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The Future of Tropical Forest Species[1]

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ABSTRACT

Deforestation and habitat loss are widely expected to precipitate an extinction crisis among tropical forest species. Humans cause deforestation, and humans living in rural settings have the greatest impact on extant forest area in the tropics. Current human demographic trends, including slowing population growth and intense urbanization, give reason to hope that deforestation will slow, natural forest regeneration through secondary succession will accelerate, and the widely anticipated mass extinction of tropical forest species will be avoided. Here, we show that the proportion of potential forest cover remaining is closely correlated with human population density among countries, in both the tropics and the temperate zone. We use United Nations population projections and continent-specific relationships between both total and rural population density and forest remaining today to project future tropical forest cover. Our projections suggest that deforestation rates will decrease as population growth slows, and that a much larger area will continue to be forested than previous studies suggest. Tropical forests retracted to smaller areas during repeated Pleistocene glacial events in Africa and more recently in selected areas that supported large prehistoric human populations. Despite many caveats, these projections and observations provide hope that many tropical forest species will be able to survive the current wave of deforestation and human population growth. A strategy to preserve tropical biodiversity might include policies to improve conditions in tropical urban settings to hasten urbanization and preemptive conservation efforts in countries with large areas of extant forest and large projected rates of future human population growth. We hope that this first attempt inspires others to produce better models of future tropical forest cover and associated policy recommendations.

RESUMEN

La deforestación y la pérdida de hábitat pueden precipitar una crisis de la extinción de especies del bosque tropical. El mayor impacto sobre los bosques tropicales existentes es la deforestación y otras actividades por humanos que viven en las áreas rurales Las tendencias demográficas humanas actuales sugieren que una reducción en el crecimiento de la población y un aumento en la urbanización podrán causar una reducción en la deforestación, una aceleración de la sucesión secundaria, y evitar la esperada extinción en masa de especies del bosque tropical. Aquí, demostramos que la proporción del potencial de la cobertura del bosque restante está correlacionada con la densidad demográfica humana entre países; esto es aplicable a las zonas tropicales y templadas. Usamos proyecciones de las Naciones Unidas sobre crecimiento poblacionales y las relaciones entre la densidad poblacional rural y el bosque existente para proyectar la cobertura del bosque tropical en el futuro. Nuestras proyecciones sugieren que las tasas de deforestación disminuiran conjuntamente con una reducción en el crecimiento poblacional, y a la vez, áreas más extensas que los sugeridos en otros estudios permanecerán con cobertura forestal. Los bosques tropicales se retraeron a áreas más pequeñas durante los repetidos eventos glaciales del Pleistoceno en el Africa y más recientemente en áreas selectas ocupadas por grandes poblaciones humanas prehistóricas. A pesar de muchas advertencias, estas proyecciones y observaciones dan la esperanza de que muchas especies del bosque tropical podrán sobrevivir la presente tasa de deforestación y crecimiento poblacional humano. Una estrategia para preservar la biodiversidad tropical puede incluir políticas para mejorar las condiciones ambientales en áreas urbanas tropicales. Esto con el objectivo de acelerar la urbanización y programas de conservación preventivos en países con áreas extensas de bosque con un alto índice de crecimiento poblacional projectado para el futuro. Esperamos que nuestro primer esfuerzo inspire a otros investigadores a producir mejores modelos para predecir la cobertura del bosque tropical y políticas asociadas con la conservacion de estos.

Key words: Brazil; conservation; deforestation; extinction; habitat loss; human population growth; secondary forest; tropical biodiversity.

The widespread destruction of the most biodiverse habitats, in particular tropical forests and coral reefs, is widely thought to be precipitating a global extinction crisis. Here, we focus on the future loss of tropical forests and its possible consequences for biodiversity and extinction. A burgeoning human population has already removed somewhere between 8 and 12 million square kilometers (between 35% and 50%) of the original closed canopy tropical forests around the world (Table 1). The net loss of tropical forest continued to average somewhere between 50,000 and 120,000 km^2/yr during the 1990s (Table 2). The loss of old growth forest has recently accelerated in tropical Asia and the Brazilian Amazon (Fearnside & Barbosa 2004, Hansen & DeFries 2004). A mass extinction is widely anticipated if these losses of tropical forest should continue unabated (Pimm & Brooks 2000, Dirzo & Raven 2003, Sohdi *et al.* 2004, Millenium Ecosystem Assessment 2005).

Predictions of extinction driven by habitat loss are based on the relationship between area and species number (Pimm *et al.* 1995). This relationship is typically well-fit by a power function, with a log-log slope between 0.25 and 0.35. Thus, when area changes by a factor of 10, species number changes by a factor of about 2. In other words, the loss of 90 percent of the area originally covered by a habitat is expected to lead directly to the extinction of about 50 percent of the species endemic to that habitat. Less severe habitat

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TABLE 1. *Recent estimates of potential and extant closed forest area for tropical and extratropical continents. Ramankutty and Foley (1999) estimated potential forest area as the area that would be covered by closed forest in the absence of human intervention using 1-km resolution satellite imagery supplemented by a global vegetation model. The FAO (2000) estimated extant closed forest cover from national forest inventories supplemented by expert opinion. Achard et al. (2002) estimated extant closed forest cover from 30-m resolution satellite imagery using a random 6.5 percent sample stratified by forest cover and recent levels of deforestation. Hansen and DeFries (2004) estimated extant closed forest cover from 8-km resolution satellite imagery using a 100 percent sample of the tropics.*

	Potential forest cover[a] Ramankutty and Foley (1999)		Extant forest cover FAO (2000)		Extant forest cover Achard *et al.* (2002)		Extant forest cover Hansen and DeFries (2004)	
Continent	(10^4 km^2)[b]	(10^4 km^2)[c]	(10^4 km^2)[b]	(%)	(10^4 km^2)[c]	(%)	(10^4 km^2)[c]	(%)
Tropical								
Africa	545	548	344[d]	63.4[d]	193	35.2	172	31.3
Americas	1085	1056	891[d]	82.1[d]	653[e]	61.8	701	66.4
Asia	661	632	256	38.7	270[f]	42.7	199	31.5
Total	2291	2236	1496[d]	65.3[d]	1116	49.9	1072	47.9
Extratropical								
Americas[g]	510		231	45.3				
Asia[h]	456		186	40.8				
Europe[h]	421		171	40.5				
Russia	1219		834	68.4				
Total	2606		1422	54.6				

[a]Includes tropical evergreen, tropical deciduous, temperate broadleaf evergreen, temperate needleleaf evergreen, temperate deciduous, boreal evergreen, boreal deciduous, and mixed evergreen/deciduous forests and woodlands (*i.e.*, biomes 1 through 8 of Ramankutty & Foley 1999).

[b]Forest area in tropical and extratropical areas is summed over countries whose geographic centers are at latitudes $\leq 24°$ and latitudes $>24°$, respectively.

[c]Forest area in the tropics is for the area between the Tropics of Cancer and Capricorn.

[d]Comparisons among sources are problematical because the FAO (2000) "closed forest" includes an unknown proportion of the extensive Brazilian cerrado, African miombo, and other relatively open formations that the other sources exclude. Such open formations are of relatively limited extent in tropical Asia.

[e]Excludes Mexico and the Atlantic coastal forest of Brazil.

[f]Includes the "evergreen and seasonal forest of the tropical humid bioclimatic zone" for all continents and also the "dry biome of continental Southeast Asia."

[g]Excludes Canada due to its unique definition of forest cover (Matthews 2001).

[h]Excludes Russia, which is reported separately.

loss is also expected to lead to extinctions but of fewer species. For example, the loss of 50 percent of habitat area should lead to the extinction of about 19 percent of habitat endemics. The global loss of tropical forest already approaches this latter threshold (Table 1).

Local and regional losses of tropical forest can be much more severe. Myers *et al.* (2000) identified 25 endemicity hotspots that collectively cover just 12 percent of the Earth's land surface yet include the entire ranges of 44 and 35 percent of all vascular plants and terrestrial vertebrates, respectively. The restricted distribution of these hotspot endemics makes them particularly vulnerable to extinction. The 16 hotspots that support tropical forest have lost staggering percentages of their original vegetation cover (range 72–97%, median = 90% cover loss; Brooks *et al.* 2002). Species-area projections that incorporate this level of habitat loss suggest that extinction already threatens *ca* 50 percent of the tropical hotspot endemics that require old growth forest cover (Brooks *et al.* 2002).

