Tropical Deforestation and Habitat Fragmentation in the Amazon: Satellite Data from 1978 to 1988

David Skole and Compton Tucker

Landsat satellite imagery covering the entire forested portion of the Brazilian Amazon Basin was used to measure, for 1978 and 1988, deforestation, fragmented forest, defined as areas less than 100 square kilometers surrounded by deforestation, and edge effects of 1 kilometer into forest from adjacent areas of deforestation. Tropical deforestation increased from 78,000 square kilometers in 1978 to 230,000 square kilometers in 1988 while tropical forest habitat, severely affected with respect to biological diversity, increased from 208,000 to 588,000 square kilometers. Although this rate of deforestation is lower than previous estimates, the effect on biological diversity is greater.

Deforestation has been occurring in temperate and tropical regions throughout history (*1*). In recent years, much attention has focused on tropical forests, where as much as 50% of the original extent may have been lost to deforestation in the last two decades, primarily as a result of agricultural expansion (*2*). Global estimates of tropical deforestation range from 69,000 km^2 $year^{-1}$ in 1980 (*3*) to 100,000 to 165,000 km^2 $year^{-1}$ in the late 1980s; 50 to 70% of the more recent estimates have been attributed to deforestation in the Brazilian Amazon, the largest continuous region of tropical forest in the world (*2, 4, 5*).

The area and rate of deforestation in Amazonia are not well known, nor are there quantitative measurements of the effect of deforestation on habitat degradation. We used 1:500,000 scale photographic imagery from Landsat Thematic Mapper data and a geographic information system (GIS) to create a computerized map of deforestation and evaluate its influence on forest fragmentation and habitat degradation. Areas of deforestation were digitized into the GIS and the forest fragments and edge effects that result from the spatial pattern of forest conversion were determined.

Background

Tropical deforestation is a major component of the carbon cycle and has profound implications for biological diversity. Deforestation increases atmospheric CO_2 and other trace gases, possibly affecting climate (*6, 7*). Conversion of forests to cropland and pasture results in a net flux of carbon to the atmosphere because the concentration of carbon in forests is higher than that in the agricultural areas that replace them. The paucity of data on tropical deforestation limits our understanding of the carbon cycle and possible climate change (*8*). Furthermore, while occupying less than 7% of the terrestrial surface, tropical forests are the home to half or more of all plant and animal species (*9*). The primary adverse effect of tropical deforestation is massive extinction of species including, for the first time, large numbers of vascular plant species (*10*).

Deforestation affects biological diversity in three ways: destruction of habitat, isolation of fragments of formerly contiguous habitat, and edge effects within a boundary zone between forest and deforested areas. This boundary zone extends some distance into the remaining forest. In this zone there are greater exposure to winds; dramatic micrometeorological differences over short distances; easier access for livestock, other nonforest animals, and hunters; and a range of other biological and physical effects. The result is a net loss of plant and animal species in the edge areas (*11*).

There is a wide range in current estimates of the area and rate of deforestation in Amazonia. Scientists at the Instituto Nacional de Pesquisas Espaciais (*12–15*) estimated a total deforested area of 280,000 km^2 as of 1988 and an average annual rate of 21,000 km^2 $year^{-1}$ from 1978 to 1988. Other studies (*2, 4, 5*) have reported rates that range from 50,000 to 80,000 km^2 $year^{-1}$ (Table 1). Additional deforestation estimates have been made for geographically limited study areas in the southern Amazon Basin of Brazil with Landsat and meteorological satellite data (*16–20*).

