biomes, only temperate coniferous forest receives a greater level of global protection [21]. Nevertheless, large numbers of tropical species have small ranges outside existing protected areas and tropical forests also comprise 65% of the global area prioritized for future protection [22]. Protected areas are also only as effective as the governments that protect them and can collapse during political and economic crises [23].
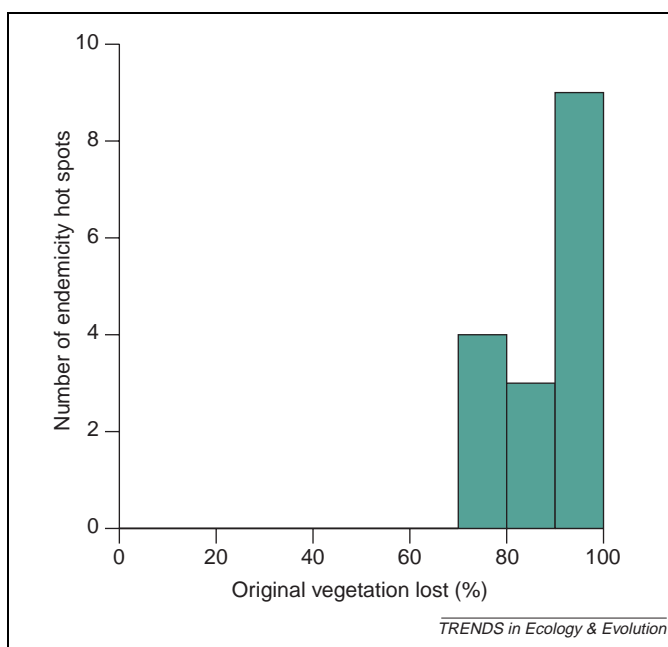
Still, protected forests suffer less degradation than do nearby unprotected forests throughout the tropics [24].

## Poachers

Few tropical protected areas exclude poachers and, as a consequence, a pantropical bush meat crisis threatens many keystone species throughout the tropics. Forest ungulates, primates and other large vertebrates provide a significant proportion of protein consumed by humans in many tropical settings [25]. Hunters routinely extirpate the more sensitive species, such as large primates and cats, which are characterized by delayed maturation and few young, and reduce the abundances of less sensitive species, such as deer and forest pigs [26]. Game species include granivores that eat large palatable seeds, browsers that eat palatable leaves, and frugivores that disperse seeds and are sometimes the only primary dispersal agents of large-seeded plants. The primates, carnivores and rodents that disperse and consume the seeds of many coccosoid palms provide an example [26]. Thus, hunting also indirectly alters the species composition of regenerating plants, favoring species with palatable foliage, palatable seeds, and seeds that are dispersed by wind, bats and small birds [26]. Habitat loss and unsustainable hunting could therefore result in species extinctions that permanently alter remaining tropical forests.

## Invasive species

Africanized bees and feral pigs have successfully invaded species-rich, old-growth tropical forests throughout the Neotropics and Australia, respectively. Invasive plants are also important components of many secondary tropical forests [17,27]. With these notable exceptions, there are relatively few reports of invasive species in tropical forests, particularly old-growth forests on continental land masses. For plants, this might reflect the tendency for humans to transport light-demanding species associated with agriculture and open habitats that are unable to regenerate in closed-canopy forest [27]. However, plantations of shade-tolerant, tropical hard woods are increasingly being established outside their native range and will increasingly provide sources of exotic propagules appropriate to conditions in old-growth forests [27]. Old-growth forests will also become more vulnerable to invasion as fragmentation and degradation intensify. Thus, invasive species are likely to become more important in future tropical forests.

## Global anthropogenic effects on lowland tropical forests

The evidence for biotic responses to global climate change is clear for high latitudes, but sparse and controversial for tropical latitudes. Many temperate and boreal species reproduce earlier, experience longer growing seasons and migrate or have extended their ranges to higher latitudes or elevations [28]. Similar changes have occurred on tropical mountains, where the elevations characterized by persistent cloud formation are increasing with global warming [28]. Lowland tropical climates are also changing in ways that are likely to affect forest organisms (Box 2). However, to my knowledge, there are no studies



**Figure 1.** The percentage of original vegetation cover lost from hotspots of endemicity that support tropical forest. Median =90% cover loss. Data from [19].

