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Conversion and recovery of Puerto Rican mangroves: 200 years of change

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ABSTRACT

Human activities have dramatically reduced the world's area of mangroves just as the ecological services they provide are becoming widely recognized. Improving the conservation tools available to restore lost mangroves would benefit from a better understanding of how human activities influence the conservation of these ecosystems. We took advantage of historical information and long-term landscape analyses to relate land use change with the area of mangroves in Puerto Rico. We found that mangroves experienced dramatic changes over the last 200 years, and four distinct eras of change were visible. During the agricultural era (1800–1940) the area of mangroves declined 45%. As the economy changed to industrial in the late 1940s the area of mangrove increase due to reduced land use pressure on the wetlands. Nevertheless, urban expansion between 1960s and 1970s produced another decline. Public concern for mangrove conservation resulted in the legal protection of all the mangroves in 1972, and since then their area has expanded. We found that past human activity altered the original proportion of mangrove species. The number and size of mangrove-forest fragments was impacted by land use, and urban areas had fewer and smaller fragments than vegetated areas. Uncontrolled expansion of urban areas emerged as a major threat to mangrove conservation. Mangroves are resilient and recover quickly when given an opportunity if the geomorphological and hydrological features of the habitat are not changed by their use. The key to conservation appears to be a combination of the type of human activity in mangrove watersheds combined with strong legal protection. The following steps are recommended: (1) identify the areas that satisfy the ecological requirements of mangrove development; (2) incorporate better zoning regulations to maintain these areas natural and to protect the fluxes of water, nutrients, and organisms in and out of the system; and (3) monitor results.

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1. Introduction

The area of the world's mangrove forests has decreased by 35% since the 1980s, at a rate of 2.1% per year, exceeding that of tropical rain forests and coral reefs (Valiela et al., 2001). Mangroves are a unique type of forest because the trees grow in saltwater at the interface between the sea and the land. The ecological and economic values that justify mangrove conservation have been extensively highlighted (Lacerda, 1993; FAO, 1994; ITTO, 2002; Lugo, 2002a); nevertheless, conversion of

mangroves for urban development, aquaculture ventures, mining, and timber extraction has led to their global decline (Valiela et al., 2001; Alongi, 2002). Authors agree that comprehensive conservation strategies are vital to guarantee the future of mangroves (Valiela et al., 2001; Alongi, 2002; Lugo, 2002b). However, in spite of the large bibliography on these ecosystems, the scientific knowledge about mangroves, particularly their response to human activities and population, is still incomplete and somewhat controversial. For example, Valiela et al. (2001) found no relationship between loss of mangroves and population density, while Alongi (2002) argued that the "destruction of mangroves is usually positively related to human population density" (p. 331) and concluded that the greatest hope for the world's mangroves future is a reduction in human population growth. Some of this discrepancy stems from equating human activity with human population pressure at the global scale, while at the local scale, mangrove loss related to human activity

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may be due to maricultural practices and changes in hydrology, which may or may not be related to population, or to urbanization of mangrove areas, which is as much related to land management as to human population density. Resolving this discrepancy is important given the implications that each viewpoint has to the conservation of these habitats. Is mangrove conservation compatible with dense human populations? Improving the management tools available to restore lost mangroves would benefit from a better understanding of how population and human activities influence the conservation of these habitats.

We had an opportunity to study this issue in Puerto Rico, where the population density has undergone dramatic increases in the last 200 years from about 50 people/km² to more than 400 people/ km² (Fig. 1, top). Puerto Rico is a case study for many efforts trying to understand the link between past human activities and today's landscape characteristics (Molina Colón, 1998; Rivera and Aide, 1998; Aide et al., 2000; Lugo, 2002b). The island, with a long history of human presence, dramatic changes in the base economy and land use, and extensive coastal urbanization, provides an opportunity for evaluating the responses of mangroves to different pressures of human activities, land cover change trends, and conservation efforts.

This study is centered in the assessment of human influences on mangroves. Our specific goals in this study were to: 1. reconstruct the area of mangroves island wide over the last 200 years, 2. relate this historic record to major land use and land cover changes that occurred in the island, 3. evaluate recent changes of individual mangrove sites in relation to the surrounding land use, 4. analyze the patch characteristics of mangrove forests and to 5. summarize the conservation lessons that emerge from the analysis of mangroves over time in Puerto Rico.

