REVIEW

Increasing human dominance of tropical forests

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Tropical forests house over half of Earth's biodiversity and are an important influence on the climate system. These forests are experiencing escalating human influence, altering their health and the provision of important ecosystem functions and services. Impacts started with hunting and millennia-old megafaunal extinctions (phase I), continuing via low-intensity shifting cultivation (phase II), to today's global integration, dominated by intensive permanent agriculture, industrial logging, and attendant fires and fragmentation (phase III). Such ongoing pressures, together with an intensification of global environmental change, may severely degrade forests in the future (phase IV, global simplification) unless new "development without destruction" pathways are established alongside climate change–resilient landscape designs.

The functioning of Earth is dominated by the redistribution of incoming solar radiation through fluxes of both energy and matter, within which life plays a pivotal role. Tropical forests are critical to this functioning as a major regulator of global climate, via water transpiration, cloud formation, and atmospheric circulation (*1*–*3*). Overall, they exchange more water and carbon with the atmosphere than any other biome: Changes in the balance of photosynthesis and respiration in tropical vegetation dominate interannual variability in Earth's atmospheric CO_2 concentration (*4*). Furthermore, over half of Earth's 5 to 20 million species reside in tropical forests (*5*, *6*).

Some 1.2 to 1.5 billion people directly rely on tropical forests for food, timber, medicines, and other ecosystem services (*7*), including both closed-canopy and more open seasonal systems (Fig. 1). This multiplicity of forest functions and services are underpinned by their diverse resident species, such that diverse forests are healthy forests (*8*). Here we consider threats to tropical forests and their impacts on forest health and the ecosystem services they supply in three parts: first, historical changes since humans began living in the tropical forest biome, because impacts can last millennia; second, the much greater changes over recent decades; and third, the future of tropical forests, given the twin pressures of further agricultural expansion and rapid global environmental change.

Historical human impacts on forest health

There are five major biogeographic regions in the moist tropics—Neo- (tropical America), Afro-, Indo-Malayan, and Australasian (largely New Guinea) tropics, plus Madagascar—each an evolutionary descendant following the breakup of Pangea ~200 million years ago (Fig. 1). Rainforest area contractions during glacial periods have left Africa depauperate in tree species (*9*), while Indo-Malayan forests are often dominated by one family of trees, the Dipterocarpaceae (*10*, *11*). Differences in structure occur: Closed-canopy African forests have fewer trees per hectare (mean, 426 stems >10-cm diameter ha^{-1}) than forests in Amazonia or Borneo (both mean, ~600 stems ha^{-1}) (*12*), while Amazonian forests have shorter trees for a given diameter (*10*) and, on average, contain one-third lower aboveground biomass (AGB) than African or Bornean forests (*12*). Thus, a priori it is expected that different regions may respond differently to environmental changes.

> ***"Beyond national networks of well-protected forested landscapes and formal collective tenure of forest lands, large-scale landscape planning will be required to maintain forest health."***

Humans began living in African tropical forests ~60,000 years before the present (yr B.P.) and have since colonized all tropical forests (since ~50,000 yr B.P. in Indo-Malayan and Australasian tropics, ~10,000 yr B.P. in Neotropics, and ~2000 yr B.P. in Madagascar). The first impact was hunting, with greater fractions of the megafauna becoming extinct in more recently colonized biogeographic regions. Thus, whereas only 18% of African megafauna were lost, some 83% disappeared in South America (*13*). Regardless of the exact contributions of hunting relative to glacial-to-interglacial climate change, these extinctions likely altered plant and animal species composition, nutrient cycling, and forest structure (*12*, *14*, *15*). The lower AGB of Amazonia may reflect long-term cascading impacts of megafauna loss (*12*).

Tropical agriculture began ~6000 yr B.P., with the area affected slowly increasing over millennia (*16*). There is debate around the extent to which farming and enrichment planting of tree crops led to tropical forests being "cultural parklands" and thus whether current "primary" forests are actually very old secondary forest and forest gardens (*17*). Archaeological remains indicate some intensively cultivated areas, including anthropogenic soil creation in Africa and Amazonia (*18*), as well as extensively cultivated areas associated with ancient empires (Maya, Khmer), forest kingdoms (West Africa), concentrated resources [Southern Amazonia near rivers (*17*)], and technological innovation [western Congo basin, 2500 to 1400 yr B.P. (*19*)]. These were always a small fraction of total forest area. Even when farming collapsed after the 1492 arrival of Europeans in the Americas, when ~90% of indigenous Americans died, pre-Colombian cultivated land likely represented <10% of Neotropical forest extent (*13*). Additionally, the tendency to compare contemporary changes only to the recent past, known as shifting baselines, gives pervasive underestimates of wildlife abundance before European arrival in the tropics. For example, 24 million Amazonian turtle eggs were harvested in 1719 alone, producing 100,000 liters of lighting oil (*20*). Overall, although pre-Colonial human activity altered parts of the tropical forest landscape, low population densities and shifting cultivation systems maintained forest health.

