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Five anthropogenic drivers—land use change, wood extraction, hunting, atmospheric change, climate change—will largely determine the future of tropical forests. The geographic scope and intensity of these five drivers are in flux. Contemporary land use change includes deforestation ($\sim 64,000 \text{ km}^2 \text{ yr}^{-1}$ for the entire tropical forest biome) and natural forests regenerating on abandoned land ($\sim 21,500 \text{ km}^2 \text{ yr}^{-1}$ with just 29% of the biome evaluated). Commercial logging is shifting rapidly from Southeast Asia to Africa and South America, but local fuelwood consumption continues to constitute 71% of all wood production. Pantropical rates of net deforestation are declining even as secondary and logged forests increasingly replace old-growth forests. Hunters reduce frugivore, granivore and browser abundances in most forests. This alters seed dispersal, seed and seedling survival, and hence the species composition and spatial template of plant regeneration. Tropical governments have responded to these local threats by protecting 7% of all land for the strict conservation of nature—a commitment that is only matched poleward of 40°S and 70°N . Protected status often fails to stop hunters and is impotent against atmospheric and climate change. There are increasing reports of stark changes in the structure and dynamics of protected tropical forests. Four broad classes of mechanisms might contribute to these changes. Predictions are developed to distinguish among these mechanisms.

Keywords: above-ground biomass; atmospheric change; climate change; deforestation; fuel wood; hunting; land-use change; protected areas; reforestation; secondary forest; tree turnover; timber

Introduction

Anthropogenic change to tropical forests will impact human well-being in several ways. Tropical forests are a key component of the global carbon cycle and contribute more than 30% of terrestrial carbon stocks and net primary production.^{1,2} Tropical forests are a key component of global hydrological cycles and evapotranspiration from tropical forests contributes to precipitation at higher latitudes as well as within the tropics.³ Tropical forests are the epicenter of global biodiversity and support 50% of all described species and an even larger percentage of undescribed species.⁴ Tropical forests provide drinking water, fuel wood, and animal protein to perhaps 500 million people.⁵ Anthropogenic changes to these forests have the potential to alter global carbon and hydrological cycles, impact global biodiversity, and af-

fect the livelihoods of many of the world's poorest people.

Anthropogenic change affects every tropical forest today. The modern drivers of tropical forest change include ancient human activities—hunting, agriculture, and wood extraction—scaled up to unprecedented levels by new technologies and population growth. The modern drivers also include unforeseen consequences of the Industrial Revolution including changes to the composition of the atmosphere and global climate. The mix of drivers differs with proximity to modern infrastructure. Remote forests escape clearing for agriculture and fuel wood extraction, are increasingly accessible to hunters and commercial timber extraction, and bear the full brunt of many aspects of global atmospheric and climate change including rising atmospheric CO_2 concentration and temperature. Every tropical forest is affected.

This review concerns the consequences. What will tropical forests look like in the future? The review is divided into three sections. The first attempts a comprehensive overview of the modern drivers of forest change and emphasizes temporal trends in their intensity and geographic reach. An understanding of the mechanistic causes of organism-level and forest-level responses is an essential precursor to model and anticipate the full implications of anthropogenic change for tropical forests. With this in mind, the second section of this review focuses on subtle changes observed in remote forests and forests in successful protected areas. Here, drivers with obvious impacts—contemporary land-use change and wood extraction—are absent; however, cryptic drivers—atmospheric and climate change and possibly hunting—are present. I evaluate the evidence for and hypothesized causes of change in forest plant communities under these circumstances. The final section of this review evaluates the implications for the conservation of biodiversity in the new human-modified forests.

Subtropical and tropical forests include four biomes.⁶ The four biomes and their potential area before agriculture are moist broadleaf (19.8×10^6 km²), dry broadleaf (3.01×10^6 km²), coniferous (0.71×10^6 km²), and mangrove (0.35×10^6 km²) forests. The geographically extensive moist broadleaf forest biome is the crown jewel of global biodiversity. As just one example, this single biome supports 20,000 species of terrestrial vertebrates and far more endemic terrestrial vertebrate species than the 13 remaining terrestrial biomes combined.⁷ Perhaps not surprisingly, most tropical literature focuses on moist forest or pools biomes. This masks relatively severe conservation problems in the three smaller tropical forest biomes. For example, about 55%, 40%, and just 25% of the dry broadleaf, coniferous, and moist broadleaf biomes had been converted to human use by 1990, respectively⁷ (Mangroves were not evaluated.). Nonetheless, I consider tropical forests in the broad sense because individual biomes cannot be extracted from most studies and because key information is missing for the three smaller biomes.

Drivers of anthropogenic change

This section updates two aging reviews of the drivers of anthropogenic change in tropical forests^{8,9} and

extends those reviews through an emphasis on geographic extent and recent temporal trends. I divide the drivers into the following five broad categories: land-use change, wood extraction, hunting and defaunation, atmospheric change, and climate change.

Drivers—land-use change

Past land-use change

Humans have modified tropical forests for at least 10,000 years.¹⁰ Hunter gatherers used fire to limit forest expansion, open forest undergrowth, and replace forest with grasses and open woodlands. Many crops were first domesticated in the tropics, including bananas in New Guinea, rice in China, yams in Africa, and corn in Mexico. Agriculture based on these and other tropical crops has been practiced for millennia throughout the tropics with the exception of Australia. Iron tools greatly increased the potential to convert forest to agriculture at the beginning of the Iron Age in the Old World Tropics and with the arrival of Europeans in Australia and the New World Tropics.

Tropical land-use change has waxed and waned for millennia. Several monumental cultures rose and fell with dramatic impacts on forest cover in northern Mesoamerica.¹¹ The first Spaniards found large agricultural populations in the Greater Antilles, Mexico, and the dry Pacific plain of Central America.^{12,13} Even the wet Caribbean coast of southern Central America, which supports extensive rain forest today, was largely deforested in 1498.¹³ Soil charcoal ¹⁴C dates implicate humans as an agent of ancient Amazonian fires.¹⁴ Amazonian fire frequency “surged” between 200 and 600 AD, fluctuated around a high level until 1600 and then abruptly returned to low background levels. Changes in fire frequency at 200–600 AD and 1600 coincide with archeological evidence for the adoption of agriculture and depopulation precipitated by the arrival of Europeans, respectively.¹⁴ A recently discovered urban culture in the Upper Xingu region rose and fell at about these dates.^{15,16} In Africa, prehistoric people smelted iron using charcoal as fuel, soil charcoal and pottery are frequent, and the prehistoric imprint on modern forests is often evident.^{17,18} Anthropogenic pressure on forests was not disrupted by European contact in Africa and Asia, and the modern wave of tropical deforestation overlays prehistoric land-use change throughout the tropics.^{19,20}

Historical cropland inventory data suggest two and in some regions three phases of tropical land-use change between 1700 and 1992.²¹ In the first, forest was converted to cropland at a slow steady rate. The second phase was marked by continuous acceleration in the rate of forest-to-cropland conversion. The second phase began about 1800 in South Asia, 1850 in Southeast Asia, and the late 1800s in tropical Africa, Mexico, and Central and South America. A third phase marked by a decelerating forest-to-cropland conversion rate began about 1950 in Mexico and Central America and 1980 in South Asia and South America. Although Ramankutty and Foley²¹ omit the conversion of forest to uses other than cropland, their analysis captures the broad temporal dynamic of tropical deforestation from 1700 to 1992.

Contemporary land-use change

Contemporary tropical land-use change is surprisingly poorly documented. The best known estimates of forest area are compiled from national forest inventories by the UN Food and Agricultural Organization. These FAO Forest Resource Assessments reported large net losses of tropical forest cover between 1980 and 2005.²² The quality of the national forest inventories varies widely among countries and through time; however, and back projections to improve earlier estimates of forest area largely offset the reported losses.²² Grainger²² concludes “. . . that it is difficult to demonstrate [tropical forest decline] convincingly using available tropical forest area data . . .” and assembles evidence consistent with the possibility that moist tropical forest area has changed little since the 1970s, with the area deforested being largely offset by reforestation.

Satellite imagery readily detects the abrupt change from tall forest to cleared land that accompanies deforestation. Four pantropical analyses of land-use change based on satellite imagery provide five estimates of deforestation rates since the 1980s (Table 1). Conversion to small holder agriculture is the most frequently reported driver of deforestation in all regions.²³ Unfortunately, remote sensing studies of land-use change use different methods to evaluate slightly different biomes, regions and time intervals, and estimates of forest area and deforestation rates vary accordingly (See forest definitions and footnotes to Table 1). Biomes, geographic

coverage, and methods are now being standardized.^{24,25} In the meantime despite methodological differences, several robust results emerge. Tropical forest covers approximately 11,000,000 km² today or an area 20% larger than the United States including Alaska. Absolute deforestation rates are greatest in the Americas, intermediate in Asia, and lowest in Africa. Relative deforestation rates expressed as a percentage of forest cover averaged 0.58%/yr for the tropics as a whole and are greatest in Asia.

