

Recovery of a Subtropical Dry Forest After Abandonment of Different Land Uses¹

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ABSTRACT

We studied the ecological characteristics of 45–50-yr-old subtropical dry forest stands in Puerto Rico that were growing on sites that had been deforested and used intensively for up to 128 yr. The study took place in the Guánica Commonwealth Forest. Our objective was to assess the long-term effects of previous land use on this forest—*i.e.*, its species composition, structure, and functioning. Previous land-use types included houses, farmlands, and charcoal pits. Stands with these land uses were compared with a nearby mature forest stand. The speed and path of forest recovery after deforestation and land-use abandonment depended on the conditions of the land. Study areas where land uses had removed the forest canopy and altered soil conditions (houses and farmlands) required a longer time to recover and had a different species composition than study areas where land uses retained a forest canopy (charcoal pits). Different forest attributes recovered at different rates. Crown area index, stem density, and litterfall rate recovered faster than stemwood and root, biomass, tree height, and basal area. Where previous land uses removed the canopy, *Leucaena leucocephala*, a naturalized alien pioneer species, dominated the regrowth. Native species dominated abandoned charcoal pits and mature forest. The change in species composition, including the invasion of alien species, appears to be the most significant long-term effect of human use and modification of the landscape.

RESUMEN

Estudiamos las características ecológicas de rodales de un bosque seco subtropical en Puerto Rico que tenían 45–50 años de recuperación después de haber sido usados intensamente durante 128 años. El estudio se realizó en el Bosque Estatal de Guánica. Nuestro objetivo fue el de evaluar los efectos a largo plazo de los distintos tipos de usos del terreno en la composición de especies, la estructura y el funcionamiento. Los usos de terreno en el pasado incluyeron viviendas, terrenos agrícolas y carboneras. Estos rodales fueron comparados con un rodal de bosque maduro en un área cercana. La rapidez de recuperación y la manera en cómo sucede depende de las condiciones del terreno después de ser abandonado. Las áreas de estudio en las que se había removido el dosel y alterado las condiciones del suelo (casas y terrenos agrícolas) necesitaron más tiempo para recuperarse y reflejaron una composición de suelo diferente a las áreas de estudio donde el dosel se mantuvo (carboneras). Los diferentes atributos forestales se recuperaban a ritmos diferentes. El índice del área foliar de la copa, la densidad de tallos y la caída de hojarasca se recuperaron más rápido que la biomasa de tallos y raíces, la altura de los árboles y el área basal. La especie pionera naturalizada, *Leucaena leucocephala* (Lam.) de Wit-Fabaceae, fue la especie dominante en los bosques donde se había removido el dosel. Las especies nativas dominaban las carboneras abandonadas y el bosque maduro. El cambio en la composición de especies e incluso la invasión de especies foráneas, parece ser el efecto a largo plazo más significativo del uso humano y de la modificación del paisaje.

Key words: alien species; biomass; Caribbean forests; disturbances; dry forests; land-use change; litterfall; plant diversity; Puerto Rico; rehabilitation; secondary succession; subtropical forests.

RESEARCH ON DISTURBANCE ECOLOGY IN THE TROPICS is focused on both natural (Walker *et al.* 1991, 1996a,b; Zarin 1993; Holbrook *et al.* 1995; Byron & Shepherd 1998; Cochrane & Schulze 1998; Kinnaid & O'Brien 1998; Uhl 1998) and anthropogenic disturbances. The study of anthropogenic disturbances has mostly focused on their immediate negative impacts on mature forests. For example, Laurance and Bierregaard (1997) and Johns (1997) reviewed the substantial literature on the effects of deforestation, fragmentation, and logging on tropical forests. Another line of research focuses on forest succession after abandonment of agricultural fields or pastures (Uhl 1982, 1987; Uhl *et al.* 1988). These studies rarely span a decade of succession and involve lands used for relatively short-term before abandonment. Other studies use chronosequences to reconstruct the recovery of mature forests after short-term agricultural use

(Saldarriaga 1994; Kennard 2002; Peña Claros 2003). Less attention has been given to the reestablishment of forests after abandonment of long-lasting (over 100 yr) land uses such as human dwellings, agriculture, and charcoal production on deforested lands. Yet, these activities are common in the dry tropical landscapes populated by subsistence farmers. Moreover, land-use effects are major ecological factors in the tropics due to cycles of deforestation and fragmentation followed either by permanent conversion, land degradation, or land-use abandonment with forest recovery or arrested succession (Lugo & Helmer 2004). An increasing human population density that requires more space fuels the land-use cycle in the tropics, which leads to millions of hectares of degraded lands (Grainger 1988) but also to land abandonment and subsequent forest recovery (Brown & Lugo 1990).

Among tropical forests, dry forests face the greatest anthropogenic effects, and their response will affect the lives of millions of people. In Central America and the Caribbean, for example, nearly 90 percent of the dry forestlands are deforested or impacted

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in numerous ways by humans (Janzen 1986; Maass 1995). There are proposals to restore these forests (Brown & Lugo 1994), but the capacity of restored forests to support the needs of people through products and ecological services is largely unknown. Equally important is the need to understand plant succession after abandonment of prevalent land uses throughout the tropics (Meyer & Turner 1994).

Deforestation in Puerto Rico peaked in the 1940s (Birdsey & Weaver 1982, 1987), and forest recovery following cessation of intensive land-use is now quite advanced in time and space (Lugo *et al.* 1996). This provided us with an opportunity to examine the recovery of a dry forest after long-term anthropogenic disturbances. The analysis—presented here as a case study—assesses natural forest recovery several decades after the cessation of land uses that had taken place for over a century.

