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Novel dry forests in southwestern Puerto Rico

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ABSTRACT

We report results of new research on (1) community composition of novel subtropical dry forests developing on abandoned pastures and agricultural fields in both private and protected public lands and (2) seed germination and growth rates of plantings of native tree species on degraded soils. We found that novel dry forests were dominated by introduced species, which accounted for 59 percent of the Importance Value (IV) of stands. These forests had high species dominance, with the most dominant species averaging 51 percent of the IV but reaching values as high as 92 percent. The floristic similarity between novel and mature native forests was low (5.6 percent) compared with the similarity among novel forest stands (26 percent). Collectively, the emerging novel forests had relatively high species richness (39 species/1.2 ha). After 45–60 years of growth and development, novel forests lagged mature native forests in basal area, tree density, and species richness, and lagged stands of similar age and past land use inside a protected area. Novel forest stands inside the protected Guánica Forest had higher species richness than those located outside in private lands. Most regeneration was from seed (67 percent of the new stems were single stems). The results from the germination and planting experiment show that seeds of 17 of 21 native tree species germinated in the laboratory and grew successfully in abandoned pastures when planted and watered for a period of 13 months. Our research shows that after the initial invasion and dominance of introduced species on degraded sites, the stands diversify with native species thus evolving towards new forest types with novel species combinations.

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1. Introduction

Caribbean dry forests are among the least conserved of the tropical dry forests (Lugo et al., 2006). They have low floristic diversity and stature and high density of small and medium sized trees. These forests occur mostly on porous limestone substrate with shallow soils, exposing them to greater water stress and nutrient limitations than other non-calcareous dry forests with similar rainfall. Caribbean dry forests also experience periodic hurricanes and insidious anthropogenic disturbances.

Most of our information about resilience of dry forests in Puerto Rico originates from stands within a protected area, the Guánica Forest Biosphere Reserve, from now on Guánica Forest (Lugo et al., 1978; Murphy and Lugo, 1986; Murphy et al., 1995; Van Bloem et al., 2003; Molina Colón and Lugo, 2006). Stands outside the Guánica Forest tend to be younger because of recurrent use and disturbance, and they also tend to grow on degraded sites relative to stands inside the reserve recovering after abandonment. Degraded sites are characterized by all or a combination of the following characteristics: compacted shallow soils, reduced or very little soil organic matter, evident soil erosion, grazed and/or trampled understory vegetation, altered species composition tending towards few dominants that are usually thorny, higher species dominance than in undisturbed stands, fewer large trees, ragged canopies, and invasions of introduced tree species (Lugo et al., 2006). When fire and grazing are chronic components of these degraded stands, arrested succession ensues at stages that are dominated by grasses and thorny shrubs. At this point, it is difficult to reverse the degradation process. Usually, a new forest emerges that is persistent and reaches maturity in its degraded state, but which is clearly different from the original (Pérez Martínez, 2007).

Under these more extreme anthropogenic effects ecological succession after the abandonment of agricultural lands can lead to changes in species composition and to a different mature state than the original. Hobbs et al. (2006) termed these new emerging ecosystems "novel ecosystems" because they were the result of deliberate or inadvertent human action and were unlike any other forests present prior to disturbance. Hobbs et al. wrote (p. 2): "Novel ecosystems arise either from the degradation and invasion of 'wild' or natural/seminatural systems or from the abandonment of intensively managed systems". Lugo and Helmer (2004) discussed the conditions under which Puerto Rican novel forests emerge and their successional pathways. For our study, the novel forests emerged

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after degradation and abandonment of agricultural fields and pastures.

We addressed the following questions regarding novel forests outside the Guánica forest. Are there differences in the structure and species composition of novel dry forests located at different distances from the Guánica forest reserve? What will these young novel forest look like and will they be dominant in future dry forest landscapes? Can the establishment of native dry forest tree species be accelerated through planting on degraded pastures? To address these questions we combine the results of new research from Puerto Rico outside Guánica forest with published information from elsewhere. We also report the results of seed germination and planting experiments designed to anticipate solutions to forest restoration problems in degraded dry forest conditions.

2. Methods

2.1. Vegetation surveys

We used aerial photographs from 1936, 1950–1951, 1963, 1971, 1983, and 1989 to identify 10 abandoned farms both inside and outside the Guánica forest in the USGS quadrangles of Guánica and Punta Verraco, southwestern region of Puerto Rico (Fig. 1). Prior to 1936, the region had been under agricultural activity for over a century. We learned from landowners which farms were used for cultivation, grazing, or both. We conducted the statistical analyses as if the uses were different (cultivation or grazing) and for combined data, independently if the farms were first used for cultivation or grazing. The abandoned farms vary in size (5–65 ha), time of abandonment (20–60 years), and distance from seed sources (85–2800 m). The distance to seed sources was estimated using all aerial photos to identify the nearest forest patch that remained forested since 1936 upwind from the study farm.

Most of the data in this study are for 10 farms ranging in age from 45 to 60 years. We sampled additional farms to gather information from younger stands (20 years), but these data were only used for an analysis of the changes with age of stands. All soils were derived from limestone but they varied in structure (clay, loam, and rocky), depth, and slope.

