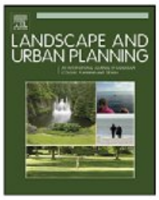
Landscape and Urban Planning 87 (2008) 129–139

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan



Causes of habitat loss in a Neotropical landscape: The Panama Canal corridor

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ARTICLE INFO

Article history:
Received 4 March 2007
Received in revised form 10 May 2008
Accepted 14 May 2008
Available online 25 June 2008

Keywords:
Habitat loss
Tropical rainforests
Biophysical factors
Socio-economic factors
Urbanization
Agriculture
Republic of Panama

ABSTRACT

We studied drivers of habitat conversion in the Panama Canal region, where rich biodiversity in tropical rainforests currently coexists with two major growing cities and a plethora of economic opportunities. We examined existing administrative units (counties) with known biophysical (e.g., rainfall, topography) and socio-economic (e.g., population density, road density) characteristics. To identify associations between those characteristics and likelihood of habitat conversion to agriculture or urbanization, we used canonical correlation analysis. Two axes accounted for most of the variation among administrative units: one for urbanization and the other for agriculture. Rainfall and topography were negatively associated with urbanization, whereas population wealth was positively associated with land conversion to urban. Agriculture was most strongly associated with elevation variability and topographic complexity. To a lesser extent, agriculture was associated with rural population density, mean annual human population growth and poverty level. We hypothesize that most future habitat loss in the Panama Canal region will be from urbanization as Panama City expands and populations grow along the highway system. Decision-makers will need to emphasize preservation of forests on the edge of developments, where risk of loss is highest. These forested lands tend to become more expensive as urbanization approaches, putting them at greater risk of being converted. Nevertheless, they are still important for protection of the Canal watershed and the high levels of biodiversity in watershed forests. Land planners and decision-makers should consider the influence of socio-economic and biophysical factors when selecting forests to protect for conservation.

1. Introduction

When tropical forests are disturbed by human activities, biodiversity in those forests usually declines (Laurance and Bierregaard, 1997). Studies of birds, for example, show that both fragmentation and habitat loss reduce diversity (Robinson et al., 2000, 2004; Laurance et al., 2002b; Gaston et al., 2003; Waltert et al., 2005; Rompré et al., 2007). Major factors associated with fragmentation and habitat loss, and therefore loss of biodiversity, are high levels of human population density (Cincotta et al., 2000; McKee et al., 2003; Scharlemann et al., 2004), density of roads (Maki et al., 2001; Laurance et al., 2002a, 2006; Gutzwiller and Barrow, 2003; Glennon and Porter, 2005), changes in agricultural practices (Meyer and Turner, 1992; Huston, 1993), logging (Köhler et al., 2002; Rudel, 2005), and hunting (Brashares et al., 2001; Laurance et al., 2006).

If we are to provide conservation solutions and recommendations for modified landscapes, so that needs of humans and biodiversity can be balanced, we need a better understanding of factors driving habitat change, especially the influence of socio-economics factors. Socio-economics include demographic, economic, technological, political, and cultural factors (Brooks et al., 2001; Lambin et al., 2003; Lepers et al., 2005), all of which contribute to rates of human population expansion and landscape change (Contreras-Hermosilla, 2000). Environmental attributes also influence patterns of habitat conversion (Lambin et al., 2003). A better understanding of forces driving habitat conversion will include both socio-economic and biophysical factors (Veldkamp and Lambin, 2001; Laurance, 2007).

The interplay of socio-economic and biophysical factors makes quantifying causes of habitat conversion challenging (Southgate et al., 1991; Contreras-Hermosilla, 2000; Veldkamp and Lambin, 2001; Lambin et al., 2003; Laurance, 2007). Such a situation can be found in central Panama. This part of Central America harbours forests rich in biodiversity neighbouring two growing cities (including the country's capital) within a relatively small area (Condit et al., 2001). After nearly a century of U.S. military presence, which limited economic and development opportunities in the canal region, departure of the U.S. in December 1999 released lands for possible conversion by Panamanians (Cho, 2001; Condit et al., 2001; Dale et al., 2003; Robinson et al., 2004). New roads, railroads, and bridges quickly followed as urban sprawl around Panama City increased (Cho, 2001). Recent plans for canal expansion to increase shipping

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doi:10.1016/j.landurbplan.2008.05.006

volume (Rubin, 2007) indicate economic opportunities show no signs of slowing. Therefore, decisions must be made to balance natural ecosystem protection and the economic decisions from the Panamanian government (Heckadon-Moreno et al., 1999; Condit et al., 2001). Historically, biophysical factors such as mountains with steep slopes, dense vegetation, and high annual rainfall influenced which habitats were occupied by humans (Suarez, 1981). Yet, today, despite a human population of more than 1.3 million and intense economic pressures, 50% of the region still has forest (Heckadon-Moreno et al., 1999; Condit et al., 2001; Ibañez et al., 2002; Robinson et al., 2004). These forests are still considered vital to protect the Canal watershed and to preserve the regional hydrologic system for Canal operations (Heckadon-Moreno et al., 1999). Economic pressures are expected to increase as human populations grow by 2.6% per year through 2020 (Prieto et al., 1999).

Given the increasing demands for land in the Panama Canal area, we asked what factors might be used to predict patterns of habitat conversion. By studying the current landscape and how it differs from its historic pattern of complete forest coverage, we sought to improve our understanding of what future land-use patterns may be. In particular, we had two primary objectives. (1) Describe the patterns of habitat change and deforestation via land-use allocation across the Panama Canal region. (2) Associate spatial patterns of human land use with biophysical and socio-economic components of the local environment and human population, and evaluate the relative importance of each variable according to general land-use types, namely, agriculture and urban. Our analysis incorporates the most recent data available on land use in the region from surveys conducted by the Panamanian government and agencies, which include potentially important anthropogenic and biophysical factors whose effects have not yet been measured in central Panama. These might prove useful to predict future habitat-loss scenarios and how those scenarios influence the distribution of biodiversity.

