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## Forest recovery in the karst region of Puerto Rico

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### Abstract

Widespread deforestation has led to an increase in secondary forest in the tropics. During the late 1940s in Puerto Rico, forest covered only 6% of the island, but a shift from agriculture to industry has led to the increase of secondary forest. This study focuses on the regeneration of forest following the abandonment of pastures and coffee plantations located in the karst region of Puerto Rico. Alluvial terraces and sinkholes were the principal features used for pastures, shifting agriculture, and coffee plantations, whereas mogotes (limestone hills of conical shape) were burned periodically or cut for charcoal or wood production. Abandoned pasture sites had a greater woody species diversity in comparison with coffee sites. The density of woody stems was greater in the abandoned pasture sites and *Spathodea campanulata* was the dominant species. In coffee sites *Guarea guidonia* was the most abundant species. There was no difference in basal area between the two land uses. Canonical Correspondence Analysis applied separately to adults and seedlings clearly separated each community according to land use. Seedling composition in coffee sites indicates a resistance to change in terms of the dominant species while in the pasture sites the composition will change as the dominant species *S. campanulata* is replaced with more shade tolerant species. Patches of forest that remained on the steep sides of mogotes and the presence of bats appears to have enhanced forest recovery, but the land use history of these sites has affected the pattern of regeneration and will continue to affect forest dynamics for many years. The karst area is a critical environment for water resources and biodiversity and its conservation and restoration is essential. © 1998 Elsevier Science B.V. All rights reserved.

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### 1. Introduction

Deforestation in the tropics has converted forests to grasslands, reduced biodiversity, degraded soils, increased hydrologic instability, and affected regional and global water and carbon cycles (Lugo et al., 1981; Uhl, 1982). By 1980, 44% of neotropical forests were felled and converted to pastures (Garcia-Oliva et al., 1994). Typically these pastures

lose their productivity, are abandoned, and deforestation continues in adjacent forested lands (Uhl, 1982). This process can lead to irreversible loss of biodiversity, but economic incentives often promote deforestation (Uhl et al., 1988). Although there are frequent calls for restoration and sustainable use of these deforested areas, we still know little about the processes of secondary forest regeneration in tropical ecosystems (Uhl et al., 1988; Finegan, 1992; Brown and Lugo, 1994; Aide et al., 1995).

Agricultural activity in Puerto Rico (PR) led to extensive deforestation mostly because of the culti-

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vation of coffee and sugar cane and the creation of pastures to raise cattle (Dietz, 1986). At the peak of deforestation in the 1940s, only 6% of the island was covered in forest (Birdsey and Weaver, 1987). A shift to an industrial base economy resulted in the abandonment of agriculture lands (Thomlinson et al., 1996) and an increase in forest cover (Lugo et al., 1981; Birdsey and Weaver, 1987). Aide et al. (1995) studied the succession in abandoned pastures in two replicate chronosequences in eastern PR that ranged in age from 0 > 60 years. They did not observe a substantial increase in woody biomass until 15 years after abandonment and the pioneer species were different from those present after natural disturbances in the adjacent Luquillo Mountains. Zimmerman et al. (1995) studied forest regeneration in the Luquillo Experimental Forest in 60-year-old abandoned pasture and coffee plantations and compare them with forested stands. They found no effect of past land use on species diversity, basal area, or stem density, but land use had a strong effect on the species composition.

Studies of forest recovery in Puerto Rico have focused in areas of igneous bedrock geology (Aide et al., 1995; Aide et al., 1996; Zimmerman et al., 1995), but few studies have investigated forest recovery in areas of karst geology (Chinea, 1980). Karst geology covers 20% of Puerto Rico and occurs in all of the Greater Antilles, and parts of Central America (Kelly et al., 1988). The topographic features of the karst region are sink-holes, caves, cliffs, alluvial terraces (long and narrow valleys) and mogotes (limestone hills of conical shape) (Monroe, 1976; Kelly et al., 1988; Zanoni et al., 1990). Alluvial terraces and sinkholes were the principal features used for pastures, shifting agriculture, and coffee plantations. As in the rest of Puerto Rico, this region was densely populated with numerous small agricultural holdings during the early 1900s, but economic changes in the 1940s, resulted in a large proportion of the rural population migrating to the cities. The abandonment of these agricultural lands has allowed the secondary forest to recover and today most of the area is covered with forest. At present, this recovery is threatened by road construction, fires, and commercial and housing development that could permanently destroy this unique landscape.

