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Socioeconomic factors and tropical deforestation

Despite worldwide concern about habitat degradation in the tropics, deforestation in tropical countries continues unabated[1]. In 1979, 75,000 km^2 was deforested, but by 1991 this figure had increased to 132,000 km^2 (ref. 2). The underlying causes of deforestation are, however, poorly understood. Here we examine the correlation between deforestation in the tropics and 14 socioeconomic variables, and show that the most significant correlates of deforestation vary from region to region. Furthermore, the relative importance of the most significant correlates of deforestation varies with the statistical model used.

Tropical forests provide important ecosystem services, and have large concentrations of biodiversity and genetic resources. Policy options concerning conservation and management of tropical forests are often presented in general, global terms[3], reflecting a poor understanding of the causes of deforestation[4]. International comparisons of data from individual countries attribute major roles to population pressure[5], wealth[5,6], external debt[7] and competition for land[4,8]. Deforestation is caused by many factors[9,10], but quantitative analysis of the relative importance of these factors throughout the tropics is lacking.

We obtained data for 70 tropical countries from the World Resources Institute database[11]. The 14 socioeconomic variables used were grouped into five categories: population, economic indicators, land use patterns, extraction of forest products and energy use. Pooling results over the entire tropics, deforestation rate was correlated positively with 11 of the 14 variables, and negatively with per capita traditional fuel consumption (Table 1). There were, however, strong regional differences.

Table 1 **Correlation coefficients between log annual deforestation rate and selected variables**

Variable (log)	All countries	Africa	Asia	Latin America
Population				
Rural population density	0.63*** (69)	0.53** (32)	0.59* (15)	0.75*** (22)
Urban population density	0.69*** (70)	0.45** (33)	0.73** (15)	0.77*** (22)
Total population density	0.68*** (68)	0.51** (32)	0.66** (15)	0.77*** (21)
Economic				
Per capita GNP	0.07 (66)	−0.16 (33)	0.23 (13)	−0.43 (20)
Per capita external debt	0.41** (62)	0.27 (33)	0.38 (11)	0.20 (18)
Forest products extracted per unit forest area				
Fuel-wood and charcoal	0.45*** (70)	−0.25 (34)	0.64* (15)	0.78*** (21)
Industrial roundwood	0.60*** (69)	0.04 (34)	0.67** (15)	0.76*** (20)
Panel-wood	0.28* (52)	−0.29 (24)	0.59* (14)	0.23 (14)
Land Use				
Cattle density	0.60*** (70)	0.46** (34)	0.09 (14)	0.88*** (22)
Crop-land area/total land area	0.74*** (69)	0.59*** (33)	0.90*** (14)	0.80*** (22)
Pasture area/total land area	0.10 (68)	−0.02 (36)	−0.12 (13)	0.79*** (19)
Land in other use/total land area	0.43*** (66)	−0.01 (33)	0.51 (13)	0.74*** (20)
Per capita energy consumption				
Traditional fuel	−0.41*** (67)	−0.17 (35)	−0.91*** (12)	−0.23 (20)
Commercial energy	0.40*** (66)	0.05 (34)	0.38 (14)	−0.13 (18)

Correlation coefficients are listed with their significance levels: *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$. The number of countries analysed is given in parentheses.

For Africa, deforestation rate was more strongly correlated with rural population than with urban population, but the opposite trend was observed for Asia. Pasture-land area and the area of land in use other than as pasture or for crop growth are correlated with deforestation only in Latin America, whereas cattle density was significant in Africa and Latin America but not in Asia. With respect to forest products, panel-wood production was correlated with deforestation in Asia but not in Latin America, and none of the forest product variables were correlated with deforestation in Africa. Per capita traditional fuel consumption showed a significant negative correlation with deforestation rate in Asia alone.

