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Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon

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The distribution of sources and sinks of carbon among the world's ecosystems is uncertain. Some analyses show northern mid-latitude lands to be a large sink, whereas the tropics are a net source¹; other analyses show the tropics to be nearly neutral, whereas northern mid-latitudes are a small sink^{2,3}. Here we show that the annual flux of carbon from deforestation and abandonment of agricultural lands in the Brazilian Amazon was a source of about 0.2 Pg C yr⁻¹ over the period 1989–1998 (1 Pg is 10¹⁵ g). This estimate is based on annual rates of deforestation, regrowing forests and biomass. Logging may add another 5–10% to this estimate⁴, and fires may double the magnitude of the source in years following a drought⁴. The annual source of carbon from land-use change and fire approximately offsets the sink calculated for natural ecosystems in the region^{5,6}. Thus this large area of tropical forest is

nearly balanced with respect to carbon, but has an interannual variability of ± 0.2 PgC yr⁻¹.

We determined the annual flux of carbon with a 'bookkeeping' model^{7,8} that tracks the annual emission and uptake of carbon that follow the clearing of forest for agriculture and the regrowth of secondary forests on abandoned agricultural land. Changes in carbon include (1) the immediate loss of carbon to the atmosphere from plant material burned at the time of clearing, (2) the slower release of carbon from decay of dead plant material left on site (slash) and removed for wood products, and (3) the accumulation of carbon during forest growth. Changes in soil carbon were not included in this analysis, as they are small relative to the changes in biomass and are inconsistent in direction^{9–12}.

We used two estimates of deforestation, three estimates of biomass and two estimates of the rate of decay of organic matter to calculate a range of net carbon emissions attributable to land-use change. The first estimate of deforestation was obtained from the Brazilian Space Agency (INPE), where data from the Landsat satellite are delineated manually for each state to determine both annual rates of deforestation and cumulative areas deforested for each year between 1988 and 1998 (except 1993). The annual and cumulative data are not entirely consistent, and we used the cumulative areas deforested to calculate annual rates of change (Table 1). INPE also determined the area deforested in 1978; before 1960 rates of deforestation were negligible¹³.

The second estimate of deforestation was based on a map of land cover derived from classification of 1986 Landsat multi-spectral scanner data (Fig. 1). Areas classified as deforested in 1986 were consistently lower than INPE's 1988 estimate of deforested area. Because the dates were different, we interpolated a rate for 1988 based on maps of land cover derived from 1986 and 1992 Landsat data. The interpolated area deforested in 1988 was still about 25% lower than INPE's estimate, although the actual percentage varied among states (Fig. 2). We used this lower estimate for a second estimate of deforestation, varying it annually in proportion to the rates from INPE.

According to the Landsat-derived land-cover classification, about 30% of the deforested area was in secondary forest in 1986—presumably as a result of the abandonment of agricultural land^{14–17}. The percentage varied from 5% in Gois to 65% in Maranhao. As we lacked data to suggest temporal trends in abandonment, we assumed that cleared lands were abandoned annually at the rate defined by the ratio of secondary forest to deforested area in 1986.

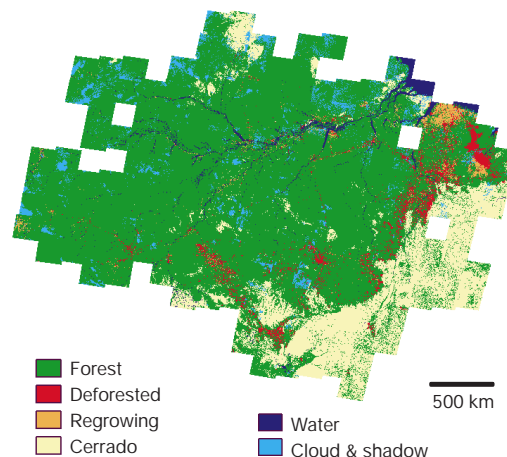


Figure 1 Land cover in Brazilian Amazonia as of 1986, based on a classification of Landsat MSS data. The classification identifies seven classes of land cover: forest, deforested land, regrowing forest, water, clouds, cloud shadow and *cerrado* (savanna). Here data for cloud and cloud shadow are grouped together.