Autotrophic plants require $CO_2$, light, water and nutrients and their metabolism varies with ambient temperature. Anthropogenic change affects each of these factors either globally ($CO_2$, temperature and light) or regionally in the tropics (precipitation, nutrients and possibly light) and must, therefore, also affect plant function [39].

Atmospheric $CO_2$ concentrations have increased by 30% since the 19th century. This might increase photosynthetic carbon uptake, particularly where other resources (i.e. water, nutrients and light) are not limiting. This will also decrease transpirational water loss when plants respond by reducing stomatal aperture.

Tropical temperatures have increased by 0.26°C per decade since the 1970s, with minimum night-time temperatures increasing more rapidly than day-time temperatures [65]. Global climate models driven by anthropogenic greenhouse gas emissions predict overall increases in tropical temperatures of 1–4°C in the 21st century [1]. Higher temperatures increase respiratory $CO_2$ losses by all plants [55], and higher day-time temperatures might also affect photosynthesis [39].

Solar irradiance penetrating the atmosphere decreased by 4% to 6% from ~1960 until the late 1980s and has increased by a similar amount since then [66,67]. The cause is believed to be anthropogenic loading of the atmosphere with particulates followed by effective air pollution control, economic change in Eastern Europe, and recovery from the 1991 eruption of Mt Pinatubo [67]. Solar irradiance limits net primary production by closed-canopy tropical forests because leaf area indices ($m^2$ of leaf area per $m^2$ of ground area) range from four to six or seven and heavy shade limits photosynthetic carbon uptake by most leaves. Experimental augmentation of light increased carbon uptake, stem elongation and reproduction by a tropical canopy tree [58], confirming that changes in solar irradiance will have large effects on forest carbon balance and dynamics.

Precipitation is unchanged since the 1970s in tropical America, has decreased significantly in tropical Asia, and has decreased more strongly in Africa, particularly across the northern margin of the African moist tropics [65]. Global climate models predict that tropical precipitation will change regionally with local increases of as much as 8% and local decreases of as much as 35% [1]. Reduced precipitation will limit seasonally dry tropical forests by extending the seasonal drought.
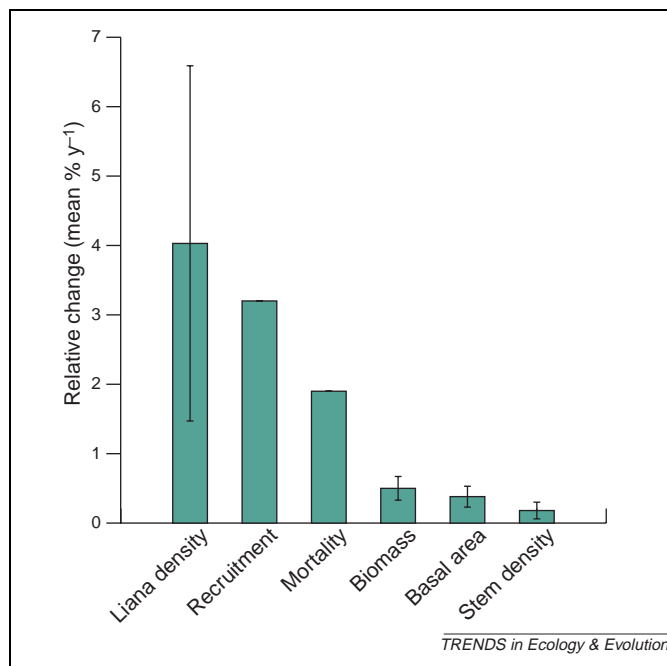
Nitrogen deposition falls off with distance from human sources and is now relatively modest ($1–7.5 \, kg \, ha^{-1} \, y^{-1}$) over most extant tropical forests [68]. Much higher levels ($10–50 \, kg \, ha^{-1} \, y^{-1}$) are projected for 2050 as industry and fertilizer use intensifies [68]. Deposition is greatest in tropical Asia, intermediate in tropical Africa, and lowest in tropical America [68]. The deposition of other pollutants is often well correlated with nitrogen deposition [39]. Multiple pollutants (e.g. nitrogen, ozone, sulfates, etc.) are also likely to stress tropical forests.