2. Methods

2.1. Definitions and terms

The term mangrove has two general meanings in ecology (Lugo and Snedaker, 1974). One refers to an ecological group of halophytic species belonging to some 12 genera in eight different families. The other refers to the complex of plant communities fringing tropical oceans and is generally considered to mean tidal forests. Lugo and Cintrón (1975) classified the Puerto Rican mangroves into two groups based on climate and other criteria. The northern-coast mangroves are subject to high wave energy, high precipitation, and river runoff. The southern-coast mangroves are subject to low wave energy regime, low precipitation and low river runoff if any. Basin and riverine mangroves predominate on the northern-coast type mangroves, while fringe mangroves predominate on the southern-coast type mangroves. All types are subtropical (*sensu* Holdridge), and subject to the same temperature regime.

We used the term "mangroves" to refer to the mangrove forests, similarly to the research literature and mapping efforts. We used the term "mangrove ecosystems" to refer to all salt-influenced wetlands that are part of the tidally driven coastal complex, including the community of mangrove trees, adjacent salt and mudflats, halophytic herbaceous and shrub vegetation, and saline lagoons often associated with mangrove trees (Cintrón et al., 1978). This distinction is important for evaluating inventories and studies conducted over a period of more than 80 years, and in comparing assessments derived from various data sources and methodologies. We used the term "mangrove cover" as a surrogate of extent or area of mangrove forests. It is known that during longterm droughts some mangrove forests contract while salt flats



Fig. 1. Human population (top) and forest cover (bottom) in Puerto Rico between 1800 and 2000. Source for population: Vázquez-Calzada (1988) and IITF (2005). Source for forest cover: IITF (2005), Ramos and Lugo (1994), Helmer et al. (2002).

expand, and during wet periods, the forest expands at the expense of salt flats (Cintrón et al., 1978). Similar responses can result from changes in sea level and sedimentation or erosion cycles. In addition, and according to the 1989s National Inventory of Mangroves for Puerto Rico (Torres Rodríguez, 1994), there are 97 "mangrove sites", or places where mangrove ecosystems occur around the island; these sites contain typically various fragments (i.e., patches) of mangrove forest. Finally, we used the term "urbanization" from a land use perspective to refer to the expansion of urban areas (cities, towns) and developed/built-up lands, as more people leave in those areas (Alig et al., 2004).

2.2. Approach

First, we evaluated the historical changes in the extent of Puerto Rican mangroves by collating and revising published information, and we evaluated (inferred) the relationship of these estimates with anthropogenic events that have been hypothesized to influence their abundance during the last 200 years (e.g. deforestation for agriculture, urban growth, population density, and legal protection). Secondly, we conducted a detailed analysis of mangrove cover change over the last 25 years for which we had a chronosequence of land cover maps and inventory information. We paid particular attention to the fate of the individual mangrove sites and their relationship to surrounding land use. How did the mangroves in urban sites experience similar changes as those

Table 1

Estimates of the area of mangroves in Puerto Rico

located in rural lands? Was there any difference among sites located inside and outside reserves? Finally, we evaluated the size distribution of mangrove fragments from the most recent vegetation map. How many forest fragments are there and how big are they? Is there a different pattern of fragmentation depending upon the surrounding land use?

In addition, we reviewed the trajectory of change in land cover, land use, and population density of the island's landscape, with special attention to the lowlands and coastal areas. Based on this, we evaluated how mangroves have responded to human activities, and how this differs from the other forests of the island. From the analysis, we formulate recommendations about the conservation of mangroves.

2.3. Data sources-utility, limitations, and preparation

2.3.1. Mangrove cover

The collection of studies and surveys aimed to estimate the extent of mangroves starts in 1918 and continues up to the present; it includes a modeled estimation for 1800s, and of the potential maximum area based on soil conditions (Table 1). The US Forest Service was responsible for the majority of these estimates. Aerial-photo interpretation was the primary source of these data, particularly for those surveys conducted before the 1990s. More recently, new estimates have been developed as part of island-wide efforts to map land cover, vegetation, and benthic habitats, using satellite imagery and aerial photography, including

