BIOTROPICA 28(4a): 525–536 1996

Land-Use Dynamics in a Post-Agricultural Puerto Rican Landscape (1936–1988)[1]

John R. Thomlinson

Terrestrial Ecology Division, University of Puerto Rico, PO Box 363682, San Juan, Puerto Rico 00936-3682, U.S.A.

Mayra I. Serrano, Tania del M. López, T. Mitchell Aide

Department of Biology, University of Puerto Rico, PO Box 23360, San Juan, Puerto Rico 00931-3360, U.S.A.

and

Jess K. Zimmerman

Terrestrial Ecology Division, University of Puerto Rico, PO Box 363682, San Juan, Puerto Rico 00936-3682, U.S.A.

ABSTRACT

Anthropogenic alteration of the landscape is a long-term disturbance both in duration and consequences. This study addresses land-cover responses to a history of human land use in northeastern Puerto Rico. Analysis of aerial photographs indicated that the pattern of land use in the municipality of Luquillo changed dramatically between 1936 and 1988. In 1936, sugar cane and pasture were the dominant land uses, occupying about one third of the study area each, while dense forest was rare. Pasture still occupied about a quarter of the area by 1988, but the area of sugar cane had declined to zero. Most sugar cane land was transformed to pasture after abandonment, while much of the pasture at higher elevations reverted to forest. More than half the study area in 1988 was occupied by dense forest, and the degree of forest regeneration was greatest adjacent to the Luquillo Experimental Forest and around patches that were dense forest remnants in 1936. The overall trend was from high-intensity agriculture to dense forest, but urban areas increased more than 2000 percent between 1936 and 1988 and are presently encroaching on forested areas. It is unclear from one study whether the same pattern would hold true at other sites in the tropics, but our study indicates the importance of preserving remnants of mature forest as sources of forest regeneration. In addition, the nature of the patches in the Luquillo landscape has changed as the land use has changed. In 1936, dense forest was highly fragmented, the patches were small and many of them had linear configurations (riparian corridors and hedgerows). By 1988, the average patch size of dense forest had increased greatly, although with one exception the patches were still small relative to other land-cover types.

RESUMEN

La alteración antropogénica del paisaje es una fuente de perturbación a largo plazo tanto en duración como en consecuencias. Este estudio se enfoca en el efecto que ha tenido la covertura del terreno respecto a la historia en el uso de tierra en la parte noreste de Puerto Rico. El análisis de fotografiás aéreas indicó que el patrón de uso de tierra en la municipalidad de Luquillo ha cambiado dramáticamente entre 1936 y 1988. En el 1936, los usos más predominantes eran la caña de azúcar y los pastizales. Cada uno ocupaba cerca de un tercio del área de estudio mientras que existía poco bosque denso. En 1988, un cuarto del área de estudio estaba ocupada por pastizales, en cambio el área que ocupaba la caña de azúcar disminuyó a cero. La mayoría de la caña de azúcar pasó a ser pastizal luego de su abandono, mientras que la mayoría del pastizal en altas elevaciones pasó a ser bosque. En el 1988, más de la mitad del área de estudio estaba cubierto por bosque denso, y el grado de regeneración de bosque era mayor, tanto adyacente al Bosque Experimental de Luquillo (LEF, por sus siglas en inglés) como cerca de parches de bosque denso que existían en 1936. La tendencia general fue el cambio de agricultura intensa a bosque denso, pero las áreas urbanas aumentaron más de 2000 por ciento entre 1936 y 1988, amenazando actualmente las áreas de bosque. Con un solo estudio es difícil precisar si estas tendencias serían aplicables en otras áreas tropicales, pero lo que sí queda claro es la importancia que tiene el preservar parches de bosque maduro como fuente para la regeneración. En adición, la naturaleza de los parches en el paisaje de Luquillo ha cambiado a medida que el uso del terreno ha ido cambiando. En 1936, la porción de bosque denso se encontraba altamente fragmentado, los parches eran pequeños y muchos de ellos tenían configuraciones lineales (corredores de vegetación riparia y "hedgerows"). En 1988, el tamaño promedio de los parches de bosque denso aumentó grandemente, aunque todos los parches, excepto uno, eran aun pequeños comparados a otros tipos de coberturas.

Key words: agriculture; forest regeneration; GIS; landscape characteristics; land-use change; Puerto Rico.

[1] Received 20 September 1995; revision accepted 10 April 1996.

Human land use affects future ecosystem properties, both in the tropics and in temperate zones (Padoch & Vayda 1983, Hamburg & Sanford 1986, Foster 1992, Zou *et al.* 1995), and much recent work has focused on these effects (Shukla *et al.* 1990, Saunders *et al.* 1991, Waide & Lugo 1992). The level or intensity of agricultural activity has a marked impact on the land-cover change trajectory (García-Montiel & Scatena 1994, McCook 1994) as well as on the level of human involvement that may be required if land is to return to mature forest (Brown & Lugo 1994). Zimmerman *et al.* (1995) found that the "footprint" of human activity in the Luquillo Mountains of Puerto Rico was clearly visible on species composition after 60 yr of abandonment and two major hurricanes. Changes in agricultural practices and abandonment of agricultural lands can therefore leave distinct traces on the landscape even as forests regenerate (Foster 1993). Anthropogenic alteration of land cover is a long-term disturbance both in duration (for example, the first Europeans landed in Puerto Rico over 500 years ago) and consequences. It should therefore be considered a part of the long-term disturbance regime of an area along with other changes that are not anthropogenic, including hurricanes and landslides.

The economic base of Puerto Rico has changed dramatically during the last 60 yr, from a largely agricultural system to a more urbanized economy with an emphasis on manufacturing (Morales-Carrión 1983). In 1934, approximately 43 percent of the island's gross national product (GNP) was from agricultural products, primarily sugar cane and coffee, while that figure had decreased to four percent by 1980 (Dietz 1986). At the same time, the manufacturing sector increased from seven percent to 48 percent of the GNP. Associated with these economic changes was the movement of people from rural to urban areas. In 1940, 45 percent of employment was in agriculture, compared to only five percent in 1982. The conversion of land from sugar cane cultivation was mainly due to the overall decline in competitiveness of Puerto Rican sugar on the world market (Morales-Carrión 1983). An additional factor was the 1941 Land Law that restricted corporate land holdings and broke up some of the large sugar estates (Koenig 1953, Dietz 1986).