To summarize, remote anthropogenic drivers have altered all aspects of the abiotic environment that influence plant function in the tropics. Although forest plants are likely to respond to these changes, the size, and even the direction, of the net response is unclear.



**Figure 2.** Relative change (mean % $y^{-1}$ ± 95% CI) in various indices of the structure and dynamics of old-growth Neotropical forests [29–33]. All values are for the most inclusive data set and incorporate the original author's corrections for possible biases. I annualized recruitment and mortality rate changes assuming exponential change between mean values reported for two census intervals in [31].

usually 10 cm in diameter at breast height (dbh), and median plot area is ~1 ha. Significant changes in tree species composition have been detected from repeated censuses of such plots in the central Amazon [29]. The RAINFOR network brings together investigators with similar data from across the Amazon (http://www.geog.leeds.ac.uk/projects/rainfor/). RAINFOR authors have recently reported significant increases in recruitment rates, mortality rates, aboveground biomass, basal area, stem density and liana stem density for old-growth forests [30–33]. The reported rates of change are quite astonishing (Figure 2). A hectare of forest that initially supported $200 \, Mg \, ha^{-1}$ and $600 \, stems \, ha^{-1}$ would just one decade later support $210 \, Mg \, ha^{-1}$ and $611 \, stems \, ha^{-1}$. Changes of this magnitude involve globally significant amounts of carbon and should be of central importance to most biologists working in tropical forests because their study organisms are adjusting to rapid changes in forest structure and dynamics.

*The evidence questioned*
The first report of rapid change from repeated censuses of lowland tropical forest plots was published in 1994 [34,35], and possible methodological biases were soon being discussed [36–38]. RAINFOR authors have evaluated many of these biases and conclude that rapid change is real [31–33,39,40]. This discussion has, however, overlooked two possibilities.

First, increases in recruitment, stem density, basal area and aboveground biomass could reflect the discovery of previously overlooked trees as census personnel changed. Trees, particularly small ones, are inevitably overlooked when plots are first censused. Known trees are systematically relocated in subsequent censuses, but newly

addressing the response of a resident lowland tropical forest animal to climate change. The evidence for plants is also limited and sometimes contradictory [29–40]. Here, I emphasize limitations, contradictions and alternative interpretations in the hope of stimulating new analyses of the responses of lowland tropical forests to global change.

*The changing structure and dynamics of lowland tropical forests*
The evidence for change in old-growth tropical forests comes mainly from censuses of the woody stems of trees and lianas that are larger than a threshold size in fully enumerated plots [29–33]. The threshold stem size is

recruited trees and previously overlooked trees might not be located. The RAINFOR plots were also established by many different investigators with many different objectives. For example, zoologists interested in stand-level fruit production or botanists interested in local diversity might have tended to overlook sterile trees near the minimum size threshold. Many plots were subsequently recensused by RAINFOR personnel. The possible bias that might result could be evaluated by tracking changes in census personnel and apparent plant community responses.

The implicit assumption of equilibrium and the use of minimum size thresholds raises a second possible bias. Forest dynamics and structure should be stable at equilibrium. Thus, any spatially consistent temporal trend becomes evidence for an effect of global change. Alternatively, most forests might not be at equilibrium but might instead be recovering from past disturbance. In this case, a spatially consistent temporal trend would be consistent with widespread disturbance. Have sites scattered widely across the Neotropics been disturbed recently? More precisely, have disturbances occurred in the relevant past, but not since tree plots were first established during the 1970s (only one of 97 RAINFOR plots was established earlier, in 1967 [31])? The relevant past reaches back several centuries because tropical trees routinely survive this long. For example, when 20 emergent trees from the central Amazon were $^{14}$C dated, the youngest individual was >200-years old, six individuals were >600 years old, and the oldest individual was >1400 years old [41].

