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RESEARCH ARTICLE

Forest recovery in a tropical landscape: what is the relative importance of biophysical, socioeconomic, and landscape variables?

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Abstract Socioeconomic changes in many areas in the tropics have led to increasing urbanization, abandonment of agriculture, and forest re-growth. Although these patterns are well documented, few studies have examined the drivers leading to landscape-level forest recovery and the resulting spatial structure of secondary forests. Land cover transitions from agricultural lands to secondary forest in the island of Puerto Rico have been ongoing since the 1940s. This study is a glimpse into this landscape level trend from 1991 to 2000. First, we relied on Landsat images to characterize changes in the landscape structure for forest, urban, and agricultural land classes. We found that although forest cover has increased in this period, forest has become increasingly fragmented while the area of urban cover has spread faster and become more clustered. Second, we used logistic regression to assess the relationship between the transition to forest and 21 biophysical, socioeconomic, and landscape variables. We found that the percentage of forest cover within a 100 m radius of a point, distance to primary roads and nature reserves, slope, and aspect are the most important predictors of forest recovery. The resulting model predicts the spatial pattern of forest recovery with accuracy (AUC-ROC = 0.798). Together, our results suggest that forest recovery in Puerto Rico has slowed down and that increasing pressure from urbanization may be critical in determining future landscape level forest recovery. These results are relevant to other areas in the tropics that are undergoing rapid economic development.

Keywords Secondary forest succession · Forest transition · Agricultural abandonment · Urbanization

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Introduction

Estimates of the Earth's land surface that has either been transformed or degraded by human activity range between 39 and 50%, with agriculture accounting for the vast majority of these changes (Vitousek et al. 1997; Kareiva et al. 2008). Although much of the focus of research on land use change in the tropics has been on deforestation, socioeconomic changes and abandonment of agricultural land and pastures have led to an increase in secondary forest cover in many tropical regions (Franco et al. 1997; Rudel et al. 2000; Chang and Tsai 2002; Klooster 2003; Read et al. 2003; Hecht et al. 2006). The extent of secondary forests in the tropics was recently estimated at 850 million hectares (ITTO 2002).These secondary forests provide many of the services attributed to primary forests including regulation of water quality and flow, erosion control, carbon sequestration, restoration of nutrients and soil properties in former agricultural lands, biodiversity conservation, and enhanced connectivity of fragmented landscapes (ITTO 2002; Chazdon 2003).

The unprecedented rate of forest clearing in the tropics and the increasing importance of secondary forests calls for an evaluation of the effects that human activities have on forest recovery. The effects of former land uses, particularly agriculture, on ecosystems may be long-lived (Dupouey et al. 2002; Thompson et al. 2002; Uriarte et al. 2004). However, variation in both agricultural practices and the ecological matrix make it difficult to draw generalizations about forest recovery processes although some general patterns are apparent (Guariguata and Ostertag 2001; Chazdon 2003). Spatial patterns of clearing at the landscape scale are critical since close proximity of seed sources in remnant forest patches accelerates forest regeneration (Thomlinson et al. 1996; Toriola et al. 1998). Recovery of forests is also constrained by soil fertility, with more intense land uses leading to longer recovery times and often requiring direct restoration interventions (Chinea 2002; Lugo et al. 2004).

At the landscape scale, forest recovery may depend more critically on socioeconomic than on physical and biological factors. By affecting land prices, distance to urban areas or roads may be an important predictor of forest recovery at the landscape scale. For instance, Thomlinson et al. (1996) observed that areas far from urban centers and close to forest in Puerto Rico, typically those at higher elevations and with steeper slopes, were more likely to increase in forest cover. Although rural-urban migration can lead to a first wave of forest recovery away from urban centers, subsequent urban sprawl can cause a decrease in forest cover (Thomlinson and Rivera 2000; McDonald and Rudel 2005; Irwin and Bockstael 2007). Therefore, understanding the effects that socioeconomic changes in tropical regions will have on the trajectory of forest recovery is critical to predicting the future of secondary tropical forests.

Puerto Rico is a densely populated island with little history of land use planning. Socioeconomic changes in the island during the past 50 years have resulted in dramatic and dynamic landscape transformations (Birdsey and Weaver 1982; Rivera and Aide 1998; Pascarella et al. 2000; López et al. 2001; Chinea 2002; Helmer et al. 2002, 2008; Grau et al. 2003; Helmer 2004; Lugo and Helmer 2004; Martinuzzi et al. 2007). Widespread abandonment of agriculture has led to expansion of secondary forest from less than 10% of the island area in the 1930s to about 42% in 1991. A recent study of the distribution of people throughout the island, coupling remote sensing images with population census data, showed that over 40% of the island is in some degree of urban sprawl (Martinuzzi et al. 2007), defined as "peripheral growth that expands in an unlimited and non-contiguous way outward from the solid built-up core of a metropolitan area" (Transportation Research Board 2002). Urban sprawl may negatively affect rates of forest recovery from agriculture by directly competing for agricultural land, restricting dispersal processes, affecting watershed hydrology, or increasing pollution.

