Early recovery of subtropical dry forest in south-western Puerto Rico

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Photograph 1.
Appearance of vegetation on June 16, 1997, after a 12 hectares burn on northern Tinaja. This fire was the last to occur before the tract was completely fenced and the livestock removed. The Sierra Bermeja hills are visible in the background. Photograph J. J. Schwagerl.

RÉSUMÉ

REPRISE PRÉCOCE DE LA FORÊT SÈCHE SUBTROPICALE AU SUD-OUEST DE PUERTO RICO

Un inventaire de la couverture forestière et de la composition florale a été réalisé en 1998, 2003 et 2010 suite à l'élimination des pâturages et brûlis dans les 32 hectares inférieurs de la zone de Tinaja, au sein du refuge national de faune de Laguna Cartagena dans le Sud-Ouest de Puerto Rico. Les inventaires de la forêt sèche subtropicale montrent pour la période de 1998 à 2010 une augmentation de 3,9 fois pour les tiges, 6,7 fois pour les arbres, 3,3 fois pour la surface terrière et de 4,4 fois pour la biomasse, et cela avec des variations notables en fonction des sites. Sur 10 parcelles le long de la limite sud, plus proche de la couverture forestière résiduelle, ont été relevés un nombre plus important de tiges et d'arbres, une surface terrière plus grande et, en général, davantage de biomasse que sur les 22 parcelles du côté nord, et ce durant les trois années d'inventaire. Pour quatre parcelles situées dans des criques et une parcelle bordant une clôture, les valeurs sont également plus élevées que les moyennes respectives pour l'ensemble des 32 parcelles du Tinaja inférieur. Les autres tendances notables relevées pour la période de 1998 à 2010 sont les suivantes : les essences exotiques augmentent en proportion de 70 à 84 % en tiges et de 70 à 86 % en arbres ; le rapport entre tiges et arbres diminue de 2,3 à 1,3 ; *Leucaena leucocephala* (Lam.) DeWit augmente de 7 à 53 % en tiges et de 14 à 64 % en arbres ; *Pilosocereus royenii* (L.) Byles & Rowley décroît de 10 à 2 % en tiges et de 7 à 1 % en arbres, en raison surtout d'attaques d'une cochenille des cactus, *Hypogeococcus pungens* ; enfin, la richesse floristique des essences augmente de 30 à 34.

Mots-clés : essences endémiques, composition florale, reprise de la forêt, structure forestière, forêt sèche subtropicale, Puerto Rico.

ABSTRACT

EARLY RECOVERY OF SUBTROPICAL DRY FOREST IN SOUTHWESTERN PUERTO RICO

Tree cover and species composition were surveyed in 1998, 2003, and 2010 after the elimination of grazing and fire on the lower 32 hectares of the Tinaja tract at Laguna Cartagena National Wildlife Refuge in south-western Puerto Rico. Surveys of the secondary subtropical dry forest showed that stems increased 3.9 times, trees 6.7 times, basal area 3.3 times, and biomass 4.4 times between 1998 and 2010. Notable differences occurred by site. Greater numbers of stems and trees, greater basal areas, and usually biomass were tallied on 10 plots along the southern boundary closer to residual tree cover than on the northern 22 plots in all three years of measurement. Four plots situated in arroyos and one plot along a fence-line also showed greater values when compared to the respective mean values for all 32 plots on lower Tinaja. Other major trends between 1998 and 2010 were: exotics increased from 70 to 84% of the stems and from 70 to 86% of the trees; the ratio of stems to trees declined from 2.3 to 1.3; *Leucaena leucocephala* (Lam.) DeWit increased from 7 to 53% of the stems and from 14 to 64% of the trees; *Pilosocereus royenii* (L.) Byles & Rowley decreased from 10 to 2% of the stems and from 7 to 1% of the trees, largely due to attack by the cactus mealybug, *Hypogeococcus pungens*; and tree species richness increased from 30 to 34.

Keywords: endemic species, species composition, forest recovery, forest structure, subtropical dry forest, Puerto Rico.

RESUMEN

PRONTA RECUPERACIÓN DEL BOSQUE SECO SUBTROPICAL EN EL SUDOESTE DE PUERTO RICO

Se realizó un inventario de la cubierta forestal y de la composición específica en 1998, 2003 y 2010 a raíz de la eliminación del pastoreo y las quemas en las 32 hectáreas inferiores del sector de La Tinaja en el Refugio Nacional de Vida Silvestre de Laguna Cartagena, en el sudoeste de Puerto Rico. Entre 1998 y 2010 los inventarios del bosce seco tropical han monstrado un incremento de 3.9 veces de los tallos, de 6.7 de los árboles, de 3.3 en la área basal y de 4.4 para la biomasa, con notables diferencias según los sitios. En 10 parcelas a lo largo del límite sur, más cerca de la cubierta forestal residual, se contabilizaron más tallos y árboles, una mayor área basal y, por lo general, más biomasa que en las 22 parcelas del lado norte durante los tres años que duró el inventario. Cuatro parcelas situadas en arroyos y una parcela a lo largo de una cerca, mostraron asimismo unos valores más altos que los valores medios respectivos del conjunto de las 32 parcelas de la parte inferior de La Tinaja. Otras tendencias destacadas registradas en el período de 1998 a 2010 fueron las siguientes: las especies exóticas aumentaron del 70 al 84% en tallos y del 70 al 86% en árboles; la relación entre tallos y árboles disminuye de 2.3 a 1.3; *Leucaena leucocephala* (Lam.) DeWit asciende del 7 al 53% en tallos y del 14 al 64% en árboles; *Pilosocereus royenii* (L.) Byles & Rowley baja del 10 al 2% en tallos y del 7 al 1% en árboles, debido en buena parte al ataque de la chinche harinosa de los cactus, *Hypogeococcus pungens*; por último, la riqueza de especies arbóreas aumentó de 30 a 34.

Palabras clave: especies endémicas, composición de especies, recuperación de los bosques, estructura forestal, bosque seco subtropical, Puerto Rico.

Introduction

About 40% of the earth's tropical and subtropical landmass is occupied by open or closed forest, and about 42% of that area is classified as dry forest (Murphy, Lugo, 1986a). Dry forest ecosystems account for 70 to 80% of the forested areas of Africa and tropical islands, about 22% of South America, and nearly 50% of Central America. Nearly 20% of Puerto Rico and the U.S. Virgin islands are occupied by the subtropical dry forest life zone (Ewel, Whitmore, 1973). Worldwide, these forests have been harvested for timber and fuel, burned, grazed, and farmed under shifting agriculture for centuries.