Table 1 Rates of deforestation in the states of Brazilian Amazonia

Years	Rate of deforestation (10^6 ha yr^{-1})									
	78–88	88–89	89–90	90–91	91–92	92–94	94–95	95–96	96–97	97–98
Acre	0.064	0.090	0.050	0.040	0.040	0.048	0.124	0.044	0.036	0.057
Amapa	0.006	0.020	0.030	0.040	0.004	0.000	0.005	0.000	0.002	0.002
Amazonas	0.180	0.200	0.050	0.100	0.080	0.037	0.189	0.080	0.059	0.092
Maranhao	0.269	0.150	0.110	0.070	0.114	0.037	0.178	0.158	0.041	0.105
Mato Grosso	0.515	0.810	0.400	0.290	0.467	0.622	0.854	0.699	0.527	0.581
Para	0.751	0.780	0.490	0.380	0.379	0.428	0.865	0.713	0.414	0.556
Rondonia	0.258	0.180	0.170	0.110	0.226	0.260	0.410	0.250	0.199	0.239
Roraima	0.026	0.090	0.020	0.040	0.028	0.024	0.016	0.024	0.018	0.016
Tocantins	0.184	0.070	0.060	0.050	0.041	0.033	0.067	0.034	0.027	0.036
Brazilian Amazonia	2.253	2.390	1.380	1.120	1.379	1.490	2.708	2.001	1.323	1.684

Data provided by INPE.

Thus, for example, the rate of abandonment in Maranhao each year was equivalent to 65% of the rate of deforestation.

We constructed three estimates of forest biomass. The first and second were based on Projeto RADAMBRASIL (Brazilian forest inventories) of stem-wood volumes on thousands of plots between 1973 and 1983¹⁸. We converted these volumes to total biomass with equations from refs 19 and 20, including an additional 20% for below-ground biomass^{19,21}. Total biomass was assumed to be 50% carbon. The intersection of this map of total biomass with the 1986 land-cover map (Fig. 1) defined the number of deforested pixels in each biomass class. We defined five broad classes of biomass (<100, 100–130, 130–160, 160–190 and >190 Mg C ha^{-1}), and calculated the area-weighted mean biomass for each class in each state on the basis of the classes deforested as of 1986 (Fig. 3). For this estimate, the classes of biomass ranged from 66 to 277 Mg C ha^{-1} .

A second estimate of biomass was based on a conversion of RADAMBRASIL stem-wood volumes to biomass²⁴. This conversion yielded an Amazonia-wide estimate 60% higher than one based on equations from ref. 18. We assumed that the larger estimate for the entire region applied to each cell. Thus the spatial distribution of biomass was equivalent to the first estimate, but each cell was 60% higher (Fig. 3).

A third estimate of biomass was based on 56 sites where live above-ground biomass was determined either indirectly (from large-area surveys of stem-wood volumes) or directly (from harvest of trees on plots between 0.2 and 2 ha). For sites where dead above-ground biomass or below-ground biomass was not measured, we increased live above-ground biomass by 10% (average of 20 sites) and 24% (ref. 21), respectively, to obtain total biomass. Multiple

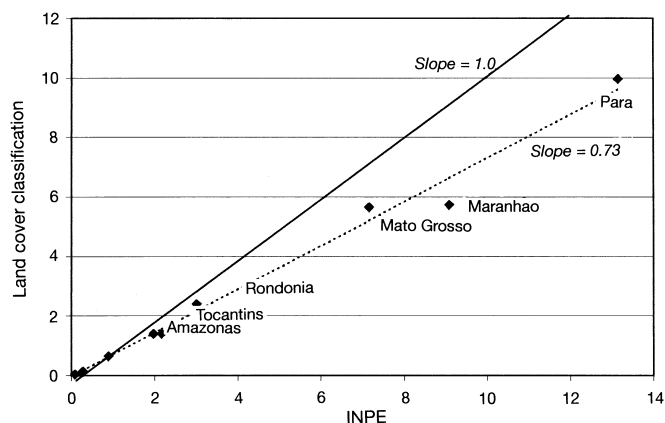


Figure 2 Comparison of two sets of estimates of the areas deforested by 1988 (10^6 ha) in each state of Brazilian Amazonia. 'INPE' indicates estimates from the Brazilian Space Agency, INPE. The rates obtained from a land-cover classification are based on an interpolation of 1986 and 1992 data.

measurements at the same location were averaged so that each site was represented by a single value. These values were distributed over Amazonia with a simple two-dimensional interpolation (Fig. 3).

