

The Ecological Consequences of Socioeconomic and Land-Use Changes in Postagriculture Puerto Rico

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Contrary to the general trend in the tropics, forests have recovered in Puerto Rico from less than 10% of the landscape in the late 1940s to more than 40% in the present. The recent Puerto Rican history of forest recovery provides the opportunity to study the ecological consequences of economic globalization, reflected in a shift from agriculture to manufacturing and in human migration from rural to urban areas. Forest structure rapidly recovers through secondary succession, reaching mature forest levels of local biodiversity and biomass in approximately 40 years. Despite the rapid structural recovery, the legacy of pre-abandonment land use, including widespread abundance of exotic species and broadscale floristic homogenization, is likely to persist for centuries.

Keywords: land-use and land-cover change, Puerto Rico, secondary succession, exotic species, globalization

Since the origin of agriculture, the human population and human consumption of resources have increased steadily throughout the world. As a consequence, forests and other natural areas have been transformed into agriculture, pastureland, and cities. Land-use and land-cover change (LUCC) represents one of the most important components of global environmental change. Widespread effects of LUCC include habitat loss and fragmentation, soil degradation, species introductions, and changes in vegetation. Indirectly, LUCC affects the interactions between the biosphere and the atmosphere (through alterations of biogeochemical cycles) and between ecosystems and cultural systems (Turner et al. 1990). Land-cover change is very intense in tropical developing countries that are characterized by agriculture-based economies and rapidly increasing human populations (Watson et al. 2001). Consequently, most research on the ecological implications of LUCC in the tropics focuses on the dominant pattern of deforestation and fragmentation (e.g., Houghton 1999, Laurence et al. 2002), which is driven by the prevailing socioeconomic and demographic factors.

The most recent predictions, however, indicate that the world's human population will stop growing before 2100 (Lutz et al. 2001), and current trends of economic globalization promote agriculture intensification, industrialization, and migration of rural population to urban areas. A potential consequence of these trends is that areas of marginal agriculture will be abandoned, leading to forest recovery. Forested areas

are already expanding in developed countries where the economic base has shifted from agriculture to industry (Ausubel 1996). Although most forest recovery is occurring in temperate ecosystems (e.g., Foster et al. 1998), some examples exist in tropical countries where manufacturing is replacing agriculture, such as Taiwan (Chang and Tsai 2002) and Puerto Rico (Franco et al. 1997, Rudel et al. 2000). The recent Puerto Rican history, characterized by a major shift from agriculture to manufacturing in the late 1940s (Dietz 1986), provides an excellent opportunity to study the ecological consequences of socioeconomic changes associated with economic globalization in a tropical environment. In this article we describe how economic changes have affected the

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patterns of land use and ecosystem dynamics, and we assess the pros and cons of Puerto Rico as a model for other Neotropical regions.

The natural environment

Puerto Rico, centered at 18° 15' north, 66° 30' west, is the smallest of the Greater Antilles, with an area of approximately 8900 square kilometers. The rugged topography covers an elevational range from sea level to 1300 meters. The island includes ecological life zones ranging from subtropical dry forests to subtropical rain forests; the annual rainfall in these zones ranges from 900 to 5000 millimeters, and the mean annual temperature ranges from 19°C to 26°C. The largest climatic zone includes moist evergreen broadleaf forests (Ewel and Whitmore 1973). The geology of the island includes sedimentary rocks on the north and south coasts (with a karst region in the northeast and sand and alluvial soil in the central-north and central-south coasts), old volcanic and sedimentary (cretaceous) rocks in the central mountainous area, and some serpentine soils (figure 1a).

The disturbance regime is characterized by hurricanes throughout the island, landslides in the wettest and steepest areas (Brokaw and Walker 1991), and fires in the dry southwest (Ewel and Whitmore 1973). The biota of Puerto Rico is mostly of Neotropical origin, with strong taxonomic affinities with the Greater Antilles. With the exception of extant native mammals (restricted to 13 species of bats), it is characterized by relatively high biodiversity, including more than 2400 species of plants, more than 200 species of birds, and more than 80 species of reptiles and amphibians, many of which are endemic (Figuroa Colón 1996).

Socioeconomic drivers and land-cover change

After the arrival of the Spanish in 1493, the economy of Puerto Rico was dominated by gold mining, and the human population at the end of the 16th century was less than 4000. By 1776 the population had grown to more than 80,000, and agriculture was still a minor activity in a landscape dominated by forests (Dietz 1986). During the 19th century, changes accelerated. Human population exhibited a 10-fold increase (figure 2a), and agriculture (sugarcane, coffee, plantain, corn, cotton, and rice) spread throughout the island (Dietz 1986). Even though political control of Puerto Rico shifted from Spain to the United States in 1898, socioeconomic conditions did not change during the following decades. Until 1940, Puerto Rico's economy resembled that of most Neotropical countries. Pastureland, the most common type of land use in the Neotropics, covered 55% of the island in 1899, and in 1934 agriculture (including cattle production) represented about 45% of the gross national product (GNP), while manufacturing only accounted for 7% (figure 2b). Population growth before 1940 was accompanied by a consistent decrease in forest cover (figure 2a), a typical pattern in tropical countries (Turner et al. 1990).

