analysis, with HTLV-III$_B$–LTR containing plasmid as a hybridization probe.
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Deforestation History of the Eastern Rain Forests of Madagascar from Satellite Images

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Madagascar is biologically one of the richest areas on Earth, and its plants and animals are among the most endangered. Satellite images and vegetation maps based on earlier aerial photographs were used to determine the extent of eastern rain forests in Madagascar and to monitor the rate of deforestation over a 35-year period. In 1985, 3.8 million hectares of rain forest remained, representing only 50 percent of the 7.6 million hectares existing in 1950 and 34 percent of the estimated original extent (11.2 million hectares). Between 1950 and 1985, the rate of deforestation averaged 111,000 hectares per year. Deforestation was most rapid in areas with low topographic relief and high population density. If cutting of forests continues at the same pace, only forests on the steepest slopes will survive the next 35 years.

MADAGASCAR, LOCATED SOME 400 km east of Africa, is the world's fourth largest island, with an area of about 587,000 km^2. Biologically it is widely regarded as one of the richest areas on Earth containing nearly 8000 endemic species of flowering plants (*1–3*). Species diversity of both plants and animals is concentrated primarily in the rain forests of eastern Madagascar. This area also has a high species richness per unit area, generally more than in any similar area in Africa (*1, 4*).

Many plant and animal species are severely threatened (*5, 6*). Numerous habitats of Madagascar have been degraded since the arrival of humans 1500 to 2000 years ago, and extinctions of species of large mammals and birds have been severe (*7, 8*). With a current human population of about 11.6 million, a population growth rate of 3.1% per year, and a per capita income of around \$230 per year (*9*), the major threats to the remaining forest are driven by subsistence needs and cutting for fuel (*10–12*). The tropical rain forests of Madagascar before human colonization are thought to have covered much of the eastern coastal plains and the eastern escarpment of the central plateau that runs along most of the 1600-km length of the island (*13, 14*). Estimates of the extent of the remaining eastern rain forests have ranged from 2.5 million to 6.9 million ha (100 ha = 1 km^2) (*3, 10, 12, 15–17*), and between 10,000 to 20,000 and 165,000 ha of forest are estimated to have been cleared per year (*17, 18*). None of these estimates were based on reliable ground or aerial surveys, and each consisted of extrapolations from earlier estimates. Whether the deforestation rate is increasing or decreasing is also uncertain (*5, 12*).

We have used maps of Humbert and Cours Darne based on aerial photography from 1950 (*13*) together with satellite image data from 1972 to 1973 and 1984 to 1985 to estimate the area of eastern rain forests of Madagascar and the rate of deforestation over this 35-year period (Fig. 1). Satellite-based remote sensing provides a powerful tool for monitoring deforestation and biodiversity, but it has not been systematically applied globally or in Madagascar (*19*).

Remotely sensed satellite images at optical wavelengths (0.5 to 1.1 μm) have been available since 1972 from the Landsat series of satellites (*20*). Madagascar's eastern rain forests have been successfully distinguished from surrounding savannah and secondary vegetation for limited regions of eastern Madagascar with the use of analog image interpretation applied to Landsat (0.6 to 0.7 μm, visible red light) images (*21, 22*). Continuous forest, either primary rain forest or large tracts of closed-canopy secondary forest, is characterized by a dark homogeneous

Table 1. Area of the eastern rain forest of Madagascar, for the period and population density specified.

Year	Aerial* extent (ha × 10^6)	Forest remaining (%)	Forest† perimeter (km × 10^3)	Deforestation rates from 1950 to 1985 (ha × 10^3/year)
		High (>10 per square kilometer)		
Original	4.7	100	3.5	
1950	2.4	50	7.8	{43
1985	0.89	19	4.5	
		Medium (5 to 10 per square kilometer)		
Original	3.4	100	2.2	
1950	2.5	76	4.9	{37
1985	1.3	38	5.0	
		Low (<5 per square kilometer)		
Original	3.1	100	3.4	
1950	2.7	86	5.0	{31
1985	1.6	51	6.1	
		Total		
Original	11.2	100	9.1	
1950	7.6	67	17.7	{111
1985	3.8	34	15.6	

*A measure of the error in aerial extent at each time period can be estimated by using the number of digitization grid cells (81 ha each) that include forest boundary. The greater the number of these cells, the larger the potential errors. We estimate this error to be ±2%, ±6%, and ±11%, respectively, for original coverage, 1950, and 1985. †Perimeter lengths from 1:1,000,000 scale maps may be underestimated during the digitization process because small-scale features of forest boundaries are lost. We calculate this error to be approximately 10%.