Satellite imagery is less good at detecting the relatively subtle change from degraded pasture or cropland to the first stages of forest regeneration on abandoned land. Nevertheless, the pantropical analyses of land-use change based on satellite imagery provide four estimates of newly tree covered land since the 1980s (Table 1). The FAO²⁶ reports transitions among 10 forest cover types, which precludes comparisons with the three remaining estimates. New tree cover averaged 10,700 km²/yr (± 700 km²/yr = ± 1 SE) or about 17% of the pantropical deforestation rate of 64,000 km²/yr (± 3200 km²/yr) for these three remaining estimates (Table 1). This figure underestimates the area of new tree cover for two reasons in addition to the difficulty of detecting the early stages of forest regeneration from satellite imagery.²⁴ First, one study estimated land cover change from a stratified random sample of 30-m resolution Landsat imagery focused on known hotspots of deforestation.²⁷ Hotspots of deforestation are unlikely to also be hotspots of reforestation, and an alternative sample focused on hotspots of forest regeneration would detect greater increases in tree cover. A second study used 8-km resolution satellite imagery.²⁸ Pasture and cropland are often abandoned at much smaller spatial scales. The estimates of new tree cover also include plantations as well as naturally regenerating forests. Better estimates of natural forest regeneration are needed.²⁴

The FAO provides an independent estimate of plantation area for 1990, 2000, and 2005 compiled from national forest inventories.²⁹ The total area in plantations grew by 5300 km²/yr in the 1990s and 5400 km²/yr between 2000 and 2005 across West and Central Africa, South and Southeast Asia, and Central and South America. The 1990s figure can be compared with the estimate of 10,100 km²/yr of newly tree covered land obtained from

Table 1. Potential and extant forest area and rates of deforestation and reforestation estimated from satellite imagery for the tropics

Definition of forest	Year(s)	Africa	Americas	Asia	Pantropical
Potential forest area (km ²)					
Evergreen and deciduous ^a	—	1,890,000	9,390,000	5,740,000	17,020,000
Extant forest area (km ²)					
Dense (≥80%) tree cover ^b	1997	1,720,000	7,010,000	1,990,000	10,720,000
Evergreen and seasonal ^c	1997	1,930,000	6,530,000	2,700,000	11,160,000
Closed (>40% tree cover) ^d	2000	2,630,000	6,790,000	1,940,000	11,350,000
Deforestation rate (km/yr)					
All tree cover ^b	1984–1990	4300	43,000	18,000	65,000
All tree cover ^b	1990–1997	3700	43,000	26,000	73,000
Evergreen and seasonal ^c	1990–1997	8500	25,000	25,000	59,000
Closed (>40% tree cover) ^d	1990–2000	8400	39,000	20,000	68,000
Humid forest biome ^f	2000–2005	3000	33,000	19,000	55,000
Reforestation rate (km ² /yr)					
All tree cover ^b	1984–1990	5600	2800	3500	11,900
All tree cover ^b	1990–1997	4300	3700	2600	10,600
Evergreen and seasonal ^c	1990–1997	1400	2800	5300	9500
Closed (>40% tree cover) ^d	1990–2000	1100	1300	1100	3500

^aDISCover 1-km resolution satellite imagery supplemented by a model of climax vegetation cover wherever crop cover exceeded 50% or natural vegetation fell below 20%. Calculated from 0.5° latitude-longitude land cover data provided by http://www.sage.wisc.edu/in_depth/global_potveg/global_potveg.html for all land between 23.5°S and 23.5°N.

^bCoarse-resolution AVHRR imagery for all land between the Tropics.²⁸ Trees are defined to be > 5 m tall.

^cCoarse-resolution AVHRR imagery for the “humid tropics” which is defined to include “evergreen and seasonal forest of the tropical humid bioclimatic zone” plus the “dry biome of continental Southeast Asia” and to exclude Mexico and the Brazilian Atlantic coastal forest.²⁷

^dHigh-resolution Landsat imagery for a 10% sample of the tropics stratified by subregion and forest cover. Excludes plantations and fragmented forests. Values are from Table 46.3 of FAO.²⁶

^eHigh-resolution Landsat imagery for a stratified 6.5% sample of the humid tropics (see footnote c). Stratification emphasized deforestation hotspots identified by “environmental and forestry experts.”

^fHigh-resolution Landsat imagery for a stratified 0.32% sample of the humid forest biome as defined by Olson *et al.*⁶ Stratification emphasized deforestation hotspots identified using 500-m resolution satellite imagery.³³

pantropical analyses of satellite imagery for 1990–1997 (Table 1). This comparison suggests that pantropical remote sensing studies detected 4700 km²/yr of natural forest regeneration in the 1990s. Data assembled by Asner *et al.*³⁰ show that this figure substantially underestimates the true extent of natural forest regeneration.

Asner *et al.*³⁰ provide the first pantropical estimate of natural forest regeneration. They identified 23 local, national and regional studies that document “net regrowth lasting about 10 years or more” (as opposed to temporary fallows) through repeated analyses of satellite imagery or extensive ground

surveys. The area of regrowth summed to 235,000 km² or 1.2% of the moist forest biome.³⁰ Their estimate of 1.2% of the moist forest biome is misleading because it was not corrected for the total area surveyed in the 23 studies. I compiled these values, which summed to 56%, 6%, and just 0.0005% of the tropical humid forest biome of the Americas, Asia, and Africa, respectively (Table 2). Natural forest regeneration actually averaged 11.8% (±2.0% = 1 SE) of the area evaluated in the 23 studies (Table 2). It would be inappropriate to extrapolate this order-of-magnitude larger estimate of regrowth area to the entire tropics because Asner *et al.*³⁰ omitted studies

Table 2. Reforestation estimated from repeated analyses of satellite imagery or extensive ground surveys

Country	Ecosystem	Regrowth area (km ²)	Area (km ²)	Regrowth area (%)	Topography	Time-scale	Regrowth rate (km ² /yr)	Source
South America								
Argentina	Tropical moist	50	699	7.2	Hilly	1949–2006	1	153
Bolivia	Humid montane, lowland	1460	34,000	4.3	Mountains	1990–2000	146	154
Brazil	Tropical moist	3991	70,818	5.6	Hilly	1970–1996	154	155
Brazil	Tropical moist	157,973 ^a	5,022,602	3.1	Lowlands	1989–1994 ^a	15,165 ^a	156
Peru	Tropical moist	242	4148	5.8	No info	1986–1997	22	157
Central America and Caribbean								
Costa Rica	Tropical dry and moist	2000	10,200	19.6	Hilly	1960–2000	50	158
Dominican Republic	Tropical moist	2550	16,000	15.9	Mountains	1984–2002	142	159
El Salvador	Tropical dry, moist, wet	4800	21,041	22.8	Mountains	1990–2000	480	160
Honduras	Tropical mesic	101	989	10.2	Mountains	1987–1996	11	161
Mexico	Tropical montane	800	4884	16.4	Mountains	1972–1980	100	162
Mexico	Tropical moist	131	278	47.1	No info	1979–2000	6	163
Mexico	Tropical moist	424	18,703	2.3	No info	1987–1997	42	164
Puerto Rico	Tropical dry, moist, wet	1032	8607	12.0	Mountains	1991–2000	115	165
Panama	Tropical dry, moist, wet	5077	74,927	6.8	Hilly	1992–2000	635	166
Asia/Oceania								
China	Subtropical moist	6	42	14.2	Uplands	1990s	1	167
Laos	Sub-tropical	10,203	48,035	21.2	Uplands	1990s	1020	168
Nepal	Tropical moist	11	111	9.9	Uplands	1980s–90s	1	169
Nepal	Tropical moist	38	543	7.0	Uplands	1980s	4	170
Nepal	Tropical moist	4	254	1.6	Uplands	1980s–90s	—	171
Philippines	Tropical moist	7100	56,066	12.7	Uplands	1988–2002	507	172
Thailand	Tropical moist	100	1215	8.2	Lowlands	1990s	10	173
Vietnam	Tropical moist	37,116	325,500	11.4	Uplands	1990s–2003	2855	174
Africa								
Madagascar	Tropical moist	0.4	11	3.8	Hilly	1980s–90s	—	175

Asner *et al.*³⁰ compiled the 23 studies and their regrowth area. The area evaluated, regrowth area as a percentage of the area evaluated, and regrowth rate are added here.

^aThe value of 157,973 km² of naturally regenerating forest includes all regenerating forests regardless of age, which can be more than 20 years. My estimate of the rate of natural forest regeneration uses only forests less than 5 years old, which constituted 48% of all naturally regenerating forests in the Brazilian Legal Amazon.¹⁵⁶

that lacked regrowth. Still, the 23 regrowth estimates suggest that continent-wide levels of natural forest regeneration are substantially larger than previously realized.

Returning to estimates of the rate of natural forest regeneration, I used the 23 studies assembled by Asner *et al.*³⁰ to calculate regrowth rates (regrowth area divided by the number of years between

surveys) and summed over studies to obtain an estimate of 21,467 km²/yr of natural forest regeneration (Table 2). This figure, which is based on 23 studies that covered just 29% of the humid tropical forest biome, is nearly five times larger than the 4700 km²/yr of natural forest regeneration estimated from pantropical analyses of satellite imagery after correcting for plantations (Table 2). A single study of Amazonian Brazil contributed 15,165 of the 21,467 km²/yr of natural forest regeneration (Table 2). If this study is omitted, the estimate of natural forest regeneration falls to 6300 km²/yr. This reduced estimate is still 35% larger than the 4700 km²/yr estimated from pantropical analyses of satellite images after correcting for plantations; however, the reduced estimate is based on 22 studies that cover just 3.6% of the humid tropical forest biome. The inescapable conclusion is that past analyses of land-use change based on pantropical analyses of satellite imagery have severely underestimated natural forest regeneration.

Taken together the best available estimates of deforestation, natural forest regeneration and plantation establishment are potentially consistent with limited change in the area of tree cover (plantations plus natural forests) over recent decades in the moist tropics. This possibility, which was first raised by Grainger,²² runs counter to an extensive literature. As just one example, Lewis³¹ reviews two of the studies summarized in Table 1, overlooks their reforestation estimates entirely, suggests their deforestation estimates are too low, and defends the much larger and widely discredited deforestation rates compiled by the FAO from national forest inventories.²⁶ Our remarkably different interpretations highlight the need for better tropical land cover data.^{22,24,25}

Future land-use change

Three independent models project surprisingly similar levels of tropical forest cover in 2050 (Table 3). The three models differ in complexity. In the simplest model, Brook *et al.*³² assume the net deforestation rate (d) expressed as the proportion of remaining forest lost each year is constant at present-day levels. This “business as usual” model can be written down as $F_{p+y} = F_p \times (1-d)^y$, where F_p and F_{p+y} represent forest area today and y years into the future, respectively. When parameterized with F_{1997} and 1990s values of d provided by Achard *et al.*²⁷

and Hansen and DeFries³³ (Table 1), this “business as usual” model predicts that 80% and 73% of 1997 tropical forest cover will remain in 2050, respectively (Table 3).