The Amazon Basin of Brazil has been defined by law to include the states of Acre, Amapá, Amazonas, Pará, Rondônia, and Roraima plus part of Mato Grosso, Maranhão, and Tocantins and is referred to as the Legal Amazon (*21*). It covers an area of

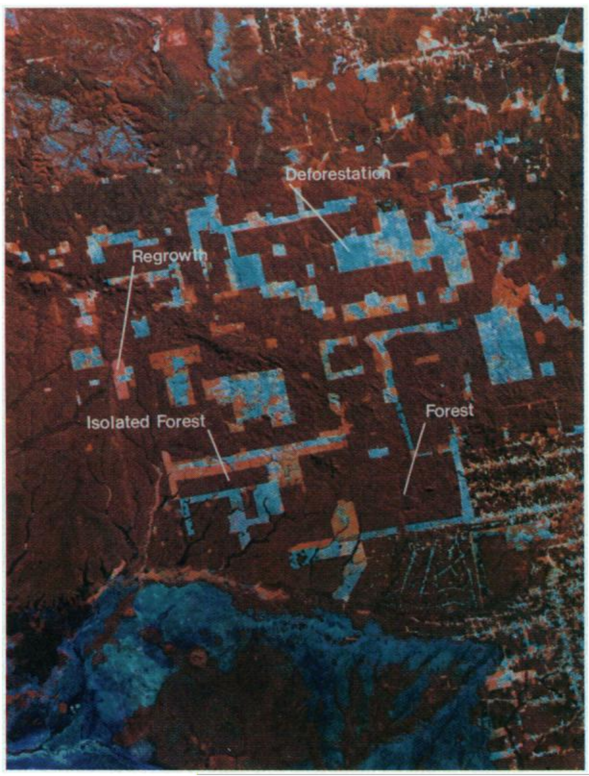

Fig. 1. Landsat Thematic Mapper color composite image of southern Rondônia state, Brazil, for path 230 and row 69 acquired on 5 June 1988. Areas of tropical forest, deforestation, regrowth, and isolated forest are labeled. The area identified as isolated forest is about 3 km by 15 km in size.

D. Skole is with the Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH 03824. C. Tucker is with the Laboratory for Terrestrial Physics, NASA Goddard Space Flight Center, Greenbelt, MD 20771.

Table 1. Tropical forest area (*3*) and reported tropical deforestation rates by country. The deforestation rates from the 1970s are from the Food and Agriculture Organization (FAO) (*3*). The 1980s data are from Meyers (*2*) and the World Resources Institute (WRI) (*5*).

Country	Total forest area (km^2)	Percent of world total	Deforestation rate, 1970s (km^2)	Percent of world total	Deforestation rates, late 1980s			
					Myers (km^2)	Percent of world total	WRI (km^2)	Percent of world total
Brazil	3,562,800	30.7	13,600	19.7	50,000	36.1	80,000	48.4
Indonesia	1,135,750	9.8	5,500	8.0	12,000	8.7	9,000	5.4
Zaire	1,056,500	9.1	1,700	2.5	4,000	2.9	1,820	1.1
Peru	693,100	6.0	2,450	3.6	3,500	2.5	2,700	1.6
Columbia	464,000	4.0	8,000	11.6	6,500	4.7	8,200	5.0
India	460,440	4.0	1,320	1.9	4,000	2.9	15,000	9.1
Bolivia	440,100	3.8	650	1.0	1,500	1.1	870	0.5
Papua, New Guinea	337,100	2.9	210	0.3	3,500	2.5	220	0.1
Venezuela	318,700	2.7	1,250	1.8	1,500	1.1	1,250	0.8
Burma	311,930	2.7	920	1.3	8,000	5.8	6,770	4.1
Others*	2,829,930	24.4	33,300	48.3	44,100	31.8	39,610	23.9
Total	11,610,350	100.0	68,900	100.0	138,600	100.0	165,440	100.0

*Sixty-three other countries.

~5,000,000 km^2, of which ~4,090,000 km^2 is forested, ~850,000 km^2 is cerrado or tropical savanna, and ~90,000 km^2 is water (Table 2). Confusion has arisen among researchers regarding the stratification of the Brazilian Amazon into forest, cerrado, and water strata. A Food and Agriculture Organization (FAO)–United Nations Environmental Program (UNEP) study (*3*) found 3,562,800 km^2 of forest, whereas Fearnside and co-workers claim there is 4,195,660 km^2 of forest, 793,279 km^2 of cerrado (*17*), and 4,906,784 km^2 total (*13*). Meanwhile, an IBGE study (*22*) found 20,972 km^2 of water, 3,793,664 km^2 of forest, and 1,149,943 km^2 of cerrado for a total of 4,964,920 km^2. These differences prevent comparison of different deforestation studies.

