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Factors influencing spatial pattern in tropical forest clearance and stand age: Implications for carbon storage and species diversity

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[1] Little is known about the tropical forests that undergo clearing as urban/built-up and other developed lands spread. This study uses remote sensing-based maps of Puerto Rico, multinomial logit models and forest inventory data to explain patterns of forest age and the age of forests cleared for land development and assess their implications for forest carbon storage and tree species richness. Accessibility, arability and spatial contagion emerge strongly as overriding spatial controls on tropical forest age, determining (1) the pattern of agricultural abandonment that permits forest regrowth, and (2) where humans leave old-growth forest remnants. Covariation between the factors patterning forest age and land development explains why most forest cleared for land development is younger. Forests are increasingly younger in more accessible and fertile areas where agriculture has lasted longer and land development is most common. All else equal, more species-rich older forest on less arable lands are somewhat less likely to undergo development, but they are still vulnerable to clearing for land development if close to urban centers and unprotected. Accounting for forest age leads to a 19% lower estimate of forest biomass cleared for land development than if forest age is not accounted for.

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1. Introduction

[2] The spatial distributions of urban/built-up lands and secondary forest age have implications for the climate, water resources, habitat distributions, and ecosystem processes of landscapes. Urban lands change surface radiation budgets, for instance, affecting local temperatures [*González et al.*, 2005]. Old-growth and older secondary tropical forests generally store more carbon and have more tree species than lands with younger forests, where agricultural or pastoral abandonment is more recent [*Aide et al.*, 2000; *Brearley et al.*, 2004; *Brown and Lugo*, 1990; *Chinea and Helmer*, 2003; *Gehring et al.*, 2005; *Guariguata and Ostertag*, 2001; *Kennard*, 2002; *Kumar et al.*, 2006; *Lugo and Helmer*, 2004; *Muñiz-Castro et al.*, 2006; *Turner et al.*, 1997]. Other forest biophysical features, like radiation balance and spectral reflectance, also change with age [*Giambelluca et al.*, 1999; *Moran et al.*, 1994]. Landscape and urban planning, management of conservation reserve networks, far-sighted agricultural development, and many types of process models can all benefit from understanding the spatial relationships between these two important aspects of land cover and land-cover change.

[3] Studies have used econometric methods to reveal landscape controls on tropical forest age or land-cover change to urban/built-up lands [*Etter et al.*, 2005; *Helmer*, 2000, 2004; *Kline et al.*, 2001; *Wear and Bolstad*, 1998]. Studies have also addressed how urbanization impacts timber management in temperate regions [*Barlow et al.*, 1998; *Kline*, 2004; *Munn et al.*, 2002]. Recent work in Puerto Rico quantifies the ages and types of forest cleared for land development. Most of the cleared forest falls into younger age classes; with 55 percent aged 1–13 yr and 32 percent aged 14–40 yr. About 12 percent of the cleared forest, however, is older (41 to > 55 yr) [*Kennaway and Helmer*, 2007]. A possible explanation for these results is the finding that much of the older forest in Puerto Rico is protected, has rugged topography or is wetland. Another interpretation is that a preference exists for clearing younger forest. Site preparation costs may be smaller for younger forest, or perhaps an interest in forest conservation discourages older forest clearing. Although *Helmer* [2004] found that forest canopy development did not influence whether land underwent urbanization in Puerto Rico from 1977 to 1991, the relationship between canopy development and forest age is not uniform across forest ecosystems.

[4] No studies comprehensively model the relative significance of potential landscape controls on the age of forests that undergo urbanization. In addition, we have little detailed information on the ecosystem attributes of the cleared forests. Filling these knowledge gaps is the goal

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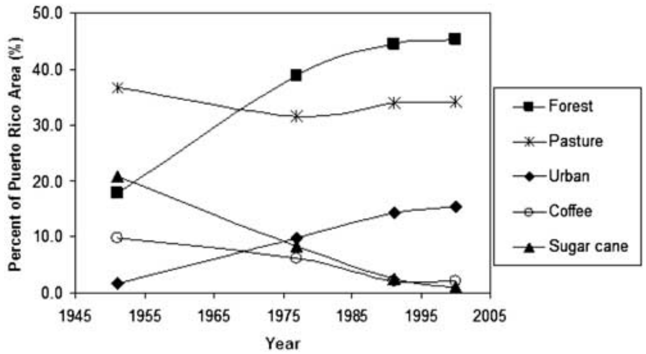

Figure 1. Major land-cover changes in Puerto Rico from 1951 to 2000. Since 1951, cover of forest and urban or developed lands has increased in Puerto Rico while area of cropland has declined, particularly areas of sugarcane and coffee cultivation. (Estimates compiled from published and unpublished data, described in *Birdsey and Weaver* [1983], *Helmer et al.* [2002], and *Kennaway and Helmer* [2007].) Area of sugarcane in 1991 includes active and recently inactive cane fields. Area of sugarcane in 2000 includes active and recently inactive cane fields and small areas of other herbaceous crops. Coffee area excludes inactive shade coffee in 1977, 1991, and 2000.

of this study. Our first objective is to develop synthetic econometric models for the Caribbean island of Puerto Rico to reveal overriding landscape controls on (1) forest age, (2) the age of forests that undergo clearing for land development, and (3) the locations of forest that undergo development, testing whether forest age is influential. The second objective is to assess whether the interactions between spatial patterns of forest age and land development are in fact relevant to the aboveground live biomass (AGLB) and tree species richness (S) of the forests subject to clearing. A final objective is to synthesize our findings with other studies on land development or tropical forest recovery after clearing to reveal general patterns in human-impacted landscapes.

[5] Puerto Rico is ideal for studying the interactions between the spatial distributions of land development and tropical forest age. It has a well-known history of near complete forest clearing for agriculture followed by large-scale forest recovery [*Franco et al.*, 1997] (Figure 1). It has also recently experienced rapid land-cover changes to urban/built-up or surface mined lands [*del Mar López et al.*, 2001; *Helmer and Ruefenacht*, 2005]. Some studies conclude that through this history Puerto Rico exemplifies how other tropical forest landscapes may evolve [e.g., *Grau et al.*, 2003]. In fact, recent studies reveal that Puerto Rico is definitely no longer unique among tropical countries in its history of secondary forest recovery accompanied by increased land development. Puerto Rico is simply decades ahead of other tropical countries in the patterns of land-cover and land-use change. Forest area increased in many tropical countries from 1990 to 2000 [*Kauppi et al.*, 2006] as economies tilted away from agriculture. On other Caribbean islands, sugarcane cultivation has declined or ended [*Mitchell*, 2005]. On several of these islands, the agricultural decline has been accompanied by large increases in forested and urban/built-up lands between 1945 and 2000 [*Helmer et al.*, 2008]. Mechanization of sugarcane cultivation in other countries, like Brazil, depressed prices for this commodity, and price subsidies have been in decline, making sugarcane cultivation on Caribbean islands unprofitable.

2. Methods

[6] To characterize the relationship between tropical forest age and land-cover change to urban/built-up or other developed lands, we estimated parameters for three logit models. Data for the response variables in these models were from previously published, remote sensing-based maps. We then used forest inventory data to assess whether tree species richness (S) of forest cleared for land development may differ from that of other forest types in the landscape. Finally, we used the inventory data to illustrate how spatial patterns of forest age and land development may affect the biomass of forest cleared for land development.