Our results show that correlates of deforestation are many and varied, with complex interactions. The relative importance of each factor depends on the model and variables used. Multiple regression analysis of the relative magnitude of direct effects places proportion of crop-growing land area ahead of population density, then per capita external debt as having the greatest effect on deforestation when all tropical countries were considered, but when Latin America and Asia were looked at separately external debt was the second most important factor (Fig. 1). In Africa, population density was more important than external debt followed by crop-land area. These three variables plus fuel-wood and charcoal

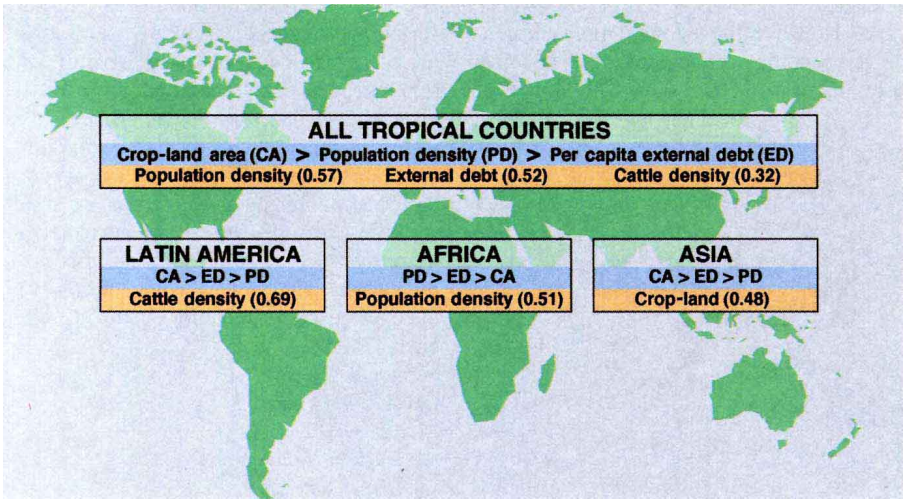

Figure 1 **Relative magnitude of direct effects (β) of population density, per capita external debt, proportion of crop-land area, fuel-wood and charcoal production and per capita traditional fuel consumption on rate of deforestation as revealed by multiple regression analysis, using a model comprising one variable from each group. The variables together explained 42% (all tropical countries), 33% (Africa), 96% (Asia) and 48% (Latin America) of variance. The three most important variables are shown in blue. Results of forward stepwise regression, using independent variables that showed significant correlation ($P<0.05$) with the rate of deforestation in tropical countries, are shown in yellow. The most significant three variables overall, and the most important in each region are shown. β is given in parentheses. Direct effects are based on standardized partial regression coefficients (β), with log annual per cent deforestation in tropical countries as the dependent variable.**

production, and per capita traditional fuel consumption together explained 42% (all tropical countries), 33% (Africa), 96% (Asia) and 48% (Latin America) of variance in deforestation rate.

On the other hand, a forward stepwise regression analysis using independent variables that were significantly correlated ($P<0.05$) with deforestation in tropical countries showed that population density ($\beta=0.57$), external debt ($\beta=0.52$) and cattle density ($\beta=0.32$) are important in that order when all countries are considered together (Fig. 1). In Africa, population density has greatest effect on deforestation rate, in Asia crop-land area, and in Latin America cattle density. Again, the most significant results of our analyses are the differences between regions, also revealed by other analyses[1,9].

Our analyses point to several possible causes of deforestation and have important policy and management implications. The availability of remote-sensing imagery and local data on socioeconomic variables, give us the potential to identify accurately the causes of deforestation at smaller scales; as we have done for the Sarapiqui region in Costa Rica (A. Sanchez-Azofeifa, S. D. and K. S. B., unpublished results) and the western Ghats, India (S. Menon & K. S. B., unpublished results). Policies to stem deforestation must take into account regional as well as country-wide differences. More emphasis is needed on land distribution and agrarian reform in Latin America, where much of the land is used inefficiently for cattle ranching, and in Asia, alternatives must be found for subsistence-level agriculture, which drives agricultural frontiers onto marginal lands occupied by forests.