The use of satellite data and the GIS make it possible to explicitly stratify Amazonia on the basis of cover types (*22*), thereby providing a means of comparison with other studies. This approach is also necessary for spatial analysis of habitat fragmentation and edge effects of deforestation. Finally, GIS provides a data management tool with which we could manage large amounts of spatial data and precisely merge and geocode information from the more than 200 satellite images used in this study.

Remote Sensing

The large area of the Brazilian Amazon necessitates a straightforward and accurate method of measurement. Landsat Thematic Mapper photo products are inexpensive and of sufficient spatial and spectral resolution for the determination of deforestation. Analysis with visual interpretation techniques produces quantitative results similar to digital processing of full-resolution, multispectral data from the Thematic Mapper and SPOT (*23*).

We acquired 210 black and white photo-

Table 2. Predeforestation water, forest, and cerrado land cover for the Brazilian Amazon by state as used in this study. The values determined in this study were based on the IBGE vegetation map and by interpretation of satellite data (*22*). Areas obscured by clouds were excluded from deforestation and affected forest habitat analyses (97% of the cloud-affected data were over tropical forest).

State	Water area (km^2)	Forest area (km^2)	Cloud total (km^2)	Cerrado area (km^2)	Total area (km^2)
Acre	393	152,394	0	0	152,787
Amapá	1,188	137,444	53,566	978	139,610
Amazonas	29,842	1,531,122	94,058	14,379	1,575,343
Maranhão	1,344	145,766	13,444	114,675	261,785
Mato Grosso	4,212	527,570	8,630	368,658	900,440
Pará	49,522	1,183,571	56,807	28,637	1,261,730
Rondônia	1,462	212,214	474	24,604	238,280
Roraima	1,817	172,425	15,232	51,464	225,706
Tocantins	2,914	30,325	0	244,005	277,244
Total	92,694	4,092,831	(242,211)	847,400	5,032,925

Table 3. Tropical deforestation, forest isolated or cut off by deforestation, and the area of forest adversely affected by a 1-km edge effect from adjacent areas of deforestation in the Brazilian Amazon. Areas that were obscured by clouds were omitted from this analysis. Parentheses following the edge effect entries contain the ratio between a 500-m buffer and a 1,000-m buffer.

State	Deforested (km^2)	Isolated (km^2)	Edge effect (km^2)	Total (km^2)
		1978		
Acre	2,612	18	4,511	7,141
Amapá	182	0	368	550
Amazonas	2,300	36	6,498	8,834
Maranhão	9,426	705	13,120	23,251
Mato Grosso	21,134	776	25,418	47,328
Pará	30,449	2,248	49,791	82,488
Rondônia	6,281	991	17,744	25,016
Roraima	196	4	812	1,012
Tocantins	5,688	337	6,584	12,609
Total	78,268	5,115	124,846	208,229
		1988		
Acre	6,369	405	23,686 (0.517)	30,460
Amapá	210	1	689 (0.537)	900
Amazonas	11,813	474	36,392 (0.582)	48,679
Maranhão	31,952	2,123	28,147 (0.626)	62,222
Mato Grosso	47,568	2,542	71,128 (0.580)	121,238
Pará	95,075	6,837	116,669 (0.633)	218,581
Rondônia	23,998	2,408	52,345 (0.657)	78,751
Roraima	1,908	1	5,236 (0.521)	7,145
Tocantins	11,431	1,437	6,760 (0.659)	19,628
Total	230,324	16,228	341,052 (0.610)	587,604