In this study, we contrasted the pattern of recovery in areas of abandoned coffee and pastures in the karst region of Puerto Rico. The major objective of this research was to quantify patterns of vegetation composition, structure, and basal area accumulation in karst areas subjected to different past land uses. Specifically, we addressed the following questions:

1. How do the different types of land use affect forest regeneration in terms of basal area, density and species diversity?
2. How does the composition of seedling regeneration compare with the composition of adults in areas of abandoned pastures and coffee?

We predicted that species diversity and stem density would recover faster in pasture, and basal area would be greater in abandoned coffee plantations. Historically coffee was planted below shade trees (e.g. *Inga vera*). Recovery in an area with a close canopy should restrict the establishment and growth of shade intolerant species. On the other hand, pasture sites may be colonized by species with a wide range of light requirements.

## 2. Methods

### 2.1. Description of the study area

The study was conducted in the karst region of Puerto Rico in the municipalities of Ciales and Morovis (Fig. 1). The limestone karst region extends along the north coast of Puerto Rico from the town of Aguada to Loiza. The area is underlain by six limestone formations that range in age from Oligocene to Miocene (Monroe, 1976; Giusti, 1978). The study sites occur in Lares Limestone formation, which is the oldest limestone formation in Puerto Rico (Monroe, 1976; Giusti, 1978). The average annual rainfall in the town of Ciales was 2074 mm and ranged from 1563 to 2785 mm during the period of 1970 to 1994 (NOAA). The elevation of the sites ranged from 90 to 310 m (Appendix A).

The study site occurs in the subtropical moist forest life zone (Ewel and Whitmore, 1973). Vegetation composition varies depending on the topographic position and aspect (Chinea, 1980). The hill tops have a dry evergreen forest and the valleys and sinkholes have evergreen seasonal (Murphy, 1916;



Fig. 1. The location of study sites in the karst zone of the municipalities of Ciales and Morovis, Puerto Rico for coffee and pasture sites.

Marrero, 1950; China, 1980). Analysis of aerial photos from 1936 to 1971 show that all valleys were used for pastures, coffee, or crops, but houses were located on the slopes and dry valleys between mogote tops (Rivera, personal observation). Due to the poor soils on the tops of the hills, these areas were not used for agriculture, but the vegetation was cut for charcoal production (Murphy, 1916).

## 2.2. Site selection

This study focused on the alluvial terraces or valleys where the majority of agriculture took place. Sites were selected and time since of abandonment was determined by analyzing aerial photographs (1936, 1951, 1964, 1971, 1983, and 1994) and interviewing local land owners. Deforestation of this region was extensive and forested areas in the oldest

photographs (1936) were assumed to be shade trees in coffee plantations. Local landowners confirmed that all forested areas in the valleys were shade coffee plantations. Some of the areas classified as abandoned pastures were previously used for agriculture (e.g., beans, squash, and tobacco), but once abandoned these lands were usually kept in pasture for a few years before being completely abandoned. The 16 abandoned coffee plantations used in this study were abandoned approximately 35 years ago and the 11 pasture sites ranged in age from 15 to 35 years (Fig. 1, Appendix A).

## 2.3. Sampling and data analysis

A minimum of two and a maximum of five transects ( $2 \times 50$  m) were used in each site. We identified and measured at breast height every woody

plant  $\geq 1$  cm in stem diameter. Seedling composition was sampled in three random  $1 \times 1$  m quadrants randomly located in each transect. All plants greater than 20 cm in height and less than 1.0 cm in diameter were identified to species. The species area curve for seedlings was determined by taking the average curve of 500 randomly ordered selections of the total number of species in six  $1\text{-m}^2$  quadrats within each site. The species area curve for trees  $\geq 1$  cm diameter at breast height (dbh) was determined by taking the average curve of 500 randomly ordered selections of the total number of species in two  $100\text{-m}^2$  transects within each site. Importance values (I.V.) of each species in each site were used along with three environmental variables (e.g., elevation, age, and valley width) in a Canonical Correspondence Analysis (CCA) (McCune and Mefford, 1995). In this analysis, *Coffea arabica* was left out to reduce the direct effect of land use. I.V. were estimated as  $[(\text{relative density} + \text{relative basal area})/2] \times 100$ . Seedling relative densities in each site, excluding *C. arabica*, were used along with the three environmental variables in a second CCA.