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image tone at red wavelengths (*5, 21*), which is produced by absorption of light by chlorophyll and by shadowing in the forest canopy (*23*). Deforestation of Madagascar's eastern rain forests has resulted in a mosaic of small plots at various stages of clearing and secondary growth, which can be identified by a relatively bright and heterogeneous tone on Landsat images. Active deforestation fronts can be identified by bright patches along the forest boundary (Fig. 2).

We examined 38 separate images at 1:1,000,000 scale, each covering 185 km by 185 km (*24*). Visual interpretation of these prints permitted us to classify and map eastern Madagascar into two land cover types: continuous forest and nonforest. Nearly complete coverage of the eastern rain forest was achieved for 1985, but cloud cover restricted coverage in 1973 to areas largely south of 18°30'S (*25*) (Fig. 1, C and D). The aerial extent of rain forest was determined by digitizing these maps. The maps of Humbert and Cours Darne were analyzed in a similar manner (Fig. 1, A and B).

The original extent of the eastern rain forest at colonization was 11.2 million ha (Table 1), of which 7.6 million ha remained in 1950. By 1985 the eastern rain forests of Madagascar, as determined from Landsat images, covered only 3.8 million ha. Thus, in 1985, only 50% of the rain forests existing in 1950 remained, ~34% of that which originally existed. This yields an average rate of clearance of 111,000 ha (1.5%) per year between 1950 and 1985.

With our techniques, large tracts of closed-canopy secondary forest and tree plantations are indistinguishable from primary forest. As a result, the mapped extent of the forest in 1985 represents a maximum estimate; however, most forested (92.8%) areas in 1985 fall within the 1950 forest boundaries. These observations suggest that the establishment of closed-canopy secondary forest may have been minimal. White (*3*) reported that little former rain forest is covered by secondary forest because there are few indigenous tree species adapted to such habitats, and these species do not compete well with smaller herbaceous plants. As a result of these factors, and because of the degradation of soils when they are exposed, deforestation may be effectively irreversible throughout much of eastern Madagascar if present conditions prevail (*26*). Furthermore, pine and eucalyptus plantations may be included in our cover estimates; however, the resultant error would not exceed 1.6% in 1950 and 3.2% in 1985 (*27*).

As has been observed in other areas, deforestation has occurred preferentially on flat land (*28*). Much of the eastern boundary of the forest in 1950, and to a greater extent in 1985, was associated with the foothills of the eastern escarpment of the central plateau. As of 1985 most of the remaining forest was located on the steep slopes of this rugged terrain (*29*) (Fig. 3A).

Most of the original forest land (72%) was on low or moderate slopes (<5°); however, because of clearing, by 1985 only 6.3% of the rain forest was on slopes <1°, and only 26.7% of the forest on slopes <5° had survived (Fig. 4).

Large forest tracts on low slopes remain in the north; however, such tracts are nearly absent in the south (Fig. 3A). This dichotomy is associated with differences in human population density (*16*) (Fig. 3B). Significantly more forest has been destroyed in regions of higher population density than in those of lower density, especially on less steep slopes (Fig. 5).

More than half of the forests present in regions of low density in 1966 had survived until 1985; however, only 19% of those forests in areas of high density had survived (Table 1). In recent years the percentage of deforestation in areas of low population