The Fish and Wildlife Service (F&WS) of the U.S. Department of the Interior is responsible for the protection of 10,231 hectares (ha) of terrestrial wildlife habitat in the Caribbean Basin, including 9,687 ha in Puerto Rico and the U.S. Virgin Islands, and 544 ha on Navassa Island (Weaver, Schwagerl, 2009). Nearly 95% of the area managed by the agency is situated in subtropical dry forest (Gould *et al.*, 2001). One of the nine protected areas is the 423 ha Laguna Cartagena National Wildlife Refuge in southwestern Puerto Rico. The refuge is comprised of two areas: the laguna tract within the Lajas Valley and the adjacent Tinaja tract on the slopes of the Sierra Bermeja.

Monitoring of early dry forest recovery after agriculture has not been done previously on individual tracts of land in Puerto Rico. Although the island is included in the U.S. Forest Service's national inventory of forest resources, that program is designed to show trends for the entire island and not for individual properties (Brandeis *et al.*, 2007). The purpose of this study was to monitor vegetation change on the lower 32 ha of the Tinaja tract. This information will be useful in evaluating the rates of forest recovery, including forest structure and species composition, on abandoned pastures situated in subtropical dry forest. Given the similarities among forests in the Caribbean Basin, these results should be of regional interest.

Hereafter, Tinaja refers to the entire ~110 ha tract. Upper Tinaja refers to the 78 plots at highest elevation and lower Tinaja to the 32 plots at lowest elevation (figure 1). Moreover, within lower Tinaja, northern refers to plots 1 through 22 nearest the dirt road and southern to plots 23 through 32 bordering residual secondary forest.

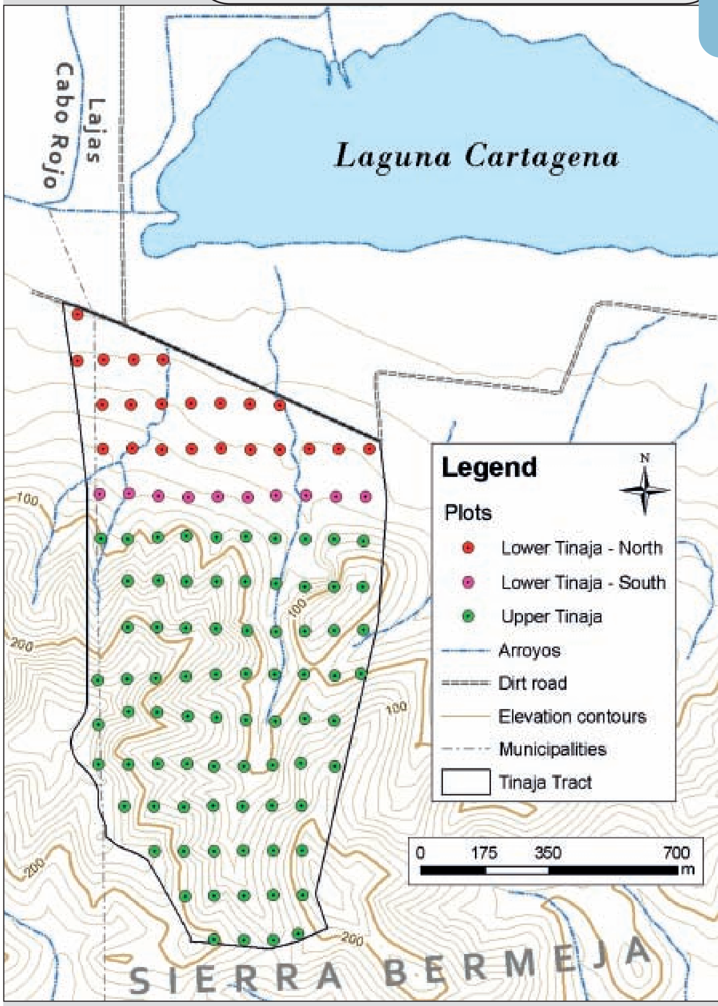

Figure 1.
Map of the 110-ha Tinaja tract indicating residual forest and shrub cover on the upper 74 ha at mid-to higher-elevations (i.e., plots 33 to 110), and the lower 32-ha area sampled in this study. The lower area is divided into northern plots (1 to 22) and southern plots (23 to 32), as follows: plot 1 is alone at top; the remaining plots, numbered left to right and descending, are: 2-5, 6-12, 13-22, and 23-32. Part of the laguna tract of the Laguna Cartagena National Wildlife Refuge lies north of the dirt road.

Site characteristics

The subtropical dry forest in southwestern Puerto Rico receives about 1,000 mm of rainfall annually (Ewel, Whitmore, 1973). The rainfall normal (i.e., the 30-year record between 1971 and 2000) for the coastal site of Magueyes, about 7 km from Tinaja, was 770 millimetres per year (mm/yr). February and March were the driest months with ~30 millimetres per month (mm/mo), and September and October were the wettest with ~125 mm/mo (Weaver, Schwagerl, 2004). A 15-year rainfall record (1991 to 2005) for the laguna tract showed an average of 1,060 mm/yr, with the first 7 years averaging 925 mm/yr and the last 8 years 1,175 mm/yr. Annual rainfalls fluctuated considerably, ranging from 57 to 159% of the 15-year mean (Weaver, Schwagerl, 2009). The mean annual temperature was 27 °C, averaging 25 °C in January to 28 °C from June to August. The vegetation, particularly during dry years, is prone to wildfires.

The slopes of lower Tinaja are composed of Quaternary alluvium and unconsolidated sand and gravel with some silt and clay (Bawiec, 2001). Amelia-Magüayo gravelly clay loams predominate. They are characterized as deep, well-drained acid soils in alluvium and colluvium that occur on eroded, gentle foot slopes (Carter, 1965).

The Tinaja tract, when acquired in 1996 from the U.S. Department of Agriculture, was being used to graze livestock (Weaver, Schwagerl, 2009). Within a couple of years, fences were repaired, and fire and grazing were eliminated. A 1996 reconnaissance of vegetation of the entire tract showed 196 plant species in 59 families, with 9 species or varieties endemic to the island (Proctor, 1996). In 1998, a systematic survey of the tract revealed 141 native and 18 exotic tree species (Weaver, Chinea, 2003; figure 1). The survey also indicated that much of the upper and steepest part of Tinaja was occupied by secondary forest and shrubs. In contrast, the lower 32 ha, with gently sloping terrain between 20 and 80 metres (m), had been burned and grazed for a much longer period and contained scattered trees (notably in arroyos and along fence-lines), shrubs, and grass (photograph 1).