Year	Hectares	Additional information
1800 [*]	11,791	Wadsworth (1959). Original area (modeled).
1918 [*]	8,334	Murray Bruner (1919). First official estimate.
1938 [*]	6,475	Holdridge (1940). He estimated that mangroves had been reduced in 22% since last estimation. He indicated that there were 4371 ha in five forests of the Commonwealth Forest System, and an additional 405 ha were also in the public domain. Holdridge found that the species composition of the mangrove forest had changed as a result of human intervention, with the following before and after percentage of species composition: <i>Laguncularia</i> (30/50), <i>Avicennia</i> (30/25), <i>Rhizophora</i> (30/20), <i>Conocarpus</i> (10/5).
1959 [*]	7,285	Wadsworth (1959).
1968 [*]	6,701	Wadsworth (1969).
1971 [*]	6,718	Heatwole (1970/1971).
1972^{*}	7,074	Departamento de Obras Públicas de Puerto Rico (1972)
1974 [*]	6,487	Carrera and Lugo (1978)
1977 [*]	6,963 (7443 modified by this study)	Ramos and Lugo (1994). LC map of Puerto Rico–1977. Corresponding to the class "mangroves". Originally made by detailed visual interpretation of aerial photos by the Puerto Rico Department of Natural Resources and Environment (DNRE), later digitized by Ramos and Lugo (1994). Spatial resolution 30 m. Fragments of mangrove without direct connection to the main land, including cays, were not mapped, as well as some U.S. Army lands. Mangroves include Pterocarpus swamps.
1981		Lewis et al. (1981). 367 ha of mangroves in the island of Vieques.
1983	9,585	National Wetland Inventory (http://www.fws.gov/nwi). Corresponding to the class "forest and scrub-shrub marine wetlands". Based on visual interpretation of aerial photos. The extent of mangrove forests is much higher than the estimate for mangrove ecosystem by Torres Rodríguez (1994) for 1989 (8584 ha) and does not agree with the trends reported by DNRE. It includes Pterocarpus swamps. The resolution at which was mapped might not be the same. More information is needed.
1989	8,584	Torres Rodríguez (1994). Unique National Inventory of the Puerto Rican Mangroves. Ecosystem level approach. The number of mangrove sites increased from 89 in 1974 to 119 in 1989 (including Puerto Rico and the other islands). They ranged in area from 2030 ha in Piñones to scattered trees in Río Bayamón. The median was about 24 ha. It reported 8584 ha of mangrove ecosystems in Puerto Rico, 266 ha in Vieques, 97 ha in Culebra, and 1 ha in Mona.
1991	6,837	Helmer et al. (2002). LC map or Puerto Rico-1991-1992. Corresponding to the class "tidally and semi-permanently flooded evergreen sclerophyllous forests". Based on automatic classification of Landsat satellite imagery (30-m pixel). The class has an accuracy = 89%. Some cays and fragments of mangrove without direct connection to the main land were not mapped.
1999	6,800	N.O.A.A. Benthic Habitat Map (http://ccma.nos.noaa.gov). Corresponding to the class "mangroves". Based on visual interpretation of N.O.A.A. aerial photos. The map covers a region that results from a fixed distance from the coast, and some fragments of mangrove that occurs more interior, as well as some cays, were not mapped. It includes Pterocarpus swamps.
2002*	8,323	Gould et al. (2008). LC map or Puerto Rico—2002 (Puerto Rico Gap Analysis Project). Class "mangrove forests and shrubland". Based on automatic classification of Landsat satellite imagery (15-m pixel), improved by photo interpretation of Ikonos imagery, and resampled to 30 m. It does not include Pterocarpus swamps. All fragments of mangrove without direct connection to the mainland, including cavs, were mapped.
	14,825	Potential maximum extent. Wadsworth (personal communication, letter of June 29, 1976 to Carlos J. Carrera), Lewis (1979). Estimate based on the potential mangrove soils. There are 446 ha in Vieques. The area of wetland soils in the island including the mangrove soils is 26206 ha.

Data for the islands of Vieques, Culebra, and Mona is also shown. Years considered for the final analysis of mangrove change are marked with "**.

for the years 1977, 1983, 1991, 1999, and 2002. However, we found that the comparison of mangrove cover between these maps is difficult or even impossible. The reason for the difficulties include differences in mapping methods (visual interpretation vs. digital processing), data sources (aerial photos vs. satellite imagery), vegetation classification (mangroves and freshwater Pterocarpus swamps appear commonly combined), and inconsistency in the total area mapped (depending upon the island's boundary that was used, some fragments of mangrove were not included). We carefully analyzed the data set to arrive at the two most comparable maps of mangrove cover, corresponding to the years 1977 and 2002. To improve our assessment, we made small modifications to the 1977 map, including adding few fragments that were not included and removing the *Pterocarpus* swamps. These corrections were based on the 2002 map, and represented an increase of 7% of the original 1977s area.