At least three types of widespread disturbance have occurred over the past few centuries. First, the Spanish Conquest precipitated the collapse of many Amerindian cultures and initiated widespread secondary forest succession beginning 500 years ago in Mesoamerica and as recently as 300 years ago in parts of the Amazon [42–44]. Second, climate fluctuations associated with a ∼200–year periodicity in solar activity repeatedly destabilized pre-Colombian cultures across the Neotropics and would have impacted forests most recently during the early 1800s [45]. Third, severe El Niño events have brought drought that can increase tree mortality and the risk of forest fires across southern Mesoamerica, the Guiana Shield and the northern and eastern Amazon Basin [46,47]. These three widespread disturbances combined could provide a suitable composite of continental-scale disturbances, indicating that widely scattered forest plots might indeed be recovering from disturbances that occurred decades if not centuries ago.

Disturbance introduces cohorts of trees of similar age. The even-aged cohort might include an entire stand after a severe disturbance (i.e. fire or agricultural clearing) or a modest proportion of the trees in a stand after a moderate disturbance (i.e. drought or flooding). In either case, the even-aged cohort joins the forest canopy and will thin through time. Given the long lifetimes of tropical trees [41], the familiar signature of a thinning stand should be detectable for centuries. Aboveground biomass and basal area should increase, recruitment should be infrequent, and stem density and mortality should decrease as the smaller suppressed trees gradually die and the survivors grow.

The use of minimum size thresholds when investigating closed-canopy forests could complicate this signal. Several small trees are likely to grow past the minimum size threshold and 'recruit' into the censused population for each canopy tree that dies and falls to form a forest gap. Thus, recruitment will exceed mortality at the scale of a single treefall gap. At equilibrium, this localized burst of recruitment would be offset by mortality elsewhere as recruits died in older, recovering gaps. When past disturbance has instead established an even-aged cohort of canopy trees, suitably old gaps will be relatively rare and the rate of new gap formation and subsequent recruitment will outpace mortality as the even-aged cohort thins. Hence, recruitment will appear to increase before mortality. This is a robust outcome of the RAINFOR analyses [31]. Stem density will also increase because several small recruits replace each canopy tree that fell to create a gap. Thus, the use of minimum size thresholds in closed-canopy forests complicates the familiar pattern of change expected for a thinning stand.

RAINFOR authors have previously discounted past disturbance as a cause of observed changes in forest dynamics because increases in recruitment and stem density could not be reconciled with recovering, thinning stands. This possibility now needs to be reevaluated. RAINFOR authors have also discounted El Niño events as a source of disturbance because two very strong events occurred during 1982–1983 and 1997–1998 after most tree plots were established [31,39]. The most severe regional drought coincided with the 1925–1926 El Niño event, however, when fires were widespread and the Amazon reached the lowest level yet recorded at Manaus [48,49]. More importantly, multiple sources of past disturbance need to be evaluated. Soil charcoal deposits left by prehistoric fires have been found near three RAINFOR sites [42,50,51], which suggests that these, and possibly other sites, might be recovering from past disturbance. The implications for forest structure and dynamics could be evaluated by contrasting forest plots where the disturbance history is known. There are additional reasons to question the RAINFOR estimates of rates of change in old-growth tropical forests (Box 3) and, thus, independent assessments of the stability of lowland tropical forests are needed.

### Independent evidence of change in lowland tropical forests

To my knowledge, there have been four independent attempts to detect long-term trends that might reflect global change in lowland tropical forests. On Barro Colorado Island (BCI), Panama, the old-growth forest has escaped fire and agriculture for at least 1500 years [52]. Here, aboveground biomass was almost constant between 1985 and 2000 over 50 hectares where all stems >1 cm in dbh were censused at five-year intervals [38]. The contribution of lianas to total leaf litter production increased, however, from ∼9% to 13% between 1986 and 2002, respectively [53]. In the Kibale National Park, Uganda, a 30-year record compiled from four shorter

**Box 3. Limits on net carbon uptake by old-growth tropical forests**

Recent reports of net carbon uptake by old growth tropical forests sometimes exceed the size of the missing global carbon sink [69]. Estimates range from $\sim 0.5$ Mg C ha$^{-1}$ y$^{-1}$ for repeated censuses of forest inventory plots [33] to 1–6 Mg C ha$^{-1}$ y$^{-1}$ for eddy flux measurements of net ecosystem $CO_2$ exchange [70,71]. Three types of evidence now suggest that these values are too high.