Most tropical species are found outside these hotspots, however, and inhabit one of the four great blocks of tropical forest that once covered Indo-Malaya, Mesoamerica, the Amazon Basin and Guiana Shield, and the Congo Basin and humid western Africa. Here, for the groups that have been studied (largely plants, birds, and larger mammals), most species have large geographic distributions, which should buffer them from extinction (Rodrigues *et al.* 2004). Nonetheless, even when geographic distributions are very large, a sufficiently severe reduction of habitat area is expected to lead to the extinction of large numbers of endemic species. Will deforestation precipitate a mass extinction across Indo-Malaya, Mesoamerica, the Amazon Basin and Guiana Shield, or the Congo Basin and western Africa?

Given the importance of habitat loss to estimates of future extinctions, surprising uncertainty remains about current rates of tropical deforestation, and virtually no attempt has been made to anticipate future rates. Recent estimates of net tropical deforestation rates during the 1990s differ by 250 percent (Table 2). Simple extrapolations of these deforestation rates into the future indicate that it could take anywhere from 75 to 260 yr for the area covered by tropical forests to be reduced to 10 percent of its potential area depending on which estimate of current forest cover (Table 1) and current deforestation rates (Table 2) is used. The highest estimated rates of deforestation are based on national inventories, which may have overstated past deforestation rates (Matthews 2001, DeFries

TABLE 2. *Recent estimates of net deforestation (10^4 km^2/yr) during the 1990s for tropical Africa, America, and Asia.*

Continent	FAO Forest Resource Assessment (2000)		Hansen and DeFries (2004)	Achard *et al.* (2002)
	Country Data[a]	Remote Sensing[b]	Remote Sensing[c]	Remote Sensing[d]
Africa	5.2	2.1	−0.06[e]	0.71
Americas	4.4	4.2	3.9	2.2
Asia	2.4	2.3	2.3	2.0
Total	12.0	8.6	6.1	4.9

[a]National inventories supplemented by "expert" opinion for 1990 through 2000. Includes all lands where treecrowns originally covered 10 percent or more of the area.

[b]LandSat, 30-m resolution imagery for 1990 through 2000. The sample covered 10 percent of the tropics and included 117 images randomly located throughout wet, moist, and dry tropical forests.

[c]Advanced Very High Resolution Radiometry (AVHRR) with 8-km resolution for 1990 through 1997. The AVHRR sample covered 100 percent of the tropics. Changes in percent tree cover were converted to changes in forest area using conversion factors derived from a subsample of Landsat imagery.

[d]Landsat, 30-m resolution imagery for 1990 through 1997. The sample was stratified by prior deforestation and covered 6.5 percent of the "evergreen and seasonal forest of the tropical humid bioclimatic zone" plus the "dry biome of continental Southeast Asia" and excludes Mexico and the Atlantic coastal forest of Brazil.

[e]The negative sign indicates a net increase in forest area. The authors state that the 8-km resolution works poorly for Africa where clearing is mostly for small-scale agriculture.

et al. 2002). Further, there are reasons to believe that the rates of net deforestation recorded for the 1990s may not be sustained.

Burgeoning human populations have driven deforestation throughout the tropics (Brown & Pearce 1994, Bawa & Dayanandan 1997). In particular, slash and burn agriculturalists are believed to have caused two-thirds of past tropical deforestation (Myers 2002). Today, population growth is slowing in many tropical countries, and an intense urbanization of the population is underway in virtually all tropical countries (United Nations 2004a). Not only does this reduce pressure to cut remaining old growth forests, it also raises the possibility that total forest cover will actually increase in the future (Aide & Grau 2004, Wright & Muller-Landau 2004). Rural–urban migrants often leave agriculturally marginal lands unoccupied. After humans abandon land that previously supported old growth tropical forests, succession could result in new secondary forest cover. Forest will not be permanently lost if human activities change in appropriate ways.

Similar trends have already occurred in Europe and northern North America. In these areas, a shrinking rural population has abandoned agriculturally marginal lands, and many of these lands are covered by secondary forests or tree plantations today. There are also a handful of tropical examples—the area in secondary forests is now greater than the area in old growth forests in Puerto Rico and Costa Rica (Chazdon 2003, Lugo & Helmer 2004).

Here, we explore where and to what extent population trends are likely to relieve pressure on tropical forests over the next several decades. To do this, we first investigate the relationships between remaining forest cover and rural and urban population densities among tropical countries in Africa, the Americas, and Asia. We then examine future population projections for these same countries and predict the potential implications for future tropical forest cover if the current, cross-country relationship between population density and forest cover continues to hold. Because old growth forests are likely to play a particularly important role in biodiversity conservation, we also examine how rates of conversion of old growth forests relate to population density among Amazonian Brazilian states. Finally, we discuss the conservation implications of these future scenarios and of historical changes in forest cover.

DATASETS

FOREST COVER.—We estimated the percentage of potential forest remaining today (henceforth percent forest remaining) for each country as the area in forest in 2000 taken from the *Forest Resources Assessment 2000* (FAO 2000) standardized by the area potentially in forest taken from Ramankutty and Foley (1999).

The Forest Resource Assessment (FRA) program of the Forestry Department of the UN Food and Agricultural Organization (FAO) assesses the state of the world's forests each decade. The 2000 assessment (henceforth FRA2000) presents national-level data for both closed forest and all forests. The FAO defines "closed forest" as "formations where trees in the various storeys and the undergrowth cover . . . > 40 percent of the ground and . . . a continuous dense grass layer . . . [is lacking]. They are either managed or unmanaged forests, primary or in advanced state of reconstitution and may have been logged-over one or more times, having kept their characteristics of forest stands, possibly with modified structure and composition." "All forests" include all formations where trees cover more than 10 percent of the ground. Trees are defined as being greater than 5 m tall. The data for closed forest (Appendix 3, Table 5 in FAO 2000) are from national forest inventories taken between 1986 and 1999 for the 45 tropical countries to be considered here and between 1995 and 1999 for 30 of those countries (see below for country inclusion criteria). The data for all forests (Appendix 3, Table 3 in FAO 2000) are from the same national forest inventories but are standardized to the year 2000 (using additional partial reports on cover changes, expert opinion, and in a few cases remote sensing) and include open formations (10–40% tree cover) more typical of moist savannahs than of forests. Forest definitions used in national inventories vary among countries, and data quality is limited for many developing countries. Matthews (2001) discusses these limitations and concludes that FRA2000 is still the most comprehensive assessment of the present distribution of global forests.

Ramankutty and Foley (1999) prepared a global map of potential vegetation cover using a combination of satellite imagery and ecosystem modeling. They started with the 1-km resolution DISCover land cover data set, which is derived from satellite imagery, and reclassified those land cover classes into 15 potential vegetation types plus three additional classes: human land use, wetlands, and water. The potential vegetation type of each 5-min grid cell was then preliminarily assigned to the dominant potential vegetation type observed among the component 1-km DISCover pixels. For those cells with >50 percent crop cover or <20 percent dominant potential vegetation, the potential vegetation type was reassigned to the type predicted by the BIOME3 global ecosystem model of Haxeltine and Prentice (1996). The first eight types or biomes comprised forests or woodlands and were described as tropical evergreen, tropical deciduous, temperate broadleaf evergreen, temperate needleleaf evergreen, temperate deciduous, boreal evergreen, boreal deciduous, and mixed evergreen/deciduous, respectively. Biomes 9 and 10 comprised savanna and grassland/steppe and were dominated by grasses. Biomes 11 and 12 comprised dense shrub and open shrub and were dominated by woody plants shorter than 5 m. Biomes 13–15 comprised tundra, desert, and polar desert/rock/ice, respectively.

The accuracy of estimates of percent forest remaining depends on the match between definitions of extant and potential forest cover. The first eight biomes of Ramankutty and Foley (1999) match the FRA2000 definition of closed forest, having >40 percent treecrown coverage and lacking a continuous grass layer. But, the savannah biome presents a problem because formations with both greater and lower coverage by treecrowns are included. Thus, for example, Ramankutty and Foley (1999) classified the Brazilian cerrado as savannah while the Brazilian national inventory used by the FAO (2000) classified an unspecified portion of the cerrado as closed forest. Achard *et al.* (2002) stated that their definition of forest corresponded closely to the FAO definition of closed forest; however, different treatments of savannah caused large discrepancies in closed forest area estimated for Africa and the Americas by FAO (2000) and Achard *et al.* (2002) (Table 1). Hansen and DeFries (2004) discuss the forest vs. savannah definitions used in national inventories by different African countries in greater detail (see their Fig. 8). We used three different estimates of percent forest cover to ensure that our analyses were robust with respect to the definition of savannah. First, we standardized the FRA2000 closed forest area by the summed area in biomes 1 through 8 to exclude savannah entirely. Second, we standardized the FRA2000 closed forest area by the summed area in biomes 1 through 9 to include savannah in the denominator only. Third, we standardized the FRA2000 all forests area by the summed area in biomes 1 through 9 to include savannah in both the numerator and denominator. The third estimate was highly variable among African countries because the national inventories treated the extensive areas of savannah differently (Matthews 2001, Hansen & DeFries 2004). Otherwise, all three estimates gave qualitatively similar results. We report results for the first estimate because we believe it provides the best match between definitions of extant and potential forest cover.