In the late 1940s, the political status of Puerto Rico changed, and the postwar efforts to promote industrialization (Oper-

ation Bootstrap; Dietz 1986) shifted the economy from agriculture to light industry. Between 1940 and 1980, the percentage of Puerto Rico in farmland decreased from 85% to 37% (Cruz Baez and Boswell 1997); by 1980, agriculture represented less than 5% of the GNP, while manufacturing had grown to almost 50% (figure 2b; Dietz 1986). The human population of the island continued increasing, from slightly less than 1 million inhabitants in 1900 to more than 3.5 million in 1990 (figure 2c). Furthermore, the spatial distribution of the population changed (figure 1b), because economic changes promoted migration from rural to urban areas and to continental urban centers such as New York, Philadelphia, Miami, and Chicago (Cruz Baez and Boswell 1997, Rudel et al. 2000). Since the 1940s, while out-migration dominated the central-western mountains, immigration and population growth mainly occurred in the urban areas and along the northeast coast. Urban areas now cover more than 14% of the island (López et al. 2001). Between 1940 and 1990, the rural population did not change significantly (figure 2c), but the rural working population (between 15 and 64 years old) decreased (Cruz Baez and Boswell 1997), reflecting the decrease in agricultural activities.

The fate of the abandoned agricultural lands depends on different factors (table 1). Forest recovery tends to occur in areas of marginal agriculture: at high elevations, on steep slopes, within reserve areas, far from roads, in areas with net population out-migration, and in small farm areas located near preexisting forests. Urban areas expand at lower elevations, on flat topography, and closer to roads and urban areas (Thomlinson et al. 1996, Helmer 2003). The landscape features that favor urbanization are the same ones that favor intensive agriculture. For example, between 1977 and 1994, new urban areas replaced 6% of the island's prime agricultural lands (López et al. 2001).

The interaction between the two expanding types of land cover (forest and urban) and the receding agricultural lands is well documented in the municipality of Luquillo in northeastern Puerto Rico (figure 3), which includes the interface between one of the oldest forest reserves in the Caribbean (Luquillo Experimental Forest) and the urbanized San Juan metropolitan area. In 1936, sugarcane and pastures each covered about one-third of the area, and closed-canopy forests covered only 15%. By 1988, the area of sugarcane had declined to zero, and more than half of the area was occupied by dense forest (Thomlinson et al. 1996). Between 1936 and 1988, the area classified as "urban" in Luquillo increased by more than 2000%; it continued to grow rapidly (a 31% increase) during the following 5 years, resulting in a loss of 5% of forested areas (Thomlinson and Rivera 2000). Whereas high-density urban areas expanded mostly into pastures and low-density forests, low-density housing expanded mostly in areas of dense forest. Similar patterns have been found in the United States (Greene 1997, Paterson and Connery 1997) and represent a major challenge for landscape planning efforts to balance urban growth with the preservation of forests. Other areas of the island show similar patterns of forest

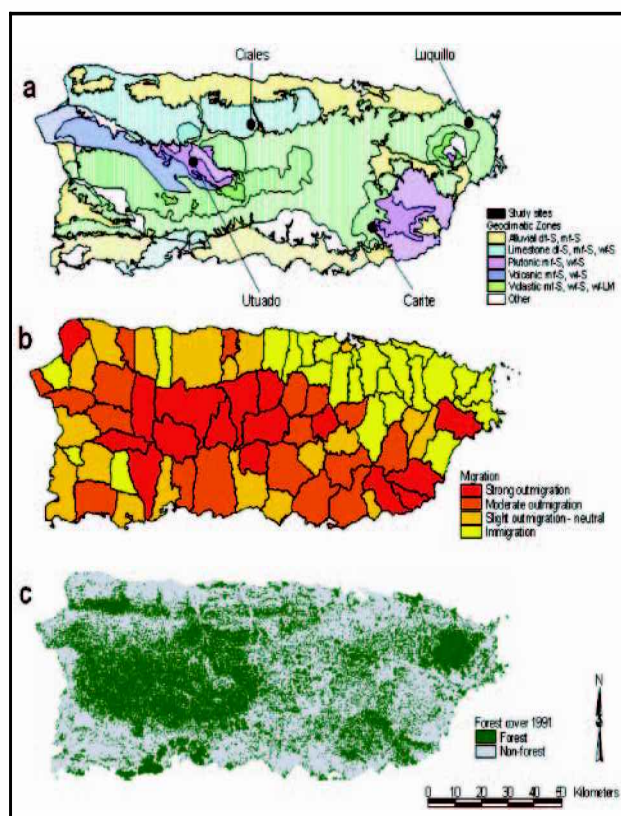


Figure 1. (a) Geoclimatic zones in Puerto Rico. Abbreviations: *df*, dry forest; *mf*, moist forest; *wf*, wet forest; *S*, subtropical; *LM*, lower montane. (b) Human population migration in and out of each municipality of Puerto Rico between 1940 and 1990. (c) Forest cover in 1991, derived from a 30-meter pixel-level classification of Landsat Thematic Mapper imagery dated 1991–1992. Because it did not undergo resampling, its minimum mapping unit is probably about 3 to 5 pixels and less than 0.5 hectares. Using data in the published error matrix, we estimate that overall forest versus nonforest classification accuracy is about 93%. Source: Briggs and Akers 1965, Ewel and Whitmore 1973, Cruz Baez and Boswell 1997, and Helmer et al. 2002.

expansion and a decrease in forest fragmentation (Lugo 2002). For example, between 1936 and 1989, forest expanded from 35% to 59% in the dry area of the municipality of Guánica (Lugo et al. 1996) and from 35% to 90% in a montane area located in the municipality of Utuado (Sued 2003).

