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Research

Biophysical and Socioeconomic Factors Associated with Forest Transitions at Multiple Spatial and Temporal Scales

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ABSTRACT. Forest transitions (FT) occur when socioeconomic development leads to a shift from net deforestation to reforestation; these dynamics have been observed in multiple countries across the globe, including the island of Puerto Rico in the Caribbean. Starting in the 1950s, Puerto Rico transitioned from an agrarian to a manufacturing and service economy reliant on food imports, leading to extensive reforestation. In recent years, however, net reforestation has leveled off. Here we examine the drivers of forest transition in Puerto Rico from 1977 to 2000 at two subnational, nested spatial scales (municipality and barrio) and over two time periods (1977-1991 and 1991-2000). This study builds on previous work by considering the social and biophysical factors that influence both reforestation and deforestation at multiple spatial and temporal scales. By doing so within one analysis, this study offers a comprehensive understanding of the relative importance of various social and biophysical factors for forest transitions and the scales at which they are manifest. Biophysical factors considered in these analyses included slope, soil quality, and land-cover in the surrounding landscape. We also considered per capita income, population density, and the extent of protected areas as potential factors associated with forest change. Our results show that, in the 1977-1991 period, biophysical factors that exhibit variation at municipality scales (~100 km^2) were more important predictors of forest change than socioeconomic factors. In this period, forest dynamics were driven primarily by abandonment of less productive, steep agricultural land in the western, central part of the island. These factors had less predictive power at the smaller barrio scale (~10 km^2) relative to the larger municipality scale during this time period. The relative importance of socioeconomic variables for deforestation, however, increased over time as development pressures on available land increased. From 1991-2000, changes in forest cover reflected influences from multiple factors, including increasing population densities, land development pressure from suburbanization, and the presence of protected areas. In contrast to the 1977-1991 period, drivers of deforestation and reforestation over this second interval were similar for the two spatial scales of analyses. Generally, our results suggest that although broader socioeconomic changes in a given region may drive the demand for land, biophysical factors ultimately mediate where development occurs. Although economic development may initially result in reforestation due to rural to urban migration and the abandonment of agricultural lands, increased economic development may lead to deforestation through increased suburbanization pressures.

Key Words: *agricultural abandonment; deforestation; forest transition; Puerto Rico; reforestation*

INTRODUCTION

Over the past two centuries, population growth, urbanization, and industrialization have induced a prolonged decline and then a partial recovery in the extent of forest cover in many regions across the globe (Mather 1992, Rudel et al. 2005). Mather (1992) argued that this pattern of forest change is related to a nation's social and economic development: as a nation develops economically, forest cover typically declines. With increasing development, however, this loss may halt and actually reverse, leading to an increase in the extent of forest cover. The point of inflection in this

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transition occurs when the rate of reforestation exceeds that of deforestation, a phenomenon described as the forest transition (FT).

Since its inception, FT theory has focused on understanding the factors that lead to these transitions. Net increases in forest cover have been associated with a number of social, economic, and biophysical factors such as the development of industry, increased agricultural efficiency and abandonment of unproductive agricultural lands (Mather 1992, Mather and Needle 1998, Perz and Skole 2003, Rudel et al. 2009), international trade, urban migration, changes in sources of energy (DeFries et al. 2010), and overall economic development (Mather et al. 1999, Southworth and Tucker 2001, Grau and Aide 2008). The enumeration of these drivers, however, leaves unanswered how important these social and biophysical factors are relative to one another and how they interact to induce land cover change at different spatial and temporal scales (Rudel et al. 2005).

Spatially, data constraints have largely restricted the study of FT to the national scale, ignoring possible consequences of a nation’s forest transition on larger, e.g., regional or global, and smaller, e.g., subnational, spatial scales (Hecht et al. 2006, Perz 2007, Meyfroidt and Lambin 2009). Many forest transitions may not reflect net gains in global forest cover, but rather an offshoring of agricultural demand that causes compensatory deforestation in other countries or regions (Meyfroidt and Lambin 2009, DeFries et al. 2010, Pfaff and Walker 2010). Similarly, examining national-scale trends can mask important variation at a subnational level. At this smaller scale, patterns of forest change may be better described by the opportunity costs of maintaining forest cover or converting the land to an alternate, more profitable use (Barbier et al. 2010). Biophysical factors such as topography, soil fertility and slope may lead to concentration of agriculture on flatter and more fertile lands, allowing reforestation of marginal, abandoned agricultural areas (Rudel et al. 2000, Wright and Samaniego 2008, Crk et al. 2009). Socioeconomic variables, such as urban-rural migration or the connectivity of the land to urban centers, may reduce the probability of reforestation by increasing relative land value (MacDonald and Rudel 2005, Crk et al. 2009). Forest cover change may also be mediated by external factors, such as technological advances, market forces, government policies, and institutional factors (Izquierdo et al. 2008, Barbier et al. 2010).

Temporally, FT theory describes a long-term, historical dynamic process but many empirical studies are restricted to a single time period (e.g., Rudel et al. 2000, Thomlinson and Rivera 2000). However, biophysical and socioeconomic factors associated with forest change may vary temporally because of shifting policies or changes in external influences on land values (Barbier et al. 2010, DeFries et al. 2010). Furthermore, as socioeconomic development proceeds and societies transition from rural to urban environments, forest regeneration may level off, in some cases reverting to net deforestation from suburbanization pressures (Thomlinson and Rivera 2000, McDonald and Rudel 2005, Irwin and Bockstael 2007). Examining forest transitions over longer time scales or across multiple periods would determine whether predictors of forest change remain constant through time.

Finally, the emphasis of FT theory on net forest change ignores the fact that reforestation and deforestation are different processes that may respond to distinct factors (Rudel et al. 2005, Lambin and Geist 2006, Meyfroidt and Lambin, 2009). Proximate causes of deforestation include infrastructure development, agriculture expansion, and wood extraction, which are in turn driven by ultimate economic, technological, political, and cultural factors (Lambin and Geist 2006). Although abandonment of agricultural land is often seen as a prerequisite for secondary forest regrowth, the proximate and ultimate drivers for reforestation may be as diverse as those of deforestation, including wood shortages, changes in fire regime with increased population density, and insecure land tenure. The common aggregation of reforestation and deforestation into net forest change makes it unclear whether the factors that favor deforestation will simultaneously hinder reforestation. By separately examining patterns of deforestation and reforestation, we can illuminate the potentially different predictors of these two processes.

The forest transition and related phenomena have been extensively studied on the Caribbean island of Puerto Rico from both a socioeconomic (Rudel et al. 2000) and a forest dynamics perspective (Aide et al. 2000, Grau et al. 2003). Economic decisions at the end of the Second World War and a special relationship with the U.S. led to fast-paced economic development in Puerto Rico that changed an agrarian economy to one based on light industrial activities (Weisskoff and Wolff 1977, Dietz 1986, Rudel et al. 2000), drawing laborers to the cities and to the mainland U.S. The integration of households into the global economy via labor migration and remittances led to an initial wave of forest recovery, which was sustained until the 1990s. Forest cover in Puerto Rico increased from less than 20% in 1951 to about 57% today (Brandeis et al. 2007). Population increased from 2 to 3.9 million over this time period (Grau et al. 2003). Lately, the increase in forest cover has decelerated and even reversed at some scales (Martinuzzi et al. 2007). Given these drastic changes in forest cover over a prolonged period, Puerto Rico is an ideal location to examine the social and biophysical drivers of forest change through time.