2. Methods

2.1. Study area

2.1.1. General description

We studied causes of habitat loss in an area of 65 km × 45 km along the Panama Canal corridor, central Panama (Fig. 1). Natural habitat in the region includes dry seasonal forests on the Pacific slope (mean annual precipitation as low as 1500 mm/year) to wet evergreen lowland and premontane rainforests on the Caribbean slope (>4000 mm/year) (Windsor et al., 1990). Altitude varies from sea level to 500 m ASL. Human impact is strong in the canal corridor, especially because urban influences are concentrated around 2 major cities (Panama City, the capital, and Colon). Yet, Central Panama still has a high percentage of forest cover close to its major cities; almost 50% of the current forest cover of the area is contained in national parks and other protected areas. The remainder of the forest is not protected, and mostly consists of a mosaic of fragments interspersed with regenerating second-growth (*matorales*), pastures (*portreros*), and urban areas. Most remaining forests in the canal region are considered mature secondary forest (disturbed more than 100 years ago) with few interspersed mature patches (not disturbed in modern history; Panamanian Service of Forest Administration [ANAM], 2003). Old-growth forests are present in both protected and non-protected lands (ANAM, 2003). Depending on location in the region, <10–100% of forest cover has been converted to urban and/or agricultural uses (Fig. 1). Satellite imagery from the Canal watershed shows that between 1.7% and 3% of forested habitat was converted to pasture and agriculture, and only 0.2% to urban annually between 1980 and 1998 (Panama Canal Watershed Monitoring Project, 1999; Dale et al., 2003). We believe urbanization has probably increased substantially since 2000 (Condit et al., 2001; Ministry of Housing [MIVI], 2005). Presently, more than 1.3 million people currently live in the study area. Biodiversity increases from the Pacific to the Caribbean along a steep rainfall gradient (Condit, 1998; Condit et al., 2001; Pyke et al., 2001). For example, forest bird species richness increases from 4 dry-forest specialists to more than 170 wet-forest specialists along this gradient (Ridgely and Gwynne, 1989; Angehr, 2006; Robinson et al., 2004; Rompré et al., 2007). The same pattern occurs in tree species richness (Condit, 1998; Pyke et al., 2001).

2.1.2. Brief history of human colonization

Humans have lived in the region since 11,000 years B.P. (Piperno et al., 1990), where Paleo-Indians first disturbed the forests for agricultural practices. Before then, the region was entirely forested (Piperno et al., 1990; Bush et al., 1992). From that period on, forests in flatter terrain were often converted for agriculture (see also Robinson et al., 2000). Trading routes used by the Spaniards during early colonization undoubtedly caused local forest disturbances across the isthmus. Panama City was first established on the Pacific coast, and then was followed by the city of Colon on the Caribbean coast. According to Suarez (1981), early colonization followed climatic, geographic and topographic relief criteria. Expansion of Panama City from the first city centre (*Casco Viejo*) avoided very wet regions with thick 'jungle' and steep terrain. Savannahs, present mostly on the Pacific slope, were favoured for colonization. Today, 90% of the human population is concentrated on the Pacific slope (Suarez, 1981). Most internal migration of humans is toward Panama City (Varela, 1998b) which has grown along an east–west axis parallel to the coast. Expansion of Panama City to the west was limited by the US Canal Zone. Meanwhile, Colon, the only urbanized area on the Caribbean side, remained limited in extent until a highway connected Colon to Panama City in the 1960s. The *Transistmica* highway allowed industrial expansion north of Panama City, and led to proliferation of small settlements along the highway (Dale et al., 2003). With the announcement in the late 1970s of withdrawal of US military, expansion of Panama City on the east and west sides of the Canal began. Expansion to the east continues where terrain is flat, but is limited to the north by mountain ranges and risk of landslides (MIVI, 2005).

2.1.3. Selection of subregions

We divided the study region into subregions based primarily on boundaries of politically administered counties (*corregimientos*). This approach was necessary since all human population survey data are available at the county level. As some counties were much larger than others, we reduced the biophysical and socio-economic variability among counties by dividing some of the larger ones into smaller subregions based on obvious differences in underlying geology, topography, or elevational range. This resulted in 33 subregions that formed the basis of our comparisons.

2.2. Biophysical characteristics of subregions

Each subregion was characterized by a combination of biophysical factors that can potentially help one understand patterns and causes of habitat loss (Table 1). These factors were chosen based on their known direct or indirect effects on habitat loss in other regions in temperate or tropical countries (Southgate et al., 1991; Laurance et al., 2001; Seabloom et al., 2002; Lambin et al., 2003 and references therein).

Mean annual precipitation data were obtained from the Panama Canal Authority (ACP) and atlases (see also Condit, 1998; Pyke et al., 2001). We calculated mean annual rainfall for each subregion from

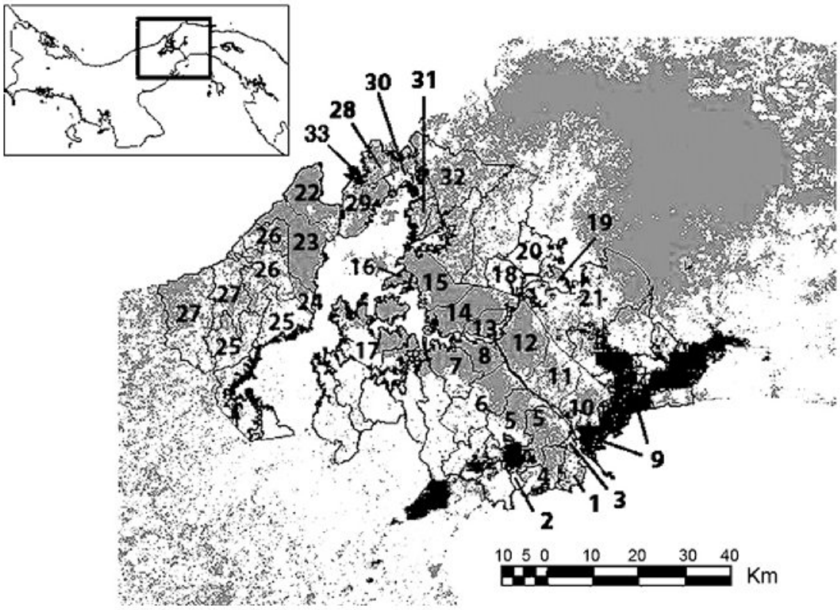

Fig. 1. Subregions in the Panama Canal corridor. Black lines and numbers indicate the regions used for the study. Dark grey represents the forests; lighter shades of grey represent the shrubs and pastures; and black represents the urban (black areas on the south side of the canal represent Panama City and suburban surroundings while smaller areas on the north side of the canal represent the city of Colon). Water from the canal and oceans is indicated in white. Digitized map from 1999 provided with kind permission of the ACP (Panama Canal Authority).