The economic shifts in the past few decades have created a range of vegetation types of various ages (primarily pastures and coffee plantations) with varying proximity to remnant forests and urban centers in which we can study the process of vegetation transition from agriculture. Previous studies have focused on identifying island-wide drivers of deforestation, through urbanization (López et al. 2001; Helmer 2004) and land development (Helmer et al. 2008). Other studies have examined forest recovery and associated drivers at relatively small scales (e.g., single municipality, Thomlinson et al. 1996; Thomlinson and Rivera 2000). Given the potential conflict between forest recovery and urbanization in the island, it is important to identify the factors that determine forest recovery at the landscape scale.

Here we examine the drivers of forest recovery after agricultural abandonment for the whole island of Puerto Rico. First, we characterize changes in the landscape structure of forest, urban, and agricultural patches and ask whether these patterns differ with proximity to remnant forests and urban areas. Second, we use statistical modeling to investigate the importance of a number of socioeconomic, biophysical, and landscape variables on forest recovery over a 10 year period with the goal of identifying the factors that best explain the conversion of agricultural lands to forest at a landscape scale.

Methods

Study area

Puerto Rico is a mountainous Caribbean island (latitude range: 17°45′N–18°30′N; longitude range: 66°15′W–67°15′W) that stretches 160 km across and 55 km north to south. The trade winds approach the island from the northeast and as a result of encountering the mountains create a distinct precipitation gradient with areas in the southwest receiving less than half the annual rainfall (~ 750 mm) than areas in the northeast (~ 1,500–2,000 mm). Mean annual temperatures range between 19.4 and 29.7°C with cooler temperatures occurring at higher elevations (Daly et al. 2003). This climate gradient, a large elevation range, and a complex geology have generated a large amount of environmental variation within this small island.

Puerto Rico was largely an agricultural economy prior to World War II, when forest was reduced to less than 10% of the total land cover by the late 1930s to make way for sugar cane, coffee plantations, and cattle pastures (Grau et al. 2003). In the 1940s, a government—sponsored industrialization program fostered an economic shift from agriculture to manufacturing, which led to increases in urban area, concomitant abandonment of agriculture, and subsequent increases in forest cover (Rudel et al. 2000; Grau et al. 2003). Forest recovery has been continuous since the 1940s although recent expansion in urban areas calls into question the persistence of this trend (Thomlinson and Rivera 2000; Martinuzzi et al. 2007).

Land cover data

Two Landsat TM and ETM + mosaics of images taken circa 1991–1992 and 2000 with 30 × 30 m resolution were used to examine patterns and drivers of recent land cover changes (Kennaway and Helmer 2007). The images were originally classified into eleven land cover classes, which we reduced to nine for our analyses (see below). Details of classification accuracy are provided in Helmer and Ruefenacht (2005). In brief, their method correctly classifying 85.4% of points and yielded an error matrix with a Kappa coefficient of agreement of 0.66 ± 0.12. For this paper, analyses of land cover changes were conducted in ArcGIS v. 9.2.

Quantifying landscape structure

Since we were primarily interested in understanding how the transition from agriculture to forest may be affected by urban expansion, we calculated a number of patch statistics for each of the agricultural classes, forest, and urban cover classes, including mean patch size, number of patches, shape indices, and landscape pattern metrics. We generated patch statistics for both 1991 and 2000 using the FRAGSTATS module in ArcGIS (McGarigal et al. 2002). To better understand the role that elevation and proximity to urban centers had on landscape structure, we calculated these metrics for the island as a whole and for high (>400 m) and low (≤400 m) elevations. Elevations below 400 m correspond to the "plains" landform defined by Gould et al. (2005), while hills and mountains correspond to elevation above 400 m. Since high elevation areas are far from large urban centers, this analysis also provided indirect information on the effects of increasing urbanization on landscape structure (Martinuzzi et al. 2007).

Evaluating the importance of landscape, biophysical, and socioeconomic variables to forest recovery

Sample selection

We relied on the land cover classification maps from 1991 to 2000 to build a land use transition matrix from which we sampled a random set of pixels for analysis. We limited the analysis to land cover transitions that could represent forest recovery. In 1991 pasture accounted for the largest percentage (33.03%) of land area in the island, while other agricultural classes represented only 4.51% of the total land area. To avoid sampling biases due the small number of pixels in some of the agricultural classes, we aggregated transitions from agriculture to forest into two classes: (1) herbaceous agriculture included cotton, sugar cane, pineapple, tobacco, corn and crops; (2) woody or tree-based agriculture included active sun coffee, coconut, plantains and bananas, citrus, mangos, and other fruits (see Kennaway and Helmer 2007 for details). Similarly, transitions from these same categories to non-forest classes were aggregated and considered collectively as transitions from agriculture to non-forest.

To obtain a representative sample for analysis, we selected a random set of 15,000 pixels using choice-based, or endogenous, stratified sampling (King and Zeng 2001). To avoid spatial autocorrelation in the dependent variable, we eliminated points within 300 m of each other. This distance was determined based on the grain of the process under study (Helmer 2000), namely the radius of most agricultural patches in 1991 (Table 1), which is based on the mean patch size assuming the patches are circular. After filtering using this criterion we had a sample of 11,092 points for analysis.

Potential drivers

A total of 21 potential drivers of land cover transitions were initially considered (Table 2). Drivers included landscape, socioeconomic, and biophysical variables and were selected because they have been shown to influence either the rate of urbanization or forest recovery (Helmer et al. 2008; Chazdon 2003; Helmer 2000, 2004; Rudel et al. 2000; Thomlinson et al. 1996; Chinea and Helmer 2003).