2.1. Study Area

[7] The Caribbean island of Puerto Rico (17°45′ N 66°15′ W) is part of the Greater Antilles and encompasses about 8,800 km^2. Moist broadleaf evergreen and seasonal evergreen forest types cover much of the island, but its forests also include drought deciduous and semideciduous (including semievergreen) forests as well as cloud forests in its two main mountain ranges (Figure 2). All forests in Puerto Rico are subtropical [*Holdridge*, 1967]. Tree species composition varies not only with climate but also with geology, differing somewhat between volcanic or alluvial, limestone, and serpentine substrates [*Ewel and Whitmore*, 1973]. Previous land use also has a lasting impact on species composition [*Aide et al.*, 1996; *Marin-Spiotta et al.*, 2007; *Thompson et al.*, 2002]. Environmental factors interact with previous land use to determine species composition over the landscape, and today new forest communities include forests of the introduced *Spathodea campanulata* emerging on abandoned sugarcane fields and former pasture [*Abelleira Martinez and Lugo*, 2008; *Chinea and Helmer*, 2003; *Rivera and Aide*, 1998].

[8] Forest clearing for agriculture began with European settlement and continued until about the 1940s. Large-scale forest recovery during the second half of the 20th century has followed [*Franco et al.*, 1997] as the Puerto Rican economy shifted toward industry and services. Both lowland crops, mainly sugarcane and pineapple, and woody agriculture at mid to high elevations, mainly shade coffee, declined 95 and 88 percent, respectively [*Kennaway and Helmer*, 2007]. Sugarcane cultivation, for example, declined from 182,000 ha in 1951 to 72,750 ha in 1977, less than 23,125 ha in 1991, and less than 9,700 ha in 2000 (from data described in *Kennaway and Helmer* [2007] and *Helmer et al.* [2002]). Meanwhile, island-wide forest cover increased from 18 percent in 1951 to 45 percent in 2000 (including all woodlands and forested wetlands). With a more generous definition of forest as lands with 10 percent stocking, forest cover estimates range as high as 57 percent in 2004 [*Brandeis et al.*, 2007].

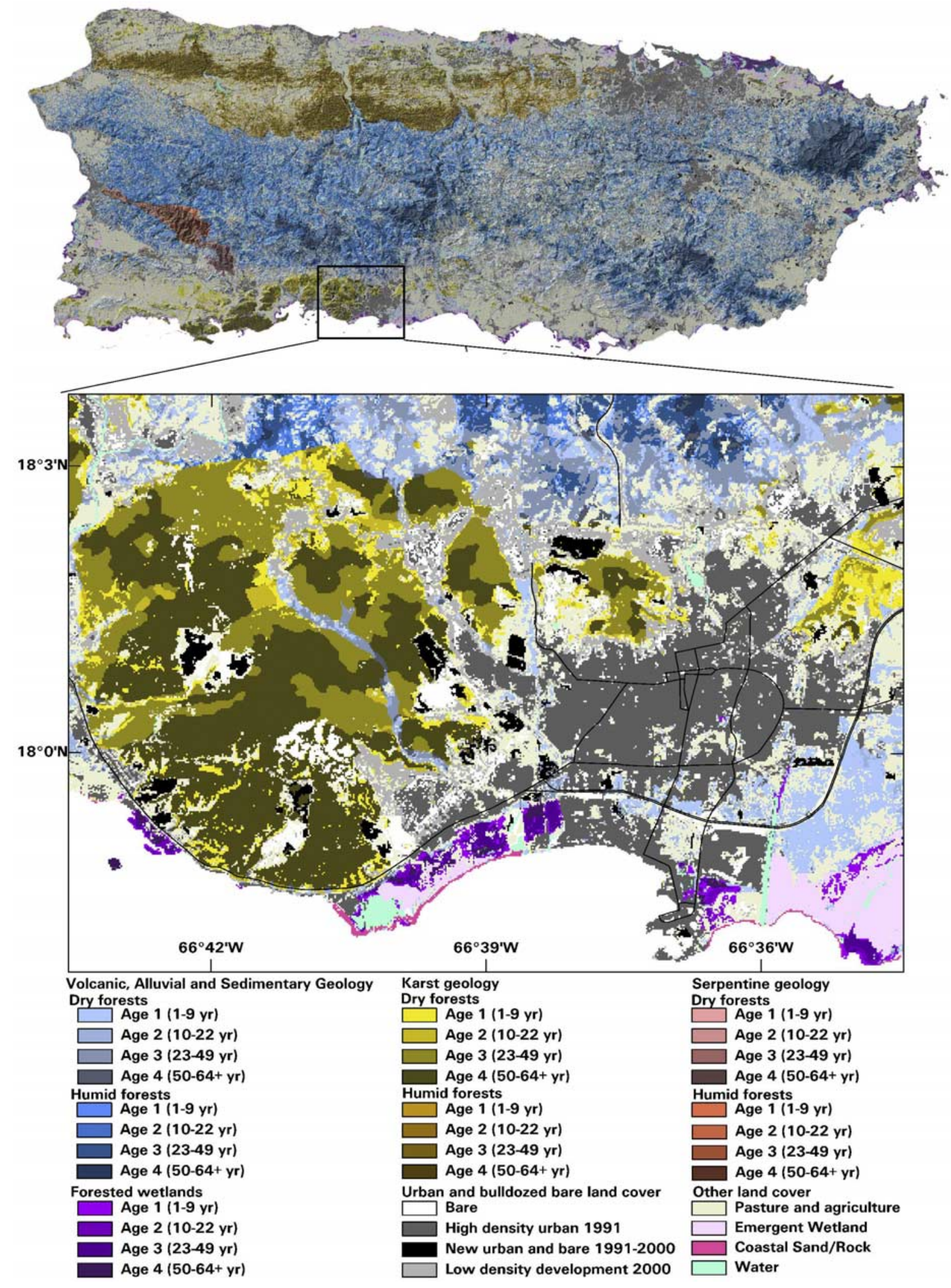

Figure 2. Forest types classified by age and their relationship to topography and surface geology on the Caribbean island of Puerto Rico. An overlay of hill shade onto forest types and age shows that forest on more rugged land and at higher elevations is older for all forest types on the island. The close-up around the city of Ponce, Puerto Rico, shows that older forests near urban areas on rugged but unprotected karst geology undergo change to urban/built-up or surface mined lands.

[9] Forested wetlands in Puerto Rico include various mangrove communities, *Pterocarpus officinalis* swamps, swamps in limestone sinkholes, and forested wetlands recovering from previous clearing for agriculture. New land-cover data for 1991 re-classifies some forest as wetlands and suggests that forested wetland area increased from 1977 to 2000 [*Chinea and Agosto*, 2007; *Kennaway and Helmer*, 2007]. In addition, some recovering forests now identified as nonwetland forest may have recovered the hydric soils, flooding regime or hydrophilic species that would qualify them as forested wetland.

2.2. Maps of Land Cover, Land-Cover Change, and Forest Age

[10] Maps for the econometric modeling and analyses of forest attributes were remote sensing-based maps of land development from 1991 to 2000, as well as land cover, forest type, and forest age in both 1991 and 2000. *Helmer and Ruefenacht* [2005] produced the land development map with a minimum mapping unit of 1 ha from two Landsat satellite image mosaics merged into one multidate image. They validated the map with aerial photos from both dates. It accurately detects land-cover change due to new residential developments and new development within urban centers, which are the major types of land development in Puerto Rico. It also includes two patches of forest cleared for limestone surface mining. The two image mosaics resulted from filling cloudy areas in Landsat TM and ETM+ scenes with imagery from other dates after regression tree normalization, which reduces inter-date image differences more than linear methods [*Helmer and Ruefenacht*, 2007].