As agriculture has declined in Puerto Rico, forest cover has increased. At the peak of agricultural activity, in the late 1940's, forest cover was reduced to five percent of the island, with about the same area in shade coffee plantations (Koenig 1953), but by 1985, 34 percent of the island was forested (Birdsey & Weaver 1987). Before agriculture declined and forest regeneration began, most of the remaining forest was located in isolated mountainous areas such as the Luquillo Mountains. The increase in forest cover over the last 50 yr is in contrast to the deforestation occurring in most of the tropics (Schmidt 1987, Grainger 1988, Brown & Lugo 1990, Johnson & Cabarle 1993, Singh 1993).

Little is currently known about landscape-level patterns of forest regeneration in the tropics because most areas are not increasing in forest cover, presumably because few tropical areas have been subject to economic programs similar to those implemented in Puerto Rico. There are certainly differences between the ecosystems studied here and those found in much of the rest of the Neotropics. Luquillo has a history of hurricane disturbance (Fassig 1929, Miner-Solá 1995), a low incidence of fire, a large expanse of protected forest nearby, and small pasture size. In other areas, where not all of these conditions are met, one might expect different rates, and possibly trajectories, of land-cover change following agricultural abandonment. It is even difficult to generalize about Puerto Rico, since different parts of the island have had different land-use histories and different population densities. However, the landscape dynamics in Luquillo present an opportunity to study what might happen to neotropical ecosystem structure and function as lands with different histories of agricultural use are abandoned and forest regenerates. The objectives of this study were to quantify changes in the extent of different land uses in the Luquillo municipality, to determine the landscape characteristics that influence the land-cover change trajectories, and to describe the landscape patch characteristics at the different stages of forest regeneration.

STUDY SITE

The study area is within the municipality of Luquillo in northeastern Puerto Rico (18°22′30″N, 65°42′30″W; Fig. 1), ranging from sea level to 310 m above mean sea level (amsl). It is almost entirely within the subtropical moist forest life zone except for a small amount of higher-elevation land in the subtropical wet life zone (Ewel & Whitmore 1973). These two life zones combined occupy 85 percent of the land surface of Puerto Rico. The presettlement land cover of Puerto Rico is not known with certainty, but it is thought that the lowlands were forested with large tree species characteristic

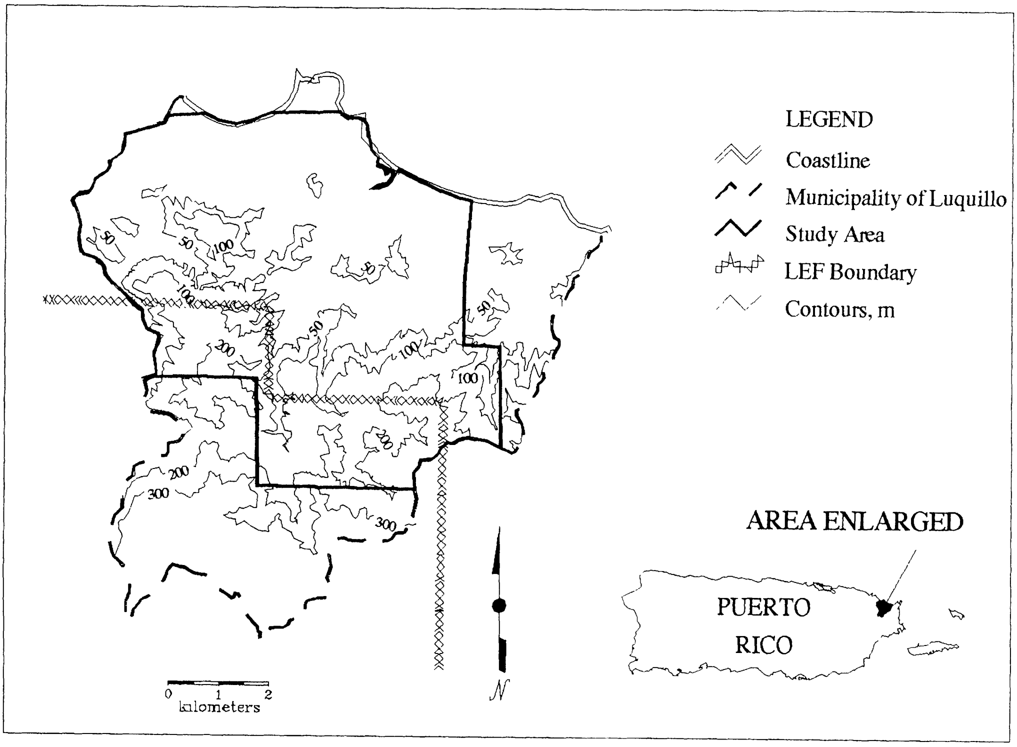

FIGURE 1. Location of the study area (solid thick line) relative to the coast and boundary of the municipality of Luquillo, Puerto Rico. The LEF boundary and selected elevation contours are also shown.

of other areas of the Caribbean basin (Wadsworth 1950). The soils are predominantly clay and clay loam inceptisols and ultisols of the Coloso-Toa-Bajura and Caguabo-Mucara-Naranjito associations (Boccheciamp 1977). We selected the largest possible area within the municipality that was covered by three overlapping sets of aerial photographs (1936, 1964, and 1988). We excluded forested land within the Luquillo Experimental Forest (LEF) boundary because it had not been subject to the same type of agricultural practices as the rest of the study area. The study area comprised 4333 ha, or about 65 percent of the total area of the Luquillo municipality. Luquillo was chosen for this study because it is located in a region that has undergone major land-use changes in the last 50 yr, and there is an extensive archive of aerial photographs available that document the progression of change. Furthermore, it is adjacent to the LEF, which contained mature forest at the start of the agricultural abandonment period, and where there has been both natural forest regeneration and active reforestation by the U.S. Forest Service (Brown *et al.* 1983, Scatena 1989).