(1) Landscape variables

1.1 *Percent of given land cover type within a 100 m buffer*. A larger percentage of pasture or forest in a region may indicate increased potential for forest recovery while a larger percentage of urban cover may be indicative of an increased potential for deforestation in the area (Helmer 2004; Thomlinson et al. 1996; Pascarella et al. 2000). To account for these regional land cover effects, we calculated the percent of urban, forest, pasture, and coffee cover within a 100 m radius in the 1991 land cover map

(2) Socioeconomic variables

2.1 *Distance to nearest roads*. Proximity to roads may deter forest recovery because areas with easy access to good roads are more likely to undergo development (Lugo 2002; Pfaff et al. 2007). Four road types were considered in the analysis: highways, primary, secondary, and tertiary roads. Each sampled point was linked to each road type separately, generating a

Table 1 Patch statistics for 1991 and 2000 generated for classes of interest for the landscape as a whole and including only patches greater than or equal to 3,600 m^2 (4 30 × 30 m pixels)

	Forest			Pasture			Coffee			Herbaceous agriculture			Urban		
	1991	2000	%Δ	1991	2000	% Δ	1991	2000	% Δ	1991	2000	% Δ	1991	2000	% Δ
MSI	1.64	1.66	0.94	1.65	1.68	1.52	1.57	1.57	0	1.70	1.60	−5.88	1.59	1.62	1.73
MPS	17.94	17.17	−4.30	7.87	7.11	−9.67	1.67	1.49	−10.41	80.34	71.25	−11.31	4.24	4.43	4.59
Skew	132.04	75.95	−42.48	86.46	94.19	8.97	21.36	32.61	52.67	7.50	8.50	13.31	152.85	155.56	1.77
NumP	20,762	21,866	5.32	36,581	40,217	9.94	5,951	8,447	41.94	365	136	−62.74	25,895	26,617	2.79
CA	372,551	375,482	0.79	287,749	285,745	−0.70	9,910	12,603	27.17	29,325	9,691	−66.96	109,787	118,026	7.50
PT	42.76	43.10	0.79	33.03	32.80	−0.70	1.14	1.45	27.17	3.37	1.11	−66.96	12.60	13.55	7.50

MSI stands for mean shape index, or the perimeter to area ratio (McGarigal and Marks 1995; MPS stands for mean patch size in hectares; Skew is the skewness of the distribution of patch sizes; NumP is the number of patches; CA is the class area in hectares as defined by Irwin and Bockstael (2007); PT is the percent of the total landscape occupied by the given class (= (CA*100)/Total landscape area)

Table 2 Summary of the 21 drivers used in logistic model

Explanatory variables		Data sources
Landscape	Percent forest cover within 100 m radius of a point	IITF/USDA Forest Service
	Percent forest cover within 300 m radius of a point	–
	Percent coffee cover within 300 m radius of a point	–
	Percent pasture cover within 300 m radius of a point	–
	Percent urban cover within 300 m radius of a point	–
Socioeconomic	Euclidean distance to nearest highway	IITF/USDA Forest Service
	Euclidean distance to nearest primary road	–
	Euclidean distance to nearest secondary road	–
	Euclidean distance to nearest tertiary road	–
	Euclidean distance to nearest large urban patches (≥500 ha)	IITF/USDA Forest Service
	Euclidean distance to nearest urban patches (≥1 ha)	–
	Euclidean distance to nearest commonwealth forest reserves	IITF/USDA Forest Service
	Euclidean distance to nearest federal forest reserves	–
	Presence in a given municipality	IITF/USDA Forest Service
Biophysical	Elevation	USGS
	Slope	N/A
	Aspect	N/A
	Annual precipitation	IITF/USDA Forest Service
	Annual maximum temperature	–
	Annual minimum temperature	–
	Soil agricultural capacity	IITF/USDA Forest Service

N/A is for 'not applicable' as this data was calculated directly from the elevation layer. –Indicates that the data source is the same as that listed above and that it belongs in a category of variables that was generated using a similar protocol

distance attribute for each point to the nearest road of a given type.

2.2 *Distance to nearest urban patches*. Areas closer to large urban centers are more likely to undergo development (Helmer 2004). For our analysis, we used the 1991 land cover layer to determine proximity to large urban centers greater than 500 ha in area (i.e., San Juan, Mayaguez, Ponce, Arecibo, Caguas) as well as to smaller urban patches (greater than 1 ha in area).

2.3 *Distance to Commonwealth and Federal Reserves*. Proximity to protected areas may increase the likelihood of forest recovery as these areas may act as seed sources for adjacent lands (Thomlinson et al. 1996; Helmer 2004). The magnitude of seed inputs may depend on the time the reserve was established or on the uses and regulations followed by the management authority. In Puerto Rico, commonwealth reserves were established as early as 1800s and up to 2005 and are managed by the Department of Natural and Environmental Resources (DNER). Federal reserves were established as early as 1903 and are managed by the United States Fish and Wildlife Service (USFWS), Forest Service (USFS), and National Park Service (USPS).