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Kinked DNA

Kinks are thought to be important in DNA–protein interactions[1] but evidence for their existence in free DNA has previously been indirect. The atomic force microscope (AFM) allows direct visualization of molecular structure *in situ*[2,3], and using our newly developed AFM (magnetic a.c. mode or MacMode)[4] we have observed small DNA circles change from smoothly bent to abruptly kinked shapes. This effect was dependent on the presence of specific divalent cations. The DNA was bent smoothly in the presence of Mg^{2+}, but consisted of nearly straight segments connected by kinks in the presence of Zn^{2+}.

Tandem sequence repeats of $d(A)_5$ and d(GGGCC[C]) bend DNA[5]. We ligated the following oligomer:

CCCAAAAAGGGCCAAAAAGGGCCCAAAAAGGGCCAAAAAGGG
TTTTTCCCGGTTTTTCCCGGGTTTTTCCCGGTTTTTCCCGGG

to produce DNA circles. Maximum formation of circles occurs when the ligated oligomers are 126-base-pairs long. DNA longer than this forms superhelices, and thermal fluctuations are needed to bring the ends together. As a result, the larger closed circles are axially strained on ligation. We extracted circles and purified them as described elsewhere[6]. We placed DNA solutions (0.5 mg ml^{-1} in 1 mM Mg^{2+} or Zn^{2+}) into the sample cell of a scanning probe microscope (PicoSPM; Molecular Imaging Corp., Phoenix, Arizona) where the molecules adsorbed spontaneously onto a mica substrate. Images were obtained *in situ* and remained stable on repeated scanning.

DNA images obtained in the MacMode had an average full-width at half-height of 3.5 nm, so the instrumental broadening is little more than 1 nm, a significant improvement in resolution over previous AFM technologies. DNA circles of 168 base pairs in 1 mM $MgCl_2$ are smoothly curved, with less than one abrupt bend or kink per molecule (Fig. 1a).

When molecules from the same sample are imaged in 1 mM $ZnBr_2$, their appearance changes dramatically (Fig. 1b). The DNA consists of nearly straight segments connected by abrupt kinks. This phenomenon was not observed in 126-base-pair circles, so we conclude that axial strain is required for this conformational change. The relative lack of kinks in the presence of Mg^{2+} and the absence of kinks in smaller circles under all ionic conditions demonstrate that single-strand breaks did not cause the kinks.

The strong enhancement of kinking observed here in the presence of Zn^{2+} is qualitatively consistent with earlier electron microscopy[7] and electro-optical[8] studies. If kinks are readily generated *in vivo* through a combination of axial strain and appropriate ionic conditions, then one might speculate that local writhing stress, to which DNA is subjected during various regulatory events, may promote the formation of localized kinks at specific DNA sequences. These could serve as signals for the assembly and/or localization of nucleoprotein complexes.

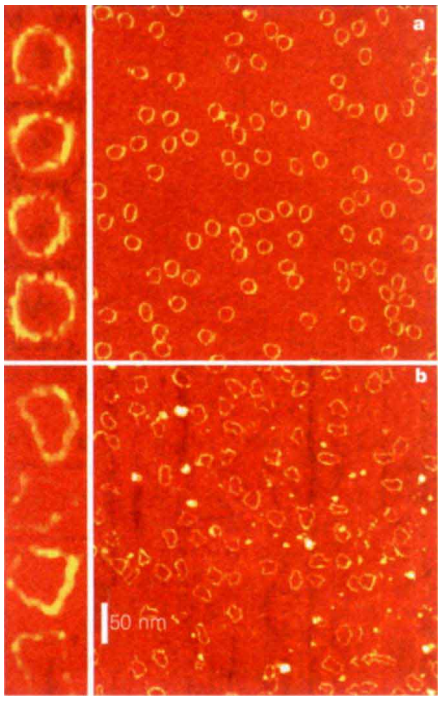

Figure 1 **Images of 168-base-pair DNA minicircles in 1 mM $MgCl_2$** (a) **and 1 mM $ZnBr_2$** (b)**, showing a fourfold increase in kink density in Zn^{2+}. Selected molecules are displayed magnified by a factor of four to the left of each image. The tip was oscillated at 25 kHz with an amplitude of 5 nm and the image was acquired in five minutes.**

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