Previous studies offer some insight as to which factors may be driving land use and land cover change (LUCC) in Puerto Rico. Reforestation has been associated with outmigration, decreases in agricultural production, protected area status, and proximity to forest patches (Rudel et al. 2000, Helmer et al. 2008, Crk et al. 2009). The major drivers of deforestation appear to be rising household incomes and material consumption, development of suburbs, and household sorting behavior across neighborhoods within major metropolitan areas (Parés-Ramos et al. 2008, Martinuzzi et al. 2007). Despite this extensive work on the FT in Puerto Rico, previous studies have typically emphasized individual aspects of the FT, e.g., social or biophysical factors, focused on particular spatial scales, e.g., pixel, county, or island, and considered net reforestation or deforestation only (Rudel et al. 2000, Grau et al. 2003, Martinuzzi et al. 2007, Helmer et al. 2008, Parés-Ramos et al. 2008). This study builds on previous work by simultaneously considering the social and biophysical factors previously found to drive forest transitions within one study, by considering these same drivers of forest change at multiple spatial and temporal scales, and by examining how these drivers influence reforestation and deforestation separately. By examining all of these components within one analysis, this study offers a comprehensive understanding of the relative importance of various social and biophysical factors for forest transitions at multiple scales in Puerto Rico.

We accomplish these goals by fitting hierarchical models for each process (reforestation and deforestation) and time period (1977-1991 and 1991-2000) separately and comparing the standardized coefficients associated with each predictor in the four resulting models. To understand the spatial scale at which these factors act, we use predictors and forest change data measured at the submunicipality (barrio) scale and include random effects at the municipality scale. Through the use of multilevel R^2 we are then able to explore the degree to which individual predictors explain variance in forest change at the municipality and submunicipality scales. Our hypotheses for the effects of specific predictors on deforestation and reforestation are summarized in Table 1.

METHODS

Study site

Puerto Rico is the easternmost island of the Greater Antilles, measuring 160 km E-W and 55 km N-S. Annual precipitation varies across the island from approximately 1500-2000 mm in the northeast mountains (900-1100 meters) to approximately 750 mm on the south coast. Mean annual temperatures range between 19.4 and 29.7°C with cooler temperatures occurring at higher elevations (Daly et al. 2003). The steep climate gradient, large elevation range, and a complex geology have generated striking environmental variation within the island. Vegetation ranges from dry, semideciduous forests in the southwest part of the island, to moist forests throughout most of the island and rain forests at higher elevations (Daly et al. 2003).

In this study we investigate forest transition at both the municipality and barrio (submunicipality) scales. Puerto Rico is comprised of 78 municipios (municipalities range from 13.2 to 328.9 km²) that are further subdivided into approximately 875 barrios (submunicipalities range from 0.12 to 64.13 km²). These two scales represent the legal and political subdivisions of Puerto Rico. Zoning laws are defined at the municipality level but these laws are poorly implemented and regulated (Dietz 1986,

Table 1. Explanatory variables and associated hypotheses for analyses of forest change in Puerto Rico.

Explanatory Variables	Data Source	Hypothesized Relationship	Rationale
Socioeconomic			
Population density (1980, 1990)	U.S. Census	+ Defor - Refor	Higher population density will be associated with greater land use intensity.
Population density change (1980-1990, 1990-2000)	U.S. Census	+ Defor - Refor	Urban-rural migration may drive deforestation for suburban development (MacDonald and Rudel 2005).
Normalized per capita income (1980[†], 1990)	U.S. Census	+ Defor - Refor	Rising local incomes may be associated with higher local land use intensity and suburbanization (Margo 1992).
Normalized income change (1980-1990[†], 1990-2000)	U.S. Census	+ Defor - Refor	Short-term increases in local income may reflect suburban development (Parés-Ramos et al. 2008).
Percent of area in reserve/protected area	GAP (Gould et al. 2007)	- Defor + Refor	Protected areas can deter forest cover change (Helmer 2004).
Biophysical			
Life zones	USGS (2009)	w/ ↑Moisture, - Defor + Refor	Precipitation is likely to affect vegetation dynamics and favor regrowth (Daly et al. 2003) or alternatively, reforestation may be slower in drier areas because of fires (Brandeis et al. 2007).
Median slope	USGS (2009)	- Defor + Refor	Slope affects development and agricultural cost (Turner et al. 2009, Crk et al. 2009).
Median soil agricultural capacity (1 is most fertile, 10 is least fertile)	USGS NRCS (2007)	+ Defor - Refor	Marginal lands are often the first areas to reforest because they are more likely to be abandoned than areas with high quality soil (Mather and Needle 1998).
Total forest cover (1977, 1991)	IITF/USDA Forest Service	+ Refor	By facilitating seed dispersal to abandoned sites, the extent and spatial distribution of forest cover can influence the rate of forest recovery (Thomlinson et al. 1996, Helmer et al. 2008, Crk. et al. 2009).

[†] Per capita income data for 1980 only available at the municipality scale.
IITF = International Institute of Tropical Forestry