MATERIALS and METHODS

AERIAL PHOTOGRAPH INTERPRETATION.—We examined three sets of 9 × 9 inch black-and-white aerial photograph stereopairs to create land-use maps of the study area. The photographs were from 1936, at a scale of 1:18,696; and 1964 and 1988, both at a scale of 1:20,000. We delineated all polygons greater than 3 × 3 mm on the photographs using a mirror stereoscope, traced their outlines onto acetate overlays of each photograph, and assigned each polygon to one of seven land-use classes (Table 1). The three forest classes differed in species composition as well as density, changing from early-successional shrubby species in Forest 1 to canopy species in Forest 3. Each polygon was coded according to the Puerto Rico Department of Natural Resources land-use mapping system, and subclasses unique to this project (for forest and urban) were added. We then verified the classification of the more confusing land-cover types on the 1988 photographs by field checking.

For each year we created a base map by tracing geographic control features, such as roads, rivers,

TABLE 1. *Land-use classes used in the aerial photography classification.*

Class	Characteristics
Sugar cane	Even texture, uniform color, no trees
Pasture	Stippled texture, up to 20 percent tree cover
Forest 1	20–50 percent tree cover
Forest 2	50–80 percent tree cover
Forest 3	80–100 percent tree cover, hedgerows, riparian zones
Urban 1	Scattered buildings in loose association
Urban 2	Towns, subdivisions, ground stripped and levelled for building

and shore lines, onto acetate overlays from United States Geological Survey 1:20,000 topographic maps. For the 1964 and 1988 photographs we were able to transfer polygon lines directly from the photograph overlays to the base maps by using the central portion of each photograph, thereby minimizing distortion. We transferred the polygon boundaries from the 1936 photograph overlays to the base map using a zoom transfer scope because of the change of scale. Each base map was then digitized into the ARC/INFO version 6 geographic information system (GIS) package (ESRI 1991). The digitized data layers were transformed into Universal Transverse Mercator (UTM) Zone 20 coordinates to allow accurate area measurements and overlay with other geographic data sets.

GIS DATABASE CONSTRUCTION AND ANALYSIS.—Attribute data files containing a unique identifier for each polygon, its land-use class, and any ancillary information, were created for each year. These files were put into ARC/INFO. Each land-use map and its associated attribute information constituted a coverage (*sensu* ARC/INFO; ESRI 1991), and the three coverages comprised the basis for the GIS used for the remainder of the project. Three overlay coverages were created by combining, respectively, 1936 and 1964; 1964 and 1988; and 1936 and 1988 coverages. Exported files of areas and land-use history of each derived polygon were used as input for statistical analyses. We constructed four different transition matrices (Forman & Godron 1986, Cherrill & McClean 1995) for each two-year combination of land uses, 1936 to 1964, 1964 to 1988, and 1936 to 1988. The matrices were expressed as (1) area of each land-use transition, ha; (2) area of each transition as a percentage of the study area; (3) area of each transition as a percentage of the area of each land use at the earlier of the two dates to determine the proportional fate of each land use; and (4) area of each transition as a percentage of each land use at the later of the two dates to determine the proportional history of each land use. Transition type (3) is analogous to the method of Markov-chain transition probabilities (White & Mladenoff 1994).

We conducted a series of analyses to examine the spatial pattern of forest regeneration in the study area. First, we selected all polygons in the combined 1936–1988 coverage that demonstrated a history of increasing forest cover as indicated by changes from any non-forest class to any forest class or from a less-dense to a more-dense forest class. Next we created a coverage of distance, or buffer, classes (0–1 km, 1–2 km, and > 2 km) from the boundary of the LEF, and overlaid it with the increasing-forest-class coverage. The same series of operations was repeated for elevation classes (0–50 m, 50–100 m, 100–200 m, and 200–300 m amsl) and distance from patches that were dense forest (Forest 3) in 1936 (0–100 m, 100–200 m, 200–400 m, and > 400 m). Areas of increasing forest class were expressed as percentages of the area of each buffer zone or elevation interval exclusive of land that was dense forest in 1936, and therefore incapable of increasing in forest cover. The percentages were compared using the log-likelihood statistic (Zar 1984). For this and the subsequent statistical analyses, we used a significance level of 0.05.

Finally we looked at area and shape of different land-use polygons in the different years (Forman & Godron 1981). The area of each land-use polygon gave an overall measure of the dominance and fragmentation of that land use, while the shoreline development index (SLD), borrowed from limnology, (Lind 1985; $SLD = \text{perimeter}/2\sqrt{(\text{area}\cdot\pi)}$) was a measure of the shape of polygons. As SLD increased from a theoretical minimum of one, it indicated an increasing ratio of perimeter to area and thus a greater exposure of the patch center to patch edge. Differences in area or SLD between different years for the same land-use type, or among different land uses for the same year were compared using the Wilcoxon rank-sum test in SAS version 6 PROC NPAR1WAY (SAS Institute 1992).

RESULTS

AREAL TRENDS.—Land-use practices changed dramatically between 1936 and 1988 (Fig. 2). One of the most marked changes was the rapid decrease in

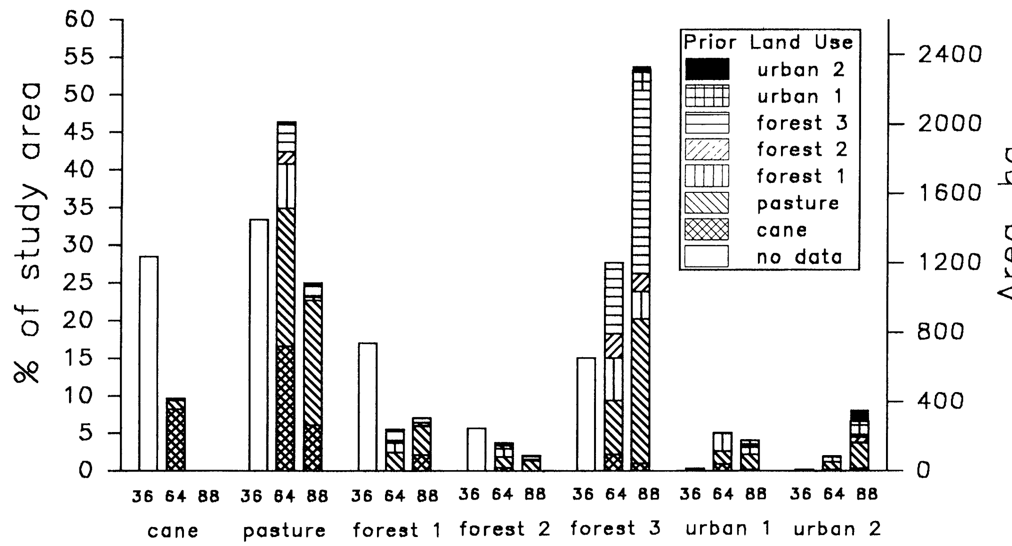

FIGURE 2. Percentage of study area and number of ha covered by each land-use class from 1936 to 1988. The different patterns in each bar and in the legend show the relative contributions of other land uses from the previous study year to each land use listed on the abscissa.