### 3. Results

#### 3.1. Forest characteristics

##### 3.1.1. Species diversity in trees $\geq 1.0$ cm dbh

A total of 87 species greater than 1 cm dbh were observed in the vegetation transects (total area sampled =  $7100 \text{ m}^2$ ) and 17 species (19.5%) were exotic. A total of 21 species (24%) occurred exclusively in coffee sites, 33 species (38%) were unique to pastures, and 33 species occurred in both land uses. There was no difference between land uses in the occurrence of exotic species. The total number of species was greater in the pasture sites in comparison with coffee sites (Fig. 2), but the number of species in each site did not differ between land uses (Fig. 3, Mann-Whitney Test  $P = 0.3001$ ). On average each site had approximately 12 species per  $200 \text{ m}^2$  (Fig. 3). The species area curve for coffee sites began to plateau sooner than the species area curve for pastures and a total of 53 species occurred in a sample

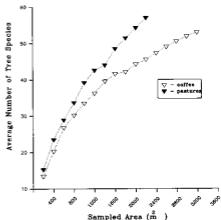


Fig. 2. The average species area curve for abandoned coffee and pastures sites (trees  $\geq 1.0$  cm dbh).

area of  $3200 \text{ m}^2$  (Fig. 2). Even though a smaller area was sampled ( $2200 \text{ m}^2$ ) in pastures, a total of 57 species were identified. With this sampling scheme the species area curve did not plateau either in pastures nor in coffee, suggesting that the diversity was even greater.

##### 3.1.2. Species diversity in seedlings and saplings $< 1.0$ cm dbh (greater than 20.0 cm in height)

A total of 43 seedlings species were observed in abandoned coffee and pastures including 4 exotic species (9.3%) in a total sampled area of  $213 \text{ m}^2$ . There were 12 species that occurred exclusively in coffee sites, 16 species were unique to pastures, and 15 occurred in both land uses. The species area curve for coffee seedlings began to plateau and a total of 26 species were identified in a sample area of  $96 \text{ m}^2$  (Fig. 4). Even though a smaller area was sampled in pastures ( $66 \text{ m}^2$ ), a total of 28 species were identified (Fig. 4). With this sampling scheme, the species area curve did not plateau in pastures suggesting that the seedling diversity was even greater in these sites.

##### 3.1.3. Density

Tree density was significantly higher in abandoned pastures (median =  $6001 \text{ stems ha}^{-1}$ ), in

comparison with abandoned coffee plantations (median = 3000 stems  $\text{ha}^{-1}$ ), (Mann–Whitney  $U$  Test;  $P = 0.0006$ , Fig. 3). In coffee sites, density ranged from 1000 to 6333 stems  $\text{ha}^{-1}$  and, in pastures, the density ranged from 2950 to 9550 stems  $\text{ha}^{-1}$ . The coffee with the highest density (#5: 6333 stems  $\text{ha}^{-1}$ ) occurred in the second widest valley (Appendix A). The coffee sites with the lowest densities, <2000 stems  $\text{ha}^{-1}$ , (sites #10, 11, 12) occurred in the narrowest valleys (Appendix A). In the pasture sites, there was a larger range in densities possibly due to a greater range in site age and valley widths (coffee =  $28.4 \pm 7.1$  m; pastures =  $39.4 \pm 13.4$  m;  $t = 2.79$ ,  $P = 0.01$ ). There was a trend toward higher densities in wider valleys, but this was not significant in either land use (Pearson Correla-

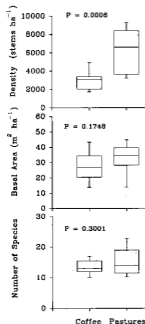


Fig. 3. The estimates of density (stems  $\text{ha}^{-1}$ ), basal area ( $\text{m}^2 \text{ha}^{-1}$ ) and number of species for coffee and pastures sites.  $P$ -values are for a Mann–Whitney Test. Estimates of density and basal area were based on all transects in each site. The number of species was based on only two transects ( $200 \text{ m}^2$ ) per site.