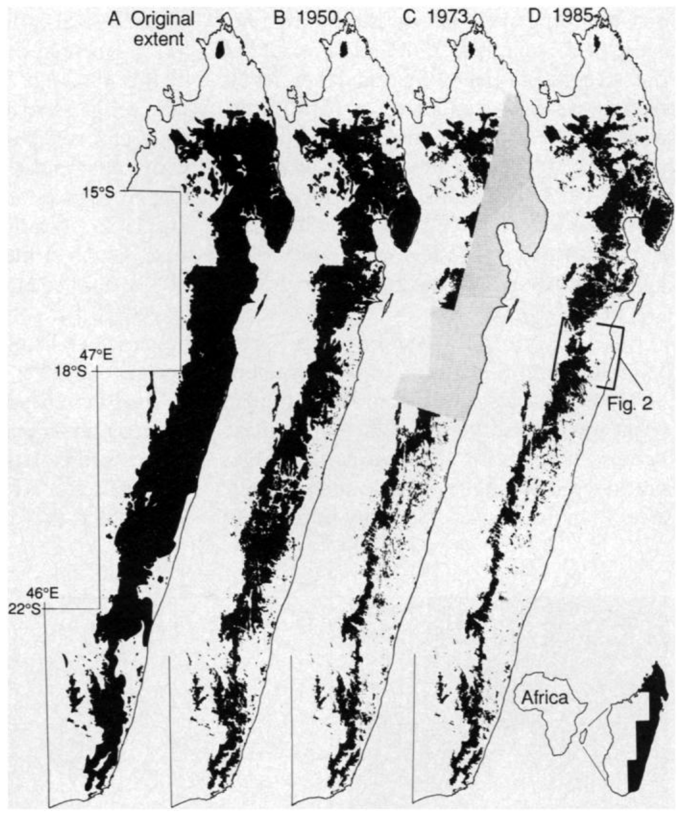

Fig. 1. Maps of distribution of rain forest in eastern Madagascar through time. Before human colonization, forest is thought to have covered much of eastern Madagascar including most of the eastern coast (**A**). Forest cover was mapped for 1950 (**B**) based on vegetation maps of Humbert and Cours Darne (*13*) derived from aerial photography and for 1973 (**C**) and 1985 (**D**) with the use of Landsat images. Extensive cloud cover permitted only partial mapping in 1973. Boxed area in (D) is shown in Fig. 2.

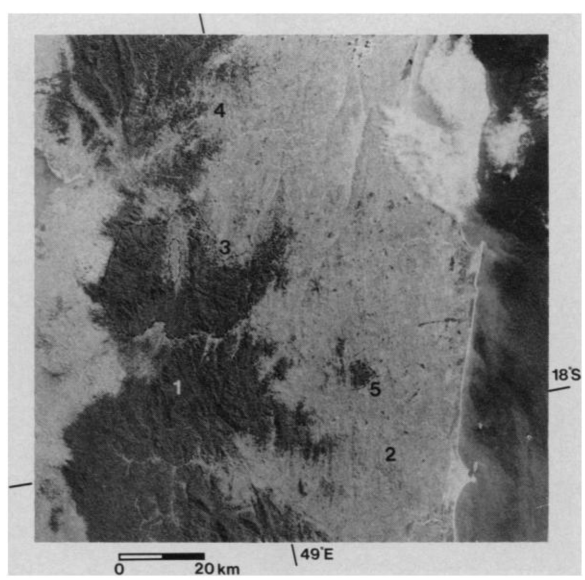

Fig. 2. Landsat Multispectral Scanner image (0.6 to 0.7 μm) acquired on 6 September 1984. Continuous forest cover, characterized by a dark homogeneous tone, is largely restricted to steeper slopes of mountainous areas (1), whereas the low slopes of the coastal plain have been largely deforested for subsistence agriculture and are characterized by a brighter heterogeneous tone (2). Nature reserve boundaries are indicated by a dashed line. An active deforestation front within the northeast part of Reserve No. 3 (Zahamena) is characterized by bright patches indicative of recent clearing (3). Subsistence clearing of forests on low slopes produces a diffuse forest boundary made up of patchwork of small isolated stands (4). Reserve No. 1 (Betampona) includes one of the last remaining tracts of eastern lowland forest (5).

density has nearly attained the level of destruction mapped in areas of high density in 1950.

Comparison of the maps of forest extent in 1950 and 1985 and the partial map for 1973, which includes 68% of the high population density areas, allows calculation of deforestation rates for the intervening 35 years. For these high population density areas, deforestation rates have fallen since 1973. Between 1950 and 1973, rain forest in these areas was cleared at a rate of 51,000 ha (2.5%) per year; this rate slowed to 16,000 ha (0.79%) per year between 1973 and 1985. This trend appears to result from a diminishing pool of accessible forest because of the elimination of forests on all but the steepest slopes. Whereas large forest tracts were destroyed south of 18°30′S before 1973, Landsat images reveal little change in forest extent in these areas between 1973 and 1985. The deforestation that has occurred since 1973 has taken place at the expense of the few stands of coastal lowland forest remaining in 1973 (Fig. 1, C and D).