Recent changes in forest function and health

Three major trends dominate tropical forest function and health in the recent past: conversion to nonforest, mostly for farmland (*21*, *22*) and mining (*23*); degradation of remaining forest, via hunting (*24*), selective logging (*11*), fire (*25*), and fragmentation and associated edge effects (*26*); and regeneration of secondary forest (*8*). Logging is a frequent gateway to degradation and conversion, although other routes occur (Fig. 2A). These trends are driven by socioeconomic factors that scale from local use to international markets and that occur legally and illegally, making their management and mitigation complex.

The extent of these changes is large: ~100 million ha of tropical forest were converted to farmland between 1980 and 2012, a rate of ~0.4% $year^{-1}$, commonly for soybean or oil palm production (*21*, *22*). Selective logging affected ~20% of tropical forests between 2000 and 2005 (*27*). Only a minority remain as Intact Forest Landscapes: i.e., areas >500 km^2 and >10 km wide with no settlements or industrial logging (Fig. 1) (*28*). Across the world's extant tropical forests a recent estimate suggests, 24% are intact, 46% fragmented, and 30% otherwise degraded (*29*). Because even structurally intact forests are hunted, including in protected areas (*30*), threats are global.

Global carbon and water cycle impacts

Changes in forest extent alter biogeochemical cycles and the biophysical properties of Earth's surface. Net tropical land carbon flux estimates have high uncertainty, with studies giving net zero exchange or a modest source over recent decades (*31*, *32*). Net values mask large and uncertain opposing gross fluxes: to the atmosphere

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from deforestation and degradation (2.0 to 2.8 Pg C year^{-1}); and from the atmosphere in intact (0.5 to 1.0 Pg C year^{-1}) and regenerating forest [1.4 to 1.7 Pg C year^{-1}; the three pairs of figures are central estimates, the first from (*33*) and the second from (*34*), over the early 2000s]. Thus, intact forest provides a valuable service, avoidable emissions from deforestation and degradation are globally significant, and substantial carbon sequestration via permanent forest restoration is possible (compared to 7.8 Pg C year^{-1} emitted from fossil fuels over 2000 to 2010).

Deforestation and degradation also cause biophysical changes, including albedo, surface roughness, and evapotranspiration. Deforestation leads to warming: Simulations of complete tropical deforestation lead to a 0.9°C global temperature increase, due to both carbon cycle and biophysical changes (*35*). Conversely, tropical forest restoration cools Earth, unlike in boreal zones where albedo effects dominate, because albedo changes are small in tropical forests while evaporative cooling and carbon sequestration are high (*35*). The impacts of land-cover change on rainfall are highly scale dependent: Local deforestation has little effect, but at the mesoscale rainfall increases, whereas very large-scale forest loss likely reduces it (*1*–*3*).

Subtracting and adding species

Hunting for local consumption is likely sustainable if population density is about one person km^{-2} and smaller, higher-fecundity species are targeted (*24*). Higher densities of forest-dwelling communities and commercial hunting to supply larger towns or the international wildlife trade (e.g., tiger bone; rhinoceros horn; elephant tusk) drive the "empty forest syndrome" where expansive forests contain few to no large-bodied vertebrates (*20*). Increasing rarity raises prices and makes it economically viable to seek out even the last individuals of a species (*36*). For example, the last Javan rhino (*Rhinoceros sondaicus annamiticus*) in mainland Southeast Asia was shot in 2010 for its horn, commanding a higher price than gold (Fig. 2B) (*37*).

Large-bodied vertebrates, which disperse large-seeded trees, are vital to healthy tropical forests. In their absence, seed dispersal becomes more clustered and seedling survival is reduced, as documented in Borneo (*38*), Congo (*14*), and Amazonia (*39*). Altered tree seedling communities suggest longer-term impacts on tree species composition and carbon stocks because larger-seeded trees tend to have higher wood density than wind-dispersed species (*40*). Given increasing hunting pressure, with 62% of Africa's forest elephants killed in the decade to 2011 (*41*), such changes may become the norm for Africa and Amazonia. By contrast, defaunation may not reduce AGB in areas of Asia where wind-dispersed dipterocarps dominate (*38*).

Human activity has not only selectively removed species from forests but added them, too. A suite of invasive species and diseases have been introduced to tropical forests, particularly on oceanic islands, driving species extinctions that have degraded pollination, dispersal, and predation functions that underpin forest health. Hunting, introduced predators, and avian malaria have decimated birds in the Pacific, where some 2000 endemic species were lost (*42*). Cascades of extinction often unfold: Over a century, the loss of Hawaiian endemic birds drove 31 plant species that they pollinated to extinction (*43*). On Guam, the introduction of brown tree snakes (*Boiga irregularis*) led to the extinction of all forest bird and bat frugivores, stopping seed dispersal services, including to secondary forest areas dominated by an invasive tree species, thereby arresting its carbon stock recovery (*44*). Away from islands, an invasive fungus has contributed to the extinction of several mainland Neotropical amphibian species (*45*).