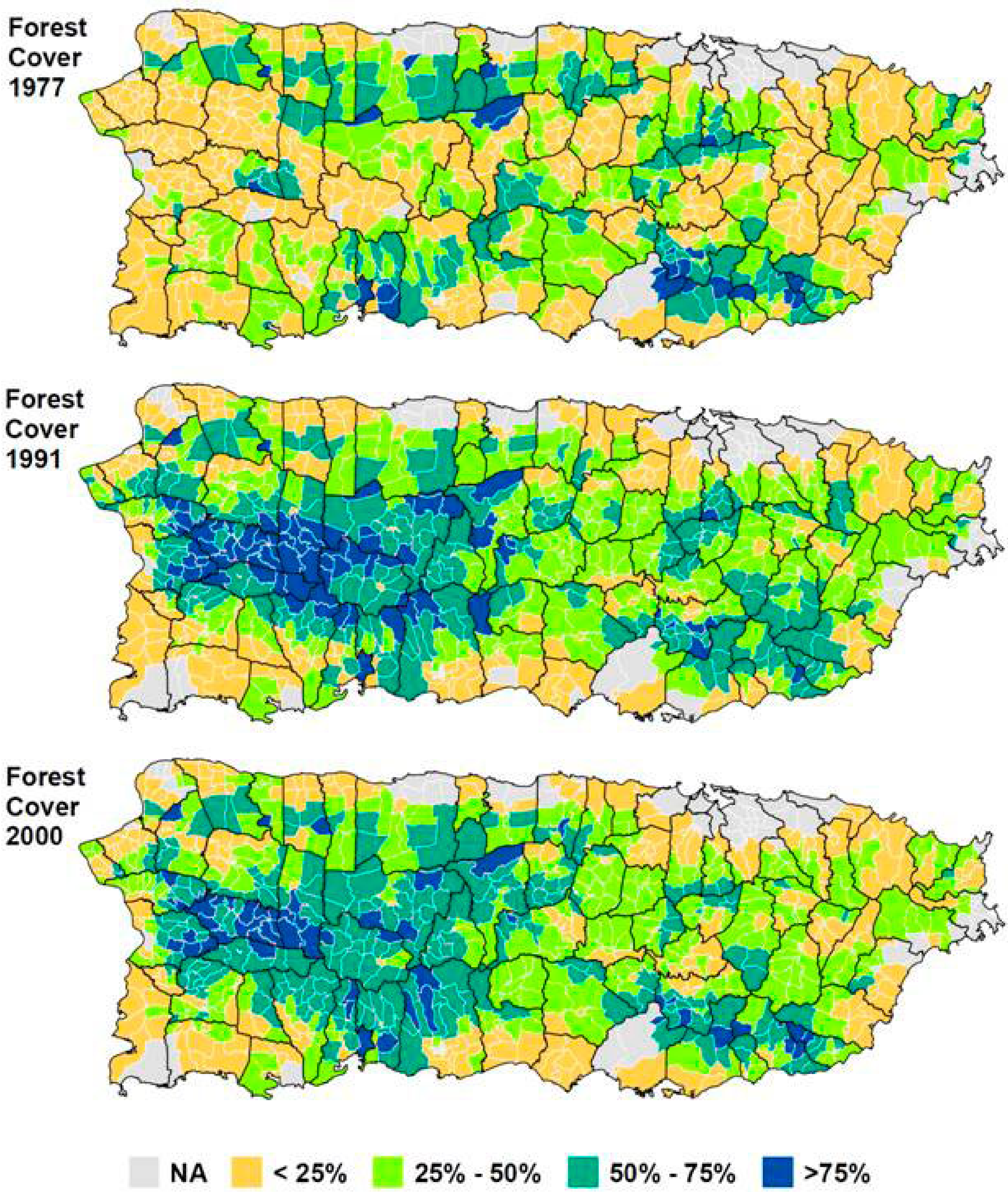
Hunter and Arbona 1995). Because the majority of land in Puerto Rico is privately owned, developers and private land owners often make the decisions that result in land use/land cover change at the barrio level. Because we were primarily interested in reforestation and deforestation outside of city-centers, we used the 1977 land cover map to exclude 84 urban barrios that had greater than 50% urban land cover from our analysis. In addition, barrios with zero total forest cover or unavailable socioeconomic data were excluded (Fig. 1).

Data collection

Land cover

Three land cover GIS layers (“maps”) were used to examine changes in land cover patterns over time. The earliest map was generated by manual interpretation of 1:20,000 scale aerial photographs from 1977 and 1978 and digitized to polygons by Ramos and Lugo (1994). We converted this map to raster at a lower, 30 m pixel scale resolution. The two other land cover maps were based on Landsat

Fig. 1. Percentage forest cover in 1977, 1991, and 2000 land cover/use GIS layer calculated at the barrio (submunicipality) scale. Barrio boundaries are shown in white and municipio boundaries in black (See Appendix for data sources).



TM and ETM + mosaics of images taken ca 1991-1992 and 2000 with 30 m resolution (Kennaway and Helmer 2007). Details on land cover classification and accuracy are provided in Appendix 1.

Biophysical predictors

Biophysical characteristics can influence forest transition through their effects on land use patterns (Table 1). We used a 30 x 30 m Shuttle Radar Topography Mission digital elevation model (USGS 2009) to calculate median elevation and slope for each barrio. Elevation was not included in the analysis because it was highly correlated with slope at both spatial scales ($r = 0.73$, both $p < 0.001$). We also used a categorical classification of land into dry, moist, and wet life zones (Daly et al. 2003).

To explore the effect of soil quality on forest transitions, we used a measurement of soil agricultural capacity that groups soils into 10 classes based on characteristics such as erosion and moisture retention potential, soil depth, and presence of toxic salts, with 1 being the most fertile and 10 being least fertile (USDA NRCS 2007; Table 1). We used the median agricultural capacity of each barrio for this analysis.

We included the percentage of forested area in each administrative unit at the beginning of each period as a predictor of reforestation. The total amount of forested area, however, was not included in the deforestation analyses because it was already implicit in our model; only areas that are forested can become deforested.

Socioeconomic predictors

Socioeconomic conditions can also influence patterns of land use change and forest transition (Table 1). In Puerto Rico, socioeconomic factors include rising incomes and substantial rural-urban migration. We extracted per capita income (in 2000 US$) and total population from the 1980, 1990, and 2000 U.S. Decennial Census for each barrio.

To normalize for differences in area among administrative units, we converted total population into population density. We also normalized income for each administrative unit with respect to mean income across the island at each time period. Finally, we included change in population density and income in each time period. Because we were unable to obtain per capita income data for 1980 at the barrio scale, we used 1990 income data as a proxy because per capita income values were highly correlated among all years ($r > 0.90$, $p < 0.001$), and omitted income change as a predictor in the 1977-1991 analysis.

Finally, we calculated total protected area in each barrio from the Puerto Rico Gap Analysis Project (Gould et al. 2007). We included the percentage of protected areas in each barrio as a predictor. Travel time to the nearest urban center (> 500 ha in the 1977 map) was originally included but was dropped because preliminary analyses failed to show significance. Although many other socioeconomic variables are cited as important in the literature, for example, land value, land ownership, institutional variables, these data were not readily available for Puerto Rico.