We considered four different previous land-use types (houses, baseball park, agriculture, and charcoal production) and tested the general hypothesis that they now have reached different levels of recovery depending on their initial type of disturbance (Ewel 1980). Specifically, we addressed the following questions: 1) Are there any differences in plant species composition and species richness, rate of forest structure recovery, or current forest production among stands recovering from different land-use types?; 2) How similar are these stands to nearby relatively undisturbed mature forest stands?; 3) How does this dry forest respond to anthropogenic disturbances?; and 4) What are the common attributes of vegetation that is recovering from different land uses?

METHODS

HISTORY OF LAND USE.—The study was conducted at five locations within the Guánica Commonwealth Forest Biosphere Reserve (Guánica forest), on the Antillean island of Puerto Rico. One location was a mature forest adjacent to the four locations with known land uses. This forest was the only mature stand within the region of our study and was not a primary forest. The stand was a closed forest in the aerial photos of 1936 and 1950. There was no evidence of logging within the mature forest since the turn of the 20th century. The various second growth areas—abandoned for 45 yr—varied in size and configuration (Fig. 1), reflecting past patterns of land use. Fieldwork took place between November 1992 and May 1994, and was followed up in 1998.

Twenty-three families lived in the locality called El Maniel (Fig. 1) for 128 yr (1820–1948) before it became part of the Guánica forest. Inhabitants of El Maniel maintained small farmlands; pastured goats, horses, cattle, and other domestic animals; and harvested green tree stems and branches for charcoal production. The latter practice was the predominant use of the forest and was an activity practiced throughout Puerto Rico at the turn of the 20th century. It involved thinning stands, selecting green wood for processing, placing wood in soil pits scattered throughout the stand to minimize hauling, covering wood with dirt, and slowly burning it to produce charcoal. Pit area was *ca* 4 m². Other land uses in this forest were subsistence agriculture, tree plantations (Wadsworth 1990),

grazing, and logging. A baseball park and school were located within the forest boundary. Baseball was introduced to Puerto Rico before the American invasion in 1898 and rapidly became popular. The school was a house similar in size to the other dwellings. The relocation of people from El Maniel involved the removal of all structures from the study area and the abandonment of all land uses.

All human activities at El Maniel caused extensive modifications in vegetation and soil structure. We anticipated that the patchy landscape observed today is a result of the different disturbance types that affected forest stands over time. None of the previous forest succession studies conducted in Guánica forest (Ewel 1971; Dunevitz 1985; Murphy & Lugo 1986a,b; Murphy *et al.* 1995) considered long-term forest recovery.

STUDY AREA.—The study area was originally a combination of deciduous and semievergreen forest located in an upper valley about 100 m above sea level with slopes varying from 0° to 18°. It is classified as subtropical dry forest (*sensu* Holdridge 1967) with a mean annual rainfall of 860 mm and a mean annual temperature of 24°C (Murphy & Lugo 1986b). Rainfall is variable both seasonally (Murphy & Lugo 1986b) and on a long-term basis (Lugo & García Martínó 1996). A long-term rainfall record shows annual extremes of 300 and 1300 mm. A 10-yr running average of annual rainfall shows periods of increasing (1927–1935 and 1968–1986) and decreasing (1935–1968 and 1986–1996) annual rainfall.

In general, soils in Guánica forest, described by Roberts (1942), are shallow, alkaline, and derived from limestone rock. Soil at the baseball park is Ensenada clay, characterized by a 5–10 cm friable, permeable, softly granular, reddish-brown, neutral or alkaline, and highly colloidal brown to red surface soil. This horizon is underlain by friable, permeable, brownish-red clay that rests on gray, medium-hard CaCO₃ limestone at a depth ranging from 20 to 30 cm. Soil and rock are both high in Ca and Mg (Roberts 1942). The depth to bedrock ranges from 15–30 cm. Aguilita clay is the soil type under houses and farmlands. On average, this soil type has a friable, granular, and calcareous dark grayish-brown clay surface soil 20 cm thick. No rock outcroppings were observed on this soil type and the soil profile was *ca* 60 cm deep. In charcoal pits and mature forest stands, the soil type was Aguilita stony clay, which differs from Aguilita clay in that it occurs on a steeper relief, has many outcroppings, and a thinner surface layer. Soil depth is about 30–60 cm. Differences among soils reflected human choices for particular activities, *i.e.*, agriculture and houses in the relatively deeper soils, and forest stands on the rockier soils; but in general these differences did not affect soil structure or chemistry.

We collected data in five land-use types based on information provided by past residents and aerial photographs, *i.e.*, baseball park, former human settlement areas (houses), farmlands, charcoal pits, and mature forest. We will use the previous land-use type to refer to forest stands or plots on these locations at the time of the study, recognizing that land-use ceased 45–50 yr ago. We established five circular plots with a radius of 11.3 m on each past land-use type; however, for the purpose of statistical analysis of plot data, we combined land uses into three types (houses [houses *sensu stricto* and baseball park], farmlands, and charcoal pits), according to the