sugar cane cultivation, from 28 percent of the study area in 1936, to 10 percent in 1964, to 0 percent in 1988 (Fig. 3). This was matched by a dramatic increase in dense forest (Forest 3), which occupied 15 percent of the study area in 1936, increased to 28 percent in 1964, and reached 54 percent in 1988. Other important changes were in pasture, which peaked in 1964 at 46 percent, and the combined urban classes, which grew from one percent in 1936 to 12 percent in 1988.

Once sugar cane was abandoned, 52 percent became pasture from 1936 to 1988, while 18 percent succeeded to dense forest (Table 2). However, only a small area of sugar cane became forested without first becoming pasture (9 % between 1936 and 1964, and 10 % from 1964 to 1988; Fig. 2). Of the area covered by pasture in 1936, 50 percent succeeded to dense forest, while 23 percent remained in pasture (Table 2). Virtually all low- and medium-density forest (Forest 1 and Forest 2) succeeded to dense forest (Forest 3). Approximately 36 percent of the low-density urban (Urban 1) changed to pasture between 1936 and 1988, while 41 percent reverted to dense forest as isolated farms were abandoned.

Looking at the changes in the other direction, conducting a back-trajectory, 85 percent of the land that was covered by sugar cane in 1964 had also been cane in 1936. In 1988, 65 percent of the low-density (early-successional) forest had been sugar cane in 1936, while 27 percent had been pasture (Table 3). Approximately 60 percent of mid-density forest had been pasture in 1936. Dense forest was comprised of almost equal areas that had been dense forest, low-density forest, and pasture in 1936. Most of the pasture had previously been sugar cane, while low-density urban was predominantly on old pastures. High-density urban (Urban 2) was about evenly split between old pastures and abandoned sugar cane. Approximately 22 percent of the study area had the same land use in 1988 as it had in 1936.

Buffer analyses.—The amount of land with increasing forest cover from 1936 to 1988 decreased as distance from the LEF boundary increased (Log-likelihood test; $P < 0.001$; Fig. 4a). Approximately 73 percent of the land area within 1 km of the LEF boundary increased in forest cover, compared to 61 percent between 1 km and 2 km and only 34 percent more than 2 km away. The whole study area was within 4.5 km of the LEF boundary. The area of increasing forest cover also differed with elevation (Log-likelihood test; $P < 0.001$; Fig. 4b). Almost all the land between 100 m and 300 m amsl (86 percent above 200 m and 94 percent between 100 m and 200 m) increased in forest cover from 1936 to 1988, while the amount of land with regenerating forest decreased downslope from 100 m elevation. Of the land above 200 m amsl that