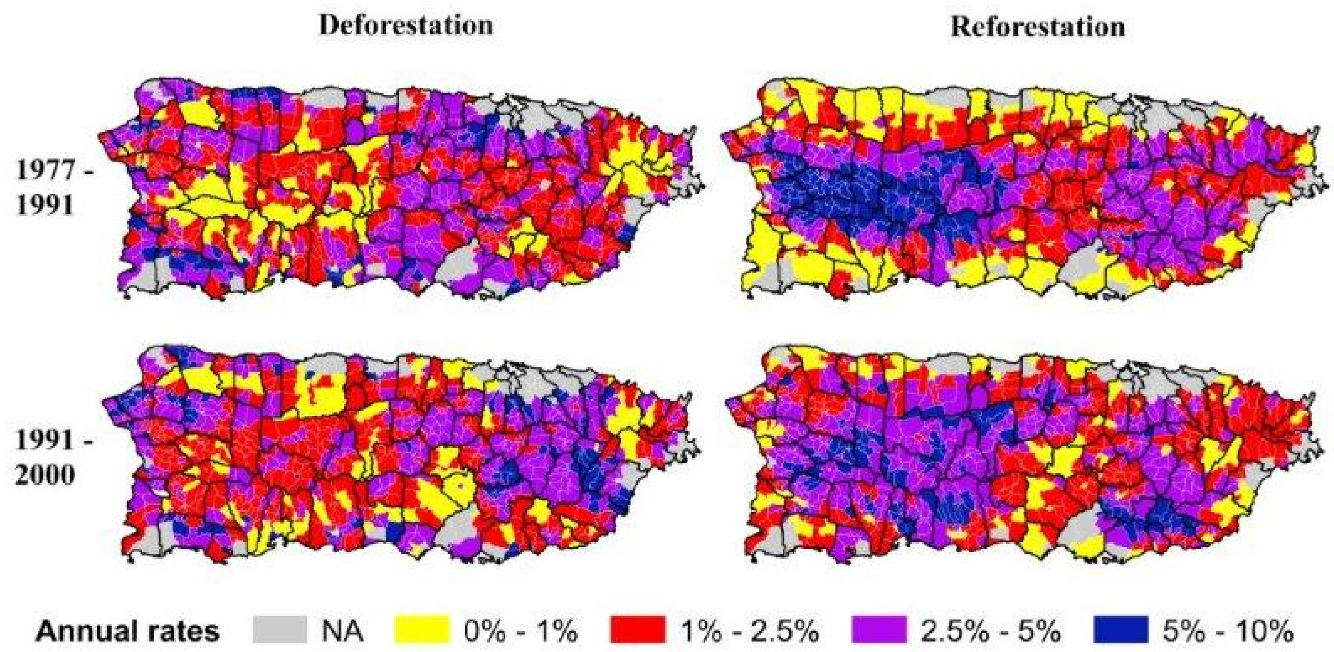
Statistical analyses

For each period (1977-1991, 1991-2000) and transition type (reforestation or deforestation) we fit separate statistical models where the response variable was the number of pixels that became reforested or deforested in a barrio during the time period. The log of the number of potential pixels that could be reforested/deforested was included as an offset. We used the logarithm as the link function in our analysis and initially used a Poisson distribution. However, initial model residuals showed over-dispersion so the final results reported here are all based on negative binomial generalized linear mixed models with a log link.

For each separate period and transition type, we selected the best submodel based on Deviance Information Criterion (DIC; Spiegelhalter et al. 2002). Starting with the full model (Table 1), we compared it to the set of all submodels formed by dropping each one of the predictors independently. If the full model had the lowest DIC, we stopped; otherwise we selected the submodel with the best DIC and compared it to the set of models formed by dropping additional predictors.

To facilitate interpretation of effect magnitudes among covariates, all continuous predictors were standardized by subtracting their mean and dividing by twice their standard deviation. Life zone was

Fig. 2. Barrio (submunicipality) scale reforestation and deforestation rates calculated for 1977-1991 and 1991-2000 time intervals. Barrio boundaries are shown in white and municipio boundaries in black.



treated as a categorical covariate. To ensure that parameter estimates between the two periods could be easily compared, the log of the number of years in the period was included as an offset. Coefficients for all other parameters were estimated using WinBugs with weakly or noninformative priors and models were judged to converge when r-hats for all parameters were &#8804 1.1 (Gelman and Rubin 1992).

Because we were interested in how barrio-level predictors could explain variance at both the municipal and barrio levels, we calculated multilevel goodness of fit (R^2) as the proportion of explained variance at the barrio and municipality levels, using methods derived from Gelman and Pardoe (2006).

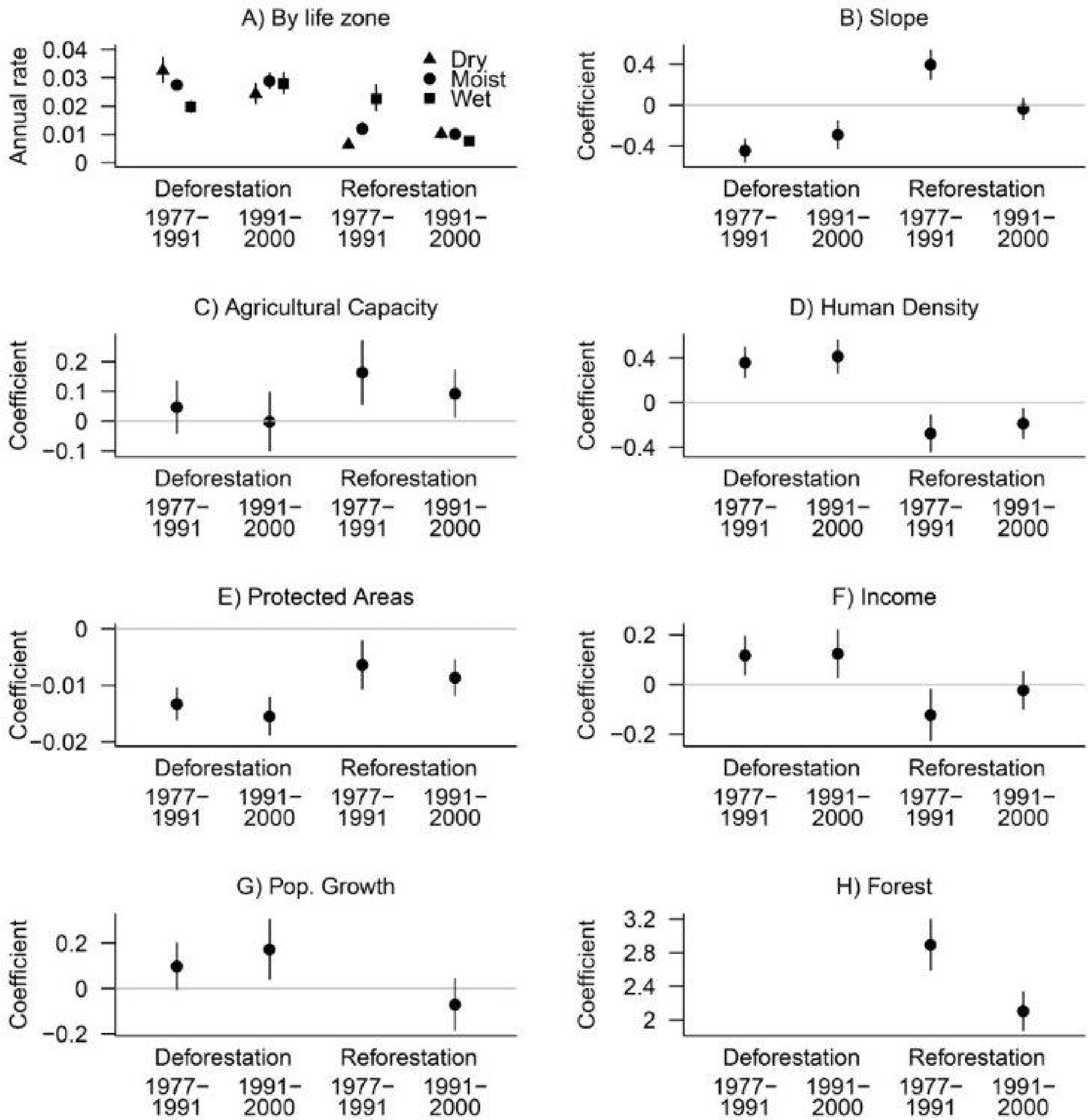
To evaluate the unique contribution of each predictor, we calculated multilevel R^2 for each of the submodels formed by dropping predictors from the best model. By comparing R^2 between these submodels and the best model, we inferred the degree to which the missing predictor uniquely contributed to the R^2 in the full model.

