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Survival and rebound of Antillean dry forests: Role of forest fragments

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ABSTRACT

Antillean dry forests have experienced high levels of human impact for almost five centuries. Economic changes in the second half of the 20th century have facilitated forest recovery in Puerto Rico. We quantified the extent of forest cover and the community composition of representative forest fragments in the subtropical dry forest life zone (*sensu* Holdridge, 1967) in southwestern Puerto Rico. Forest cover, which was largely eliminated by the 1940s, stood at 48% in the western dry forest life zone in 1993. Fragments varied in land-use history and supported from 1% to 86% of the reference species sampled in Guánica Forest, a 4000-ha protected area. Reference species were well represented in forest fragments, even those smaller than 1 ha, if they had never been completely cleared, but were uncommon in forests regenerating on previously cleared sites. The studied fragments are novel ecosystems which combine native and introduced elements; *Leucaena leucocephala* (Lam.) De Wit, an introduced legume, was the most common species, regardless of land-use history.

1. Introduction

The insular Caribbean has a history of anthropogenic disturbance dating, in some cases, to the 16th century. The islands juxtapose some of the highest population densities in the world (Ambio, 1981; Maunder et al., 2008) with high rates of endemism and extinction (Myers et al., 2000; Maunder et al., 2008). As is true throughout the northern Neotropics (Portillo-Quintero and Sánchez-Azofeifa, 2010) most Antillean dry forests have been cleared and converted to non-forest uses, or been used for the production of timber and fuel wood.

Structural changes in the economies of many of these islands allowed the return of forest cover (Lugo, 2002; Rudel, 2005). In Puerto Rico, economic changes in the postwar period facilitated forest recovery. Between 1940 and 2003 forest cover of the overall island increased from about 7% to over 50% (Brandeis et al., 2007), the highest rate of reforestation anywhere in the world during that interval (Rudel et al., 2000). These 'emerging forests' (Lugo and Helmer, 2004) are often made up of patches with different land-use histories and range from species-poor to species-rich forests dominated by both introduced and native tree species (Molina Colón and Lugo, 2006; Molina Colón et al., 2011).

Antillean dry forests are able to recover after severe disturbance (Molina Colón, 1998; Murphy et al., 1995; Molina Colón and Lugo, 2006; Oatham and Boodram, 2006). Most dry forest tree species sprout readily after cutting (Ewel, 1971; Murphy and Lugo, 1986a,b; Murphy et al., 1995; McLaren and McDonald, 2003a) and pre-disturbance species compositions can recover within a few decades even in cut-over forest patches (Molina Colón, 1998; Murphy et al., 1995). Recovery is slower in areas where more intensive land use precludes sprouting from stumps or root collars (Molina Colón, 1998; Ray and Brown, 1995; Roth 1999). Low recruitment rates from seed (Ray and Brown, 1994; Murphy et al., 1995; McLaren and McDonald, 2003b) also slow succession. Molina Colón (1998) found that land used for farming, housing, or recreation supported species-poor forests dominated by *Leucaena leucocephala* (Lam.) De Wit. (an introduced legume) after 50 years of abandonment, whereas areas used only for charcoal production were indistinguishable from older forests. In St. John, US Virgin Islands a 33-year-old forest on abandoned pasture was similarly dominated by *L. leucocephala*, but a 50-year-old forest was dominated by the native *Bourreria succulenta* Jacq. (Ray and Brown, 1995). Similar patterns of succession were observed in dry forests in the Dominican Republic (Roth, 1999) and in Mexico (Burgos and Maass, 2004; Lebrija-Trejos et al., 2008) where dry forests on abandoned agricultural land were species poor and dominated by native or introduced leguminous shrubs.

We documented the spatial patterns and extent of forest cover in the western portion of the dry forest life zone in southwestern Puerto Rico, and compared the species composition of 39 forest

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fragments with a reference list compiled in Guánica Forest. Central to this study were three questions: what was the nature, extent and distribution of forest cover in the dry forest life zone in southwestern Puerto Rico, how well have native species survived in forest fragments, and, as forest cover has returned to the landscape, to what extent have these species managed to recolonize the new forests? Dry forest trees resprout readily after cutting, but establish poorly from seed; this should favor their persistence on the landscape, but not their ability to recolonize new forests.

2. Materials and methods

2.1. Study region

Field work was carried out between May 1995 and August 1997 in the subtropical dry forest life zone (*sensu* Holdridge, 1967) in southern Puerto Rico, a coastal strip between approximately 18°N 66° 35′W and 18°N 67° 12′W (Fig. 1). Mean annual rainfall in the region ranges from 600 to 1000 mm (Ewel and Whitmore, 1973). Rainfall is seasonal, mostly occurring in the major wet season between August and November, or in the minor wet season in April and May (National Oceanic and Atmospheric Administration, 2001). Annual ratios of potential evapotranspiration to precipitation averaged 1.4 (Murphy and Lugo, 1986b). Evaporative demands exceeded water supply for 9 months of the year, with soil moisture deficits occurring in 10 months (Lugo et al., 1978). On average, Puerto Rico experiences one hurricane every 8 years (Quiñones, 1992) but return rates on the south coast are about one every 25 years (Van Bloem et al., 2005). While 37 hurricanes hit Puerto Rico between 1700 and 1999, the eyes of only 12 of these came near the dry forest zone (Van Bloem et al., 2005).

The life zones of Puerto Rico and the US Virgin Islands were mapped by Ewel and Whitmore (1973) using a combination of climatic data and field surveys. An updated map, produced by Gould et al. (2008) used climatic, substrate and topographic data to delimit 57 landscape units. The combination of the sixteen dry forest landscape units and two wetland units was used to produce an updated delineation of the dry forest life zone. Due to the paucity of forest cover in the eastern part of the dry forest life zone (Ramjohn, 2004), this study focused on the part of the life zone that is located to the west of the city of Ponce (Fig. 1).