We superimposed 5-min resolution maps of biomes and political boundaries to calculate the area within each country potentially covered by forest. We excluded countries smaller than 10,000 km^2. We included humid tropical countries defined to be those countries whose geographic center fell within 24° of the equator and whose potential vegetation was forest over 40 percent or more of the national territory. Angola met these criteria but was excluded because the FAO estimate of Angola's forested area increased threefold from 1990 to 2000 suggesting an unresolved definitional problem (Matthews 2001). The 45 humid tropical countries that remain supported 89.6 percent of all extant closed tropical forest (FAO 2000) and 89.9 percent of all potential tropical forest cover (calculated from Ramankutty and Foley (1999)). Among extratropical countries, we excluded Canada because the national inventory uses a unique definition of forest (Matthews 2001).

HUMAN POPULATIONS.—The United Nations (UN) Population Division has compiled (or interpolated) data on the total, urban, and rural population of each country at 5-yr intervals for 1950–2000 and projected these numbers forward to 2030 (United Nations 2001, 2004a). Low, medium, and high variant projections make different assumptions about changes in fertility, mortality, and international migration rates. For example, the medium variant projection assumes that (1) fertility declines following the past experience of countries with declining fertility between 1950 and 2000 and with a floor of 1.85 births per woman; (2) mortality declines based on models of change in life expectancy that incorporate the HIV/AIDS epidemic; and (3) international migration follows past patterns modified by country-specific policies toward future immigration.

Rural–urban projections are based on a logistic model of the growth of the proportion urban (P). The logistic model incorporates the difference between the urban and rural population growth rates (Δ) and is modified to reflect reductions in the pool of potential rural–urban migrants as P increases. The modification estimates future values of Δ as a weighted average of the most recent value actually observed, Δ_o, for a country and a second value, Δ_i, interpolated from the most recently observed or projected value of P for that country and the linear relationship between Δ_o and P observed for the 113 most populous countries in 1995. Subsequent 5-yr projections assigned weights of 0.8, 0.6, 0.4, 0.2, and 0 to Δ_o and the complement of these weights to Δ_i. The definition of urban varies among countries and may be based upon minimum population size or density, specific places, or administrative, economic, and/or infrastructural criteria. Definitions based on minimum population size include 500 (Papua New Guinea), 1500 (3 countries), 2000–5000 (15), and 10,000 (2) inhabitants for the humid tropical countries considered here (United Nations 2004a). Total population data and projections (rural and urban) were taken from United Nations (2001, 2004a).

OLD GROWTH FOREST COVER AND POPULATION IN BRAZIL.—Brazil's National Institute for Space Research (INPE) has used LANDSAT imagery to estimate the area of old growth deforested between 1978 and 1988 and, with one exception, for each year thereafter for each Brazilian Amazon state (http://www.obt.inpe.br/prodes/prodes_1988_2003.htm). INPE also estimated the original area in old growth forest, but has only released those figures as maps

(P. Fearnside, pers. comm.). We combined the INPE deforestation data, Fearnside's (1994) estimates of original forest cover based on the INPE maps (column B in his Table 2), and Fearnside's (1994) estimates of the area deforested between 1960 and 1988 (column F in his Table 2) to calculate the proportion of original forest cover remaining at the national censuses of 1980, 1991, and 2000 for each Brazilian Amazon state. Census data were taken from the Instituto Brasileiro de Geografia e Estatícas (http://www.ibge.gov.br). The states of Maranhao and Tocantins had less than 50 percent potential forest cover and were excluded.

EXTANT FOREST COVER AND DEFORESTATION RATES

Extant forest cover includes old growth forests as well as secondary, logged, and otherwise degraded forests. The FAO (2000) consistently provides larger estimates of extant forest area than do two recent satellite-based surveys for each of the tropical continents (Table 1). This reflects different definitions of forest. FAO (2000) includes land with >40 percent coverage by treecrowns, Hansen and DeFries (2004) include land with >60 percent coverage by treecrowns, and Achard *et al.* (2002) include "evergreen and seasonal forest of the tropical humid bioclimatic zone." More surprisingly, the relative ranking of the continents varies among the three estimates. Tropical Asia has the least extant forest in the FAO (2000) assessment, while tropical Africa has the least extant forest in the two recent satellite-based surveys. This probably reflects regional differences in the extent of dry forest and in its treatment in the national inventories compiled by FAO (2000) (Ramankutty & Foley 1999, Matthews 2001, Hansen & DeFries 2004). The two satellite-based surveys use relatively consistent forest definitions across continents (but see footnotes e and f in Table 1); however, the correspondence to the definition used in the potential forest cover calculations remains unclear.

The percent forest remaining, defined as extant forest area divided by potential forest area (times 100), is surprisingly low for tropical Asia and Africa (Table 1). The percent forest remaining is consistently low for all three estimates of extant forest area for tropical Asia and for the two satellite-based surveys for tropical Africa. The percent forest remaining is already as low or lower for tropical Asia and Africa as for the temperate and boreal regions of the Americas, Asia, and Europe (Canada and Russia excluded).

Estimates of net tropical deforestation rates also vary widely for the 1990s (Table 2). The FAO (2000) provides the largest estimates of net forest loss of 86,000 and 120,000 km^2/yr (Table 2). The two recent satellite-based surveys provide remarkably similar pantropical estimates of net deforestation of 49,000 and 51,000 km^2/yr, but this masks large, offsetting differences among the tropical continents (Table 2). Tropical deforestation occurs first in drier, more open forests (FAO 2000); thus, it is not surprising that the FAO, which includes drier, more open forests, reports higher net deforestation rates. The satellite-based estimates suggest that about 2.2 percent of the *potential* closed canopy tropical forest is being removed each *decade*.

The remainder of this paper will use the FAO (2000) estimates of extant closed canopy forest because this is the only estimate of extant forest cover available by country. The reader should keep in mind that this probably overestimates the actual extant forest cover.

THE RELATIONSHIP BETWEEN FOREST COVER AND HUMAN POPULATION DENSITY

Humans cause deforestation, and it is widely recognized that recent deforestation rates are positively related to local human population density while the percent forest remaining is often negatively related to human population density in the tropics (Brown & Pearce 1994, Bawa & Dayanandan 1997). To demonstrate that the latter relationship is not unique to the tropics or to "developing" countries (as defined by the United Nations (2004a) plus Albania), we performed an analysis of covariance (ANCOVA) to evaluate how percent forest remaining related to latitudinal zone and total population density. Countries whose potential vegetation was closed forest over more than 40 percent of their national territory were included. The categorical variable latitudinal zone was scored as tropical for countries whose geographic center was below 24° latitude and temperate for all other countries. Untransformed values of percent forest remaining and logarithms of population density fulfilled ANCOVA assumptions throughout.

Percent forest remaining is indistinguishable for tropical and developed temperate countries after controlling for variation in total population density (Fig. 1). Percent forest remaining was closely related to the logarithm of total population density for 84 temperate and tropical countries ($r = -0.65$). The five developing temperate countries were outliers from the relationship for the more developed temperate countries (Fig. 1) and were therefore excluded from the

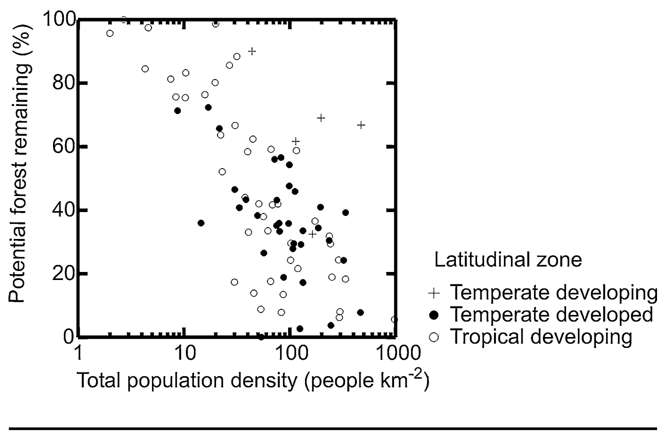

FIGURE 1. The relationship between the percentage of potential closed forest remaining and total population density for 79 humid tropical and temperate countries. The relationship is statistically indistinguishable for tropical countries and developed temperate countries. Five developing temperate countries (Albania, Bhutan, Nepal, North Korea, and South Korea) were excluded from this analysis. Closed forest is the potential vegetation over 40 percent or more of the national territory for each country.