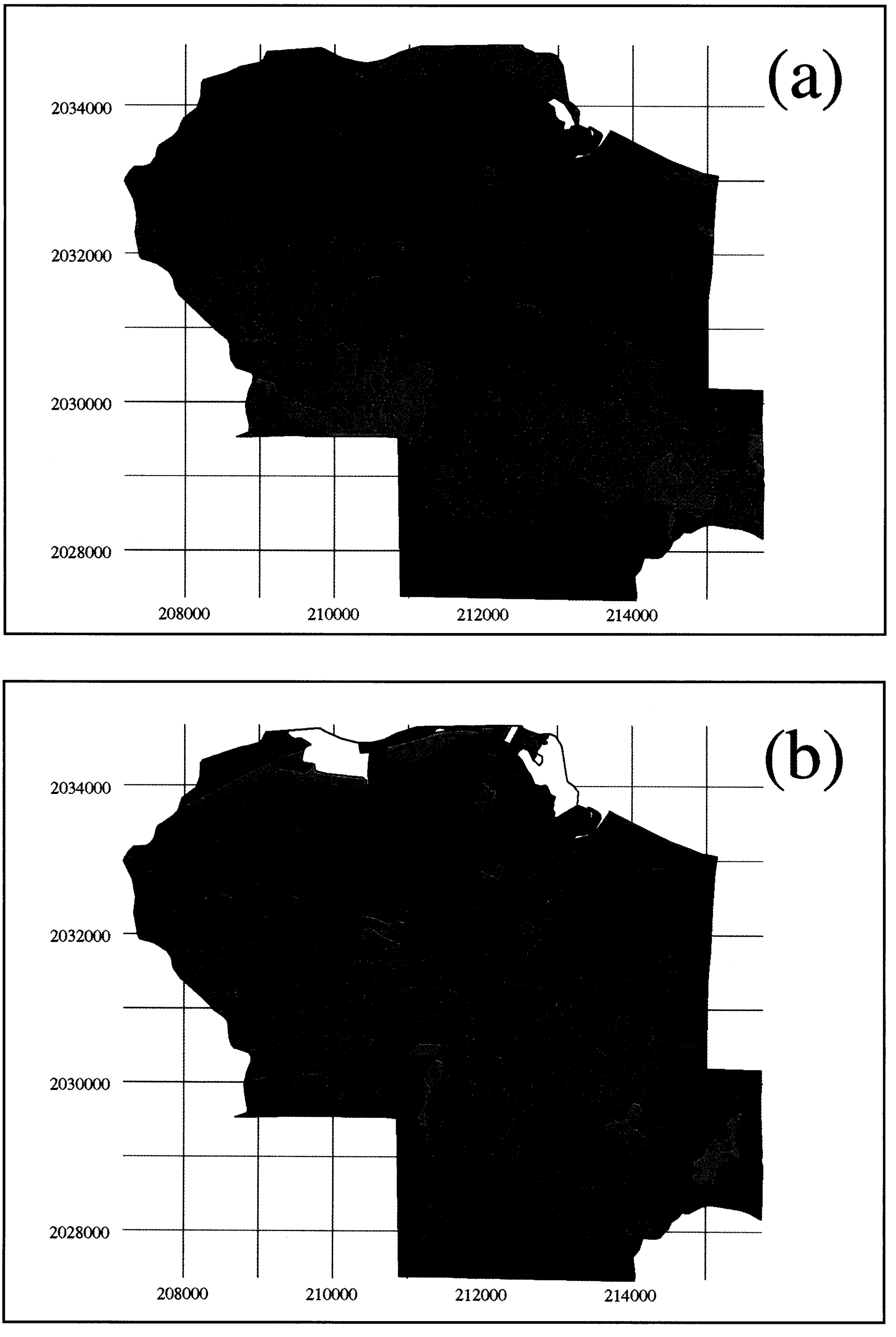

FIGURE 3. Land-use classes in the study area in (a) 1936, showing the dominance of sugar cane and pasture; (b) 1964, showing the increasing area of pasture, largely at the expense of sugar cane; and (c) 1988, showing the dominance of dense forest. Values in parentheses in the legend show the percent canopy closure for each of the three forest classes.

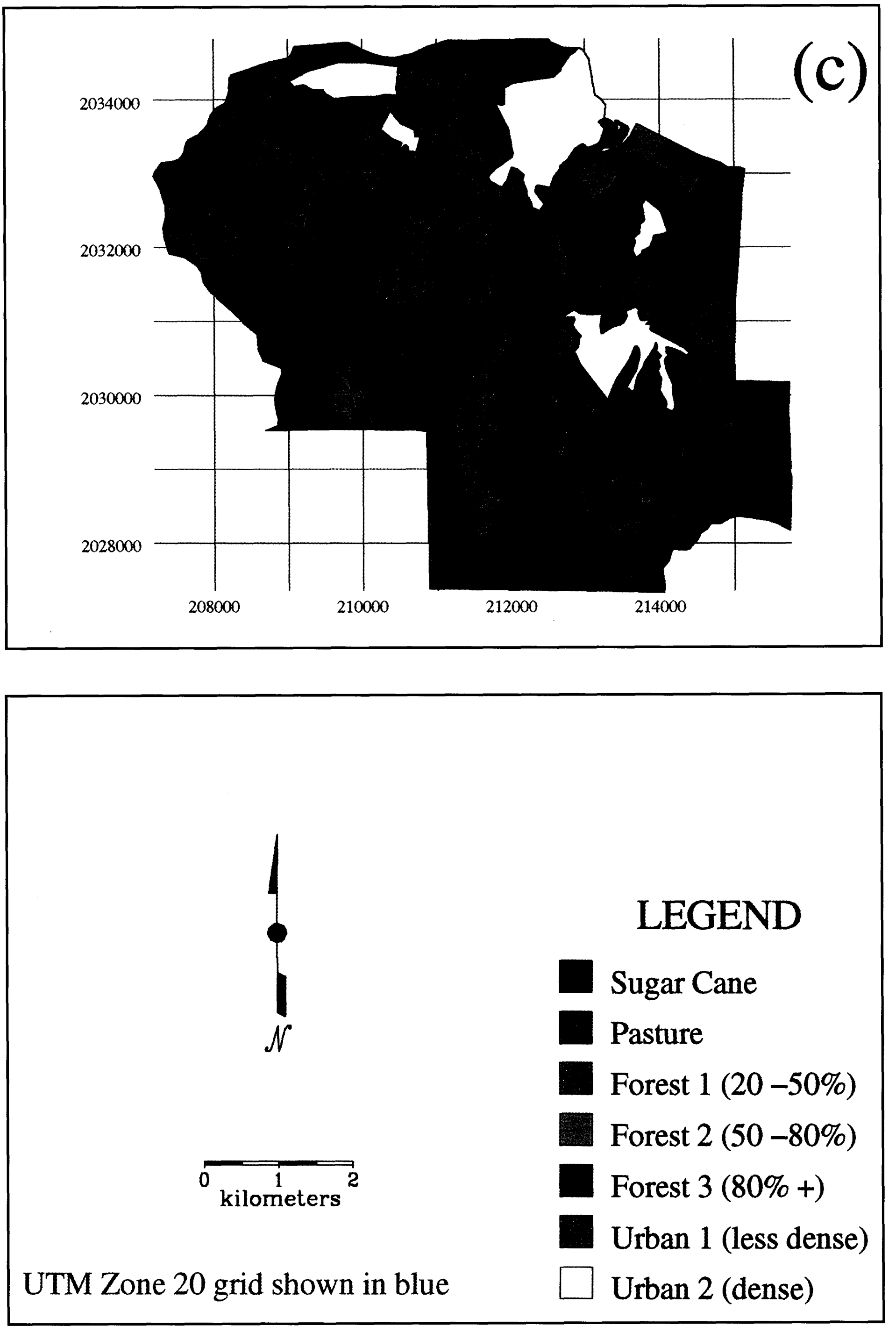

FIGURE 3. Continued.

TABLE 2. *Land-use transition matrix (forward trajectory) showing the fate in 1988 of each 1936 land-use type. Values in the table are the percentages of the area occupied by each of the land uses in 1936 (the rows) that changed to each particular land use in 1988 (the columns).*

1936 land use	1988 land use						
	Sugar cane	Pasture	Forest 1	Forest 2	Forest 3	Urban 1	Urban 2
Sugar cane	0.0	51.7	16.0	1.0	18.2	1.0	12.2
Pasture	0.0	23.2	5.6	3.6	49.9	7.6	10.2
Forest 1	0.0	8.4	1.1	1.9	79.2	4.0	5.4
Forest 2	0.0	4.8	2.2	2.2	87.3	2.8	0.6
Forest 3	0.0	4.9	1.6	0.6	89.5	3.0	0.4
Urban 1	0.0	36.3	12.0	0.0	41.0	1.0	9.7
Urban 2	0.0	0.0	0.0	0.0	0.0	0.0	100.0

did not increase in forest cover, 71 percent became urban. The amount of land with increasing forest cover also differed with distance from the dense forest (Forest 3) remnants present in 1936 (Log-likelihood test; $P < 0.001$; Fig. 4c). Regeneration of forest was greatest within 100 m of the forest islands and riparian zones and decreased with increasing distance from them.