With deforestation, the fractions of initial forest biomass burned, left as slash, removed for products and converted to 'elemental carbon' through burning were 0.2, 0.7, 0.08 and 0.02 (refs 23, 24), respectively. We assumed rates of decay as follows: woody material removed from the site (wood products) decayed with a rate constant

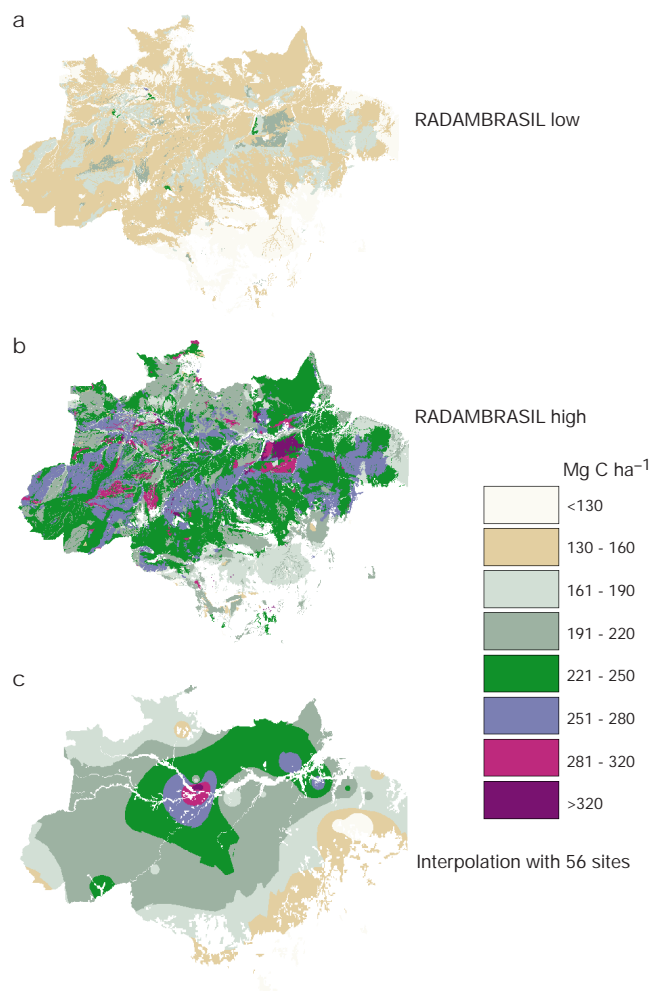


Figure 3 The spatial distribution of biomass in Brazilian Amazonia. **a**, RADAMBRASIL wood volumes converted to biomass with equations from refs 18, 19 (low estimate). **b**, RADAMBRASIL volumes converted to biomass (from ref. 21) (high estimate). **c**, Biomass interpolated from 56 sites (medium estimate).

Table 2 Eight combinations of data used to calculate a range of estimates of carbon flux

	Deforestation	Biomass	Decay rate	Carbon released 1989–1998	Carbon still to be released from slash products accumulated by 1998	Carbon to be accumulated in regrowth
1.	INPE	High	Low	2.64	3.03	3.12
2.	INPE	Medium	Low	2.14	2.46	1.32
3.	INPE	Medium	High	2.37	1.05	1.32
4.	INPE	Low	Low	1.63	1.87	1.00
5.	Land cover	High	Low	1.66	2.12	1.44
6.	Land cover	Medium	Low	1.34	1.72	1.17
7.	Land cover	Medium	High	1.59	0.77	1.17
8.	Land cover	Low	Low	1.02	1.31	0.88
			Mean	1.80	1.79	1.43

Shown are total amount of carbon (Pg C) released from deforestation and agricultural abandonment in Brazilian Amazonia over the period 1989–1998, carbon still to be released from slash and products remaining in 1998, and the total amount of carbon to be accumulated in forest growth if secondary forests remain undisturbed over the next 75 years.

of 0.1 yr⁻¹; elemental carbon decayed at 0.001 yr⁻¹. Dead wood left on site decayed exponentially with one of two decay constants: 0.1 yr⁻¹ for a ‘best estimate’, and 0.4 yr⁻¹ to test the model’s sensitivity to this parameter. Both values are within the range reported for 25 forests in Venezuela²⁵.