Residuals of the best model were tested for spatial autocorrelation using Moran's I test. In all four cases there was no evidence of spatial autocorrelation so no adjustments of standard errors were required. All statistical analyses were conducted in R 2.10 (R Development Team 2010).

RESULTS

Total forest cover increased dramatically during our first time period (1977-1991) but only slightly from 1991 to 2000 (Fig. 2). Analysis of deforestation patterns between 1977 and 2000 indicates that forest was most likely to be replaced by pasture, followed by urban land cover (Appendix Table A3). During the first period there were clear spatial signatures for both reforestation and deforestation, with reforestation concentrated in the abandoned coffee-growing regions in western Puerto Rico and deforestation around major cities and along the coast (Fig. 2). The spatial trends in the second period were similar, but the magnitude of change was smaller.

Fig. 3. Estimated annual deforestation and reforestation rates during the two study periods for the (A) three life zones (with all other covariates set to their mean values) and standardized regression coefficients for (B) slope, (C) soil agricultural capacity, (D) population density, (E) percentage of municipality in protected areas, (F) average income (in 2000 US$), (G) population growth rates during the analyses period, and (H) total amount of forest (only included in reforestation models). Bars indicate two standard errors above and below estimated means.



Although there were idiosyncrasies between the different time periods and processes, there were also general patterns in the significance and magnitude of the predictors that generally supported our hypotheses (Table 1, Fig. 3). In general, greater per capita income, population growth, and population density led to greater deforestation and lower reforestation. Areas with steeper slopes and lower soil fertility were more likely to reforest than flatter slopes and more fertile soils whereas the reverse was true for deforestation. As we hypothesized, most variables made mirror predictions (with opposite signs) for reforestation and deforestation (Fig. 3), with two exceptions. Agricultural capacity had positive effects on both reforestation and deforestation over the study period. Areas with protected status had lower rates of both deforestation and reforestation.

Most variables had similar effect sizes among the first and second time periods (Fig. 3), with two important exceptions. Areas with high mean slopes had increased rates of reforestation in the first period only. Similarly, variation between life zones in deforestation and reforestation rates was much greater during the first period (Figs. 3 and 4) with deforestation concentrated in the drier life zones and reforestation concentrated in the wettest areas.

The efficacy of models in explaining variance at each scale varied depending on the time period and transition type (Table 2), and the factors that uniquely explained the most variance often differed between scales of analysis. At the municipality scale, the models' efficacy (R^2) in explaining patterns of deforestation decreased over time whereas the opposite was true for reforestation (Table 2). At the barrio scale, predictors of deforestation accounted for a greater proportion of the variance in 1977-1991 than in 1991-2000 but we did not find any difference in the efficacy of the reforestation model. Through the use of multilevel R^2, we were able to explore the degree to which individual predictors explained variance in reforestation and deforestation across the two time periods at both the municipality and submunicipality scales. Results are outlined in Table 2.

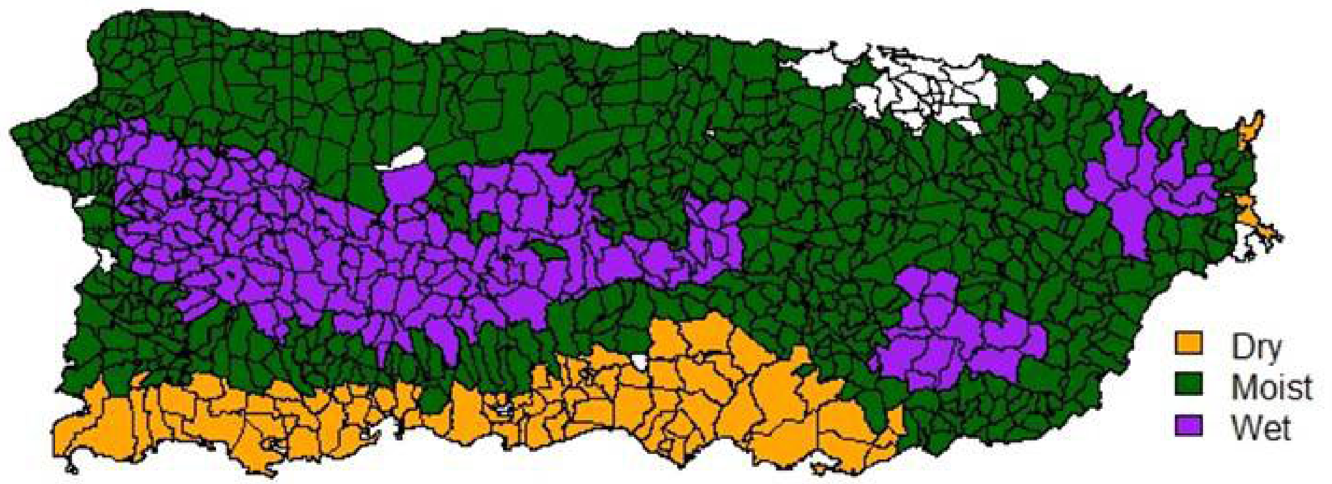
- Deforestation 1977-1991: Removal of life zones from the model led to a large drop in explained variance at the municipio scale (Table 2). At the barrio level, however, removal of life zones led to little change in explained variance. In contrast, removal of percent protected area led to a large drop in explained variance at the barrio but not at the municipal scale.
- Deforestation 1991-2000: During this time period, removal of protected areas led to the largest drop in explained variance at both municipal and barrio scales.
- Reforestation 1977-1991: Removal of either life zones or slope led to large drops in explained variance at the municipio scale, but none of the predictors seemed to uniquely explain much variance at the barrio scale.
- Reforestation 1991-2000: Dropping forest cover as a predictor led to large declines in explained variance at both municipio and barrio scales, despite the fact that effect size of forest cover was lower during the second period.

DISCUSSION

Broadly, our results show that in 1977-1991, forest dynamics in Puerto Rico were primarily driven by the abandonment of marginal agricultural land in the western-central highlands and by the development of pastureland and urban areas along the flat, coastal regions of the island. This agricultural abandonment resulted in net reforestation across the island, in agreement with previous studies that have examined forest transitions in Puerto Rico since the 1950s (Rudel et al. 2000, Brandeis et al. 2007, Helmer et al. 2008). These land use changes mirror the shifts in the island's agricultural production (Rudel et al. 2000), which transitioned away from cash crops like coffee to the production of more perishable commodities that are difficult to import like dairy. It is important to note that Puerto Rico, given its special relationship with the U.S., was able to make the transition away from agriculture relatively quickly given the availability of inexpensive food imports (Lopez et al. 2001).