PATCH CHARACTERISTICS.—The average area of a land-use patch almost doubled, from 9.1 ha in 1936 to 17.6 ha in 1988, while the average SLD stayed more or less constant over the period, changing from 1.68 to 1.74 (Table 4). The polygon area boxplot (Fig. 5) mirrored the increasing average area trend ($P \leq 0.0307$). The areas of polygons of sugar cane decreased from 1936 to 1964 ($P = 0.0105$), and by 1988 there was no sugar cane. Dense forest patches increased in area from 1936 to 1964 ($P = 0.0111$) and again from 1964 to 1988 ($P = 0.0187$). In each study year, one or two polygons accounted for a large proportion of the total area in dense forest: in 1936, one polygon contained 63 percent; in 1964, two polygons comprised 56 percent; and in 1988 one polygon accounted for 84 percent. When those polygons were excluded, the average polygon sizes increased from 2.1 ha in 1936 to 3.9 ha in 1964 to 6.8 ha in 1988, a three-fold increase. Polygon areas of the urban classes ($P = 0.0008$) and pasture ($P = 0.0001$) increased from 1936 to 1988. Shoreline development indices of polygons of individual land-use classes were generally unchanged from year to year, although they decreased for cane between 1936 and 1964 ($P = 0.0215$) and increased for dense forest between 1964 and 1988 ($P = 0.0031$).

Spatial characteristics of polygons varied among the different land uses in each year. In 1936, sugar cane had the largest individual land-use polygons (Wilcoxon; $P \leq 0.0019$), while dense forest had the smallest ($P \leq 0.0107$) except for combined urban (comparison of dense forest and combined urban non-significant, $P = 0.9079$); dense forest also had the largest shoreline development indices (SLD; $P = 0.0001$). By 1964, the pattern was less distinct, although dense forest still had the smallest individual polygons ($P \leq 0.0084$) (except when compared to urban, $P = 0.0686$) and the largest SLD's ($P \leq 0.0061$). The same pattern was re-

TABLE 3. *Land-use transition matrix (backward trajectory) showing the source from 1936 of each 1988 land-use type. Values in the table are the percentages of the area occupied by each of the land uses in 1988 (the columns) that came from each particular land use in 1936 (the rows).*

1936 land use	1988 land use						
	Sugar cane	Pasture	Forest 1	Forest 2	Forest 3	Urban 1	Urban 2
Sugar cane	0.0	58.7	64.9	13.7	9.6	6.7	42.8
Pasture	0.0	31.0	26.6	59.6	30.9	61.8	42.2
Forest 1	0.0	5.7	2.7	15.8	25.1	16.5	11.3
Forest 2	0.0	1.1	1.8	6.2	9.1	3.9	0.4
Forest 3	0.0	3.0	3.4	4.6	25.0	11.0	0.7
Urban 1	0.0	0.5	0.6	0.0	0.3	0.1	0.4
Urban 2	0.0	0.0	0.0	0.0	0.0	0.0	2.2

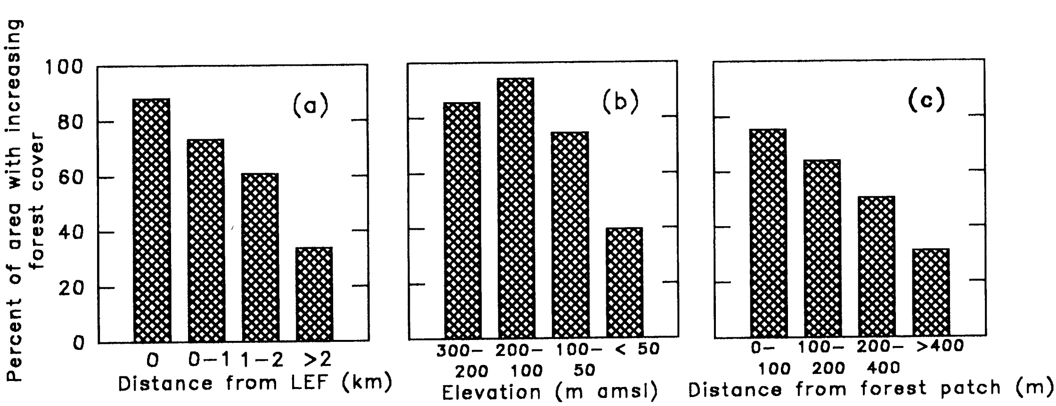

FIGURE 4. Area of increasing levels of forest cover from 1936 to 1988, expressed as percentages of total area, as a function of (a) distance from the LEF boundary; (b) elevation; and (c) distance from polygons that were dense forest in 1936.

peated in 1988. The average area of dense forest polygons in 1988, however, was much greater than that of any other land-use class except high-density urban. The high average value was the result of one very large dense-forest polygon (representing 45 percent of the study area) in the south of the area (Fig. 3c). Without that polygon, dense forest had the smallest average patch size (6.8 ha) of any land-cover class.

DISCUSSION

The pattern of land use in Luquillo has changed dramatically between 1936 and 1988 (Fig. 3). In 1936, sugar cane and pasture were dominant, occupying about one third of the study area each, while by 1988 there was no land under sugar cane cultivation. By 1988, pasture covered a quarter of the area, but more than half the study area was occupied by dense forest. While earlier successional stages of forest were never very common, they had almost disappeared by 1988. There was a definite trend from high-intensity agricultural use to dense forest. In addition, the area of the combined urban classes increased over 2000 percent between 1936 and 1988, and photographs taken in 1993 (J. R. Thomlinson, pers. obs.) suggest that the urban areas are continuing to increase on recently forested areas.