Directly degrading tropical forest health

Over 400 million ha of tropical forest are within the permanent timber estate (*46*). Logging in tropical forests usually selectively removes only valuable trees (Fig. 2, C and D). Logging intensity varies regionally (1 to 2 trees ha^{-1} in Amazon and Congo, >10 in Southeast Asia) and locally with topography and variation in timber stocks (*11*, *47*). Such forests retain 76% (range, 47 to 97%) of carbon stocks shortly after logging (*47*) and maintain large-scale hydrological processes (*11*). Though logging is less extensive than hunting, it has greater consequences for forest health. Critically, logging provides road access to hunters, increasing the number of empty forests (Fig. 2D).

Studied logged forests, averaging across logging intensities, retain similar species richness (*11*, *47*) but have altered community composition (*11*). Reductions in biodiversity are lower at lower logging intensities (*48*), under reduced-impact logging (*49*), and when areas of primary forest are spared within concessions (*11*). The contribution of invertebrates to litter decomposition, seed predation and removal, and invertebrate predation is reduced by up to one-half on Borneo, but increases in the abundance of small mammals, amphibians, and insectivorous birds compensate to retain these ecosystem processes

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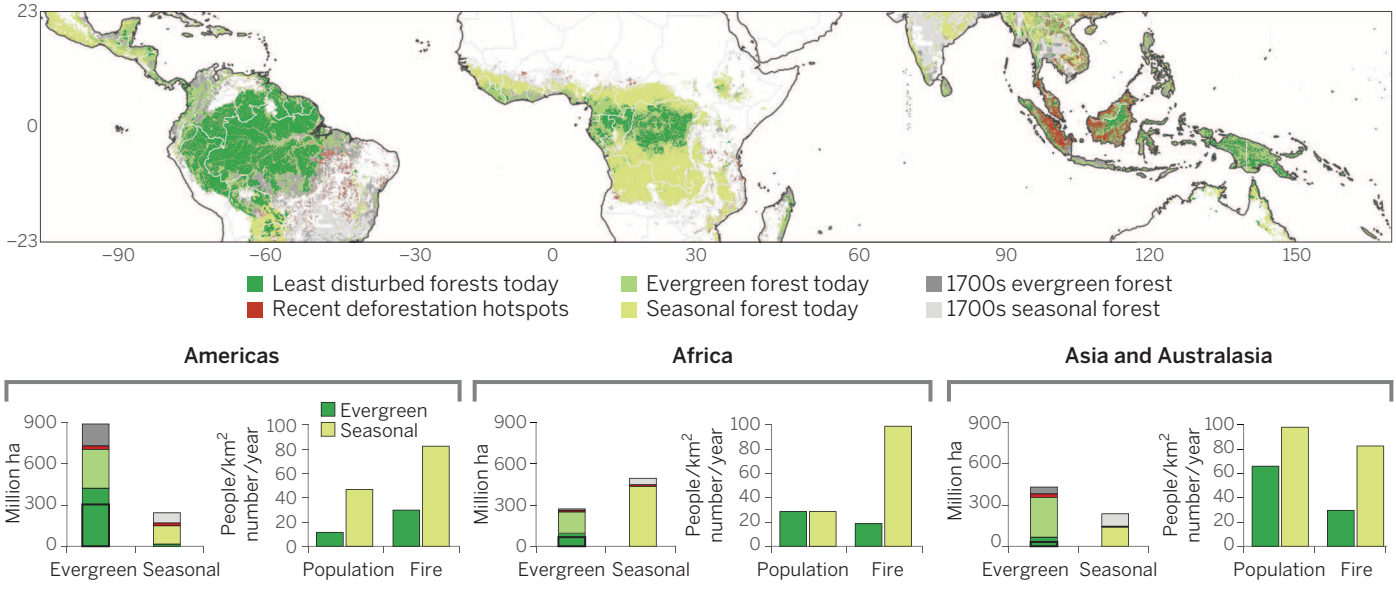

Fig. 1. Map of current and historical evergreen and seasonal tropical forest extent. The figure is adapted from (*88*). Gray shading represents the extent of forest before the Industrial Revolution [~1700; based on (*89*)]. Green indicates current extent. Darkest green represents Intact Forest Landscapes, 95% of which are evergreen forests (*28*). Red represents recent intense land-cover change [2000 to 2012, ≥10% deforestation per 10 km^2 (*22*)]. Below, for each continent, a pair of bar plots summarize forest area data (left) and human population density plus fire numbers within forested areas (right); dark boxes denote a more conservative definition of least disturbed forests: a 5-km buffer from any high-intensity human influence.

at primary forest levels (*50*). Forest health is therefore maintained, but only if the forest is not further degraded or deforested [Fig. 2A, (*11*)].