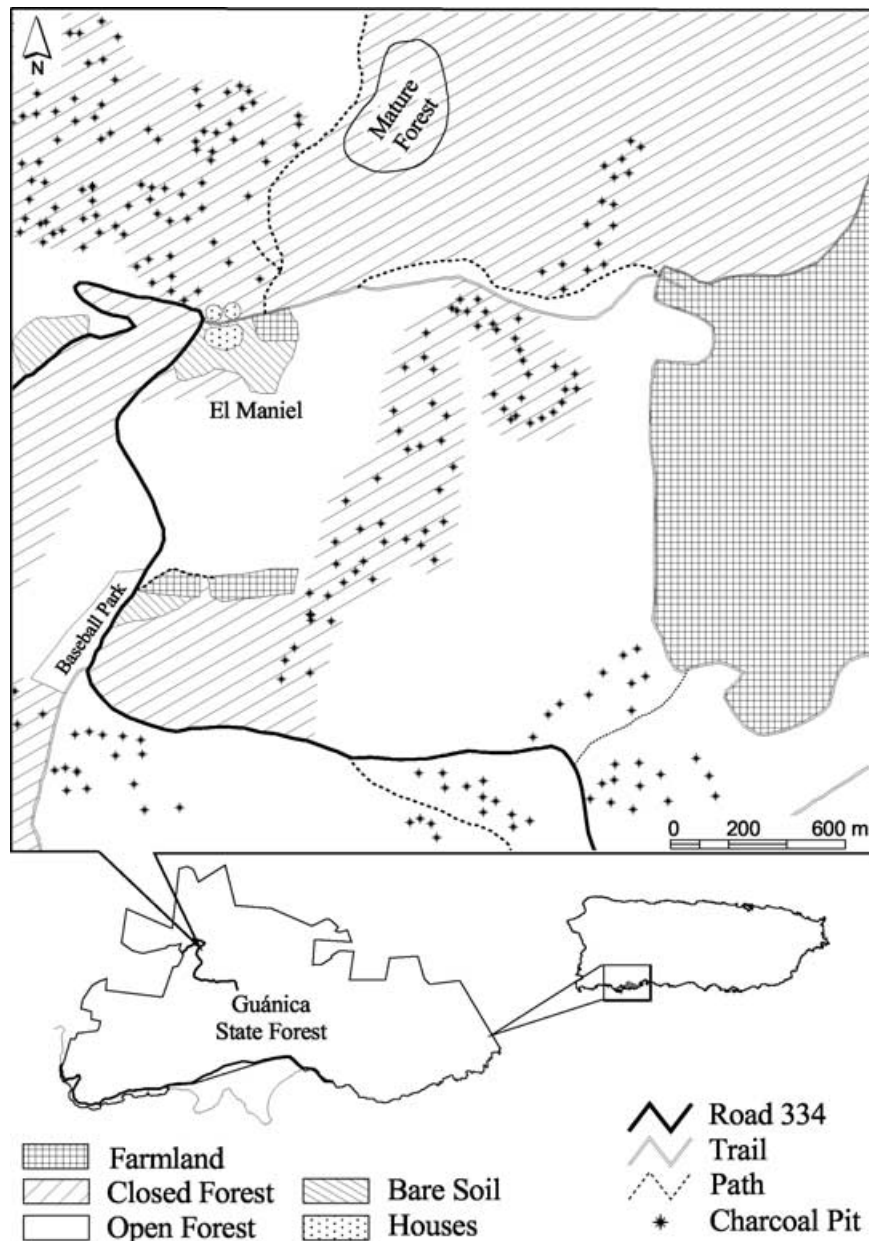


FIGURE 1. Map of the study area based on a 1936 air photo. The charcoal pits shown in this map are those that were active (burning) at the time the air photo was taken. For this reason, the locations of the charcoal pits sampled do not correspond with the pits in this illustration.

geographic location of individual replicate plots within each of the land-use types. The baseball park plots were combined as were three house plots (Fig. 1) to form two independent data sets. The two other house plots completed four independent data sets for houses. We also combined two farmland plots that were in close proximity, so that we also had four independent data sets for farmlands.

When selecting plots, we controlled as much as possible for topography, distance from roads, and aspect. All plots, except four—two each for charcoal pits and mature forest—had flat topography (slopes 0 to $<15^\circ$). The four exceptions had slopes of 15° (charcoal

pits) and 18° (mature forest). The aspect of most plots was either north (12 stands) or south (8 stands). The aspect for two farmland and two charcoal pit plots was to the east, and for another farmland plot, to the west. The prevailing wind at the study area is from the northeast, but moisture can also reach stands from the south as sea breezes. Variation among plots in distance from trails was minimized (most were about 20 m from a trail). Total plot area was 0.2 ha for each land use.

The following parameters were analyzed with pooled data: basal area, stem density, crown cover (CC), crown area index (CAI),

and stemwood biomass. For other parameters, individual plot data, rather than pooled plot data by past land use, were used in the analysis. For example, we tested the similarity within and among land uses using the Sørensen similarity index (below) with individual plot data for tree species composition.

PLANT SPECIES COMPOSITION AND SPECIES RICHNESS.—We identified each plant species and classified them as native and/or endemic to Puerto Rico (Liogier & Martorell 1982), alien and/or naturalized alien (Francis & Liogier 1991), and pioneer or non-pioneer. A naturalized alien species is an introduced species that is now regenerating naturally in Puerto Rico without human interference. Criteria used for the pioneer species group included size of propagules, number of seeds per fruit, fruiting period, age of first reproduction, required soil conditions for germination, shade tolerance, gap size preferences, growth rate, and/or longevity (Little & Wadsworth 1964; Little *et al.* 1974; and our own field observations). We deposited specimens of all identified plants in the Herbarium of the Pontifical Catholic University of Puerto Rico in Ponce, Puerto Rico.

Species density (number of species per area) was estimated for tree, sapling (woody plants <2.5 cm DBH [diameter at breast height measured at 1.3 m] and ≥ 1 m height), and ground vegetation (woody or herbaceous < 1 m height). Seedlings were included in the ground vegetation. We classified trees into two groups: small (2.5 to < 5 cm DBH) and large (≥ 5 cm DBH). The similarity between plots representing different past land-use types (Sørensen Index; Kent & Coker 1996) was also calculated. We compared all plots within a land-use type and all plots of different past land-use types, including those from the mature forest.