2.2. Landscape characterization

Forest cover in 1993 was mapped in a portion of the dry forest life zone (as delineated by Gould et al. 2008) west of the city of Ponce using 1-m resolution 3.75-min digital orthophoto quadrangles (DOQs) taken between October and December 1993 obtained from the USGS Earth Explorer website (http://earthexplorer.usgs.gov/). Forest cover for 1936 and 1963 was obtained from a published land-use map (Vélez Rodriguez, 1995a,b); areas not covered by the map were digitized from 1:18,000 black and white photographs (obtained from the Oficina de Fotogrametria, Autoridad de Carreteras y Transportacion, San Juan, Puerto Rico) and supplemented with 1930 aerial photographs obtained from the Porto Rico 1930 Aerial Image Database (http://pr1930.revistatp.com/). Forest patches with more than 50% of the ground visible were classified as open forest, while those with less ground visible were classified as closed forest (FAO, 1993). Areas of closed forest which supported forest cover both in 1936 and in 1963 were classified as relict forest; closed forest areas which did not were classified as regrowth.

Landscape elements were digitized and converted to Esri ASCII Grid format using Quantum GIS version 1.74 Wroclaw (Quantum GIS Development Team, 2012). Landscape indices were calculated using FRAGSTATS version 4.0 (McGarigal et al., 2012).

Aerial photographs (1:33,000 color-infrared photographs December 1993), obtained from the United States Geological Survey, Eros Data Center, Sioux Falls, South Dakota, were used to locate fragments across the dry forest life zone of southern Puerto Rico. A random subset of these fragments in the western half of the dry forest life zone (Fig. 1) was selected for further study. Fragments which were active pasture supporting monodominant stands of *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth, an introduced leguminous tree species, were discounted. Beyond this, we did not attempt to control for land-use history or recentness of disturbance. Forty fragments were subject to detailed study. Fragments were classified as relict (>75% of the fragment was continuously wooded throughout the sequence of aerial photographs), regrowth (<25% continuously wooded) or mixed (25–75% continuously wooded). Fragment turnover was low – once an area reverted to forest, it persisted as forest (with few exceptions), although several declined in size. One forest fragment lay outside the area for

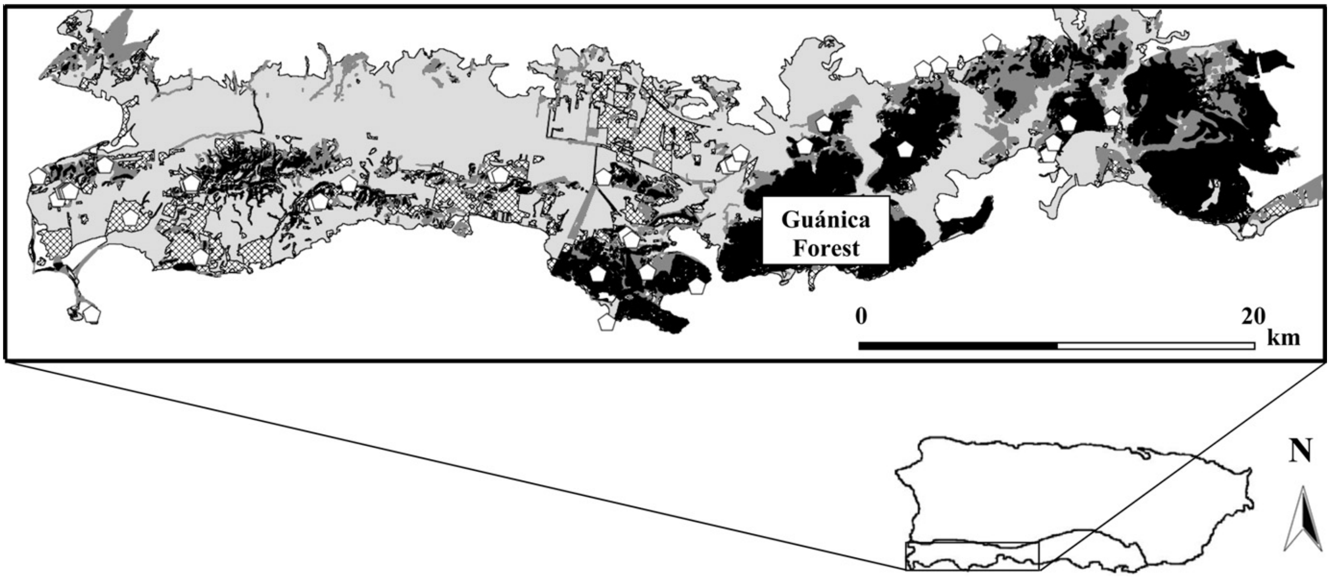

Fig. 1. The location of study area in the dry forest life zone of southwestern Puerto Rico. Inset map of Puerto Rico showing the dry forest zone in southwestern Puerto Rico (after Ewel and Whitmore, 1973) and the area from which the detailed map was selected. Closed forest cover is in black (relict forest) and gray (regrowth), open forest cover is hatched and non-forest is pale gray. Focal forest fragments are indicated with pentagonal symbols.

which coverage was obtained; no history could be constructed for this fragment.