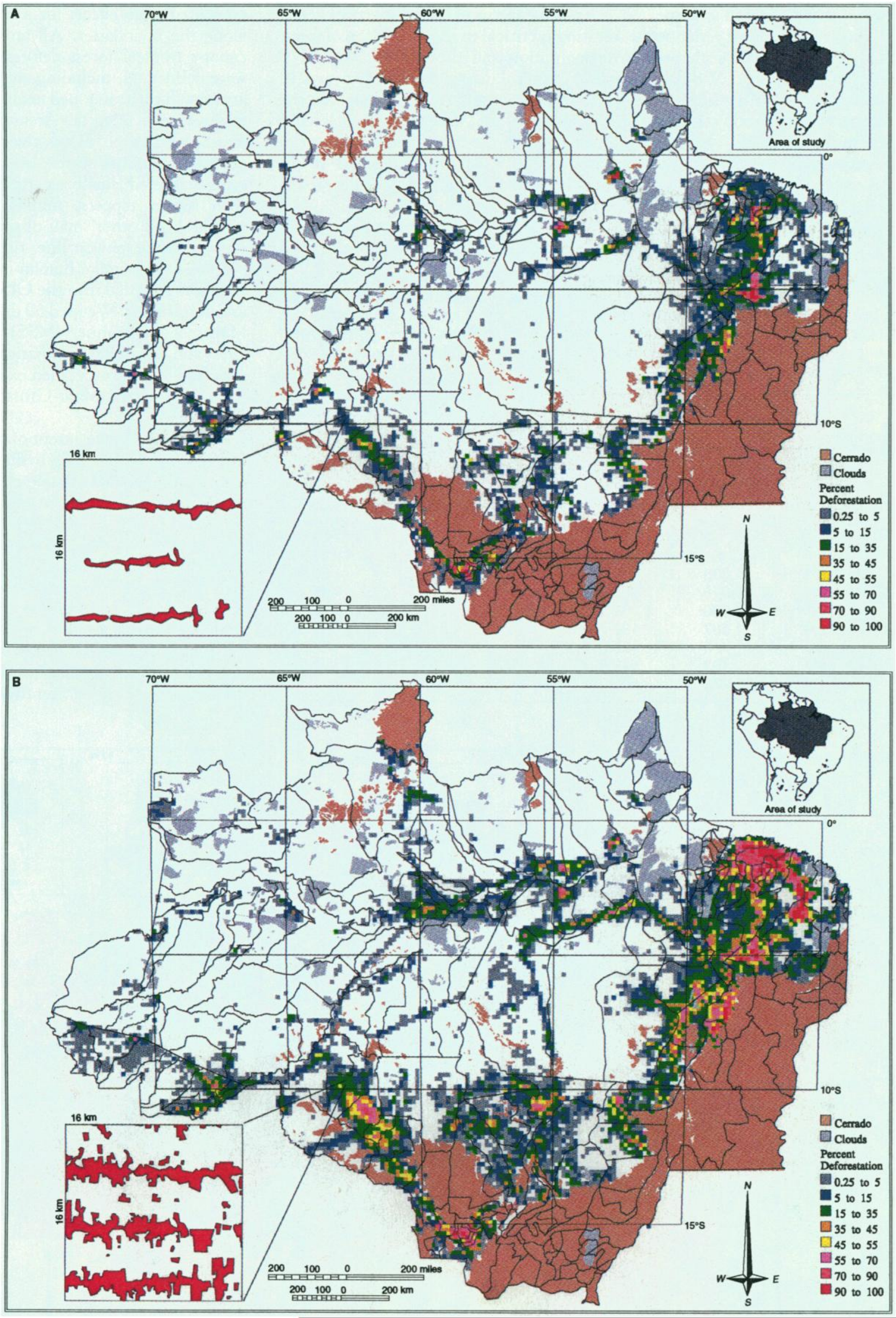

Fig. 2. Representation of deforestation in the Amazon of Brazil from (**A**) 1978 and (**B**) 1988. The deforestation represented in these figures is confined exclusively to the forest strata. The data were averaged into 16 km by 16 km grid cells.

graphic images of the entire Brazilian Amazon. They were obtained with channel five of the Landsat Thematic Mapper (1.55 to 1.75 μm) at 1:500,000 scale and were primarily from 1988 (*24*). We digitized the deforested areas with visual deforestation interpretation and standard vector GIS techniques (Fig. 1). The digitized scenes were projected into equal-area geographic coordinates (latitude, longitude), edge matched, and merged in the computer to form a single, seamless data-set for the entire Brazilian Amazon.