ANCOVA. The homogeneity of slopes assumption was satisfied for the 79 remaining countries, and the insignificant interaction between latitudinal zone and the logarithm of population density ($F_{1,75} = 3.36$, $P = 0.071$) was removed. The reduced ANCOVA model explained 62 percent of the variance in percent forest remaining, with a significant effect of the logarithm of population density ($F_{1,76} = 105.2$, $P < 0.001$) but not latitudinal zone ($F_{1,76} = 0.38$, $P = 0.54$). Anthropogenic forest loss is a global problem, not a tropical problem.

We performed a second ANCOVA to quantify the relationship between percent forest remaining and human population density in different tropical regions. We treated rural and urban populations separately because rural populations are expected to have a greater direct impact on forests, clearing forest at agricultural frontiers and maintaining agricultural landscapes that prevent secondary forest regrowth. This second ANCOVA evaluated relationships among percent forest remaining (dependent variable), tropical continent, and rural and urban population densities. The categorical variable tropical continent took the following values: Africa, the Americas including North and South America and the Caribbean, and Indo-Malaya including South Asia, Southeast Asia, and Papua New Guinea.

Percent forest remaining was negatively correlated with the logarithm of rural population density for each tropical continent (Fig. 2; $r = -0.83$, -0.93, and -0.89 for Africa, the Americas, and Indo-Malaya, respectively). The homogeneity of slopes assumption was satisfied, and the insignificant interactions between continent and the logarithms of rural and urban population densities ($F_{2,36} = 0.48$, $P = 0.62$ and $F_{2,36} = 0.087$, $P = 0.92$, respectively) were removed. The reduced ANCOVA model explained 76 percent of the variance in percent forest remaining, with significant effects of continent ($F_{2,40} = 4.48$, $P < 0.02$) and rural population density ($F_{1,40} = 25.0$, $P < 0.001$) but not urban population density ($F_{1,40} = 0.041$, $P = 0.84$). Logarithms of rural and urban population densities were closely related ($r = 0.84$, $P < 0.001$). Therefore, residuals from relationships among percent forest remaining, continent, and the two types of population densities were examined directly. Residuals from the relationship including rural population density were unrelated to urban population density ($r = 0.014$, $P = 0.93$). Residuals from the relationship including urban population density were negatively and nearly significantly related to rural population density ($r = -0.24$, $P = 0.057$, one-tailed test). A strong relationship between percent forest remaining and rural population density is not improved by incorporating urban population density. Percent forest remaining averaged 43.2 percent greater for Indo-Malaya than for Africa and the Americas (Fisher's least significant difference, $P < 0.005$ and $P < 0.05$, respectively) and was indistinguishable for Africa and the Americas ($P = 0.48$) in *post hoc* comparisons that controlled for variation in rural population density.

Net forest loss has proceeded further in tropical Asia than in the tropical Americas (FAO 2000). It is perhaps less widely recognized that net forest loss is as severe for tropical Asia as for extratropical Asia, Europe, and North America (Table 1). It is certainly less widely appreciated that net forest loss per capita is actually significantly lower for tropical Asia than for the tropical Americas and Africa (Fig. 2). The per capita human impact on forests is greatest in the tropical Americas and Africa.

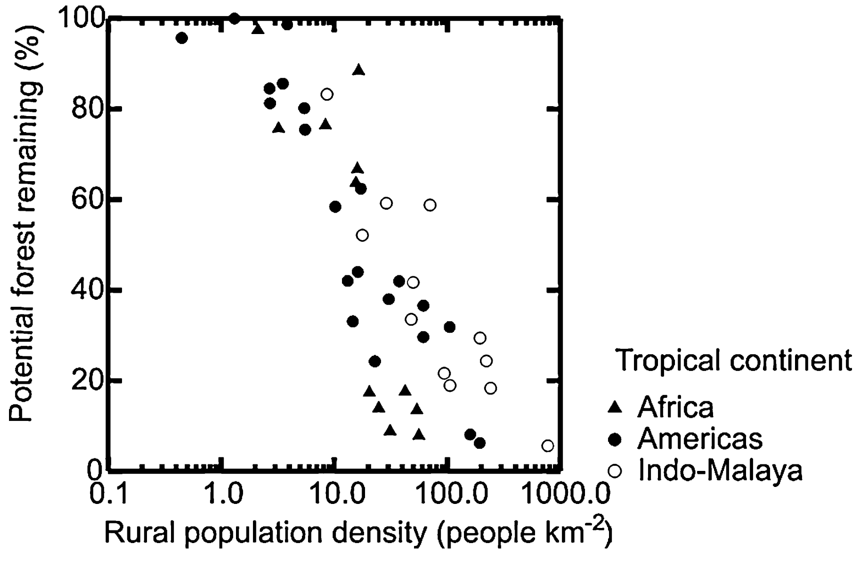

FIGURE 2. The relationship between the percentage of closed forest remaining and rural population density for 45 humid tropical countries. Potential forest cover (the denominator of the ordinate) includes the forest and woodland biomes of Ramankutty and Foley (1999). Extant closed forest cover (the numerator of the ordinate) was taken from FAO (2000). Humid tropical countries were defined to be those countries with closed forest being the potential vegetation over 40 percent or more of their national territory and whose geographic centers were at latitudes below 24°.

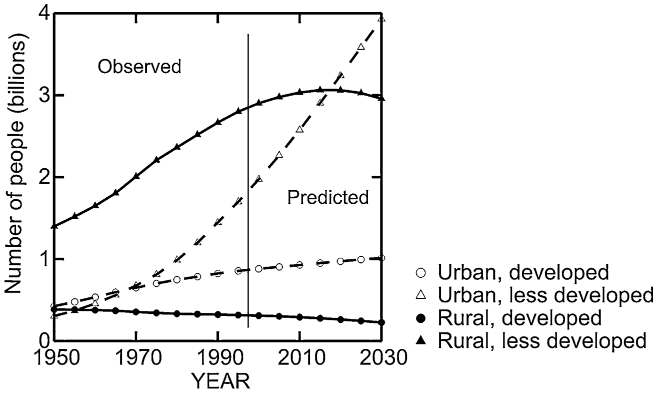

FIGURE 3. Global population size partitioned among more and less developed countries and rural and urban settings. Values from 1950 through 1995 were observed or interpolated, those from 2000 through 2030 were predicted (United Nations 2004a). The more developed regions comprise Europe, northern North America, Australia, New Zealand, and Japan. The less developed regions comprise Africa, Asia (excluding Japan), Latin America and the Caribbean, Melanesia, Micronesia, and Polynesia following United Nations (2004a).

PROJECTIONS OF HUMAN POPULATION GROWTH

The UN Population Division projects that the global human population will increase by 34 percent from 6.1 billion in 2000 to 8.1 billion in 2030 with the growth concentrated in urban areas (United Nations 2004a). Globally, urban populations are projected to increase by 73 percent while rural populations are projected to *decrease* by 1 percent. Urbanization has long characterized the more developed countries, whose urban and rural populations grew by 1.45 percent/yr and shrank by 0.43 percent/yr, respectively, between 1950 and 2000 (Fig. 3). In 2000, the percentage of people living in urban settings was 79.1 and 72.7 percent in the developed countries of northern North America and Europe, respectively. Urbanization has also been underway in the developing countries, whose urban and rural populations grew by 3.73 and 1.46 percent/yr, respectively, between 1950 and 2000 (Fig. 3). In 2000, the percentage of people living in urban settings was a surprising 75.5 percent in Latin America and the Caribbean and just 37.1 percent in both Africa and Asia. The trend toward urbanization is expected to intensify through 2030. This is particularly true for the less developed nations where urban and rural populations are projected to grow by 2.29 and 0.06 percent/yr, respectively, between 2000 and 2030.