2.3.2. Mangrove sites

The mangrove sites mapped by the 1989s National Inventory of Mangroves (Torres Rodríguez, 1994) were the framework for evaluating (1) recent changes in the extent of mangroves (1977–2002), and (2) actual patterns of fragmentation of mangrove forests. Since we were particularly interested in the effects of human activities in the mangroves, we categorized each mangrove site based on the surrounding land cover and land use. For this, we used a map of urban and rural land uses of Puerto Rico (Martinuzzi et al., 2007), and a map of protected lands (Gould et al., 2008). Urban land use refers to areas with predominant developed/built-up surfaces, such as urban centers, while rural land use refers to areas with predominant open spaces (Martinuzzi et al., 2007).

We found that from the total of 97 mangrove sites, 14 were located within urban areas ("urban sites"), 62 sites were located in rural areas ("rural sites"), and 21 mangrove sites were surrounded by both land development and open spaces ("urban/rural sites). At the same time, 33 mangrove sites were located within protected lands ("protected sites"), 40 sites were outside reserves ("nonprotected sites"), and 24 mangrove sites had a portion within protected lands and a portion outside protected lands ("partially protected sites").

2.4. Land cover and land use history in Puerto Rico

Puerto Rico had an agricultural economic base until the late 1940s, when the economy shifted to one of industry (Dietz, 1986). As a result, the island experienced rapid changes in human activities, population distribution, and land cover. In a few decades,

the lowlands were transformed from an agricultural into an urban/ residential landscape. During the agricultural era, which started in the 1800s, the island was almost completely deforested, with only about 6% of the original forest cover remaining by 1948 (Birdsey and Weaver, 1987) (Fig. 1, bottom). The lowlands were the most deforested regions due to their flat topography, moist climate, and rich soils.

As the economy shifted towards industrial in the late 1940s, people abandoned the rural areas and migrated to the coastal lowlands, where the centers of commerce, industry, and transportation are located. As a result, the coastal lowlands experienced rapid urbanization, and simultaneously, forests began to recover on the abandoned lands (Thomlinson et al., 1996; López et al., 2001; Chinea and Agosto, 2007). Urban development expanded rapidly, the process turned into a disorganized urban sprawl, disconnected from the core of the urban centers and consuming large portions of the lowlands. This urban sprawl phenomenon emerged in the 1960s, grew rapidly during the 1970s, and slowed during the 1980s (Santiago, 2004). Today, built-up surfaces cover nearly one third of the lowlands and continue growing (Martinuzzi et al., 2007). The largest urban centers of Puerto Rico, such as the San Juan Metropolitan Area, Ponce, and Mayagüez, are located in the coast. The population of the island increased from half a million in 1800 to almost four million people today (Fig. 1, top).

Agricultural abandonment and subsequent urbanization has led to a natural increase in forest cover equivalent to 44% of the island by 1992 (Helmer et al., 2002) (Fig. 1, bottom). This process was, however, less important in the lowlands than in the rest of the island. In the lowlands, plantations of sugar cane continued their decreasing production until its final collapse in the late 1980s and now pastures and other minor agricultural practices occur on these lands. As a result, the coastal lowlands, where mangroves occur, are today landscapes dominated by humans: urban developments, industries, pastures, agricultural/hay fields, and wetlands cover these lands.

3. Results

3.1. Changes in mangrove cover (1800-present)

The changes that we observed in the extent of mangroves in Puerto Rico during the last 200 years can be divided into four distinct periods (Fig. 2). The first period is from 1800 to 1938, identified as the agricultural period since it corresponded to most of the agricultural era of the island. During this time, the area of mangrove decreased by 45% from 11,791 ha to 6475 ha. The



Fig. 2. Extent of the mangrove cover in Puerto Rico, including the four historical periods of change (between parenthesis). Original estimates for the years 1968, 1971, 1972, and 1974 (white diamonds) where averaged and combined into one single value for 1971. Data for other years is showed in black squares.

lowlands were transformed into sugar cane fields and pastures. Mangroves were extensively used for fuel wood and charcoal and stands were converted to agricultural fields. The hydrology of coastal wetlands was altered mostly by drainage to protect agricultural crops or for irrigation. Many mangrove stands were affected by the combined agricultural activities of the period. Protection of mangroves in Puerto Rico began in 1919, with the proclamation of thousand of hectares of mangroves within the Commonwealth Forest System, including San Juan, Aguirre, Ceiba, Guánica, and Boquerón (see Holdridge, 1940 in Table 1). This protection must have prevented a major reduction in mangroves.