Spatial analysis of the geometry of deforestation is critical to the estimation of forest fragmentation and the edge effect. If 100 km^2 of tropical deforestation occurs as a 10 km by 10 km square and we assume that the edge effect is 1 km, the total area affected is $\sim$143 km^2. In contrast, if the 100 km^2 of deforestation is distributed as ten strips, each 10 km by 1 km, the affected area is $\sim$350 km^2.

We extracted forest fragments <100 km^2 that were isolated by deforestation and computed edge effects for a zone of 1 km along the boundaries. All areas of closed-canopy tropical forest deforested by 1988 were delineated, including areas of secondary growth on abandoned fields and pastures where visible (Fig. 1). Areas of long-term forest degradation along river margins in central Amazonia were also included, as were scattered small clearings associated with rubber tappers, mining operations, airfields, and other small disturbances. All visible roads, power line right of ways, pipelines, and similar human-made features were also digitized into the GIS and treated as deforestation. We used 50 digital Landsat Multispectral Scanner (MSS) scenes from 1986 and 15 digital Thematic Mapper images from 1988 for detailed examination of Acre, Amazonas, Mato Grosso, Pará, and Rondônia.

To determine the extent of deforestation in 1978, we used the GIS to digitize maps of scale 1:500,000 from single-channel Landsat MSS data, produced jointly by the Instituto Brasiliero de Desenvolvimento Florestal (IBDF) and the Instituto de Pesquisas Espaciais (INPE) in the early 1980s (*12, 23*). These maps did not differentiate between forest and cerrado clearing. We compiled forest, cerrado, and water data by combining a vegetation map with analysis of Landsat images and meteorological satellite data (*25*). Our deforestation and affect-

Table 4. Spatial characteristics of isolated and remaining tropical forest within the Legal Amazon as determined by analysis of 1988 Landsat Thematic Mapper imagery. Isolated forest refers to areas of forest <100 km^2 surrounded by deforestation. Remaining forest refers to tropical forest that has not been deforested and includes both isolated and larger areas of forest. Many of the largest remaining areas of tropical forest are contiguous among states. Areas affected by clouds were omitted from this analysis.

State	Isolated forest		Undisturbed remaining forest		Range of areas (km^2)	
	Area (km^2)	Polygons (no.)	Area (km^2)	Polygons (no.)	Minimum	Maximum
Acre	405	603	146,025	605	<1	139,215
Amapá	1	2	83,676	3	<1	83,675
Amazonas	474	464	1,425,253	465	<1	1,424,779
Maranhão	2,123	1,035	100,554	1,042	<1	70,057
Mato Grosso	2,542	2,016	478,619	2,027	<1	471,792
Pará	6,837	4,030	1,032,194	4,032	<1	1,021,263
Rondônia	2,408	1,587	187,743	1,588	<1	185,335
Roraima	1	2	155,326	6	<1	152,414
Tocantins	1,437	493	18,894	508	<1	6,982
Total	16,228	10,232	3,628,284	10,276		