Estimates of deforestation rates since 1973 for regions north of 18°30′S (regions of predominantly low and medium human population density) are difficult to make because high cloud cover in some images precluded mapping. Forest boundaries near areas of high population density in 1985 are characteristically distinct at a scale of 1:1,000,000 and generally occur where there is an abrupt change in slope (Fig. 3A). In contrast, many large forest tracts near areas of low population density (<5 people per square kilometer) do not have boundaries associated with steep slopes but rather are diffuse, made up of a patchwork of isolated stands cut by a series of deforested corridors and subject to clearing from all sides (Fig. 2, northern part). A similar dissected pattern was present in 1950 near 21°30′S (Fig. 1B), an area virtually cleared of forest by 1973.

The ratio of forest perimeter to area can be used as a measure of the extent cutting has fragmented the forest. For regions with high population density this ratio increases with progressive deforestation. By 1985 the ratio of forest perimeter to area in regions with low population densities had exceeded that in regions with high density in 1950 (Table 1). Nearly 70% of those forested areas that had human population densities of <10 per square kilometer in 1966 now exceed 10 per square kilometer (*30*), densities at which massive deforestation has been documented over the past 35 years.

The last remaining large tracts of primary eastern rain forest in Madagascar are found in the northeastern part of the island. Many of these tracts are not on steep slopes (Fig. 3A); rather, they have escaped deforestation

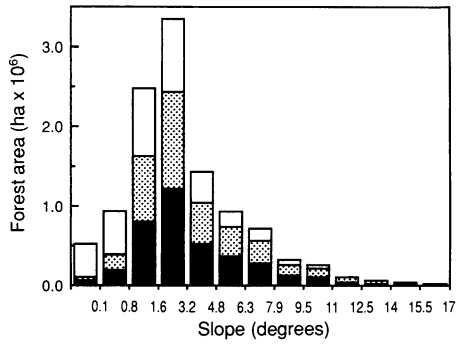

Fig. 4. Forest area remaining at a given slope circa 1985 (solid bar), 1950 (dotted bar), and for the original estimated extent (open bar). Deforestation has greatly reduced forest cover at low and moderate slopes (<5°).

because the population density in this area is relatively low (Fig. 3B).

Establishment of reserves in itself does not guarantee protection. The Landsat images (Fig. 2) vividly show active deforestation fronts cutting into the northern parts of nature Reserve No. 3 (Zahamena). The last remaining small tracts of southern coastal plain forest are also severely threatened. Natural Reserve No. 1 (Betampona) was established in 1927 on land of low slope on the coastal lowlands, between 300- and 550-m elevation, to help preserve the fauna and flora of the low altitude eastern rain forest (*31*). Landsat images reveal that deforesta-