Contrary to the general trend of deforestation in the tropics (Turner et al. 1990, DeFries et al. 2000, Watson et al. 2001), the main result of Puerto Rican socioeconomic changes has been a process of forest recovery. In the late 1930s, about 90% of Puerto Rico was in some form of agriculture (Dietz 1986, Birdsey and Weaver 1987); by 1991, forest covered 42% of the island (figures 1c, 2a; Helmer et al. 2002). These changes are directly associated with the decrease in agricultural areas caused by economic changes that have promoted industrialization and urbanization of the human population.

Table 1. Influence of landscape attributes on land-cover changes from agricultural areas to urban areas or secondary forests.

Variable	Urban	Secondary forest
Distance to existing urban areas ^a	+	NT
Population ^b	NT	–
Elevation ^{a, b, c, d}	–	+
Distance to roads ^{a, c}	–	+
Percent slope ^{a, c}	–	+
Farm size ^b	NT	–
Surrounding proportion of pasture and agriculture ^c	NT	–
Distance to reserved area	+	–

+, positive relationship; –, negative relationship; NT, variable not tested.

a. Islandwide (Helmer 2000, 2003, López et al. 2001).

b. Islandwide (Rudel et al. 2000).

c. Montane Costa Rica (Helmer 2000).

d. Northeastern Puerto Rico (Thomlinson et al. 1996).

Changes in biotic communities through succession

Recovery of forest structure is a key process for recovering ecosystem processes (e.g., hydrologic or biogeochemical cycles) and habitats. The analysis of sites with different ages of abandonment (chronosequences) can be used to assess patterns of vegetation recovery. In Puerto Rico, pastures have been gradually abandoned through the second half of the 20th century, providing the opportunity to quantify trends in vegetation structure over several decades.

The analysis of 71 plots of different ages, climates, and types of geology across the island showed that, after 40 years of succession, secondary forests growing in abandoned pasturelands cannot be distinguished from mature old-growth forests in terms of stem density and basal area (figure 4; Aide et al. 2000). Initial forest recovery on some abandoned pastures is slower than that following other natural or anthropogenic disturbances (Aide et al. 1995), but recovery accelerates after 10 to 15 years, when woody vegetation shades out the dominant grasses. In the karst region, differences in pre-abandonment land uses produced little differences in basal area and diversity recovery rates (Rivera and Aide 1998). Although distance from the forest edge affects the patterns of seed rain (Zimmerman et al. 2000, Cubiña and Aide 2001), this is not a main factor controlling the rates of recovery of forest structure in Puerto Rican forests at a landscape scale (Aide et al. 1996).

In general, the recovery rates of structural parameters in Puerto Rico are comparable to those of other tropical secondary forests that are not limited by seed sources or recurrent disturbances (e.g., Finegan 1996, Grau et al. 1997). The small size of the farms (< 30 hectares [ha]) and the infrequent use of fire seem to be the factors that facilitate rapid forest structure recovery in Puerto Rican abandoned lands.

During the early stages of succession, species composition is controlled by the local microenvironmental conditions and by the effects of pre-abandonment land use. In particu-

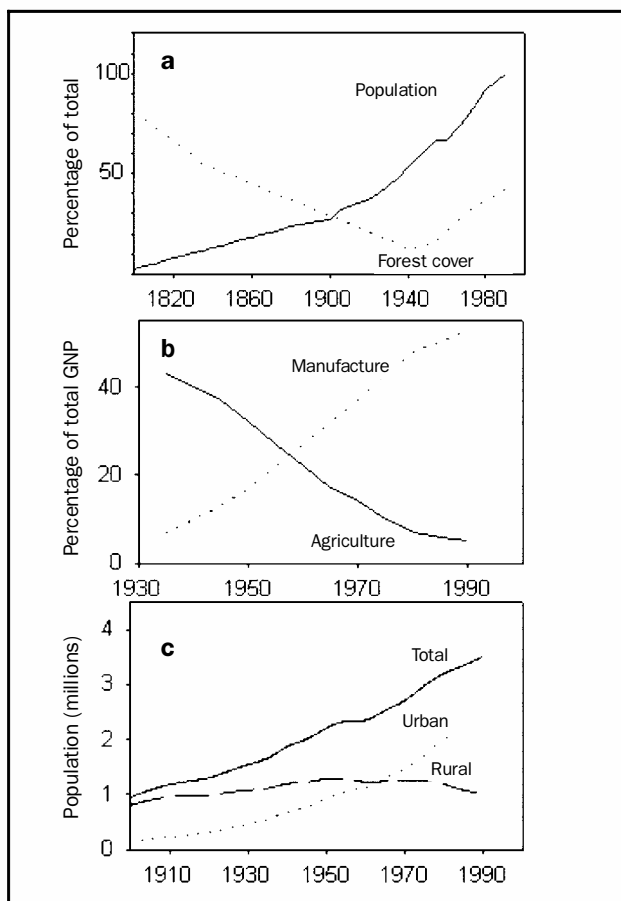


Figure 2. (a) Population growth (as a percentage of current population) and forest cover (as a percentage of total land area) since 1800, (b) percentage of gross national product attributed to agriculture and manufacturing since 1930, and (c) rural and urban population during the 20th century. Source: Dietz 1986, Cruz Baez and Boswell 1997, López et al. 2001, Helmer et al. 2002, Helmer 2003.