the ACP data (1994–2003). Rain gauges from the ACP were not available for all subregions, therefore we interpolated precipitation data from isohyets available from atlases; these data were concordant with other studies in the same area (Condit, 1998; Pyke et al., 2001; Santiago and Mulkey, 2005; Rompré et al., 2007). Variability in elevation was determined by calculating maximum altitude above sea level (ASL) in each subregion minus minimum altitude (ASL), which was often the altitude of the canal waters. Calculations were done using topographic maps and digital elevation data. Maximum elevation variability was 500 m. We estimated topographical variation within each subregion on a scale of 1–5 (1 being relatively flat with little variability in slopes and few irregular basins, 5 having high variability in slopes and many ridges and ravines). To do this, we used topographic maps and digital elevation data (resolution of 3 arcsec or 90 m; available at http://www.mapart.com).

Geologic information was obtained from the most recent U.S. Geological Survey map of superficial geology (Woodring et al., 1980). In the area covered by the 33 subregions of our study, 11 different geological formations were recorded (Table 2). Formations found in a single subregion can be very patchy, thus occasionally several types were recorded; our data represent the main formation type, which covered most of the area in a given subregion (over 60%).

Forest age classes were determined for each subregion by following an age classification scheme already available (Pyke et al., 2001; ANAM, 2003). Categories which are based on species composition and forest disturbance history include: (1) secondary forest, (2) mature secondary, and (3) old-growth or primary forest. Age classification was: secondary forests were disturbed in relatively recent history (<100 year), mature secondary forests were disturbed more than 100 year ago, and old-growth forests were considered never to have been logged or cultivated in modern history (>500 year, see Denslow and Guzman, 2000; DeWalt et al., 2003). In cases where forest age varied within a single subregion (Pyke et al., 2001), we considered only the dominant relative age of the forests for the analysis (when >60%).

Table 1
Biophysical and socio-economic variables used to compare the 33 subregions of the Panama Canal region

Biophysical variables	Sources
Mean annual precipitation (Rainfall, mm)	Canal Authority of Panama, Pyke et al. (2001), Santiago and Mulkey (2005)
Elevation variability (Elev., maximum less minimum elevation recorded, m)	Topographic maps
Geological formation (Geol., all class numbered from 1 to 10)	Woodring et al. (1980)
Topography complexity (Topo., class of 1, flat, to 5, high complexity)	Digital elevation data, Topographic maps (see text)
Age (1 = secondary forest, 2 = mature secondary, 3 = primary mature forest)	ANAM, Pyke et al. (2001)
Agriculture area (Agric. Area, expressed by km^2 of agriculture area within each subregion) [dependent variable]	Digitized maps (ACP, Panama)
Urban area (Urban area, expressed by km^2 of urban area within each subregion) [dependent variable]	Digitized maps (ACP, Panama)
Socio-economic variables	
Human population density in 2002 (urban population size *and* rural population density)	General Comptroller of the Panama Republic (2003)
Human annual population growth	Idem
Road density (Road dens., km of road/km^2)	Digitized maps (ACP, Panama)
Distance of subregion centroid to the next main city (Dist city, km)	Digitized maps (ACP, Panama)
Distance of subregion centroid to the next main highway (Dist highway, km)	Digitized maps (ACP, Panama)
Human level of poverty (%)	Ministry of Housing (2005)

Table 2

Characteristics of the 33 subregions covering the lowland rainforest and urban areas of the canal corridor, Panama

SR[a]	Total area (km^2)	Urban area (%)	Agriculture area (%)	Annual rainfall (mm)	Geology	Topo	Road density	Urban pop. size	Rural pop. density	Lev. poverty (%)	Projected value[b]
1	19.1	24.5	24.7	1525	Tp	1	3.14	218.7	69.2	0.41	149
2	18.9	42	39	1400	Tb	2	1.46	930.39	804.3	0.19	400
3	4.4	30	25.8	1650	Tl	1	4.27	41.3	72.4	0.41	100
4	36.2	18	27	1800	Tp	3	1.54	563.8	75.7	0.41	149
5	106.7	17.7	17.2	1890	Tb	3	1.48	3659.4	104.4	0.28	1471
6	78.6	1.2	42	2100	Tb	3	0.69	2304.2	14.8	0.43	113
7	52.5	1	17.3	2300	pT-Tb	4	0.12	1744.0	5.7	0.55	0
8	28.2	0	4	2300	Tb	5	0.12	0	0.4	0.43	0
9	46.9	97.9	0.1	1633	Tp	1	14.48	415964.0	0	0.15	4887
10	54.7	30.7	29.8	1770	Tp	2	2.81	136.4	22.8	0.18	900
11	55.7	2	40.8	1935	Tp	3	0.66	1256.5	18.4	0.18	100
12	66.9	0.1	11	2200	Tcr-Tlc	4	0.34	16750.0	2.7	0.18	30
13	20.1	3.1	6.8	2250	pT-Tb	3	1.03	161.3	1.7	0.3	0
14	57.3	0	5.4	2450	pT-Tb	4	0.09	0	0	0.3	0
15	58.6	0	1	2600	pT-Tb	4	0.26	0	0	0.3	0
16	11.2	0	4	2550	Tbo	2	0	0	0	0.3	0
17	67.7	0	37.3	2441	Tb-Tue	2	0	0	14.7	0.65	0
18	27.3	0	75	2287	Tgo	1	0.46	0	20.2	0.53	169
19	17.8	1	4.4	2132	Tam	1	1.02	4229.0	10.5	0.18	100
20	40.9	7	75.7	2287	Tgo	2	0.91	1903.6	246.5	0.45	272
21	158.2	10.6	39	2132	Tgo	3	0.92	3818.4	99.8	0.33	980
22	52.7	0	6	3250	Tam	2	0.72	0	0	0.3	0
23	73.4	0	1.5	3200	Tg	5	0.53	0	0	0.3	0
24	11.6	0	16.7	3100	Tg	4	0.67	0	0	0.3	0
25	101.9	1	45	2750	Tg	3	0.14	3361.0	14.8	0.65	0
26	91.7	0	21.6	3200	Tc	4	0.22	0	3.5	0.63	0
27	159.8	0	20	3100	Tc	4	0.14	0	4.5	0.66	0
28	23.8	24	18	3400	Tg	1	1.92	779.7	141.7	0.3	678
29	49.4	13.5	22	3200	Tg	1	2.41	1386.1	83.3	0.26	1357
30	21.8	29.6	30	3400	Tg	2	2.19	899.4	366.0	0.39	332
31	17.3	1.1	27	3000	pT-Tb	3	1.20	2786.4	47.9	0.4	63
32	111.7	36.1	22.3	3500	pT-Tb	5	0.54	795.9	57.4	0.35	160
33	2.9	100	0	3400	Tg	1	13.00	42133.0	0	0.4	318