The eddy flux measurements are suspect for two reasons. The method models air movement and $CO_2$ concentrations between the vegetation and the atmosphere. The model assumptions fail at the low wind speeds commonly observed at night in tropical forests, which alone could fully explain the reports of substantial net carbon uptake by tropical forests [70]. The second possibility is that early eddy flux studies might have been conducted in maturing forests, where net $CO_2$ uptake is to be expected. Large net $CO_2$ losses have recently been reported from an Amazonian old-growth forest [71]

A forest dynamics model indicates that the more modest net uptake values of $\sim 0.5$ Mg C ha$^{-1}$ y$^{-1}$ might also be too high [72]. The model incorporated tree mortality, growth and recruitment rates observed for the central Amazon. Growth rates were then increased by 25%, which is the maximum increase observed when $CO_2$ is experimentally doubled in the presence of ample light, water and nutrients [72]. Model simulations demonstrated that the maximum potential increase in aboveground biomass attributable to increased atmospheric $CO_2$ was much less that the increase observed from repeated plot censuses [72]. Either a more potent limiting factor has increased (light is a possibility [39]) or the central Amazonian forests are recovering from past disturbance [72,73].

The final line of evidence that suggests limited potential for increased carbon sequestration in old-growth tropical forests concerns levels of carbon storage [69]. Trees store carbon in their tissues as non-structural carbohydrates, and the tropical trees that have been examined have consistently high non-structural carbohydrate concentrations [69,74]. This suggests that current photosynthesis levels meet, or even exceed, the carbon requirements of maintenance and growth. Forest trees with large carbon stores at current atmospheric $CO_2$ concentrations and light levels are unlikely to sequester still more carbon in response to future increases in either resource unless some additional limiting resource is also augmented [69,74].

records suggests changing levels of reproductive activity by forest trees [54]; and, at La Selva, Costa Rica, diameter growth rates decreased among surviving individuals for cohorts of nine species measured annually for 17 years [55]. To summarize, the four independent studies confirm that lianas are increasing in importance on BCI and suggest that trees are reproducing more often at Kibale; they also indicate that aboveground biomass is almost constant on BCI and that tree growth rates are declining at the La Selva Biological Station.

These mixed outcomes necessitate additional independent assessment of the stability of old-growth tropical forests. At least three assessments are possible based on existing long-term records. First, tree plot data and/or annual tree rings could be used to explore temporal trends in the growth rates of individual trees. Second, the many published studies of plant phenology could be used to explore possible changes in levels of plant reproduction [54]. Finally, the many published studies of fine litter production could be used to explore possible changes in this major component of net primary production. Experiments must also have a crucial role. They have been used to explore the responses of old-growth forests to increases [56] and decreases [57] in moisture availability, increases

in light availability [58] and increases in $CO_2$ concentrations for individual branches of canopy trees [59] and for understorey seedlings [60]. The tropics lack a single forest-level elevated $CO_2$ experiment and have very few, if any, long-term experiments in secondary forest. Until new data become available, we must accept the available evidence indicating that global change is causing a massive restructuring of lowland tropical forests with rapid increases in aboveground biomass, basal area, stem density, mortality, recruitment and the relative importance of lianas and canopy tree species at the expense of understorey tree species [29–33].