2.4 *Municipality*. Municipality level effects such as zoning laws or changes in population size may affect the probability of transition. Municipal zoning regulations also determine where and how urban development will occur. For these reasons, we examined the effects of municipality on forest recovery and used census data to calculate the percent change in population from 1990 to 2000.

(3) Biophysical variables

3.1. *Topography*. Three topographic variables were included in the analysis: elevation, slope, and aspect. Forest recovery tends to occur at higher elevations, where land is abandoned first (Thomlinson et al. 1996). Urban development is also less likely to occur in rugged terrain, favoring forest recovery in steep areas (Helmer 2004; López et al. 2001). Forest may also re-grow more readily on slopes facing moisture-bearing wind; in Puerto Rico these areas tend to face north-northeast (Daly et al. 2003; Weaver 1991). We used 30 × 30 m SRTM elevation data from USGS to calculate slope and aspect.

3.2. *Climate*. Precipitation and temperature were used as drivers under the assumption that cooler temperatures and relatively high precipitation in the higher elevations may accelerate forest recovery relative to warmer areas (Daly et al. 2003). However, high levels of precipitation and low temperature can also lead to soil saturation and low physiological activity leading to lower vegetation growth rates (Silver et al. 1999). Climate data included total annual precipitation (mm), and average annual minimum and maximum temperature averaged over the years 1963–1995.

3.3. *Soil*. Soil may affect forest recovery in two ways. First, agricultural abandonment is less likely to occur in fertile soils. However, for plots that undergo transition, forest recovery will proceed faster in fertile relative to poor soils. To evaluate the effect of soil fertility on forest recovery, we used soil agricultural capacity, a measure of agricultural suitability. Agricultural capacity data group soils into 12 classes according to several criteria including erosion and moisture retention potential, soil depth, and presence of toxic salts, with one being the most fertile and ten being least fertile (USDA 2007; Table 2).

Statistical analysis

We used logistic regression to determine the effects of these 21 drivers on the likelihood of transition to forest. We used a generalized mixed effects model of the form:

$$\log\mathrm{it}(y) = \log\left(\frac{y}{1-y}\right) = \beta_o + \beta X + \Phi + \varepsilon \qquad (1)$$

where y is the probability of conversion of agricultural land to forest from 1991 to 2000, β_o is the intercept, X is a vector of driving variables (fixed effects), β is a vector of parameter estimates for these covariates, Φ is a vector of random effects, and ε are pixel—level errors. Soil agricultural capacity was included as a categorical effect while municipality was included as a random effect.

To minimize parameter correlation and facilitate interpretation, all explanatory fixed variables were standardized by centering them on their mean and dividing by two standard deviations (z-score). To avoid colinearity among explanatory variables, we selected variables with correlations lower than $r = 0.5$. We then used forward variable selection to select the best model and we examined the importance of interactions of interest in the final model. In addition, we tested a number of simple to increasingly complex models that included landscape, socioeconomic, and biophysical variables. We used Akaike's Information Criterion (AIC) to select the best model.

Environmental variables tend to be spatially autocorrelated leading to lack of independence in model residuals (Rossi et al. 1992). Although we sampled points at distances greater than 300 m, we tested model residuals for spatial autocorrelation using a variogram fitting procedure and calculating Moran's I. If we detected spatial correlation in the residuals after the model selection procedure, we fitted a second logistic regression model that included a spatial correlation structure (Pinheiro and Bates 2001). We assumed that, if present, spatial autocorrelation decayed exponentially with Euclidean distance.

We used the goodness of fit approach for the final logistic regression models suggested by Hosmer and Lemeshow (1989): (1) for each point in the dataset we calculated the predicted probability of transition to forest given the estimated parameters, and (2) using the entire dataset, we then grouped the predicted probabilities of transition to forest into classes (0–10%, 10–20%, etc) and then computed the percentage of pixels in that category that converted from agriculture to forest. Thus, for pixels predicted to have a 0–10% probability of transition to forest, a model that fits well will have approximately 5% of the pixels transition from agriculture to forest. Therefore, this method gives us a visual way to compare "observed" with "expected" values given the model. These counts can then be compared using a chi-square test. It also gives us a way to determine if the model fits equally well across different prediction values.

We also evaluated the spatial performance of the model using the area under the curve (AUC) of Relative Operating Characteristic (ROC). The ROC curve is built by plotting the sensitivity (or true-positive rate) versus 1—specificity (or false-positive rate) for every possible threshold value that can be chosen to convert the predicted probability of forest transition (a continuous value predicted by the model in the interval 0–1) to actual forest recovery (a binary value). The AUC summarizes ROC plots with a measure of overall accuracy independent of a threshold. The AUC can be interpreted as the probability of the model to render a higher predicted value of forest recovery for pixels that underwent forest transition than for those that did not. An AUC value of 0.5 indicates random performance and a value of 1 perfect discrimination. All analyses were conducted using R statistical software (R Development Core Team 2008).

Results

Landscape structure

Forested areas increased by 0.79% from 1991 to 2000, while areas of herbaceous agriculture decreased by 66.96% and pasture area decreased by only 0.7%. Substantially more land converted to urban areas (7.50% increase) than to forests, in part because of large differences in land area in each class (Table 1). Mean patch size (MPS) increased only for the urban class together with a reduction in the number of small patches. All other classes of interest including forest cover showed a decline in MPS, a result of an increase in the number of small patches. The Mean Shape Index (MSI), a measure of shape irregularity, decreased only for the herbaceous agriculture class which also had the largest decrease in overall area.