Aerial photographs of the Tinaja tract in 1936 showed considerable tree cover on upper Tinaja; in comparison, tree cover on lower Tinaja was very sparse (figure 1; Weaver, Schwagerl, 2004, 2008). In 1998, the lower 32 plots were still largely grass covered. Stems on the 22 northern plots, however, averaged slightly ›60% of those on the 10 southern plots.

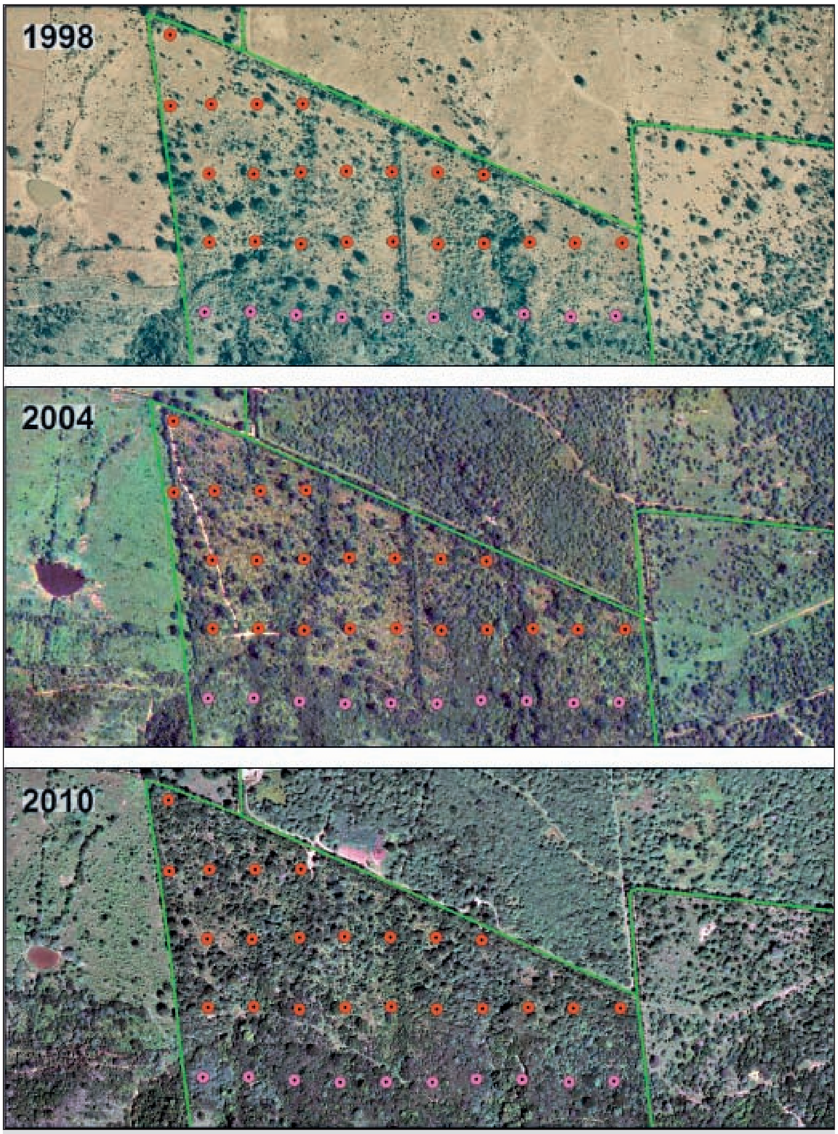

Figure 2.
Aerial photographs showing chrono-sequence of vegetation cover on the lower Tinaja tract in 1998, 2004, and 2010. In 1998, the area is mainly grass-covered (light tan color); by 2010, most of the area is covered by trees and shrubs (dark shades of gray and purple). Tree cover along arroyos and fence-lines is most notable during the earlier years.

Methods

In 1998, 109 circular plots with a radius of 10 m (~ 3.4% sample) were established and permanently marked with reinforcement bars about 1.5 m long and 2 centimetres (cm) thick as center stakes throughout Tinaja. All plots were geographically referenced. On each plot, all individual stems more than or equal to 2.5 cm of diameter at 1.4 m above the ground (dbh), including those arising from a single trunk at ground level (hereafter called a tree), were measured but not tagged. In 2003 and 2010, 32 plots on lower Tinaja were re-measured (total sample area = 1.0048 ha, rounded to 1 ha). Heights were determined with an extension pole in 1998 and 2003 but estimated in 2010 when more than 90% of the trees were still less than 8 m tall. The tallest trees, however, were verified with a range finder. All trees were identified using local literature (Little, Wadsworth, 1964; Little *et al.*, 1974). Plant nomenclature followed relatively recent taxonomic work (Liogier, 1987-97; Liogier, Martorrel, 1982).

A dot-grid was used to estimate tree and shrub cover on aerial photographs taken in 1998, 2004, and 2010 (figure 2). Numbers of stems and trees were analyzed by species and year. Stem data, including cactus, were partitioned by dbh and height classes, and used to calculate basal areas. Woody stems alone, however, were used to estimate biomass. Mean values for all parameters on the northern 22 plots were compared to the southern 10 plots using standard t-tests at the 5% level (Steel, Torrie, 1960). The structure and composition of plots within or bordering arroyos (i.e., northern plots 8 and 20, and southern plots 24 and 30) and the fence-line plot 12 were examined separately. Biomass for woody stems was estimated by equation (Chave *et al.*, 2005), as follows:

$$BIOM = 0.112 \times (pD^2H)^{0.916}$$

Where BIOM is total aboveground biomass (oven dry) per tree in kg, p is wood specific gravity in g/cm^3, D is diameter (cm), and H is total tree height (m). Dry weight specific gravities were derived from several sources (Little, Wadsworth, 1964; Little *et al.*, 1974; Rahayu, 2005; Reyes *et al.*, 1992). Specific gravities for ~10% of the stems were unknown and were estimated at 0.67 g/cm^3, the mean for all known specific gravities in the data set. All tallied trees had regenerated naturally except for three specimens of *Cordia dentata* and four of *Bursera simaruba* that were planted in lines on plot 1 after the 2003 measurements. The planting was part of F&WS restoration efforts and not a formal part of this study.

Results

Cover and Structure

Forest and shrub cover on lower Tinaja increased from ~20% in 1998, to nearly two-thirds in 2003, to ~90% by 2010 (figure 2). In 1998, most of the area was grass covered with scattered patches of trees. Three other features were readily apparent in the 1998 photograph:

- Parallel lines of trees in the middle of the property indicating the old entrance to the tract;
- Prominent tree cover in an arroyo midway between the old entrance and the easternmost boundary of the tract;
- Another arroyo crossing lower Tinaja from the south-western corner to a point on the dirt road about two-thirds of the way to the old entrance (figure 2, top panel).