The conversion of logged or intact forest, mainly to agriculture (*21*, *22*), drives fragmentation of remaining forests into smaller, isolated patches. With the exception of the vast Congo and Amazon regions (only 25% within 1 km of an edge), the majority of tropical forests are now edge affected; for example, 91% of Brazilian Atlantic forest is within 1 km of an edge (*51*). Fragmentation has two key impacts on forest health. First, landscape connectivity is reduced, disrupting metapopulation dynamics and driving species losses, particularly in the smallest fragments (*52*). Species-poor communities have reduced ecosystem function and services: for example, decreased seed dispersal mutualism in Africa (*53*) and dominance of low–wood density tree species in Amazonia (*26*). Second, fragments suffer edge effects that penetrate into the forest, such as winds and woody vines, that increase tree mortality and alter species composition (*26*). Thus, carbon stocks are reduced in fragments (*54*), particularly at their edges (*26*, *51*, *55*). Nevertheless, even after a century or more of isolation, fragments can retain appreciable biodiversity, carbon, and multiple functions (*54*, *55*), especially in hotspots of extinction risk where contiguous forest cover has been widely disrupted, such as the Brazilian Atlantic, East and West Africa, the Tropical Andes, and the Himalayas.

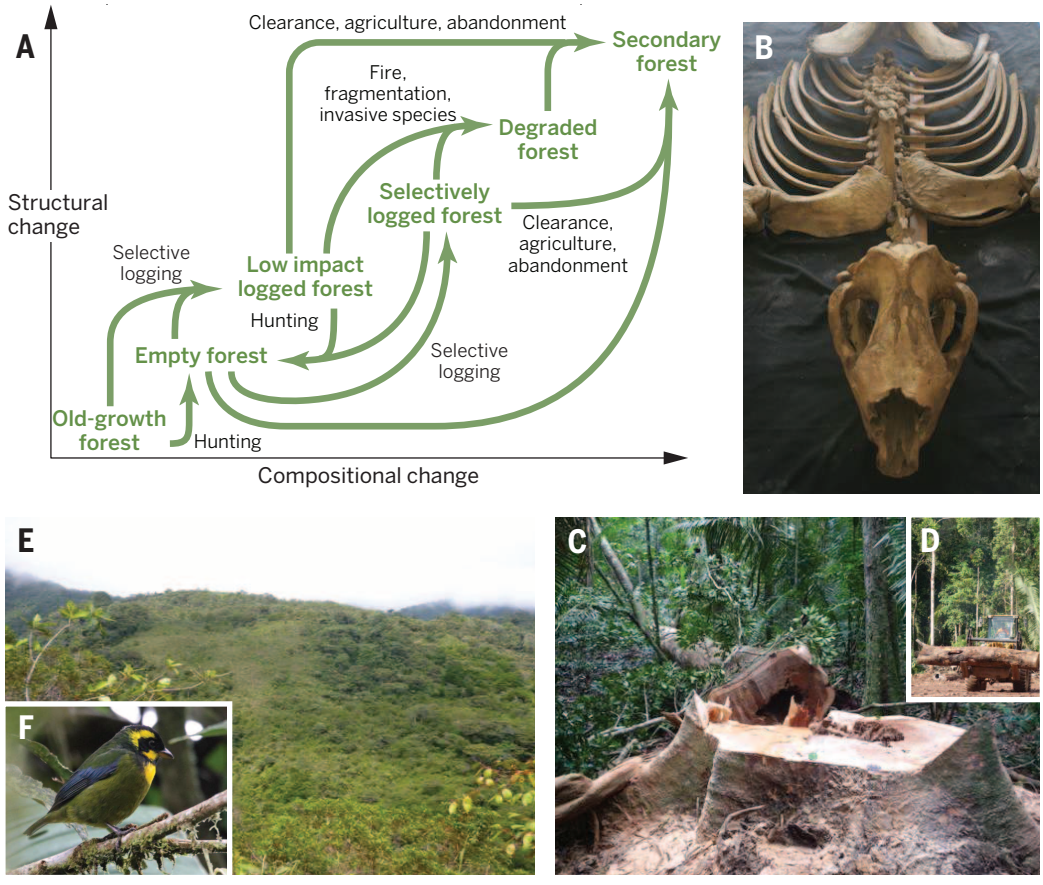

Fig. 2. Examples of direct human impacts on tropical forests. (**A**) Schematic of common land-use changes that alter forest structure and species composition; all are classified as "forest" (*8*). (**B**) Skeleton of the last Javan rhino from mainland Southeast Asia, shot in 2010 for its horn, which has been removed by hunters; an example of hunting pressure that drives the "empty forest syndrome." (**C**) A logged canopy emergent in Brazilian Amazonia. If protected from further impacts, selectively logged forest retains most biodiversity and much carbon. (**D**) Logging road in the Brazilian Amazon. By 2050, >25 million km of roads are predicted to be built across the tropics (*70*), driving further forest degradation from fragmentation and encroachment by fire and hunters. (**E**) Secondary forest in the Colombian Andes. Across the tropics, areas of marginal farmland are being abandoned followed by regeneration, providing multiple ecosystem services from carbon sequestration to reduced landslides. (**F**) The endangered gold-ringed tanager that has recolonized secondary forests in the Tropical Andes (*59*), showing their increasingly important role in tropical forest conservation. [Photo credits: (B) Sarah Brook/WWF; (C to E) David Edwards; (F) James Gilroy].