Abandoned agricultural lands reverted to forests that accumulated carbon at rates proportional to initial forest biomass. Rates ranged from about 1.5 Mg C ha⁻¹ yr⁻¹ in forests initially with biomass < 100 Mg C ha⁻¹, to about 5.5 Mg C ha⁻¹ yr⁻¹ for forests initially > 190 Mg C ha⁻¹. Growth of biomass is rapid in young forests, and declines with age²⁶. In this analysis, forests recovered 70% of their original biomass in 25 years and the remaining 30% over the next 50 years. The assumption that forests are fully regrown after as little as 75 years is probably not valid, but this analysis was largely concerned with human-induced changes over the past 10–40 years.

The two rates of deforestation described above, when used with the three estimates of biomass and two rates of decay, yielded eight estimates of annual emissions of carbon (Table 2). Annual emissions increased from zero before 1960 to between 0.1 and 0.3 Pg C yr⁻¹ in the 1990s (Fig. 4). The average rate of carbon release for the 1990s varied between 0.102 and 0.264 Pg C yr⁻¹, and the mean flux over the 10-year period (1989–98) was 0.18 Pg C yr⁻¹. The main contributor to flux is the decay of wood that had been chopped down. In contrast, the uptake of carbon in secondary growth, and the releases from burning associated with deforestation, are small (Fig. 4).

The average annual source of 0.18 Pg C yr⁻¹ from deforestation and regrowth is near the low end of the range of estimates from previous analyses of Brazil (0.174–0.336 Pg C yr⁻¹; refs 7, 27, 28), and lower than the estimate for Brazilian Amazonia (0.261 Pg C yr⁻¹; ref. 22). Many of these earlier estimates were for a single year or an average year, were based on tabular rather than spatial data, used a small number of average values for biomass and did not take into account the sources and sinks embodied in previous land-use history. Fearnside’s recent analysis²² is the most comprehensive, but his estimate is difficult to compare with ours because he computed a ‘committed’ flux that included future sources and sinks embodied in current slash pools and regrowing forests. The estimate determined here lowers the global estimate of flux for the 1980s (ref. 8) by about 0.2 Pg C yr⁻¹.

The greatest uncertainty in the calculated flux of carbon over the period 1989–1998 results from uncertainty in the biomass of forests deforested. Uncertainty in biomass, rates of deforestation and rates of decay accounted for about 60, 25 and 15%, respectively, of the range of estimates of flux. Rates of decay were relatively more important in the years following increased rates of deforestation.

The average biomass of forests was 145 Mg C ha⁻¹ for the first estimate obtained from RADAMBRASIL data, and 232 Mg C ha⁻¹ (60% higher) for the second estimate. The reasons for the discrepancy include different adjustments for below-ground biomass,

dead biomass, palms, vines, and understory vegetation, and the possibilities of bias in sampling²⁹. The third estimate of biomass, based on independent field measurements, yielded an intermediate value of 210 Mg C ha⁻¹. Despite the large uncertainty in estimates, average biomass of the forests actually deforested was only 4–6% less than the average biomass of the region’s forests, whichever estimate was used.

The deforested area reported by INPE in 1988 was about 25% higher than the deforested area interpolated between 1986 and 1992 classifications of land cover with Landsat data (Fig. 2). Both estimates of deforestation were obtained from Landsat data, and it is not clear which estimate is more accurate. INPE uses a manual approach for delineating areas deforested, whereas our land-cover classifications were based on supervised, automated techniques using digital data.

Although logging and fire were not considered in this analysis, they are important in the region and affect the storage of carbon. The net effect of logging is probably small (4–7% of the release from deforestation)⁴, because releases of carbon associated with harvest are largely offset by the accumulations in forests recovering from earlier harvests. The area annually burned is unknown, but fire may release as much carbon as is released from deliberate deforestation, particularly following the dry years associated with an El Niño event^{4,30}.