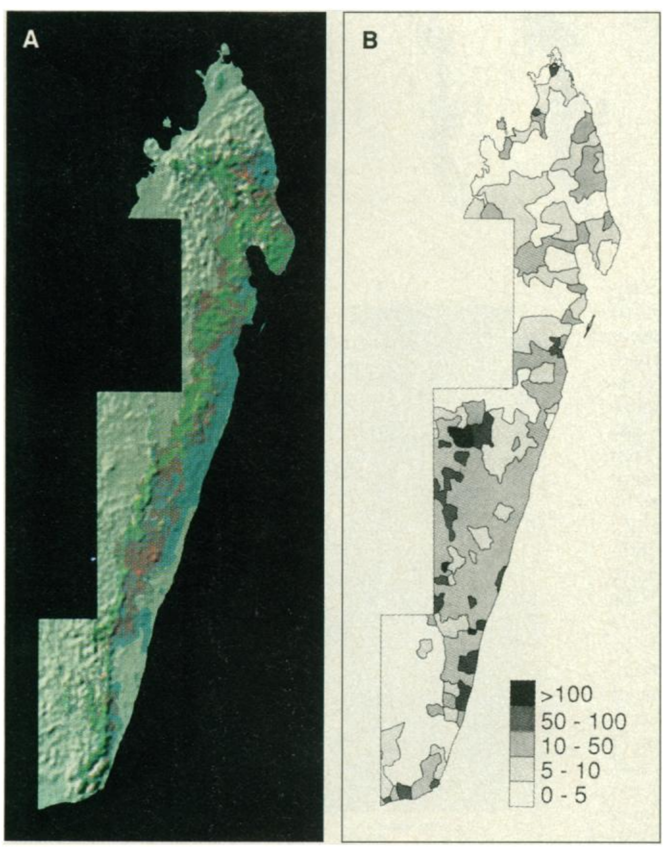

Fig. 3. (**A**) A shaded relief map of surface slope depicts steeper slopes as higher elevation. Blue areas were deforested before 1950, red areas between 1950 and 1985, and green areas were still forested in 1985. An abrupt change in slope stabilizes the deforestation front and a distinct forest boundary develops. (**B**) Human population density in persons per square kilometer is shown at subprefecture level in 1966. Regions of higher density are concentrated in the south.

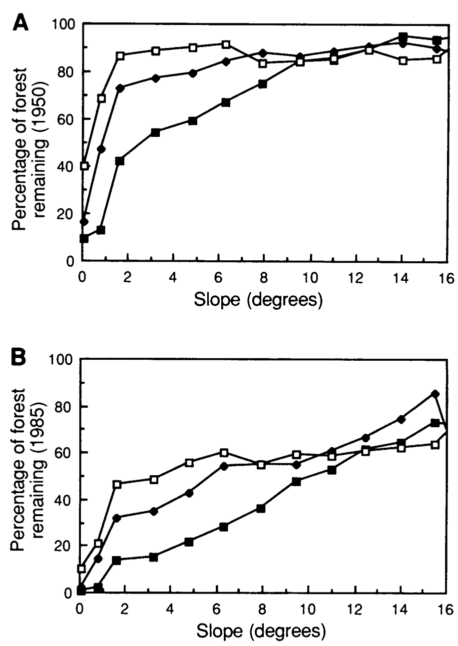

Fig. 5. Percentage of forest remaining at a given slope and population density circa 1950 (**A**) and 1985 (**B**). Regions of higher population density have experienced greater deforestation, especially at low and moderate slopes. Symbols for population density: (■), high density (>10 per square kilometer); (◆), medium (5 to 10 per square kilometer); (□), low (<5 per square kilometer).

tion has occurred recently within the reserve boundaries (Fig. 2), and continual clearing in the reserve has been reported (*32*). Soil no longer protected by forest is subject to rapid erosion from intense rainstorms and frequent hurricanes, and erosion rates as high as 250 tons of soil per hectare have been reported (*33*).

This study provides an example of how remote sensing data can be used to map forest extent and to monitor deforestation. Landsat images are already available for most of Earth's tropical forests. Many of these images are nearly two decades old and thus provide a remarkable but essentially unused database.

Sustainable agriculture and agroforestry to provide local inhabitants with needed food and fuel, accompanied by reduction of population growth, are among the prerequisites for effective tropical rain forest preservation. Detailed ethnographic studies addressing the social and economic needs of local peoples are needed if these efforts are to succeed.

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Code of Ant-Plant Mutualism Broken by Parasite

DEBORAH K. LETOURNEAU

Newly discovered *Phyllobaenus* beetles are parasites of a mutualism. *Piper* ant-plants in tropical forests provide lipid and protein-rich food cells and shelter for *Pheidole bicornis* ants while the ants remove small herbivores and vines from the foliage. In contrast to all other ant-plants, *Piper* ant-plants produce food bodies only when *Pheidole bicornis* is present in the plant. However, *Phyllobaenus* beetles can stimulate the plants to produce food bodies as if ants were present. The beetles then inhabit the plant, exploiting nest sites and food produced by the plants for ants. These beetles may also prey on ant brood, depriving the plants of resources and services provided by the ants.

PARASITES OF MUTUALISMS EXPLOIT the resources or services of the mutualists without providing reciprocal benefits (*1*). Previous examples of a third species that derives benefits from both interacting mutualists while benefitting neither have at least one characteristic in common: the parasitism depends on a mimetic rela-