Natural fires are extremely rare in moist tropical forest, but anthropogenic fires are common today (Fig. 1). Following logging and fragmentation, fuel loads (woody debris, ongoing tree mortality), conditions (drier, warmer in canopy openings), and ignition sources (people) all promote fires (*25*). Fires have major impacts on forest health: Experiments in Amazonia show 226 to 464% increases in tree mortality, 23 to 31% decline in canopy cover, and 12 to 20% decline in AGB (*56*), plus almost all primary forest birds are replaced by secondary and nonforest species (*57*). Furthermore, the risk of repeat burning increases, eventually leading to a deflected successional community of savanna or shrubby vegetation, losing most species and many functions (*58*). Severe large-scale impacts can result from drought–fire interactions: During the last major El Niño, in 1997 to 1998, ~20 million ha of tropical forest burned (*25*), contributing to a corresponding record increase in atmospheric CO_2 concentration (*31*).

Forest recovery

New extensive areas of logged and secondary forest provide enormous scope to improve forest health and ecosystem services (Fig. 2, C and E) (*59*). If fire and conversion are avoided, logged tropical forests naturally recover structure and carbon stocks over time, and if overhunting is avoided, species composition will also likely be maintained (*11*). Following conventional logging, recovery of AGB may take several decades (*60*), but stocks returned to primary levels only 16 years after reduced-impact logging in the southern Amazon (*11*). Silvicultural techniques can enhance the rate of forest recovery; nontimber tree thinning and vine cutting nearly doubled the rate of AGB recovery in Africa (*60*), and vine cutting had minimal impacts on birds and wider forest health in Borneo (*37*).

Secondary forest regrows when economically marginal farmland is abandoned, often because it is too dry, steep, or high altitude for modern agriculture, including in the Tropical Andes, Caribbean, southern Mexico, and Philippines (Fig. 2E) (*27*). With protection from fire, forest recovery is fast (*59*, *61*) and carbon sequestration high (*34*), with soil erosion, landslides, and flood risk all reduced (*62*). In the Tropical Andes, carbon stocks reached half of primary forest levels after 30 years (*59*). Biodiversity began recovering, including the return of 33 of 40 threatened bird species (Fig. 2F) (*59*). Enrichment planting can boost early forest recovery in terms of carbon uptake and biodiversity (*61*). Regrowing areas can be large: In Latin America and the Caribbean, over 35 million ha of woody vegetation began recovery between 2001 and 2010 (*63*). Restoration can therefore provide many benefits, but such forests are not, in many respects, equivalent to faunally intact old-growth forests.

Future health of tropical forests

The 21st century will see large increases in demand for products from tropical lands. Thus,

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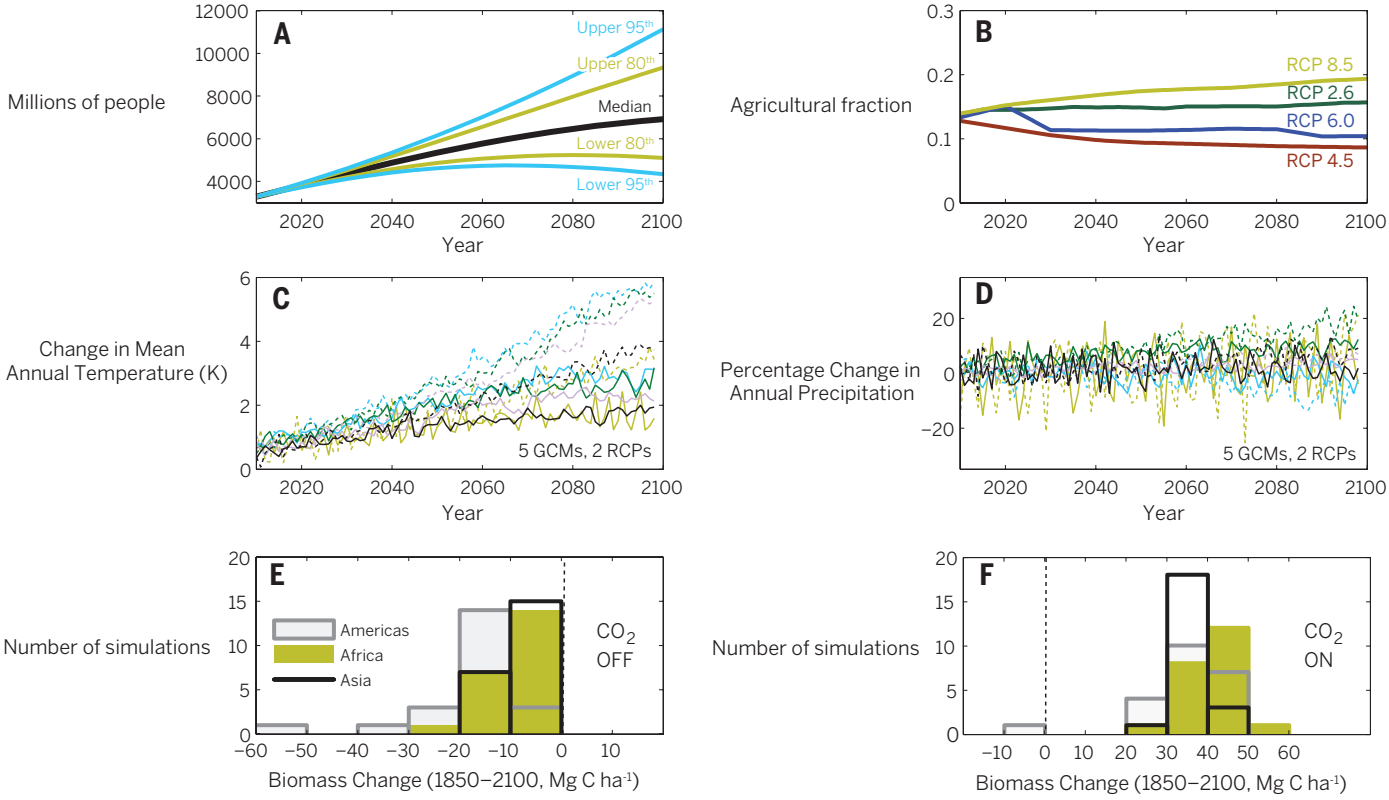