The identity and abundance of all vascular plants was collected using a variable number of 25-m^2 circular plots per fragment. The plot size was chosen to account for the fact that sampled individuals ranged in size from herbs to small trees. Collectors' curves were used to assess sample adequacy. Censuses were carried out in 34 of the forest fragments using a total of three hundred and seventy four 25-m^2 plots. Species lists were compiled for 39 of the 40 fragments by supplementing the plot-based species lists with intensive searches of the sites. Each fragment was searched and all new vascular plant species of all sizes were recorded. Identification of grasses was difficult, especially in grazed sites where there was often little more than close-cropped stubble. A system of diminishing returns was used to estimate the completeness of the search. If 1 h of search time failed to record any new species the site was considered adequately searched. Attempts were made to search each major feature of every site (*e.g.*, each major slope and valley).

Guánica Forest, a 4000-ha protected area located in the center of the study area (Fig. 1) was used as a reference community for comparison with fragments. While not a pristine example of Puerto Rican dry forest, it is the largest remaining patch of dry forest and includes many areas of high-quality forest (Ewel and Whitmore, 1973; Murphy et al., 1995). A reference list was compiled based on the species composition of a total of nineteen 25-m^2 plots stratified across the three major associations (deciduous forest, semi-evergreen forest and scrub forest; Lugo et al., 1978) in Guánica Forest. Collectors' curves were used to assess sample adequacy in each association. Species lists for all studied fragments were compared with this reference list. Nomenclature followed Acevedo-Rodríguez and Strong (2012); differences from Liogier (1985–1997) were noted.

Species were classified on the basis of their habitat affinities using the multinomial classification model presented by Chazdon et al. (2011). The model uses species abundances in two distinguishable habitat types to estimate relative abundances, correct for the fact that sampling tends to overestimate common species and underestimate rare species, and minimizes bias due to uneven sampling intensities. Classification was carried out using the R package vegan 2.0-2 (Oksanen et al., 2011; R Development Core Team, 2011), rather than the implementation supplied by Chao and Lin (2011) which was used in the original article. The vegan implementation does not require the assumption that the data show multivariate normality. The classification was based on species abundances in eighty-eight 25-m^2 plots located in regrowth fragments and 218 plots in relict fragments. As the model was designed for paired habitat types, only plots which fell in Relict or Regrowth fragments were used in the analysis.

3. Results

Forest cover stood at 48.2% of the dry forest landscape in 1993; of that, 72.5% was closed forest (47.7% relict and 24.8% regrowth forest) and 27.5% open forest (Table 1). A total of 2114 forest fragments were identified. Eighty-three percent of the fragments were between 0.04 ha (the minimum patch size) and 5 ha; these accounted for 9% of the total forest cover. Twenty-three fragments (1.1%) were larger than 100 ha; these accounted for 64% of the total forest cover. The largest closed forest fragment occupied 6.6% of the total study area, while the largest open forest fragment occupied 2.1% (Table 2).

Mean fragment area, area-weighted mean area, median area and edge density were all higher in relict closed forest fragments (Table 2). Shape metrics (perimeter-area fractal dimension, patch shape index, related circumscribing circle and the contiguity index) were largely the same for all classes of forest fragments (Table 2). Among the aggregation indices, the proximity index, clumpiness index, percentage of like adjacencies and aggregation index were all higher for closed forest fragments, while the splitting index and normalized landscape shape index were higher for regrowth close forest and open forest. The Euclidean nearest neighbor distance was highest for open forest and lowest for regrowth closed forest. All of these indicate a greater degree of aggregation among relict closed forest fragments than open forest or regrowth closed forest fragments. The patch cohesion index was similar for all forest classes (Table 2).

Table 1

Distribution of forest cover (based on aerial photographs taken in 1993), by size class, in the dry forest life zone, southwestern Puerto Rico. Totals may not precisely match the values in the columns due to rounding. Fragments with more than 50% of the ground visible were classified as open forest, while those with less ground visible were classified as closed forest (FAO, 1993). Forest fragments which supported open or closed forest cover in both 1936 and 1963 were classified as relict, while those which supported non-forest in one or both time intervals were classified as regrowth.

	Fragment size class					
	0.04–5 ha	5–10 ha	10–50 ha	50–100 ha	>100 ha	Total
Closed forest						
Relict						
Number	268	32	30	5	8	343
Area	360	235	622	378	8976	10571
% Class	3.4	2.2	5.9	3.6	84.9	100
% Study area	0.8	0.5	1.4	0.8	19.5	23
Regrowth						
Number	810	66	58	12	7	953
Area	740	471	1353	828	2108	5500
% Class	13.4	8.6	24.6	15.0	38.3	100
% Study area	1.6	1.0	2.9	1.8	4.6	11.9
Open forest						
Number	676	73	55	6	8	818
Area	908	496	1122	426	3148	6100
% Class	14.9	8.1	18.4	7.0	51.6	100
% Study area	2.0	1.1	2.4	0.9	6.8	13.2

The 40 focal dry forest fragments (Fig. 1) ranged in size from 6×10^{-3} ha to 1372 ha in 1993 (Table 3). Twenty-three of these fragments (59%) maintained some amount of forest cover between 1936 and 1993 (Table 3). Eighty-nine percent of the total area occupied by the fragments had been continuously forested since 1936, (although some stems were probably harvested for fence posts and charcoal production). Nineteen fragments were classified as relict (75–100% continuously forested), three were classified as mixed (25–75% continuously forested) and 16 fragments were classified as regrowth (0–25% continuously forested). Historical data were not available for one fragment, and difficult to interpret unambiguously for another; in the 1936 aerial photograph the latter site was occupied by short scrub which could either reflect resprouts in a recently cut site (which would make it a relict fragment) or shrub encroachment on pasture or farmland (which would result in the site being classified as regrowth). Species richness increased significantly with fragment areas (power function, $R^2 = 0.715$). *L. leucocephala* was the most widespread and the most abundant species, accounting for 12% of all recorded individuals.