Wright and Muller-Landau³⁴ use a model of intermediate complexity to project future forest cover from human population growth. They first document strong ($r^2 > 0.8$) exponential relationships between population density and the proportion of potential forest area present in 2000 for Africa, the Americas and Asia using 45 countries that supported 89% of tropical forest area in 2000. They then project forest area to 2030 assuming the same exponential forest–population relationships hold in 2030 and population growth follows the medium projection of the United Nations Population Division. I extended these projections to 2050 using high, medium, and low projections for total (rural plus urban) population growth.³⁵ The summed population of the 45 principal tropical forest countries was 2.2 billion in 2000 and is projected to increase to 2.9, 3.6, and 4.1 billion in 2050 under the low, medium, and high projections, respectively. The exponential forest–population relationships project that 64%, 68%, and 71% of 2000 forest cover will remain in 2050 under the low, medium, and high UN population projections, respectively (Table 3).

The Millennium Ecosystem Assessment (MEA) used four model scenarios to project global land-use change.⁷ Each scenario incorporates economic, population, and land-use change as well as vegetation responses to global atmospheric and climate change. Governmental behavior, individual and societal responses to incipient environmental problems and technological innovation including the adoption of biofuels vary among the four model scenarios. Thus, the MEA models a wide range of possible human behaviors. The four MEA scenarios project that 78–89% of 2000 tropical forest cover will remain in 2050 (Table 3).

Land-use change—synthesis

It is widely recognized that environmental conditions have long protected large parts of the subtropical and tropical moist broadleaf biome from permanent conversion to agriculture. Pathogens, insects, and weeds thrive in humid tropical climates and debilitate crops, domesticated animals and all too often people. In addition, high rainfall and ancient

Table 3. Recent projections of global tropical forest cover forward from about 2000 to 2050

Model	Drivers	Input	Remaining forest cover (%)	Source
Business as usual	Constant deforestation rate	Landsat 30-m resolution imagery ^a	80	32
		AVHRR 8-km resolution imagery ^b	73	
Modern forest cover–population density relationship	Population growth	UN high population projection ^c	64	34
		UN medium population projection ^c	68	
		UN low population projection ^c	71	
Global orchestration	Indirect: population, economics, politics, culture, technology Direct: climate change, nutrients, land-use change, invasive species	Global cooperation improves well-being ^d	85	7
Order from strength Adapting Mosaic		National self-interest ^d	78	
		Adaptive management of resources ^d	89	
Technogarden		Technology improves ecosystem services ^d	89	

For each model, forest cover projected to remain in 2050 is expressed as a percentage of extant forest cover in 2000.

^aParameterized with 1990–1997 annual net cover change rates and 1997 forest cover for Africa, Latin America, and Southeast Asia from Table 1 of Achard *et al.*²⁷

^bParameterized with 1984–1997 deforestation rates and 1997 forest cover for Tropical Africa, Tropical Asia, and Latin America from Table 6 of Hansen and DeFries.²⁸

^cParameterized with continent-specific relationships between forest cover and population density, country-specific FAO closed forest cover, and UN population projections for 45 tropical countries that supported 89.4% of extant closed tropical forest in 2000.³⁴

^dValues are from Table 10.4 in Carpenter *et al.*¹⁷⁶

geological formations combine to limit soil fertility over large regions. Much of the evidence for pre-historic anthropogenic impacts on tropical forests comes from dry tropical forests and forest–savannah ecotones.^{14,15} Historical deforestation rates accelerated in the 19th century but deforestation was again concentrated in drier forests.²¹ In 1990, just 25% of the subtropical and tropical moist broadleaf biome had been converted to human use; only the three coldest biomes—temperate coniferous forests, boreal forests and tundra—had lower levels of conversion to human use.⁷ Contemporary hotspots of de-

forestation are once again concentrated in relatively dry and newly accessible forests around the periphery of the moist broadleaf forest biome.^{24,27,28} The wetter forests might yet resist permanent conversion to agriculture; however, even the wetter forests are being replaced by plantations, young secondary and logged forests on a large scale. Extrapolations from current trends suggest that 64–89% of the 11,000,000 km² of tropical forest present in 2000 will remain forested 2050 (Table 3). This forest will probably be concentrated where soils are poorest, topography is most difficult and rainfall is high and

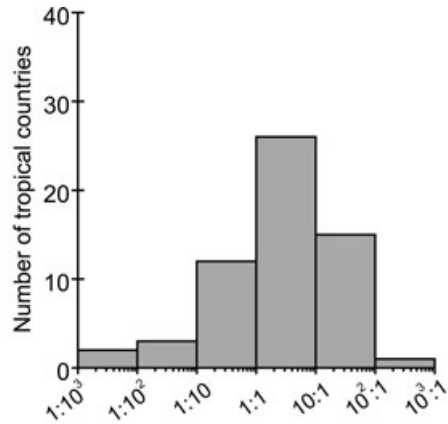
will be increasingly modified by a wide range of human activities to be considered now.

Drivers—wood extraction

Asner *et al.*³⁰ compiled the first global assessment of the extent of logging in the tropics—20% of the tropical forest biome was either actively logged or consigned to logging concessions between 2000 and 2005. About half of this area had already been heavily impacted by land-use change having previously lost more than 50% of its potential forest cover.³⁰ Commercial timber extraction has also reached into the center of Amazonia,³⁶ is expanding rapidly into new areas including Central Africa and Papua New Guinea,^{37,38} and could soon reach the last remote tropical forests.

Government reports of industrial round wood production are consistent with this dire assessment. Global round wood production changed by less than 1% between 1990 and 2005; however, there were large changes in regional production.²⁹ Production fell by 137×10^6 m³/yr across Europe, Russia, China, East Asia, and Southeast Asia. This was nearly offset by increases of 15, 20, 20, and 80×10^6 m³/yr in Central and West Africa, North America, Oceania, and South America, respectively. Among 61 tropical nations that reported wood production for 1990 and 2005, the largest percentage declines were in Indonesia, Malaysia, Philippines, and Thailand, four traditional logging nations of Southeast Asia.²⁹ Five of the 10 tropical nations with the largest percentage increases—Gabon, Surinam, Solomon Islands, Vanuatu, and surprisingly Costa Rica—have not been known for logging, yet industrial round wood constituted more than 80% of their total wood production in 2005. Illegal logging that goes unreported would probably reinforce the evidence that commercial logging is rapidly moving to new tropical countries.

Wood production for fuel is also increasing. The five remaining tropical nations with the largest 1990–2005 increases in wood production are Rwanda, Ghana, Bangladesh, Democratic Republic of the Congo, and Guatemala, and here fuel wood constituted more than 95% of total wood production. In 2005, 63 tropical nations reported total fuel wood production of 695×10^6 m³ and total round wood production of just 290×10^6 m³ (Fig. 1). Wood extraction is a multifaceted problem that affects most tropical forests located



Volume of fuelwood : Volume of industrial roundwood

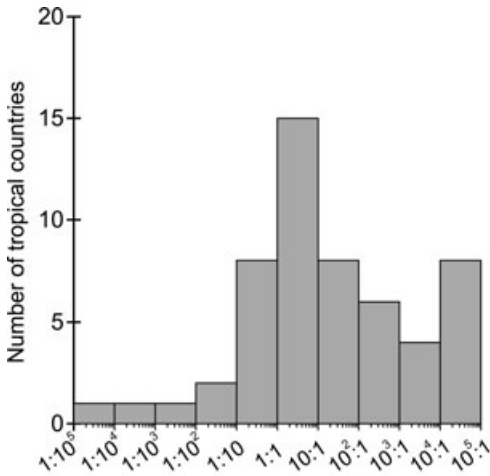
Figure 1. Most tropical countries report greater production of fuelwood than industrial roundwood. Data are from Table 17 of FAO.²⁹

near people and increasingly reaches into remote forests.

National reports of the relative extent of primary and modified natural forests are consistent with the assessment that wood extraction affects most tropical forests. Forty-one of 54 tropical nations reported more modified natural than primary forest in 2005, and 26 reported at least an order of magnitude more modified natural than primary forest (Fig. 2). These modified natural forests exclude plantations and include forests regenerating naturally on abandoned land; however, forests degraded by wood extraction are clearly quantitatively more important.