By 2010, tree or shrub cover had increased considerably and the above features were more difficult to discern (figure 2, bottom panel; photograph 2). Stems per plot, including cactus, ranged from 0 to 64 in 1998, from 0 to 115 in 2003, and from 8 to 187 in 2010 (figure 3). Comparative data excluding cactus ranged from 0 to 30, 0 to 73, and 7 to 168, respectively. Likewise, trees per plot, including cactus, ranged from 0 to 51 in 1998, 0 to 128 in 2003, and 8 to 185 in 2010. Comparative data excluding cactus ranged from 0 to 27, 0 to 73, and 7 to 166, respectively.

The number of stems on lower Tinaja increased from 497 to 1,175 to 1,928 stems/ha and the number of trees from 215 to 706 to 1,436 stems/ha in 1998, 2003, and 2010 (table I). Basal areas increased from 2.1 to 4.0 to 6.9 m^2/ha and biomass from 5.9 to 9.7 to 25.8 t/ha during the same period. The rates of change in stem density, basal area, and biomass for the tract varied between measurement periods (i.e., 1998-2003 vs. 2003-2010): for stem density, the rate declined from 136 to 108 ha/yr; for tree density, it increased slightly from 97 to 107 ha/yr; for basal areas, it remained constant at 0.4 m^2 ha/yr; and for biomass, it increased from 0.8 to 2.3 t ha/yr (table I).

Photograph 2.
Typical secondary tree cover on northern Tinaja about 12 years after the elimination of fire and grazing. Although some scattered patches of grass persist, all plots had at least 8 to 187 stems counting cactus, or 7 to 168 stems excluding cactus in 2010.
Photograph P. L. Weaver.

Stems, trees, and basal areas, and usually biomass on the southern plots exceeded or equaled those of the northern plots in all years (table I). The greatest means for the above four parameters, however, were on the arroyo and fence-line plots. Moreover, after tree planting in 2003, plot 1 showed dramatic increases in the aforementioned parameters by 2010 (table I, footnote 2).

The ratio of stems to trees was 2.3 in 1998, 1.7 in 2003, and 1.3 in 2010 (table II). In 1998, *Leucaena leucocephala*, *Pilosocereus royenii* (a multi-stemmed cactus), *Pithecellobium dulce*, and *Prosopis pallida* composed 62% of the stem density (table II). In 2003 and 2010, these same four species accounted for about 80% of the density. After 2003, *Pilosocereus royenii* abruptly declined.

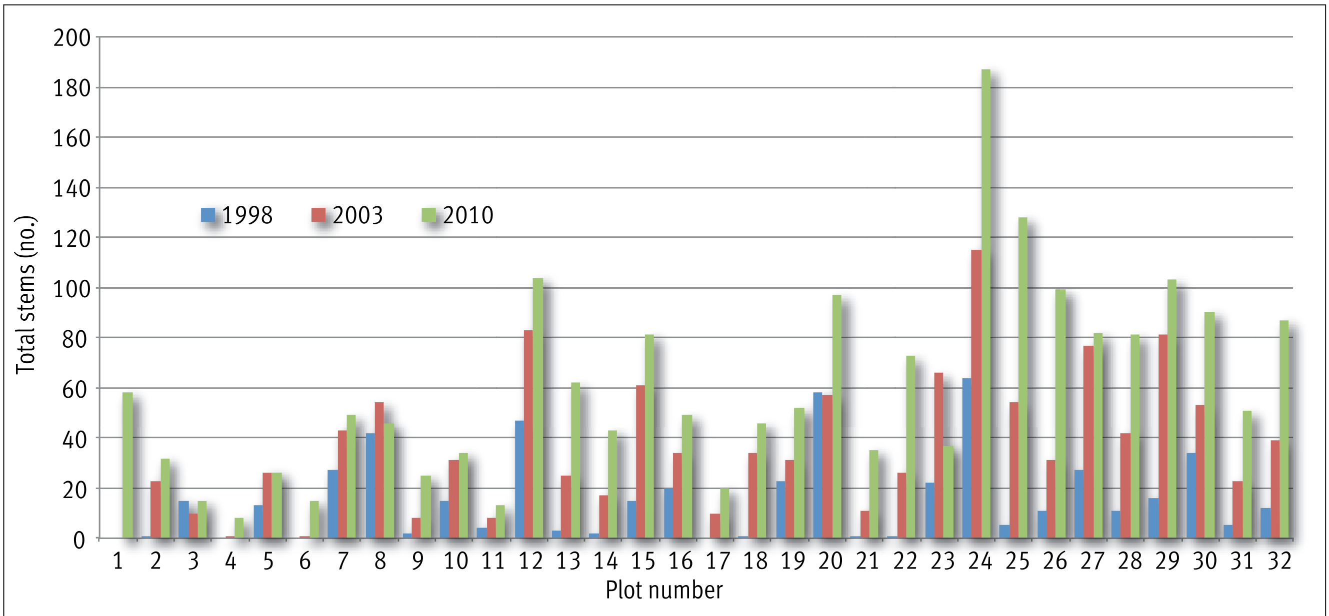

Figure 3.
Changes in stem numbers, including cactus, by plot on lower Tinaja between 1998 and 2010. Plots are: northern, 1 to 22; and southern, 23 to 32. Plot 1 was planted after 2003. Plot 12 is the fence-line plot. Plots 8, 20, 24, and 30 are in or along arroyos. The total area for all sample plots equals 1 ha.