Taking a closer look at country-level projections for population growth in general and rural population growth in particular, we see dramatic variation with latitude and, at low latitudes, among continents (Fig. 4). Total populations are expected to hold steady or decline between 2000 and 2030 for most countries located above 40° latitude and to increase for most countries located closer to the equator. The projected increases are relatively modest in the Americas and potentially much greater although highly variable among African and Asian countries (Fig. 4a). In contrast, rural populations are expected to decline often substantially for most countries located above 40° latitude and to hold relatively steady for most countries in the tropical Americas (Fig. 4b). Rural population growth is expected to be more variable among African and Asian tropical countries with many of these countries experiencing substantial increases in their rural populations, particularly in Africa. Thus, while future human population growth is mostly in the tropics, it is also concentrated in urban areas.

Projections for three important countries illustrate the regional differences in population growth expected within the tropics (Fig. 5). Brazil, Indonesia, and the Democratic Republic of the Congo contain 60, 40, and 21 percent of the closed tropical forest remaining in the Americas, Indo-Malaya, and Africa, respectively (FAO 2000). The populations of Brazil and Indonesia are expected to grow by 29 and 31 percent by 2030, respectively. This is similar to the population growth of 30 percent projected for the United States. In contrast, the population of the Democratic Republic of

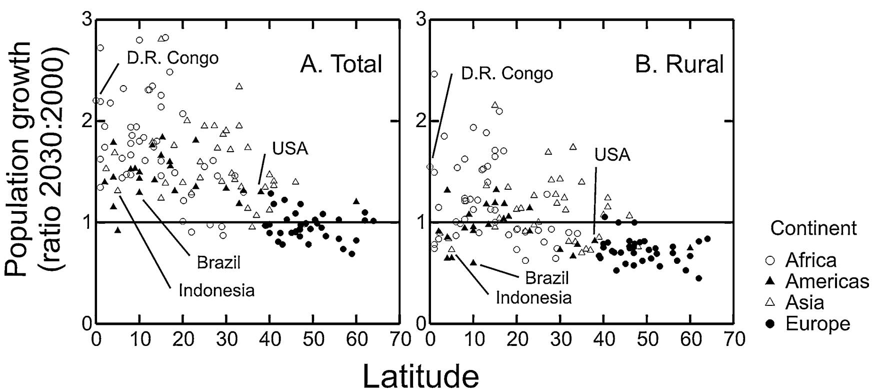

FIGURE 4. The relationship between latitude and population growth expressed as the ratio of population projected for the year 2030 by the UN Population Division to population in the year 2000 for the countries of Africa, the Americas, Asia, and Europe, for total population (a) and rural population (b). Small island nations are excluded.

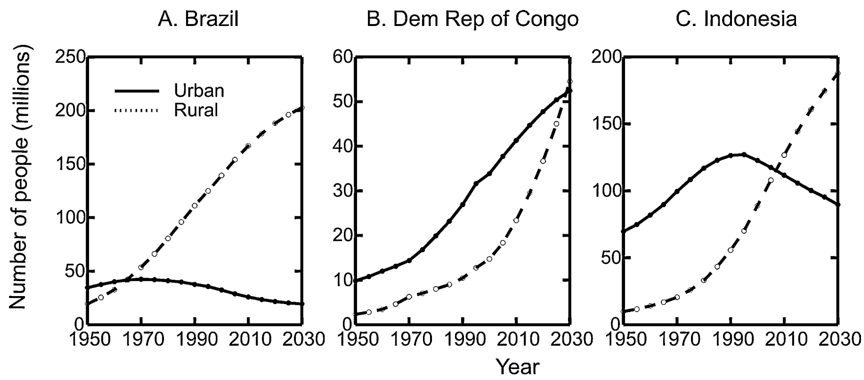

FIGURE 5. Population size partitioned among rural and urban settings for Brazil (a), the Democratic Republic of the Congo (b), and Indonesia (c). Brazil is representative of Latin America and the Caribbean where 75.5 percent of all people lived in urban settings in 2000 and future population growth and rural–urban migration are expected to further intensify urbanization. The Democratic Republic of the Congo is representative of many African countries where 37.1 percent of people lived in urban settings in 2000 and future population growth rates are expected to be very high everywhere but particularly in urban areas. Indonesia is representative of many tropical Asian countries where 37.1 percent of people also lived in urban settings in 2000 and future population growth is expected to intensify urbanization. Data or interpolations from 1950 through 2000 and projections from 2005 through 2030 are from United Nations (2004a).

the Congo is expected to grow by a sobering 220 percent. The rural population of Brazil peaked in 1975, has declined steadily since 1975, and is projected to decline from 32 million in 2000 to just 19 million in 2030. The rural population of Indonesia is believed to have peaked in 1995 and is projected to decline by more than 35 percent by 2030. In contrast, the rural population of the Democratic Republic of the Congo is projected to increase from 34 million to 52 million between 2000 and 2030. Again, rapid ongoing population growth in Africa often includes substantial rural population growth.

PROJECTIONS OF TROPICAL FOREST COVER

We combined continent-specific, cross-country relationships between the percent forest remaining and logarithms of population density in 2000 (Fig. 2) with country-specific population projections to estimate future net deforestation rates and changes in forest cover. The estimates are for the 45 humid countries considered here—countries that contained 89.6 percent of all closed tropical forests in 2000 (FAO 2000). A first estimate of future net deforestation was based on total population density, which incorporates rapid ongoing growth of urban populations (Figs. 3–5). A second estimate was based on rural population density only, which is predicted to shrink in many tropical countries (Figs. 4 and 5). These two estimates might be considered as upper and lower bounds on future rates of net deforestation.

Net rates of deforestation are predicted to decline steadily over the next 25 yr for both projections and all three tropical continents (Fig. 6). The projections based on total vs. rural population growth predict net tropical deforestation of 7.0×10^4 vs. 2.1×10^4 km^2/yr, respectively, for the 5-yr interval centered on 2005. These broad bounds compare favorably to the net global loss of closed tropical forest of 4.9×10^4 and 6.1×10^4 km^2/yr between 1990 and 1997 estimated by Achard *et al.* (2002) and Hansen and DeFries (2004), respectively.

The continent-specific deforestation projections (Fig. 6) reflect the very different levels of total population growth and urbanization anticipated by the UN Population Division (Figs. 4 and 5). The Americas in particular will experience high levels of natural forest regeneration if urbanization reduces rural population densities as expected and if land is indeed abandoned to regenerate as secondary forest. In the Asian tropics, forest cover is already very low, and is projected to remain thus through 2030, with relatively modest net changes to total cover. The situation is much grimmer for Africa where rapid growth of the total population and continued growth of rural populations are predicted to sustain high levels of net deforestation through 2030.

CAVEATS.—Our predicted rates of net forest loss should be regarded as a first attempt to bracket future forest loss. They are based on a simple model associating forest cover with local human population density. Thus, the quality of these estimates depends critically on the future constancy of the underlying relationship between percent forest remaining and population density, as well as on the accuracy of the population projections. Here, we discuss the limitations of these assumptions and the potential implications for the accuracy of our predictions.

It is important to note at the outset that our projections of forest area from human population density are not meant to imply that population density changes are the direct cause of forest clearing or regrowth. Many factors affect deforestation, both proximately and ultimately, and these factors vary regionally (Geist & Lambin 2002). In some cases, changes in rural population density are arguably a proximate cause of forest area change. For example, emigration from rural areas (whether driven by the availability of better jobs in cities, war, or other factors) may lead to land abandonment and forest regrowth. In other cases, independent external factors may drive