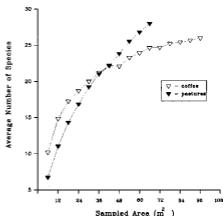


Fig. 4. The average species area curve for woody seedlings in abandoned coffee and pastures sites.

tion, valley width vs. density: pastures  $R = 0.2189$ ;  $P = 0.5178$ , and coffee,  $R = 0.4123$ ;  $P = 0.1125$ ).

*G. guidonea* had the highest mean density and accounted for 23.7% of stems in the coffee sites (Table 1). In the pasture sites, *S. campanulata* had the highest mean density and accounted for 33.2% of the stems (Table 1). *S. campanulata* was uncommon in coffee plantations, but *G. guidonea* was a second dominant species in pasture sites. In the pasture sites there was no relationship between age since abandonment and density (Pearson Correlation:  $R = 0.0275$ ;  $P = 0.9360$ ).

### 3.1.4. Basal area

There was no significant difference in basal area between the two land uses (median for pastures =  $34.6 \text{ m}^2 \text{ha}^{-1}$ , median for coffee =  $26.9 \text{ m}^2 \text{ha}^{-1}$ , Mann–Whitney  $U$ -Test:  $P = 0.1748$ ; Fig. 3). In coffee sites, basal area ranged from  $9.7$  to  $50.9 \text{ m}^2 \text{ha}^{-1}$  and in pastures from  $12.5$  to  $47.5 \text{ m}^2 \text{ha}^{-1}$  (Fig. 3, Appendix A). The two woody species that showed the greatest contribution to basal area estimates were *G. guidonea* (mean basal area =  $12.4 \text{ m}^2 \text{ha}^{-1}$ ) in coffee plantations and *S. campanulata* (mean basal area =  $18.9 \text{ m}^2 \text{ha}^{-1}$ ) in pastures (Table 1). There was no significant relationship between valley width and basal area in either land use (Pearson Correla-

Table 1  
The density (stems ha<sup>-1</sup>), basal area (m<sup>2</sup> ha<sup>-1</sup>), and mean importance value of the top 10 dominant species ( $\geq 1.0$  cm dbh) in abandoned coffee and pastures

Species	Family	Range of density	Mean density	Range of basal area	Mean basal area	Mean importance values
<i>Coffea</i>						
<i>C. gaidonia</i>	Meliaceae	333-1250	707	0.86-31.7	12.4	36.0
<i>C. arabica</i>	Rubiaceae	100-1400	510	0.01-0.24	0.1	8.4
<i>Dendropanax arboreus</i>	Araliaceae	0-900	272	0-2.34	0.33	5.2
<i>Montezuma speciosissima</i>	Malvaceae	0-167	48	0-7.95	1.97	4.6
<i>Trichilia pallida</i>	Meliaceae	0-9.50	213	0-3.43	0.46	4.5
<i>Ocotea leucocylon</i>	Lauraceae	0-700	112	0-8.82	1.1	3.9
<i>Cordia alliodora</i>	Boraginaceae	0-1000	22	0-5.53	0.98	3.9
<i>Cecropia acberrimana</i>	Moraceae	0-100	15	0-21.5	1.9	3.1
<i>Cupania americana</i>	Sapotaceae	0-400	61	0-4.3	0.67	2.4
<i>Aneliro inermis</i>	Leguminosae	0-250	60	0-7.9	1.18	2.3
<i>Pastures</i>						
<i>S. campalata</i>	Bigoniaceae	50-8233	2136	0.05-38.6	18.9	39.9
<i>G. gaidonia</i>	Meliaceae	0-2050	865	0-12.4	3.2	14.2
<i>Cassaria guianensis</i>	Flacourtiaceae	0-2800	744	0-2.2	0.47	6.0
<i>Thouinia striata</i>	Sapotaceae	0-2900	418	0-4.63	0.78	5.4
<i>A. inermis</i>	Meliaceae	50-800	259	0.01-5.5	1.1	5.0
<i>Spondias mombin</i>	Anacardiaceae	0-100	20	0-23.3	2.6	3.9
<i>Cas. ylliocaris</i>	Flacourtiaceae	0-1400	401	0-0.67	0.3	3.3
<i>Cap. americana</i>	Cap. americana	0-600	135	0-3.2	0.47	3.1
<i>Parathesis crenulata</i>	Myrsinaceae	0-960	190	0-0.03	0.04	2.5
<i>O. leucocylon</i>	Lauraceae	0-467	197	0-1.84	0.4	2.5