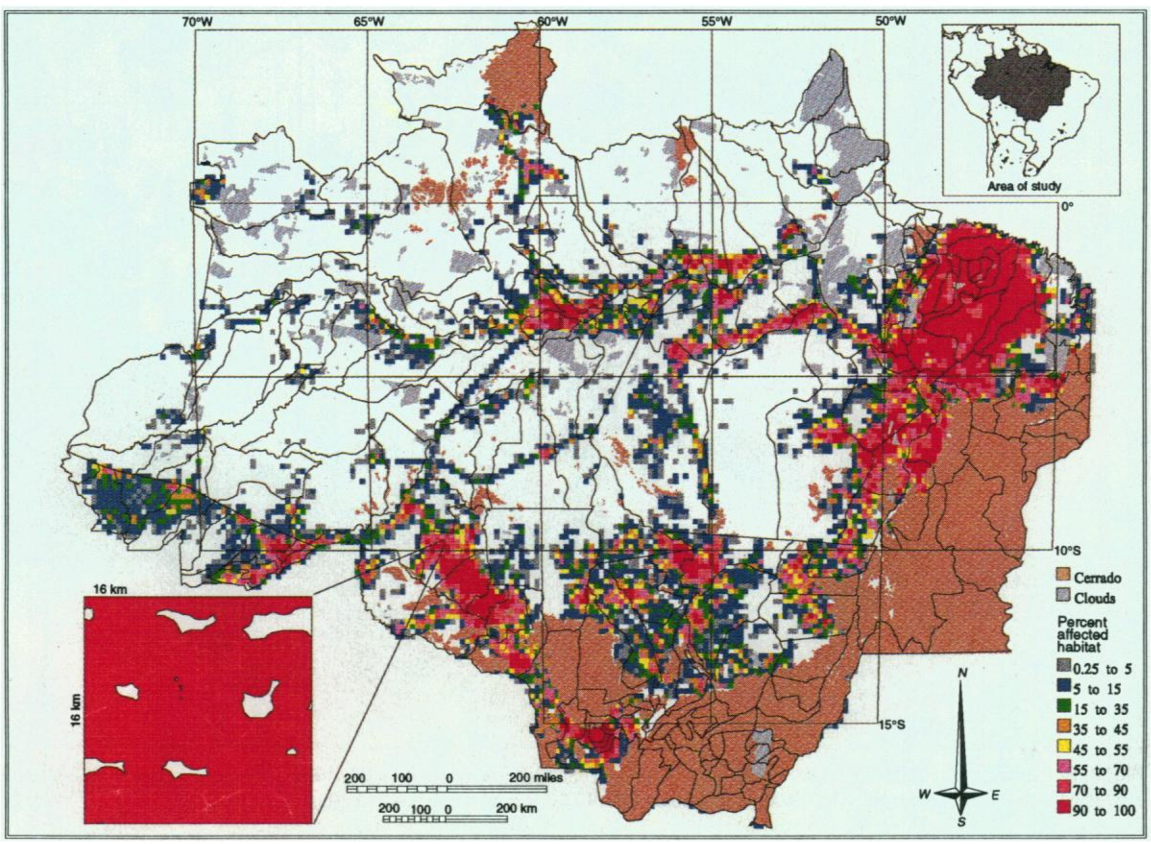

Fig. 3. Map of the Brazilian Amazon Basin showing where biological diversity was adversely affected in 1988 by deforestation, isolation of forest, and the 1-km edge effect of deforestation. The largest contributor to the area of negative effects on biological diversity was the 1-km edge effect from adjacent areas of deforestation. Isolation of forest patches was not a large contributor to this problem. The affected-habitat data were averaged into 16 km by 16 km grid cells.

ed habitat analyses for 1978 and 1988 were restricted to closed-canopy forest of the Brazilian Amazon.

Deforestation and Forest Fragmentation

Distribution of deforestation and affected habitat in the Brazilian Amazon for 1978 and 1988 (Figs. 2 and 3) was concentrated in a crescent along the southern and eastern fringe of the Amazon [a spatial pattern similar to the distribution of fires observed from thermal anomalies in data from Landsat's Advanced Very-High Resolution Radiometer (AVHRR) (*20*)] and along major transportation corridors in the interior of the Amazon. Deforestation increased between 1978 and 1988 (78,000 to 230,000 km^2), while the total affected habitat increased (208,000 to 588,000 km^2) (Table 3). The total area deforested increased by a factor of two to three or more in every state except Amapa; but it is likely that the deforested area in Amapa is higher than our assessment because excessive cloud cover in this region prevented complete analysis (Table 2). We found that 6% of closed-canopy forest had been cleared as of 1988 and ~15% of the forested Amazon was affected by deforestation-caused habitat destruction, habitat isolation, and edge effects (Fig. 2 and Table 3).