In the 10 selected farms we established thirty 400-m^2 circular plots (three per farm of ages 45–60 years). Inside these plots we measured the dbh of all adults trees with a diameter at breast height (dbh at 1.37 m) $\geq$ 2.5 cm. An additional three circular plots were established in a native mature forest randomly selected from five plots measured by Molina Colón (1998). We used the same methods in Molina Colón and Lugo (2006) to measure or estimate the following parameters of vegetation structure: tree dbh density, basal area, and height; species Importance Value (IV; defined as the sum of relative density and relative basal area expressed in percent), tree species richness, Shannon diversity (H), and homogeneity (J); and the percentage of single and multiple stems. With these data we calculated the Holdridge (1967) Complexity Index (HCI) for trees $\geq$10 cm and for all trees $\geq$2.5 cm dbh. We used the following formula (units in parenthesis): HCI = basal area (m^2/0.1 ha) * tree density (stems/0.1 ha) * number of tree species in 0.1 ha * tree height (m) * 10^{-3}.

All adult tree data presented here are for trees with dbh $\geq$ 2.5 cm. For juvenile trees (<2.5 cm dbh and height > 1 m) we used the circular plots established in four farms (two inside and two outside the Guánica forest). Inside these circular plots we established two transects perpendicular to each other. The dimension of transects were 22.6 m × 2 m (86 m^2 per plot, when sampling area is corrected to avoid double accounting of vegetation at the center of the circle). Along these transects we measured the diameter of all juvenile trees. The total sampled area for juvenile trees was 0.1 ha. We also studied plants with <1 m height. This vegetation was identified to species and counted in four randomly selected 1-m^2 subplots per plot in three plots within farm 2 inside the Guánica forest.

We estimated the floristic similarity between farms and between farms and mature forest using the Sørensen Similarity Index, Motyka variation, which corrects for species abundance (Mueller-Dombois and Ellenberg, 1974). Tree species were also classified as native, introduced, pioneer, and/or mature forest species according to their characteristics in Little and Wadsworth (1964) and Little et al. (1974). Morphological and reproductive characteristics were used as indicators to classify the species as pioneers or mature forest species. Among them were their reproductive effort, seed size and seed dispersion, life cycle characteristics, and shade tolerance. The percent of native, introduced, and pioneer species were determined for each farm. Naturalized species, i.e., introduced species capable of regeneration under natural conditions, were tallied as introduced species.

2.2. Germination experiment

A germination experiment with 21 native (17 trees, one shrub, and three cacti) species and *Leucaena leucocephala* (a naturalized species) was conducted between June and December 2000. Seeds were collected in the Guánica forest during the spring of 2000. We collected between 10 and 250 seeds per species and germinated them under controlled conditions using trays filled with Promix soil. This soil was not fertilized. Seeds were washed with running tap water and allowed to dry on towel paper before sowing. Seeds of three native species (*Amyris elemifera*, *Erythroxylon aerolatum*, and *Bunchosia glandulosa*) and *L. leucocephala* received four different treatments respectively to improve germination: acid scarification (seeds in 1 percent sulfuric acid for 15 min); and mechanical scarification using pliers, a razor, and a nail file. After sowing, trays were placed in a greenhouse, shaded with saran, and watered daily. They were watered every other day after germination. As seeds germinated, seedlings were identified to species and counted daily.

2.3. Planting experiment

The seedlings obtained in the germination experiment plus additional ones that were not used in the experiment but were also germinated from seed were maintained in a greenhouse and irrigated during the first two years of growth. On March 2002, we began a reforestation experiment in Guánica forest and in a private old field in Sierra Bermeja. On each site, we select two 50 × 50 m plots. In one of them we eliminated all vegetation (no shade) and in the other, we eliminated all vegetation except *L. leucocephala*, which was left to provide shade to the plantings. All plots had the same aspect and were divided into 11 rows with 2.5 m between rows. Each row had space for 11 plantings with a 2.5-m spacing between them. Not all planting spaces were occupied as planting location was randomly assigned to species until all available seedlings were distributed. We planted 61 plants on each plot from 13 of the 17 tree species previously germinated in the greenhouse (total number of plants was 244). Outplants were irrigated individually every two weeks. We measured the height of each plant (cm) at the time of planting and 13 months later.

2.4. Data analysis

All data were statistically analyzed using SPSS version 13 for PC. Descriptive variables (distance from seed source, time of abandonment, and farm size) as well as response variables (species richness, diversity, and homogeneity; tree diameter, height density, and basal area; species relative importance; HCI; and percent of single and multiple stems) were analyzed with descriptive statistics.