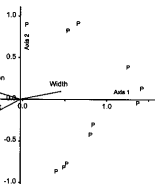


Fig. 5. The ordination (CCA) diagram showing the relationship between 16 coffee sites (C) and 11 pastures (P) with site age, elevation, and valley width. The ordination was based on the importance values of all species in each site.

tion: coffee— $R = 0.3477$ ,  $P = 0.1869$ ; pastures— $R = -0.1571$ ,  $P = 0.6446$ ), nor was there a significant relationship between age since abandonment and basal area in the pasture sites,  $R = 0.3704$ ;  $P = 0.2621$ .

### 3.2. Species composition

#### 3.2.1. Importance values

*G. guidonea* was the dominant species in the abandoned coffee plantations with a mean impor-

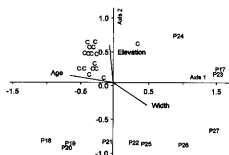


Fig. 6. The ordination (CCA) diagram showing the relationship between 16 coffee sites (C) and 11 pastures (P) with site age, elevation, and valley width. The ordination was based on the relative density of seedling and saplings of all species in each site. Numbers identify each pasture site.

tance value of 36.0% (Table 1). It exceeded the importance value of the next species by a factor of 4 (*C. arabica*; I.V. = 8.4%). With the exception of *C. arabica*, the other common species in the coffee sites were also present in the pasture sites. Although *I. vera* was an important shade species in these coffee sites its important value was only 2.2, and many large dead *I. vera* trees (dbh > 50 cm) occurred in these sites.

In the pasture site, *S. campanulata* and *G. guidonea* were the dominant species (Table 1). *Cas. guianensis* and *Spo. mombin* were the only dominant

Table 2

The mean relative density of tree seedling species for the dominant species observed in abandoned coffee plantations and pastures

Species	Family	Coffee		Pastures	
		# of individuals	Relative density (%)	# of individuals	Relative density (%)
<i>I. vera</i>	Leguminosae	196	20.4	0	0
<i>C. arabica</i>	Rubiaceae	168	17.3	0	0
<i>A. inermis</i>	Leguminosae	75	9.0	100	22.1
<i>Piper glabrescens</i>	Piperaceae	61	7.7	1	0.01
<i>O. leucoxylon</i>	Lauraceae	59	7.3	14	5.9
<i>G. guidonia</i>	Meliaceae	65	6.6	30	9.4
<i>Calophyllum brasiliense</i>	Guttiferae	47	3.9	8	2.4
<i>The. striata</i>	Sapindaceae	23	3.0	14	4.8
<i>Syzygium malaccense</i>	Myrtaceae	41	2.4	104	7.0
<i>Eugenia</i> spp.	Myrtaceae	0	0.0	21	6.4
<i>P. crenulata</i>	Myrsinaceae	21	2.4	30	6.0
<i>Pau. spinosa</i>	Malvaceae	0	0.0	82	15.1

Total number of species for coffee = 27; total number of species for pastures = 31; total number of individuals for coffee = 905; total number of individual for pastures = 455; sampled area in coffee, 114 m<sup>2</sup>; sampled area in pastures, 99 m<sup>2</sup>.

Table 3

The dominant seedlings species in abandoned pastures sites (total sampled area = 99 m<sup>2</sup>)