Drivers—hunting and defaunation

Tropical forests harbor an unmatched diversity of large, charismatic animals. These include birds of paradise, cockatoos, macaws and other parrots, currasows, eagles, fruit pigeons, guans, hornbills, tinamous, toucans and trumpeters among birds and anteaters, bears, cattle and other bovids, cats, civets, deer, elephants, flying foxes, giant armadillos, okapis, olingos, pangolins, peccaries, primates, rhinoceros, sloths, and tapirs among mammals. These and many other large animals have inhabited tropical forests for millions of years, and their ecological interactions with one another, with smaller animals, and with plants help to shape those forests. Hunters have pursued the larger species for their



Area of modified natural forest : Area of primary forest

Figure 2. Most tropical countries report more modified natural forest than primary forest. Modified natural forest includes “. . . selectively logged-over areas, naturally regenerating areas following agricultural land use, areas recovering from human-induced fires, etc. . . .”. Data are from Table 8 of FAO.²⁹ Countries are from Central and South America, South and Southeast Asia, and tropical Sub-Saharan Africa; their geographic centers are in the tropics; and each country reports >1000 km² of forest cover. Botswana, Cameroon, Democratic Republic of the Congo, Equatorial Guinea, Gabon, and Venezuela meet these criteria but did not report forest cover types.

meat and charismatic species for their hides, ornaments, and supposed medicinal properties for millennia. Modern technology (guns, wire snares, battery powered lights, outboard motors) and infrastructure has increased the efficiency of the hunt and also provides access to urban markets and previously remote forests. The result is a “bush meat” crisis.^{39,40}

Many game species have been extirpated or persist only at greatly reduced abundances in otherwise intact forests. The problem is particularly acute in Southeast Asia where human population pressure is greatest. Here, the geographic distributions of many game species have already contracted by 90% or more and extinctions are imminent.⁴¹ The situation is only marginally better in Africa, where 60% of 57 large forest mammal taxa are being harvested at unsustainable levels that threaten their extirpation from the Congo Basin.⁴² No large mammal taxon faces extirpation

throughout the Amazon Basin;⁴² however, hunting intensity varies tremendously across Amazonia and preferred game species are already effectively extirpated from large areas.⁴³ The problem is uniformly worse where once continuous forests have been fragmented by human land uses because the remaining forest fragments are readily accessible to hunters and are often too small to maintain populations of large species.^{39,44} Hunting and defaunation affect an even larger area of tropical forest than does wood extraction.

Many of the persecuted species influence forest regeneration through their interactions with plants.^{45,46} Predispersal seed predators consume immature, developing seeds. Levels of predispersal seed predation are lower and more viable seeds are produced where hunters take predispersal seed predators.⁴⁷ Primary seed dispersal agents consume fruit taken directly from the plant and inadvertently disperse living seeds. Secondary seed dispersal agents take fallen fruit or seeds from the ground and move them to new locations where the seeds are often cached for future consumption. Many studies now document reduced dispersal of larger seeded plants in hunted forests (reviewed by Stoner *et al.*⁴⁸). Postdispersal seed predators consume dispersed seeds, and rates of postdispersal predation are again altered where hunters are active.^{48–50} Collectively, these interactions determine the number, locations, and survival of dispersed seeds and seedlings and, hence, the spatial template for onward plant regeneration. Not surprisingly, plant species composition changes rapidly where hunters are active.^{51–54} The pervasive impact of hunting on large forest vertebrates sets the stage for the global extinction of many of the persecuted species and also for widespread changes in plant species composition.

Drivers—global atmospheric change

We are changing the composition of atmospheric gases. Agriculture is largely responsible for increases in methane and nitrous oxides while industry, fossil fuel use, and biomass burning associated with tropical deforestation are largely responsible for increases in CO₂.⁵⁵ The global growth rate of CO₂ emissions from industry and fossil fuels accelerated from 1.1%/ yr in the 1990s to >3%/yr from 2000 to 2004, with increases in every region.⁵⁵ The growth rate of atmospheric CO₂ concentrations

increased accordingly from 1.4 ppm/yr in the 1990s to 1.8 ppm/yr for 2000–2008.⁵⁶ The cumulative anthropogenic increase in atmospheric CO₂ concentrations now stands at 38%—from 280 ppm before the Industrial Revolution to 385 ppm in 2008. This increase potentially affects photosynthesis and evapotranspiration by every autotrophic plant.

Humans also increase concentrations of particulates and aerosols in the atmosphere, which alters atmospheric transmissivity to incoming solar irradiance. Globally solar irradiance penetrating the atmosphere decreased by 4% to 6% from 1950 through the late 1980s as industrial pollution increased and then returned to 1950s levels as air pollution was regulated in the European Union and North America and Soviet era industry collapsed across Eastern Europe and the former Soviet Union.⁵⁷ The “brown cloud” over India and China is a recent regional manifestation.⁵⁸ Solar irradiance limits carbon uptake in closed-canopy tropical forests because leaf area indices (meter square of leaf area per meter square of ground area) range from four to six or seven and heavy shade limits photosynthesis by most leaves.^{59,60} Decadal fluctuations of 4–6% of solar irradiance will affect net primary production in closed-canopy forests.⁵⁷

The particulates and aerosols added to the atmosphere by human activity include pollutants and compounds rich in nitrogen and phosphorus. These pollutants settle back to Earth at levels that fall off with distance from their anthropogenic sources. Nitrogen deposition, which is relatively well studied, is greatest in tropical Asia, intermediate in tropical Africa, and lowest in tropical America. Nitrogen deposition is relatively modest (1–7.5 kg/ha/yr) over most tropical forests today, but is projected to increase to much higher levels (10–50 kg/ha/yr) in 2050 as industry and fertilizer use intensifies in tropical countries.⁶¹ Multiple pollutants are already being deposited on forests near cities, intensive agribusiness, and sites of biomass burning.

Drivers—global climate change

Observed increases in global temperature, precipitation, and sea level all exceed the predictions of global climate models.^{62–64} By many measures, the tropical climatic belt has recently expanded by 2 to 4° of latitude.⁶⁵ Anthropogenic emissions of the greenhouse gases that are responsible are increasing in every region.⁵⁵ These accelerating changes lend

urgency to our first attempts to understand the implications for tropical forests.

Temperature

Observed temperature increases averaged 0.26° C per decade across the tropics between 1976 and 1998.⁶⁶ The IPCC evaluated 21 global climate models and each one predicts further increases.⁶⁷ The median projected increase for the tropics is 3.3° C by 2100 under an intermediate greenhouse gas emissions scenario.⁶⁷ A 3.3° C increase will raise the mean annual temperature of 75% of all forested land in the tropics above the temperature of the hottest modern forest.⁶⁸

Organisms respond to climate change through acclimation, evolutionary adaptation, and/or range shifts to cool refuges. The potential for range shifts is limited in the tropics because the latitudinal temperature gradient is shallow.⁶⁹ The minimum distance to a cool refuge for a focal location can be defined as the distance to the closest location where the temperature projected for 2100 is equal or cooler than the modern temperature in the focal location. This minimum cool refuge distance exceeds 1000 km for key tropical regions including West Africa, large portions of Amazonia and the Congo Basin, and many isolated tropical mountain ranges.⁶⁸ This calculation was based on a moderate greenhouse gas emissions scenario. Greenhouse gas emissions recently exceeded the worst scenario envisioned by the IPCC.⁵⁵ If these emission rates continue, temperature increases will be larger and range shifts to cool refuges will require dispersal over even larger distances—several thousand kilometers—for large portions of the tropics. Most tropical species will be left to cope with large temperature increases *in situ*.

Tropical species are likely to be particularly sensitive to temperature increases for two reasons. First, lowland tropical species live at or close to the highest temperatures on Earth and therefore lack populations adapted to warmer temperatures.^{68,69} Second, tropical endemics encounter limited variation in temperature. Seasonal temperature variation averages less than 4° C over 20° of latitude centered on the equator.^{68,70} Geographic temperature variation is also minimal; lowland mean annual temperature ranges from just 24 to 27° C over 31 million km² and 47° of latitude between the Tropics of Cancer and Capricorn.^{68,71} Minimal seasonal and geographic

variation in temperature permits the metabolisms of tropical species to be finely tuned to a narrow range of temperatures.⁷⁰ Both the lack of populations adapted to warmer climates and finely tuned temperature tolerances suggest that many tropical species might be unable to acclimate to rapid increases in temperature.

The temperature sensitivity of tropical insects and reptiles reinforces concern for the future of tropical species on a warmer planet.^{72,73} Deutsch *et al.*⁷² document the relationship between fitness and temperature for 38 insect species and then evaluate changes in fitness associated with temperatures projected for 2100. Temperate zone species live well below their temperature optima today, and their fitness actually increases at projected 2100 temperatures. In contrast, equatorial species live near their temperature optima today and their fitness declines at projected 2100 temperatures. In most species, fitness declines precipitously with small increases above optimum temperatures. Short generation times might enable evolutionary adaptation to higher temperatures in insects; however, precipitous declines in fitness observed for small temperature increases and the rapidity of projected temperature increases cause concern.⁷²

The acclimation capacity of tropical trees is critically important because their generation times are often measured in centuries^{74–76} and are extremely long relative to observed and projected rates of temperature increase. Many tropical trees appear to have only limited acclimation capacity.⁷⁷ Extreme daytime air temperatures already exceed optimum temperatures for photosynthesis. The impact on stand-level carbon uptake could be large as “. . .the brightly illuminated leaves that contribute disproportionately to canopy photosynthesis are warmed to the point that leaf gas exchange is curtailed.”⁷⁸ Consistent with this possibility, stand-level carbon uptake declined when air temperatures were warmest in eddy flux studies in Brazil and Costa Rica.^{59,78,79} Respiratory carbon losses also increase with temperature, which will further reduce net carbon uptake.^{80,81} Finally, tree growth rates have declined as temperatures increased in Costa Rica, Malaysia, and Panama.^{77,82} This decline is closely related to mean annual nighttime temperature and therefore to nighttime respiration in Costa Rica.⁷⁷ Collectively, this evidence suggests that many tropical forest plants are acclimating poorly to the modest

temperature increases observed to date. Changes in plant species composition appear to be inevitable as species that are relatively tolerant of warmer temperatures replace species that are relatively intolerant.