Our results illustrate a very different pattern of forest transition during the 1991-2000 period. Unlike in the earlier decades, abandonment of agriculture, as indicated by forest regrowth in former coffee growing regions, i.e., steep terrain, wet life zone, was not a strong driver of reforestation. Instead,

Fig. 4. Distribution of life zones in Puerto Rico (Daly et al. 2003).



presence of remnant forest cover was the most important explanatory factor, possibly due to greater dispersal of forest tree seeds to open areas close to forest patches relative to those far from forested land (Thomlinson et al. 1996, Aide et al. 2000, Helmer 2004, Crk et al. 2009). Deforestation, on the other hand, was influenced by a variety of biophysical and socioeconomic factors, such as slope, population growth, and income, which drive local development patterns based on relative land values (Barbier et al. 2010). Flatter areas that had higher population densities and where people had more income were more likely to be deforested, possibly because of increased suburbanization pressure (Thomlinson and Rivera 2000, MacDonald and Rudel 2005, Parés-Ramos et al. 2008). Furthermore, deforestation was least likely in areas that prohibited development. This suggests that without effective policies in place for managing secondary forests, such as protected areas, increasing urban expansion may cause a reversal in forest gains (Helmer et al. 2008, Crk et al. 2009).

Our general conclusions support previous findings of the drivers of forest change in Puerto Rico while our specific analyses provide a number of new insights into the forest transition theory. First, we comprehensively quantify the relative importance of biophysical and socioeconomic factors associated with forest change at subnational scales by simultaneously considering factors found to be important in previous individual studies. This is important because previous studies have either focused on national-scale processes (Rudel et al. 2000) or examined only a few social and biophysical drivers of subnational forest change (e.g., Thomlinson et al. 1996, Helmer et al. 2008, Parés-Ramos et al. 2008). We find that biophysical factors that show variation at municipality scales, e.g., life zones, percent forest cover, were the best predictors of forest change at subnational levels. Life zones were especially good predictors of deforestation and reforestation during the first time period at the larger municipality scale (Table 2). Although forest transitions are often imputed to socioeconomic drivers (Mather et al. 1999, Rudel et al. 2005), our analysis indicates that biophysical factors are at least equally important in mediating local patterns of deforestation and reforestation at subnational scales. This result, however, must be interpreted in the context of broader socioeconomic changes that occurred across the island, namely the shift from agricultural to dairy production and subsequent rural to urban migration (Rudel et al. 2000).

Second, we show how the importance of individual drivers changes with the spatial scale of analysis. Previous studies have typically examined the drivers of forest transitions at one spatial scale and have not quantified how the relative importance of these drivers change across scales (e.g., Thomlinson et al. 1996, Helmer et al. 2008, Parés-Ramos et al.

Table 2. Explained variance at barrio (submunicipality) and municipio levels for best models of deforestation and reforestation during two time periods (1977-1991 and 1991-2000) and explained variance in models where individual explanatory variables are removed from best model. The decrease in R^2 relative to the best model indicates the importance of that variable in predicting observed transitions. The best model does not necessarily have the best R^2 at a particular scale because model selection is based on the overall agreement between data and the model; in other words, the ability to simultaneously explain variance at all levels of a multilevel model.

	Deforestation				Reforestation			
	1977-1991		1991-2000		1977-1991		1991-2000	
	Barrio	Municipio	Barrio	Municipio	Barrio	Municipio	Barrio	Municipio
Best Model	0.53	0.64	0.45	0.24	0.64	0.49	0.63	0.64
Variable removed								
Life Zones	0.52	**0.49**	0.45	0.23	**0.60**	**0.22**	0.62	0.63
Slope	0.50	0.62	0.44	0.21	0.63	**0.38**	0.63	0.63
Agricultural Capacity	0.53	0.65	0.46	0.23	0.63	0.50	0.62	0.64
Forest Cover					0.60	0.55	**0.48**	**0.32**
Human Density	0.52	0.64	0.43	0.20	0.64	0.50	0.63	0.65
Percentage Protected Area	**0.46**	0.63	**0.39**	**0.19**	0.64	0.47	0.62	0.60
Mean Income	0.52	0.67	0.45	0.21	0.63	0.52	0.63	0.64
Population Growth	0.53	0.65	0.45	0.21	NA	NA	0.63	0.64

2008). Life zones were weaker predictors of reforestation and deforestation at the smaller barrio scale than at the municipality scale. This is not surprising given that reforestation and deforestation were spatially clustered at the regional level, resulting in limited variation in reforestation and deforestation within life zones at the finer barrio scale. Deforestation rates were best explained by the absence of protected areas during both time periods, especially at the barrio scale. This is not surprising given that expansion of pastureland and urban areas were the main sources of deforestation (Appendix Table 3), and protected areas legally prohibited this development. In the second time period and in contrast to the first time interval, drivers of deforestation and reforestation were similar across spatial scales. Finally, the predictive efficacy of the model changed across spatial scales highlighting the scale at which variation in deforestation and reforestation occurs. For instance, in the 1977-1991 period, our model captured patterns of deforestation better at the municipality scale than at the barrio scale, highlighting the importance of large-scale biophysical factors in mediating deforestation dynamics. The opposite was true for the 1991-2000 period for which our model did a better job capturing patterns of deforestation at the barrio than at the municipal level. In all likelihood, patterns of deforestation in this time period exhibited a patchy, fine-grained spatial pattern, reflecting suburbanization pressures.

Third, our analyses also suggest that examining forest transitions during multiple time periods is important given that the drivers of reforestation and deforestation in Puerto Rico changed markedly between our two study periods. For example, during the first time period characterized by high levels of agricultural abandonment and rural to urban migration, life zones were the best predictor of reforestation. During the second time period, however, when these broad socioeconomic patterns were less marked, percent forest cover was the best predictor of reforestation. Similarly, deforestation rates were best explained by life zones during the first time period because of development of pastureland and urban areas on dry, flat lands. Absence of protected areas, however, was the best predictor of deforestation in the second time period, pointing to increasing deforestation pressure from land development. These results highlight that, to understand the dynamic nature of forest transitions and their causes, it is important to consider multitemporal scale analyses. Our results add to an increasing body of literature showing the dynamic nature of LUCC drivers (e.g., DeFries et al. 2010).

Finally, our analyses show that examining net forest transitions may obscure the factors driving forest change through reforestation and deforestation. Although these two processes largely mirror each other, they are also associated with different factors depending on the spatial and temporal scales of analysis (Asner et al. 2009). These results suggest that reforestation and deforestation often have different drivers, and therefore should be examined and managed separately.