Sites	First dominant species [Relative density (%)]	Second dominant species [Relative density (%)]	# of species
17	<i>Pav. spinosa</i> (81.3)	<i>S. campanulata</i> (12.5)	3
18	<i>Eugenia</i> spp. (36.4)	<i>C. brasiliense</i> (21.2)	10
19	<i>Par. crenulata</i> (45.5)	<i>A. inermis</i> (32.0)	7
20	<i>O. leucoxylon</i> (33.0)	<i>Eugenia monticola</i> (22.2)	6
21	<i>A. inermis</i> (50.0)	<i>G. guidonia</i> (17.6)	8
22	<i>Tho. striata</i> (22.2)	<i>A. inermis</i> (16.7)	11
23	<i>Pav. spinosa</i> (74.0)	<i>A. inermis</i> (6.7)	7
24	<i>A. inermis</i> (26.3)	<i>G. guidonia</i> (10.5)	10
25	<i>A. inermis</i> (77.0)	<i>O. leucoxylon</i> (6.5)	6
26	<i>Syz. malaccense</i> (77.0)	<i>A. inermis</i> (19.3)	6
27	<i>G. guidonia</i> (45.5)	<i>Cas. guianensis</i> (18.2)	22

species in the pasture sites that did not occur in any coffee sites.

### 3.2.2. Ordination analysis

The CCA, using trees  $\geq 1.0$  cm dbh, produced a sharp separation between coffee and pasture sites (Fig. 5). The coffee sites tended to occur at higher elevations and pastures were in wider valleys, the environmental variables with the highest correlations with axis one and two were elevation ( $r = -0.90$ ) and age ( $r = -0.64$ ), respectively. Axis one grouped the majority of the coffee sites at the low end and pasture sites at the high end. Axis two separated the pasture sites due to the larger range in age (time since abandonment). The dominant species that influenced the separation between the two land uses were the high abundance of *D. arboreus*, *M. speciosissima*, *T. palida*, *Cec. schreberiana*, and *Cor. allodora* in the coffee sites and the high abundance of *S. campanulata*, *Cas. guianensis*, *Cas. sylestris*, *Tho. striata*, *Spo. mombin*, and *P. crenulata* in the pasture sites (Table 1).

The CCA for seedling and saplings (< 1.0 cm dbh and greater than 20.0 cm in height) also produced a sharp separation between coffee and pasture sites (Fig. 6). The environmental variables with the highest correlations with axis one and two were age ( $r = -0.91$ ) and elevation ( $r = 0.99$ ), respectively. In this analysis, the coffee sites were tightly clumped suggesting that they have a similar species composition. The distribution of pasture sites was scattered,

and although *A. inermis* and *Pavonia spinosa* were the most common species (Table 2), they were the dominant species in only 5 of the 11 sites (Table 3).

## 4. Discussion

### 4.1. Forest structure

Densities were higher in abandoned pastures in comparison to coffee sites, but there was no difference in basal area between the two land uses. The major differences between these land uses were the vegetation structure at the time of abandonment, age since abandonment, valley width, and light environment. The coffee sites were all abandoned approximately 35 years ago. The pasture sites are younger, and were abandoned at different times (range 15–35 years ago). It appears that coffee sites have reached a stable phase in terms of density and basal area, while the pastures are still in the thinning (density) and increment (basal area) phases. Valley width was significantly higher in abandoned pastures when compared to abandoned coffee sites. The wider valleys receive more light and at the time of abandonment the light environment in the abandoned pastures would have been much greater. The coffee plantations were all planted under shade trees (e.g., *I. vera*) and the light levels in the understory were relatively low. The light environment in these plantations should have limited colonization to species that

are shade tolerant (e.g., *G. guidonea*, *C. arabica*, *O. leucoxyton*, and *A. inermis*, Tables 1 and 2). The high light environment in the abandoned pastures has permitted colonization by pioneer species and, with time, shade tolerant species. In addition, higher light availability has contributed to higher densities and growth rate. *S. campanulata*, with a diameter growth rate of up to 5 cm year<sup>-1</sup> (Francis, 1990) made the largest contribution to basal area in pastures. *G. guidonea*, was the dominant species in the abandoned coffee plantations and although it has a rapid growth rate for forest species (0.81 cm year<sup>-1</sup>, Weaver, 1988) its growth rate is much lower than *S. campanulata*.

In addition to the differences between land uses types, there were also differences among sites of similar use. Abandoned pastures varied in time since abandonment, but there were no significant effects of age on density or basal area. Although the sites were abandoned, periodic grazing by cattle could have affected the structure of these sites. For example, cattle were observed twice in 1 year in site 23 and this was one of the sites with the lowest density (Appendix A). Cattle have been reported to eat juveniles of *S. campanulata* (Francis, 1990) and, in this site, *S. campanulata* had its second lowest importance value (4.4%). In other sites (e.g., 20, 21, 22 and 25), evidence of coppicing suggests that cutting activities after abandonment have also affected the pattern of forest recovery. In the abandoned coffee plantations, there was little variation among sites in density and higher variation in basal area. A possible cause of variation in basal area is occasional selectively logging for charcoal and wood production.