When we compared patch statistics according to elevation class (Table 3a, b), we observed that total forest area was largest among all classes of interest above 400 m for both years. Forest fragments were also larger at higher elevations. However, both forest area and MPS have decreased above 400 m but increased at lower elevations over this 10 year period although these changes are small. Below 400 m pasture occupied the largest area while herbaceous agriculture had the largest MPS. Pasture area followed the opposite pattern to forest cover in that both total area and MPS increased from 1991 to 2000 above 400 m but decreased at low elevations over the same time period. Finally, the majority of urban cover occurred below 400 m for both 1991 and 2000. Nevertheless, urban cover increased throughout the landscape in the 10 year period examined.

Quantifying the importance of socioeconomic, biophysical, and landscape drivers for forest recovery

We ran seven increasingly complex models of forest recovery that included landscape, socioeconomic, and biophysical variables and selected the best model using AIC. The best model included as fixed covariates the degree of forest cover within a 100 m radius buffer of a point (i.e., pixel), slope of the terrain, distance to primary roads and commonwealth reserves, as well as soil agricultural capacity and municipality as random effects (Table 4). It also included interactions between slope and three other variables: forest cover within 100 m radius, distance to primary roads, and distance to commonwealth reserves. All models had a significant spatial structure in their residuals so we included spatial autocorrelation in the final models as described above. The final statistical model provided an excellent fit to the data used to parameterize the model (Table 4; Fig. 1). An AUC-ROC value of 0.7982 (0.7868–0.8097, 95% CI) also indicated spatial agreement between model predictions and actual forest recovery.

Landscape, biophysical, and socioeconomic variables influenced the probability of forest recovery

Table 3 Patch statistics calculated (a) above and (b) below 400 m elevation for each year (1991, 2000)

	Forest			Pasture			Coffee			Herbaceous Agriculture			Urban		
	1991	2000	% Δ	1991	2000	% Δ	1991	2000	% Δ	1991	2000	% Δ	1991	2000	% Δ
(a)	Above 400 m														
MSI	1.72	1.71	−0.33	1.63	1.66	2.02	1.57	1.59	1.34	1.31	n/a	−100	1.53	1.55	1.04
MPS	66.90	46.32	−30.75	3.18	3.94	23.81	1.66	1.60	−3.79	0.67	n/a	−100	1.59	1.75	10.38
Skew	56.46	39.10	−30.75	63.96	43.36	−32.04	21.88	31.67	44.75	n/a	n/a	n/a	44.89	21.88	9.77
NumP	3,652	4,507	23.41	8,768	9,408	7.30	5,704	6,954	21.91	1	n/a	−100	5,271	6,075	15.25
CA	244,310	208,786	−14.54	27,909	37,078	32.85	9,480	11,120	17.30	1	n/a	−100	8,377	10,657	27.22
PT	28.04	23.96	−14.54	3.20	4.26	32.85	1.09	1.28	17.30	0	n/a	−100	0.96	1.22	27.22
(b)	Below 400 m														
MSI	1.62	1.64	1.07	1.66	1.68	1.35	1.48	1.45	−1.83	1.70	1.60	−5.94	1.61	1.64	2.06
MPS	7.50	9.60	28.12	9.34	8.07	−13.61	1.74	0.99	−42.99	80.56	71.25	−11.55	4.92	5.23	6.30
Skew	75.89	108.91	43.66	76.05	83.8	10.18	9.28	21.18	128.22	7.49	8.50	13.45	136.55	136.88	0.24
NumP	17,110	17,359	1.46	27,813	30,809	10.77	247	1,493	504.45	364	136	−62.64	20,624	20,542	−0.40
CA	128,242	166,696	29.99	259,840	248,668	−4.30	430	1,483	244.58	29,325	9,691	−66.95	101,410	107,369	5.88
PT	14.72	19.13	29.99	29.82	28.54	−4.30	0.05	0.17	244.58	3.37	1.11	−66.95	11.64	12.32	5.88

MSI stands for mean shape index, or the perimeter to area ratio (McGarigal and Marks 1995; MPS stands for mean patch size in hectares; NumP is the number of patches; Skew is the skewness of the distribution of patch sizes; CA is the class area in hectares as defined by Irwin and Bockstael (2007); PT is the percent of the total landscape occupied by the given

Table 4 Final prediction model

Variable	Parameter estimate	Standard error	*t* value	Pr(>|t|)	Sig. level
Distance to nearest primary road	−0.001	0.085	−0.01	0.989	
Percent forest cover within 100 m buffer	1.496	0.058	25.55	<0.0001	***
Distance to nearest commonwealth forest reserve	−0.122	0.076	−1.59	0.110	
Slope	0.692	0.062	11.12	<0.0001	***
Aspect	0.180	0.051	3.52	0.0004	***
Distance to nearest primary road × slope	−0.316	0.095	−3.33	0.0009	***
Percent forest cover within 100 m buffer × slope	−0.763	0.087	−8.69	<0.0001	***
Distance to nearest commonwealth forest reserve × slope	0.178	0.099	1.78	0.073	†
Intercept	−2.09	0.25	−8.21	<0.0001	***