Land use allocation (in% of total land) is divided into three categories: urban, agriculture, and forest. Details on sources for each variable are provided in Table 1. See Fig. 1 for subregion locations.

[a] SR subregions; see Fig. 4 for geographic locations.

[b] In U.S. Dollars per square meters.

We measured the area of three land uses: urban, agriculture and natural habitat (forest: see above for age categories). We combined agriculture and pastures since they are difficult to distinguish on remote sensing imagery (Dale et al., 2003). All data were obtained from Landsat ETM+ satellite maps showing the normalized difference vegetation index (NDVI) for the years 1999 and 2003 to ensure adequate coverage of all subregions (provided by ACP, Panama). Satellite data were ground-truthed by the Panamanian Service of Forest Administration (ANAM, 2003). Boundaries of the 33 physiographic subregions were obtained (or created when counties were divided by us) from digitized data from the government (General Comptroller of the Panama Republic, 2003). We merged the two data maps with ArcGIS (ESRI, 2001) to calculate the areas of the different land uses present in each subregion.

2.3. *Socio-economic characteristics of subregions*

Human population size, density and demography in each subregion were obtained from the government (General Comptroller of the Panama Republic, 2003). Data were interpolated for each subregion and verified by experts from the government. As Laurance et al. (2002a) did, we distinguished urban and rural populations, because urban population size and density are far greater than their rural counterparts, and both affect habitat loss in different ways (Laurance et al., 2001, 2002a, 2006). We used population size, not density, for urbanized areas because the latter was much less variable than the former. However, rural populations were represented by density at a spatial resolution of 1 km^2.

Road density was calculated for each subregion by dividing the total length of major paved (primary) and most important unpaved (secondary) roads by total area. Road data were obtained from digitized maps provided by the ACP (Fig. 2). From the centroid of each subregion, we calculated the distance to the nearest large city (Panama City or Colon) and the distance of the nearest highway (Pan-American or *Transistmica*). The Pan-American Highway crosses the country from east to west, on the Pacific slope, whereas the *Transistmica* highway links Panama City to Colon.

Data on human population poverty were obtained for each subregion, recently available from the government's survey in 2003 (Ministry of Economy and Finances, 2005). "Poverty" was defined as the proportion of the population earning less than $953 per year, taking into account number of family members, family consumption capacities and general household expenses (see Ministry of Economy and Finances, 2005 for details). Briefly, the data are based on an index of satisfaction and basic needs of the population, and were gathered through a combination of the 2003 quality of life survey and a nation-wide population survey in 2000. A *per capita* model was obtained via questionnaires completed by families which reported data on *per capita* income and basic household information and needs. Estimates were then obtained through average calculations made from simulations of each household in each subregion.

2.4. *Projected land value*

To compare our results with predicted economic growth, we used data from the urban development plan of the Panamanian's government (MIVI, 2005; URL http://www.mivi.gob.pa/4URBANISMO/urbanismo). To obtain a land speculation value for each subregion included in the plan, MIVI used a measure of actual and projected economic growth, current and predicted projects for employment, current and projected political influences on development (coming from state level decisions), and demographic and economic predictions in terms of population, annual population growth and average income. All subregions of our study possess a given value in Panamanian Balboas (equivalent to U.S. dollars) per square meter, representing perceived potential for economic growth. Certain subregions are classified as "untouchable", e.g., National Parks, and some regions previously used by the U.S. military bases are devoted to military training. The latter regions are considered impossible to "develop" because they are considered potentially dangerous (land with unexploded ordnance). Finally, certain subregions not under any restrictions are simply not included in the government plans because they are rural and fall under the direction of another administration. Economic plans for these regions are not always the focus of attention, are difficult to obtain, and are subject to constant changes (Suarez, 1981; Varela, 1998a,b). All unclassified and "untouchable" regions were therefore given a unit-area value of zero (Table 2) since they were not considered part of future urbanization plans of the country's government (MIVI, 2005).

2.5. *Statistical analysis*

To search for linear combinations between biophysical and socio-economic variable sets, we used a Canonical Correlation Analysis (CCA). Instead of multiple regressions or correlations, which examine the relationship between a linear combination of a set of independent variables with one dependent variable, CCA examines the relationships between a linear combination of explanatory variables with a dependent set of variables (Legendre and Legendre, 1998; SAS Institute, 1999). We defined the dependent set of variables as land-use allocation: proportion of urban or agricultural land cover (the remaining land-use being forest). This matrix was set against a first explanatory matrix, the biophysical variables; and secondly against the socio-economic variables. The CCA provides two axes of canonical variables, and verifies the association of each variable with one of the axes. We used SAS to run the analysis (PROC CANCORR). We evaluated multicollinearity among variables to avoid unstable canonical coefficients. To do so, we measured all pair-wise correlations within biophysical and socio-economic variables and when $r > 0.6$, we eliminated the variable with the weakest correlation with the axes, and excluded it from the CCA. The CANCORR procedure provides also a likelihood ratio for all canonical correlations by giving Wilks' lambda (λ), here used to test which set of variables contribute significantly to a discriminant function or which set is driving more strongly the changes observed in our data. The lambda provides a measure of discriminatory power between the two canonical axes, ranging from 0 (perfect discrimination; means differ) to 1 (no discrimination, means are the same; McLachlan, 2004; Thum and Stemberger, 2006). To complement this, we used a partial canonical analysis (Borcard et al., 1992; Legendre and Legendre, 1998) to partition variability of land-use data attributable to each of the three explanatory matrices (biophysical, socio-economic, and both groups together). We consider this method simple and efficient to determine the percent of variance explained by our analyses. Subtracting lambda values from 1 provides an index similar to the variance explained (lambda is often referred to as an "inverse" measure of a R^2 value; Rencher, 1993). As an example, a low value of lambda (e.g.: $\lambda = 0.2$) means high discriminatory power, while a high percentage obtained in the partial correlation analysis (e.g.: $R^2 = 0.80$) means a high variance explained by our data.