Twenty-three species were classified as regrowth specialists, 56 as relict specialists, and 61 as generalists; 172 species were too rare to assign to any category. Five of the regrowth specialists (21.7%) were introduced species, while only three (*Croton betulinus* Vahl, *Serjania polyphylla* (L.) Radlk. and *Ziziphus reticulata* (Vahl) DC.; 13.0%) were restricted to the West Indies and none were en-

Table 2
Selected landscape metrics for the western portion of the dry forest life zone, southwestern Puerto Rico. Fragments with more than 50% of the ground visible were classified as open forest, while those with less ground visible were classified as closed forest (FAO, 1993). Forest fragments which supported open or closed forest cover in both 1936 and 1963 were classified as relict, while those which supported non-forest in one or both time intervals were classified as regrowth.

Landscape metrics[a]	Closed forest (relict)	Closed forest (regrowth)	Open forest
Area and edge metrics			
Largest patch index (%)	6.6	1.4	2.1
Fragment area (ha)			
Mean	26.0	4.2	7.2
Standard deviation	222.8	49.0	26.7
Coefficient of variation	855.7	675.9	615.8
Area-weighted mean	1932.8	338.2	168.7
Median	0.9	1.2	0.3
Edge density (m/ha)	17.8	11.9	17.5
Shape metrics			
Perimeter-area fractal dimension	1.27	1.30	1.35
Patch shape index			
Mean	1.8	1.7	1.8
Standard deviation	0.9	0.8	0.9
Coefficient of variation	49.5	43.8	49.8
Area-weighted mean	6.1	4.3	4.9
Median	1.5	1.5	1.6
Related circumscribing circle			
Mean	0.6	0.6	0.7
Standard deviation	0.23	0.29	0.17
Coefficient of variation	37.3	48.3	26.2
Area-weighted mean	0.62	0.76	0.73
Median	0.69	0.70	0.68
Contiguity index			
Mean	0.67	0.52	0.77
Standard deviation	0.29	0.32	0.17
Coefficient of variation	44.5	62.4	22.0
Area-weighted mean	0.97	0.92	0.93
Median	0.80	0.62	0.81
Aggregation metrics			
Proximity index			
Mean	2238.3	348.1	296.4
Standard deviation	9326.1	1534.3	1628.9
Coefficient of variation	416.7	440.8	549.4
Area-weighted mean	481.4	1727.7	1084.4
Median	43.2	14.7	14.7
Euclidean nearest-neighbor distance (m)			
Mean	72.0	67.9	92.9
Standard deviation	81.2	97.5	131.7
Coefficient of variation	112.9	143.5	141.8
Area-weighted mean	28.9	51.8	59.6
Median	43.9	37.9	52.5
Clumpiness index	0.97	0.92	0.93
Percentage of like adjacencies (%)	97.4	92.7	94.0
Patch cohesion index (%)	99.6	98.4	98.8
Splitting index	103.6	2278.0	1025.7
Aggregation index (%)	97.5	92.9	94.1
Normalized landscape shape index	0.03	0.07	0.06

[a] For further details on these indices and their calculation, see McGarigal et al. (2012).

Table 3
Fragment area, the proportion continuously wooded since 1936 and the number of reference species present in studied dry forest fragments in southwestern Puerto Rico. ‘Continuously wooded’ refers to the portion of the fragments that supported tree cover through the 1936–1993 chronosequence of aerial photographs.

Area (ha)	Continuously wooded (%)	Number of reference species
Relict fragments		
1372.0	83	75
125.0	78	64
101.0	82	74
64.0	76	49
33.0	97	76
7.0	100	46
6.3	100	43
6.0	100	53
5.9	93	32
3.7	100	55
3.3	100	43
2.6	100	42
2.0	100	36
1.5	90	53
1.2	100	57
0.8	100	46
0.4	100	36
0.11	100	44
0.04	100	42
Mixed		
770.0	74	75
5.1	57	48
2.4	59	40
Regrowth		
45.0	19	–
1.5	0	34
1.5	0	22
1.0	0	21
1.0	0	6
1.0	0	35
0.2	0	21
0.2	0	40
0.1	0	26
0.09	0	1
0.07	0	30
0.07	0	27
0.02	0	24
0.01	0	13
0.01	0	18
0.006	0	15
Unknown		
3.0	–	43
1.2	–	51

demic to the Puerto Rican Bank. Of the 61 generalists, three were introduced (4.9%), 11 were restricted to the West Indies (18.0%) and five were endemic to the Puerto Rican Bank (8.2%; including two species endemic to the island of Puerto Rico – *Ipomoea steudelii* Millsp. and *Machaonia portoricensis* Baill.). Of the 56 relict specialists, one was non-native (1.8%; *Kalanchoe pinnatum* (Lam.) Pers., 15 were restricted to the West Indies (26.8%) and six were endemic to the Puerto Rican Bank (10.7%) including four Puerto Rican endemics (*Mosiera* [=*Eugenia*] *xerophytica* (Britton) Salywon, *Psychilis krugii* (Bello) Sauleda, *Thouinia striata* Radlk. var. *portoricensis* (Radlk.) Votava & Alain, and *Zamia portoricensis* Urb.).

The reference list compiled in Guánica Forest consisted of 90 species (Table 4): 34 relict specialists, 31 generalists, 7 regrowth specialists, and 18 that were too rare to assign to any category. Thirteen species were present in at least 30 fragments, 34 in at least 20 fragments, and 69 in at least 10 fragments. Eighty-eight of the species were present in at least one fragment. On average, each reference species was present in 17.4 ± 1.0 fragments (mean ± 1 standard error). Individual fragments supported 1–86% of the reference species; relict fragments averaged 55 ± 3.6%, while regrowth fragments averaged 25 ± 3.2%. Fragments 1 ha or larger supported 1–51% of the reference species (Fig. 2). Relict fragments 1 ha or smaller supported 42 ± 4.5% of the reference species while regrowth fragments 1 ha or smaller averaged 24 ± 3.5%.