lar, the availability of perches for seed dispersers and the presence of food resources (especially fruit) as attractors for dispersers play a major role in the future forest composition (Wunderle 1997). In the temperate ecosystems of New England, which experienced regional forest recovery caused by processes of industrialization and urbanization, the species composition in secondary forests is highly variable locally (from field to field) but very similar at broader scales. Foster and colleagues (1998) found that local-scale differences are caused by legacies of specific agricultural or management practices such as crop type and frequency of plowing, while broadscale floristic homogenization results from human disturbance and a relatively short recovery time. This homogenization process is reinforced by repeated human disturbance and by species introductions that favor a reduced group of secondary species whose propagules are widely available (e.g., Aragón and Morales 2003). Broadscale human disturbance and abundance of exotic species are both characteristics of

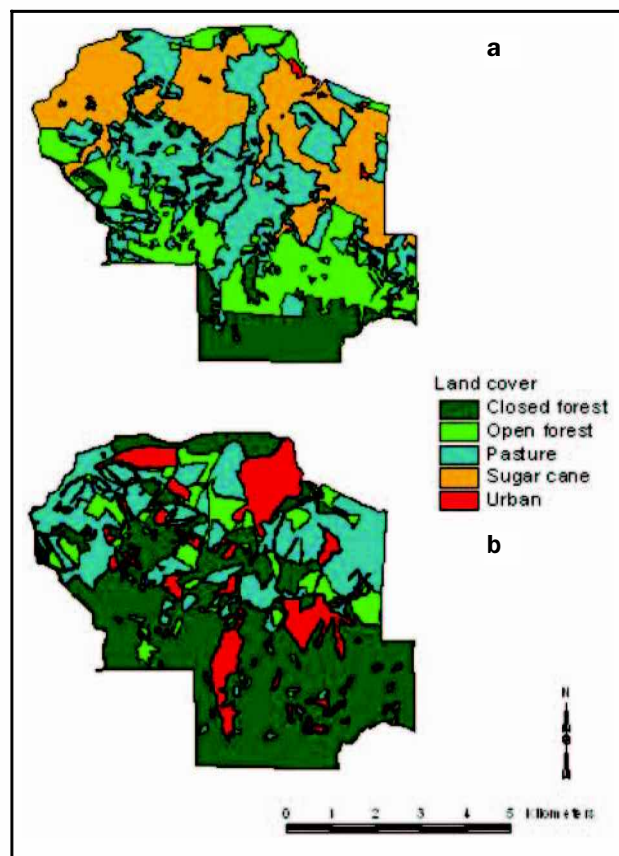


Figure 3. Land-use patterns in (a) 1936 and (b) 1989 in the Luquillo municipality of northeastern Puerto Rico.

Puerto Rican ecosystems (Aide et al. 2000, China and Helmer 2003), which suggests that this model of broadscale homogenization and local scale heterogeneity due to previous land use should apply.

In Puerto Rico, unlike New England (Foster et al. 1998), changes in scale-dependent forest homogeneity and heterogeneity relative to pre-Columbian forests cannot be characterized, because researchers lack detailed knowledge of the composition of these forests. Evidence for broadscale homogeneity comes from islandwide surveys by the US Department of Agriculture Forest Service (Franco et al. 1997), which show that forests overall are dominated by *Spathodea campanulata*, a species of African origin that was introduced as an ornamental. Among the remaining top 10 abundant species (table 2), *Syzygium jambos* is an introduced species and *Erythrina poeppigiana* is used as coffee shade. All the remaining trees are native species whose ecologies range from light-demanding pioneers (*Cecropia schreberiana*, *Schefflera morototoni*) to shade-tolerant species that probably dominated the pre-Columbian lowland forests (*Guarea guidonia*, *Andira inermis*; Franco et al. 1997).

Within regions, the dominant species often differ among the two main types of abandoned land uses, shade coffee and pasture, providing evidence of increased local-scale

Table 2. Species composition of secondary forests in Puerto Rico.

All forested land	Abandoned shade coffee land	Abandoned pasture
	Carite	
<i>Spathodea campanulata</i>	<i>Guarea guidonia</i>	<i>Ocotea leucoxydon</i>
<i>Guarea guidonia</i>	<i>Cecropia schreberiana</i>	<i>Prestoea montana</i>
<i>Inga vera</i>	<i>Inga vera</i>	<i>Tabebuia heterophylla</i>
<i>Cecropia schreberiana</i>	<i>Andira inermis</i>	<i>Cecropia schreberiana</i>
<i>Andira inermis</i>	<i>Dendropanax arboreus</i>	<i>Casearia arborea</i>
<i>Tabebuia heterophylla</i>		
<i>Syzygium jambos</i>	Ciales	
<i>Inga laurina</i>	<i>Guarea guidonia</i>	<i>Spathodea campanulata</i>
<i>Erythrina poeppigiana</i>	<i>Coffea arabica</i>	<i>Guarea guidonia</i>
<i>Schefflera morototoni</i>	<i>Dendropanax arboreus</i>	<i>Andira inermis</i>
	<i>Montezuma speciosissima</i>	<i>Cupania americana</i>
	<i>Ocotea leucoxydon</i>	<i>Casearia sylvestris</i>
	Luquillo	
	<i>Guarea guidonia</i>	<i>Andira inermis</i>
	<i>Prestoea montana</i>	<i>Schefflera morototoni</i>
	<i>Cecropia schreberiana</i>	<i>Tabebuia heterophylla</i>
	<i>Cordia borinquensis</i>	<i>Casearia guianensis</i>
	<i>Casearia sylvestris</i>	<i>Miconia prasina</i>
	Utuaado	
	<i>Guarea guidonia</i>	<i>Guarea guidonia</i>
	<i>Cecropia schreberiana</i>	<i>Spathodea campanulata</i>
	<i>Spathodea campanulata</i>	<i>Tabebuia heterophylla</i>
	<i>Ocotea leucoxydon</i>	<i>Inga vera</i>
	<i>Inga vera</i>	<i>Casearia sylvestris</i>

Note: The most common species, ranked by basal area per hectare, are shown for all forested lands in Puerto Rico. Similar data from four regions (see figure 1a) show species composition of two major land uses: abandoned shade coffee land and abandoned pastures. Ages of abandonment range from 10 to 60 years. Exotic species are shown in bold.