Precipitation

Global precipitation is expected to increase as temperatures increase because more water evaporates from warmer oceans. Measured precipitation is already increasing globally.⁶² In the tropics, this includes a significant increase over the oceans and a nonsignificant increasing trend over land.⁶²

Regional projections of future precipitation are highly uncertain. The IPCC evaluated 21 global climate models and similar numbers of models projected increases and decreases in precipitation over most of the tropical land surface.⁶⁷ Relatively consistent projections with 17 or more of the 21 models in agreement include increasing precipitation in East Africa, Southeast Asia, and New Guinea and decreasing precipitation in Mesoamerica, northern South America, and in the dry season, southeast Amazonia.⁶⁷ A network of land-based weather stations documented significant regional declines in precipitation over southwest India and most of tropical Africa between 1960 and 1998.⁶⁶

The distributions of tropical forest plants are highly sensitive to moisture availability.⁸³ Altered precipitation, rising temperature, and rising atmospheric CO₂ concentration all affect plant-available moisture. Rising temperatures increase evaporation of free water and leaf transpiration (by increasing the vapor pressure deficit between saturated leaf tissues and the atmosphere) and thereby decrease moisture availability. Rising atmospheric CO₂ concentrations permit plants to close stomata and thereby reduce transpiration and increase moisture availability. Thus, moisture available to plants might change even where precipitation is unchanged. Moist forest species are likely to expand into areas where moisture availability increases and to decline where moisture availability decreases. Forest is likely to be replaced by open woodlands, shrub lands, and savannahs where moisture availability falls sufficiently.⁸⁴ Similar shifts in vegetation cover are well documented for paleo changes in precipitation.¹⁸

The drivers of forest change—synthesis

Tropical forests have been remarkably resilient to past human activities. Many apparently pristine

forests grow on soils rich in charcoal and pottery, legacies of prehistoric agricultural societies. Extensive young secondary forests grow on recently abandoned agricultural land. The past resiliency of tropical forests is being tested in new ways today. Agriculture and other human uses now displace approximately 35% of potential tropical forest cover (Table 1). Rising temperatures affect every forest organism. Rising atmospheric CO₂ concentrations affect every autotrophic plant. Hunters take the larger reptiles, birds, and mammals from most tropical forests. Wood is extracted from most forests. Precipitation is changing regionally. Anthropogenic aerosols alter atmospheric transmissivity and solar inputs regionally. The aerosols include compounds rich in nitrogen and phosphorus as well as other pollutants, which settle onto nearby forests. Vulnerable fragmented forests remain scattered over the immense deforested area. In short, multiple human activities now affect every tropical forest. The second section of this review will evaluate the impact on the composition, structure, and dynamics of remote and protected tropical forests exposed only to the relatively cryptic impacts of atmospheric and climate change and possibly hunting.

The changing composition, structure, and dynamics of tropical forests

Mounting evidence suggests dramatic changes in the composition, structure, and dynamics of trees and woody vines in remote and protected tropical forests (Table 4). The 10 documented changes include three contradictory pairs (5 vs. 6, 7 vs. 8 and 9 vs. 10). I will evaluate this contradictory evidence first and then consider hypotheses concerning causation of spatially and temporally consistent changes.

Inconsistent changes in the composition, structure, and dynamics of tropical forests

Is stem density (number of trees/hectare) increasing or decreasing (5 vs. 6)? The answer depends on tree size. Smaller trees (1–10 cm DBH) are declining rapidly and larger trees (≥10 cm DBH) are also declining but by two to four orders of magnitude more slowly in mature forests in Panama and Amazonian Ecuador (Table 5). A nonsignificant trend toward decreasing stem density for larger trees was also observed across 18 1-ha plots near Manaus, Brazil.⁸⁵ In contrast, larger trees are increasing significantly

Table 4. The changing composition, structure, and dynamics of mature tropical forests

No.	Decadal trend documented in mature forest	Source
1	Increasing above-ground biomass (AGB) of wood	88,89,91,92
2	Increasing rates of tree mortality and recruitment	86,89
3	Increasing importance of woody vines or lianas	90,95,96
4	Decreasing abundance of species with seeds dispersed by large vertebrates	52–54
5	Increasing stem density (numbers of trees per hectare)	86
6	Decreasing stem density (numbers of trees per hectare)	177,178
7	Decreasing abundance of understory tree species	85
8	Inconsistent changes in abundance of understory tree species	88
9	Decreasing rates of tree diameter growth	77,82
10	Increasing rates of tree diameter growth	85,89

in a third Amazonian study (smaller trees were not documented), but even here larger trees increased in 32 1-ha plots and decreased in 18 plots.⁸⁶ I conclude there is no consistent trend in stem density.

Are understory tree species decreasing in abundance (7 vs. 8)? Species of small adult stature that reproduce in the understory constitute more than 50% of all tree species in many tropical forests.⁸⁷ The evidence for decreases in their abundance comes from a genus-level analysis of 18 1-ha plots near Manaus, Brazil.⁸⁵ The contradictory evidence comes from species-level analyses of 10 large (25–52 ha) plots on three continents⁸⁸ (I exclude two disturbed sites.). Understory species increased significantly at three sites, decreased significantly at two sites, and did not change significantly at five of these 10 sites. I conclude there is no consistent trend in the abundances of understory species.

Are the diameter growth rates of individual trees increasing or decreasing (9 vs. 10)? The evidence for increasing growth rates is for trees > 10 cm DBH in

Table 5. Changes in the density of individual trees (stems per hectare) in three tropical forest studies

Site	Change in density (stems/ha/yr)		Source
	<10 cm DBH	≥10 cm DBH	
25-ha plot at Yasuni, Ecuador ^a	−32.0	−0.41	178
50-ha plot at BCI, Panama ^b	−22.2	−0.03	177
50 1-ha plots at 14 Amazonian sites	−	+0.94	86

^aI excluded 0.48 ha of recently disturbed forest and calculated area weighted values for valley (7.88 ha) and ridge (16.64 ha) habitats.

^bI excluded 1.92 ha of recently disturbed forest and calculated values for the 10 cm size threshold.

20 1-ha plots near Manaus Brazil.⁸⁹ Mean diameter growth rates differed significantly among four multiyear census intervals and were smallest in the second interval, intermediate and statistically indistinguishable in the first and third intervals, and largest in the final interval.⁸⁹ There was no consistent trend through time. Evidence for decreasing growth rates comes from similar multiyear census intervals for 50-ha plots in Malaysia and Panama.⁸² In Malaysia, the declines were consistent across three census intervals. In Panama, growth rates were largest in the first two census intervals and smaller in the final three intervals; however, there was no consistent temporal trend across the final three intervals. The strongest evidence for decreasing growth rates comes from annual measurements in Costa Rica, where growth rates decline with mean annual minimum temperature rather than through time.⁷⁷ I conclude there is no consistent temporal trend for changing diameter growth rates.

To summarize, six of the 10 documented changes in the composition, structure, and dynamics of tropical forests are inconsistent across studies and sites (5 through 10 in Table 4). These changes are locally real; however, the evidence does not yet suggest that they are regionally or globally consistent. Four documented changes remain (1 through 4). I will now review the evidence for these changes, which is slim in some cases, and then evaluate hypotheses concerning causation.

Consistent changes in the composition, structure, and dynamics of tropical forests and causation

Controlled experiments to evaluate hypothesized mechanisms have not been performed over scales of time (decades) and space (hectares) commensu-

rate with the long-term trends documented in tropical forests (Table 4). The closest approximation to an experiment concerns declining abundances of species with seeds dispersed by large vertebrates (4 in Table 4).

The hypothesized mechanism is persecution of large frugivores by hunters. A natural experiment is approximated wherever protected and hunted forests occur in close proximity, with hunters maintaining the “natural” experiment. Species whose seeds are dispersed by large frugivores decline while species whose seeds are dispersed by wind, small birds, and bats increase in the seedling and sapling layers in hunted forests relative to nearby protected forests.^{52–54} This is likely to be a pantropical trend because hunters are active and target large frugivores in most tropical forests^{41–43} (See *Drivers—hunting and defaunation*). Many studies also document indirect impacts of hunters on one or a small number of plant species (Reviewed by Wright⁴⁶ and Stone *et al.*⁴⁸). In each study, hunters reduce or extirpate game species, known interactions between game species and plants fail at hunted sites, and plant species involved in mutualisms with game species (seed dispersal) decline while those involved in negative interactions (seed predation, browsing) increase at hunted relative to protected sites. The causal link between hunters and changes in plant abundance is clearly established because protected forests serve as controls that are compared with hunted forests by many studies.

There is no similar natural experiment available to evaluate the principal hypothesis advanced to explain the remaining long-term trends (1 through 3 in Table 4). This hypothesis concerns increased resource availability. The favored resource is atmospheric CO₂ although nutrients

augmented through anthropogenic deposition and light levels altered by anthropogenic aerosols are also possibilities.^{85,86,90–92} All forests experience rising atmospheric CO₂ concentrations so there is no control forest. In addition, other human activities also affect every study forest (rising temperatures) or some undocumented proportion of the study forests (hunting, altered precipitation, past disturbance). Clark⁹³ and Boisvenue and Running⁹⁴ provide excellent discussions of the pitfalls that be-devil causal inference under these circumstances. Here, I will focus more narrowly on attempts to distinguish between alternative mechanisms that might contribute to increases in above-ground biomass, tree mortality, and recruitment rates, and the importance of woody vines (1, 2, and 3 in Table 4).