[11] *Kennaway and Helmer* [2007] classified the above mentioned Landsat image mosaics using decision tree analysis, mapping land cover and forest type in both 1991 and 2000. They then coregistered the satellite image-based maps with land-cover maps from 1951 and 1977 that were based on aerial photo interpretation. With the resulting map time series, they produced maps of forest age in 1991 and 2000. They assigned three age classes (1–13, 14–40 and $\geq$ 41–55+ yr) in the forest age map for 1991 based on forest presence in 1951, 1977 and 1991. They assigned four age classes (1–9, 10–22, 23–49, and 50–64+ yr) for the year 2000. The upper end of the age range for the oldest age class in both maps assumes that lands mapped as dense forest in 1951 were at least 15 years old at that time. The age assignments also assume that woody vegetation grew older during the interval between two successive map dates. Consequently, the age maps have some error to the extent that forest clearing and regrowth occurred between map dates. However, no other time series data set of land cover is available for the entire island of Puerto Rico.

2.3. Models of Forest Age in 2000, the Age of Forests Cleared for Land Development, and Forest Clearing for Land Development

[12] The two models of forest age are multinomial (polytomous) logit models of (1) forest age in 2000, and (2) the age of forest that underwent development from 1991 to 2000. The models used age class as the categorical dependent variable. The structure of these models is similar to other spatially explicit models of land use that are simple econometric models [*Chomitz and Gray*, 1996; *Turner et al.*, 1996]. It assumes that model dependent variables are proxies for the processes that impact land use. In this study, as in *Helmer* [2000], we are considering the dependent variable of forest age to be an aspect of land use. For any forest point, the processes impacting land use have resulted in forest being a particular age. These processes are assumed to include human decisions aimed at maximizing land rent such that location and land quality determine land use. In other words, the attributes of a particular place influence if and when forest is cleared for agriculture; agriculture is abandoned and forests recover; or forest is cleared for land development. The model explanatory variables are landscape attributes, such as topography and distance to roads. The multinomial models yield sets of logistic models, each with the following form:

$$\ln\left[(\text{Pr. Age class}_i)/\left(\text{Pr. Age class}_j\right)\right] = \beta_0 + \beta_1 X_1 \ldots + \beta_n X_n \quad (1)$$

where (Pr. Age class$_i$) and (Pr. Age class$_j$) are the probabilities of forest being age class i and j, respectively, β_0 is a constant, $\beta_1 \ldots \beta_n$ are coefficient estimates, and $X_1 \ldots X_n$ are one or more explanatory variables. Here (Pr. Age class$_j$) is the probability that forest is in the youngest forest age class. Each of the two multinomial models yields a set of probability models that are each in the form of equation (1). Each of these probability models estimates the relative probabilities (odds ratios) between a forest point being in one of the older age classes relative to the youngest age class tested. The first multinomial model with four age categories, for example, output three probability models.

[13] The model of forest cleared for land development is binomial (dichotomous), and it yields one logistic model in the form of equation (2):

$$\ln[(\text{Pr. Land Dev.})/(\text{Pr. No Land Dev.})] = \beta_0 + \beta_1 X_1 \ldots + \beta_n X_n \quad (2)$$

where (Pr. Land Dev.) and (Pr. No Land Dev.) are, respectively, the probabilities of forest being cleared for land development from 1991 to 2000 or not being cleared for land development.

2.4. Explanatory Variables and Sample Design for Model Observations

[14] Spatial autocorrelation in land-use change is well-documented. Predictive land-cover change models that use cellular automata take advantage of this fact. Yet spatial autocorrelation in a dependent variable can also bias statistical models. The spatial dependence violates the assumption of independence among observations, leading to underestimation of model coefficient errors and possible bias in regression models toward spatially autocorrelated explanatory variables [*Miller et al.*, 2007]. The dilemma is that spatial autocorrelation in dependent variables can also result from neighborhood processes that significantly influence spatial pattern. Examples of such endogenous variables are amount of nearby forest as a seed source in forest regeneration models, or pricing of nearby homes in housing

price models. In these cases both an explanatory variable and the dependent variable measure the same or a closely related attribute. Understandably, these endogenous variables can greatly improve predictions from the resulting models [*Kissling and Gudrun*, 2008].

[15] Two common ways to avoid model bias from spatial autocorrelation in econometric modeling, which are often used together, are: (1) sampling to minimize the bias, or (2) including a spatial lag variable [*Kline*, 2003; *Kline and Alig*, 2001; *Kline et al.*, 2007]. Sample designs that avoid bias from autocorrelation are also common in spatial ecological models [*Miller et al.*, 2007]. As for spatial lag variables, they are meant to account for localized spatial influences (endogenous variables) and are based on some type of spatial weights matrix related to the dependent variable. Their calculation should depend on the issue under study, and they may be as simple as surrounding amount of a relevant land-cover type. One problem with spatial lag variables is that they can displace all other variables, resulting in simple, efficient models that say little about the factors that influence the dependent variable at broader scales. For this reason, *Helmer* [2000] presents models of forest age that both do and do not include explanatory variables for surrounding forest cover. In one study, *Kline et al.* [2007] found that spatial lag variables added little to models of urban development or led to results that were difficult to interpret. Spatial econometric or ecological models require common sense structures and sample designs that consider the questions being addressed and their spatial scales, as well as the goals of the modeling (predictive versus inferential) rather than focusing on removal of spatial autocorrelation [*Kissling and Gudrun*, 2008; *Miller et al.*, 2007]. Such an approach can help identify both important landscape-scale and localized variables, as appropriate.

[16] With the above considerations in mind and a goal of inferential rather than predictive modeling, we both (1) used a sample design that avoided spatial dependence, and (2) included relevant local spatial variables (described later). The sample design for the two multinomial models of forest age consisted of random sampling followed by filtering to drop observations that might not be independent of each other. The observations came from a random sample of points (pixels) in (1) the map of forest age in 2000, for the first model and (2) a map of the forest cleared for land development from 1991 to 2000 that was classified by age in 1991, for the second model. This latter map consisted of those areas in the forest age map for 1991 that were cleared for land development by 2000. We then dropped observations that were closer together than the grain of the process under study, as in other work [*Helmer*, 2000, 2004]. In this case we dropped any points in which the 90-m window surrounding the points overlapped. The window size of 90 m came from determining the average patch size of forest that underwent land development from 1991 to 2000 with a contiguity analysis (the average patch would have a diameter of 75 m if circular). We randomly selected 2,000 points from the forest age map for 2000, assuming that about 300–600 points would adequately characterize each of the four age classes. For the second model, we randomly selected 500 points. The smaller area of forest cleared for land development necessitated the smaller sample size for the second model. After eliminating points with overlapping windows, the final number of observations was 1,875 for the first model and 309 for the second one. Despite the small size of the latter sample, oversampling was not an issue. The proportions of each forest age in the sample were similar to the proportional areas of each forest age cleared (52, 37 and 11 percent versus 54, 32 and 12 percent for forest ages 1, 2 and 3, respectively).

[17] A model contrasting cleared with uncleared forest would convincingly test whether forest age influences forest clearing for land development. This model structure is problematic, however, because forest area cleared from 1991 to 2000 was tiny compared with forest area remaining in 2000. Simple random sampling would require so many points to adequately represent all ages of cleared forest that spatially filtering the dense observations of uncleared forest might amount to a stratified sample. In logistic regression, stratification on the dependent variable yields biased intercepts [*Allison*, 1999]. Moreover, rare outcomes can bias models by underestimating the probability of a rare event [*King and Zeng*, 2001]. *King and Zeng* [2001] outline corrective steps. First, they suggest selecting "roughly" two to five times more observations of the common event (no clearing) than the rare event (clearing) in separate random samples. Second, either a weighting procedure is used in model estimation or the intercept is corrected as in equation (3) below:

$$\beta_{0\mathrm{Adj}} = \beta_0 - \ln[(1-\tau)/\tau][\bar{y}/(1-\bar{y})] \tag{3}$$

[18] In equation (3), $\beta_{0\mathrm{Adj}}$ is the adjusted intercept, τ is the fraction of 1's in the population, and $\bar{y}$ is the fraction of 1's in the sample. The sets of points from the two forest age models fit these recommendations. We combined them for the model of cleared versus uncleared forest and adjusted the model intercept with equation (3).