Source: Zimmerman et al. 1995, Aide et al. 1996, 2000, Franco et al. 1997, Rivera and Aide 1998, Pascarella et al. 2000, Marciano-Vega et al. 2002.

heterogeneity in forest composition. For example, *G. guidonia* is the dominant species in abandoned shade coffee in all four regions (table 2). Surprisingly, *Inga vera* is not a dominant species in abandoned coffee, probably because it is relatively short-lived (Zimmerman et al. 1995), so its dominance across the island is not directly related to the abandonment of shade coffee but is probably a consequence of human dispersal. Certain regions have unique dominant species (i.e., *Montezuma speciosissima* and *Cordia borinquensis* in abandoned shade coffee in Ciales and Luquillo, respectively; table 2), and not all regions exhibit strong differences in species composition between land uses, particularly where frequent cutting of secondary forest may lead to stronger homogenization of seed sources. This is the case for the Utuaado region (Marciano-Vega et al. 2002), in which both *G. guidonia* and *S. campanulata* are dominant in abandoned coffee plantations and pastures (table 2).

The species composition of forests recovering from coffee plantations and pastures is often strikingly distinct, as indicated in more detailed analyses (Zimmerman et al. 1995, Rivera and Aide 1998, Pascarella et al. 2000, Marciano-Vega et al. 2002). Ordination analysis based on the species composition of forests of different regions and different previous

land uses (figure 5) shows that forests with similar histories of pre-abandonment use follow consistent patterns along the first ordination axis, while the effect of the geographic location is evident along the second ordination axis. In addition, where there are relatively intact forests, their composition is very different from that of adjacent forest areas that have recovered from human land uses (Zimmerman et al. 1995, Pascarella et al. 2000, Thompson et al. 2002).

While forest structure (density, basal area) recovers in a few decades after abandonment, differences in vegetation composition persist much longer, because early invaders differ among pre-abandonment land uses, promoting local-scale heterogeneity. The fact that early successional species in Puerto Rico are successful exotic invaders or widespread pioneers, typical of many areas in the tropics (Aide et al. 2000), supports the idea of a broadscale homogenization.

Trees determine the structure of forests by controlling the availability of resources and microhabitat for other organisms, such as different invertebrate groups. Therefore, the recovery of forest structure is expected to have strong effects on the diversity and composition of other organisms (Huston 1994).

While tree species richness increases through succession in Puerto Rico (figure 6), changes in the abundance, biomass,

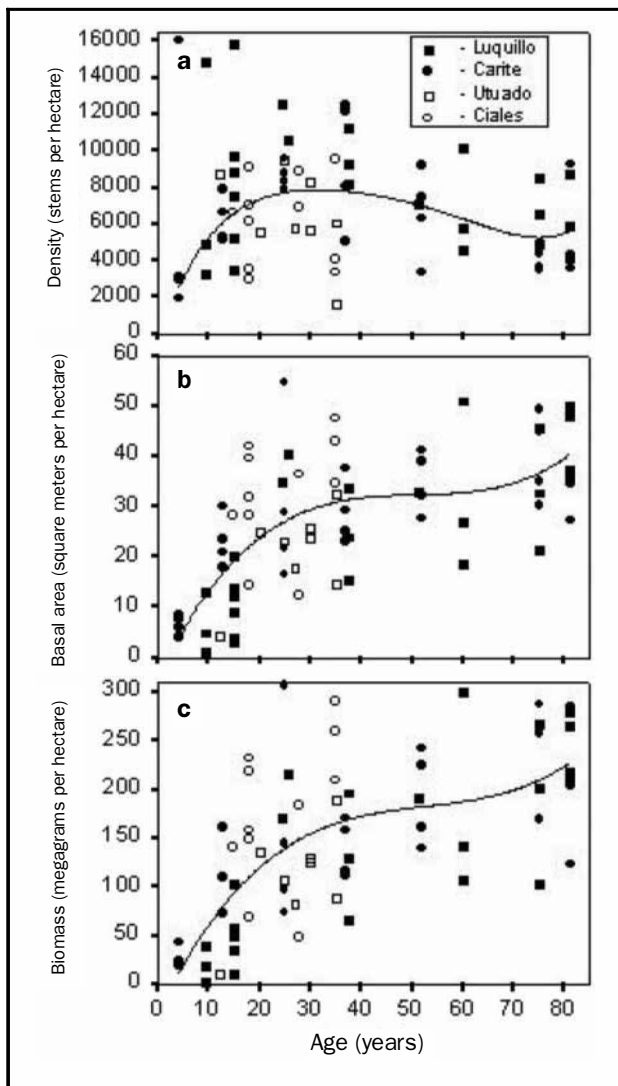


Figure 4. Relationships between time since abandonment and three forest structural parameters, (a) density, (b) basal area, and (c) biomass, in 71 abandoned pastures and old forests (> 70 years old) in Puerto Rico. Three sites with densities greater than 14,000 stems per hectare were excluded from the regression. Source: Aide et al. 2000.

and diversity of other organisms with time vary greatly. Litter insect richness increases through succession (figure 6). Species composition is different between early and late successional states, but the trophic structure remains similar through succession (Barberena-Arias and Aide 2003). Ant species richness, however, peaks at intermediate successional stages (figure 6), and species composition also differs between early and late successional forests. In a chronosequence disturbed by a recent hurricane, insect richness was much higher in pastures than in secondary forests because of the high richness of diptera. Nevertheless, differences in species composition between early and late successional stages were maintained (Barberena-Arias and Aide 2002).