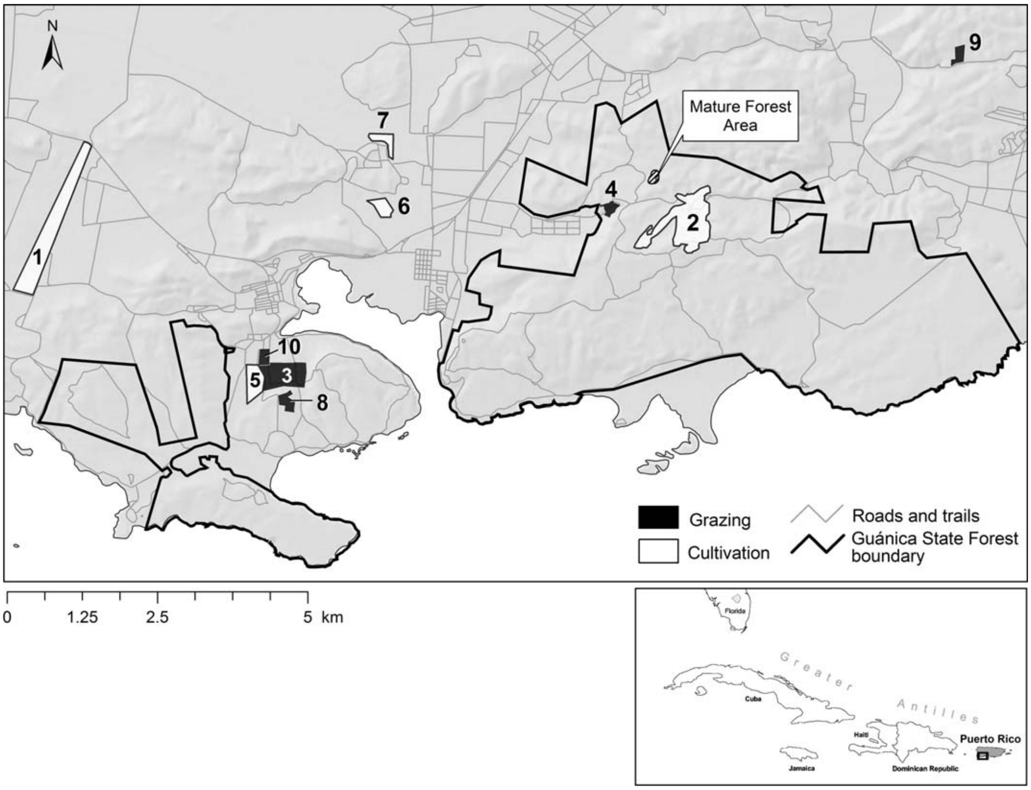

Fig. 1. Map of the study sites.

The two sets of data (cultivated and grazed farms) were compared with independent sample *t*-test. Data were also compiled by categories of time of abandonment, size of the farm, and distance from Guánica forest to perform one way ANOVA and multiple comparisons. Pearson correlation was also performed between descriptive and response variables. We also performed multiple regression analyses between response variables (dependent variables) and combinations of the descriptive variables (independent variables). Significance for all tests was set at $p \leq .05$. We applied categorical analyses (contingency table analyses) to the germination percent data for the species that received all scarification treatments and control. Also, we applied a comparison of means (one way ANOVA) for the germination time data.

We used ArcView 3.3 GIS software (ESRI, 2002), to spatially analyze the farms. First we calculated the centroid for each of the farm polygons. From each centroid, we measured the distance along lines given by the two prevalent wind directions and the point crossing the closest closed-forest fragment within and outside the Guánica forest. The perimeter to area ratio was also calculated using the feature attribute table values for each of the farm's polygons.

3. Results

3.1. Vegetation surveys

Adult trees were represented by 39 tree species in 1.2 ha sampled in the 10 farms (Table 1). Of these, 11 were introduced species, which accounted for 59 percent of the total species IV. The naturalized leguminous *Prosopis juliflora* and *L. leucocephala* were the dominant species in 8 of 10 farms. *P. juliflora* is bird- and cattle-dispersed, whereas *L. leucocephala* is wind-dispersed. Native tree species whose fruits and/or seeds are consumed by birds or bats (i.e., *Guaiacum officinale*, *Bursera simaruba*, *Bourreria succulenta*, *Pithecellobium unguis-cati*, and *Capparis* spp.) were common in the stands (Table 1). In general, species richness was low (Table 2), especially in farms far from the Guánica forest. The mean IV of the most dominant species in farms was 51 percent with a range of 21–92 percent (Fig. 2).

We found no significant difference in the structure of forests whether located in farms previously cultivated or grazed (Table 2). Thus, we combined the stands into one group and refer to these forests as "farms" to reflect their historical origin. The floristic similarity among farms was low (26 ± 2.9 percent). However, the number of stems per shared species increased when farms were located close to each other (Pearson correlation, beta value = −0.61, $n = 45$, $p = .00$).