[19] We tested model explanatory variables that other studies [*Helmer*, 2000, 2004; *Kline et al.*, 2001] identify as relating to land development or forest age (Table 1). These variables included distances to roads, urban areas, large urban areas, and protected lands; protection status; surrounding cover of pasture, forest or urban land (local spatial variables); and elevation, slope, generalized geology, and urban gravity indices for the model of land development. Forward variable selection determined which spatial variables best explained forest age in 2000, the age of forest that underwent land development from 1991 to 2000, or whether forest in 1991 underwent land development by 2000. In forward variable selection, we retained variables if their coefficients were significant at $p < 0.05$ in at least one of the output probability models. We discarded spatial lag variables of surrounding cover of each separate forest age class in the previous time step. Though efficient predictors, these variables completely dominated the resulting models, displacing variables related to forest age over broader scales.

2.5. Relationships Between Forest Age and Biomass or Plot-Level Species Richness

[20] We used forest inventory data to assess how the interactions between spatial patterns of forest age and land development affect AGLB and S of the forests cleared for

Table 1. Variables Used in Forward Variable Selection for Developing Multinomial Logit Models of (1) Forest Age in 2000, (2) Age of Forest That Underwent Development From 1991–1992 to 2000, and (3) Forest Land Clearing for Land Development From 1991 to 2000

Variable	Description
Distance Variables	
URBNDIST	Distance in km to nearest high-density urban/built-up land in 1991 of any size.
URBLGDIST	Distance in km to nearest of six largest urban/built-up areas ($\geq$225 ha in 1991).
SECONDDIST	Distance in km to nearest secondary road.
TERTDIST	Distance in km to nearest tertiary road.
ROADDIST	Distance in km to nearest primary, secondary or tertiary road.
PROTDIST	Distance in km to nearest Commonwealth, Federal or private reserve land.
Gravity Indices[a] and Forest Age Variables (Only in Model Forest Land Development)	
SIZE $\cdot$ DIST^{-2}	ha $\cdot$ km^{-2}
SIZE $\cdot$ DIST^{-1}	ha $\cdot$ km^{-1}
SIZE $\cdot$ DIST$^{-0.5}$	ha $\cdot$ km$^{-0.5}$
SIZE$^{0.5}$ $\cdot$ DIST^{-1}	ha$^{0.5}$ km^{-1}
AGE 1, AGE 2, AGE 3	
Topographic, Geology, Protection, and Forest Type Variables	
ELEVATION	Elevation in m.
PCTSLOPE	Percent slope.
Geology	Geology of substrate, including ALLUVIAL (base case), VOLCANIC, LIMESTONE, and SERPENTINE
PROTECTED	Whether the point is or is not (base case) protected.
WETLFOR	Whether the point is or is not (base case) forested wetland.
Surrounding Land Cover Variables in Models of Age of Forest Developed From 1991 to 2000 and Forest Land Development	
SFORSHR91	Percent of woody vegetation in 90-m window surrounding an observation
SPASTURE91	Percent of pasture in 90-m window surrounding an observation
SURBAN91	Percent of high or low density urban or residential lands in 90-m window surrounding an observation
SWETLFOR91	Percent of forested wetland in 90-m window surrounding an observation
QUARRY	Whether development is or is not (base case) surface mining.
Surrounding Land Cover Variables in Model of Forest Age in 2000	
SFORSHR2000	Percent of woody vegetation in 90-m window surrounding an observation
SPASTURE2000	Percent of pasture in 90-m window surrounding an observation
SWETLFOR00	Percent of forested wetland in 90-m window surrounding an observation

[a]Gravity indices calculated with contiguous urban area size in ha and distances in m. Each index is a sum of gravity indices with the indicated power coefficients for the three urban patches that yield the largest values for the observation point (assuming those urban patches are the most influential) [*Helmer*, 2004; *Kline et al.*, 2001].

land development. The inventory data included 205 plots randomly located within systematic grids over the island and surveyed from 2001 to 2003 by the U.S. Forest Service Forest Inventory and Analysis (FIA) Caribbean program [*Brandeis et al.*, 2007]. Estimates of AGLB were available from an additional 26 plots surveyed in 2004 and 2005 for a separate study. Additional plots identified as forest in the inventory but nonforest in the land-cover maps were excluded. The land-cover maps define forest as lands with $\geq$25 percent cover of trees or of shrubs mixed with young seedlings or saplings. The FIA program defines forest more generously as having at least 10 percent stocking. Each plot consists of four circular subplots, each with a radius of 7.3 m (24 ft), which are distributed over an area of about 0.4 ha. The total sampled area of the four subplots is 0.0674 ha. In each subplot, all trees are surveyed with a diameter at breast height (dbh) $\geq$ 12.5 cm. Tree saplings with a diameter between 2.5 and 12.5 cm are surveyed in one nested circular "microplot" within each subplot. The microplots have a radius of 2.1 m. Aboveground live biomass of each plot was estimated from tree dbh and height with allometric equations appropriate for each forest type, as detailed by *Brandeis et al.* [2007].

[21] Multiple regressions between forest age and S, and an estimate of the impact of forest age spatial patterns on the biomass of forest cleared for land development, served to illustrate potential differences between forests cleared for land development and other forests in the landscape. We estimated regressions for S for nonwetland plots in the following groups: (1) all plots, (2) plots on volcanic, sedimentary or alluvial substrates, and (3) plots on limestone or serpentine substrates. The numbers of cloud forest plots or plots on serpentine substrate were too few to estimate separate regressions for them. Species richness for each plot is defined as the total number of tree species found in both the subplots and microplots. A variable for sampled plot area in the regression models of S adjusted for plots with fewer than all four subplots forested. We estimated the total biomass of forest cleared for land development from 1991 to 2000 in two ways. First, for an estimate that did not account for differences between forest ages in area cleared and biomass, we multiplied the area of each forest type cleared from 1991 to 2000 by the average AGLB of each forest type from the inventory data, assuming that the cleared forests had AGLB similar to that of the inventory-measured AGLB for that type. Second, we estimated cleared forest biomass weighted by age differences in cleared forest areas and AGLB. This estimate assumed that the AGLB of different forest ages would be similar to the

Table 2. The Three Probability Models Resulting From the Multinomial Model of Forest Age in 2000[a]