There was a significant relationship between the percentage of reference species in a fragment and the natural logarithm of the fragment area ($p = 3 \times 10^{-9}$; adjusted $R^2 = 0.606$). Based on this model, it is estimated that a 0.04 ha fragment would be required to support 25%, 3.4 ha would be required for 50% and 286 ha for

Table 4
Habitat affinities and mean abundance (and standard error, s.e.) in fragments of 'reference species' compiled in Guánica Forest; n = number of samples used to calculate the mean adundance.

Growth form	Species	Mean abundance (indiv./ha)	
		Relict (s.e, n = 218)	Regrowth (s.e., n = 88)
Relict fragment specialists			
T	*Amyris elemifera* L.	569 (142)	64 (46)
T	*Stenostomum acutatum* DC.[a]	114 (28)	0 (0)
T	*Bernardia dichotoma* (Willd.) Müll.Arg.	95 (27)	0 (0)
T	*Bourreria succulenta* Jacq.	363 (51)	218 (57)
T	*Bursera simaruba* (L.) Sarg.	220 (40)	64 (18)
T	*Cynophalla flexuosa* (L.) J.Presl[b]	171 (32)	86 (26)
T	*Coccoloba diversifolia* Jacq.	479 (188)	0 (0)
T	*Coccoloba microstachya* Willd.	147 (38)	0 (0)
T	*Comocladia dodonaea* (L.) Urb.	132 (32)	45 (15)
T	*Crossopetalum rhacoma* Crantz	472 (124)	14 (10)
S	*Croton discolor* Willd.	510 (103)	27 (20)
S	*Croton glabellus* L.[c]	594 (124)	73 (31)
T	*Erithalis fruticosa* L.	367 (140)	9 (9)
T	*Eugenia axillaris* (Sw.) Willd.	127 (46)	0 (0)
T	*Eugenia foetida* Pers.	183 (60)	18 (9)
T	*Eugenia ligustrina* (Sw.) Willd.	70 (24)	0 (0)
T	*Eugenia rhombea* (O.Berg) Krug & Urb.	224 (65)	5 (5)
T	*Exostema caribaeum* (Jacq.) Roem. & Schult.	411 (87)	191 (53)
T	*Forestiera segregata* (Jacq.) Krug & Urb.	24 (10)	0 (0)
T	*Guaiacum sanctum* L.	29 (8)	0 (0)
T	*Guettarda elliptica* Sw.	46 (12)	0 (0)
T	*Guettarda krugii* Urb.	125 (52)	0 (0)
T	*Gymnanthes lucida* Sw.	875 (221)	0 (0)
V	*Heteropterys purpurea* (L.) Kunth	426 (52)	218 (51)
T	*Krugiodendron ferreum* (Vahl) Urb.	455 (98)	41 (21)
T	*Mosiera xerophytica* (Britton) Salywon[d]	161 (88)	0 (0)
E	*Psychilis krugii* (Bello) Sauleda	50 (29)	5 (5)
T	*Reynosia uncinata* Urb.	35 (14)	9 (9)
T	*Schaefferia frutescens* Jacq.	51 (15)	5 (5)
T	*Thouinia striata* Radlk. var. *portoricensis* (Radlk.) Votava & Alain	411 (64)	95 (30)
E	*Tillandsia recurvata* (L.) L.	6172 (1073)	2664 (817)
V	*Vanilla* spp.	53 (28)	0 (0)
S	Verbenaceae sp.22	37 (14)	0 (0)
S	*Wedelia calycina* Rich.	7 (4)	0 (0)
Regrowth fragment specialists			
S	*Croton betulinus* Vahl	361 (108)	705 (256)
S	*Heliotropium angiospermum* Murray	1004 (219)	1895 (503)
S	*Siphonoglossa sessilis* (Jacq.) D.N.Gibson	3508 (539)	5050 (1017)
M	*Phoradendron* spp.	24 (20)	55 (50)
V	*Serjania polyphylla* (L.) Radlk.	358 (95)	605 (228)
S	*Solanum americanum* Mill.	4881 (1180)	10264 (2737)
T	*Ziziphus reticulata* (Vahl) DC.	68 (24)	168 (59)
Generalists			
S	*Argythamnia* spp.	868 (228)	650 (224)
S	*Ayenia insulicola* Cristóbal	380 (80)	605 (169)
T	*Bucida buceras* L.	110 (20)	68 (24)
S	*Celosia nitida* Vahl	275 (124)	209 (73)
V	*Chiococca alba* (L.) Hitch.	31 (13)	32 (20)
V	*Cissus trifoliata* (L.) L.	149 (23)	123 (35)
T	*Colubrina arborescens* (Mill.) Sarg.	42 (15)	14 (10)
T	*Colubrina elliptica* (Sw.) Brizicky	62 (25)	105 (58)
S	*Commelina erecta* L.	859 (121)	1327 (260)
V	*Amphilophium lactiflorum* (Vahl) L.G.Lohman[e]	868 (103)	995 (172)
T	*Erythroxylum areolatum* L.	83 (28)	82 (49)
S	*Hibiscus phoeniceus* Jacq.	1517 (288)	1591 (593)
V	*Ipomoea steudelii* Millsp.	88 (24)	27 (19)
V	*Jacquemontia cumanensis* (Kunth) Kuntze	84 (19)	159 (43)
S	*Lantana involucrata* L.	277 (59)	368 (124)
C	*Leptocereus quadricostatus* Bello (Britton & Rose)	119 (42)	136 (86)
T	*Leucaena leucocephala* (Lam.) De Wit	9077 (1394)	12341 (2214)
V	*Dolichandra unguis-cati* (L.) L.G.Lohman[f]	1444 (126)	1859 (201)
S	*Melochia tomentosa* L.	40 (15)	45 (25)
V	*Passiflora suberosa* L.	61 (16)	27 (23)
T	*Pictetia aculeata* (Vahl) Urb.	127 (30)	155 (62)
C	*Pilosocereus royenii* (L.) Byles & Rowley	358 (54)	586 (118)
T	*Pisonia albida* (Heimerl) Britton ex Standl.	631 (238)	873 (452)
T	*Pithecellobium unguis-cati* (L.) Benth.	585 (85)	341 (74)
T	*Quadrella* spp.[g]	259 (56)	332 (122)
T	*Randia aculeata* L.	178 (34)	305 (76)
T	*Samyda dodecandra* Jacq.	51 (21)	41 (32)