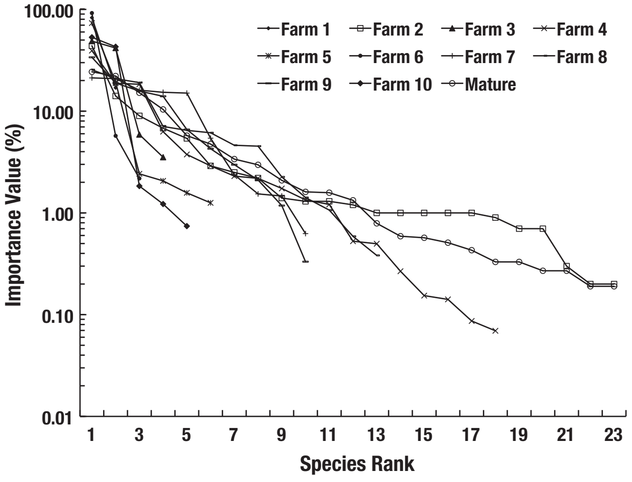

Fig. 2. Importance Value curves for tree species in the 10 study farms and a mature forest. Farmlands were recovering from cultivation and/or grazing. The mature forest had seven additional species not shown in the graph. The sampling area was the same for all forests (0.12 ha).

Table 1

Stem density, basal area, Importance Value, and type of fruit or seed for adult tree species (≥2.5 cm dbh) in abandoned farms and the top 10 tree species in mature forest located in the subtropical dry forest life zone inside and outside the Guánica state forest in southwest Puerto Rico. Farm data are from 30 circular 400 m^2 plots (1.2 ha) and mature forest data are from 3 plots (0.12 ha). Empty cells mean the information is not known. Introduced species have an asterisk (*). Basal area data are rounded. Other mature forest species present in the farms are identified by a "P" in the tree density column.

Species	Stem density (stems/ha)		Basal area (m^2/ha)		Importance Value (%)		Fruit/seed	
	Farms	Mature	Farms	Mature	Farms	Mature	Fleshy	Dry
*Leucaena leucocephala**	772		1.23		27.7			X
*Prosopis juliflora**	311		2.19		24.3		X	
Pithecellobium unguis-cati	414	934	0.54	1.16	13.9	5.8	X	
Bucida buceras	75	P	0.26		3.8			X
Guaiacum officinale	75	P	0.23		3.5		X	
Bourreria succulenta	76		0.18		3.2		X	
Guazuma ulmifolia	13		0.34		3.0			X
*Cassia siamea**	12		0.29		2.5			X
*Hura crepitans**	8		0.28		2.3		X	
Pictetia aculeata	67	P	0.08		2.2			X
Flueggia acidoton	51	P	0.08		1.8			
Bourreria virgata	57		0.058		1.8		X	
Andira inermis	37		0.076		1.5		X	
Exostema caribaeum	28	P	0.079		1.3			X
Thouinia portoricensis	21	2631	0.07	2.89	1.0	15.2		X
*Tamarindus indica**	4		0.09		0.8		X	
*Delonix regia**	3		0.08		0.7			X
Bursera simaruba	6	P	0.07		0.7		X	
Schaefferia frutescens	11	P	0.02		0.4		X	
Amyris elemifera	13	P	0.02		0.4		X	
*Melicoccus bijugatus**	1		0.03		0.3		X	
Capparis hastata	7		0.02		0.3		X	
Zanthoxylum monophyllum	8		0.01		0.2		X	
Krugiodendron ferreum	5	P	0.01		0.2		X	
*Garcinia dulcis**	3		0.02		0.2		X	
Eugenia foetida	8	637	0.01	0.59	0.2	3.4	X	
Colubrina arborescens	5	P	0.01		0.2		X	
Coccoloba diversifolia	5	4032	0.01	4.02	0.2	22.1	X	
Bunchosia glandulosa	5		0.01		0.2		X	
Trichilia hirta	4		0.01		0.2		X	
*Pithecellobium saman**	4		0.00		0.1			
Pisonia albida	1	297	0.02	0.29	0.2	1.6		X
*Haematoxylum campechianum**	4		0.00		0.1			X
Cordia nitida	1		0.01		0.1		X	
Colubrina reclinata	1	P	0.01		0.1			X
Capparis cynophallophora	4		0.01		0.1			X
*Bauhinia monandra**	2		0.01		0.1			X
Casearia aculeata	1		0.00		0.0		X	
Capparis indica	1		0.00		0.0		X	
Savia sessiliflora		4753		4.10		24.4		X
Eugenia rhombea		1867		1.92		10.4	X	
Erythroxylon rotundifolium		806		0.92		4.8	X	
Guettarda elliptica		552		0.53		3.0		X
Gymnanthes lucida		382		0.38		2.1		X
Total	2125	18,081	6.0	18.0	100	100		

There were no significant correlations (Pearson correlations, $p > .05$) between any of the descriptive variables (time of abandonment, distance from seed source, and size) and the response variables (species richness, diversity, and homogeneity; vegetation HCI; tree height, diameter, basal area, and density; species IV; and percent of single stems) when all sites were considered. Multiple regression analyses between the dependent variables: richness, homogeneity, diversity and complexity indexes and various com-

Table 2

Mean values for structural parameters of forest stands in abandoned farms previously used for grazing, cultivation, and when combined. Farms were located on the subtropical dry forest life zone in southwest Puerto Rico. Data are based on circular 400 m^2 plots (0.12 ha per farm) where trees ≥2 cm dbh were measured between 1996 and 1998. The standard error is in parentheses, $n = 5$ for the first two columns and 10 for the combined data. The differences between cultivated and grazed farms are not significant.