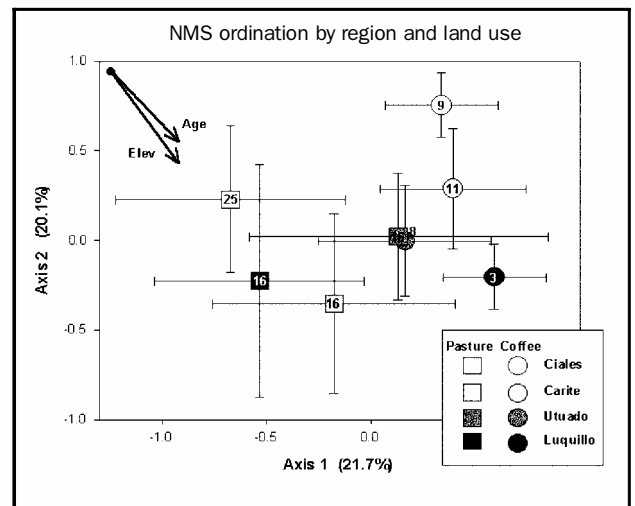


Figure 5. Nonmetric Multidimensional Scaling (NMS) ordination of Puerto Rican secondary forest communities (Bray-Curtis [Sorensen] dissimilarity index; trees > 10 centimeters in diameter at breast height) showing the relative effects of region and previous land use. Percentage variance from the original dissimilarity matrix explained by each axis is shown in parentheses. Note that the first axis clearly discriminates between forests of different pre-abandonment conditions (pastures and coffee). Values within symbols are the number of 0.1-hectare plots sampled. Error bars equal one standard deviation. Arrows in the upper left corner of the figure indicate the relative strength and direction of the correlations of environmental variables with ordination axes. Source: Kruskal and Wish 1978, Zimmerman et al. 1995, Rivera and Aide 1998, Aide et al. 2000, Pascarella et al. 2000, Marciano-Vega et al. 2002.

In contrast to patterns presented by insects, earthworm density and biomass decreased dramatically from pastures (831 worms per square meter [m^2], 175 grams [g] per m^2) to forests (32 worms per m^2 , 19 g per m^2), probably because of a decrease in fine root biomass (Zou and Gonzales 1997, Sanchez et al. 2003). Native earthworms are absent from pastures, which are almost exclusively dominated by the exotic species *Pontoscolex corethrurus*. Contrary to the abundance pattern, earthworms' species diversity increases through succession as native species colonize secondary forests (figure 6). The exotic *P. corethrurus* is the only species present along the complete chronosequence and is still the most abundant species in mature forests, although in these environments the native earthworms' biomass is higher (Zou and Gonzalez 1997, Sanchez et al. 2003).

Ecosystem processes

Given that approximately 50% of world forests are located in the tropics and that this area has the highest rate of deforestation and land conversion in the world, tropical forests are

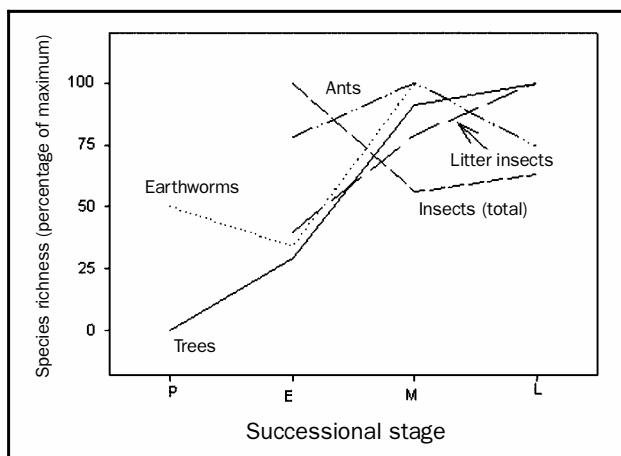


Figure 6. Changes in species richness expressed as a percentage of the maximum value analyzed along successional stages. Abbreviations: P, pasture; E, early successional (5 to 10 years of abandonment); M, midsuccessional (25 to 40 years of abandonment); L, late successional or mature (more than 50 years of abandonment).

considered to be a major source of carbon dioxide (CO_2) to the atmosphere, exceeded only by carbon (C) emissions due to combustion of fossil fuels (Houghton 1999, Watson et al. 2001). Because atmospheric CO_2 is the single most important greenhouse gas, understanding the interactions between land use and the dynamics of forest destruction, conversion, and recovery is critical for predicting global effects of LUCC on the atmosphere. Regions in which forests are expanding into agricultural areas and pasturelands, such as Puerto Rico, represent opportunities for C sequestration (Silver et al. 2000).