Table 4 (*continued*)

Growth form	Species	Mean abundance (indiv./ha)	
		Relict (s.e, $n = 218$)	Regrowth (s.e., $n = 88$)
S	*Scleria lithosperma* (L.) Sw.	119 (41)	55 (55)
V	*Stigmaphyllon emarginatum* (Cav.) A.Juss.	701 (76)	768 (112)
V	*Myriopus microphyllus* (Bertero ex Spreng.) Feuillet[h]	147 (33)	77 (26)
V	Vine sp.12	29 (11)	36 (23)
Not classified (too rare)			
T	*Canella winterana* (L.) Gaertn.	4 (3)	5 (5)
T	*Coccoloba krugii* Lindau	9 (6)	0 (0)
T	*Cordia rickseckeri* Millsp.	24 (16)	0 (0)
S	*Crotalaria lotifolia* L.	13 (10)	0 (0)
T	*Elaeodendron xylocarpum* (Vent.) DC.	4 (3)	5 (5)
T	*Erythroxylum rotundifolium* Lunan	9 (5)	0 (0)
T	*Eugenia* sp.	–	–
T	*Hypelate trifoliate* Sw.	2 (2)	0 (0)
T	*Jacquinia berteroi* Spreng.	4 (3)	0 (0)
S	*Krameria ixine* L.	0 (0)	0 (0)
C	*Melocactus intortus* (Mill.) Urb.	2 (2)	0 (0)
C	*Opuntia* sp.	–	–
T	*Plumeria alba* L.	18 (8)	0 (0)
T	*Reynosia vivesiana* Trejo[i]	2 (2)	0 (0)
T	*Sideroxylon obovatum* Lam.	13 (7)	5 (5)
T	T 012	4 (4)	0 (0)
T	*Tabebuia heterophylla* (DC.) Britton	15 (6)	5 (5)
S	*Turnera diffusa* Willd. ex Schult.	6 (4)	5 (5)

Growth form: T = tree or tall shrub frequently exceeding a diameter of 1 cm at breast height, excluding cacti; S = small shrub or suffrutescent herb; C = cactus; V = vine or liana; E = epiphyte; M = mistletoe.

[a] *Antirhea acutata* in Liogier (1985–1997).

[b] *Capparis flexuosa* in Liogier (1985–1997).

[c] Monsegur Rivera (2009) observed that what is usually called *Croton humilis* in the Puerto Rican literature is actually *Croton lucidus*. Axelrod (2011) noted that *C. lucidus* is actually a Jamaican endemic, and outside of Jamaica the species referred to *C. lucidus* was actually *C. glabellus* L.

[d] *Eugenia xerophytica* in Liogier (1985–1997).

[e] *Distictis lactiflora* in Liogier (1985–1997).

[f] *Macfadyena unguis-cati* in Liogier (1985–1997).

[g] *Capparis cynophallophora* and *Capparis indica* are now placed in the genus *Quadrella*.

[h] Axelrod considered *Tournefortia microphylla* in synonymy with *T. volubilis*. Christian Feuillet in Acevedo-Rodríguez and Strong (2012) kept the two species distinct, and transferred them both to the genus *Myriopus*.

[i] *Reynosia guama* in Liogier (1985–1997).

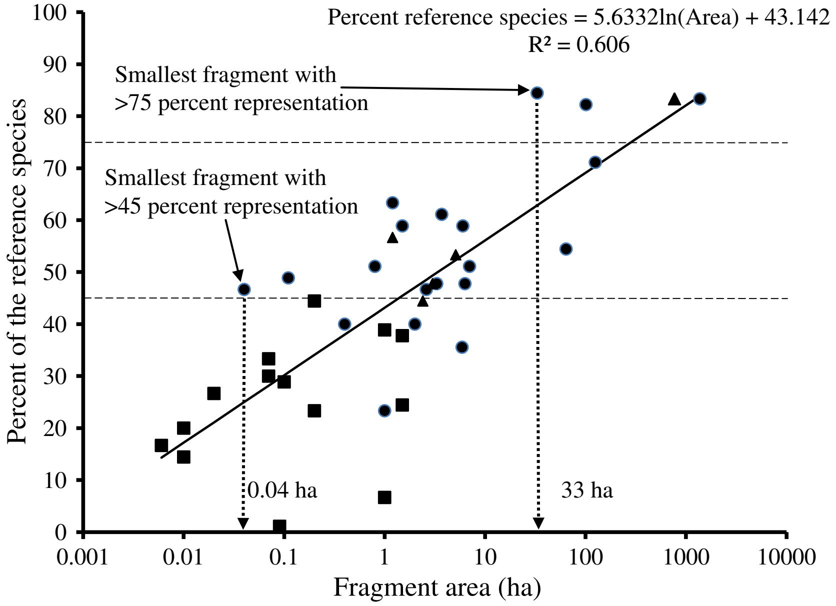

Fig. 2. The relationship between fragment area and 'representation', the proportion of reference species from Guánica Forest that were present in each fragment. Relict forest fragments are represented by circles and regrowth with squares; other categories of fragments (mixed and unclassified) are represented with triangles. Dashed horizontal lines represent 45% and 75% of the reference species. Reference species were present even in very small fragments.