The combined effects of deforestation, abandonment, logging and fire may thus yield sources of carbon that vary between 0.1 and 0.4 Pg C yr⁻¹. These fluxes are similar in magnitude (but opposite in sign) to the sink calculated recently for natural ecosystems in the

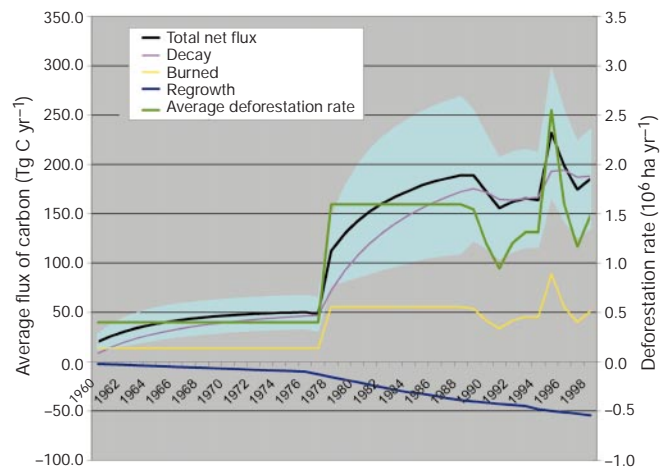


Figure 4 Annual rate of deforestation and mean annual sources and sinks of carbon in Brazilian Amazonia. Shaded area is ± 1 s.d. from the mean annual flux of carbon determined for the eight cases described in the text.

region^{5,6}. Taken together, the sources (from land-use change and fire) and the sinks (in natural forests) suggest that the net flux of carbon between Brazilian Amazonia and the atmosphere may be nearly zero, on average. However, the interannual variability of the natural fluxes, including fire, is larger than it is for the human-induced sources: the annual net flux for this significant region of the tropics may vary between a sink and a source of 0.2 Pg C yr⁻¹, occasionally more. □

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Rapid evolution of male reproductive genes in the descent of man

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A diverse body of morphological and genetic evidence has suggested that traits pertaining to male reproduction may have evolved much more rapidly than other types of character^{1–3}. Recently, DNA sequence comparisons have also shown a very high level of divergence in male reproductive proteins between closely related *Drosophila* species^{4–6}, among marine invertebrates^{7,8} and between mouse and rat⁹. Here we show that rapid evolution of male reproductive genes is observable in primates and is quite notable in the lineages to human and chimpanzee. Nevertheless, rapid evolution by itself is not necessarily an indication of positive darwinian selection; relaxation of negative selection is often equally compatible with the DNA sequence data. By taking three statistical approaches, we show that positive darwinian selection is often the driving force behind this rapid evolution. These results open up opportunities to test the hypothesis that sexual selection plays some role in the molecular evolution of higher primates.

Although positive (or directional) selection may justifiably be considered the essence of darwinian evolution, proving its action at the molecular level is often difficult, especially in humans. In the rare cases when positive selection is strong enough to rise above the background of neutral evolution or overcome other forms of selection, the rate of non-synonymous nucleotide substitution (K_A) may exceed that of synonymous substitution (K_S)¹⁰. Many of the genes cited above that function primarily in males' reproductive tissues do indeed have $K_A > K_S$. They not only suggest positive selection but also implicate selection "in relation to sex"¹¹. Evidence for sexual selection has been reported extensively in previous morphological and genetic analyses^{1–3}.

Here we attempt to find out how strong positive selection (especially in relation to sexual functions) has been in the lineage leading to modern human by analysing a cluster of three spermatid-associated protein genes and then a broad class of genes of male reproduction. We use three approaches to reveal the action of positive selection: (1) showing that the K_A/K_S ratio is significantly greater than one; (2) contrasting the pattern of intraspecific variation with that of interspecific divergence¹²; and (3) classifying amino-acid substitutions into categories based on the physicochemical properties of the residues^{13,14}. The current wealth of DNA sequence data is particularly suitable for this third approach.

Table 1 The numbers of replacement (R), silent (S) and noncoding (S') nucleotide changes

	R	S+S'	(S)
<i>Pm-1</i>			
Within (<i>n</i> = 52)	0	6	(2)
Between	9	9	(0)
No. of sites	114	483	(39)
		<i>P</i> = 0.037	(<i>P</i> = 0.018)
<i>Pm-2</i>			
Within (<i>n</i> = 32)	0	9	(0)
Between	7	11	(2)
No. of sites	224	705	(82)
		<i>P</i> = 0.035	(NC)

Within denotes 'within human populations'; *n* indicates the number of haploid genomes sampled; Between denotes 'between human and chimpanzee'. In this application of the McDonald and Kreitman test¹², we compare *R* with both *S+S'* and *S* alone (in parentheses). The *P* values given are from the one-tailed Fisher's Exact test. Total numbers of sites for each class by the method of Li *et al.*³⁰ are also given.