The exact trajectories taken by any particular patch of land can not be ascertained conclusively because of the interval between photographs, but it seemed that sugar cane was converted to pasture (which was the fate of over half the 1936 sugar cane and about two thirds of the 1964 cane). Interestingly, however, 10 percent of land that was cane in 1964 was dense forest in 1988, an interval of only 24 yr. Examination of intermediate photographs may permit us to determine the exact trajectory this land followed, but it seems that there was insufficient time for a long period of pasture establishment and use between abandonment from sugar cane and the start of forest regeneration. Pasture tended to remain in pasture or succeed to

TABLE 4. *Average areas and shoreline development indices (SLD) for all polygons of each land-cover type in each of the three study years. Dashed lines indicate value not applicable.*

	1936		1964		1988	
	Area (ha)	SLD	Area (ha)	SLD	Area (ha)	SLD
All polygons	9.1	1.68	8.5	1.64	17.6	1.74
Sugar cane	29.3	1.65	12.2	1.46	0.0	—
Pasture	6.8	1.46	8.0	1.44	8.7	1.45
Forest 1	13.2	1.60	4.8	1.40	9.8	1.57
Forest 2	7.6	1.49	7.2	1.54	9.6	1.41
Forest 3	5.6	2.23	8.9	2.15	42.4	2.61
Combined urban	1.6	1.38	13.2	1.49	19.5	1.59

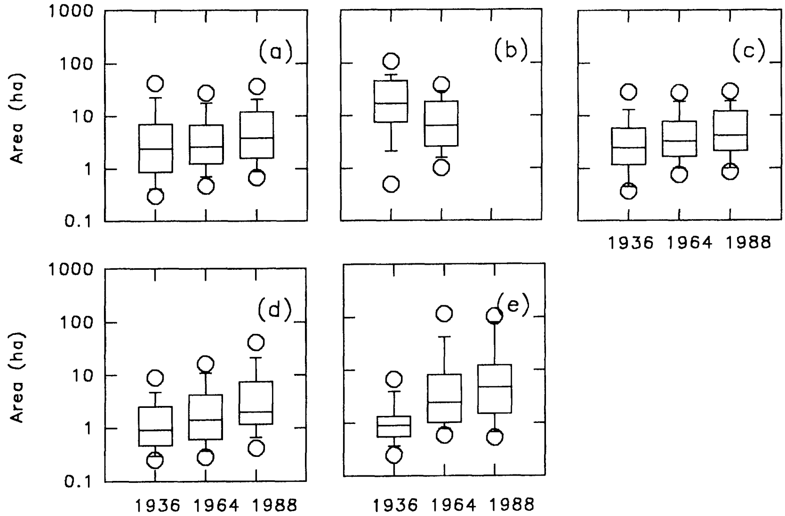

FIGURE 5. Boxplots of areas of polygons of different land-use types: (a) all polygons; (b) sugar cane; (c) pasture; (d) dense forest; and (e) combined urban, shown for each of the three study years. Horizontal lines on the box plots show the 10th, 25th, 50th, 75th, and 90th percentiles increasing up the ordinate. The open circles show the 5th and 95th percentiles.

dense forest, this latter trajectory applying to about a quarter of the pasture between 1936 and 1964 and close to half from 1964 to 1988. Looking at the process from the other direction, land that was dense forest in 1988 had previously been in one of a number of different land uses in 1936, mainly existing dense forest, low-density forest, or pasture. The approach of looking at both forward and backward trajectories allows two different perspectives. The forward trajectory gives an indication of the successional pathways and therefore possibly insight into mechanisms (Aaviksoo 1993). The backward trajectory considers the land-use history of a given patch, and it may therefore help explain existing ecosystem properties based on known past conditions.

Forest regeneration was greatest close to the boundary of the LEF and decreased as distance from the boundary increased. This may indicate that the LEF was an important source pool of seeds or simply that the land near the LEF was not as attractive for human land uses. Higher elevations of the study area, and the steep slopes found at higher elevations, are not as suitable for agricultural and urban development as the coastal plain. In addition, the higher elevations are further from the coast and the major residential areas and transportation routes. One analysis that does seem to have a more easily interpreted message is that the degree of forest regeneration decreases with increasing distance from the 1936 patches of dense forest. The forest islands and riparian corridors that were left in 1936 appear to have served as nuclei for the forest regeneration process. Further study is required to determine the mechanisms of regeneration, but it seems likely that proximity to seed pools or parent plants is the dominant factor. In addition, hedges, roadside trees, and riparian forest remnants may serve as dispersal corridors for bird- and bat-dispersed species (Saunders & de Rebeira 1991).

There are other possible factors affecting forest regeneration in the Luquillo area. These might include earlier abandonment of less-suitable sites (for example, stream-side sites may be more subject to flooding) or management decisions based on political or monetary factors. For example, land closer to the LEF may have been taken out of pasture before land further away because of the market value of land close to a protected area, and at the cooler high elevations, for home sites.

Finally, the nature of the patches in the Luquillo landscape has changed as the land use has changed. In 1936, dense forest had the smallest individual patches with the highest degree of convolution, as measured by the shoreline development index. This is a good indication of the high degree of fragmentation of dense forest at that time; many of the remnants had linear configurations (riparian corridors and hedgerows). This pattern was maintained through 1988, even though the land-use map (Fig. 3c) suggests otherwise. The large area of dense forest on the map is a single polygon, albeit a very large one, and the massive effect this has on the overall land-use pattern is not reflected in the statistical tests. The average polygon areas, while not a suitable metric for statistical comparisons, may give a more realistic view of the overall land-use dynamics in the study area.

CONCLUSIONS

In our study area, decreasing intensity of agricultural activity led to forest regeneration at a rapid pace, and the rate of regeneration was greatest close to remnant patches of mature (dense) forest. In general, the land-cover change trajectory was from sugar cane, through pasture, to forest, although a small percentage of abandoned sugar cane land appeared to revert to forest directly. It is unclear from one study whether exactly the same pattern would hold true at other sites in the tropics, or even other sites in Puerto Rico, but our study indicates the importance of preserving remnants of mature forest as sources of forest regeneration.