Variable	Estimated Coefficients[b] ln [(Pr. Age class$_2$)/(Pr. Age class$_1$)]		Estimated Coefficients[b] ln [(Pr. Age class$_3$)/(Pr. Age class$_1$)]		Estimated Coefficients[b] ln [(Pr. Age class$_4$)/(Pr. Age class$_1$)]		Mean of X[c]
Constant	−0.82 ± 0.55	**	−2.72 ± 0.79	***	−2.86 ± 0.76	***	
PROTECTED	−0.12 ± 1.00	ns	0.96 ± 0.91	*	3.02 ± 0.85	***	0.09
LIMESTONE	−0.18 ± 0.55	ns	1.92 ± 0.74	***	1.47 ± 0.66	***	0.24
SLOPPCT	0.016 ± 0.0080	***	0.028 ± 0.0084	***	0.030 ± 0.0098	***	30
ELEVATION	0.0014 ± 0.00080	***	0.0018 ± 0.00086	***	0.0035 ± 0.00103	***	287
VOLCANIC	0.48 ± 0.49	ns	1.18 ± 0.73	**	−1.03 ± 0.71	**	0.67
SPAST2000	−0.0036 ± 0.008	ns	−0.0320 ± 0.012	***	−0.0353 ± 0.016	***	6.1
ROADDDIST	0.26 ± 1.10	ns	1.34 ± 1.10	*	2.46 ± 1.14	***	0.16
TERTDIST	−0.016 ± 0.20	ns	0.282 ± 0.20	*	0.41 ± 0.22	***	0.90
SECONDDIST	−0.069 ± 0.087	ns	0.147 ± 0.087	**	0.13 ± 0.104	*	1.8
SWETLFOR00	0.039 ± 0.029	*	0.024 ± 0.032	ns	0.043 ± 0.030	*	1.4
URBLGDIST	−0.00083 ± 0.016	ns	−0.014 ± 0.017	ns	−0.025 ± 0.021	*	15
URBNDIST	0.10 ± 0.093	*	−0.033 ± 0.10	ns	0.038 ± 0.12	ns	1.91
SERPENTINE	0.61 ± 1.48	ns	1.60 ± 1.59	*	1.05 ± 1.53	ns	0.03

[a]Each model estimates the log-odds ratio that forest in the year 2000 was in an older age class relative to the youngest age class. Forests closer to cities and roads, on gentler slopes and at lower elevations are increasingly younger. Forests under protection, on rugged land, on infertile soils, or forested wetlands tend to be older. The dependent variable of each probability model is shown at the top of the column of coefficient estimates and significance for the explanatory variables. The age classes are: Age class 1, 1–9 yr; Age class 2, 10–22 yr; Age class 3, 23–49 yr, and Age class 4, 50–64+ yr. Summary statistics for the overall multinomial model are as follows: n = 1875, Log Likelihood = −2439, Restricted Log Likelihood = −2988, χ^2 = 1099, d.f. = 39, P < 0.0001. Table 1 contains variable descriptions. Without recoding mangrove to old forest as in *Kennaway and Helmer* [2007], the age distribution of forested wetland, in ha, is: 1,822 (Age 1), 1,505 (Age 2), 1,481 (Age 3), and 3,423 (Age 4). The total of 8,231 ha is a slight overestimate, and mangrove area proportions of younger and older ages are slightly overestimated or underestimated, respectively, due to slight misregistration around coastlines.

[b]Asterisks indicate coefficient p values, with ***, **, and * representing, respectively, $p < 0.0005$; $p < 0.005$; and $p < 0.05$ (ns, coefficient not significant).

[c]Mean value of explanatory variable or proportion of observations within category for discrete variables.

average of forest inventory estimates for the particular forest age and type.

3. Results

3.1. Models of Forest Age, Age of Forest Cleared for Land Development, and Land Development

[22] Each multinomial logit model yields a set of logistic models in the form of equation (1). The logistic models each estimate the log odds ratio of forest being in an older class relative to the youngest class tested (Tables 2 and 3). In the multinomial model of forest age, protection, steeper slopes or higher elevation result in progressively greater probabilities that forest is in one of the three older classes in 2000 relative to the youngest forest (1–9 yr) (Table 2). For example, protected forest is about 3 times more likely to be Age 3 (23–49 yr) than Age 1 and 20 times more likely to be Age 4 (50–64+ yr) than Age 1. For each 500-m increase in elevation, the odds of forest being older relative to the youngest class are six, 2.5 and two times greater for Ages 4, 3 and 2 (10–22 yr), respectively. Forest on limestone substrate is four to six times more likely to be in the two older classes. Less surrounding pasture, increased distance to roads, serpentine substrate, or more surrounding forested wetland, makes forest significantly more likely to be older in one or more of the probability models. A surprising result is that all else equal, the oldest forest is slightly (88 percent) more likely to be close to a large urban area, which we discuss later.

[23] The set of logistic equations from the multinomial model of the age of forest that underwent development from 1991 to 2000 has fewer significant explanatory variables

Table 3. The Two Probability Models Resulting From the Multinomial Model of the Age Class of Forest Stands That Underwent Development From 1991 to 2000[a]

Variable	Estimated Coefficients[b] ln [(Pr. Age$_2$)/(Pr. Age$_1$)]		Estimated Coefficients[b] ln [(Pr. Age$_3$)/(Pr. Age$_1$)]		Mean of X[c]
Constant	−0.31 ± 0.68	ns	−4.58 ± 1.85	***	
LIMESTONE	1.14 ± 0.78	**	4.06 ± 1.44	***	0.24
TERTDIST	−0.25 ± 0.43	ns	1.03 ± 0.62	**	0.88
SPASTURE91	−0.021 ± 0.015	**	−0.056 ± 0.037	**	16
ELEVATION	−0.0055 ± 0.0029	***	−0.0080 ± 0.0094	Ns	114
PCTSLOPE	0.029 ± 0.022	*	0.044 ± 0.043	*	17
ROADDIST	3.77 ± 3.00	*	3.58 ± 4.73	Ns	0.12

[a]Each model estimates the log-odds ratio that forest cleared for land development was in an older age class relative to the youngest age class. The ages of forests cleared for land development appear to depend mainly on the spatial patterns of forest age before forest clearing. The dependent variable of each equation is shown at the top of the column of corresponding coefficient estimates and significance for the explanatory variables. The age classes are: Age class 1, 1–13 yr; Age class 2, 14–40 yr; and Age class 3, $\geq$ 41–55+ yr. Summary statistics for the overall multinomial model are as follows: n = 309, Log Likelihood = −212, Restricted Log Likelihood = −295, χ^2 = 165, d.f. = 12, P < 0.0001. Table 1 contains variable descriptions.

[b]Asterisks indicate coefficient p values, with ***, **, and * representing, respectively, $p < 0.0005$; $p < 0.005$; and $p < 0.05$ (ns, coefficient not significant).

[c]Mean value of continuous explanatory variable or proportion of observations within category for discrete variables.

Table 4. The Probability Model Resulting From the Multinomial Model of Forest That Underwent Development From 1991 to 2000[a]

Variable	Estimated Coefficients[b] ln [(Pr. Age_2)/(Pr. Age_1)]		Mean of X[c]
Constant	−4.99 ± 0.48	***	
URBNDIST	−0.50 ± 0.21	***	1.9
URBLGDIST	−0.069 ± 0.021	***	15
SLOPPCT	−0.040 ± 0.012	***	31
PRIMDIST	−0.17 ± 0.061	***	5.8
SECONDDIST	−0.28 ± 0.12	***	1.8
PROTECTED	−1.99 ± 1.5	*	0.11
WETLFOR	−2.80 ± 2.1	*	0.012
SPASTURE91	0.014 ± 0.010	*	7.4
ELEVATION	−0.0016 ± 0.0013	*	299
AGE 3	−0.47 ± 0.45	*	0.25

[a]It estimates the log-odds ratio that forest was cleared for land development relative to not being cleared. Development likelihood balances proximity to urban areas and roads with topographic factors that affect ease and cost of land development. There is no difference in the likelihood of development between Age 1 (1–13 yr) and Age 2 (14–40 yr) forests, but Age 3 forests (41–55+ yr) are slightly less likely to undergo development. Summary statistics for the overall multinomial model are as follows: n = 2184, Log Likelihood = −485, Restricted Log Likelihood = −834, χ^2 = 698, d.f. = 10, P < 0.0001. Table 1 contains variable descriptions.

[b]Asterisks indicate coefficient p values, with ***, **, and * representing, respectively, $p < 0.0005$; $p < 0.005$; and $p < 0.05$.