To minimize parameter correlation and facilitate interpretation, all explanatory variables were standardized by centering them on their mean and dividing by two standard deviations (*z*-score)

Significance levels: † $0.1 < P < 0.05$; *** $0.001 < P$

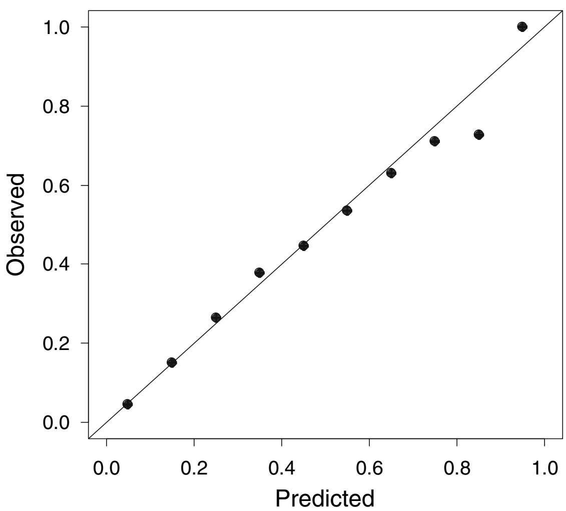

Fig. 1 Results of goodness of fit tests for the final model for observed versus predicted plot of original data ($\chi^2 = 1.23$, $df = 9$, P-value $= 0.9987$; $R^2 = 0.976$)

(Table 4; Fig. 2). Percentage of forest within a 100 m radius of a given point had the strongest positive and significant effect on forest recovery, indicating that surrounding extant forest plays a critical role in promoting forest recovery. Distance from commonwealth reserves had a small negative effect on the probability of forest transition, demonstrating that the likelihood of forest recovery decreases with distance from a reserve. As expected, steeper slopes favored forest recovery. Transitions to forest were also more likely in the north-west to north-east facing slopes (Table 4).

Although distance to primary roads had a positive effect on forest recovery, it was not significant as a single factor. However, a negative interaction term between distance to primary roads and slope suggested that steeper slopes had lower probability of development in the proximity of primary roads but had little effect in less accessible areas. In addition, the negative interaction term between percentage of forest within a 100 m buffer and slope points to the pivotal role that the degree of surrounding forests played in forest recovery in flat areas relative to a weaker role in steep terrain. Similarly, the positive interaction term between distance to commonwealth reserves and slope shows that steeper slopes did not influence the likelihood of recovery near a reserve but were critical at greater distances from protected areas.

Soil agricultural capacity reflects the properties of the soil (Fig. 3). As expected, soils with highest agricultural capacity (categories 1–3) had low probability of transition, likely as a result of their high value for agriculture. Similarly, soils with very low agricultural capacity (categories 9, 10) had lower probabilities of transition to forest. These soils may be not fertile enough to support either agriculture or forest re-growth, providing added incentive for urban development. As a result, we observed higher rates of forest recovery in soils of intermediate agricultural capacity which may be not fertile enough to make farming profitable but adequate for forest growth.

Municipality effects on forest regeneration displayed a spatially clustered pattern, with greater probability of recovery for those municipalities along

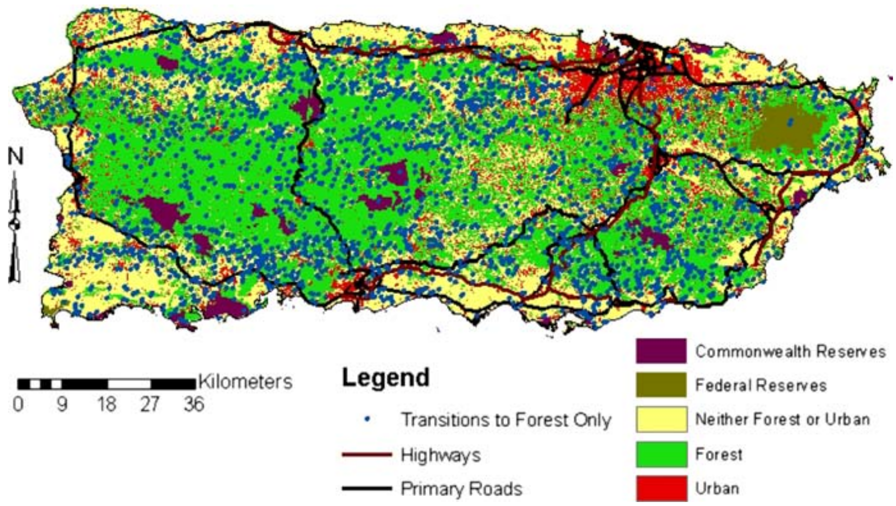

Fig. 2 Location of federal and commonwealth reserves, primary roads, and highways, forest and major urban areas in 1991. Points that transitioned to forest from 1991–1992 to 2000 are also shown

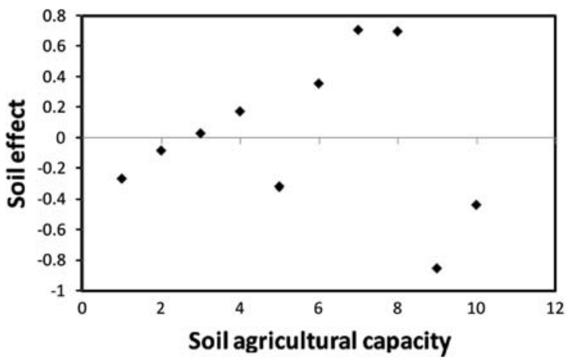

Fig. 3 Soil agricultural capacity effects. Lower capacity values have greater fertility. A positive effect indicates increasing odds of forest transition for that agricultural capacity class

the coast and near less dense urban areas. Municipalities less likely to support forest recovery were either in less accessible locations or near San Juan. There was no relationship between the magnitude of municipality effects and the percent change in population ($r^2 = 0.02$, $n = 76$).