Finally, we investigated the relationship between variables (linear or curvilinear) using simple regressions of the same combinations of variables. CCA assumes that relationships are linear. In our exploratory analyses, we discovered that rainfall and rural population density had a curvilinear relationship, thus both were log transformed to improve the linear fit to land use change data. Since CCA assumes linearity in relationships, the transformation

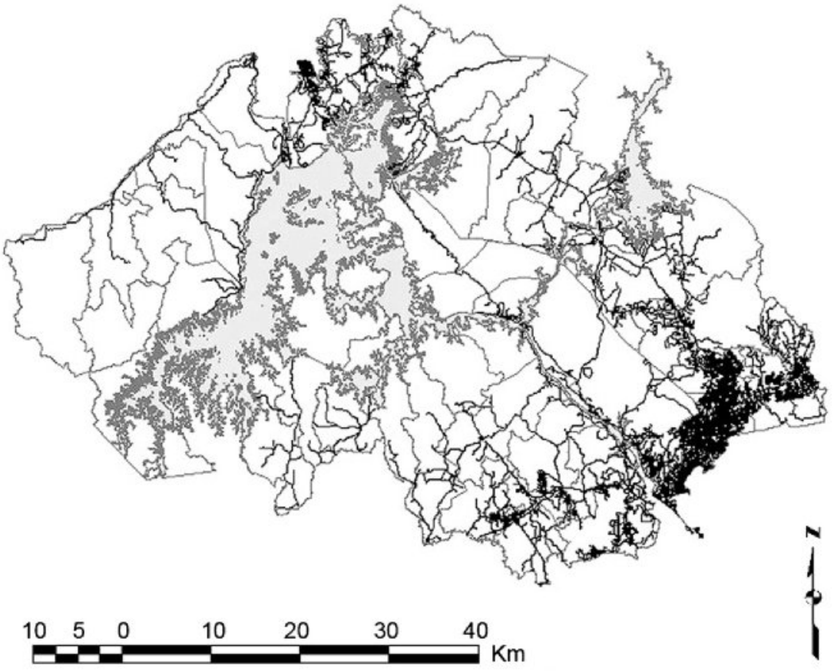

Fig. 2. Roads in each subregion used for the analysis in the Panama Canal corridor. Subregions are delineated by light grey lines, while roads are represented by black lines.

of nonlinear variables prior to inclusion in canonical correlation is a standard procedure (SAS Institute, 1999). Our data are spatially structured and spatial autocorrelation may be an issue, because of its potential effect on the effective sample size (Dale and Fortin, 2002). One of the simplest ways to deal with spatial autocorrelation is to adjust the Type I error rate to a more conservative level than the usual $\alpha = 0.05$ (Dale and Fortin, 2002). Accordingly, we chose an error rate of $\alpha = 0.01$ when declaring results significant for all of the canonical analyses.

3. Results

Our preliminary analysis revealed that some of the variables we examined were intercorrelated. Within the biophysical variables, topography was highly associated with forest age ($r = 0.84$, $p < 0.0001$). Similarly, geology was highly correlated with rainfall ($r = 0.76$, $p < 0.0001$). Within the socio-economic variables, road density was strongly associated with urban population size in 2002 ($r = 0.76$, $p < 0.0001$). Topography, rainfall and road density had slightly stronger correlations with the CCA axes, and therefore we included them in the analysis.

3.1. *Canonical correlation analysis*

Within the 33 subregions of central Panama, the CCAs produced two canonical axes of correlations (Fig. 3) each of which accounted for a significant amount of variance (Axis 1: $F = 10.07$, d.f. = 12, $p < 0.0001$; Axis 2: $F = 4.05$, d.f. = 6, $p = 0.002$). The first CCA was done comparing land-use allocation with biophysical variables, while the second CCA was done comparing land-use with socio-economic variables (Fig. 3). Socio-economic factors ($\lambda = 0.03$; high discrimination) explained the data better than biophysical factors ($\lambda = 0.48$). Thus one of the two axes explained most of the variance, while the other explained the variance partially (Table 3). We emphasized values greater than 0.6 as the most important correlations in our results, but we considered all correlations at 0.3 or higher to be interpretable and meaningful. Results from partial canonical analysis were similar (Table 4), with a higher proportion of the variance explained by the socio-economic variables than by the biophysical variables. Although weaker, variances explained by biophysical variables were significant.