[c]Mean value of continuous explanatory variable or proportion of observations within category for discrete variables.

because it has fewer observations and less variable conditions. The observations of cleared forest, for example, include little or no cloud, serpentine or protected forest. Relative to the youngest forest cleared for land development from 1991 to 2000, less surrounding pasture, steeper slopes, or limestone substrate increase the likelihood that cleared forest was older (Table 3). If the forest that was cleared for land development was on limestone substrate, it was almost 60 times more likely to be in the oldest class compared with the youngest one. As with the model of forest age in 2000, the coefficients for these variables increase in absolute magnitude with forest age, and amount of surrounding pasture displaces amount of surrounding forest in forward variable selection. Forest that underwent development is more likely to be in the second oldest age class if it is at higher elevations and further from any road. It is more likely to be in the oldest age class if it is further from a tertiary road.

[24] The model contrasting forest cleared for land development from 1991 to 2000 with the forest that remained suggested that the most significant influences on whether forest is cleared for urbanization or surface mining are proximity to existing urban areas and roads as well as slope (Table 4). Clearing is also more likely at lower elevations and with more surrounding pasture. Clearing is less likely if forest is protected or a wetland. The likelihood of land development did not differ between Age 1 and Age 2 forests, but Age 3 forests were about 40 percent less likely to be developed.

3.2. Relationships Between Forest Age and Biomass or Species Richness

[25] As expected, the square root of forest inventory plot species richness was significantly related to forest age in 2000, with younger ages having successively fewer species than the base case of the oldest class (Table 4). On serpentine and karst substrates, S values for Ages 3 and 4 forests were not significantly different, but Age 1 to 2 forests had successively fewer species. The estimate of total forest biomass cleared for land development from 1991 to 2000 was 19 percent less when age differences in areas and biomass of cleared forest were accounted for (Table 5). Average AGLB of some old forest types was less than AGLB of corresponding intermediate-aged forest. We attribute this result to three main sources of uncertainty in the biomass and age estimates. First, some categories of forest type and age had relatively few samples because of the systematic sample design of FIA plots. Second, errors in the age maps from misclassifications, misregistration, or forest clearing and regrowth between map dates, likely led to errors in age assignment for some plots. For example, much former coffee shade was classified as Age 2 forest but could be older as mentioned. Finally, finely scaled topographic changes cause large variability in AGLB of drier forest types, particularly those on karst and serpentine substrates. As a result, small AGLB of old forests of these types could be an artifact of the particular places sampled.

4. Discussion

4.1. Landscape Controls on the Spatial Distribution of Tropical Forest Age

[26] Accessibility, arability and spatial contagion seem to be the overriding spatial controls on the age of tropical forest recovering from clearing for agriculture (Table 7). Though their importance differs with economic conditions and landscape structure, these factors emerge strongly from this study and other recent studies. Accessibility and arability determine (1) the spatial patterns of the agricultural abandonment that permits forest recovery, and (2) where

Table 5. Models of the Relationship Between Forest Age Class and Plot-Level Species Richness (S) in Nonwetland Forest Inventory Plots[a]

	All Nonwetland Plots[b]	Volcanic, Sedimentary, and Alluvial Substrates[b]	Limestone and Serpentine Substrates[b]
		Response Variables	
	$S^{0.5}$	$S^{0.5}$	$S^{0.5}$
Explanatory Variables			
Age_4 (Intercept)	2.11***	1.83***	2.21***
Age_3	−0.36**	−0.47*	-0.07^{ns}
Age_2	−0.46***	−0.41*	−0.47*
Age_1	−0.75***	−0.79***	−0.59*
Plot area	18.88***	22.86***	17.39**
R-square	0.25	0.27	0.26
Pr > F[c]	<0.0001	<0.0001	<0.0001
N	205	128	77

[a]Models include all plots, only plots on volcanic, alluvial, or sedimentary substrate, and only plots on serpentine or limestone substrate. The age classes are for the year 2000: Age class 1, 1–9 yr; Age class 2, 10–22 yr; Age class 3, 23–49 yr, and Age class 4, 50–64+ yr. Plots with all subplots forested have a total area of 0.0674 ha.

[b]Asterisks indicate probabilities of erroneously rejecting the null hypothesis that the coefficient estimate is zero, based on a two-sided t-distribution, ***$p \leq 0.0005$, **$p \leq 0.005$, *$p \leq 0.05$, ns not significant at $p \leq 0.05$.

[c]Pr > F is the probability of erroneously rejecting the null hypothesis that there is no significant relationship between the response and explanatory variables.

humans leave old-growth forest remnants. Spatial contagion can spur recovery of tree species that were present in the original forest [*Franklin and Rey*, 2007; *Guevara et al.*, 1986; *Muñiz-Castro et al.*, 2006; *Oosterhoorn and Kappelle*, 2000; *Purata*, 1986; *Uhl et al.*, 1988]. Though natural disturbances are outside the focus of this study, they of course also affect the spatial distribution of forest stands of different ages.

[27] This study covers a broader range of forest types than similar studies in tropical landscapes, which are limited to cloud forests [*Helmer et al.*, 2000], higher elevation forests on volcanic or limestone substrate [*Rudel et al.*, 2000], or lowland forests [*Etter et al.*, 2005]. Over Puerto Rico, forests range from lowland dry and moist to montane cloud forests and occur on karst, serpentine, volcanic and alluvial substrates. Across this range, forest age decreases as accessibility increases. Forests closer to roads, on gentler slopes and at lower elevations are increasingly younger. Forests on rugged land, on infertile soils, or forested wetlands tend to be older. These areas are abandoned first when agriculture no longer dominates the economy of a region. Protected forests are also older. Less surrounding pasture (and correspondingly more surrounding forest) also implies older forest. The model explains why nonwetland forests on alluvial or volcanic substrates, or on flat limestone substrates, have 10 percent or less of their area in old forest. In contrast, more than 60 percent of cloud forests and serpentine forests were at least 50–64 yr old in 2000. Forty to fifty percent of forested wetlands and forests on rugged limestone (karst) geology were at least 50–64 yr old [*Kennaway and Helmer*, 2007]. The least accessible or arable lands are also where old-growth forest remnants may remain. In Puerto Rico, some old-growth forest remnants remain in protected areas. These remnants appear to include areas of cloud forest, evergreen forest on volcanic substrate in the Luquillo Experimental Forest, dry forest on karst substrate in the Guánica reserve, and some forested wetlands, including *Pterocarpus* swamp and a large portion of mangroves.

[28] In similar studies, logistic models of tropical forest age (secondary versus old-growth forest) for montane Costa Rica show that age increases with elevation, distance from roads, distance from agriculture and pasture, and protection level. Land is more likely to be secondary forest as compared with agriculture as amount of surrounding old-growth forest increases. Socioeconomic forces, like accessibility, and biophysical forces, like nearby forest seed sources, seed vectors, and microclimate, probably combine to create the secondary forest patterns [*Helmer*, 2000]. In lowland Colombian landscapes, forest age directly correlates with amount of surrounding forest, and age decreases with accessibility and soil fertility [*Etter et al.*, 2005]. *Rudel et al.* [2000] document that as shade coffee cultivation declined in the coffee-growing region of Puerto Rico, agricultural abandonment and forest regrowth were more likely at higher elevations and on less fertile soils as farmers sought off-farm income in an urbanizing economy. The relative importance of accessibility and arability, however, do change with economic conditions. In Western Honduras, forest recovered on accessible lands with lower soil fertility when higher elevation lands became accessible for coffee cultivation [*Nagendra et al.*, 2003].