Table I.
Forest structure and composition on lower Tinaja.[1]

Plots[2] Parameters	Northern-22	Southern-10	Arroyo	Fence-line	All-32
Estimated values 1998					
Stems (no./ha)	422±116	662±181	1,584	1,504	497±98
Trees (no./ha)	176±47	299±102	760	640	215±46
Basal area (m^2/ha)	1.9±0.6	2.3±0.7	7.0	5.1	2.1±0.5
Biomass (t/ha)	5.3±1.6	7.1±2.6	16.7	17.6	5.9±1.4
Mean species (no./plot)	2.3±0.5	4.2±1.2	9.2	6	2.9±0.5
Total species (no.)	22	24	24	6	30
Estimated values 2003					
Stems (no./ha)[3]	865±150*	1,859±278*	2,232	2,656	1,175±188
Trees (no./ha)[3]	502±97*	1,155±207*	1,320	1,824	706±189
Basal area (m^2/ha)	3.8±0.9	4.6±0.9	10.3	8.8	4.0±0.7
Biomass (t/ha)	9.7±2.6	9.3±3.3	23.0	30.2	9.3±2.0
Mean species (no./plot)	3.9±0.5	5.7±0.8	10.0	7	4.5±0.5
Total species (no.)	24	23	20	7	31
Estimated values 2010					
Stems (no./ha)[3]	1,430±181*	3,024±418*	3,360	3,328	1,928±221
Trees (no./ha)[3]	1,004±141*	2,387±433*	2,752	2,144	1,436±199
Basal area (m^2/ha)	6.4±1.0	8.2±0.7	11.8	13.1	6.9±0.7
Biomass (t/ha)	23.6±3.6	31.0±1.6	49.5	75.2	25.8±3.0
Mean species (no./plot)[3]	5.3±0.4*	7.6±1.0*	10.5	6	6.0±0.5
Total species (no.)	25	30	24	6	34

[1]Explanation: Northern 22 plots with sparse tree cover in 1998; southern 10 plots with scattered small stems from nearby residual forest in 1998. Four arroyo plots (i.e., 8, 20, 24, and 30) and fence line plot 12 with residual cover in 1998.
[2]Plot 1 was planted after 2003. Plot 1 values (in units as above) in 2010 were: stems = 1,856; trees = 736; basal area 8.2; biomass = 20.4; and both total and mean number of species = 7.
[3]Asterisks indicate significant differences between northern vs. southern plots.

The number of stems in all dbh classes increased from 1998 to 2010. Except for the smallest two dbh classes in 1998 and 2003, the proportions of stems remained relatively constant (table III). In comparison, the proportion of stems in height classes showed a notable shift to classes more than 4 m tall (table III). The largest trees measured on the lower Tinaja plots were an *Albizia lebbeck* with a dbh of 37.7 cm and *Melicoccus bijugata* that reached 16 m in height in an arroyo.

Composition

Forty-two species were tallied at some time during the three surveys (table II). The number of species present increased from 30 through 31 to 34 in 1998, 2003, and 2010. Seven species were gained and six lost from 1998 to 2003; similarly, five species were gained and two lost from 2003 to 2010. *Thouinia striata*, the only recorded endemic on lower Tinaja, increased slightly in numbers of stems and trees.

During the measurement period, the mean number of species for all 32 plots increased from 2.9 through 4.5 to 6.0 (table I), with 29 plots increasing in species, two remaining the same, and one decreasing (figure 4). At each measurement, the mean number of species on the southern plots exceeded those on the northern plots. Arroyo plots, regardless of location, supported the greatest species richness (table I).

Exotic species dominated the tract, increasing from 70 to 73 to 84% of the stems and from 70 to 80 to 86% of the trees for the three measurement years, respectively (table II). Similarly, *Leucaena leucocephala* was the most abundant species, ranging from 7 to 35 to 53% of the stems and from 14 to 50 to 64% of the trees. Other exotics that increased notably were *Albizia lebbeck, Pithecellobium dulce*, and *Prosopis pallida*. Between 1998 and 2010, *Tamarindus indica* entered the tract and *Bauhinia monandra* and *Calotropis procera* disappeared. By 2010, *Leucaena leucocephala* was encountered on all plots (table II). *Albizia lebbeck*, *Pithecellobium dulce*, and *Prosopis pallida* were also well distributed, occurring on 47 to 69% of the plots.

Table II.
Changes in tree species, stem numbers, basal areas, and tree distributions at Tinaja.[1]

Species name	Stems (no./ha)			Trees (no./ha)			Basal areas (m^2/ha)			Occurrence (%)[2]		
	1998	2003	2010	1998	2003	2010	1998	2003	2010	1998	2003	2010
Native species												
Andira inermis (W. Wright) HBK	3	4	4	2	3	2	0.02	0.02	0.01	6	6	6
Bourreria succulenta Jacq.	17	8	24	7	2	15	0.15	0.14	0.18	9	3	19
Bursera simaruba L. Sarg.	1	1	7	1	1	7	0.01	0.01	0.16	3	3	12
Capparis cyanophallophora L.	1	0	0	1	0	0	0.00	0.00	0.00	3	0	0
Capparis flexuosa L.	2	0	0	2	0	0	0.00	0.00	0.00	3	0	0
Capparis frondosa Jacq.	0	0	3	0	0	2	0.00	0.00	0.00	0	3	6
Capparis hastata Jacq.	4	4	11	2	2	6	0.02	0.03	0.05	6	6	9
Capparis indica (L.) Fawc. & Rendle	0	0	6	0	0	6	0.00	0.00	0.01	0	3	12
Citharexylum fruticosum L.	4	4	12	2	3	10	0.01	0.01	0.05	6	6	22
Coccoloba diversifolia Jacq.	0	1	1	0	1	1	0.00	0.01	0.01	0	3	3
Coccoloba swartzii Meisner	1	0	0	1	0	0	0.00	0.00	0.00	3	0	0
Cordia alliodora (Ruiz & Pav.) Oken	0	1	1	0	1	1	0.00	0.00	0.00	0	3	3
Cordia collococca L.	0	2	0	0	1	0	0.00	0.00	0.00	0	3	0
Cordia dentata Poir.	0	0	17	0	0	4	0.00	0.00	0.05	0	3	3
Erythroxylum rotundifolium Lunan	1	0	1	1	0	1	0.00	0.00	0.00	3	0	3
Eugenia biflora (L.) DC.	3	4	8	2	3	6	0.00	0.01	0.01	6	6	16
Guapira fragrans (Dum.-Cours.) Little	0	2	8	0	2	4	0.00	0.00	0.02	0	3	9
Guazuma ulmifolia Lam.	8	11	17	2	2	6	0.08	0.12	0.18	6	9	16
Gymnanthes lucida Sw.	1	2	5	1	1	4	0.00	0.00	0.01	3	3	3
Hymenaea courbaril L.	7	8	7	7	7	7	0.07	0.09	0.15	3	3	22
Lantana camara L. var. camara	3	7	20	3	6	17	0.00	0.00	0.02	9	6	28
Lonchocarpus domingensis (Pers.) DC.	3	3	0	1	2	0	0.05	0.06	0.00	3	3	0
Palicourea crocea (Sw.) Roem. & Schult.	0	1	2	0	1	1	0.00	0.00	0.00	0	3	3
Pictetia aculeata (Vahl) Urban	0	3	5	0	1	1	0.00	0.01	0.01	0	3	3
Pilosocereus royenii (L.) Byles & Rowley	52	203	41	15	68	14	0.23	0.96	0.23	25	66	21
Randia aculeata L.	7	3	4	4	3	4	0.01	0.00	0.00	3	6	12
Rauvolfia nitida Jacq.	6	14	21	2	8	11	0.08	0.10	0.13	6	9	6
Sabinea florida (Vahl) DC.	1	0	0	1	0	0	0.00	0.00	0.00	3	0	0
Securinega acidoton (L.) Fawc. & Rendle	12	21	49	6	14	41	0.02	0.03	0.08	6	12	25
Trichilia hirta L.	7	2	3	1	1	2	0.01	0.00	0.01	3	3	6
Trichilia pallida Sw.	0	0	13	0	0	8	0.00	0.00	0.02	0	3	16
Thouinia striata Radlk.[3]	6	11	13	1	4	9	0.00	0.01	0.01	3	3	3
Zanthoxylum monophyllum (Lam.) P. Wilson	0	0	14	0	0	8	0.00	0.00	0.01	0	3	12
Subtotals[4]	150	320	317	65	137	198	0.77	1.60	1.40	41	78	88
Exotic species												
Acacia farnesiana (L.) Willd.	29	21	16	7	8	10	0.02	0.04	0.06	16	6	22
Albizia lebbeck (L.) Benth.	15	59	72	12	38	53	0.22	0.35	0.95	22	41	47
Bauhinia monandra Kurz.	5	0	0	3	0	0	0.01	0.00	0.00	3	0	0
Calotropis procera (Ait.) f.	14	3	0	11	3	0	0.03	0.01	0.00	19	9	0
Leucaena leucocephala (Lam.) DeWit	33	410	1020	31	353	920	0.08	0.48	2.14	19	72	100
Melicoccus bijugatus Jacq.	28	32	42	17	22	30	0.13	0.21	0.34	6	6	12
Pithecellobium dulce (Roxb.) Benth.	131	187	252	35	70	123	0.59	0.93	1.10	44	50	69
Prosopis pallida (H.& B. ex Willd.) HBK	92	142	202	34	74	95	0.20	0.42	0.91	41	56	53
Tamarindus indica L.	0	1	7	0	1	7	0.00	0.00	0.03	0	3	12
Subtotals[4]	347	855	1611	150	569	1238	1.28	2.45	5.52	81	94	100
Totals[4]	497	1175	1928	215	706	1436	2.05	4.05	6.92	88	97	100