Fig. 3. Projected 21st-century trends for tropical forest regions: human population, agricultural extent, annual surface air temperature, annual precipitation, and changes in forest biomass. (**A**) Human population projections for tropical forest–containing countries (*64*). Median, black line; 80% probability interval, olive lines; 95% probability intervals, blue lines. (**B**) Mean agricultural-cropland and pasture fraction of land points in tropical-forest–containing regions, for four IPCC Representative Concentration Pathway (RCP) scenarios (*82*). Each land-use scenario uses a different integrated assessment model: IMAGE, green line (RCP2.6); MiniCAM, brown line (RCP4.5); AIM, navy line (RCP6.0); and MESSAGE, olive line (RCP8.5). Data from http://luh.umd.edu/data.php. (**C**) Change in mean annual temperature of land points in tropical-forest–containing regions, relative to the 1960 to 2005 mean, for RCP4.5 (solid lines), and RCP8.5 (dashed lines), each from five CMIP5 general circulation models (GCMs): GFDL-ESM2M, olive line; HadGEM2-ES, blue line; IPSL-CM5A-LR, green line; MIROC-ESM-CHEM, lilac line; and NORESM1-M, black line (*82*). Data from http://pcmdi9.llnl.gov. (**D**) Identical to (C), but reporting percentage change in mean annual precipitation. (**E**) Histograms of biomass change between 1850 and 2100 for tropical moist forest areas of the Americas, Africa, and Asia (Indo-Malayan and Australasian tropics combined) simulated by the MOSES-TRIFFID land-surface model, run with climate data outputs from 22 different CMIP3 general circulation models under an A2 emissions scenario (relatively high emissions), excluding the impacts of CO_2 fertilization on plants (*74*). (**F**) Identical to (E) except that plants also respond to CO_2 increases. The impacts of climate change are generally projected to be negative, and CO_2 positive, on tropical forest biomass. Panels (A) to (D) include areas of evergreen and seasonal forests (see Fig. 1), (E) and (F) evergreen only.

the greatest threats will likely continue to be conversion and degradation but will be increasingly combined with the impacts of rapid climatic changes (Fig. 3). The outcomes for forests will depend on their natural resilience plus management interventions that increase or decrease their vulnerability to multiple environmental changes. Here we synthesize model results and suggest alternative policy responses to maintain forest health.

Continued forest conversion

Predicting the future of land-use change in the tropics is challenging, given complex interactions among biophysical, economic, policy, and behavioral factors. Six billion people are projected to live in the tropics by 2100, rising from 40 to 55% of global population, with growth centered on Africa (Fig. 3A) (*64*). Gross domestic product (GDP) is projected to increase three- to sixfold by 2050 in rapidly industrializing nations, including Brazil, China, and India (*65*). These trends imply increased demand for commodities from tropical lands. For individual countries, Forest Transition Theory shows a slowing and reversal of net forest cover loss as country GDP increases and marginal farmlands are abandoned, thereby reverting back to forest (*66*). However, a global forest transition is unlikely because agricultural and forestry products are then obtained from other countries, leaking deforestation and degradation elsewhere (*67*).