[29] The modeling suggests that tropical forest recovery proceeds like deforestation in reverse. Support for this concept also comes from landscape pattern analyses. Tropical forest recovery tends to spread outwards from existing forest patches [*Kramer*, 1997; *Turner et al.*, 1996] and fill in cleared areas surrounded by forest. Because secondary forest surrounds or is surrounded by old-growth forest, it geometrically increases forest mean patch size and core area in landscapes, reducing forest patch number and buffering old-growth forest. These same outcomes have been documented in montane Costa Rica, northwest Costa Rica, Palau, lowland Amazonia and montane Mexico [*Cayuela et al.*, 2006; *Endress and Chinea*, 2001; *Etter et al.*, 2005; *Helmer*, 2000; *Kramer*, 1997].

4.2. Landscape Controls on the Age of Forests Cleared for Land Development

[30] Of the 6,670 ha of land converted to urban or surface mined lands from 1991 to 2000, 22 percent was forest (Table 6). In the model contrasting this cleared forest with remaining forest, the most significant factors reflect decisions that balance proximity to and size of existing urban areas and roads with topographic factors that probably affect ease and cost of land development. These factors are similar to those that influence urbanization of any land-cover type in Puerto Rico [*Helmer*, 2004]. All else equal, the likelihood of land development did not differ between the two younger forest ages (1–13 yr and 14–41 yr old). Land development likelihood was slightly smaller for the oldest forests (41–55+ yr) compared with the youngest ones, implying that the average stand in this class has some protection that is not accounted for by the other model variables we tested. Otherwise, the ages of forests cleared for land development appear to depend mainly on the spatial patterns of forest age before forest clearing. More of the youngest forest is cleared for land development mainly because of how the spatial patterns of forest recovery and land development intersect. Supporting this conclusion are the similarities between the model of forest age in 2000 and the model of cleared forest age. In both models, older forest is on less accessible lands where agriculture is less feasible: further from roads, at higher elevations, on steeper slopes, or on limestone substrate.

[31] The possibility that land owners may allow forest to regenerate on land they expect to undergo development may increase the amount of young forest cleared. In the U.S., more young forest clearing may be due to declines in forest management where land development or population density increase. Lands formerly managed for timber undergo parcelization, and residential lands become dispersed within them. The management declines are evidenced by lower stocking levels, less pre-commercial thinning, less replanting, and less production or harvest [*Barlow et al.*, 1998; *Kline*, 2004; *Kline and Alig*, 2005; *Munn et al.*, 2002; *Wear et al.*, 1999]. Agricultural management may also decline in the face of land development. Either way, however, agriculture has remained active longer and forest is younger in the same more accessible places that are most desirable for land development.

[32] At the same time, some older forest is close to urban areas. In fact, all else equal, forest present in 2000 is slightly more likely to be in the oldest age class if it is close to a large urban area. This seemingly contradictory result

Table 6. Areas of Forest Cleared for Land Development From 1991 to 2000 by Type and Age Class (Forest Types Are Generalized From Kennaway and Helmer [2007]), Aboveground Live Biomass (AGLB) of Forest by Age and Type, and Total AGLB of Forest Cleared for Land Development From 1991 to 2000 Assuming (1) Uniform Age and Biomass of Cleared Forest (Non-Age-Weighted Biomass Cleared), and (2) Area and Biomass of Cleared Forest Varying With Age (Age-Weighted Biomass Cleared)[a]

Forest Type	Area Urbanized of Youngest[b] Forest, ha	Area Urbanized of Intermediate Aged[c] Forest, ha	Area Urbanized of Old[d] Forest, ha	Total Forest Area Urbanized, ha	AGLB of Young[b] Forest, Mg ha^{-1}	AGLB of Intermediate Aged[c] Forest, Mg ha^{-1}	AGLB of Old[d] Forest, Mg ha^{-1}	AGLB of All Ages, Mg ha^{-1}	Non-Age-Weighted Biomass Cleared, Mg	Age-Weighted Biomass Cleared, Mg
Semideciduous and drought deciduous forests on alluvial, volcanic, or flat limestone geology	108	58	19	187	53.6	66.3	-	60.7	11,354	10,879
Evergreen and seasonal evergreen forests on alluvial or volcanic geology	610	298	21	928	72.4	107.1	136.1	104.4	96,885	78,830
Semideciduous, drought deciduous and mixed forests on karst geology	36	63	108	207	34.5	71.7	53.6	56.8	11,762	11,545
Seasonal evergreen, semideciduous, and evergreen forest complex on karst geology	33	40	23	97.1	51.4	87.6	93.6	83.3	8,090	7,364
Semideciduous and seasonal evergreen forest on serpentine	0.5	3.4	0	3.9	16.4	79.2	16.7	47.9	187	277
Evergreen forest on serpentine	0	0	0	0	–	25.3	79.6	61.5	–	–
Elfin, sierra palm, transitional, and tall cloud forest	0.4	0	0	0.4	–	128.2	134.5	132.6	53	51
Forested wetlands[e]	10	4.2	1.5	15.7	0.75	–	142.6	114.3	1,794	701[f]
Total	797	466	173	1,439					130,125	109,649

[a]All biomass estimates are as dry weight.
[b]Age 1–13 yr in 1991; 1–9 yr in 2000.
[c]Age 14–40 yr in 1991; 10–49 yr in 2000.
[d]Age 41–55+ yr in 1991; 50–64+ yr in 2000.
[e]AGLB of old forested wetlands includes two *Pterocarpus* swamp plots and may be large compared with most mangrove and secondary forest wetlands in Puerto Rico.
[f]Based on average forested wetland biomass.

reflects the fact that some of the oldest forests in the landscape are near urban centers, because they are protected wetlands, are in the largest forest reserve, or are forest on rugged karst geology. Humans either leave these forests undisturbed or abandon them sooner because of topography, regulations, ownership or low agricultural potential.

[33] Limestone geology is significant when modeling the age of forests cleared for land development, because many observations of developed old forest were on limestone substrate. Twenty percent of forests cleared for land development from 1991 to 2000 were growing in areas of karst physiography, accounting for more than 75 percent of the oldest forest cleared. These forests include much of the oldest forest on the island that is not protected. They were among the first to reforest as economics on the island changed, even though some karst areas are adjacent to or within large urban areas. These lands are apparently now valuable for urban development or surface mining if they are close to an urban center. Likewise, before mangroves were under regulatory protection, some large stands near the capitol city of San Juan were cleared and filled for residential development. Financial profitability of land development may be much greater than agricultural profits ever were. Older forests that are not historically convenient to roads and urban centers may also be vulnerable to land development if they are in a desirable natural setting. However, this latter process is not as well-documented in Puerto Rico.

4.3. Plot-Level Species Richness and Biomass of Forest Cleared for Land Development

[34] The youngest Puerto Rican forests are apparently still young enough that, on average, their plot-level species richness and AGLB are smaller than comparable old forest present in 1951. A positive outcome (with respect to the conservation of species diversity) of the way that spatial patterns of forest age and land development interact is that most forest cleared for land development tends to have less biomass and fewer species. Despite the inherent uncertainties in the map-based estimates of forest age, the broad age classes explained about 25 percent of variation in plot-level S. In addition, accounting for age variation in both cleared forest area and biomass resulted in an estimate of total AGLB cleared for land development that was 19 percent less than if age variation was ignored. A negative aspect of these patterns is that fertile low- to mid elevation ecological zones, once important for agriculture, are the least protected and most disturbed zones and under the most land development pressure [*Helmer*, 2004]. Another cautionary note is that even though most of the forest cleared for development is younger, old forest remains vulnerable to land development.