Four studies provide evidence that woody vines or lianas are increasing in importance through time. Several indices of the importance of large lianas (≥ 10 cm DBH) increased by 50–100% in just 20 years across 74 Neotropical sites.⁹⁰ The proportion of total leaf fall comprising liana leaves increased by 50% and flower production averaged over 33 liana species increased by 80% in 17–20 years in Panama.^{95,96} Lianas also increased through time in a warm temperate forest but not in a cool temperate forest.^{97,98} Additional studies are clearly needed to determine geographic scope. In the meantime, the increasing importance of lianas appears to be widespread at least in the Neotropics.^{52,90,95,96}

Four mechanisms have been hypothesized to explain increasing importance of lianas relative to trees. Decreasing rainfall might favor lianas;⁹⁹ however, rainfall has not decreased in the Neotropics and this first possibility can be discounted. Hunting might favor lianas because approximately 60% of tropical liana species have wind-dispersed seeds while approximately 80% of tropical tree species have frugivore-dispersed seeds.¹⁰⁰ In Panama, the proportion of seedlings constituting lianas averages 100% larger at 11 hunted sites than at nine protected sites, and the increase at hunted sites is entirely due to liana species whose seeds are dispersed by wind or by bats and small birds that are not hunted.⁵² A third hypothesis to explain increasing importance of lianas postulates that liana species respond more strongly to rising atmospheric CO₂ than do tree species.⁹⁰ The final hypothesis postulates increasing rates of tree mortality and formation of tree fall

gaps, which favor lianas.⁹⁰ The final three hypotheses are mutually compatible. Hunting pressure is increasing throughout the Neotropics,⁴³ atmospheric CO₂ concentrations are rising everywhere, and tree mortality rates are increasing across Amazonia (2 in Table 4, see below). Information concerning recent tree mortality rates and hunting intensity might enable future analyses to distinguish among these three hypotheses.

The evidence for increasing above-ground biomass (AGB) and increasing tree mortality and recruitment rates (1 and 2 in Table 4) has been questioned repeatedly and defended vigorously.^{101,102} I will not reopen that debate. Rather, I will evaluate three mechanisms hypothesized to explain the increases. I will refer to the three mechanisms as resource availability, climate variation, and stand history.

The resource availability hypothesis posits a shift in forest structure and dynamics toward greater AGB and tree turnover caused by increased carbon uptake associated with rising atmospheric CO₂ concentrations and/or solar inputs.^{92,103} Free air CO₂ enhancement (FACE) experiments have evaluated the hypothesis that rising atmospheric CO₂ concentrations increase AGB in three temperate zone forests (I discount two FACE studies of newly planted seedlings.). A transitory AGB increase disappeared after the first year of CO₂ enhancement in a 10-year-old broadleaf plantation.¹⁰⁴ AGB increased with CO₂ enhancement in a 13-year-old pine plantation with larger increases for 5 years before canopy closure and smaller increases for the first 5 years after canopy closure.^{104,105} AGB was unaffected by CO₂ enhancement in a relatively mature Swiss forest, but the number of manipulated trees was small.¹⁰⁶ The fraction of above-ground net primary production allocated to wood increased with CO₂ enhancement in the pine plantation but not in broadleaved plantations.¹⁰⁵ The experimental evidence is mixed and lends limited support to the hypothesis that rising atmospheric CO₂ will cause sustained increases in forest AGB; however, the relevance of temperate zone forests and in particular young plantations is questionable.

Two additional predictions of a CO₂-mediated resource availability hypothesis have been evaluated. The predictions concern growth rates of individual trees and stand-level AGB. If atmospheric CO₂ concentrations are limiting, then both growth

rates should increase through time as the limiting atmospheric CO₂ concentrations increase. Stand-level AGB growth rates tended to increase through time for 50 1-ha plots in Amazonia.⁸⁶ Stand-level AGB growth rates fluctuated through time with no consistent trend for three large (50–52 ha) plots in Borneo, Panama, and Peninsular Malaysia.⁸⁸ Individual tree growth rates have been evaluated for four tropical forests and are decreasing through time in two forests, possibly decreasing in a third forest, and possibly increasing in the fourth forest.^{77,82,89} An analysis of individual tree growth rates for the 50 Amazonian plots would be timely. In the meantime, tests of the prediction that tree growth rates should be increasing are mixed and provide little evidence for a CO₂-mediated resource availability hypothesis.

The climate variation hypothesis posits recent climate fluctuations that favor greater AGB and tree turnover and/or an absence of recent climate fluctuations with the opposite effects. This class of hypotheses is viable because increasing AGB and tree turnover have been observed for a short period relative to the lifetimes of individual tropical forest trees, which range up to 1400 years.⁷⁴ The observations began in the 1980s and even 1990s with a very few census plots established earlier.^{86,92} Tree growth rings often record multiple decades of sustained high or sustained low growth rates associated with natural climate fluctuations (For a tropical example see¹⁰⁷). The same Amazonian plots that provide evidence for increasing AGB recently provided evidence consistent with the climate variation hypothesis. During the first strong drought recorded since census plots were established, AGB losses averaged 5.3 Mg/ha/yr wherever average water deficits increased by 100 mm over a multiyear census interval.¹⁰⁸ A similar effect was observed in Panama, Borneo, and Peninsular Malaysia with AGB losses during severe droughts associated with El Niño events.^{88,109,110} Favorable climate variation and/or an absence of unfavorable climate variation might contribute to decadal increases in AGB.

The stand history hypothesis posits tree cohorts established after one or more past disturbances.^{9,111,112} This hypothesis predicts increased stand-level AGB but decreasing growth rates as forest stands recover from past disturbances. Phillips *et al.*¹⁰³ discount this hypothesis because tree recruitment increases before tree mortality in their

Amazonian data. For the stand history hypothesis to accommodate this observation, Phillips *et al.*¹⁰³ reason: “Assuming [cohort regeneration] dominates in Amazonia, *and* that our plots tend to start around the point that a few big trees are dying and finish around the point that self-thinning mortality is accelerating, *then* the pattern of recruitment leading mortality during the particular time-window glimpsed by the plots could actually reflect a longer-term mortality-led process initiated originally by a much earlier large-scale climate event across the Amazon.” There are two problems with this reasoning.

The first concerns the assertion that censuses must “. . . start around the point that a few big trees are dying and finish around the point that self-thinning mortality is accelerating . . .” This is not necessary. Instead, all that is required is that senescence-related mortality of large trees increases between the first and last censuses and that each large tree is replaced by more than one small tree on average. Mortality rates increase as large senescent trees die. Small trees quickly fill each tree fall gap. Recruitment will exceed mortality immediately if, on average, more than one of these small trees recruits to the minimum size threshold during the multi-year census interval. The minimum size threshold is 10 cm DBH. Gaps opened by the death of a single large tree often hold several new trees of this size within a few years.¹¹³ The second problem with the reasoning of Phillips *et al.*¹⁰³ concerns their assertion of spatial consistency. The observation advanced as being inconsistent with a stand history hypothesis does not “dominate in Amazonia.” Rather, tree recruitment is greater than tree mortality for 31 and 34 of 50 sites in two census intervals.⁸⁶ Recruitment will exceed mortality at 25 of 50 sites by chance. Stand history could explain the disparity between observation and chance if stand history affected tree dynamics at 12 and 18 of the 50 study sites in the two census intervals. Is this likely?

Stand history has been documented for just two mature tropical forests.^{75,76} In one, the tree cohort that now dominates the canopy established after a catastrophic disturbance in the mid 1800s and additional discrete pulses of tree establishment followed widespread disturbances in the 1910s, 1940s, and 1960s.⁷⁵ In the second, long-lived pioneers dominate the canopy layer and are failing to recruit.⁷⁶

Both forests are likely candidates for senescence-related increases in mortality of large canopy trees. Unfortunately, the stand history hypothesis cannot be evaluated directly until the histories of many more forests are known.⁹³

The resource availability, climate variation, and stand history hypotheses are all consistent with increasing AGB and increasing tree recruitment and mortality rates. The three mechanisms are also mutually compatible and might all contribute to observed increases in AGB and tree turnover. It will be difficult to disentangle their relative importance. This is an important exercise because the increases in AGB in tropical forests appear to have been a globally significant carbon sink in recent decades.⁹² The mechanism responsible will determine how this sink changes in the future.

The changing composition, structure, and dynamics of tropical forests—synthesis

The species composition, structure, and dynamics of plant communities are changing in many tropical forests. Some of these changes are not consistent among forests. Stem density, tree growth rates, and the abundance of short-statured tree species are increasing in some forests and decreasing in others (5 through 10 in Table 4). Other changes are consistent across forests but have been evaluated infrequently. This includes increases in liana abundance documented by four studies and decreases in abundances of large-frugivore dispersed species documented for three hunted forests. Other changes have been documented more frequently, including increases in above-ground biomass and rates of tree mortality and recruitment, but multiple alternative hypotheses of causation cannot yet be discounted. Broad trends are clear, however. Ubiquitous increases in temperature and atmospheric CO₂ concentrations are accelerating in severity. The local and regional impact of hunters, wood extraction, altered precipitation, and deposition of nitrogen and other pollutants are also increasing. Many species are persecuted directly (for timber, fuel wood, and meat). Many others are affected indirectly. Some species will respond positively, others will respond negatively, interactions among species will change accordingly, and changes in species composition will inevitably follow.¹¹⁴ Those changes will have wide-ranging implications for the conservation of tropical biodiversity.

Implications for conservation

Implications for conservation—habitat loss

Habitat loss is a leading cause of documented extinctions and this threat has long dominated tropical conservation. The rate of conversion of tropical forests to cropland accelerated continuously for approximately 100 years²¹ and conservation biologists understandably projected tremendous future losses of tropical forests. For example, Dirzo and Raven¹¹⁵ conclude: “It is therefore doubtful that more than 10% of the tropical forests will be protected, and probably more realistic to think of 5% surviving the next 50 years.” Fortunately, net deforestation rates have stopped accelerating and are decreasing in some regions (Table 1). Recent projections now predict that 64–89% of 2000 tropical forest cover will remain in 2050 (Table 3).