RATE OF RECOVERY.—Basal area, stem density, tree diameter and height, CAI, root and stemwood biomass, stemwood biomass accumulation, litterfall, and soil organic matter were measured as indicators of forest recovery after abandonment. The value of each of these parameters over the time elapsed since abandonment is a linear rate of recovery in terms of vegetation growth and productivity. To facilitate comparisons, we standardized the measured rates as a percent of the mature forest value. Vegetation was sampled between June 1993 and April 1994.

The diameter at breast height (DBH), height, and CC of all large trees were measured in all plots. We established a 5-m radius subplot within each plot to measure the same parameters on small trees. Saplings were sampled along two perpendicular 22.6 m-long and 2-m wide transects on each circular plot. We used four systematically located 1 m² subplots on each circular plot to count and identify to species all ground vegetation, including seedlings. All grass blades attached to a particular underground stem were considered an individual when counting grass mats.

Basal area was estimated from tree DBH. All multiple stems at DBH were counted and measured individually. We estimated height with a measuring rod. CC was estimated by the formula:

$$CC = \left[\frac{D_1 + D_2}{4} \right]^2 \times \pi$$

where D_1 and D_2 are replicate measurements of crown diameter taken at right angles (Mueller-Dombois & Ellenberg 1974). The result was expressed in square meters of CC per tree. We multiplied CC by tree density (trees/m²) to estimate CAI (m²/m²).

Importance value (IV-200) of all tree species was expressed in percent and calculated as the sum of relative stem density and relative basal area divided by two. The IV allowed the determination of any difference in dominance of tree species within each category of past land-use type.

We collected roots from known soil volumes by systematically selecting four sampling points corresponding to N, E, S, and W directions on each plot at 5 m from the center. At each sampling point, we took two cores from each of two depths (0–5 cm and 5–10 cm). We collected different soil volumes from each depth due to the conical shape of the corer, 177 cm³ for 0–5 cm and 150 cm³ for 5–10 cm, and we combined the two cores from each depth in paper bags. Samples were washed free of soil and separated by depth and root diameter (<2 mm, 2–5 mm, and >5 mm). Samples were then oven-dried to constant weight at 70°C. We calculated biomass from dry weight (g) per soil volume (cm³), and multiplied by depth (cm) to obtain g/m². Here, we only report total root biomass.

We estimated stemwood biomass by multiplying individual tree volume data (basal area times height) by wood density. Wood density values were obtained from Little and Wadsworth (1964), Little *et al.* (1974), and Reyes *et al.* (1992). We collected wood samples for species with unknown wood density and dried samples at 70°C to constant weight and their volume determined by water volume displacement. In June and July 1998, we remeasured 1735 trees tagged in 1993. These data were converted to stemwood biomass as described above and used to estimate an annual rate of stemwood biomass accumulation for each stem.

Fine litterfall was collected monthly for a year using four randomly located 50 × 50 cm litter traps on each plot for a total of 100 baskets. The contents of each basket was oven-dried at 70°C to constant weight, and sorted into leaves, wood, flowers, and seeds. Here we only report total litterfall.

SOIL SAMPLING.—Soil samples were collected between November 1992 and January 1993. Sampling followed the same procedure used for root biomass but we collected two cores from each depth for organic matter, and bulk density determinations (20 determinations per parameter per location). Samples for bulk density were processed separately from those used for chemical and physical determinations. Each bulk density sample was analyzed individually, while samples for physical analysis were combined by depth and placed in a labeled cloth bag. Samples for bulk density were oven-dried at 105°C for 48 hours. After cooling, samples were weighed to the nearest 0.0001 g. We sieved soil samples used for pH and organic matter through an 850 μ m mesh. Soil pH was measured with an Orion Ion Analyzer Microprocessor (model 901) with a combination pH electrode in a 1:1 soil-water solution. Soil organic matter was determined with a modified Walkley Black method (Nelson & Sommers 1982).

DATA ANALYSIS.—We tested the pooled plot data by category of past land-use type for normality and constant variance. We tested data distribution by one sample Kolmogorov–Smirnov test on actual data as well as residuals. We compared data with normal distribution with one-way ANOVA and *post hoc* multiple comparisons (Bonferroni test). Basal area, stem density, stemwood biomass, root biomass, CAI, stemwood biomass production, total litterfall, similarity index, and soil chemistry data had normal distribution. Tree height and CC data did not have a normal distribution. For these, equivalent nonparametric tests were used, *i.e.*, Kruskal–Wallis and Mann–Whitney *U*-test. Contingency table analysis was applied to determine whether the frequency of the diameter and height classes differed among forests. The level of significance alpha was set at 0.05 for all statistical analyses. All statistical analyses were done with a Statistical Package for Social Sciences for Macintosh (SPSS 1999).

RESULTS

PLANT SPECIES RICHNESS AND COMPOSITION.—Charcoal pits had the highest tree species density (47 species/0.2 ha) followed in order by mature forest (37), farmlands (35), and houses (25). Houses had more ground vegetation species (53/40 m²) and charcoal pits had more sapling species (49/221 m²). All land-use types had more ground vegetation and sapling species than in mature forest.

Leucaena leucocephala, a naturalized alien pioneer species (Parrotta 2000), was the most important tree species in the former houses, and its IV was high in comparison with the IV of the dominant species at other locations (Table 1). *Leucaena* and *Pisonia albida*, a native nonpioneer species, were the most important species in farmlands. *Bucida buceras*, another native nonpioneer species, was dominant in charcoal pits and *Coccoloba diversifolia*, also a native nonpioneer species, dominated in the mature forest.

Stands of similar land use had a mean Sørensen similarity index of 0.50, with the exception of former farmland plots (Table 2). For trees, the highest similarity among locations was between charcoal pits and mature forest (two of the most structurally developed stands) followed by a progression of decreasing similarity with farmlands and houses. Species composition in former house sites was more similar to that of farmlands than to charcoal pits or mature forest.