These results have important implications for land use policy. First, broader socioeconomic changes in a given region or even globally may drive demand for land, but biophysical factors ultimately mediate where development occurs. In the case of Puerto Rico, a socioeconomic transition away from agriculture led to the abandonment of agricultural lands, however, biophysical factors influenced which areas were actually abandoned and subsequently reforested. These patterns were the result of variations in topography. In agreement with this result, a recent review by Asner et al. (2009) found that a majority of reported forest transitions occurred in areas with steep topography. Second, our results suggest that even though socioeconomic development may result in net reforestation levels at the national level, actual reforestation and deforestation patterns vary subnationally. This is important to note given that net reforestation may mask the loss of important primary and secondary forests at the subnational scale. Finally, our results highlight that although economic development may initially result in reforestation because of rural to urban migration and the abandonment of agricultural lands as predicted by FT Theory, increased economic development may lead to deforestation through increased suburbanization pressures. In fact, previous studies have suggested that as people's purchasing power increases, they prefer to migrate to low-density suburban areas near existing forest cover, resulting in significant deforestation (Thomlinson and Rivera 2000, Parés-Ramos et al. 2008).

One important caveat to our study is the degree to which our findings can be generalized to other tropical regions across the globe. Puerto Rico is unique compared with much of the tropics given its special relationship with the United States and its high population density and subsequent high demand for urban cover. Thus, factors that drove forest dynamics in Puerto Rico may not be important in other tropical regions that have no ties to large industrialized countries and have low rates for urban development. Considering Puerto Rico's special relationship with the United States, we argue that the industrialization process in Puerto Rico was only the initial economic trigger and that the present drivers of forest transition, e.g., land values, reflect general processes at work in other developing tropical regions (Grau et al. 2003). Furthermore, although broad national-scale forest transitions vary across the tropics, we argue that an increasing demand for agricultural products, urban cover, and development that is being driven by globalization and increased wealth across the tropics (Hecht et al. 2006, Perz 2007, DeFries et al. 2010) will result in similar local-scale drivers of reforestation and deforestation over the upcoming decades. The importance of land value for explaining local-level forest change is supported by similar findings from other tropical regions: reforestation is concentrated in rural, higher-altitude municipalities while deforestation is concentrated on the coast in southern Brazil (Baptista 2008), forest cover is concentrated in low population density, low income districts in Panama (Wright and Samaniego 2008), and land abandonment and subsequent reforestation is more frequent in farms with marginal soil quality and high forest cover in southern Chile (Díaz et al. 2011). We expect our results to most directly apply to other regions that have already undergone a significant amount of forest recovery and are rapidly developing, such as Hong Kong, Taiwan, and other Caribbean islands. Our results, however, may not apply to sparsely populated areas with flat topography and high potential for commercial agriculture (Grau and Aide 2008, Asner et al. 2009).

Our study suggests that to understand the complexity of forest transitions in the tropics, it is important to monitor such transitions at different temporal and spatial scales, and place them in dynamic social and institutional settings. Land transformations need to be considered as an intricate cycle where human decisions affect the landscape, altered landscapes affect ecological processes, these processes influence the way humans monitor and respond to land transformations, and these responses set in motion a new set of social drivers of land use change. Temporally, human transformations of landscapes are driven by historical and current social, economic, and ecological drivers (de Jong 2010, Lawrence et al. 2010). Spatially, these transformations respond not only to local needs and concerns but also to regional and global drivers. Understanding forest transition dynamics will improve the ability of decision makers to promote forest conservation and regrowth at multiple spatial scales and increase our understanding of how deforestation and reforestation drivers can change over time.

Responses to this article can be read online at: *http://www.ecologyandsociety.org/vol16/iss3/art15/responses/*

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Appendix 1: Mapping Methodology

This study is based on analyses of land-cover change derived from three land-cover maps (1977-78, 1991, 2000). Land-cover maps for 1991 and 2000 were derived from Landsat TM and ETM + mosaics of images taken at 30 m resolution (Kennaway and Helmer 2007). The 1977-78 maps were derived from vector-based, photo-interpreted maps of forest cover. Potential problems with this approach to the study of land-cover change are related to challenges in post-classification change detection, reconciling different data types, and differences between aerial photo interpretation and machine imagery classification. In change detection using classified images, misclassification errors can accumulate through time. Nevertheless, this approach was used successfully by Kennaway and Helmer (2007) and Helmer *et al*. (2008).

Reconciliation of the vector-based (1977-78) and pixel-based (1991-2000) mapping methods was made easier by the relatively good geo-registration between the two methods. In order to compare all three maps, we used ArcGIS 9.2 to correct minor boundary errors between the 1977-78 images, rasterize the 1977 map (a 30 m cell size was assigned to the 1977-78 map by majority rule), and calculate total forest area and transitions across time periods (1977-1991 and 1991-2000). Residual misregistration errors between the rasterized 1977-78 vector boundaries and the 1991 pixel-based map can be mistaken for land-cover change. Differences between aerial photo interpretation and machine classification of satellite imagery can also affect the accuracy of detecting various types of changes. Although manual photo interpretation and machine classification can both result in detailed classification schemes (see Tables A1 and A2), we conservatively restricted them to eight distinct classes. Classification of moderate-resolution (e.g., 30 m) satellite imagery often results in scattered misclassified pixels, but it may also correctly identify small patches that a manual interpreter would aggregate into different classes (Kennaway and Helmer 2007).

Although gross errors in classification of individual land-covers are possible between the 1977-78 and 1991 maps, they are unlikely. Despite widespread shifts in land-cover and agricultural production (Appendix Table 3), there is great concordance between the 1977-78 and 1991 maps (52.0% identical). The 1977-78 and 1991 maps differ most in the forest cover of the western highlands, which remain forested today (Brandeis *et al*. 2007). Large declines in Puerto Rican coffee production immediately preceded agricultural abandonment of the western uplands (*Fagan, unpublished data*), lending indirect support to the accuracy of the 1977-78 and 1991 maps. Finally, only 5.3% of the 1977-78 and 1991 maps appear to be obviously misclassified change (i.e., loss of urban cover, or conversion from land to water).

During our study period, urban cover increased from 12.1 to 15.5% of island area, and forest cover increased from 34.8 to 45.1% of island area. Although our figure of 45.1% forest cover contrasts with the 57% forest cover reported by Brandeis *et al*. (2007), this is likely because of differences in methodology and imagery resolution. Brandeis *et al*. (2007) used high-resolution photos to map forest cover over the island, and defined forest as land with greater than 10% forest cover. It is unsurprising that our moderate-resolution land-cover maps have lower forest cover, because coarser-resolution images typically underestimate true forest cover (Fagan and DeFries 2009). Non-forest areas with small patches of forest interspersed (e.g., pastures, suburbs, etc.) would have their forest patches mapped in high-resolution imagery, while moderate-resolution imagery would be classified to the dominant land-cover type. Similarly, the expansive forest definition employed by Brandeis *et al*. (2007) would cause small changes in tree cover from 1990 to 2004 to count as much greater changes in forest area than those observed by Landsat. In effect, the Landsat estimate of forest area is more conservative, but not inaccurate as a measure of large-scale change. We refer the interested reader to Brandeis *et al*. (2007), who discuss this issue extensively. Our estimates of forest cover agree with those of Pares-Ramos *et al* (2008) who use a different methodology and higher-resolution imagery to arrive at 52.4% forest cover. Our estimate of urban cover in 2000 is higher than that of Pares-Ramos *et al*. (2008) (11.3% of island area), but their lower estimate likely arises from their higher-resolution mapping and the relatively small building footprint of suburban development in Puerto Rico.