75% of the reference species. Four of the six fragments 33 ha or larger supported more than 75% of the reference species. All fragments 7 ha or larger supported more than 50% of them. The smallest of these, Site 7, covered 33 ha. A total of 14 sites supported more than 50% of the reference species; the smallest of these was Site 28 (0.8 ha). Site 36, a 0.04-ha fragment, supported

42 reference species (47%) including 18 of 34 Relict specialists, two of seven Regrowth specialists, 19 of 31 generalists and three of 18 species too rare to classify.

4. Discussion

Puerto Rico is the smallest and most densely populated of the Greater Antilles, with over 400 people per km^2 (López et al., 2001). The study region supported well-developed agricultural societies in pre-Columbian times (Torres, 2005), but the indigenous population was decimated in the 16th century (Anderson-Córdova, 2005). Population of the coastal zone peaked during the 20th century with the development of the sugar industry following the American conquest of the island in 1898. Between 1899 and 1910, while the population of Puerto Rico grew by 17.3%, that of Guánica Municipality, which lies in the study area, grew by 121.4% (Dietz, 1986). Forest resources were largely depleted during the Spanish colonial period (Wadsworth, 1950), but deforestation probably peaked early in the 20th century, with most suitable land used to cultivate sugar cane or to supply fuel wood for sugar refineries or for domestic use (Murphy, 1916).

Forest cover, which had been largely eliminated by the 1940s (Lugo et al., 1996), stood at 48.2% in the western part of the dry forest life zone in 1993. During the second half of the 20th century, the Puerto Rican economy underwent a structural transformation, resulting in an unprecedented level of forest recovery (Rudel et al., 2000). Between 1949 and 1997, the acreage devoted to sugar cane production declined by 95% (Carro-Figueroa, 2002), while employment in agriculture declined from 35% of the labor force in 1940 to 3.7% in 1990 (Rivera-Batiz and Santiago, 1996). Net emigration to the US mainland increased from 73,000 people in the first four decades of the 20th century to 1,002,000 people between 1940 and 1990. Over that same period (1940–1990) the population of the island shifted from being two thirds rural to 72% urban 1990 (Rivera-Batiz and Santiago, 1996). These forests recovered on substrates which were degraded relative to undisturbed stands in these areas (Landres et al., 1999) and this resulted in novel forested ecosystems (Lugo, 2004; Hobbs et al., 2006; Seastedt et al., 2008).

The ability of dry forests to return after the removal of the stressor which has kept them off the landscape (in this case, agriculture) is necessary for their persistence. The recovery of dry forests can be hindered by fires, free-roaming livestock and soil erosion which can inhibit the establishment of trees (Griscom and Ashton, 2011); in many parts of the insular Caribbean this has prevented the reestablishment of dry forests (Mitchell, 1999). Although fire poses a threat to the development of forests on abandoned pasture land (Santiago-García et al., 2008; Wolfe and Van Bloem, 2012), it has not prevented the reestablishment of extensive forest cover in southwestern Puerto Rico.

4.1. Forest cover and species richness in southwestern Puerto Rico

Closed forest cover was high in the eastern part of the study area; five large blocks of closed forest – four of them predominantly relict, one mostly regrowth – dominated the landscape (Fig. 1). This accounted for most of the forest cover in the entire dry forest life zone (Ramjohn, 2004) and strongly influenced all three categories of landscape metrics calculated. Regrowth closed forest was generally in close proximity to relict forest, often surrounding and connecting relict fragments. Open forest fragments were small and were frequently interspersed within larger blocks of closed forest. This observation was supported by the aggregation-related metrics which found that levels of connectivity and adjacency were higher for closed forest that open forest (Table 2). The pattern of forest cover was different in the western part of the study area. Overall forest cover was lower, with large patches of open forest and smaller, more heavily fragmented closed forest. Much of the closed forest – both relict and regrowth – was located in narrow valleys and ravines in the mountainous Sierra Bermeja (Fig. 1).

Overall, most forest fragments were small, but a small number of large fragments accounted for most of the forest cover, a pattern that is similar to other long-term fragmented landscapes. In Brazilian Atlantic Rainforest, Ranta et al. (1998) found that 48% of fragments were smaller than 10 ha and 7% were larger than 100 ha. In this study, 91% of forest fragments were smaller than 10 ha, but these only accounted for 14.5% of the total forest cover. At the other extreme, while 1.1% were larger than 100 ha, these fragments accounted for 64% of forest cover (Table 1).

Large patches of habitat are important for biodiversity conservation, and Guánica Forest, is a critical refuge for native biodiversity (Murphy et al., 1995). Small fragments, on the other hand, support fewer species (Table 3) and tend to be more strongly influenced by edge effects (Laurance et al., 2011). However, this does not mean that large forest patches are necessarily valuable habitat, nor does it mean that small fragments should be neglected. The forests that have established since the middle of the 20th century are primarily regrowth, and are dominated by generalists (notably *L. leucocephala*) and regrowth specialists. Although these patches of forest can be larger than small relict fragments, they may support far fewer reference species (see Fig. 2).