Discussion

Landscape structure

We characterized the landscape pattern of forest patches and agricultural land in Puerto Rico. As in previous research, we found increases in both urban and forest cover (Kennaway and Helmer 2007; Pares-Ramos et al. 2008). Additionally, we found that while increases in forest area are leveling off, urban area is spreading much faster with fragments converging and creating larger patches. Conversion of pastures to forests accounted for most forest recovery. Most of the herbaceous agriculture class converted to pasture and a much smaller percentage transitioned to urban and forest classes (see Kennaway and Helmer 2007 for details).

Mean forest patch size decreased slightly from 1991 to 2000 and the number of patches also showed a minor increase. This result contrasts with previous studies that have shown increasing MPS over time as secondary forests appear next to existing older patches (Helmer et al. 2008). Previous work has found secondary forests will buffer older forest patches and that larger forest patches will converge on the smaller, effectively reducing their number and increasing MPS. However, our results suggest that forest cover is also increasing in areas away from larger patches, suggesting that these two processes may occur simultaneously. Nevertheless, these patterns may be clarified by investigating where forest patches are emerging and by observing the impact that suburbanization may have on forest re-growth (Pares-Ramos et al. 2008).

When we bisected the landscape at a 400 m elevation threshold we observed that urban area increased throughout the landscape. In contrast, forest area expanded only at lower elevations and actually diminished at higher elevations. These trends deviate from our assumption that forest cover would increase in the higher elevations as a result of reduced accessibility, steeper slopes, and presence of older forest. Our model indicates that these variables are still affecting probability of forest recovery but at lower elevations. Similarly, urban area is expected to increase in the lower elevations for the opposite reasons. Although urban area is spreading into higher elevations, the change in forest area at lower elevations far exceeds this amount compensating for this urban spread. Therefore, the two competing classes are expanding in each other's domain.

Quantifying the importance of socioeconomic, biophysical, and landscape drivers for forest recovery

We examined the importance of a number of socioeconomic, biophysical, and landscape variables on forest recovery over a 10 year period representative of the ongoing socioeconomic changes on the island. Through statistical modeling we identified the factors that best explain the conversion of agricultural lands to forest on a landscape scale. Some of the variables examined here and their effects on forest recovery are similar to those from other studies: positive effects of remnant forests nearby, increasing distance to roads, and steeper slopes, and a negative effect of distance to forest reserves (Helmer 2000; Rudel et al. 2000; Chazdon 2003). These results confirm that economic development and increasing urbanization have played a key role in forest recovery in Puerto Rico.

The percentage of forest within a 100 m radius of a point had the greatest positive effect on probability of forest transition. Helmer et al. (2008) suggest that surrounding forest cover is an efficient predictor of forest recovery. Previous research has found that remnant forest patches are a source of seeds for colonization of cleared and degraded areas and act as critical habitat for animal seed dispersers (Uhl et al. 1988; Chazdon 2003). In addition, proximity to remnant forest patches has been linked to increasing species richness, density, and aboveground biomass (Chinea 2002; Guariguata and Ostertag 2001). In Puerto Rico, Thomlinson et al. (1996) found that forest recovery in the Luquillo municipality was greatest within 100 m of extant forest patches and decreased at further distances. Lugo (2002) reported much the same trend, whereby small remnant forest patches accelerated reforestation and reduced fragmentation. In addition to the degree of forest cover in the area, proximity to commonwealth reserves had additional beneficial effects on forest recovery. This positive effect could be the result of larger populations of animal dispersers, greater numbers of seed sources, or a reduced likelihood of development near reserves.

As in previous work (Helmer et al. 2008), our results indicate that reforestation is more likely to occur in steeper slopes and at higher elevations, which is often attributed to relatively poor soil quality for agriculture (Chinea 2002), low accessibility (Thomlinson et al. 1996), and wetter climates (Rudel et al. 2000; Lugo 2002). In addition, the positive effect of aspect can be the result of moisture-bearing trade winds arriving from the north-east that release the moisture on north facing slopes (Rudel et al. 2000; Daly et al. 2003). Significant interaction terms between slope and proximity to roads attest to the role of topography in mediating the effect of urban encroachment (Martinuzzi et al. 2007).