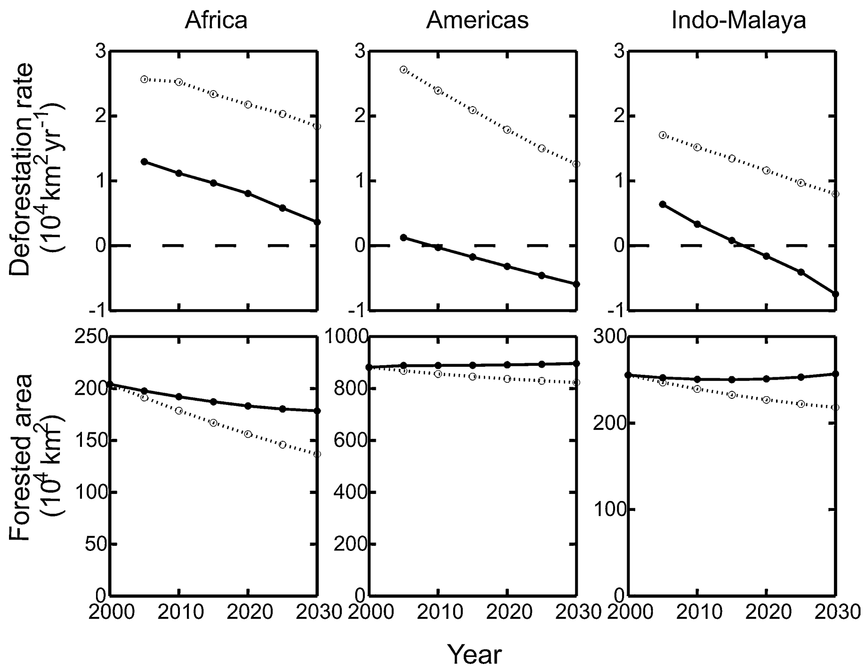

FIGURE 6. Future net deforestation rates (upper panels) and forested area (lower panels) predicted from total (open symbols, dotted lines) and rural (solid symbols and lines) population growth. The dashed horizontal lines represent zero net deforestation in the upper panels. Negative net deforestation rates represent net increases in forest area. The predictions incorporate continent-specific, cross-country relationships between forest area and population density in 2000 (see Fig. 2) and population growth anticipated by the UN Population Division (see Fig. 4). All figures are for the 45 humid tropical countries that support 89.6 percent of all extant tropical closed forest (see *Data sets: Forest cover*).

changes in both population density and forested area. For example, road-building may increase access to markets and to immigrants, and thus result in increased population density and forest clearing for agriculture. Many studies have found correlations between various measures of forest cover or change and human population density or change (Brown & Pearce 1994). In using population projections to predict forest area, we are not suggesting a particular causal relationship, rather we use a strong phenomenological relationship to predict a quantity for which we have little basis for prediction (future forest remaining) from one that is much-studied and often-predicted (human population density).

The existence of a relationship between population density and forest area today does not necessarily mean that the relationship will take the same form in the future, as assumed in our projections. Our data provide limited evidence on the reliability of this assumption. The slope of the relationship is relatively consistent among regions at very different stages of development and with different histories (Figs. 1 and 2), suggesting that it may be consistent in time as well. However, the intercept varies among regions (it is higher for Indo-Malaya, Fig. 2), suggesting that it may vary in time too—in which case, future relationships may indicate more or less forest area for a given human population density. A full test of our assumption requires accurate human population and forest cover data from multiple time periods. Pre-2000 FAO forest cover data were obtained in a different manner than the 2000 data and are considered less reliable (Matthews 2001), and thus are unsuitable for such analyses. Future studies should seek to obtain and analyze consistent data for multiple time periods to assess the constancy of the relationship between population density and forest cover through time.

In principle, there are reasons to expect this relationship to change in the future. Rural population density may be so closely related to forest area today in part because the predominant uses of cleared land are currently labor-intensive (*e.g.*, small-holder agriculture), and most employment is directly or indirectly related to the use of cleared land. If agricultural practices in tropical countries continue to become more energy- and input-intensive and less labor-intensive as expected, cleared land may be used and maintained in a less labor-intensive way in the future. In this case, we could expect to find lower forest cover for a given population density than we observe today. This phenomenon may already be apparent in some areas—for example, it may explain why the Brazilian state of Rondonia, which contains many large soybean farms geared toward the global market, has less forest than expected based on its population density (Fig. 7a). On the other hand, if job opportunities that do not involve forest clearing or cleared land become more abundant in rural areas, then we may see higher forest cover for a given population density in the future. This possibility seems likely for Indo-Malaya. We expect that there will be significant changes in the labor-intensity of land use and in rural employment options in tropical countries as development and globalization proceed. How these changes will interact to affect the relationship between rural population density and forest area remains to be seen.

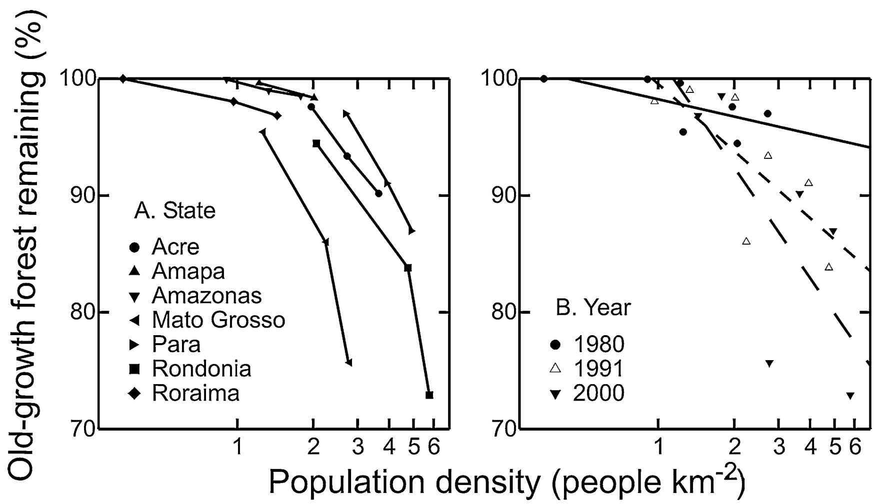

FIGURE 7. The relationship between total population density and the percentage of old growth forest remaining for the seven states of the Brazilian Amazon where old growth forests originally covered more than 50 percent of the territory. Panel (a) presents the data for each state. Panel (b) presents the same data for the three most recent national censuses (1980, solid circles and line; 1991, open triangles and finely dashed line; 2000, solid triangles and coarsely dashed line).

Our forest area projections depend not only on the future constancy of the relationship between population density and forest area, but also critically on the accuracy of the human population projections themselves. There are many uncertainties in predicting human demographics, with different assumptions producing very different estimates of future total population sizes. Reflecting these uncertainties, the UN Population Division produces not only the median population projection used here, but also high and low projections which predict global population in 2030 to be 8.8 and 7.5 billion or 108.5 and 91.6 percent of the median projection, respectively. These differences correspond to 1.6–2.5 percent less tropical forest area remaining in 2030 for the high variant and 1.7–2.8 percent more forest area remaining for the low variant for projections based on rural and total populations, respectively. Additional uncertainty enters our projections from rural population density, as these depend critically on the predictions of how future populations will be divided between urban and rural areas. The United Nations (2004a) bases this last prediction on a purely phenomenological fit to past data and provides no high and low variants. Changing economic conditions and government policies could potentially cause major unforeseen changes in rural–urban migration.

Both the UN population projections and our projections of forest data from population extrapolate past and current relationships into the future. They are phenomenological models. Like all phenomenological models, they are liable to fail if the causal relationships that have produced historical or current patterns change. More complex and mechanistic models of the underlying economic, social, and political factors have been applied to understanding deforestation rates (Barbier & Burgess 2001, Geist & Lambin 2002). These models may provide a better basis for projection of future forest area if the relevant causal factors—prices of agricultural commodities, rural wages, road-building, tenure insecurity, etc.—can be reliably projected into the future. However, projecting these factors may prove as difficult as projecting forest area itself, and result in no overall improvement in the accuracy of forest area estimates.

The specifics of our projections will almost certainly prove wrong, but we believe the qualitative predictions will prove correct. Specifically, we expect that in the next 25 yr the rate of net tropical deforestation will slow on all continents. Further, we predict a switch to a net increase in forest area in Latin America and Asia if not within 25 than at least within 50 yr, and in Africa within 100 yr. The fundamental causes of such changes will be stabilizing human populations and thus stabilizing demand for agricultural commodities, increased nonagricultural economic opportunities in developing countries, and increased agricultural land use efficiency due to continuing technological improvements and their more widespread use. Our optimism is consistent with past changes in population size, agricultural yields, and cropland area in developing countries. Between 1960 and 2000, an increase of just 20 percent in cropland area was able to support an increase of 133 percent in population because agricultural yields increased by 100 percent (Green *et al.* 2005). Agricultural yields continue to increase steadily and developing country yields still lag 20 yr behind those realized in developed countries (Green *et al.* 2005). Finally, there is reason to believe that in tropical countries in the future, as in developed temperate countries in the past, increasing per capita income will eventually bring increasing demand for environmental goods, including native forest protection (Barbier & Burgess 2001).