ACKNOWLEDGMENTS

We are grateful to the Puerto Rico Department of Natural Resources for their assistance with some of the aerial photographs. This study was supported in part by grants from the National Aeronautics and Space Administration Institutional Research Awards for Minority Universities Program (NAGW-4059) and the National Science Foundation Minority Research Centers for Excellence (HRD-9353549), and in part under grant DEB-9411973 from the National Science Foundation to the Terrestrial Ecology Division, University of Puerto Rico, and the International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by the Forest Service (U.S. Department of Agriculture) and the University of Puerto Rico. We also thank the students of the scientific writing seminar at the UPR–Río Piedras campus and two anonymous reviewers for their helpful comments on the manuscript.

LITERATURE CITED

Aaviksoo, K. 1993. Changes of plant cover and land use types (1950's to 1980's) in three mire reserves and their neighbourhood in Estonia. Landscape Ecol. 8: 287–301.

Birdsey, R. A., and P. L. Weaver. 1987. Forest area trends in Puerto Rico. U.S. For. Serv. Res. Note SO-331. New Orleans, Louisiana.

Bocchecíamp, R. A. 1977. Soil survey of the Humacao area of eastern Puerto Rico. U.S. Soil Cons. Serv., San Juan, Puerto Rico.

Brown, S., and A. E. Lugo. 1990. Tropical secondary forests. J. Trop. Ecol. 6: 1–32.

———, and ———. 1994. Rehabilitation of tropical lands: a key to sustaining development. Rest. Ecol. 2: 97–111.

———, ———, S. Silander, and L. Liegel. 1983. Research history and opportunities in the Luquillo Experimental Forest. U.S. For. Serv. Gen. Tech. Rep. SO-44. New Orleans, Louisiana.

Cherrill, A., and C. McClean. 1995. An investigation of uncertainty in field habitat mapping and the implications for detecting land cover change. Landscape Ecol. 10: 5–21.

Dietz, J. L. 1986. Economic history of Puerto Rico: Institutional change and capitalist development. Princeton University Press, Princeton, New Jersey.

ESRI. 1991. Arc/info version 6.0, 6.1. Environmental Systems Research Institute, Inc., Redlands, California.

Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the United States Virgin Islands. U.S. For. Serv. Res. Pap. ITF-18, Río Piedras, Puerto Rico.

Fassig, O. L. 1929. On the frequency of hurricanes in the vicinity of Porto Rico. Porto Rico J. Pub. Health Trop. Med. 5:106–113.

Forman, R. T. T., and M. Godron. 1981. Patches and structural components for a landscape ecology. Bioscience 31: 733–740.

———, and ———. 1986. Landscape ecology. Wiley, New York, New York.

Foster, D. R. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. J. Ecol. 80:753–771.

———. 1993. Land-use history and forest transformations in central New England. *In* M. J. McDonnell and S. T. A. Pickett (Eds.). Humans as components of ecosystems, pp. 91–110. Springer-Verlag, New York, New York.

García-Montiel, D. C., and F. N. Scatena. 1994. The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. For. Ecol. Manage. 63: 57–78.

Grainger, A. 1988. Estimating areas of degraded tropical lands requiring replenishment of forest cover. Int. Tree Crops J. 5: 31–61.

Hamburg, S. P., and R. L. Sanford, Jr. 1986. Disturbance, *Homo sapiens,* and ecology. Bull. Ecol. Soc. Am. 67: 169–171.

Johnson, N., and B. Cabarle. 1993. Surviving the cut: natural forest management in the humid tropics. World Resources Institute, Washington, DC.

KOENIG, N. 1953. A comprehensive agricultural program for Puerto Rico. U.S.D.A. For. Serv. Washington, DC.
LIND, O. T. 1985. Handbook of common methods in limnology. Second edition. Kendall/Hunt, Dubuque, Iowa.
MCCOOK, L. J. 1994. Understanding ecological community succession: causal models and theories, a review. Vegetatio 110: 115–147.
MINER-SOLÁ, E. 1995. Historia de los huracanes en Puerto Rico. First Book, San Juan, Puerto Rico.
MORALES-CARRIÓN, A. 1983. Puerto Rico, a political and social history. Norton, New York, New York.
PADOCH, C., AND A. P. VAYDA. 1983. Patterns of resource use and human settlement in tropical forests. *In* F. B. Golley (Ed.). Tropical rain forest ecosystems, pp. 301–313. Elsevier, New York, New York.
SAS INSTITUTE. 1992. SAS/STAT user's guide, volume 2, version 6, fourth edition. SAS Institute Inc., Cary, North Carolina.
SAUNDERS, D. A., AND C. P. DE REBEIRA. 1991. Values of corridors to avian populations in a fragmented landscape. *In* D. A. Saunders and R. J. Hobbs (Eds.). Nature conservation 2: The role of corridors, pp. 221–240. Surrey Beatty, Chipping Norton, New South Wales, Australia.
———, R. J. HOBBS, AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. 5: 18–32.
SCATENA, F. N. 1989. An introduction to the physiography and history of the Bisley experimental watersheds in the Luquillo Mountains of Puerto Rico. U.S. For. Serv. Gen. Tech. Rep. SO-72. New Orleans, Louisiana.
SCHMIDT, R. 1987. Tropical rain forest management. Unasylva 39(156): 2–17.
SHUKLA, J., C. NOBRE, AND P. SELLERS. 1990. Amazon deforestation and climate change. Science 247: 1322–1325.
SINGH, K. D. 1993. The 1990 tropical forest resources assessment. Unasylva 44(174): 10–19.
WADSWORTH, F. H. 1950. Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. Caribb. For. 11:38–47.
WAIDE, R. B., AND A. E. LUGO. 1992. A research perspective on disturbance and recovery of a tropical montane forest. *In* J. G. Goldammer (Ed.). Tropical forests in transition, pp. 173–190. Birkhäuser Verlag, Basel, Switzerland.
WHITE, M. A., AND D. J. MLADENOFF. 1994. Old-growth forest landscape transitions from pre-European settlement to present. Landscape Ecol. 9: 191–205.
ZAR, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey.
ZIMMERMAN, J. K., T. M. AIDE, M. ROSARIO, M. SERRANO, AND L. HERRERA. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. For. Ecol. Manage. 77: 65–76.
ZOU, X., C. P. ZUCCA, R. B. WAIDE, AND W. H. MCDOWELL. 1995. Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. For. Ecol. Manage. 78: 147–157.