Our study also demonstrates that the rate of forest recovery is constrained by soil fertility. Forest recovery was less likely in areas of extremely low soil fertility although high fertility also led to low rates of reforestation. Previous studies have demonstrated that soils of high fertility are usually the last to be abandoned (Chinea 2002; Arroyo-Mora et al. 2005). Additionally, in Puerto Rico most of these soils are in the coastal plains where land values are high (López et al. 2001; Martinuzzi et al. 2007). As a result of these interacting processes, forest recovery occurred primarily in areas of intermediate fertility where soils are less productive for agriculture. Additionally, land use can itself alter soil fertility. In Puerto Rico, secondary forests that were former pastures have a faster recovery of soil carbon, one important measure of soil fertility, than former agricultural fields (Weaver et al. 1987; Silver et al. 2000). Therefore, forest recovery at the landscape scale may depend on an interaction between land use history and underlying soil fertility (Guariguata and Ostertag 2001; Arroyo-Mora et al. 2005).

Most forest transitions occurred along the forest periphery at some distance from a nearby primary road (Fig. 2). This pattern appears to be the result of urban development near roads possibly as a result of increased accessibility (Lugo 2002), flatter slopes, and proximity to extant urban areas (López et al.

2001; Helmer 2004). Puerto Rico has the greatest road density among all of the Caribbean islands. At 2.5 km of road per km^2, this facilitates the process of development even in areas far from the largest urban centers (López et al. 2001). From 1977 to 1994 alone, 42 % of new urban areas expanded into former agricultural areas (López et al. 2001). This trend may also explain why soils of high quality and fertility have lower probability of forest recovery since they are either maintained as agriculture or converted to urban areas.

There was no clear link between the municipality effect on forest recovery and percent change of population size by municipality for this time period (i.e., 1990–2000, Pares-Ramos et al. 2008). Although municipalities in the east of the island that are experiencing increased population growth tend to experience lower rates of forest recovery, this is not the case in western Puerto Rico. Fast-growing municipalities in western Puerto Rico, including the coastal regions, had greater rates of reforestation than municipalities elsewhere on the island. Some of the most isolated municipalities in the western side of the island had very low probability of reforestation, a counterintuitive result. These patterns may be the result of zoning regulations. Most land in Puerto Rico is privately owned (Collins et al. 2006). The island contains 78 municipalities which exert varying degrees of control over land use planning decisions (Puerto Rico Planning Board http://www.jp.gobierno.pr/). The degree of forest recovery at the municipality level may reflect both decision-making autonomy and the existence and effectiveness of land use plans that limit land development. This result is intriguing and worth exploring because it suggests that land use policies can have a large effect on forest recovery, reinforcing findings elsewhere (Lambin and Geist 2006).

Urban development and forest recovery are both occurring in abandoned agricultural land, but so far growth of the two is positive (Grau et al. 2003; Helmer 2004; Martinuzzi et al. 2007; Pares-Ramos et al. 2008). Most of the literature and our study suggest that the conversion of agriculture to either urban or forest cover is a non-random and highly patterned trend, making the transitions easier to manage (Thomlinson et al. 1996; López et al. 2001). However, Thomlinson and Rivera (2000) demonstrated that low-density urban development has shifted to higher slopes, elevations, at some distance to roads, and to generally more remote areas of the Luquillo municipality, placing pressures on existing forests. As the El Yunque National Forest is within the study area, it suggests that its reserve status may not be enough to limit urbanization within its boundaries. Martinuzzi et al. (2007) also found that a large percentage of low density urban development was occurring in the hills. This pattern seems to be largely driven by consumer choice and a dense road network that serves to attract development (Thomlinson and Rivera 2000). Indeed, the decentralization of urban areas and expansion to suburban neighborhoods has been noted island-wide for 1990–2000, with population increases reported in the coastal hills and central mountain regions and at all elevations (Pares-Ramos et al. 2008). Reportedly, forest recovery rate peaked between 1959 and 1974 as a result of maximum agricultural abandonment (Rudel et al. 2000), but this trend seems to have slowed (Kennaway and Helmer 2007) or even reversed at some scales (Thomlinson and Rivera 2000 citing unpublished data). Given the critical ecosystem services secondary forests provide in Puerto Rico (Brandeis et al. 2007), this knowledge is a cause for concern and calls for development of land use plans that direct the concentration of urban development.

Some researchers have argued that the forest transition observed in Puerto Rico over the past decades is simply the result of its close association with the United States, which provided access to labor markets and promoted the abandonment of agriculture (Walker 1993; Vandermeer and Perfecto 1995; Rudel et al. 2000). An alternative explanation is that forest resurgence was the result of an aggressive industrialization program that provided incentives in the form of tax exemptions for industries in the 1930s (Rudel et al. 2000). In practice, it is difficult to separate these two potential causes: many of the companies that established in Puerto Rico were American and much of their production was exported to the US without tariffs. The US also provided access to a vast labor market (Rudel et al. 2000). Some have suggested that the factors that drove forest resurgence in Puerto Rico are unlikely to be important in other tropical regions with no ties to large industrialized countries. However, we argue that the industrialization process was only the initial economic trigger and that the present drivers of forest recovery reflect general processes at work in other tropical regions undergoing development (Grau et al. 2003). Moreover, foreign actors and globalization are playing an increasingly important role in forest cover change in many tropical regions by driving demand for agricultural products and labor (Hecht et al. 2006; Perz 2007). Therefore, understanding the role that socioeconomic drivers have on forest recovery relative to biophysical and landscape variables is critical to land use planning and maximization of the ecosystem services secondary forests provide.

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