[1]Stem numbers refer to all stems with a measurable dbh. Tree number refers to the number of trunks at ground level, many of which had multiple stems at dbh. Cactus (*Pilosocereus royenii*) is treated similarly. Total area sampled = 1 ha.
[2]Percent of plots on which the species was recorded, rounded to nearest integer.
[3]Endemic species.
[4]Under occurrences only: subtotals reflect the percentages of plots on which native or exotic species occur by year; totals reflect the percentages of plots occupied by any species by year.

Table III.
Distribution of stem diameters and heights for plots on the lower tinaja tract in 1998, 2003, and 2010.[1]

Category (sizes)	1998	2003	2010
		Stems/ha (%)	
Diameter (cm)			
2.5-3.9	156 (31.4)	515 (43.8)	688 (35.6)
4.0-5.9	149 (30.0)	269 (22.9)	621 (32.2)
6.0-7.9	92 (18.5)	202 (17.2)	325 (16.9)
8.0-9.9	56 (11.3)	110 (9.4)	142 (7.4)
10.0-14.9	20 (4.0)	43 (3.6)	97 (5.0)
15.0-19.9	16 (3.2)	21 (1.8)	27 (1.4)
20.0-24.9	5 (1.0)	9 (0.8)	17 (0.9)
≥25.0	3 (0.6)	6 (0.5)	11 (0.6)
Total	497 (100.0)	1,175 (100.0)	1,928 (100.0)
Height (m)			
‹2	14 (2.8)	50 (4.2)	4 (0.2)
2.0-3.9	257 (51.7)	731 (62.2)	212 (11.0)
4.0-5.9	180 (36.2)	324 (27.6)	1,022 (53.0)
6.0-7.9	39 (7.9)	53 (4.5)	547 (28.4)
8.0-9.9	5 (1.0)	15 (1.3)	98 (5.1)
≥10.0	2 (0.4)	2 (0.2)	45 (2.3)
Total	497 (100.0)	1,175 (100.0)	1,928 (100.0)

[1]Total area sampled = 1 ha.

During the same years, native species showed changes. *Trichilia pallida* and *Zanthoxylum monophyllum* entered the tract and *Capparis hastata*, *Citharexylum fruticosum*, *Guapira fragrans*, *Lantana camara*, and *Rauvolfia nitida* showed modest gains (table II). The most dramatic flux was experienced by *Pilosocereus royenii*, which increased from 10 to 17% of the stems and from 7 to 10% of the trees between 1998 and 2003, and then sharply declined to 2% of the stems and 1% of the trees by 2010 (table II). Also by 2010, *Citharexylum fruticosum*, *Hymenaea courbaril*, *Lantana camara*, and *Securinega acidoton* were recorded on ›20% of the plots. *Pilosocereus royenii*, although greatly reduced in stem and tree numbers, was still found on ›20% of the plots.

Discussion

Dry climate, sporadic tree harvest, recurrent fires, and extensive grazing slowed forest recovery at Tinaja during most of the 20th century. *Pithecellobium dulce* and *Prosopis pallida*, planted as forage and shade for livestock in the past, provide scattered cover on much of the island's southwestern landscape. Planted grasses like *Panicum maximum* Jacq. (syn.: *Megathyrsus maximus* (Jacq.) B.K. Simon & J.W.L. Jacobs; Guinea grass) and *Pennisetum purpureum* Schumach. (Elephant grass), both native to Africa, spread rapidly attaining more than 2 m in height. Today, the grasses form a dense cover that slows the regeneration of all but the most aggressive exotics like *Albizia lebbeck* and *Leucaena leucocephala*, notably the latter.