RATE OF RECOVERY.—We found significant differences between past land-use types in the recovery of basal area ($P \leq 0.01$), mean tree height ($P \leq 0.001$), mean CC ($P \leq 0.001$), stemwood biomass ($P \leq 0.05$), and root biomass ($P \leq 0.001$). Areas used for charcoal production recovered species richness and vegetation structure faster than abandoned houses or farmlands (Figs. 2a and b). Moreover, after the abandonment of charcoal production, the forest exceeded the basal area and species density of nearby mature forests. Houses and farmlands showed faster recovery of their structure, litterfall, and stemwood biomass productivity (range of 0.3–1.5 Mg/ha/yr) than of their stemwood biomass, relative abundance of large-diameter trees, or types of dominant tree species (native vs. naturalized alien

or pioneer vs. nonpioneer; Figs. 2b and c, and 3, Table 1; complete list available from authors).

Stem density, CAI, total litterfall, and stemwood biomass production did not differ significantly among land-use types. Houses and farmlands had lower basal area, mean tree height, mean CC, and stemwood and root biomass than charcoal pits and mature forest. Houses ranked last in mean tree height (4.8 ± 0.04 m; $N = 732$), mean CC (7.7 ± 0.04 m²; $N = 732$), and stemwood biomass (36 ± 4.8 Mg/ha; $N = 4$); but were similar to farmlands in basal area (10 ± 0.6 vs. 14 ± 2.2 m²/ha; $N = 4$) and root biomass (270 ± 10 ; $N = 10$ vs. 296 ± 48 g/m²; $N = 20$).

The frequency of tree diameter classes differed significantly between land-use types and mature forest ($\chi^2 = 93.4$, $P \leq 0.01$). The most frequent tree diameter classes in all stands were stems <2.5 cm (saplings) and 2.5–4.9 cm DBH (small trees), independently of land-use type (Fig. 3). Less than 1 percent of the trees had a DBH between 10–69 cm. Mature forest had fewer saplings and more trees with diameters between 10–69 cm. The frequency of height classes also differed significantly between land-use types and mature forests ($\chi^2 = 357$, $P \leq 0.01$). Most trees in all land-use types and mature forest stands belong to the 1.0–2.9 m and 3.0–4.9 m height classes (not shown). The distribution of the tallest tree height classes shows an increasing trend from houses and farmlands to mature forest, where they reach the highest values (between 9–19 m).

SOIL.—Soil bulk density differed significantly between locations ($P \leq 0.001$). The highest bulk density (0–5 cm depth) corresponded to houses and farmlands (0.8 g/cm³), and the lowest to the mature forest and charcoal pits (0.4 and 0.6 g/cm³, respectively). Soil pH (7.6 – 7.8) and soil organic matter content (36 – 45 Mg/ha) did not differ significantly among land-use types.

DISCUSSION

In an earlier study of dry forests following deforestation, Opler *et al.* (1977) estimated that 150 yr would be required for lowland tropical dry forests to reach maturity after deforestation. Our study in Guánica forest suggests that after 45 yr of growth, recovery had advanced significantly suggesting resilience, but not all stands were at the same level of recovery for the parameters measured (Figs. 2a–c). Moreover, some forest properties recovered faster than others. Variables with fast turnover rates (fast variables *sensu* Carpenter *et al.* 2001) recover faster than slow variables because it takes time to accumulate basal area, biomass, or large trees (all slow variables), and the rate of accumulation is slowed down by the degree of land degradation (Aide *et al.* 1995; Zimmermann *et al.* 1995; Silver *et al.* 2000; Dupouey *et al.* 2002).

The results of the similarity index were similar to those of González Iturbe *et al.* (2002) who studied the recovery of Yucatan's dry forests after the long-term cultivation of *Agave fourcroydes*. In both studies, the highest similarity indices observed were about 0.50; the similarities were variable within and across sites, with some values as low as 0.11. Both of our studies underscore Ewel's (1980) suggestion that the path to maturity follows many alternatives.

TABLE 1. Basal area (BA in m^2/ha), stem density (D in stems/ha), and importance value (IV in%) of the fifteen most important tree species in plots developing on different former types of land-use 45 yr after abandonment, and plots of mature vegetation in the Guánica Commonwealth Forest, Puerto Rico. Data are also shown for each species at locations where it was not among the top 15 species in IV. Data are for trees with DBH ≥ 2.5 cm. Importance values are rounded off, and reported when ≥ 1 . Of the 120 plant species found in the study, 64 percent were trees, 18 percent were herbaceous and 10 percent were vines; 11 percent were alien, 6 percent were endemic, and 24 percent were pioneers.