## The future of tropical forests

The broad outline of the future of tropical landscapes is clear. As the populations of tropical countries increase by two billion over the next 25 years, agriculture will replace extensive tracts of old-growth forest [61]. Elsewhere, secondary forests will become more important as degraded land is abandoned and urbanization intensifies [13,14]. Given that 18% of moist and humid tropical forests and 9% of dry tropical forests have governmental protection [21], future tropical landscapes will also include islands of secondary forest and protected old-growth forest isolated in a sea of land converted to agriculture and other human uses. This resembles modern temperate landscapes except more old-growth forest is likely to survive in the tropics.

The future of those surviving tropical forests is uncertain. There is no information about the possible responses of secondary tropical forests to global change, and old-growth forests might already be undergoing a massive restructuring (Figure 2) [29–33]. Positive feedback might intensify global change effects; for example, an increase in tree mortality might favor the proliferation of lianas that then further increase tree mortality [30,62]. It is equally easy, however, to imagine negative feedback mechanisms. For example, the proliferation of lianas might favor tree species with straight trunks, smooth bark and other traits that inhibit lianas. In my opinion, the present understanding of long-term change in tropical forests is too limited to speculate about possible feedback mechanisms.

Other direct effects can be anticipated, however. Many of the remaining forests will be degraded and valuable timber will often be removed. The well known influences of edges and fragmentation will alter the dynamics and structure of many surviving forests as land converted to human use comes to dominate the landscape [8]. More exotic species will invade as sources of propagules are established ever closer to these remaining forests [27]. Game species will be removed wherever human poverty and forests meet [25,26].

The scientific community has an important role to play as the future of the tropics unfolds [63]. Basic research will help to understand the dimensions and mechanisms of forest responses to anthropogenic forcing. Conservation scientists will help to mitigate the number of species lost to extinction by enhancing the effectiveness of the network of protected areas [21,22]. Other applied research will help to rehabilitate degraded lands and to improve agricultural yields and living standards. The tropics support over half

of all species and over two-thirds of all people. Without an appropriate commitment from the scientific community, the two are unlikely to continue to coexist.