THE FUTURE OF OLD GROWTH FORESTS OF BRAZIL

The forest cover data discussed so far includes degraded and secondary forests, which have lower conservation value than old growth forests. Because of their importance for tropical species diversity, we now take a closer look at what is happening to old growth forests in particular. We use the example of Brazil, where extensive data are available.

The percentage of old growth forest remaining has declined approximately linearly with the logarithm of human population density for five of the seven Brazilian Amazon states whose original vegetation cover was more than 50 percent forest (Fig. 7a). The two exceptions are Mato Grosso and Rondonia. Industrial agriculture, which requires relatively little human labor, has driven recent deforestation in Rondonia (W. F. Laurance, pers. comm.) and is probably responsible for the recent steep decline there in percent old growth forest remaining relative to human population density. The slope of the relationship between percent old growth forest remaining and the logarithm of population density became progressively steeper from 1980 to 1991 and on to 2000 (Fig. 7b). An ever steeper slope is to be expected when old growth forests are preferentially cleared while, at the same time, secondary forests develop on previously deforested land. Secondary forests already covered 30 percent of the deforested lands of the Brazilian Amazon in 1986 (Houghton *et al.* 2000). The recovery of secondary forests will buffer the net loss of forest cover even as the rate of loss of old growth forest accelerates in the Brazilian Amazon (Fearnside & Barbosa 2004).

THE NATURE AND DISTRIBUTION OF FUTURE TROPICAL FORESTS

Already today all forests worldwide are significantly affected by human activities, and the magnitude of human influences will continue to grow. These influences can be grouped into two broad categories—direct effects of local human activities such as land clearing, timber extraction, and hunting, and indirect effects of regional and global human industrial activities through influences on the Earth's atmosphere and climate. We expect that net deforestation, hunting, and other local human influences (but not timber extraction) will peak within the next century and then decline, in parallel with projected trends in rural human population density in the tropics. However, the history of such activities will leave a legacy of changed forest structure and species composition that will endure for centuries after the activities themselves cease. Further, the more diffuse influences caused by anthropogenic change to the global atmosphere and climate are expected to continue to grow for the foreseeable future.

In the future, most tropical forests will be secondary forests regenerating after previous clearing. This transformation is already underway. Secondary forest succession offset one of every six or seven hectares deforested during the 1990s (Achard *et al.* 2002, Hansen & DeFries 2004). The regrowth of secondary forest is expected to reduce and in some cases eventually reverse losses in total forested area. However, such secondary forests differ systematically in species composition and forest structure from the original primary forests (Chazdon 2003, Lugo & Helmer 2004). At best, it is expected to take hundreds of years for secondary forests to return to a state resembling primary forest, and such a return will not be possible in all areas. Because clearing is often preferentially of primary forests, the total proportion of forested area in secondary forests will continue to grow and the average age of forests continue to fall for many years even after net deforestation rates begin to decline.

Relatively undisturbed old growth or primary forests will become increasingly rare, and even these forests will be ever more affected by anthropogenic increases in atmospheric CO_2, nitrogen deposition, and air pollution, as well as by climate change. While the effects of these factors on tropical forests remain largely unknown at this point, preliminary evidence suggests that they can cause major changes in species composition and forest structure (Phillips *et al.* 2002, Clark *et al.* 2003, Laurance *et al.* 2004, Lewis *et al.* 2004, Wright *et al.* 2004, Wright & Calderón 2006, Wright 2005). These more diffuse influences on tropical forests due to anthropogenic changes in global biogeochemical and climatic cycles are caused by global human industrial activities. Because global industrial activity is expected to grow three- to sixfold by 2050 (Millenium Ecosystem Assessment 2005), we expect corresponding continued rapid increases in the impacts of changes to the global atmosphere and climate on tropical forests. In sum, most tropical forests of the future will be significantly degraded, affected by previous and ongoing human harvesting and land conversion, as well as by anthropogenic changes in global atmosphere and climate. Most temperate forests are already in a similar state of degradation.

In the future, forests in the tropics will be increasingly restricted to areas that have low human population densities and are not valuable for agriculture or other development and to effective protected areas. Tropical forests in areas that are highly useful for agriculture are often already gone or nearly so. For example, the Mesoamerican dry forests, which are located on relatively fertile soils, have a climate favorable to the health of humans and their domestic animals, and can easily be cleared through burning in the dry season, are virtually all gone (Janzen 1988). The Atlantic coastal forests of Brazil are suffering a similar fate as the land in this area of favorable climate and easy coastal access is valuable for agriculture and is not coincidentally the most densely populated region of Brazil today (Brooks *et al.* 2002). On the flip side, tropical forests in areas of low human population density, with climates unfavorable to human health and/or having soils poorly suited to agriculture are those most likely to remain intact. These are disproportionately very wet forests, because abundant rainfall favors many disease vectors and leaches nutrients from the soil. Forest conversion is also reduced where political boundaries, lack of transportation infrastructure, or other limits on access prevent immigration and keep local human population densities low. Thus, percent forest remaining is currently particularly high ($>80\%$) in the Amazon basin, Guyana, French Guiana, Surinam, Papua New Guinea, and Gabon and is likely to remain high even as old growth forests are replaced by degraded and secondary forests. Forest cover is also largely intact in protected areas (Bruner *et al.* 2001), which cover 18 and 9 percent of all tropical moist and dry forests, respectively. Moist tropical forest has a larger percentage of its area protected than all but one of 16 major biomes (Brooks *et al.* 2004).

IMPLICATIONS FOR THE EXTINCTION OF TROPICAL FOREST SPECIES

Habitat loss must be quantified to predict subsequent levels of extinction from simple species-area considerations. Our analyses, based on 45 humid tropical countries that now support 89.6 percent of all extant closed tropical forest, confirm substantial past losses of these forests and suggest that future losses driven by human population growth will slow over the next 25 yr (Fig. 6). Conditions are certainly best (or perhaps least bad) in the American tropics where more than half the potential forest cover remained in 2000 and net deforestation is projected to decline rapidly. Conditions are considerably worse in Indo-Malaya, where just 39 percent of the original forest cover remained in 2000 and 33–39 percent is predicted to remain in 2030. The FAO survey suggests that past deforestation has been less severe in Africa; however, much greater rates of population growth and net deforestation are anticipated and just 38–50 percent is predicted to remain in 2030. The projections for Africa in particular may be overly optimistic: if we assume that satellite-based measurements provide both more accurate readings of forest cover and a good match to the potential forest definition, then the percent forest remaining in Africa in 2000 is already only 31–35 percent, and proportional reductions in projected forest cover suggest that just 18–28 percent of potential forest cover will remain in 2030.

Based on these projections of future forest cover, a power function relationship between species number (S) and area (A) with an exponent (z) of 0.25 (or $S = cA^z$, where c is a constant) predicts that 21–24 and 16–35 percent of the species of the Asian and African tropics, respectively, will be threatened with extinction by 2030. Different treatments of the extensive Brazilian cerrado by our data sources preclude continent-level estimates of forest loss and associated extinctions for the Americas.

These extinction estimates are uncertain for several reasons. First, as discussed in previous sections, our estimates of future forest losses may be wrong. Second, as discussed in the "Introduction," deforestation rates may be greater in certain endemicity hotspots and our analyses are intended to be applied only to the great continental blocks of tropical forest. Third, simple species-area considerations may not predict extinctions accurately at this scale. This third possibility has been evaluated for birds for the North American deciduous (Pimm & Askins 1995) and Brazilian Atlantic coastal forests (Brooks & Balmford 1996). In both cases, the species-area formulation given in the previous paragraph accurately predicted the number of extinct or globally endangered species.

A fourth source of uncertainty arises because the net forest cover changes considered here treat all forest types equally. Pristine, old growth forests are being replaced by secondary forests and logged forests throughout the tropics. Net forest change is insensitive to these processes. This will cause systematic underestimates of future extinctions if old growth forests support greater numbers of species or different species. Old growth forests and secondary forests just 20–40 yr old support similar numbers of species of many tropical animal groups; however, animal species composition often differs with forest age (reviewed by Dunn 2004). Secondary forests also support fewer and different tree species than do old growth forests (Turner *et al.* 1997, Chazdon 2003, Lugo & Helmer 2004). In contrast, logged forests support similar numbers and types of tree species as do pristine, old growth forests (Cannon *et al.* 1998, ter Steege *et al.* 2002). Secondary and logged forests clearly have substantial conservation value as do many agricultural landscapes (Green *et al.* 2005); however, neither degraded forests nor agricultural landscapes will protect old growth specialists such as the extinct Passenger Pigeon, which once required old growth, North American deciduous forest (Pimm & Askins 1995). This final source of uncertainty cannot be resolved until the proportion of tropical species that require old growth forests is known.