Species	Houses			Farmlands			Charcoal pits			Mature forest		
	BA	D	IV	BA	D	IV	BA	D	IV	BA	D	IV
<i>Leucaena leucocephala</i> ^{a,b,c}	3.06	1821	36	1.84	878	15	0.28	167	2	0.01	5	
<i>Pithecellobium unguis-cati</i> ^{d,e}	1.24	1232	20	0.23	163	2	0.61	567	5	0.26	249	2
<i>Bursera simaruba</i> ^{d,e}	0.53	73	4	0.27	66	2	1.09	60	3	1.27	30	3
<i>Thouinia portoricensis</i> ^{d,e,f}	0.45	221	5	0.85	855	10	1.36	1117	10	1.18	524	7
<i>Machaonia portoricensis</i> ^{d,e,f}	0.13	127	2				0.35	233	2			
<i>Comocladia dodonea</i> ^{d,e}	0.10	130	2				0.03	26				
<i>Colubrina arborescens</i> ^{d,e}	0.59	355	7	1.55	1102	15	1.15	541	6	0.08	20	
<i>Exostema caribaeum</i> ^{d,e}	0.11	68	1	0.11	45	1	0.75	365	4	0.06	30	
<i>Prosopis juliflora</i> ^{a,b,c}	1.05	156	8	2.01	417	11						
<i>Bunchosia glandulosa</i> ^{d,e}	0.14	48	1	0.09	61	1	0.06	20				
<i>Bourreria vigata</i> ^{d,e}	0.06	36	1									
<i>Pisonia albida</i> ^{d,e}	0.16	45	1	2.56	694	16	2.79	760	12	1.24	266	5
<i>Securinea acidoton</i> ^{d,e}	0.11	61	1	0.22	147	2	0.27	121	1	0.05	15	
<i>Guapira obtusata</i> ^{d,e}	0.03	18								0.51	45	2
<i>Coccoloba diversifolia</i> ^{d,e}	0.06	15	1	0.23	111	2	1.06	689	7	3.68	1856	23
<i>Guaiacum officinale</i> ^{d,e}	0.21	114	2	0.43	182							
<i>Melicoccus bijugatus</i> ^{c,b}	0.17	10	1			3						
<i>Bourreria succulenta</i> ^{d,e}	0.09	58	1	0.64	227	4	0.07	35		0.09	20	
<i>Krugiodendron ferreum</i> ^{d,e}	0.05	51	1	0.07	30		0.03	51		0.19	70	1
<i>Swietenia mahagoni</i> ^{c,b}	0.19	10	1	0.09	30	1						
Unknown lugume	0.15	8	1									
<i>Croton astroites</i> ^{d,c}	0.04	64	1									
<i>Capparis cynophallophora</i> ^{d,e}	0.06	36	1									
<i>Erythroxylum areolatum</i> ^{d,e}	0.03	18		0.22	122	2	0.03	5		0.06	35	
<i>Capparis hastata</i> ^{d,e}	0.02	13		0.27	95	2	0.02	26				
<i>Amyris elemifera</i> ^{d,e}	0.02	15		0.16	142	2	0.17	147	1	0.14	66	1
<i>Forestiera segregata</i> ^{d,e}	0.01	13		0.27	10	1						
<i>Bucida buceras</i> ^{d,e}	0.01	13		0.01	5		5.16	210	14	5.21	381	16
<i>Eugenia foetida</i> ^{d,e}	0.01	13		0.02	26		1.18	1113	10	0.72	614	6
<i>Tabebuia heterophylla</i> ^{d,c}	0.01	15					0.29	125	2	0.22	76	1
<i>Eugenia rhombea</i> ^{d,e}							0.21	131	1	0.53	565	5
<i>Erythroxylum rotundifolium</i> ^{d,e}				0.04	51	1	0.29	126	1	0.87	267	4
<i>Guettarda krugii</i> ^{d,e}							0.17	209	2	0.04	15	
<i>Hypelate trifoliata</i> ^{d,e}				0.06	51	1	0.38	95	2	0.45	55	2
<i>Antirhea lucida</i> ^{d,e}							0.25	147	2	0.10	20	
<i>Savia sessiliflora</i> ^{d,e}							0.08	81	1	0.68	687	7
<i>Gymnanthes lucida</i> ^{d,e}							0.11	81	1	0.44	432	4
<i>Guettarda elliptica</i> ^{d,e}	0.01	2					0.20	168	2	0.21	234	2

^aNaturalized alien.

^bAlien.

^cPioneer.

^dNative.

^eNonpioneer.

^fEndemic.