The chronosequence studies in Puerto Rico indicate that forests accumulate about 150 megagrams (Mg) per ha of aboveground biomass during the first 30 years (figure 4c), a level similar to that of other tropical secondary forests (Brown and Lugo 1990, Silver et al. 2000). In Puerto Rico, after 11 years of secondary succession, forests already contain between 40 and 50 Mg per ha of belowground biomass, and secondary forests originating from pastures and agricultural land recover the belowground biomass content of mature forests (approximately 100 to 150 Mg per ha) in approximately 50 years (Brown and Lugo 1990, Cuevas et al. 1991). Litterfall rate in secondary forest was also similar to mature forest rates after 50 years of succession (Zou et al. 1995).

Other consequences of large-scale deforestation on C dynamics, however, may persist even when forest structure is recovered. For example, CO_2 soil efflux due to decomposition is positively correlated with earthworm activity (Camilo and Zou 2001). Consequently, the high density and biomass of exotic earthworms (a legacy of the broadscale transformation of forest into pastures) significantly accelerates the decomposition of plant litter and increases CO_2 flux from the soil to the atmosphere (most likely through changes in microbial activity; Liu and Zou 2002), indicating an increase in the turnover of soil organic C.

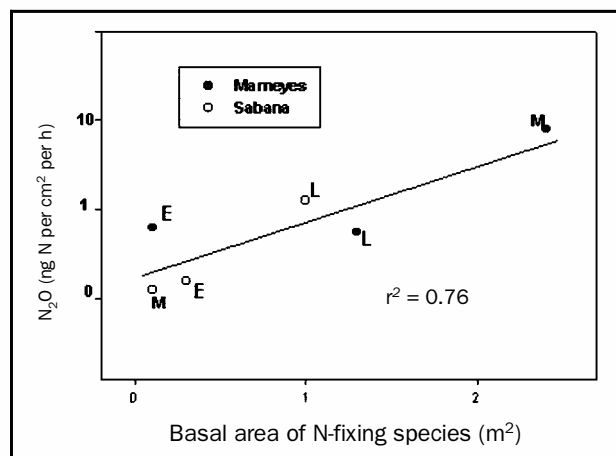


Figure 7. Nitrous oxide (N_2O) emissions (in nanograms of nitrogen per square centimeter per hour) as a function of the basal area of nitrogen-fixing species in forest stands sampled from two chronosequences, Mameyes and Sabana. E, early successional; M, midsuccessional; L, late successional. Source: Erickson et al. 2000.

Another important effect of tropical LUCC with implications for global change is soil emission of the greenhouse gas nitrous oxide and the tropospheric ozone precursor nitric oxide. Aggrading forests are expected to be nutrient conserving (Vitousek and Reiners 1975), with low levels of nitrogen (N) turnover and gaseous emissions compared with older stands. In Puerto Rico, Erickson and colleagues (2000) did not find a consistent positive relationship between stand age and N emissions. In fact, one midsuccessional forest exhibited emissions exceeding 9 milligrams N per square centimeter per hour, the highest ever recorded in an unfertilized forest. The key factor explaining this relationship was the high basal area of N-fixing leguminous trees (mainly *A. inermis*) in the forest stand (figure 7). Enhanced N fixation probably caused low litter C:N ratios and high values of soil N mineralization and other indexes of soil N turnover. If this pattern is confirmed, then unlike the C balance, which is affected mostly by stand age, N fluxes are affected mostly by forest composition, which largely depends on land-use history.

Land-use intensification often leads to increased soil erosion, which can become a serious economic and environmental problem. For example, the La Plata reservoir in Puerto Rico—which supplies water for 36% of San Juan, with more than 1.5 million people—has lost 30% of its storage capacity because of sediment accumulation (López et al. 1998). Suspended sediments, an index of low-quality stream habitat, are significantly higher in first-order streams surrounded by pastures than in those surrounded by forests (Heartsill-Scalley and Aide 2003). Erosion rates are controlled by rainfall intensity, soil erodability, slope, land cover, and management practices. In the tropics, which are usually characterized by relatively intense rainfall, poor soil conservation practices, and relatively fragile soils, LUCC can severely affect rates of erosion (Lal 1990). A detailed study showed that

a watershed dominated by agriculture (the Río Grande de Loiza) yielded about 50% more landslides and suspended sediments than a forested watershed located in the Luquillo Experimental Forest (Larsen 1997).

By analyzing the spatial distribution of land-cover types, topography, and parameters of soil erosion in the Guadiana watershed (a major water source for San Juan), López and colleagues (1998) found that on a river basin scale, the amount of erosion was largely dependent on the distribution of the cover types. Erosion rates varied from 534 Mg per ha per year in bare soil to 8 Mg per ha per year in closed-canopy forest, with intermediate values for open-canopy woodlands (26), agriculture (22), pastures (17), and low-density urban areas (15). Relatively small changes in the type of land cover could have major effects on rates of soil erosion. For example, if only the 5% of the watershed with the highest erosion rates (bare soil, agriculture on steep slopes) is transformed into closed-canopy forests, erosion in the watershed will decrease by 20%. If open woodlands are transformed through succession into closed-canopy forests, erosion will decrease by 7%. If instead the landscape is transformed into a mixture of pasture and agriculture, as it was during the first half of the 20th century, total basinwide erosion will increase between 33% (all pasture) and 103% (all agriculture).

Soil erosion is also controlled by the invasion of exotic earthworms. In plots in relatively undisturbed forest where exotic earthworms were 90% excluded through electroshock, the water runoff doubled, and the transport of mineral soil and fine litter increased by factors of 5.3 and 3.4, respectively. This pattern is probably due to reduced soil porosity derived from decreased earthworm activity.