Several individual biophysical variables were more strongly related to the axes than others (Fig. 3). Complex topography was associated with low urbanization and high agricultural development. Elevation variability was also associated with high levels of agricultural development, but not with urbanization. Rainfall was negatively, but weakly, associated with urbanization, but not with agriculture. Among the socio-economic factors, road density

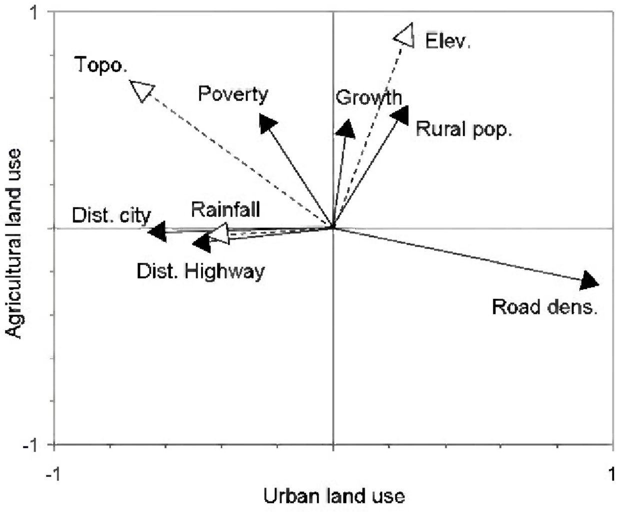

Fig. 3. Biplot from Canonical Correlations Analysis (CCA) of land use allocation (in % of total land) and the biophysical and socio-economic variables defined in Table 1. Land-use categories are: urban and agriculture (forests are the remaining land use in each subregion). Correlations between the explanatory variables and axes are represented by arrows: biophysical variables (dashed) and socio-economic variables (solid). Angles between the arrows and axes reflect their correlation (the smaller the angle, the greater the correlation).

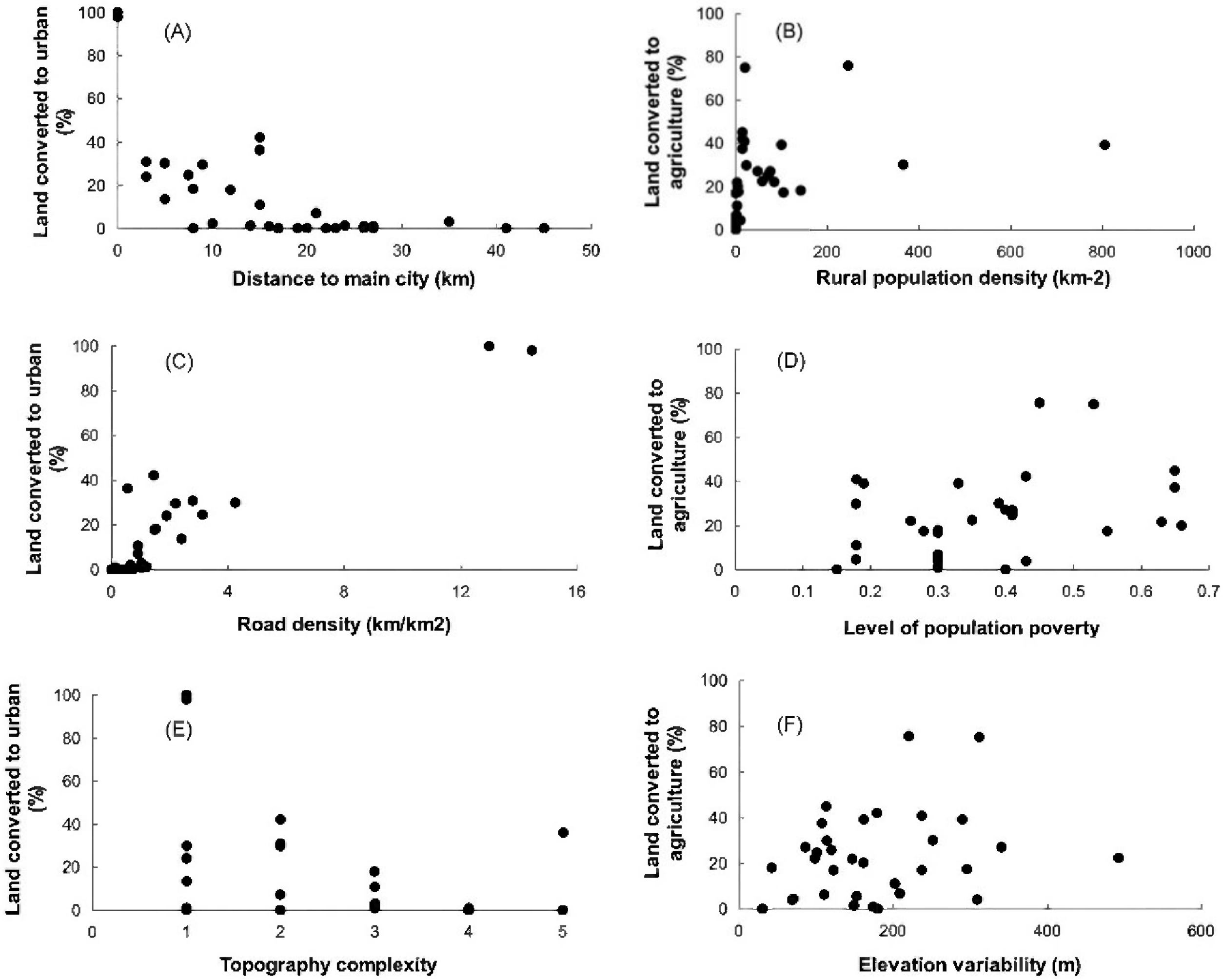

Fig. 4. Relationships between land-use changes with selected biophysical and socio-economic variables in the Panama Canal corridor. Habitat converted to urban is plotted against the distance to a main city (A), road density (C), and topography complexity (E); while habitat converted to agriculture is plotted against rural population density (B), level of poverty (D), and elevation variability (F). Each point represents a single subregion ($n = 33$).

and proximity to main cities and highways were strongly associated with high levels of urbanization, but not with agriculture. The socio-economic factors most positively associated with agriculture were rural population density, poverty level, and annual population growth. These factors had smaller or no associations with urbanization. Fig. 4 shows some individual relationships between different combinations of variables.

Table 3
Canonical correlation analysis (CCA) of land use (urban or agriculture) and biophysical or socio-economic explanatory variables

Variables	Urban land use	Agricultural land use
Biophysical variables		
Mean annual rainfall (*censu* geology)	−0.41	−0.10
Elevation variability	0.21	**0.98**
Topography complexity (*censu* forest age)	**−0.76**	**0.65**
Socio-economic variables		
Road density (*censu* urban population size)	**0.95**	−0.26
Rural population density	0.27	0.53
Annual population growth	0.06	0.47
Distance to main city	**−0.63**	−0.02
Distance to main highway	−0.49	−0.19
Level of poverty	−0.25	0.50

Absolute values greater than 0.6 in bold typeface. Each value can be interpreted as the association between the variable and the corresponding CCA axis

Projected land values were highest near or in urbanized and partially urbanized areas around major cities, especially Panama City (Table 2). Projected value was positively correlated with urban population size ($r = 0.90$, $n = 33$, $p < 0.001$), but was negatively correlated with distance to urban centre (distance from centroid to nearest main city; $r = -0.45$, $n = 33$, $p = 0.01$). The projected value was not associated with annual population growth ($r = 0.17$, $n = 33$, $p = 0.34$), and tended to be negatively correlated with the level of poverty ($r = -0.38$, $n = 33$, $p = 0.03$).