The second period between 1938 and 1959 was characterized by a brief, yet marked natural recovery of mangroves. This period was the ending of the agricultural era and the beginning of the industrial period. The population was on the move to urban centers and was abandoning agricultural lands, mostly in the mountains and to a lesser degree on the coastal plains. Mangrove land cover increased by 12% to 7285 ha. This recovery occurred naturally, facilitated by the lower pressure for agriculture in the wetlands. In addition, some planting occurred within protected lands (Wadsworth, personal communication). The other forests of the island showed a similar increasing response (Fig. 1, bottom).

The third period of mangrove cover change was between 1959 and 1971, and was characterized by a rapid decline in mangrove cover due to rapid urbanization. The area of mangrove decreased by 540 ha, to 6745 ha. This period corresponded with the great expansion of coastal urbanization and the peak of urban sprawl (Santiago, 2004). Many mangrove forests were converted to housing developments and garbage dumps. Urban drainages were channeled through mangroves, and insidious garbage deposition slowly filled the mangroves, facilitating conversion. For example, neighborhoods of the San Juan Metropolitan Area, such as Barrio Obrero and Puerto Nuevo were constructed on large mangrove forests. While the mangrove area was reduced by coastal urbanization, the forest cover in the rest of the island continued in an increasing trend.

The current period of mangrove cover change started in 1971 and we term it as mangrove recovery through protection. Since 1971, the area of mangrove forests has increased by 23% to the highest historical level of 8323 ha. This expansion was particularly rapid during the first years. The combined effect of legal protection of all mangroves, restoration of wetlands, and the end of the sugar cane industry, resulted in a rapid increase in the total area of mangroves. Simultaneously, the population and the forest cover of the island continued in an increasing trend.

3.2. Changes in mangrove cover at a site level (1977–2002)

Between 1977 and 2002 the mangrove cover of Puerto Rico increased by 12%, from 7443 ha to 8323 ha. However, from the total of 97 sites where mangroves occur, they increased in area in nearly half of them, 47; in 30 it did not change; and in 20 decreased.

In absolute terms, the area of mangroves increased in rural and urban/rural sites, but not in urban ones (Fig. 3, top). Mangroves expanded by 568 ha (14%) in rural sites and by 238 ha (8%) in urban/rural ones. In urban sites the mangroves decreased by 2%. However, we found that in all three types of landscapes, i.e., urban, urban/rural, and rural, there were individual mangrove sites that



Fig. 3. Changes in forest cover between 1977 and 2002 for the different types of mangrove sites, including urban, urban/rural, and rural (top), and protected, partially protected, non-protected (bottom). Data include, for each type of site, the absolute change in mangrove cover, the number of mangrove sites, and the relative change, i.e., the proportion of sites that increased, decreased or did not change in forest cover. For the purposes of this study, only changes in forest cover larger than both 10% and 1 ha were considered.

increased, decreased, or did not change in mangrove cover, but these changes occurred in different proportions. The first tendency for mangroves located in rural and urban/rural landscapes was to increase in area, while in urban sites the first tendency was to remain the same, secondly to decrease, and ultimately, to increase.

On the other hand, the mangrove cover increased almost similarly in protected, partially protected, and non-protected sites, ranging between 9% and 15%. This was translated into an absolute forest expansion of 466 ha in protected sites, 167 ha in partially protected sites, and 162 ha in non-protected sites (Fig. 3, bottom). For the three types of sites, the tendency of the mangroves was firstly to increase in area, secondly to remain the same, and ultimately to decrease; although, the proportion of sites that increased in mangrove cover was barely higher in fully and partially protected areas, and the proportion of sites that decreased in mangroves cover was barely higher in nonprotected ones.

As a result, 55% of today's mangroves are located in rural sites (4560 ha), 38% in urban/rural sites (3097 ha), and 7% in urban sites (565 ha) (Fig. 3). At the same time, 59% are located in protected sites, or within reserves (4906 ha), 26% are in partially protected sites, or sites that are partially included within reserves (2055 ha),

and 15% are in non-protected sites, or outside reserves (1260 ha). We also found small fragments of mangrove forest that were present in the land cover maps from 1977 and 2002 that were outside the sites mapped in the 1989s inventory, totalizing 78 ha for 1977 and 97 ha for 2002.

3.3. Fragment characteristics of mangrove forests

We found that by 2002 there were 1286 fragments of mangrove forests distributed within the 97 sites identified for the island. There was one outlier forest fragment that accounts for 1475 ha, located in Piñones (adjacent to the San Juan Metropolitan Area see Fig. 4), and the rest were distributed in a continuous fashion between 353 ha and less than 1 ha (Fig. 5). The mean size was 6.5 ha when considering Piñones, and 5.3 ha without. The median was 0.3 ha. We found that 930 from the 1286 fragments were less than one ha in size.