Structural parameter	Grazed farms	Cultivated farms	All farms
Species richness	10.0 (2.6)	8.8 (3.8)	9.4 (2.2)
Species diversity (H')	2.2 (0.4)	1.6 (0.5)	1.9 (0.3)
Species homogeneity (J')	68.8 (4.6)	50.4 (11.5)	59.6 (6.6)
Complexity ≥ 10 cm dbh	0.4 (0.2)	0.7 (0.6)	0.5 (0.3)
Complexity ≥ 2.5 cm dbh	17 (13)	13 (8)	15 (7)
Tree density (stems/ha)	2518 (710)	2948 (727)	2733 (485)
Basal area (m^2/ha)	6.5 (1.8)	8.7 (1.2)	7.6 (1.1)
Tree height (m)	5.2 (0.2)	5.6 (0.2)	5.4 (0.2)
Tree diameter (cm)	6.7 (0.3)	7.5 (1.3)	7.1 (0.7)
Single stem trees (%)	54.8 (10.3)	79 (6.8)	66.9 (7.1)
Importance Value of the most dominant species (%)	40.2 (4.9)	62.6 (13.2)	51.4 (7.6)

Table 3
Density and basal area of juvenile and adult trees in four farms on two contrasting locations. Farms 2 and 4 were located inside the Guánica forest, and farms 7 and 9 were located in private lands. Juvenile trees had a diameter at breast height (dbh) < 2.5 cm and were taller than 1 m, while adult trees had a dbh ≥ 2.5 cm.

Farm ID	Juvenile trees		Adult trees	
	Density (trees/ha)	Basal area (m^2/ha)	Density (trees/ha)	Basal area (m^2/ha)
2	4252	0.66	4231	8.1
4	927	0.16	5128	13.6
7	618	0.09	1114	11.3
9	6146	0.79	2899	5.1

binations of the independent variables: time of abandonment, size of farmland, and distance from a seed source were all not significant ($\alpha > 0.05$). However, the two farms located within Guánica forest and the closest one outside (<500 m) had more than double the species diversity and richness of those that were more than 1000 m from the reserve (independent *t*-test, $t = 3.31$, df = 8, $p = .01$). Similarly, stem density increased with age after abandonment. Stem density was significantly different in farms abandoned for 20 years (1877 stems/ha) in comparison to farms abandoned for ≥45 years (4653 stems/ha). Stem density was also significantly different between farms abandoned for 30 years (1954) vs. those abandoned for ≥45 years (Bonferroni Test, $p \leq .05$).

We enumerated 34 species of juvenile trees in 0.1 ha of four farms. Of these 34 species, 88 percent were native species, 23 were found as adult trees, and 11 were not when compared against the adult trees in the four farms. Juvenile tree density was similar to adult tree density in some farms and either higher or lower in others (Table 3). In all farms the basal area of juvenile trees was low and there was no pattern associated with the location of the farms. We found eight species as plants <1 m height in farm 2 inside the Guánica forest (six tree and two cacti species; Table 4).

3.2. Germination experiment

The germination experiment resulted in a range of germination of 1–88 percent (Table 5). *L. leucocephala* had 57 percent germination. Seeds from five of the native species did not germinate. The native species *E. aerolatum*, *Capparis cynophallophora*, *A. elemifera*, and *Pisonia albida* (trees) and *Pilosocereus royenii* and *Melocactus intortus* (cactus) had higher germination than *L. leucocephala*. There was no difference in the mean germination time between scarification treatment and control (one way ANOVA; $F = 0.04$; total df = 71; $p = .10$), and the values range from 20 (scarification with blade) to 29 days (scarification with pliers). Time of germination under control conditions was 26 days. The scarification techniques and control were all equal on germination percent by species (contingency table analyses; Chi square = 107.90; df = 8, $p > .05$).

3.3. Planting experiment

Fifteen saplings died during the planting experiment, six percent mortality on each site. The mortality was independent of site, shade conditions, and the species involved. Among the surviving saplings, 27 percent decreased in height due to insect herbivory or drought. The rest increased 40–50 cm and this increment was independent of site or shade conditions (Table 5). Nevertheless, there was a significant difference between the height at the time of planting and the height 13 months later (pair samples *t*-test; $t = -18.20$; df = 173; $p < .00$) and was negatively correlated with the height at the time of planting (regression analyses; $R^2 = 0.07$; df = 173; $p < .00$) such that the tallest saplings grew less than short ones.

Table 4
Density of trees <1 m height and cacti in a farm inside the Guánica forest. The asterisk identifies introduced species.