Our analysis of the spatial pattern of deforestation found a strong tendency toward spatial concentration; areas of undisturbed tropical forest tended to be sizable (Table 4). This is more pronounced than Table 4 indicates because many of the large areas of undisturbed tropical forest are contiguous among states.

For the entire Brazilian Amazon, our deforestation estimate is close to, but lower than, the estimates of Fearnside *et al.* (*13*) and the INPE (*15*) of ~280,000 km^2 as of 1988. The difference is a result of three factors: (i) different stratification of forest, cerrado, and water; (ii) slightly different estimates of secondary growth, which is spectrally similar to intact forest in channel five; and (iii) positional accuracy, interpretation, and boundary generalization. We estimate that ~30,000 km^2 of the difference is from a different evaluation of the forest-cerrado boundaries in Mato Grosso and Tocantins. By comparison, our analysis suggests that deforestation estimates based on coarse-resolution meteorological satellite data in the southern Amazon of Brazil have overestimated deforestation by ~50% (*18*, *23*).

The average deforestation rate in the closed-canopy forests from 1978 to 1988 (~15,000 km^2 $year^{-1}$) (Table 3) is higher than the rate from 1975 to 1978 (*3*) but considerably lower than recent estimates (*2*, *4*, *5*, *20*). Our estimates can be used in assessments of net flux of carbon from land clearing and biomass burning in the Brazilian Amazon. Current estimates of these fluxes have largely been based on model calculations with deforestation values much higher than we report. In addition, many deforested areas are in stages of regrowth following abandonment (*26*). If regrowth is widespread, estimates of the net flux of carbon should be further reduced because carbon accumulates in regrowing biomass.

The preponderance of affected habitat results from proximity to areas of deforestation (~341,000 km^2 for a 1-km edge effect) and not from isolation of forest (~15,000 km^2) or deforestation per se (~230,000 km^2). While the rate of deforestation averaged ~15,000 km^2 $year^{-1}$ in the Brazilian Amazonia from 1978 to 1988, the rate of habitat fragmentation and degradation was ~38,000 km^2 $year^{-1}$. Implications for biological diversity are not encouraging and provide added impetus for the minimization of tropical deforestation.

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24. Images: 7 from 1989, 175 from 1988, 8 from 1987, and 20 from 1986. All data from the Brazilian Landsat receiving station. The exact boundary between intact forest and deforested land was digitized in the Universal Transverse Mercator projection and then edited and error-checked with use of clear velum plots of the line-work overlaid on each photographic image. Each Landsat scene contained coordinate control points in decimal degree units, such that each scene could be geographically registered within precise tolerances and mosaicked together. For digitization, vertices were placed approximately every 50 m of ground position. Tests of positional accuracy in digitizing followed those of R. Dunn, R. Harrison, and J. C. White [*Int. J. Geograph. Inf. Syst.* **4**, 385 (1990)] and indicated encoding; hence, area-estimation errors were less than 3% (*23*). The variance associated with interpretation and delineation of boundaries between intact forest and deforested areas was less than 10% overall. Further accuracy assessment was made in test sites established in Rondonia, where fragmentation was very high. An explicit spatial comparison between our estimate of deforestation and the same derived from high-resolution (20-m resolution) SPOT satellite imagery was highly correlated ($r^2 = 0.98$; $y = 1.11x - 57.358$). Additional ground checking and verification was done in eastern Para state (north of Manaus) and along the Rio Negro, both in Amazonas.
25. Fundamental to our analysis was a specified representation for water, cerrado or savanna, and forest for the Brazilian Amazon. We used a vegetation map (*23*) that was augmented by Landsat Thematic Mapper and meteorological satellite imagery for more accurate depiction of cerrado and water. This GIS representation is available upon request.
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RESEARCH ARTICLE