Because of the merging of land-cover classes and the source of the 1977-78 maps, it is difficult to evaluate the overall accuracy of the three land-cover maps. The accuracy of the 1991 and 2000 imagery was quantified by Kennaway and Helmer (2007); these maps correctly classified 72% and 82% of points, respectively, with an error matrix having Kappa coefficients of 0.69 ± 0.02 and 0.81 ± 0.02. Due to aggregation from 29 to eight land-cover classes, the accuracy of the 1991 and 2000 maps is higher than reported in Kennaway and Helmer (2007). However, we lack an estimate of accuracy for the 1977-78 map. Although we cannot quantify the classification accuracy of the 1977-78 map, the aerial photos were interpreted by a team of professional photo interpreters using sound methodology (DNRA 1998) (Table A1). Therefore, we assume low classification error for the 1977-78 land-use map. The analyses in this study assume that none of the potential error sources discussed here are large enough to influence our conclusions. In addition, forest change from 1977-1991 was dramatic, providing a strong signal-to-noise ratio, while most of the urban forest change occurred from 1991-2000, a period for which we have an estimate of error (Kennaway and Helmer 2007).

Table A1: Class conversions from the original 1977 map to the classifications used in our analyses**.** The twelve land-cover classes in the 1977 land-cover map discussed by Ramos and Lugo (1994) were reduced to eight classes in our analysis, following the same methodology as Crk *et al*. (2009).

Original 1977 class	**Old Class**	**New Class**	New Class Name
Development, non-productive land	12	1	Urban/developed
Agriculture	2	2	Herbaceous/coffee/mixed woody agriculture
Pasture	3	3	Pasture/grass
Highly dense canopy forest	4	4	Forest/woodland/shrubland
Dense canopy forest	5	4	Forest/woodland/shrubland
Low canopy density forest	6	4	Forest/woodland/shrubland
Shrub	7	4	Forest/woodland/shrubland
Mangrove	8	5	Forested wetland
Wetlands and salt-flats	9	6	Non-forest wetland
Rocky areas	10	7	Non-vegetated
No class	13	--	No class (omitted)
Water bodies	11	8	Water

Table A2: Class conversions from the original 1991 and 2000 maps**.** The twenty-nine land-cover classes in the 1991 and 2000 land-cover maps created by Kennaway and Helmer (2007) were reduced to eight classes in our analysis, following the same methodology as Crk *et al.* (2009).

Original 1991/2000 Class	Old Class	New Class	New Class Name
High-Medium Density Urban	1	1	Urban/developed
Low-Medium Density Urban	2	1	Urban/developed
Herbaceous Agriculture - Cultivated Lands	3	2	Herbaceous/coffee/mixed woody agriculture
Active Sun Coffee and Mixed Woody Agriculture	4	2	Herbaceous/coffee/mixed woody agriculture
Pasture, Hay or Inactive Agriculture (e.g. abandoned sugar cane)	5	3	Pasture
Pasture, Hay or other Grassy Areas (e.g. soccer fields)	6	3	Pasture
Drought Deciduous Open Woodland	7	4	Forest/woodland/shrubland
Drought Deciduous Dense Woodland	8	4	Forest/woodland/shrubland
Deciduous, Evergreen Coastal and Mixed Forest or Shrubland with Succulents	9	4	Forest/woodland/shrubland
Semi-Deciduous and Drought Deciduous Forest on Alluvium and Non-Carbonate Substrates	10	4	Forest/woodland/shrubland
Semi-Deciduous and Drought Deciduous Forest on Karst (includes semi-evergreen forest)	11	4	Forest/woodland/shrubland
Drought Deciduous, Semi-deciduous and Seasonal Evergreen Forest on Serpentine	12	4	Forest/woodland/shrubland
Seasonal Evergreen and Semi-Deciduous Forest on Karst	13	4	Forest/woodland/shrubland
Seasonal Evergreen and Evergreen Forest	14	4	Forest/woodland/shrubland
Seasonal Evergreen Forest with Coconut Palm	15	4	Forest/woodland/shrubland
Evergreen and Seasonal Evergreen Forest on Karst	16	4	Forest/woodland/shrubland
Evergreen Forest on Serpentine	17	4	Forest/woodland/shrubland
Elfin, Sierra Palm, Transitional and Tall Cloud Forest	18	4	Forest/woodland/shrubland
Emergent Wetlands Including Seasonally Flooded Pasture	19	5	Non-forest wetland
Mangrove	21	6	Forested wetland
Seaonally Flooded Savannahs and Woodlands	22	6	Forested wetland
Pterocarpus Swamp	23	6	Forested wetland
Salt or Mud Flats	20	7	Non-vegetated
Coastal Sand and Rock	26	7	Non-vegetated
Bare Soil (including bulldozed land)	27	7	Non-vegetated
Background/water	0	8	Water
Water - Permanent	28	8	Water
Tidally Flooded Evergreen Dwarf-Shrubland and Forb Vegetation	24	n/a	n/a
Quarries	25	n/a	n/a

Table A3: Key land-cover transitions in Puerto Rico, 1977-2000. Land-cover change calculated from the GIS land-cover maps described above. Deforestation measures transitions from forest to non-forest land-covers, and is broken down by non-forest category. Similarly, reforestation marks transitions from non-forest to forest land-covers, broken down by non-forest category. The “other” category includes all other non-forest categories (listed in Table A2). Net forest change subtracts deforestation from reforestation, and urbanization measures transitions from all land-covers to urban cover. Total hectares for the island of Puerto Rico were similar between land-cover transition maps, with minor changes (0.05% of total area) due to classification error with water (excluded here). See Kennaway and Helmer (2007) for detailed land transition matrix.

	1977-1991		**1991-2000**	
	Hectares	**Normal %***	**Hectares**	**Normal %***
Deforestation				
to pasture	64,272	5.31	49,077	6.31
to agriculture	4,144	0.34	9,333	1.20
to urban	16,549	1.37	15,526	2.00
to other	1,043	0.09	705	0.09
subtotal	86,008	7.11	74,640	9.60
Reforestation				
from pasture	70,732	5.85	63,160	8.12
from agriculture	85,397	7.06	4,985	0.64
from other	14,164	1.17	10,989	1.41
subtotal	170,293	14.07	79,134	10.18
Land-use shifts				
Net forest change	84,285	6.97	4,494	0.58
Urbanization	59,850	4.95	47,876	6.16
Total hectares	864,233		863,775	

***The normalized % expresses land-cover change at the island level calculated over a standard 10-year period. Changes in hectares are calculated over a 14-year and 9-year period, respectively.

References

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