Table 4
Variance partitioning results from the partial canonical analysis

Analysis	Variance explained (%)	*F*-ratio	*p*
Urban vs. biophysical	1.8	2.8	0.05
Urban vs. socio-economic	46.6	61.7	0.0001
Agriculture vs. biophysical	1.1	2.9	0.05
Agriculture vs. socio-economic	3.0	3.9	0.006

Proportions represent the variance explained by each group of explanatory variables (biophysical and socio-economic) used to analyse the land-use allocation (urban or agriculture). 47.5% of the variance in land use was unexplained.

4. Discussion

Several factors explain a complex pattern of land-use conversion in the Panama Canal corridor. The canonical correlation analysis (CCA) showed that habitat loss is best explained by a combination of factors (see also Lambin et al., 2003; Rudel, 2005; Laurance, 2007). The two axes accounted for over 50% of the variation in conversion of habitat to urban and agricultural areas. Given the complexities of land use, that degree of explanatory power is relatively high. Other similarly designed and analyzed studies (e.g., Seabloom et al., 2002) also obtained two meaningful CCA axes, one dominated by agricultural land use and a second dominated by population density and urban land use. Although our sample size is relatively low for this type of analysis (33 subregions), this study is the first of its kind at this spatial scale in the Neotropics. A possible next step would be to validate our model with independent data to evaluate the robustness and precision of our approach.

4.1. Conversion to urban land use

Apart from the historical influence of the canal on colonization and land use conversion patterns, we noticed that drier regions (low mean annual precipitation), with flatter topography provided the most attractive regions for urbanization. In our study area, low mean annual precipitation means drier seasonal forests compared to thicker "jungles" in more humid subregions (Condit, 1998; Rompré et al., 2007). Likewise, in Amazonia, deforestation is greater in seasonal areas and regions with low precipitation (Fernside and Ferraz, 1995; Steininger et al., 2001; Laurance et al., 2002a). Our results, excluding Colon, which is the only large city on the Caribbean coast of the entire country (Suarez, 1981; MIVI, 2005), indicate urbanization clearly occurs in the drier subregions of the study area. Complex topography is often associated with more mature-intact forests than areas with flatter terrain, because ease of access for harvesting and development is limited (Kerr and Packer, 1997; Steininger et al., 2001; Veldkamp and Lambin, 2001; Laurance et al., 2002a; Rompré et al., 2007). In this study, areas with flatter terrain tend to occur on the drier slope where forests are usually younger and more disturbed by human activities (Condit, 1998; Pyke et al., 2001). We also found that young forests are often positively associated with urbanization as well. Despite the low but significant explanatory power of biophysical factors such as rainfall and topography (Table 4), their importance was apparent and we encourage additional research that includes more than just socio-economic factors in analyses of land-use change in the Neotropics.

On the other hand, results from CCAs confirm the importance of socio-economic factors. Subregions with high urban population size, wealthy populations, high density of roads (which allows easier access to new lands), proximity to major cities and highways, were all associated with conversion to urban areas. These patterns are familiar and have been documented quantitatively in other landscapes as well (Carvalho et al., 2001; Steininger et al., 2001; Laurance et al., 2002a). High population size (and associated high road density) can have a strong direct influence on habitat conversion for urban and suburban housing (McKinney, 2002; Lambin, 2005). They can also have indirect influence through demands for forest resources (Browder and Godfrey, 1997; Laurance et al., 2002a; Laurance, 2007), human migration (immigrants in city increase population size and needs for space) (Varela, 1998b; Lambin and Geist, 2002) and other social factors (see Browder and Godfrey, 1997). Proximity to roads is known to increase rates of urbanization (McKinney, 2002; Soares-Filho et al., 2004). Highways may provide easier access to resources and markets (e.g., trees and cattle), which accelerates forest loss (see Rudel, 2005). Suarez (1981) and more recently Dale et al. (2003) stressed the importance of the construction of the *Transistmica* highway between the two cities for industrialization and urbanization north of Panama City (see also Varela, 1998b). Another interesting result from our analysis is the negative association between poverty and urbanization. It appears that wealthier populations have easier access to new areas, which might be caused by improved road transportation, more efficient bus systems, or simply more vehicles (Pfaff, 1996; McKinney, 2002; MIVI, 2005; Rudel, 2005) that in turn encourage expansion of suburbs.

The pattern of forest conversion in the Panama Canal area may not apply in other Neotropical landscapes because about 50% of current forests are protected as parks. Nevertheless, half the region is susceptible to conversion for other uses. With its two major cities, urbanization in Panama might be the most important factor influencing habitat change (MIVI, 2005), which is similar to many rapidly changing tropical landscapes (Laurance, 2007). Because urbanized sites cover such a low proportion of the world's land surface (2%, Grübler, 1994), urbanization may not have properly received the attention it deserves in land-use change studies in the tropics (Lambin et al., 2001). In central Panama, as in other less-developed countries, urbanization tends to "outbid" all other land uses in close proximity to a city (Lambin et al., 2001). McKinney (2002) points out that urbanization is generally more lasting and permanent than other types of habitat conversion (see also Rodiek, 2008). With current economic opportunities associated for example with the new Panama waterway (Rubin, 2007), central Panama is facing a population and development explosion (MIVI, 2005; Rubin, 2007), much of which may result in higher rates of urban habitat conversion. We suggest that habitat conversion to urban areas should not be taken lightly in central Panama or anywhere else in the tropics, as this may be the most important factor driving habitat loss in the future (Laurance, 2007).