Arrestin Function in Inactivation of G Protein–Coupled Receptor Rhodopsin in Vivo

Patrick J. Dolph, Rama Ranganathan, Nansi J. Colley, Robert W. Hardy, Michael Socolich, Charles S. Zuker*

Arrestins have been implicated in the regulation of many G protein–coupled receptor signaling cascades. Mutations in two *Drosophila* photoreceptor-specific arrestin genes, *arrestin 1* and *arrestin 2*, were generated. Analysis of the light response in these mutants shows that the Arr1 and Arr2 proteins are mediators of rhodopsin inactivation and are essential for the termination of the phototransduction cascade in vivo. The saturation of arrestin function by an excess of activated rhodopsin is responsible for a continuously activated state of the photoreceptors known as the prolonged depolarized afterpotential. In the absence of arrestins, photoreceptors undergo light-dependent retinal degeneration as a result of the continued activity of the phototransduction cascade. These results demonstrate the fundamental requirement for members of the arrestin protein family in the regulation of G protein–coupled receptors and signaling cascades in vivo.

Rhodopsin is a member of a class of receptors containing seven membrane-spanning domains that transduce extracellular signals to specific intracellular effector molecules through the activation of heterotrimeric guanosine triphosphate–binding proteins (G proteins). This large superfamily of proteins, collectively known as G protein–coupled receptors, includes receptors for a variety of environmental signals such as hormones, neurotransmitters, peptides, light, and odorants (*1, 2*).

The events that lead to the stimulation of G protein–coupled receptors, and the subsequent activation of their corresponding effector molecules [such as adenylyl cyclase, guanosine 3′,5′-monophosphate (cGMP) phosphodiesterase, and phospholipase C] have been well characterized (*2, 3*). However, the mechanisms effecting the termination of the activated state of these receptors and the downstream signaling molecules in vivo are not well defined. Such information is essential for an understanding of the regulation of receptor function and the role of this regulation in modulating receptor-mediated cellular processes.

Much of the data on mechanisms of inactivation of G protein–coupled receptors has come from in vitro reconstitution studies of the β-adrenergic receptor (*4, 5*) and bovine rhodopsin (*6*). The inactivation of metarhodopsin, the activated state of rhodopsin, is thought to result from the action of at least two proteins, rhodopsin kinase and arrestin. According to this model, light-activated rhodopsin is a substrate for rhodopsin kinase, which phosphorylates rhodopsin in a cluster of serine-threonine residues located in the COOH-terminal tail of the protein (*7–9*). The light-activated, phosphorylated rhodopsin interacts stoichiometrically with arrestin, an abundant cytosolic protein that competes with the G protein for receptor binding and terminates, or arrests, the activated state of the receptor (*10, 11*). Although this model is consistent with biochemical studies of arrestin function in vitro, little is known about the function of this protein in vivo (*12*).

Arrestin was originally identified as an abundant, soluble 48-kD protein (also known as soluble antigen or S antigen) found in the vertebrate retinal and pineal photoreceptors (*13*). Human and bovine S antigen are highly immunogenic and have been linked to autoimmune disorders that affect vision (*14*). Functional homologs of visual arrestin have been isolated from nonretinal tissue and have been implicated in the desensitization and inactivation of the β-adrenergic receptor (β arrestins) (*15–17*). Similar proteins have been thought to act as mediators of the inactivation of many G protein–coupled receptors (*18*) and therefore, the molecular mechanisms of receptor inactivation may be shared among members of this receptor superfamily.

Drosophila provides an excellent model system for studying the function of arrestin and the regulation of G protein–coupled receptors in vivo (*19–21*). Mutants with defects in key regulatory components of the phototransduction cascade can be isolated and studied genetically, physiologically, and biochemically. Phototransduction in *Drosophila* begins with the light activation of rhodopsin (*19, 21*). Rhodopsin consists

The authors are in the Howard Hughes Medical Institute and Departments of Biology and Neurosciences, University of California at San Diego, La Jolla, CA 92093–0049.

*To whom correspondence should be addressed.