Global land-use scenarios are included within the latest Intergovernmental Panel on Climate Change (IPCC) scenarios of greenhouse gas concentrations, termed "Representative Concentration Pathways" (RCPs). However, each of the four RCP scenarios utilizes a different Integrated Assessment Model driven by different assumptions. Thus, land-use projections within RCPs appear idiosyncratic and include both increases and decreases in agricultural area in 2100 (Fig. 3B). Uncertainty is also seen in the Agricultural Model Inter-comparison Project (AMIP), showing an average 200 million ha increase in cropland by area 2050, primarily in the tropics, yet 7 of the 10 economic models report a 10 to 25% increase in croplands, two a very modest increase, and one a decrease (*68*). Such uncertainty is unsurprising, as current models, both stochastic and deterministic, have largely failed to capture observed deforestation patterns, such as the large decline in deforestation rates in Brazilian Amazonia between 2004 and 2011 (*69*). The RCP and AMIP scenarios may grossly underestimate forest loss, as major new road infrastructure—some 25 million km by 2050 (*70*)—and highly lucrative mining and oil extraction look set to expand further (*23*). Despite the predictive challenges, there is agreement that land-use change is a much more important driver of tropical forest loss than climate, even under the most extreme emissions scenario (RCP8.5) (*71*).

Impacts of a changing climate

Climatic risks to tropical forests emerged from some early models that incorporated a dynamic

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link between vegetation and the atmosphere and simulated severe drying and warming over Amazonia, with considerable loss ("dieback") of forests (*72*). By contrast, more recent ensemble-based approaches, in which vegetation models are forced with output from multiple climate models, project gains in tropical forest biomass and cover under most future scenarios across the tropics (*73*, *74*). These changes reflect a balance of carbon losses due to climate change—higher air temperature and in some regions less rainfall—and carbon gains from increasing atmospheric CO_2, with gains generally outweighing the losses (*74*) (Fig. 3, C to F). By contrast, climate envelope-type approaches show a decreasing "niche space" for tropical forests but do not include the direct influence of CO_2 on photosynthesis and water-use efficiency (*75*). Thus, forest responses to CO_2 are critical to understanding the resilience of tropical forests to global change (compare Fig. 3, E and F).

Indeed, the balance of sensitivities to increasing CO_2 and a changing climate may be overly optimistic in most vegetation models. First, observations from 321 intact long-term inventory plots across Amazonia report net gains in AGB, in line with CO_2 fertilization, but also show these gains declining over the past two decades (*76*). That is, sink strength is declining, whereas vegetation models show the opposite (*74*, *77*). Second, current vegetation models fail to capture the doubling of tropical land sensitivity to increased temperatures over the past five decades (*4*) or the observed reductions in biomass under extreme drought (*77*). Third, the models generally lack representations of the mechanisms expected to curtail CO_2-related biomass increases such as soil phosphorus availability, which limits productivity in many tropical forests.

Changes not captured by plant physiology–based models will also occur, such as the responses to the projected 2° to 9°C temperature increase over tropical lands by 2100, depending on the emissions scenario and model (*74*). Populations will adapt, move, or die. In the montane tropics, some species are moving upslope (*78*), but in extensive low-altitude areas, including the Amazon and Congo basins, species would have to travel 0.33 km $year^{-1}$ to maintain their temperature niche over the 21st century (A1B scenario, ~4°C increase over tropical lands by 2100) (*79*). This implies high levels of population extinction. However, some tolerance of higher air temperatures may exist, as some species are old enough to have encountered Pliocene temperatures that were warmer than that of today (*80*), while others may exploit cool microhabitats to survive extreme weather events (*81*).

In contrast to air temperature, tropical precipitation projections vary considerably across climate models (*82*) (compare Fig. 3, C and D). There is some regional agreement: Southern and eastern Amazonia see longer dry seasons and East African forests become wetter (*82*). Longer dry seasons may lead to shorter forests through disproportionate mortality of tall canopy trees (*83*) and rapidly altered species composition: A 40-year rainfall decline in West Africa was accompanied by a dramatic shift to dry-adapted and deciduous species (*84*). Both drought and higher temperatures increase fire risk, potentially overwhelming all other changes and increasing the risk of widespread "savannization" of once-moist forest regions (*25*, *56*).

A choice of futures

Human-induced changes to tropical forests can be synthesized in stages: phase I, hunting and megafauna extinctions; phase II, low-intensity shifting cultivation; and phase III, global integration. This latest phase is defined by permanent intensive agriculture, often driven by distant socioeconomics directing land-use change, frontier industrial logging for export, cross-continental species invasions, and the early impacts of global atmospheric and climatic changes, where even the most remote forests are affected (*76*, *34*). A phase IV may occur: global simplification, in which species are lost across landscapes through a combination of rapid changes in climate, population isolation in fragmented landscapes, competition from invasive species, and the impacts of increasing disturbances—notably, fires combining with logging. Such changes would adversely affect local communities and global ecosystem services.

Human activity will dictate the future of tropical forests (*13*). Therefore, management decisions will deliver benefits to some groups over others and strongly influence the future health of tropical forests. The central policy question is, who derives benefits, and who bears the costs? In the face of widespread poverty in tropical forest regions, a goal of "development without destruction" would allow prosperity without undermining current ecosystem services—that over a billion people rely on—or globally critical functions (*2*, *7*, *34*). From a human rights perspective, forest-dwelling communities should be the overwhelming recipients of benefits flowing from tropical forests (which has not been the case with industrial logging or export farming). From a policy perspective, avoiding deforestation is often best achieved by allocating forest-dwellers legal rights over their land. An analysis of 292 protected areas in Brazilian Amazonia found that indigenous reserves were the most effective at avoiding deforestation in locations with high deforestation pressure (*85*). Furthermore, a pan-tropical study of 80 forest commons in 10 countries showed that collective long-term use rights maintain forest cover and carbon stocks better than other management systems (*86*). Such human rights–conservation win-win scenarios are gaining traction (*87*).