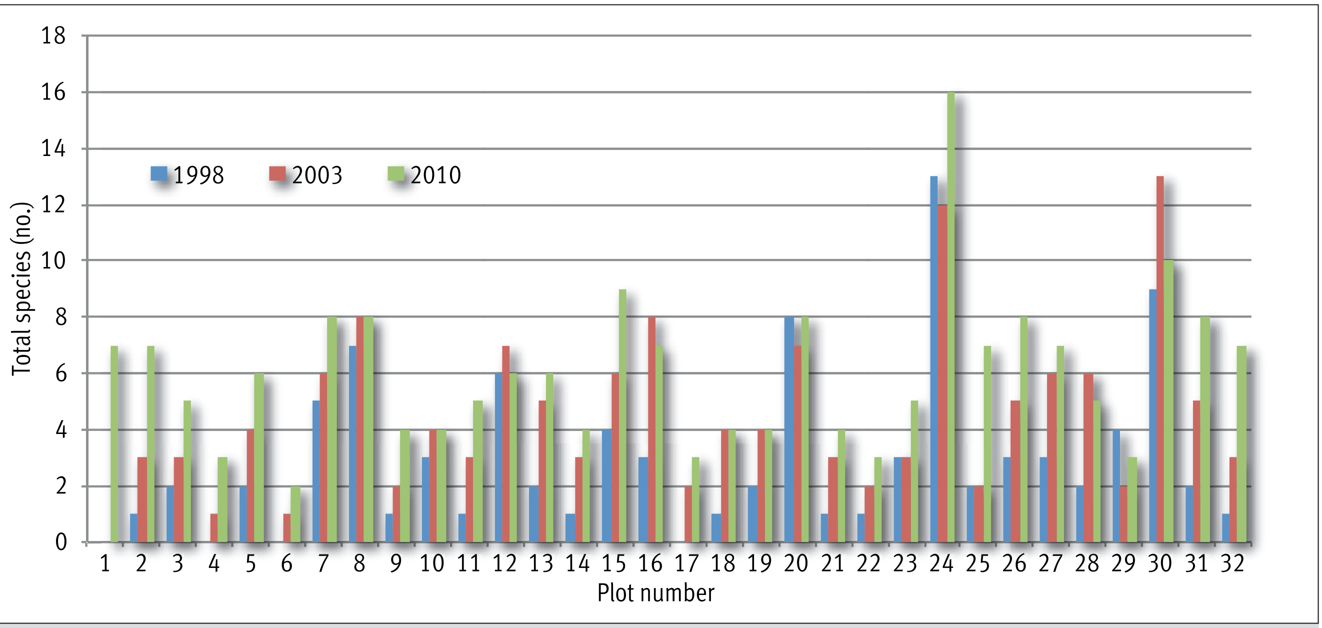

Figure 4.
Changes in the number of species by plot for all 32 plots in lower tinaja between 1998 and 2010.

Increases in forest and shrub cover are apparent when northern Tinaja and the laguna tract north of the dirt road are compared with the cattle ranch to the west (figure 2). Since 1998, both Tinaja and the laguna tract have been protected, and the latter also planted, whereas the farm has been grazed continuously during that period.

The decline in the rate of stem density increase after 2003 was caused by heavy cactus mortality resulting from the invasive mealybug *Hypogeococcus pungens*, a South American pest on columnar cacti (Segarra-Carmona *et al.*, 2010). Some cacti may also have succumbed to increasing shade from regenerating trees and masses of vines (photograph 3). The rate of basal area increase, however, remained constant as the loss of cactus was offset by gains in broadleaf stems. The decline in the ratio of stems/trees is due to heavy losses of the cactus after 2003 accompanied by significant gains of *Leucaena leucocephala*, more than 90% of which are single stems. The rate of biomass accumulation increased because woody stems nearly doubled and residual stems increased in dbh and height.

Stem density, basal area, biomass, and species richness on lower Tinaja remain low reflecting the relatively short period of recovery (table I). By comparison, in 1998, the entire Tinaja tract was about 50% in shrubs, 43% in open canopy forest, and 7% in pasture (Weaver, Chinea, 2003). All of the pasture was in lower Tinaja. Moreover, the entire tract contained 141 native tree species, or slightly more than 25% of the island's total. The high number of native species is impressive considering the relatively small size of Tinaja and its land use history. Similarly in 1998, the mean stem density for the entire tract averaged 4,350 stems/ha and its mean basal area was 5.8 m^2/ha. The largest trees observed while traversing Tinaja (i.e., outside of established plots) were the natives *Bucida buceras*, *Ceiba pentandra*, and *Hymenaea courbaril*, and the exotics *Melicoccus bijugatus* and *Tamarindus indica*, all of which were more than 60 cm in dbh.

Comparable data on early forest recovery are lacking for other sites within Puerto Rico's subtropical dry forest. Information does exist, however, for the nearby 4,000 ha Guánica Forest where forest type, soils, and time since past disturbances are different. About 60% of Guánica is occupied by deciduous forest on limestone-based soils. After 50 years of protection from human disturbance, including fire, the deciduous type had more than 12,000 stems/ha (i.e., minimum dbh = 2.5 cm) and a total plant biomass of 90 tons per ha (t/ha) (Murphy, Lugo, 1986b; Murphy *et al.*, 1995). When the type was experimentally cut-over, stump and root sprouts helped to recover >40% of the initial aboveground biomass in only 13 years. Guánica Forest, occupying an area nearly 40 times that of Tinaja, contains 169 tree species (Little, Wadsworth, 1964; Little *et al.*, 1974).

Photograph 3.
Pilosocereus royenii (Stove pipe cactus) overgrown with vines and suffering from an early infestation of *Hypogeococcus pungens* (mealybug) on northern Tinaja. Cactus stems increased considerably between 1998 and 2003 but subsequently declined dramatically. The pods of *Leucaena leucocephala*, a species present on all plots by 2010, are visible on the top right.
Photograph P. L. Weaver.

Habitat differences

The recovery of secondary forest and reforestation of grass covered areas help to reduce wildfires and to improve wildlife habitat. Scattered trees in savannas or grasslands and remnant trees surviving after clearing may function in a role analogous to gaps in forested areas (Belsky, Canham, 1994; Guevara *et al.*, 1986). Birds and bats transport fruits and seeds to isolated trees where they consume them. Often fragments of fruit or seeds drop to the soil where the microclimate, soil conditions, and sparse grass cover are more favourable for tree regeneration than in the surrounding areas of dense grass cover. The greater forest structure and species composition associated with arroyos, fence-lines, and forest borders highlight the importance of existing vegetation in the recovery of relatively large, mostly open areas like northern Tinaja (figure 1, table I).

Planting experience on the refuge

Between 1980 and 1998, nearly 9,100 seedlings of 33 species had been planted on both the Cabo Rojo and Laguna Cartagena wildlife refuges by the Fish and Wildlife Service (Weaver, Schwagerl, 2008). Of these, 10 natives (*Andira inermis*, *Bourreria succulenta*, *Bucida buceras*, *Bursera simaruba*, *Ceiba pentandra*, *Colubrina arborescens*, *Cordia sulcata*, *Erythroxylum areolatum*, *Guazuma ulmifolia*, and *Trichilia hirta*) and 2 exotics (*Samanea saman* and *Swietenia mahagoni*) showed both good survival and growth. Several other species were rated as fair.