Species	Density (plants/ha)
Trees	
*Leucaena leucocephala**	140,000
Bourreria succulenta	4167
Guaiacum officinale	1667
Flueggia acidoton	1667
Ziziphus reticulata	833
Erythroxylon areolatum	833
Cacti	
Opuntia repens	833
Pilosocereus royenii	833

4. Discussion

At the outset we asked whether forests recovering from grazing or land degradation after cultivation in private lands would form stands similar to those native stands in the vicinity and if not, what would they look like? We knew from studying forests on lands abandoned after a variety of uses within the Guánica forest that after 45 years of recovery the emerging forests would be different from the original native forests in terms of species composition and structural development (Molina Colón and Lugo, 2006). However, in this study, we searched for stands with a variety of ages in private lands where the agricultural use pressure and human disturbances were expected to be higher or at least more recent than within the protected confines of the Guánica forest. We expected that under greater anthropogenic disturbances, land degradation would be greater and forest recovery proportionally slower. Our results did show differences in the level of response of the farms from this study with those studied by Molina Colón and Lugo (2006) but they also showed some similarities that suggest a common pattern of forest response when developing on abandoned agricultural lands.

4.1. Forest structure and rate of recovery

4.1.1. Adult trees

Forest stands in the farms exhibited less structural development (Table 2) than native forest stands in the Guánica forest, which are taller, richer in species composition and have higher HCI (Lugo et al., 1978; Murphy and Lugo, 1986, 1995; Murphy et al., 1995). Holdridge (1967) proposed the HCI for comparisons of mature vegetation using a minimum dbh of 10 cm as the basis of the calculation. The scarcity of trees with dbh ≥ 10 cm results in reduced HCI in Guánica forest (Lugo et al., 1978). Our results for trees with dbh ≥ 10 cm are even lower (Table 2). Even if we calculate the HCI for trees with dbh ≥ 2.5 cm, the result was also lower (15) than the 170 reported by Lugo et al. (1978) for mature native forests in the Guánica forest. However, both mature native and recovering farmland stands have similar tree density and basal areas (Lugo, 1988; Lugo et al., 1978; Murphy and Lugo, 1986, 1995; Molina Colón, 1998; Molina Colón and Lugo, 2006). Thus, the level of maturity and species composition are the main differences between novel forests in farms and native mature forests.

Farms had recovered 40 percent of tree basal area, density and species richness in comparison with the mature native forest, whereas, 77 and 66 percent of recovery was estimated for tree

Table 5

Germination (Germ) in percent and annual height growth (cm) of plantings under shade or without shade at the Guánica forest (GF) and Sierra Bermeja (SB). Empty cells mean either that germination was not studied for a particular species or that the seedlings failed to grow or died. *Leucaena leucocephala* was not planted. Height growth values are rounded to the nearest cm.

Species	Germ	Shade		No shade	
		GF	SB	GF	SB
Amyris elemifera	84	56	67	27	58
Bumelia krugii	0				
Bunchosia glandulosa	40	39	74	50	115
Capparis cynphallophora	64	73	41	0	44
Coccoloba diversifolia	44	39	8	51	41
Coccoloba krugii	0				
Colubrina arborescens	2	9		2	
Crossopetalum rhacoma		29	52	53	32
Erithalis fruticosa	1				
Erythroxylon aerolatum	61	24	5	12	5
Erythroxylon rotundifolium			24	10	57
Eugenia rhombea	22				
Exostema caribaeum	14	4			
Guaiacum sanctum	42	54	33	35	28
Gymnanthes lucida		16		7	
Helicteres jamaicensis	0				
Jacquinia arborea	50	66	69	48	33
Krugiodendron ferreum	0				
Lantana arida[a]	0				
Leptocereus quadricostatus[b]	53				
Leucaena leucocephala	57				
Melocactus intornus[b]	62				
Pilosocereus royenii[b]	88				
Pisonia albida	84	14			
Reynosia uncinata	11	2	10	10	73
Zanthoxylum caribaeum		74		24	

[a] Shrub.

[b] Cactus.

height and species diversity, respectively (Fig. 3). These measured levels of recovery relative to the mature native forest are lower than those reported for stands recovering after agricultural use inside the reserve (Molina Colón and Lugo, 2006). For example, Fig. 2 in Molina Colón and Lugo (2006) compares forest stands recovering from agricultural use with the same mature forest that we used in this study. The recovery percentages in that figure are higher than those in our Fig. 3. Nevertheless, the pattern of regeneration in our 10 farms is similar to the regeneration pattern from abandoned farms and houses inside the Guánica forest, with height recovering faster than basal area or presence of large trees. The regeneration by single stems is predominant in lands previously used for agriculture (67 ± 7 percent), suggesting that most trees regenerate from seed as opposed to sprouting.

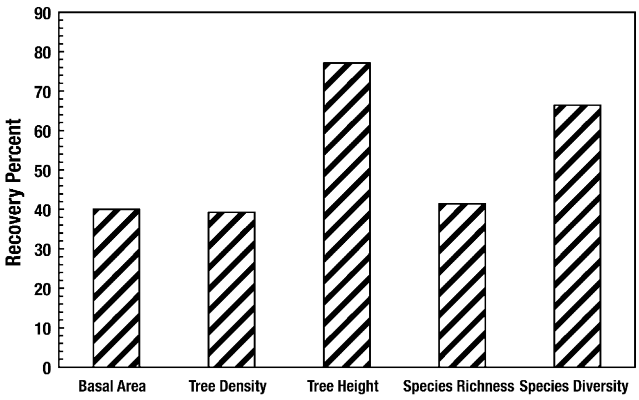

Fig. 3. Recovery of structural parameters in forest stands located in 10 abandoned farms after cultivation or grazing. Recovery is expressed as a percent of the corresponding value in a nearby mature native forest. The mature forest values were: basal area – 19 m²/ha, tree density – 6959 stems/ha, tree height – 7 m, species richness – 22.7 species/0.12 ha, species diversity – 2.83.