Species-area curves are crude tools, and much better estimates of the proportion of threatened taxa can be made if projected future habitat maps are combined with current distributions of individual species. Unfortunately, the fundamental distributional information needed to assess extinction risk in this way is lacking for many tropical taxa. Most species of small-bodied taxa including insects are undescribed; their distributions and dependence on old growth forests are of course unknown. Distributions are best known for vertebrates, and here recent analyses have compared the spatial distributions of threatened species and protected areas (Rodrigues *et al.* 2004). Most vertebrates of the Congo Basin, the Guyana Shield, and the Amazon Basin have broad geographic distributions that include existing protected areas. In contrast, many vertebrates of South Asia, Southeast Asia, the Caribbean, Central America, and the Brazilian Atlantic coastal forests have relatively limited distributions and are wholly outside protected areas. Our analyses suggest that the long-term survival of such species will require new protected areas for species dependent on old growth forests while species able to persist in secondary and logged forests are likely to survive without further direct protection. Direct assessment of the extinction risk faced by most other tropical forest species will require better distributional and habitat requirement data.

INSIGHTS FROM PREHISTORIC FOREST AREA CHANGES

Historical changes in tropical forest area may provide additional insight into the implications of future area changes for extinction rates. The distribution of tropical forest waxed and waned through multiple Pleistocene glacial cycles (Morley 2000). Tropical forest retracted during cooler and drier glacial conditions and expanded during warmer and wetter interglacial conditions that lasted on the order of 100,000 yr and 10–20,000 yr during each cycle, respectively. Temperatures were *ca* 6°C cooler during the most recent glacial maximum, rainfall was lower by an unknown amount, and the distribution of tropical forests is hotly debated. If the reduction in rainfall had been relatively large, drought would have restricted tropical forests to scattered moist refugia and to gallery forests along rivers. Alternatively, if the reduction in rainfall had been relatively modest, low temperatures would still have restricted modern lowland forests to the warmest areas near sea level. These alternative scenarios predict very different forest cover during the glacial maxima for South America and Southeast Asia where there are extensive areas near sea level. In contrast, both scenarios predict strong contractions of African tropical forests because most of the Congo Basin is on a high plateau at 600 m elevation and even a small reduction in rainfall would drastically restrict West African forests (Morley 2000). African tropical forests occupied far less than 38–50 percent (Table 1, or even 18–28%, see "Implications for the Extinction of Tropical Forest Species") of their modern potential range during most of the Pleistocene. This suggests that African species in particular should be able to survive the current reduction in forest area.

Prehistoric humans also caused large reductions in tropical forest cover in the past 10,000 yr. High prehistoric human population densities have been documented in areas now covered by closed tropical forest in Africa, the Americas, and Asia (Willis *et al.* 2004). Human populations were particularly dense in northern Mesoamerica where Mayan population densities were greater than modern population densities for many centuries, crashed about 1100 YBP, recovered, and crashed again with the Spanish Conquest (Gómez-Pompa & Kaus 1999). These two population cycles occurred without "major changes in floristic composition at a genus level in the last 5–6 thousand years" (Gómez-Pompa & Kaus 1999). History suggests that Mesoamerican species should also be able to survive the current reduction in forest area.

The insight gained from historical changes in forest area must be qualified because modern and prehistoric conditions differ. Modern hunters use guns, motorized vehicles, and battery-powered lanterns that prehistoric hunters lacked—game species face unique threats today (Wright 2003). Modern forests face increasing atmospheric concentrations of CO_2; changing levels of solar radiation attributed to changing atmospheric opacity (Wild *et al.* 2005); and a changing climate with increases in temperatures, altered rainfall patterns, and possibly more frequent El Niño events (Malhi & Wright 2004). There are preliminary indications that these global changes are having differential effects on forest species, with understory trees decreasing and canopy trees and lianas increasing in importance (Phillips *et al.* 2002; Laurance *et al.* 2004; Wright *et al.* 2004; Wright & Calderón 2006). Possible synergisms with extinction risk are unexplored.

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Current human demographic trends—slowing population growth and intense urbanization (Figs. 3–5)—give reason to hope that deforestation will slow, forest regeneration through secondary succession will accelerate, and a mass extinction of tropical forest species can be avoided. Our projections suggest that more than 33 percent of potential closed tropical forest will remain in forest in 2030. Tropical forests retracted to even smaller areas during repeated Pleistocene glacial events in Africa and more recently in selected areas that supported dense prehistoric human populations. Despite caveats—forest loss is particularly intense in selected endemicity hotspots, old growth forest is being replaced by secondary and logged forest, global change and technology will have unforeseen impacts—these projections and observations provide hope that many tropical forest species will be able to survive the current wave of deforestation and human population growth. The long time lags observed between habitat loss and species extinctions (Brooks *et al.* 1999) favor this possibility, providing time for secondary forests to mature and reestablish habitat suitable for forest residents.

At a regional scale, the situation is most favorable in Latin America. Here, percent forest remaining is relatively high (Table 1), low projected population growth and intense urbanization suggest that a substantial net increase in forest area may occur before 2030 (Fig. 6), and the population is expected to grow by just 10 percent between 2030 and its peak level in 2065 (United Nations 2004b). The situation is less good in Southeast Asia and especially Africa. In Southeast Asia, percent forest remaining is already very low (Table 1), our population-driven projections suggest less scope for net increases in forest area before 2030 (Fig. 6), and the human population is expected to grow by 13 percent between 2030 and its peak level in 2060 (United Nations 2004b). The political and economic problems facing Indonesia further exacerbate the problems facing Southeast Asian forest species (Curran *et al.* 2004, Sohdi *et al.* 2004). Africa may soon encounter similar problems. Here, an intermediate level of percent forest remaining (Table 1) confronts continued high population growth. Our population-driven projections suggest strong net deforestation through 2030 (Fig. 6), and the human population is predicted to grow by yet another 65 percent between 2030 and its peak level in 2100. The conservation crisis that threatens the Asian tropics today is likely to affect the African tropics in the near future.

Additional research will be needed to refine estimates of the extinction threat facing tropical forest species. Crucial unknowns include forest area to be lost or gained; possible synergisms between forest loss and other local, regional, and global threats; and the unique contribution of old growth forests. Here, we have attempted to address the first unknown. Our projections of net forest area change are only as good as our central assumption that the cross-country relationship of Figure 2 holds through time. This assumption should be evaluated for historical time series of forest cover and population density. Synergisms among extinction threats are being investigated for temperate organisms; similar research is badly needed in the tropics where vastly greater numbers of species are threatened. Finally, old growth tropical forests are likely to continue to disappear rapidly and to be replaced by secondary and logged forests. Many tropical biologists already have a good understanding of the proportion and types of species that are dependent on old growth forests. This information urgently needs to be quantified and applied to refine extinction threats.

Finally, we offer two policy recommendations in the hope of stimulating discussion. First, economic opportunity in urban centers and the quality of urban life should be improved throughout the tropics (Aide & Grau 2004). Policies designed to keep people in the tropical countryside have rarely preserved forest (Terborgh

1999). Greater opportunities in urban centers will hasten rural–urban migration, relieve some sources of pressure on old growth forests, and allow marginal agricultural lands to return to forest. It is important to recognize, however, that human cultural diversity is even more threatened than tropical biodiversity—any policy to favor rural–urban migration should be sensitive to indigenous cultures.

Our second recommendation is more a question. Where will today's conservation efforts be most effective? Should the focus be on countries in crisis today? Haiti retains just 6 percent of its potential forest cover. Should the focus be on countries likely to be in crisis in the future? The Congo retains 78 percent of its potential forest cover but its population is projected to grow by 219 percent by 2030. Or, should the focus be on countries where there is even more breathing room? Guyana retains 89 percent of its potential forest cover and its population is projected to decline by 8 percent by 2030. There is clearly a role for conservation in every country; however, preemptive conservation efforts might best be targeted at countries like the Congo that combine ample forest cover today and high projected population growth.

While many studies have examined past deforestation rates, few have quantitatively predicted future tropical deforestation rates, natural forest regeneration rates, and thus future forest area. This information is critical for predicting effects on tropical forest species. We hope that our work here, with all its limitations, inspires others to produce additional and better projections of future tropical forest cover around the globe.

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