## References

1 IPCC (2002) *Climate Change 2001: The Scientific Basis*, Cambridge University Press
2 Dirzo, R. and Raven, P.H. (2003) Global state of biodiversity and loss. *Annu. Rev. Environ. Resources* 28, 137–167
3 United Nations (2004) *World Urbanization Prospects: The 2003 Revision*, UN Department of Economic and Social Affairs
4 Pimm, S.L. and Askins, R.A. (1995) Forest losses predict bird extinctions in eastern North America. *Proc. Natl. Acad. Sci. U. S. A.* 92, 9343–9347
5 Ramankutty, N. and Foley, J. (1999) Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochem. Cycles* 13, 997–1027
6 Hansen, M.C. and DeFries, R.S. (2004) Detecting long-term global forest change using continuous fields of tree-cover maps from 8-km Advanced Very High Resolution Radiometer (AVHRR) data for the tears 1982–99. *Ecosystems* 7, 695–716
7 Fearnside, P.M. and Barbosa, R.I. (2004) Accelerating deforestation in Brazilian Amazonia: towards answering open questions. *Environ. Conserv.* 31, 7–10
8 Laurance, W.F. (2004) Forest–climate interactions in fragmented tropical landscapes. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359, 345–352
9 Skole, D. and Tucker, C.J. (1993) Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* 260, 1905–1910
10 Achard, F. *et al.* (2002) Determination of deforestation rates of the world's humid tropical forests. *Science* 297, 999–1002
11 Perz, S.G. and Skole, D.L. (2003) Social determinants of secondary forests in the Brazilian Amazon. *Soc. Sci. Res.* 32, 25–60
12 Perz, S.G. and Skole, D.L. (2003) Secondary forest expansion in the Brazilian Amazon and the refinement of forest transition theory. *Soc. Nat. Res.* 16, 277–294
13 Aide, T.M. and Grau, H.R. (2004) Ecology – globalization, migration, and Latin American ecosystems. *Science* 305, 1915–1916
14 Wright, S.J. and Muller-Landau, H.C. The future of tropical forest species. *Biotropica* (in press)
15 Dunn, R.R. (2004) Recovery of faunal communities during tropical forest regeneration. *Conserv. Biol.* 18, 302–309
16 Chazdon, R.L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst* 6, 51–71
17 Lugo, A.E. and Helmer, E. (2004) Emerging forests on abandoned land: Puerto Rico's new forests. *For. Ecol. Manage.* 190, 145–161
18 Myers, N. *et al.* (2000) Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858
19 Brooks, T.M. *et al.* (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* 16, 909–923
20 Janzen, D.H. (1988) Tropical dry forests: the most endangered major tropical ecosystem. In *Biodiversity* (Wilson, E.O., ed.), pp. 130–137, National Academy Press
21 Brooks, T.M. (2004) Coverage provided by the global protected-area system: is it enough? *Bioscience* 54, 1081–1091
22 Rodrigues, A.L. (2004) Global gap analysis: priority regions for expanding the global protected-area network. *Bioscience* 54, 1092–1100
23 Curran, L.M. (2004) Lowland forest loss in protected areas of Indonesian Borneo. *Science* 303, 1000–1003
24 Bruner, A.G. *et al.* (2001) Effectiveness of parks in protecting tropical biodiversity. *Science* 291, 125–128
25 Fa, J.E. *et al.* (2003) Bushmeat and food security in the Congo Basin: linkages between wildlife and people's future. *Environ. Conserv.* 30, 71–78
26 Wright, S.J. (2003) The myriad effects of hunting for vertebrates and plants in tropical forests. *Perspect. Plant Ecol. Evol. Syst.* 6, 73–86
27 Fine, P.V.A. (2002) The invasibility of tropical forests by exotic plants. *J. Trop. Ecol.* 18, 687–705
28 Walther, G. (2002) Ecological responses to recent climate change. *Nature* 416, 389–395
29 Laurance, W.F. *et al.* (2004) Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* 428, 171–175
30 Phillips, O.L. *et al.* (2002) Increasing dominance of large lianas in Amazonian forests. *Nature* 418, 770–774
31 Phillips, O.L. *et al.* (2004) Pattern and process in Amazon tree turnover 1976–2001. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359, 381–407
32 Lewis, S.L. *et al.* (2004) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359, 421–436
33 Baker, T.R. *et al.* (2004) Increasing biomass in Amazonian forest plots. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359, 353–365
34 Phillips, O.L. *et al.* (1998) Changes in the carbon balance of tropical forest: evidence from long-term plots. *Science* 282, 439–442
35 Phillips, O.L. and Gentry, A.H. (1994) Increasing turnover through time in tropical forests. *Science* 263, 954–958
36 Clark, D.A. (2002) Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecol. Appl.* 12, 3–7
37 Clark, D.A. (2004) Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359, 477–491
38 Chave, J. *et al.* (2003) Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *J. Ecol.* 91, 240–252
39 Lewis, S.L. *et al.* (2004) Fingerprinting the impacts of global change on tropical forests. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359, 437–462
40 Phillips, O.L. *et al.* (2002) Changes in the biomass of tropical forests: evaluating potential biases. *Ecol. Appl.* 12, 576–587
41 Chambers, J.Q. *et al.* (1998) Ancient trees in Amazonia. *Nature* 391, 135–136
42 Bush, M.B. *et al.* (1989) A 6000 year history of Amazonian maize cultivation. *Nature* 340, 303–305
43 Heckenberger, M.J. *et al.* (2003) Amazonia 1492: pristine forest or cultural parkland? *Science* 301, 1710–1714
44 Willis, K.J. *et al.* (2004) How "virgin" is virgin rainforest. *Science* 304, 402–403
45 Schimmelmann, A. *et al.* (2003) Palaeoclimatic and archaeological evidence for a ∼200-yr recurrence of floods and droughts linking California, Mesoamerica and South America over the past 2000 years. *Holocene* 13, 763–778
46 Cochrane, M.A. (2003) Fire science for rainforests. *Nature* 421, 913–919
47 Nepstad, D. *et al.* (2004) Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. *Glob. Change Biol.* 10, 704–717
48 Schöngart, J. *et al.* (2004) Teleconnection between tree growth in the Amazonian floodplains and the El Niño-Southern Oscillation effect. *Glob. Change Biol.* 10, 683–692
49 Sombroek, W. (2001) Spatial and temporal patterns of Amazon rainfall. *Ambio* 30, 388–396
50 Piperno, D.R. and Becker, P. (1996) Vegetation history of a site in the central Amazon Basin derived from phytolith and charcoal records from natural soils. *Quat. Res.* 45, 202–209
51 Sanford, R.L. *et al.* (1985) Amazon rainforest fires. *Science* 227, 53–55
52 Piperno, D. (1990) Fitolitos, arquelogia y cambios prehistoricos de la vegetacion en un lote de cincuenta hectáreas de la isla de Barro Colorado. In *Ecologia de un Bosque Tropical* (Leigh, E.G., Jr. *et al.*, eds), pp. 153–156, Smithsonian Institution Press
53 Wright, S.J. *et al.* (2004) Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85, 484–489
54 Chapman, C.A. (2005) A long-term evaluation of fruiting phenology: importance of climate change. *J. Trop. Ecol.* 21, 31–45
55 Clark, D.A. *et al.* (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984-2000. *Proc. Natl. Acad. Sci. U. S. A.* 100, 5852–5857
56 Cavelier, J. *et al.* (1999) Effects of irrigation on fine root biomass and production, litterfall and trunk growth in a semideciduous lowland forest in Panama. *Plant Soil* 211, 207–213