Urban sites had fewer and smaller forest fragments (mean and maximum size) than rural or urban/rural sites, as well as a lower proportion of the smaller forest fragments (less than 1 ha in size) (Table 2). On the other hand, non-protected sites had smaller fragments (both mean and maximum size) than protected or



Fig. 4. Map of the distribution of mangroves and land use patterns, complemented by insets from the 2002 land cover map (Gould et al., 2008) and aerial photography (Source: IITF). The background of the top figure corresponds to the urban (in dark gray color) and suburban and rural land uses (in light gray) from Martinuzzi et al., 2007. Inset 1 shows mangroves within the San Juan Metropolitan Area (i.e., urban sites); in this area, Caño Martín Peña (site "a" in the lower image) increased in mangrove forest cover between 1977 and 2002 due to restoration efforts, while Rio Puerto Nuevo (site "b") decreased. Inset 2 shows an urban–rural site, which decreased in forest cover, and inset 3 correspond to a rural site, which increased. In the top map and just next to inset 1 is Piñones, the largest mangrove of the island.



Fig. 5. Distribution of mangrove-forest fragments based on size.

partially protected sites; however, the proportion of fragments of different sizes was similar.

4. Discussion

4.1. Responses of mangroves to human activities in Puerto Rico

Over the last 200 years the Puerto Rican mangroves have experienced changes that were associated with the different types of human use of the land. Agriculture and urban growth caused mangroves to decline by changing the hydrology, sedimenting and asphyxiating the trees, mechanically removing the trees, and/or reducing the habitat. As humans reduced pressure on the land and/ or implemented protection strategies, the area of mangroves increased (see Table 3 and Fig. 2).

In Puerto Rico, agricultural activity did not occur on areas occupied by mangrove forest due to the salinity. The reductions in mangrove cover were mainly a secondary result of agricultural activity due to drainage and changes in hydrology

Characteristics of the mangrove-forest fragments for the different sites

or excessive sedimentation. Draining was common in permanently flooded mangroves in the humid coasts, but not in the dry coast. In the former, agricultural use was possible when soil salinity was reduced by rainfall and seawater penetration was prevented, process that took place behind the red mangrove (*Rhizophora* sp.) belt. Agricultural utilization of areas occupied by black mangroves (*Avicennia* sp.) and buttonwood (*Conocarpus* sp.) is more common in the south if abundant irrigation is available.

Mangroves and other island forests experienced similar trends in land cover including a net decrease during the agricultural era, and a net increase in the industrial period (compare Fig. 1, bottom and Fig. 2). Nevertheless, the forces that explain the recovery of these habitats and the way human legacy is expressed on them are somewhat different. Over the last 60 years, terrestrial forests expanded by natural recovery, that is, by simply re-growing over abandoned lands, for the most part without human intention or plan. Much of this was on the stepper slopes of the island interior less attractive for development. Mangroves occupy flat coastal areas which, when drained and filled, are attractive for development. Thus, for mangroves, the expansion between 1940s and 1960s was a result of natural recovery, but as urban areas started to expand, mangrove areas decreased rapidly. Although some mangroves were protected since 1920s, the establishment of legal protection for all the mangroves in the early 1970s was a key development that prevented further reductions in area in spite of continuing urbanization. Without legal protection of mangroves, the widespread and continuous expansion of urban areas, coupled with a high demand for lands near the shoreline, would have resulted in a net decline of mangrove cover. Other forest types that used to be common in the lowlands but did not benefit from such protection, such as riparian and alluvial forests, and Pterocarpus swamps, are today almost non-existent (Lugo, 2005). The recent

Type of site	Number of forest fragments	Average fragment (ha)	Largest fragment (ha)	%Fragments		
				<1 ha	1-10 ha	>10 ha
Urban	145	3.9	62.3	57	33	10
Urban/rural	281	5.8 [°]	195.5 [†]	70	20	10
Rural	779	5.9	353.2	76	17	7
Non-protected	382	3.3	137.7	73	20	7
Partially protected	325	6.3	241.1	74	17	9
Protected	501	6.9 [‡]	353.2 [†]	70	21	8

Protected, non-protected, and partially protected refer to the location of mangrove sites in relationship with reserves (see Section 2).

* 11.1 if consider Piñones.

[†] 1474.8 with Piñones.

[‡] 9.8 if consider Piñones.