The resilience of Puerto Rican landscapes

The dramatic shift in the land-use and land-cover history of Puerto Rico is equivalent to a large-scale ecological experiment, allowing us to assess the resilience of an ecosystem of almost 1 million ha that was submitted to intense human disturbance for approximately a century and later progressively abandoned. Our results show that the degree of resilience of the Puerto Rican landscape depends on what factor is considered. Chronosequence studies indicate that the vegetation structure and the local (alpha) diversity of several taxa have recovered in less than 50 years and are relatively independent from the pre-abandonment land use. Similarly, rates of soil erosion and C sequestration recover to levels comparable to those of mature forest ecosystems in a few decades through unmanaged forest succession. In contrast, the local-scale species composition of secondary forests is strongly affected by pre-abandonment land use, and some ecological processes, such as N effluxes, are very sensitive to forest composition. At a regional scale, there seems to be a homogenization of species composition in which exotic species have profound and long-lasting ecological impacts. These species, ranging from trees to earthworms, establish early in succession and are still dominant in the oldest secondary forests. This suggests that a period of little more than a century of intensive LUCC will

continue to influence the ecology of the whole island for much longer periods of time, most likely several centuries.

Puerto Rico as a model

Can the Puerto Rican experience be extrapolated to other Neotropical countries? The biota, climate, soils, and major crops of Puerto Rico are very similar to those of many other areas of the Neotropics. Furthermore, the patterns of forest recovery following economic changes observed in Puerto Rico are being repeated in other areas. For example, forest cover has increased on marginal agricultural lands as rural populations migrate to urban centers in Argentina (Ramadori and Brown 1997) and the Dominican Republic (Rudel et al. 2000). The broadscale floristic homogenization and local-scale heterogeneity due to pre-abandonment land use observed in Puerto Rico are consistent with observations in temperate ecosystems of the northeastern United States (Foster et al. 1998) and the subtropical ecosystems of northwestern Argentina (Grau et al. 1997, Aragón and Morales 2003), regions that have experienced forest recovery following abandonment of extensive agricultural areas. These observations suggest that the ecological responses to economic changes in Puerto Rico are representative of other tropical areas as well as some temperate systems.

Two geographic conditions limit the potential for extrapolation of the Puerto Rican experience to the rest of the Neotropics. First, hurricanes, a rare phenomenon in most continental Neotropical regions, have profound effects on Caribbean ecosystem dynamics, including forest succession and ecosystem fluxes (Lodge and McDowell 1991, Zimmerman et al. 1995, Rivera and Aide 1998, Pascarella et al. 2000, Lomáscolo and Aide 2001). While it is unclear to what degree hurricane disturbance “blurs” the effects of previous land use (Foster et al. 1999), hurricanes nonetheless play an important role in defining landscape-scale forest structure (Brokaw and Walker 1991). Second, the unique socioeconomic history of Puerto Rico has generated a human-dominated landscape characterized by small farms interspersed with forest fragments, which facilitates the availability of seed and tree establishment and creates conditions unfavorable for fire spread. In large areas of the continental Neotropics, land-use patterns are very different. These areas are usually dominated by large properties with extensive cattle ranching managed with fire, which generates degraded soils and very long distances to seed sources (e.g., Cavelier et al. 1998, Nepstad et al. 2001). Under these conditions, forest recovery is expected to be much slower than in Puerto Rico.

Conclusions

The environmental history of Puerto Rico exhibits a turning point, which is captured by the change in the relationship between the curves of human population and forest cover through time (figure 2a). Before 1940, as in a typical tropical country, there was a negative relationship between human population and forest cover. During the second half of the 20th century, the relationship became positive, as in several

developed countries, where economic and urban growth were accompanied by forest expansion. Both forest and urban areas have expanded rapidly during the last 50 years, closely tracking the patterns of economic and demographic change. At an islandwide scale, urbanization may reinforce forest expansion, because migration into urban areas is the main driver of land abandonment and subsequent forest regeneration. At a local scale, however, particularly in areas adjacent to the most intensively urbanized areas, an opposite pattern emerges: Low-density residential use invades forest. In addition, urban expansions occur over the most productive agricultural areas, a process that greatly reduces the island's capacity to re-adapt to an economy less dependent on external food sources.

The recent environmental history of Puerto Rico is unusual in that socioeconomic changes toward a manufacture-based economy have been strongly influenced by extratropical economies (Dietz 1986). However, given the current globalization trends, this degree of economic linkage may become more common. Puerto Rico has yielded a unique broadscale experiment from which three main conclusions emerge: (1) Forest structure and the ecological factors depending on it (e.g., biomass, erosion rates, alpha diversity) recover in a few decades in conditions of small farm sizes and infrequent use of fire; (2) in spite of rapid forest recovery, large-scale human disturbances have effects on biotic communities that may last for several centuries; and (3) the invasion by exotic species plays a key role in these long-lasting ecological effects, which include a large-scale floristic homogenization.

Acknowledgments

Most of the studies described in this article were supported by an Institutional Research Award from the National Aeronautics and Space Administration to the University of Puerto Rico (UPR). Additional support was provided by the National Science Foundation to UPR's Center for Research Excellence in Science and Technology (HRD-9353546) and the Luquillo Experimental Forest Long-Term Ecological Research program (DEB-9411973 and DEB-9705814) and by the University of Puerto Rico and the International Institute of Tropical Forestry (US Department of Agriculture Forest Service). Alfredo Grau, Maria Fernanda Barberena-Arias, Gary Toranzos, and four anonymous reviewers provided helpful comments on different stages of the manuscript.

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