57 Nepstad, D.C. *et al*. (2002) The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *J. Geophys. Res.* 107, 1–18

58 Graham, E.A. *et al*. (2003) Cloud cover limits net $CO_2$ uptake and growth of a rainforest tree during tropical rainy seasons. *Proc. Natl. Acad. Sci. U. S. A.* 100, 572–576

59 Lovelock, C.E. *et al*. (1999) Effects of elevated CO2 concentrations on photosynthesis, growth and reproduction of branches of the tropical canopy tree species, *Luehea seemannii* Tr. & Planch. *Plant Cell Environ.* 22, 49–59

60 Würth, M.K.R. *et al*. (1998) *In situ* responses to elevated CO2 in tropical forest understorey plants. *Funct. Ecol.* 12, 886–895

61 Geist, H.J. and Lambin, E.F. (2002) Proximate causes and underlying driving forces of tropical deforestation. *Bioscience* 52, 143–150

62 Körner, C. (2004) Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359, 493–498

63 Bawa, K.S. *et al*. (2004) Tropical ecosystems into the 21st century. *Science* 306, 227–228

64 FAO (2000) *Global Forest Resource Assessment 2000 – Main Report*, FAO Forestry Paper 140, United Nations Food and Agricultural Organization

65 Malhi, Y. and Wright, J. (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359, 311–329

66 Pinker, R.T. *et al*. (2005) Do satellites detect trends in surface solar radiation? *Science* 308, 850–854

67 Wild, M. *et al*. (2005) From dimming to brightening: decadal changes in solar radiation at Earth's surface. *Science* 308, 847–850

68 Galloway, J.N. *et al*. (2004) Nitrogen cycles: past, present, and future. *Biogeochemistry* 70, 153–226

69 Körner, C. (2003) Carbon limitation in trees. *J. Ecol.* 91, 4–17

70 Martens, C.S. *et al*. (2004) Radon fluxes in tropical forest ecosystems of Brazilian Amazonia: night-time $CO_2$ net ecosystem exchange derived from radon and eddy covariance methods. *Glob. Change Biol.* 10, 618–629

71 Saleska, S.R. *et al*. (2004) Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. *Science* 302, 1554–1557

72 Chambers, J.Q. *et al*. (2004) Response of tree biomass and wood litter to disturbance in a Central Amazon forest. *Oecologia* 141, 596–614

73 Chambers, J.Q. and Silver, W.L. (2004) Some aspects of ecophysiological and biogeochemical responses of tropical forests to atmospheric change. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359, 463–476

74 Würth, M.K.R. *et al*. (2005) Non-structural carbohydrate pools in a tropical forest. *Oecologia* 143, 11–24