These numbers should not cause complacency for at least two reasons. First, they mask large ongoing changes in the types of forest cover with mature forests being replaced by plantations, natural secondary forests, and forests modified by timber and fuel wood extraction (Table 2, Fig. 2). Second, global and continental-scale estimates of forest cover mask local variation in the extent of forest loss. Habitat loss still threatens local endemics where forest losses are large and species that are unable to persist in the new secondary and modified forests.

Conservation hotspots focus attention where habitat losses and numbers of endemic species are large.^{116,117} The 34 hotspots each support more than 1500 endemic plant species and have lost more than 70% of their original vegetation. The 18 hotspots located entirely or almost entirely within subtropical and tropical forest biomes^{6,117} offer an opportunity to compare the area of original or pristine vegetation cover with the total area of tree cover in key areas of endemism. Those 18 hotspots cover 10,998,000 km² or 46% of the distribution of subtropical and tropical forest before agriculture (Table 6). I calculated tree-covered area for these 18 hotspots using data provided by the Global Land Cover 2000 Project¹¹⁸ and compared tree-covered area with the area of original vegetation provided by Mittermeir *et al.*¹¹⁷ There is substantially more tree cover than original vegetation (Table 6, paired $t = 6.02$, $P < 0.001$).

This difference has at least three causes. A small contribution comes from plantations, which

Table 6. Land cover and area of 18 conservation hotspots where subtropical and tropical forest is the dominant potential vegetation^a

Hotspot name	Hotspot area (km ²) ^b	Original vegetation (%) ^b	Tree cover (%) ^c	Other cover (%) ^d	Human use (%) ^e	No data (%) ^f
Brazilian Atlantic Forest	1,233,875	8	21	18	61	0
Caribbean Islands	229,549	10	20	28	52	0
Coastal Forests of Eastern Africa	291,250	10	69	27	4	0
East Melanesian Islands	99,384	30	68	17	11	4
Eastern Afromontane	1,017,806	11	27	31	42	0
Guinean Forests of West Africa	620,314	15	36	7	58	0
Indo Burma	2,373,057	5	26	37	37	0
Madagascar and the Indian Ocean Islands	600,461	10	23	66	12	0
Madrean Pine Oak Woodlands	461,265	20	70	19	11	0
Maputaland-Pondoland-Albany	274,136	24	55	33	13	0
Mesoamerica	1,130,019	20	56	7	37	0
New Caledonia	18,972	27	25	46	29	0
Philippines	297,179	7	25	8	68	0
Polynesia-Micronesia	47,239	21	22	45	13	20
Sundaland	1,501,063	7	48	10	42	0
Tumbes-Choco-Magdalena	274,597	24	31	26	43	0
Wallacea	338,494	15	54	15	30	0
Western Ghats and Sri Lanka	189,611	23	55	9	36	0

^aThe Himalaya and Tropical Andes hotspots include tropical forest but are excluded because other biomes predominate.

^bValues from Table 1 of Mittermeir *et al.*¹¹⁷ c, d, e, and f. Calculated using ARCGIS software, shape files for hotspots provided by Conservation International¹⁷⁹ and shape files for land cover in 2000 provided by the Global Land Cover Project.¹¹⁸

^cIncludes eight land cover types identified by “Tree cover” and the following descriptors: “broadleaved deciduous closed,” “broadleaved deciduous open,” “broadleaved evergreen,” “mixed leaf type,” “needle leaved deciduous,” “needle leaved evergreen,” “regularly flooded fresh water,” and “regularly flooded saline water.”

^dIncludes nine land cover types described as follows: mosaic of tree cover and other natural vegetation; shrub cover, closed-open, evergreen; shrub cover, closed-open, deciduous; herbaceous cover, closed-open; sparse herbaceous or sparse shrub cover; regularly flooded shrub and/or herbaceous cover; bare areas; snow and ice; and water bodies.

^eIncludes five land cover types described as follows: tree cover, burnt; cultivated and managed areas; mosaic of cropland, tree cover and other natural vegetation; mosaic of cropland, shrub and/or grass cover; and artificial surfaces and associated areas.

^fNo data occur where the Global Land Cover Project¹¹⁸ provides no data and due to slight misalignment of shape files.

constituted 2% of tropical tree cover in 2005²⁹ and are not distinguished from natural forests by the Global Land Cover Project.¹¹⁸ A larger contribution comes from other nonforested but tree-covered landscapes. As an example, tree cover estimated by the Global Land Cover Project¹¹⁸ is 59% larger than forest cover estimated from Landsat imagery for Costa Rica¹¹⁹ (Plantations constitute just 0.2% of Costa Rican forest²⁹). The Global Land Cover Project¹¹⁸ apparently categorizes some nonforested landscapes as tree covered.

To minimize this possibility, I excluded three land cover types that included trees. Those three are burnt tree cover, mosaics of trees and other natural vegetation, and mosaics of trees and cropland (See footnotes to Table 6). The final contribution to the difference in tree cover and original vegetation cover reflects forests regenerating naturally on abandoned land and forests degraded through wood extraction and other means. This final contribution is apparently substantial; 15 of the 18 tropical hotspots have 100% to nearly 600% more

tree cover than original vegetation. A key question concerns the conservation value of these modified forests and wooded landscapes.

Some conservation biologists implicitly assume only the original vegetation has conservation value. As an example, Myers *et al.*¹¹⁶ state “As many as 44% of all species of vascular plants and 35% of all species in four vertebrate groups are confined to 25 hotspots comprising only 1.4% of the land surface of the Earth.” The 25 hotspots actually constituted 17,444,300 km² or 11.8% of the land surface of the Earth. The value 1.4% refers to the area of original vegetation only, and the assertion that every endemic species is confined to that 1.4% reflects the implicit assumption that only the original vegetation has conservation value. To focus attention on this implicit assumption, Wright and Muller-Landau³⁴ explicitly assume the opposite—that all forests (plantations excluded) have equal conservation value. Both assumptions are false. Every species has characteristic habitat requirements and an unknown number require mature forest habitats.

The key question is how many. Gardner *et al.*¹²⁰ conclude a “data vacuum” precludes an answer. Dent and Wright¹²¹ compiled 69 published comparisons of faunal composition for mature tropical forests versus naturally regenerating or secondary forests. Species composition and relative abundances were quite similar when regenerating forests were just 20 years old (also see¹²²). Species composition is also quite similar for logged and unlogged forests.^{123,124} These comparisons suggest that the conservation value of naturally regenerating tropical forests is potentially large.

The key question remains unanswered, however. We still need to know how many tropical species require mature forest habitats. If mature forest specialists tend to be rare or to have small geographic distributions, their impact on comparisons of faunal composition might belie their diversity. Studies of species’ global habitat distributions are required. This has been attempted for Neotropical birds and Central American nonvolant, terrestrial mammals. Stotz *et al.*¹²⁵ identify 10% of Neotropical forest birds as “trash” species able to persist in regenerating forests. Their brief definition of regenerating forest includes a photograph that appears to show a banana plant in the foreground and a dense tangle of low scrub in the background. This definition of regenerating forest is biologically unreasonable in the

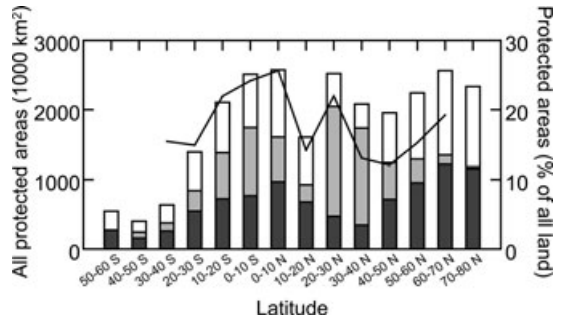


Figure 3. The latitudinal distribution of all land area in protected areas (*histogram*) and the percentage of all land this constitutes (*line*). The histogram distinguishes strict (*dark shading*; IUCN categories I to IV); cultural, recreational and sustainable use (*light shading*; IUCN categories V and VI) and undesignated protected areas (*open portion of bars*). Updated from Brooks *et al.*¹⁵¹ Data are from the World Database on Protected Areas.¹⁵²

tropics where many aspects of forest structure are reestablished after just 20 years of secondary succession.¹²⁶ In contrast, Pereira and Daily¹²⁷ conclude that just 54% of the nonvolant, terrestrial mammals of Central America tolerate human modified habitats and just 46% require “native habitats.” An even smaller percentage requires mature native habitats because Pereira and Daily included naturally regenerating habitats as native habitats. New studies that incorporate clear, reasonable definitions of naturally regenerating forests are required to determine how many tropical species require mature forest habitat. These studies will help to identify the species threatened by the tremendous reductions in mature primary forest in most tropical countries (Fig. 2).

Implications for conservation—protected areas

Forest stewardship is the responsibility of local people and governments. Protected areas are a key means of discharging this responsibility. Protected areas can be managed strictly for the conservation of nature; for cultural, recreational, and extractive use and by indigenous peoples.¹²⁸ Protected areas constitute more than 20% of all land between 20°S and 10°N (Fig. 3) and those managed strictly for conservation constitute more than 7% of all land between 20°S and 20°N (Fig. 4). Outside the Tropics, similar values are only found in lightly populated regions

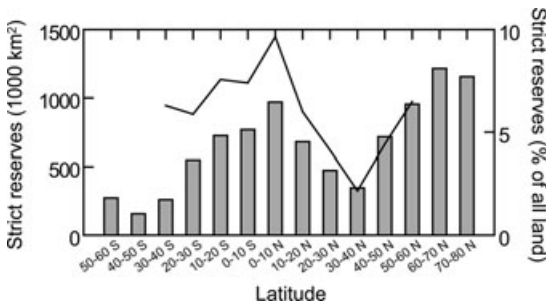


Figure 4. The latitudinal distribution of land in strict protected areas (*histogram*) and the percentage of all land this constitutes (*line*). Strict protected areas include IUCN categories Ia, Ib, II, III, and IV. Updated from Brooks *et al.*¹⁵¹ Data are from the World Data Base on Protected Areas.¹⁵²

poleward of 40°S and 70°N. The commitment of land to protected areas is greatest in the tropics.