Table 3

Table 2

Causal forces of mangrove loss and gain, including the mechanism responsible for each force and the human activity that these two apply to

	Mechanism	Applies to
Causal forces of mangrove loss		
Change in hydrology	Drainage, ditching, diversion of terrestrial runoff	Agricultural activity, mosquito control, urbanization
Mechanical removal	Deforestation, excessive exploitation	Charcoal production, urbanization
Tree and sediment asphyxiation	Filling, excessive sedimentation	Construction, land conversion, runoff with heavy sediment loads from urban and/or agricultural areas
Reduction of habitat	Invasion of salt and mud flats, construction on floodplains and coastal fringe, river canalization	Urbanization
Causal Forces of Mangrove Gain		
Protection	Laws, regulations, land purchasing	Government action
Reinstatement of hydrological conditions	Filling of drainage canals, collapse of levies	Abandonment of agricultural activity
Reduced pressure on mangroves	No more cutting or habitat incursions	Abandonment of charcoal production activities
Planting	Forest management	Government and NGO's

recovery of mangroves was, hence, the result of a combined effect of natural recovery under legal protection.

From an inland-wide perspective, the changes in land cover of mangroves were not associated with the amount or density of people living in the island. Ironically, the mangroves almost disappeared when the population density was lower than today, when mangroves are expanding. The increase in population density was not an impediment for the recovery of these habitats. This observation coincides with one of the original principles that explain the recent history of the landscape in Puerto Rico: "population growth is compatible with forest recovery" (Lugo, 2002b). The compatibility of mangroves with high population density depends on the management practices and economy of the social system. This observation reflects the fact that forests can recover on abandoned agricultural land or restored wetlands as urban areas increase in population. Population increase can be compatible with forest recovery in the short-term if the rate of forest regeneration exceeds the rate of urban expansion, both occurring at the expense of agricultural or abandoned land, and in the long-term only if abandoned open space is preserved, urban expansion limited, and population density increased. Developed land has little chance of mangrove forest recovery (Ellison and Farnsworth, 1996), although this can occur with strong management action. Urban expansion always occurs at the expense of agricultural areas, abandoned lands, or wildlands, while population increase may not necessarily be equated with urban expansion. Additionally, the historical and spatial context of this statement differs when applied to mangroves or terrestrial forests. Mangroves have recovery in the same region that experienced the highest population growth, i.e., the lowlands (observe the location of mangroves and developed lands in Fig. 4, top map), while most of the other forests have recovery in areas from where people emigrated, i.e., the interior mountains. In any case, this argument demonstrates that population growth can be compatible with forest recovery, at both regional (e.g. lowlands) and islandwide scales. The key to the harmony between mangroves and people rests on the social protection of the ecological conditions under which mangroves survive. Because there are no longer agricultural activities in mangrove sites, and their conversion is prohibited by laws, mangroves can thrive irrespective of the population density as long as the urban system does not encroach, poison, flood, fill, or cut the mangroves. Urbanization is compatible with mangroves if it protects the mangrove area (the habitat) and does not excessively disturb the hydrological regime of the forest. However, a lot of urban drainage is channeled through mangroves with insidious garbage deposition filling the mangroves and inviting conversion. As a result, while there has been a net overall increase in mangrove cover, population, and urban areas in the island over the last decades, certain sites have experienced a decrease in mangrove cover.

One of the major ecological lessons from the Puerto Rican experience with recovering forest cover has been that human legacy on the landscape impacts tree species composition (Rivera and Aide, 1998; Lugo, 2002a; Lugo and Brandeis, 2003; Lugo and Helmer, 2004). A result of past human activities is that today's terrestrial forests have novel combinations of alien and native tree species that may potentially remain for centuries (Lugo, 2002a). However, this did not occur in the recovery of mangroves. In spite of all the changes that have occurred in the coastal areas, the original species composition remains unaltered (Lugo, 1998). The reason is that only mangroves can tolerate the hydrological and edaphic conditions that prevail in these habitats, making it impossible for non-halophitic tree species to invade (Lugo, 1998). However, human legacy is reflected in the proportion of mangrove species that are present today. Laguncularia and Avicennia were less affected by agriculture than Rhizophora (Holdridge, 1940, see Table 1). Avicennia grows in the most saline, thus the less agriculturally suited soils. During the rapid decline for urbanization (1960s–1970s), much of the encroachment on mangroves has been from the landward side where species such as *Avicennia, Laguncularia*, and *Conocarpus* predominate; consequently, these species have been reduced to a much greater extent than has *Rhizophora* (Heatwole, 1985). More recently, we observe an expansion of the landward portions of mangroves, particularly the zones dominated by *Laguncularia* and the fern *Achrostichum*, because of the abandonment of drainage canals and the expansion of the flooded areas behind the mangroves.