4.2. Conversion of land to agriculture

The relationships between conversion factors and agriculture in the Canal area are less clear. The strongest biophysical factors present in our analysis were elevation variability and topography complexity. Factors associated with higher altitude and uneven topography did not impair habitat conversion to pastures and agriculture. Our results differ from other studies, especially those in Andean countries, where uneven topography can be a major obstacle to many kinds of agriculture (Pichon, 1997; Maki et al., 2001; Steininger et al., 2001). Altitude probably does not play a strong negative role in central Panama because elevation variability may not be high enough (<500 m) compared with other, more mountainous landscapes. In habitat conversion to agriculture, mature forests (strongly associated with complex topography) do not appear to be an obstacle, as is the case for urbanization. Occurrence of agriculture was not influenced by rainfall; agriculture occurred in all non-urbanized subregions.

In terms of socio-economic variables, the most important factors were level of poverty, annual population growth and rural population density. Contrary to urbanized areas, poverty level is positively correlated to agricultural land-use, meaning poorer populations live in rural subregions. Data from the government (Ministry of Economy and Finances, 2005) indicate that up to 61% of the rural population lives below the poverty threshold, whereas the proportion is 22% for urban populations. Poverty has been often mentioned as a major factor contributing to habitat loss in other parts of the tropics (Rudel, 1993; Pichon, 1996, 1997; Rudel and Roper, 1997). Rudel and Roper (1997) add that poor rural populations often do not have other economic opportunities than to clear land for agricultural purposes (see also Durand and Lazos, 2004). Furthermore, Pfaff (1996) and Laurance et al. (2002a) indicate that the relation between rural population density and habitat loss to agriculture is not linear. We found a similar relationship in the Panama Canal region (Fig. 4b). Pfaff (1996) (see also Pichon, 1997; Laurance et al., 2002a) hypothesized that early settlers have a greater impact on natural habitat, while later settlers can only have a smaller impact, as little habitat is left to be converted. At that point, emigration from rural areas toward urbanized regions may increase (Rudel and Roper, 1997); this phenomenon has been especially strong in Panama in recent years, especially toward Panama City (Varela, 1998b). Thus, poverty may conceal more important and complex social, political and infrastructural changes in rural populations (Lambin et al., 2001). The apparent effect of annual population growth on conversion to agriculture may indicate a strong link between growth, poverty, population density and deforestation (Mather and Needle, 2000; Lambin et al., 2001). Our results also show that neither distance to a main highway or major city, nor road density or urban population size influenced conversion of habitats to agriculture. These contrast with results from larger land areas in other studies (e.g., Amazon basin) where road construction is known to facilitate deforestation by small-scale agriculture (Maki et al., 2001; Steininger et al., 2001; Durand and Lazos, 2004).

4.3. Projected value of the land for economic growth and recommendations

Future urban growth and land value projected by the Panamanian's government (MIVI, 2005) show strong similarities with our results from the CCA, especially Axis 1, which described urbanization. Future urban growth will happen where there are already large populations, in proximity to urbanized areas, and also where the populations are wealthy. The strong relationship between our results and the projected land value for economic growth shows the accuracy of our approach (incorporating all the variables, either biophysical or socio-economic together). Forested habitat remaining in the different subregions characterized by low altitude, flat topography and in proximity of the cities and urbanized areas are at greatest risk of conversion or fragmentation. Since these lands are getting rare due to recent rates of development (Rubin, 2007), they tend to become more expensive and consequently are less likely to be preserved. A strong awareness exists in the population concerning the biodiversity of the forests in the area and its value for ecotourism (Condit et al., 2001; Ibañez et al., 2002). Suburban populations, with their increasing density, wealth and political influence, can play a critical role in social support of conservation and awareness (McKinney, 2002; Lambin, 2005; Zhu and Zhang, 2008). Unfortunately, the comparison between our results and the projected land value holds only for urbanization, and therefore does not provide much detail on what can happen to rural regions. Our study mentions that lands already under protection or under other administration are not included in any “development plans” (MIVI, 2005). This lack of available data raises some concern for rural areas; there is no plans for monitoring or following what may occur in these isolated subregions. Lambin et al. (2000) argue that it is extremely difficult to provide specific predictions of the driving forces in agricultural land-use models. One reason for this might involve too restrictive decision-making by land owners and managers in face of limited ranges of options (Lambin et al., 2000; Rudel, 2005). A good example of this might be the growing human settlements found within National Parks in the canal watershed and elsewhere in the tropics (Condit et al., 2001; Ibañez et al., 2002; Dale et al., 2003; see also Funch and Harley, 2007).

We suggest that future research be directed towards the complex issues of rural areas and their populations in Panama or any other areas in the tropics where anthropogenic growth directly interacts with the highest levels of biodiversity. Urban planning authorities and decision-makers should be made aware of conservation issues and of the importance of forests, even in fragmented or suburbanized landscapes, for biodiversity. Both short- and long-term repercussions of habitat loss on local climate changes and other changes should be considered; such changes may affect socio-economics as well, especially in situations like the Panama Canal region where alteration of watershed dynamics can influence continuing operation of the Canal itself (Heckadon-Moreno et al., 1999; Dale et al., 2003; but see also Lambin et al., 2003).

Acknowledgments

This study was supported by the Natural Sciences and Engineering Research Council of Canada, via a Ph.D. fellowship to G. Rompré. Research in Panama was possible thanks to the generous help of: Smithsonian Tropical Research Institute (STRI), Autoridad Nacional del Ambiante (ANAM), Autoridad del Canal de Panama (ACP), Autoridad de la Region Interoceanica (ARI), Centro de Estudio de Accion Social Panameno (CEASPA), Ministerio de Vivienda (MIVI), and Contraloria General de la Republica de Panama. Elena de Lombardo, Maria Leone, Oris Ovecedo, Benjamen Ordoñez (STRI), Charlotte Elton (CEASPA), and Sayda de Grimaldo (ARI) made things easier in the field by giving access and helping coordinate and organize the field work. A special thanks to people and staff at STRI, ACP, ARI, MIVI and Contraloria General for access to important data bases and sharing thoughts during the analysis and writing process. We are grateful to William F. Laurance, Catherine Potvin, Louis Bélanger and two anonymous reviewers for their valuable revisions and comments on the various versions of the manuscript.

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