#### 4.2. Species diversity and composition

Species diversity of trees greater than 1 cm dbh was high in abandoned pastures in comparison with abandoned coffee plantations even though fewer pasture sites were sampled. The higher diversity in the abandoned pasture sites may be due to the presence of both light demanding and shade tolerant species that co-occur at this stage of forest development (Table 1). Even though these areas have a closed canopy, the dominant species, *S. campanulata* is deciduous during the drier part of the year. Increased

light in the understory, may allow the establishment of a greater diversity of species. *G. guidonia*, the dominant species in the abandoned coffee plantations, is evergreen and produces a dense canopy that reduces light in the understory during the whole year and possibly reduces the establishment of some species. Saldariaga et al. (1988) suggested that the heterogenous crown structure of old growth forests was responsible for a greater number of establishment sites in comparison with the relatively uniform canopy of young secondary forests. In our study, the occurrence of pastures in wider valleys and the deciduousness of *S. campanulata* appear to combine to create more establishment sites in comparison with the low light understory in the abandoned coffee plantations.

The ordination analysis clearly separated the abandoned coffee plantations from the abandoned pasture sites. *S. campanulata* was the dominant species in the pasture sites and *G. guidonia* was the dominant species in the coffee sites and the second most dominant species in the pastures. The high importance values of *G. guidonia* may be due to its high abundance on the slopes that have facilitated its dispersal into the valleys. This tree produces large seed crops of medium size seeds that have an average weight of 0.23 g (range, 0.12–0.31 g) and the seeds are dispersed by birds or runoff during heavy rains. The frequent observation of *G. guidonia* in abandoned coffee plantations (Weaver and Birdsey, 1986; Zimmerman et al., 1995, present study) may be due to its ability to increase photosynthetic capacity in response to increase soil nitrogen (Fernández, 1997). *I. vera*, a nitrogen fixing legume (Rodríguez, 1990), has been used as a shade tree species in these plantations. Most plantations were in use for more than 30 years, and the presence of *I. vera* has likely increased soil nitrogen content. We suggest that *G. guidonea* dominates these sites because there were nearby seed sources and because it can respond to the high soil nitrogen content.

*S. campanulata* is an exotic species that dominated the pasture sites. Mean basal area of *S. campanulata* was approximately six times greater than the second most important species, *G. guidonia*. *S. campanulata* produces many wind-dispersed seeds that can be dispersed hundreds of meters. In the study area, this species was used as an ornamental

and live fence which has facilitated its dispersal into abandoned agricultural lands. *S. campanulata* has a fast growth rate, but because it is shade intolerant there were few juveniles in these secondary forest and it appears that *G. guidonia* will eventually dominate these forest.

The CCA analysis demonstrated that the species composition of seedlings was very similar in the coffee sites and highly variable in the pastures sites. The microhabitats in the abandoned coffee sites were probably more uniform in comparison with the pastures. The understorey in the coffee plantation had lower levels of light ( $n = 5$ ; 2.1% of PAR) in comparison to pastures ( $n = 8$ ; 17.7% of PAR), (Rivera unpublished data). The similarity in species composition among the coffee sites was due to the high seedling densities of *I. vera* and *C. arabica*, demonstrating the long term effect of past land use on regeneration. Seedlings of *A. inermis*, *Pip. glabrescens*, *O. leucoxyton*, *G. guidonia*, and *Cal. brasiliense* were also common in the coffee sites. With the exception of *Pip. glabrescens*, these species are all canopy trees that are also considered potential timber species (Weaver and Birdsey, 1986). These results show that even after 35 years of abandonment the past land use continues to influence the species composition. The presence of some native tree species implies that eventually the canopy will be replaced by a slightly more diverse group of species. The seedling composition in the pastures was more variable. Many factors (e.g., years since abandonment, occasional grazing, valley width, selective logging, variation in seed sources) could have contribute to this variation. *A. inermis* was the most common seedling species in the pastures and this species is dispersed by bats. The large seed of *A. inermis*, should facilitate the colonization of this species. In contrast to the coffee sites, seedling composition in the pastures is different from that of the adults. *S. campanulata* was the dominant canopy species, but it was not even in the top 10 seedling species due to its intolerance to shade. This suggests that *S. campanulata* will be replaced by *A. inermis* and *G. guidonia*. The seedling composition data suggests that successional pathways of the pasture sites could be site specific. Although many of the same species occur in both coffee and pasture sites, the pasture sites tend to be dominated by one or two species. If

these species are shade tolerant, this can have a long term effect on the future dynamics and species composition of the site.