4.2. Legal protection-performance and threats to conservation

The overall results of legal protection were positive: First, the early protection of mangroves within the Commonwealth Forests System by 1919 prevented a major decrease in mangrove area during the agricultural period. And second, mangroves experienced a net expansion since the enactment of the 1972 organic law that established the Puerto Rico Department of Natural and Environmental Resources. Since then, twenty-five state and nine federal laws and regulations were implemented to protect mangroves (Torres Rodríguez, 1994). Since the 1970s, all mangroves have been protected and have subsequently expanded throughout the coastal areas of the island, including inside and outside reserves, in rural areas, as well as in landscapes with some presence of land development. However, we found some failures in the system that put the future of these ecosystems at risk. Twenty percent of the sites where mangroves occur experienced some type of reduction. We found that the shorter the distance to urban areas, the higher the probability for mangrove forest cover to decrease. In fact, urban centers experienced a net reduction in mangrove forests, and today they have smaller and fewer forest fragments than other parts of the island. A notable exception to this is Caño Martín Peña, within San Juan, which increased in forest cover as a result of an intense restoration effort (see inset 1 in Fig. 5). Protection by reserves was not an important factor affecting the changes in mangrove forests, expanding even in non-protected areas (although the size of the fragments in non-protected areas is smaller). Helmer (2004) found that for terrestrial forests in Puerto Rico, areas adjacent to protected areas were less likely to develop than areas without any protection or close to urban areas.

The presence of mangrove forests declining even if located under "ideal" conditions (i.e., far from urban centers, within reserves), suggests that (a) the negative effects of urbanization or other human activities expand beyond urban centers, and (b) natural events might be causing reductions in mangrove forests. Although there are chances for both of them to occur, there are several studies that support the first option. Land development can negatively affect the mangroves by many ways without involving the conversion of large areas (Lugo, 1988, 2002b). Considering the amount of widespread developments that occurs in the coastal plains of Puerto Rico (Martinuzzi et al., 2007), and the extensive road system, there are realistic opportunities for this concern to occur. In addition, damages can result from excessive recreational uses without implying land development at all (DNER, 1990).

Although direct and indirect effects of urbanization emerge as major threat for the conservation of mangroves in Puerto Rico, charging humans for all possible reduction in mangrove forests might result a gross error. For example, hurricanes can flatten mangroves such as happened in Aguirre in 1928 (Wadsworth, personal communication). More recently, we have observed forest retrocession at expenses of salt flats in Jobos Bay National Estuarine Research Reserve, an event that reverted rapidly after a strong precipitation event that occurred in 2003.

4.3. Recommendations

Systematic multi-scale monitoring of mangroves can improve our understanding of the rates, causes, and consequences of natural and human-induced processes that change these habitats over time. It is surprising that, as one of the most protected ecosystems in Puerto Rico, mangroves have been inventoried only once, in 1989. Additionally, most of the available data with potential use for monitoring, such as land cover and vegetation maps, has been inconsistent in the way they map the mangroves. The development of standard methods for mapping and classification of the coastal areas are desirable. The development of an official monitoring system for the mangroves appears as an important task to be completed in support of coastal monitoring, improving zoning, and designing more effective regulations.

5. Conclusion

During the last 200 years, human activities in Puerto Rico have had negative and positive impacts on the mangroves. Mangroves are resilient and recover quickly when given an opportunity if the geomorphological and hydrological features of the habitat are not altered by their use.

The future of the mangroves in Puerto Rico depends on human decisions, and on the legal and social attitude aimed to conserve them. Although the law protects the mangroves anywhere they occur, this approach has not prevented negative effects of human decisions and activities related to mangroves and coastal ecosystems in general. As a result, while the area of mangroves has increased over the last decades for the entire island, it has decreased in certain sites. In order to guarantee the future of mangroves in places with high human activity and limited space such as Puerto Rico, conservation strategies should be clear in (1) defining the areas that satisfy the ecological requirements of these ecosystems, (2) incorporating more effective zoning regulations to maintain these areas natural and to protect the fluxes of water, nutrients, and organisms in and out of the system, and (3) developing monitoring programs that include all the components of these habitats. These will help ordering and directing human activities, facilitating the delimitation of urban growth boundaries and conservation areas, as well as understanding the causes and consequences of natural and human-induced processes on these important coastal ecosystems.

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