Beyond national networks of well-protected forested landscapes and formal collective tenure of forest lands, large-scale landscape planning will be required to maintain forest health. This would include halting deforestation (*87*), improving yields on existing agricultural lands, implementing low-impact logging methods for timber production (*37*, *49*), carefully targeting new road construction (*70*), and effective fire management (*37*, *58*). Some forest restoration will be required as species are moving under a rapidly changing climate; therefore, unbroken forested corridors linking tropical forest landscapes with those ~4°C cooler will be necessary to reduce levels of extinction. Combining these measures with near–real-time satellite monitoring, and effective enforcement to curb illegal activity, would substantially benefit forest-dependent communities, increase the resilience of tropical forests, and maintain the flow of ecosystem services they provide. This would lessen the unwelcome shocks that living in the Anthropocene will bring this century.

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REVIEW

Planted forest health: The need for a global strategy

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Several key tree genera are used in planted forests worldwide, and these represent valuable global resources. Planted forests are increasingly threatened by insects and microbial pathogens, which are introduced accidentally and/or have adapted to new host trees. Globalization has hastened tree pest emergence, despite a growing awareness of the problem, improved understanding of the costs, and an increased focus on the importance of quarantine. To protect the value and potential of planted forests, innovative solutions and a better-coordinated global approach are needed. Mitigation strategies that are effective only in wealthy countries fail to contain invasions elsewhere in the world, ultimately leading to global impacts. Solutions to forest pest problems in the future should mainly focus on integrating management approaches globally, rather than single-country strategies. A global strategy to manage pest issues is vitally important and urgently needed.

Forests and woodland ecosystems are a hugely important natural resource, easily overlooked and often undervalued (*1*–*3*). Globally, one in six people is estimated to rely on forests for food (*3*), and many more depend on forests for other critical ecosystem services, such as climate regulation, carbon storage, human health, and the genetic resources that underpin important wood and wood products–based industries. However, the health of forests, both natural and managed, is more heavily threatened at present than ever before (*4*–*6*). The most rapidly changing of these threats arise from direct and indirect anthropogenic influences on fungal pathogens and insect pests (hereafter referred to as pests), especially their distribution and patterns of interactions.

Here we focus on the importance of pests of planted forests, which are particularly vulnerable to invasive organisms yet are of growing importance as an economic resource and for various ecosystem services. Planted forests are typically of a single species. In plantations in the tropics and Southern Hemisphere, they are usually of non-native species, such as species of *Pinus*, *Eucalyptus*, and *Acacia*. Northern Hemisphere plantations often comprise species of *Pinus*, *Picea*, *Populus*, *Eucalyptus*, and other genera, often in native areas or with closely related native species. These intensively managed tree farms cover huge areas [currently 7% and potentially 20% of global forests by the end of the century (*1*)], and they sustain major industries producing wood and pulp products. These tree genera have become natural resources of global importance, much like major agricultural crops, and are unlikely to be easily replaced.

Planted forests face various serious health threats from pests (Fig. 1). Non-native trees in plantations are in part successful because they have been separated from their natural enemies. However, when plantation trees are reunited with their coevolved pests, which may be introduced accidentally, or when they encounter novel pests to which they have no resistance, substantial damage or loss can ensue (*7*). The longer these non-native trees are planted in an area, the more threatened they become by native pests. Where the trees are of native species, they can be vulnerable to introduced pests. But the relative species uniformity of monoculture stands in intensively managed native plantation forests can make them especially susceptible to the many native pests occurring in the surrounding natural forests (*8*–*10*).

There are many opportunities to mitigate potential losses caused by pests in planted forests through exclusion (e.g., pre-export treatments and quarantine), eradication of newly established pests, and avoidance of disease through pest containment and management. Yet the lack of investment and capacity, especially in poorer countries, as well as the limited coordination of efforts at a global level, means that the impact of these tools to stem the global problem is limited. Unless this is addressed, pest problems will continue to grow and will threaten the long-term sustainability of forests and forestry worldwide. It should be recognized that the sustainable use of these tree "crops" will require the same global focus and investment to manage pest threat as that of agricultural crops.

Prevention is important but remains porous

Biological invasions of alien pests have been shown to be growing at constant or even increasing rates—and not only for those affecting trees (*4*–*6*, *11*). Few pests are ever eradicated or completely suppressed, leading to an an ever-changing and increasing number of management programs to juggle. Phytosanitary measures are the major line of defense available to limit the global movement of pests, and various international policies seek to promote them [such as the International Standards For Phytosanitary Measures No. 15 (ISPM 15)

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Increasing human dominance of tropical forests

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