4.1.2. *Juvenile trees*

Juvenile trees had a significant contribution to the structure (Table 3) and species composition of these novel forests. Their basal area was small but their stem density in some farms doubled the value of this structural measure. The result was that these forests are very dense stands. Of significance to plant succession is the fact that the species composition of juvenile trees is 91 percent native compared to 72 percent for adult trees. These juvenile tree species represent the future composition of these forests and it is notable that 32 percent of the species tallied were not represented in the overstory of the stands.

4.2. *Community organization*

A species IV is an indirect measure of its relative productivity in a community and its use of resources. Species IV curves assess how a community divides its use of ecological space (Whittaker, 1970). Whittaker described geometric species IV curves as usually associated with communities with few species in severe environments, while the lognormal IV curves reflect species-rich communities in less severe environments (Whittaker, 1970). The species IV curves of forest stands in most farms we surveyed approach a geometric series (farms 1, 3, 5, 6, 7, 9, 10), while that of the more diverse mature forest is less vertical with high IV for its most dominant species (Fig. 2). Farms 2 and 4 had high dominance and high species richness with an IV curve similar to that of the mature forest but with fewer species. Both farms were inside the Guánica forest, close to abundant seed sources and under protection from anthropogenic disturbances.

Native dry forests, like most forests in Puerto Rico, exhibit high dominance and a tendency for geometric IV curves (Lugo, 2005). When anthropogenic disturbances alter dry forests, the level of species dominance increases (Lugo, 1991). Molina Colón and Lugo (2006) found that the most dominant species in recovering farms inside the Guánica forest had higher IV (32 percent) than the most dominant one in the mature forest (23 percent). In our farms, the average species IV of the dominant species was 51 percent and in some farms it was as high as 92 percent. This higher level of dominance probably reflects the greater level of anthropogenic disturbance in farms outside the Guánica forest.

4.3. Species composition and its variability

A striking feature of forest stands in abandoned farms was the dominance of introduced species (Tables 1 and 4). Introduced species constitute the core of these forest stands, contributing the majority of their basal area, tree density, height, and biomass. However, observations in other forests (Aide et al., 2000) suggest that the high dominance of introduced species might change in the future. The change appears to be in favor of native species, even if introduced species now exert a high dominance in these forests or continue to dominate in the near future (Lugo, 2004). One can surmise this change in our study area by comparing juvenile tree species composition with canopy tree species composition. We found that of 34 species of juvenile trees, only 23 were represented among adult trees, a finding that coincides with the results of Pérez Martínez (2007) from the Guánica forest. The proportion of introduced species declined from 28 percent in the adult tree species list to 9 percent in the juvenile species list. Of interest to the conservation of rare species, we found saplings of *Bumelia obovata*, and seedlings of *Ziziphus reticulata*. Both are uncommon species in Guánica forest.

We also found dramatic differences in the species composition of abandoned farm plots compared to that of the mature forest. For example, the mean Similarity Index of tree species between mature forest and farms was 5.6 ± 1.8 percent. This low level of similarity was independent of distance between the mature forest and the farm polygon centroids, and the time of abandonment of the farming activities (multiple regression, $n = 10$, $p > .05$). It would appear that introduced species are the early colonizers of abandoned agricultural lands and this leads to their high dominance. Over time, the dispersal of seeds by wind and animals from adjacent forests diversify stands, and it appears that most of the new arrivals are native species and/or that the environmental conditions under the canopy have changed favoring the germination and establishment of native tree species. Table 1 shows that collectively all farms share 16 tree species with the mature forest, or 41 percent of their 39 species. Yet, each farm accumulates a particular group of native species, probably depending on seed sources as well as local growth conditions. This enrichment process leads to different species assemblages among farms and strong species differences between those in the canopy and those in the understory. The presence of introduced species adds to the level of uniqueness of each farm.

4.4. Landscape-level species richness

We found 39 tree species in 1.2 ha of abandoned farms (Table 1), which is low in comparison with the 50 species per hectare inside the Guánica forest (Lugo, 2005). Nevertheless, when we combine all our 10 farms into one data set, the higher aggregate species richness reduces the dominance of the community to levels similar, although still higher, to those of native forests. This raises a point of relevance to the landscape-scale level of analysis. The low similarity between farms (26 percent) coupled to their scattering over the landscape, makes the landscape richer in species, even if individual forest patches are species-poor. Collectively the forests of these farms provide refuge to a larger number of species, in spite of the fact that they individually are species-poor and even if collectively they still lag the species richness of protected landscapes.