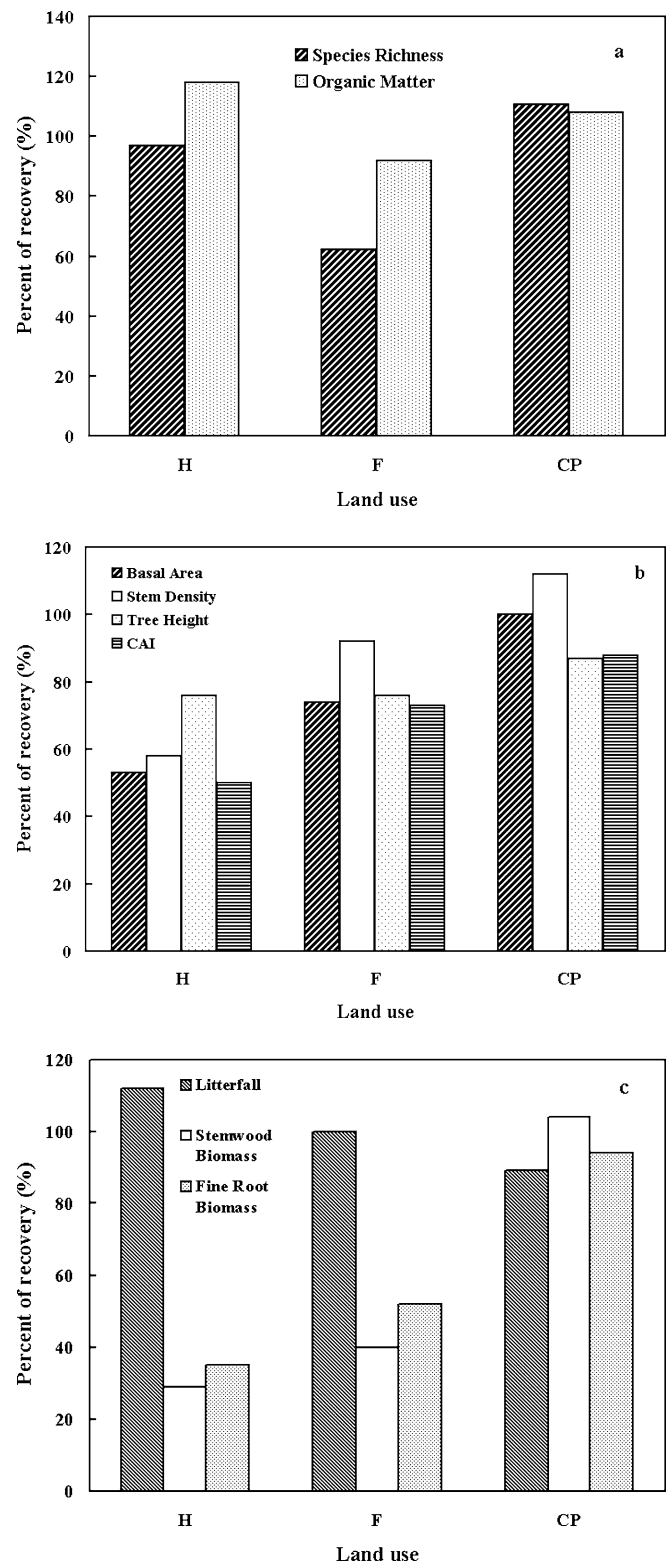


FIGURE 2. The level of recovery of various forest parameters on 45-yr-old stands with the indicated types of past land use: (a) total species richness and soil organic matter, (b) vegetation structure, and (c) primary productivity. All values are expressed as a percentage of the parameter in a nearby mature forest stand that was not converted to a nonforest land-use. Stands are located in the Guánica Commonwealth Forest, Puerto Rico. H = houses, F = farmlands, CP = charcoal pits, MF = mature forest, and CAI = crown area index.

TABLE 2. Mean Sørensen Similarity Index for trees (DBH ≥ 2.5 cm) of stands on locations of differing types of former land-use 45 yr after abandonment, and a nearby stand of mature vegetation in the Guánica Commonwealth Forest, Puerto Rico. Comparisons are based on 400 m² circular plots. Standard error is in parentheses. Values with the same letters along rows (comparing between past land uses) and the first (bottom) diagonal (comparing within past land uses) are not statistically different at $P \leq 0.05$.

	H	F	CP	MF
Houses (H)	46 (1.9) ^a	34 (2.3) ^b	19 (1.4) ^c	12 (0.8) ^c
Farmlands (F)		25 (5.0) ^b	22 (2.7) ^c	17 (2.3) ^c
Charcoal Pits (CP)			44 (2.3) ^a	44 (1.7) ^a
Mature Forest (MF)				56 (2.7) ^a

Replicate stands on each of the land-use types—except farmlands—developed comparable floristic composition but differed from those developing after other land-use types.

Forests developing on former abandoned house plots supported the least developed community, followed by farmlands, and charcoal pits. Houses and farmlands had the greatest abundance of pioneer species, lower floristic richness, and highest dominance compared with charcoal pits and mature forest (Table 1). We believe forest stands followed different successional pathways because of the condition of soil and vegetation at the time of abandonment of a type of land-use (below).

FOREST RESPONSE TO ANTHROPOGENIC DISTURBANCES.—Interpreting forest response to land-use types requires knowing the ways that human activity modifies site conditions. Each type of modification

affects a different component of the ecosystem (*i.e.*, canopy, soil, understory, etc.) and has a different effect on ecosystem response.

Charcoal production burns aboveground biomass and leaves nutrient-rich ash and charcoal fragments on the forest floor and soil profile. Charcoal production also created many small gaps within the forest and the soil was not heavily affected except in the site of the pit. These gaps favor seed germination from soil seed bank or seed rain, and/or the elongation of suppressed saplings, thus increasing the density of trees and favoring high species richness of native species (Fig. 2a). High stem density (4734–7826 stems/ha) and development of multiple stems of the cut trees increased stand basal area (Fig. 2b). Tree height and CC did not recover as fast as basal area and stem density because cutting altered apical dominance, which kept trees small and their crowns pruned.

In contrast to charcoal pits, all vegetation was removed from house sites, including roots, altering soil conditions through compaction and erosion. Conditions in former house sites resulted in the slowest rates of succession among all land uses because of total woody plant removal. These sites showed the lowest values of basal area, biomass, height, and species density (Figs. 2a and b). Moreover, this land use enabled invasion by *Leucaena*, a nitrogen-fixing pioneer species, well suited to the harsh conditions of a compacted, vegetation-free site. *Leucaena* creates vegetation cover in a short time, and facilitates the establishment of shade-tolerant species by providing shade and adding nutrients and organic matter to the soil (Parrotta 1993). The highest seedling density occurred under this *Leucaena* canopy (90 vs. 15 seedling/m² in mature forest).

Houses and farmlands had a particular effect on soil conditions. On the one hand, humans removed all litter and compacted the soil in house locations, but on the other, they concentrated organic matter and nutrients and thus enhanced soil fertility. Farmers altered farmland locations by plowing the soil and enriched their farms and house locations with alien species. Humans removed the original