Many species present in Guánica Forest were found in forest fragments, including, in one case, 42 of the 90 reference species in a fragment as small as 0.04 ha. On average, more than half of the reference species were present in relict fragments, while regrowth fragments supported only 25% of them. This pattern held even in fragments smaller than 1 ha. The difference in species richness between more and less intensively used sites has been shown before (Molina Colón, 1998; Molina Colón and Lugo, 2006); this difference was also observed in forest fragments. Site 36, a 0.04-ha fragment, was able to support 47% of the reference species despite the fact that it was located in an active pasture and had been isolated since at least 1936. While the degree of aggregation among forest patches may facilitate the dispersal of native species into these forests, the presence of relict fragments within this matrix of regrowth can be an important source of colonists.

Fragmentation effects in mainland moist forests are more pronounced in small sites, where edge effects may extend through the entire forest patch and lead to extensive tree mortality (Laurance et al., 2011). Insular dry forest fragments are likely to be more resistant to edge-related mortality (Pither and Kellman, 2002; Terborgh et al., 2006), especially in hurricane-adapted Puerto Rican dry forests (Van Bloem et al., 2005). In the case of Site 36, not only did it support almost half the reference species (Fig. 2), the proportions of relict specialists and generalists are close to the overall proportion of reference species present. On the other hand, rare species were disproportionately absent, but that should be expected given the sampling effect – rare species are less likely to have been present when the fragment was initially isolated.

4.2. Biogeographic patterns

The proportion of introduced species was highest among the regrowth specialists, and lowest among the relict specialists. Similarly, the proportions of species endemic to the West Indies, the Puerto Rican Bank, and to Puerto Rico itself were all highest among the relict specialists. The generalists included *L. leucocephala*, the most abundant species on the landscape, disturbance-associated native species like *Pithecellobium unguis-cati* (L.) Benth. and *Pisonia albida* (Heimerl) Britton ex Standl., common vines like *Cissus trifoliata* (L.) L., *Dolichandra* [=*Macfadyena*] *unguis-cati* (L.) L.G. Lohman and the endemic *I. steudelii*, and native forest trees like *Bucida buceras* L. and *Erythroxylum areolatum* L. Regrowth specialists were mostly herbs, vines and small shrubs, together with a few fast-growing trees. Relict specialists include many of the trees which dominate undisturbed forest. Some of these, like *B. succulenta* and *Amyris elemifera* L., were present in both relict and regrowth fragments. Others like *Gymnanthes lucida* Sw., *Coccoloba diversifolia* Jacq. and *Eugenia ligustrina* (Sw.) Willd., were very rare in or absent from regrowth fragments.

5. Conclusions

Native species were able to survive in small forest fragments and at least some were able to establish successfully in regrowth forests. However, prolonged, landscape-level deforestation of southwestern Puerto Rico produced a set of ecological conditions that are novel for Puerto Rican dry forests. Native species do poorly in open, grass-invaded habitats. *L. leucocephala* seedlings, on the other hand, grow faster and have lower mortality rates (Wolfe and Van Bloem, 2012). Native seedlings showed better growth and lower mortality after fire under a nurse crop of *L. leucocephala* (Santiago-García et al., 2008). Thus, management of dry forests in southwestern Puerto Rico should be approached from a novel ecosystems paradigm (Seastedt et al., 2008) and should attempt to maximize the ecosystem services provided by *L. leucocephala* forests, while working to enhance the role of native species in these new forests.

L. leucocephala played a major role in the reforestation of abandoned agricultural land; extensive blocks of closed forest included substantial areas dominated by this species. It is likely that it will remain an important element of these forests, even as native species become more abundant. For example, Puerto Rican dry forests stands dominated by *L. leucocephala* show nitrogen dynamics which differ from stands dominated by native tree species (Erickson et al., 2002). This reflects differences in species functional types (native leguminous trees are rare in mature dry forest stands) and soil factors (erosion, soil compaction and altered soil biota), but for native species these comprise a set of conditions that are likely to be outsider of historical norms. Understanding these dynamics, and the ways in which they differ from mature dry forests, is important for effectively managing these forests in the future.

Native Antillean dry forests are short in stature with high stem densities (Murphy and Lugo, 1986a) and a high proportion of belowground biomass (Murphy and Lugo, 1986b). These factors combine to make them resilient to hurricanes and drought, and allow them to recover rapidly from cutting (Lugo et al., 2006). It is also likely that these factors explain the survival of native species in fragmented forests. Four of the six fragments larger than 33 ha supported more than 80% of the reference species (Table 3). Consequently, special attention should be given to relict fragments 25–50 ha or larger in size, as they are likely to support a large assemblage of native species.

The value of very small forest fragments (like Site 36, just 0.04 ha) is not simply their potential to serve as habitat for native species, but also as a source of propagules for native species in regrowth (Griscom and Ashton, 2011). While the absence of *G. lucida* from regrowth might reflect either dispersal limitation or unfavorable growing conditions in *L. leucocephala*-dominated forests, the relative rarity of other relict specialists like *A. elemifera* and *Eugenia foetida* Pers. probably reflects dispersal limitation, since Pérez-Martínez (2008) found both of these species to be among the most common in the sapling layer in certain *L. leucocephala*-dominated stands.

Although the return of forests to southwestern Puerto Rico can be seen as an emergent property driven by structural changes in the economy, it is also the product of individual decisions by landowners who allowed their land to reforest. In that sense, it is a vulnerable recovery that can be undone by other individual decisions. It is thus important to communicate to the public some idea of the ecosystem services provided by these forests – local issues like erosion control and aquifer recharge, or global ones like carbon sequestration. Since native tree species are often slower growing with denser wood and a large proportion of belowground biomass, they are likely to be more resilient than *L. leucocephala*, especially as a warming climate may make the region drier (Lin, 2003).

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