5. Conclusions and Implications

[35] In tropical landscapes recovering from large scale clearing for agriculture, this study and the other studies mentioned above suggest that accessibility, arability and spatial contagion are the main spatial factors that control patterns of forest age, though natural disturbances are also important (Table 7). An outcome of these factors is that older forest and old-growth remnants are more common on

Table 7. Landscape Controls on Spatial Patterns of Secondary Forest Age and the Age and Types of Forests Cleared for Land Development (Urban Development or Surface Mining), and the Outcomes of These Patterns

	Controls and Outcomes
Spatial controls on tropical forest age	Accessibility - topography, ownership or protection, and transport routes.
	Arability - topography and soil fertility (depth, texture, chemistry, hydrologic regime).
	Spatial contagion - proximity to seed sources and vectors, milder microclimate, and vulnerability to disturbance.
	Natural disturbances.
	Current economic conditions and opportunities.
Outcomes of spatial controls on forest age	For a given economic condition, older forest and old-growth remnants are more common further from roads and rivers, have more surrounding forest and are on less fertile soils, in wetlands and under protection. Often they are also at higher elevations and on steeper slopes.
	Forest patch size and core area increase and forest patch numbers decrease with forest recovery, buffering older forest.
	Recovering forest may have more old-growth forest species if closer to old-growth.
	Changing economic or ownership conditions may lead to forest recovery or old-growth forest clearing on more accessible but less fertile lands.
Spatial controls on land development	Accessibility - topography, ownership or protection, and transport routes.
	Desirability - including desirable natural settings.
	Spatial contagion - distance to large urban centers very important.
	Current economic conditions and opportunities.
Outcomes of spatial controls on land development	Lands on gentler slopes and closer to large urban centers and roads are most likely to undergo clearing for land development.
	Lands that were formerly remote, rugged or otherwise inaccessible or had low arability may become profitable to develop.
Outcomes of the intersections between spatial controls on land development and forest age	Land development impacts the same areas that were most impacted by agriculture (where agriculture remained active longer), and most of the forest cleared for urban development is younger and less species-rich.
	If recovering forests are still relatively young, the total forest biomass cleared for land development is less than if forest age was uniform over the landscape.
	Forest management may decline as developed lands spread.
	More species-rich older forests on less arable lands, where agriculture was abandoned first, also undergo some clearing for land development because profit potential is great.

steeper slopes, under protection, further from roads and rivers, on less fertile soils, in wetlands, have more surrounding forest and in many landscapes are at higher elevations. Accessibility, arability, and spatial contagion also tend to control patterns of forest clearing by humans [*Chomitz and Gray*, 1996], which is well-known. Old-growth forest logging that increases accessibility to forest often leads to outright forest clearing [*Asner et al.*, 2005]. When considering both forest recovery and clearing of old-growth forest, the relative importance of these spatial factors depends on changing economic conditions or ownership (and protection level). New access to more remote lands where a more profitable or newly profitable crop can thrive may, for example, result in secondary forest recovery on less fertile lands near roads [*Nagendra et al.*, 2003]. On the other hand, when technology and commodity prices permit profitable farming on less fertile soils, accessibility alone controls spatial patterns of old-growth forest clearing [*Jasinski et al.*, 2005].

[36] As for land development, spatial patterns of land-use are again directed by accessibility and spatial contagion. Close proximity to large urban centers and roads serves to increase land development and is an example of the importance of spatial contagion in this process. As a result, much of the forest cleared for land development is young relative to other forests in the landscape. If young enough, as is apparently is the case in Puerto Rico, much of this cleared forest may, on average, have less biomass and fewer species than older or remnant old-growth stands. In our analysis, accounting for age variation in cleared forest areas and biomass resulted in a 19 percent lower estimate of the total biomass cleared for land development from 1991 to 2000. However, because land development has apparently been more profitable than agriculture has been since about 1951, some old forest is cleared that may have greater conservation value. A desirable natural setting can also lead to higher housing prices [*Bockstael*, 1996] and, presumably, more profitable land development.

[37] Whether land development pressures will prevent longer-term forest recovery in fertile low to mid-elevation ecological zones, where much agriculture was once concentrated, is difficult to predict. The answer to this question, however, has implications for future carbon storage and species diversity of tropical landscapes recovering from large scale forest clearing. For similar rainfall regimes, tree species richness of old-growth tropical forests tends to increase with soil fertility and decline with elevation (though endemic species are often associated with high elevation or low soil fertility) [*Givnish*, 1999]. This trend implies that lower elevation forests have more potential to accumulate species. Moreover, seasonal or post-storm animal migrations can encompass forest over a range of elevations [*Covich and McDowell*, 1996; *Powell et al.*, 2000]. Furthermore, low and mid-elevation forests are often in moist climatic zones where forest productivity and potential carbon storage are largest [*Brown and Lugo*, 1982].

[38] The Puerto Rican example may have implications for landscapes currently subject to old-growth forest clearing for agriculture. Large-scale clearing of old-growth forest for soybean cultivation in Brazil, Bolivia and other South American countries is well-documented [*Jasinski et al.*, 2005; *Steininger et al.*, 2001]. Old-growth tropical forest clearing for other crops that are usable as biofuels, such as sugarcane and oil palm, is a current concern in Africa and Asia as well. These agricultural products are commodities. As such, where they are grown affects their production costs and profitability but not their selling price. Their selling prices are subject to the laws of supply and demand. If they eventually lose their profitability because of supply or demand changes, the biogeographical uniqueness of the cleared old-growth forest may be difficult to recover unless steps are taken now, as agricultural development proceeds, to avoid that outcome. A well-dispersed network of old-growth forest might help maintain some of the biogeographical uniqueness of each landscape and help to hedge against a future collapse of commodity agriculture. Such a dispersed network probably deserves continued attention and planning.

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Errata:

The heading for the second column of Table 4 should read as:
ln [(Pr. Land Dev.)/(Pr. No Land Dev.)]. *A corrected Table 4 is shown below.*

Table 4. The multinomial model of forest that underwent development from 1991 to 2000 resulted in one probability model. It estimates the log-odds ratio that forest was cleared for land development relative to not being cleared. Development likelihood balances proximity to urban areas and roads with topographic factors that affect ease and cost of land development. There is no difference in the likelihood of development between Age 1 (1-13 yr) and Age 2 (14-40 yr) forests, but Age 3 forests (41-55+ yr) are slightly less likely to undergo development. Summary statistics for the overall multinomial model are as follows: n = 2184, Log Likelihood = -485, Restricted Log Likelihood = -834, χ^2 =698, d.f. = 10, P < 0.0001. Table 1 contains variable descriptions.

Variable	Estimated Coefficients[a] ln [(Pr. Land Dev.)/(Pr. No Land Dev.)]		Mean of X[b]
Constant	-4.99 ± 0.48	***	
URBNDIST	-0.50 ± 0.21	***	1.9
URBLGDIST	-0.069 ± 0.021	***	15
SLOPPCT	-0.040 ± 0.012	***	31
PRIMDIST	-0.17 ± 0.061	***	5.8
SECONDDIST	-0.28 ± 0.12	***	1.8
PROTECTED	-1.99 ± 1.5	*	0.11
WETLFOR	-2.80 ± 2.1	*	0.012
SPASTURE91	0.014 ± 0.010	*	7.4
ELEVATION	-0.0016 ± 0.0013	*	299
AGE 3	-0.47 ± 0.45	*	0.25

[a]Asterisks indicate coefficient p values, with ***, **, and * representing, respectively, $p < 0.0005$; $p < 0.005$ and $p < 0.05$.
[b]Mean value of continuous explanatory variable or proportion of observations within category for discrete variables.