By the end of 2001, about 300 seedlings had also been planted in one area of north-eastern Tinaja outside of the measured plots (Weaver, Schwagerl, 2004). The species were *Bourreria succculenta*, *Bursera simaruba*, *Ceiba pentandra*, *Citharexylum fruticosum*, *Cordia dentata*, and *Ficus citrifolia*. Subsequent surveys showed that the effort was successful (photograph 4). The plantings of *Bursera simaruba* and *Cordia dentata* on plot 1 showed good survival and growth in only 7 years. The three *Cordia* trees developed 17 stems and the 4 *Bursera* trees averaged between 17.4 and 22.8 cm in dbh. In addition, the plantings may have facilitated the rapid regeneration of nearby exotics such as *Acacia farnesiana*, *Albizia lebbeck*, *Leucaena leucocephala*, *Pithecellobium dulce*, and *Prosopis pallida*, which totaled 14 trees and 37 stems.

Recent work in the Sierra Bermeja hills near Tinaja suggested that scattered *Leucaena leucocephala* (table II) might serve as nurse trees and help in the establishment of other species (Santiago-García *et al.*, 2008). *Leucaena*, which casts a light shade that reduces grass cover, is abundant and increasing throughout the sampled area. *Leucaena*, however, may also grow in extremely dense, nearly impenetrable stands like those at Las Cabezas de San Juan along Puerto Rico's north-eastern shore (Weaver, personal observation). Regardless, the current status of the northern Tinaja plots and the success of planting on plot 1 and elsewhere on the refuges suggest that this may be an opportune moment to interplant native tree species to hasten the recovery of a more diverse secondary forest.

The role of exotic species to help restore native forest remains a controversial issue (Weaver, Schwagerl, 2004). A point often overlooked is that Puerto Rico's southwest has changed dramatically since the island's discovery. Today's secondary forests do not have the stature, biological diversity, organic matter content, or moisture holding capacity of the original forests. Native species should be favored in planting operations but scattered exotics like *Tamaridus indica* and *Prosopis pallida* provide crown extension, drought tolerance, and longevity. Their shade not only reduces the potential of fires that could set early secondary forest back to grass cover but also provides foraging and nesting sites for local wildlife instrumental in forest recovery.

Photograph 4.
About 3,700 trees were planted at the Laguna Cartagena National Wildlife Refuge, including 300 on northern Tinaja. Surveys recorded survival, height, diameter, and were used to determine survival and growth.
Photograph P. L. Weaver.

Photograph 5.
Puerto Rican Tody (*Todus mexicanus*), one of six endemic bird species recorded on the 110 hectares Tinaja tract. Despite past land use and small size, the tract contains 141 native tree species and 17 bird species.
Photograph I. Vicéns.

Refuge flora and fauna

The entire Tinaja tract, relatively small in size, has a diverse flora and fauna. Of the 141 native tree species recorded, 7 were endemics (Weaver, Chinea, 2003): *Eugenia woodburyana* Alain; *Garcinia hessii* (Britton) Alain; *Leptocereus quadricostatus* (Bello) Britton & Rose; *Machaonia portoricensis* Baill.; *Rondeletia inermis* (Spreng.) Krug & Urban; *Tabebuia haemantha* (Bert.) DC.; and previously mentioned *Thouinia striata*. Moreover, 17 bird species were recorded, including six endemics (Weaver, Schwagerl, 2009): *Caprimulgus noctitherus* (Puerto Rican nightjar), *Dendroica adelaidae* (Adelaide's warbler), *Loxigilla portoricensis* (Puerto Rican bullfinch), *Melanerpes portoricensis* (Puerto Rican woodpecker), *Todus mexicanus* (Puerto Rican tody) (photograph 5), and *Vireo latimeri* (Puerto Rican vireo). The nightjar, thought to be extinct, was rediscovered in Puerto Rico's southwest during March, 1961 (Reynard, 1962). Later recorded at Tinaja (Vilella, Zwank, 1993), the species was seen on the ground in dense leaf litter and overhanging branches during field work for this study. The proximity of Tinaja to the laguna tract (figure 1), where 146 bird species have been recorded, suggests that new surveys at Tinaja would likely disclose additional species.

Current trends in south-western Puerto Rico pose concerns for the region's wildlife. The mealybug infestation, which reduced the number of cacti stems on lower Tinaja from 17 to 2% of the total in only 7 years, has affected about 1,400 km^2 of Puerto Rico's south-west (table II, Segarra-Carmona *et al.*, 2010). The cacti, also present on steep, eroded slopes at higher elevations on upper Tinaja, are an important source of food for several wildlife species. In addition, the human population in the municipality of Cabo Rojo, which borders the Tinaja tract (see figure 1, upper left for municipality boundaries), has grown significantly during the past 25 years due to new summer home construction and increased tourism. Human expansion into the Lajas municipality seems likely in the future because of the pleasant climate and proximity to beaches. Presently, lower Tinaja contains less than one-quarter of the native tree species recorded for the entire tract (table II; Weaver, Schwagerl, 2009). The development of a more diverse native tree cover, including species useful as forage for birds and bats, would increase the value of the refuge for wildlife.

Conclusions

Tinaja has been cutover, burned, sporadically planted with exotic trees, and heavily grazed for decades, a situation common in dry forests of the Caribbean islands and elsewhere. The elimination of grazing and fire on lower Tinaja currently allows the invasion of trees and shrubs of different species, notably exotics. These secondary forests are a product of several factors – time, landscape variables like elevation and topography (i.e., arroyos), past human influences (i.e., fence-lines and tree planting), and proximity to residual secondary forest.

Restoration plantings on plot 1 at Tinaja and elsewhere on Fish and Wildlife Service refuges in south-western Puerto Rico have been successful. Moreover, aggressive exotic species like *Albizia lebbeck*, *Leucaena leucocephala*, and *Pithecellobium dulce* continue to spread, shading surrounding grasses and reducing the threat of fire. Their current abundance and scattered shade offer an opportunity to interplant native trees to enhance species richness and improve wildlife habitat.

Finally, with regard to past surveys of the entire Tinaja tract, it is apparent that relatively small areas largely surrounded by grazing lands may still support a rich native flora and fauna, even after a century of heavy use. Their acquisition and protection are critical to the conservation of wildlife species, including many endemics.

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