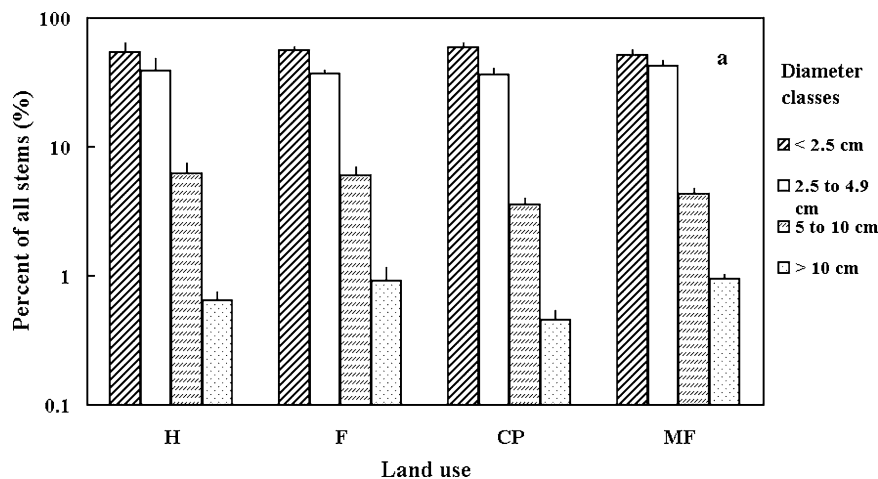


FIGURE 3. Diameter class distributions for saplings (<2.5 cm DBH) and trees ≥ 2.5 cm DBH in 45-yr-old forest stands developing at locations with the indicated types of past land use and for a nearby mature forest. Stands are located in the Guánica Commonwealth Forest, Puerto Rico. The largest tree was 69 cm DBH. Standard error of the mean is shown for each class ($N = 4$ for houses and farmlands, and $N = 5$ for the other two): H = houses, F = farmlands, CP = charcoal pits, and MF = mature forest.

vegetation from house and farm locations, but planted trees and nonforest plants at both locations. This type of site use depletes root systems and natural vegetation. Therefore, pioneer species invaded houses and farmlands, and the vegetation was closely associated among them (Table 2). Probably because of better soil conditions, trees in farmlands developed more height (5.3 vs. 4.8 m), CC (9.0 vs. 7.7 m²), and stemwood biomass (54 vs. 36 Mg/ha) than houses and had higher tree species density after 45 yr of growth (35 vs. 25 species/0.2ha). After 45 yr of abandonment, farmlands and houses had the highest number of herbaceous species among the four land uses (data not shown).

CHARACTERISTICS OF VEGETATION RECOVERING FROM ANTHROPOGENIC DISTURBANCES.—The most severe disturbances were those that stripped vegetation and damaged soil and root systems, houses, and farmlands. Vegetation under these conditions regenerated by seed rain, mostly of pioneer species (data not shown). Dry tropical forests have few viable seeds in the soil seed bank (Vázquez-Yanes & Orozco-Segovia 1993; Miller 1999); most tropical seeds have low dormancy and do not tolerate adverse soil conditions for prolonged periods. These factors create opportunities for alien species invasions in these communities, but the success of alien species invasions in terms of the number of species was low. The same was true in the early stages of regeneration of Yucatan dry forests after abandonment of *Agave* plantations (González Iturbe *et al.* 2002). However, those alien species that regenerated at these locations were extremely successful in terms of abundance, basal area, and IV. The alien species with high IVs in our study (*Leucaena* and *Prosopis juliflora*) were naturalized woody aliens. Those in Yucatan, however, were herbaceous invaders.

Apparently, the main regeneration mode in former houses and farmland stands is by seed germination instead of vegetative regeneration by multiple stems. These results contrast with those of Ewel (1971, 1977, 1980) and Dunevitz (1985) who found high rates of coppiced trees in the early regrowth after clear-cutting experimental dry forest plots. The difference in these results is the intensity and scale of the disturbance. Experimental cuts were acute events of small scale. In contrast, our locations were subject to 128 yr of use over landscape-level scales. As a result, our locations experienced greater change in soil and vegetation than those in experimental cuts. The resulting community at our study area had dominant species with high IV (Table 1), but species richness can be low or high, depending on the rate of recovery. Recovery was limited by poor root development and harsh soil conditions.

Some anthropogenic disturbances enhance rates of forest recovery. Soil enrichment and planting of vegetation, even if alien, in houses and farmland locations probably contributed to fast accumulation of species and fast rates of litterfall. The high dominance of the nitrogen-fixing *Leucaena* in these plots further contributed to soil enrichment. Thinning and burning of branches for charcoal production resulted in a species-rich and productive forest that exceeded the basal area, biomass, and species richness of nearby mature forest (Figs. 2a–c). The dominant species in this forest had a low IV because more species per unit area shared resources.

LONG-TERM LEGACIES OF LAND USE.—We compared the results of our study with the results of other studies that examined the recovery of forest structure and composition in mature stands established after abandonment of known long-term land uses. The locations were: subtropical wet forests in Puerto Rico (García Montiel & Scatena 1994; Aide *et al.* 1995, 1996, 2000); subtropical moist forests in Puerto Rico (Rivera & Aide 1998; Marciano Vega *et al.* 2002); tropical dry forests in Mexico and Bolivia (González Iturbe *et al.* 2002; Kennard 2002); and temperate moist forests in New England (Foster 1992; Foster *et al.* 1997, 1998; Fuller *et al.* 1998). In all of these locations, the structural development of stands varied with local conditions and type of past land use, but the common pattern to all studies was that the species composition and/or the relative IV of the species in the recovered mature forests was different from those present in the preconversion forests. It appears that forests recover after abandonment of a variety of land-use types, even chronic use as in our study, but the species composition of the emerging forest, while impossible to predict, will be different from what it was before forest conversion. In most instances, alien species form part of the mature forest state, and even after nearly 100 yr of development, the original species composition does not return in the emerging forests (Aide *et al.* 1996; Foster & Motzkin 1998; Fuller *et al.* 1998; Dupouey *et al.* 2002; Lugo 2004; Lugo & Helmer 2004). This emerging pattern of forest response to land-use change requires the attention of ecologists and land managers who strive to restore damaged lands to their original species composition, because the previous land use might have already precluded the recovery of the original species composition (Dupouey *et al.* 2002).

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