4.5. Factors that regulate forest response

Molina Colón and Lugo (2006) suggested that the type of human use of dry forestlands influenced the conditions of forest recovery. Where the intervention was mechanical removal of aboveground biomass, forest recovery was fast and for some parameters exceeded the mature forest e.g., abandoned charcoal pits. For interventions such as agricultural uses where the vegetation and its roots were removed and soil degraded, recovery after abandonment was slower. In the 10 farms from this study we found no difference in the recovery of forests after grazing or cultivation, perhaps because both types of use removed all original vegetation and altered root structure, thus considerably setting back succession in both types of land uses. Moreover, the presence of cattle probably influenced the abundance of *P. juliflora*, a tree that is consumed and propagated by cattle in dry forest zones.

Another confounding effect on forest recovery was the geographic location of farms, which influences the supply of seeds for forest regeneration. Native forests surrounded farms inside and closest to Guánica forest whereas the farthest farms had topographical and urban barriers between them and the nearest forest stands, placing them at greater distance (both ecologically and geographically) from seed sources. We found that farms inside the Guánica forest (numbers 2 and 4, Fig. 2) are floristically more similar to forest stands within the reserve and have higher species richness, diversity, and homogeneity than farms located in private lands far from the Guánica forest. Nearby forest fragments are not only seed sources but also harbor seed dispersers that further facilitate the dispersal of tree species. Frugivore birds (Carlo et al., 2003) and bats (Gannon et al., 2005) might be the dispersal agents from forest areas to abandoned farms.

4.6. Management options

Scattered dry forests fragments of <1 ha size contribute to the recovery of isolated farms. Ramjohn (2004) found that these forest patches retain species richness and tree composition and documented 12 rare or endangered species out of a total of 53 species in at least one of 40 dry forest fragments that he examined. The species recovery pattern that emerges from our study and Ramjohn's (and also Pérez Martínez, 2007) is that over time, native species invade degraded stands but do not completely displace the dominant introduced ones. Instead, the end point of species succession appears to be a new mix of native and introduced species. Therefore allowing time to exert its influence on species enrichment is a cost-free management option for restoring native species to degraded lands but there is no expectation that the end game will be a stand with only native species (Weaver and Schwageri, 2008).

Tree planting becomes an option at small scales if natural recovery is too slow or if there is an interest in promoting particular species combinations for particular conditions. Weaver and Schwageri (2008) document a successful restoration through tree planting of native tree species in dry forests. They used a suite of species different from those that we used (only two species overlapped the two studies). Their field trials and the high percent of germination that we found among 15 native tree species (Table 5) suggest that the germination and seedling stage does not represent an obstacle for forest rehabilitation in dry forest environments. Although tree growth rate was slow in both studies, reforestation of abandoned lands was successful due to the high percent of germination and survivorship. We found no difference in the growth of seedlings under shade or sunlit conditions, which means that seedlings are tolerant to the field conditions under which reforestation projects might take place. However, this option is costly due to the requirements for watering and taking care of plantings. Nevertheless, secondary succession on lands adjacent to plantings further

Table 6
Ecological characteristics of novel Antillean dry forests.

Ecological characteristic	Notes
High Importance Value for the dominant species	Usually greater than 50 percent
Dominant species usually not native	Invasive native species might also dominate
Low basal area, small trees, high tree density	At least for 100 years of growth, these structural parameters remain below (or above for tree density) the corresponding values for mature native forests
Predominance of single stems	Multiple stems occur when cutting is insidious
Native species regenerate after the canopy is established	Deep shade prevents many pioneer species from regenerating; but periodic canopy openings allow them to survive at low densities
Low similarity index between tree strata within a stand and low similarity index of comparable strata between stands	Similarity indices are lower than observed when comparing native forest stands
Understory vegetation structure variable	Ranges from dense to open in terms of vegetation cover
Ground litter is variable	Ranges from thick litter layers to exposed soil
Species richness increases over time	Species richness increase is accelerated when seed sources are near by

accelerated the recovery of the overall landscape. These results provide management options for accelerating or redirecting succession in small patches of degraded dry forestlands.

4.7. Characteristics and future of novel dry forests

We developed a list of characteristics of novel dry forests (sensu Lugo and Helmer, 2004 and Hobbs et al., 2006) on abandoned agricultural lands (Table 6) based on our results and those of Molina Colón and Lugo (2006) in southwestern Puerto Rico, the island-wide study of Brandeis et al. (2009), and our observations throughout the Caribbean. The list is not exhaustive and is bound to expand with further research. Moreover, not all novel dry forests share all these characteristics. However, all the novel forests have been exposed to the effects of human activity. Human activity provides the impetus for the emergence of novel combination of species in relation to normal succession in the particular environment (Hobbs et al., 2006).

The growth of novel forest stands on degraded lands, particularly in dry forest areas, is slowed down by lack of moisture, compacted and eroded soils, nutrient limitation, high temperatures, etc. These conditions lead to slower succession and reduced development of biomass and large trees. Our results (Table 2) reflect the low level of structural development of our farms and we discussed above that our study sites lag in development behind abandoned farms surrounded by native forests within the Guánica forest. Lugo (1988) termed the delayed effects of degradation as a “time tax” because time is required for organisms to overcome the limitations imposed by degradation. The phenomenon has also been observed in wet forest conditions after abandonment of degraded pastures (Aide et al., 1995).

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