There is concern about the effectiveness of tropical protected areas because funds for their management are often limited¹²⁹ and several tropical protected areas have conspicuously failed.¹³⁰ Satellite image analyses have recently been used to evaluate the effectiveness of hundreds of humid tropical protected areas. Protected status was associated with substantial reductions in deforestation, logging and fire frequency relative to nearby unprotected forests.^{36,131–134} The impressive network of tropical protected areas is generally effective.¹³⁵

Despite the vast commitment to tropical protected areas, the top priorities for new protected areas are overwhelmingly (85%) in the tropics.^{136,137} New tropical protected areas are required because many threatened tropical species have small geographic ranges that fall entirely outside existing protected areas.¹³⁷ Because many of the poorest nations have already dedicated large percentages of their land resources to conservation, additional commitments should include financial help from the global community.¹³⁸

The number of threatened tropical forest endemic species is so large that many will only survive in human-modified landscapes outside protected areas. Fortunately, a wide range of tropical forest species are able to survive in human-modified landscapes,^{127,139} and new research programs are increasingly focused on management to increase the conservation value of human modified, tropical landscapes.^{140–144}

Implications for conservation—atmospheric and climate change

The conservation implications of global atmospheric and climate change are profound. As just one example, a leading hypothesis for the recent extinction of several hundred species of tropical frogs concerns subtle temperature changes that favored a fungal pathogen.¹⁴⁵

The primary response to the conservation threat posed by global atmospheric and climate change has been to propose new targeted protected areas.^{146,147} The new protected areas would (1) protect physiological and genetic diversity to facilitate *in situ* acclimation and evolution in response to climate change and (2) maintain connectivity along environmental gradients to facilitate dispersal in response to climate change.

Protected areas can also mitigate regional climate change. A large portion of Amazonian rainfall is generated by evapotranspiration within the basin. If deforestation reduced evapotranspiration and rainfall sufficiently, savannah could replace large areas of forest.¹⁴⁸ It has recently been suggested that Amazonian protected areas already include enough forest to prevent this scenario.¹⁴⁹

Forest protection offers a cost-effective means to reduce current greenhouse gas emissions and to remove CO₂ from the atmosphere and thereby mitigate global atmospheric and climate change. Biomass burning associated with tropical deforestation contributes approximately 20% of global anthropogenic CO₂ emissions.⁷ The inclusion of Reduced Emissions from Deforestation and Degradation as a mechanism for mitigating climate change within United Nations climate-change agreements will enable payments to conserve mature tropical forests and thereby reduce greenhouse gas emissions. Secondary succession removes carbon from the atmosphere more quickly in tropical forests than in any other biome.¹²⁶ Additional payments could help to expand tropical forest cover on marginal agricultural land, which is often abandoned anyway (Table 2). The forests to be protected by payments for carbon could then be targeted to protect physiological and genetic diversity and landscape connectivity.

Financing to mitigate rising atmospheric CO₂ concentrations through the protection of tropical forests might be borne in proportion to cumulative contributions to the CO₂ problem. The United

States, the European Union, and Japan are responsible for more than 60% of the cumulative increase in atmospheric CO₂ concentrations since the Industrial Revolution⁵⁵ and should contribute to solutions accordingly.

Implications for conservation—synthesis

Several of the anthropogenic drivers that confront tropical forests today have run their course in temperate broadleaf forests. Temperate broadleaf forests grow on abandoned agricultural land, except where rugged topography precluded agriculture. Even here apex predators, the largest herbivores and timber are gone. Deposition of nitrogen altered availability of a key limiting nutrient and other pollutants acidified soils and freshwater over entire continents. A similar fate awaits many tropical forests.

Three key differences between the temperate zone and the tropics will, however, save many tropical forests from this fate. The first difference concerns agriculture. Soils tend to be poorer, rainfall higher and pathogens, insects and weeds more aggressive in the humid tropics than in the temperate zone. These conditions have protected many humid tropical forests from long-term conversion to agriculture for millennia and continue to do so today wherever humid forests are converted to agriculture and then quickly abandoned. Development informed by an understanding of the environmental limits on agriculture could preserve many mature humid tropical forests.

The second difference between temperate and tropical broadleaf forests concerns the extraordinary regeneration capacity of tropical forests. Persistent “old fields” are largely a temperate zone phenomenon. Secondary succession quickly reestablishes forest structure and provides suitable habitat for many forest species in just a few decades in the humid tropics.^{122,126} The conservation value of abandoned tropical lands is potentially large and is receiving increasing attention.^{121,150} This new attention should include investigations of the limits on conservation value of regenerating and logged forests through the identification of species with absolute habitat requirements for mature forests.

A third difference between temperate and tropical forests concerns the splendid network of tropical forest protected areas (Figs. 3 and 4). These protected areas were largely established before being logged and while faunas were intact. This vast in-

vestment could ensure that mature forests and ecologically viable populations of apex predators and large herbivores survive in the tropics. Additional protected areas might focus on species that require old-growth forests. This is a global responsibility; residents of London and Sao Paulo enjoy similar benefits from remote Amazonian protected areas. A new mechanism is needed to apportion the cost of tropical protected areas equitably and globally.¹³⁸

Climate change is a wild card. As just one example, Cook and Vizy⁸⁴ simulated twice modern atmospheric CO₂ concentrations of 757 ppm and found that forest was replaced by semiarid caatinga vegetation over eastern and southern Amazonia. Their simulations are credible because they carefully selected a potential vegetation model (PVM), a regional climate model (RCM), and a global climate model (GCM) that successfully recreated the modern vegetation and climate of South America. The GCM, which was produced by the Canadian Center for Climate Modeling and Analysis, provided lateral boundary conditions and sea surface temperatures. The coupled RCM-PVM used these inputs to simulate vegetation change over South America. Atmospheric CO₂ concentrations of 757 ppm and concomitant increases in the severity of climate change become increasingly likely as the rate of greenhouse gas emissions continues to accelerate.⁵⁵ Climate change and the potential for tropical forest collapse is the greatest threat to tropical biodiversity today.

Conclusions

The single word change captures the future of all tropical forests. Twelve key trends contributing to change follow:

1. The widespread conversion of mature forests to agriculture continues.
2. No. 1 leads to large net losses in forest area in deforestation hotspots concentrated in South America and Southeast Asia.
3. The abandonment of marginal agricultural land to natural regeneration offsets 1 in other regions where the net change in forest area is reduced accordingly; however, young secondary forests replace mature forests.
4. Commercial logging is rapidly moving from depleted forests of Europe and Asia to new

forests in Africa, Melanesia, New Guinea, and South America.

5. Fuel wood comprises 71% of tropical wood production and is taken from forests accessible to poor people.
6. Modified natural forests constituted well over half of all tropical forest cover in 2005 as a consequence of 3, 4, and 5.
7. Tropical governments have protected 20% of all land between 20°S and 10°N and manage >7% of all land between 20°S and 20°N for the conservation of nature. This vast protected area is generally effective at limiting deforestation and logging and, in some cases, hunting.
8. Elsewhere hunters access even more remote forests and remove frugivores, granivores, and browsers whose absence alters plant regeneration and forest structure.
9. Anthropogenic aerosols reduce atmospheric transmissivity to solar inputs regionally and are deposited as pollutants locally. Deposition is projected to increase dramatically in the next 50 years as industry and agriculture intensify in the tropics.
10. Rising atmospheric CO₂ concentrations potentially affect every autotrophic plant through increased photosynthesis and decreased evapotranspiration.
11. Rising temperatures potentially affect every tropical organism.
12. Climate change might also alter regional precipitation; however, precipitation projections are extremely uncertain.

Changing tropical land use dynamics (1 through 7 above) have been incorporated into a variety of models to project future forest cover. These models agree that the extreme levels of habitat loss once anticipated will not be realized and project that 64–89% of the tropical forest cover present in 2000 will remain in 2050. A large portion of the forests of 2050 will have been stripped of valuable timber, game species, and fuel wood (4, 5, and 8). The establishment of an immense system of protected areas (7) has the potential to protect many mature tropical forests from these local threats. Global threats are another matter.

The species composition, structure, and dynamics of remote and protected tropical forests are already changing in response to anthropogenic ac-

tivities. Widespread changes include increases in above-ground woody biomass, tree turnover rates, tree species composition, and the importance of woody vines. A mechanistic understanding of the causes of these changes is necessary to predict consequences for conservation and global carbon and hydrological cycles. Global atmospheric and climate change (10, 11, and 12 above) are frequently mentioned among the possible causes of change in otherwise intact forests. Multiple, compatible mechanisms might contribute to each of the documented changes; however, and the evidence to distinguish among the possibilities is largely unavailable.

Whether these trends are good or bad is largely moot—they are already here and are increasing in intensity and geographic extent. Almost five billion people live in the tropics including 2.2 billion living in the 45 countries that supported 89% of tropical forest in 2000. The willingness of these people to protect an immense area for the conservation of nature and the resiliency of tropical biota inspire hope for the future of tropical forests and their species.

Meanwhile global greenhouse gas emissions continue to increase despite international accords. These increases raise the specter of large increases in temperature and changes in precipitation and the possibility of regional forest collapse wherever moisture availability declines sufficiently. In my opinion, global climate change is the greatest threat facing tropical forests and most other biomes today. The management of human-modified landscapes will be an essential component of conservation everywhere as global atmospheric and climate change alters conservation priorities in unexpected ways.

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Conflicts of interest

The authors declare no conflicts of interest.

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