#### 4.3. Comparison with other studies

Secondary forests in the karst region appear to recover faster in comparison with secondary forest in other geological/soil formations of Puerto Rico. In the karst region, the mean basal area in the abandoned pastures (age 15–35 years) was  $32.4 \text{ m}^2 \text{ ha}^{-1}$ , whereas the mean basal area in pastures of similar age (15–37 years) in eastern Puerto Rico was only  $19.4 \text{ m}^2 \text{ ha}^{-1}$  (Aide et al., 1995). In the karst region, the dominant pioneer species was *S. campanulata*, while in the pastures in eastern Puerto Rico, shrub species were the most important pioneer species. The early establishment of the fast growing tree, *S. campanulata*, is probably the major reason of high basal area in the karst pastures. In another study, Zimmerman et al. (1995), reported a similar mean basal area ( $30 \text{ m}^2 \text{ ha}^{-1}$ ) in pastures there were at least twice the age (60 years) of those in the karst region.

Abandoned coffee plantations in the karst region (subtropical moist forest) also have recovered faster in comparison with plantations in other areas of Puerto Rico. In this study, basal area in 35 years old abandoned plantations (median  $26.9 \text{ m}^2 \text{ ha}^{-1}$ ) was greater than the basal area in plantations > 30 years old ( $14 \text{ m}^2 \text{ ha}^{-1}$ ) studied by Weaver and Birdsey (1986) on volcanic soils in subtropical wet forest. Zimmerman et al. (1995) reported a higher basal area ( $45 \text{ m}^2 \text{ ha}^{-1}$ ) in plantations in the Luquillo Mountains in subtropical wet forest, but these sites were at least 25 years older than those of the present study. Although the differences in the rate of recovery in these abandoned coffee plantation could be due to different climates, we believe that the topography of the karst region may have also contributed to the rapid recovery.

#### 4.4. Topography

The unique topography of the karst region may be the most important factor contributing to the rapid recovery of secondary forest. Karst topography includes long narrow valleys surrounded by hills with steep slopes. This topography protects the valleys

from strong winds during hurricanes and tropical storms. In addition, the accumulation of soil and organic matter in the valley bottoms creates better conditions for plant growth. The long narrow valleys will be more protected from direct sun light (maintaining high humidity) and less soil erosion (maintaining high nutrient inputs from runoff of surrounding mogotes) in comparison with others non karst soils. In addition, the topography may reduce the environmental changes associated with deforestation. For example, there was virtually no use of bulldozer

in agricultural areas due to the lack of roads in these areas.

As in other regions of the Caribbean, areas of steep slope were rarely used for intense agriculture (Lugo et al., 1981). The abrupt topography of the mogotes restricted the majority of agriculture to the valleys and vegetation that survived on the steep slopes and top of mogotes were important seed sources. Agricultural land near riparian vegetation or forest reserves appear to recover faster (Thomlinson et al., 1996) and in the cases of the karst region most

## Appendix A

Forest characteristics for 16 abandoned coffee sites and 11 abandoned pastures sites, C = coffee, and P = pastures)

Site	Prior land use	Time of abandonment	Elevation (m)	Site width (m)	# of transects (100 m <sup>2</sup> )	# of species in 200 m <sup>2</sup>	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Density (stems ha <sup>-1</sup> )	Sampling Date 1995
1	C	≈ 1960	260	32	2	13	19.9	3400	May
2	C	≈ 1960	260	31	3	10	34.1	2000	May
3	C	≈ 1960	260	25	2	12	32.8	3450	May
4	C	≈ 1960	250	30	2	14	9.7	3300	May
5	C	≈ 1960	235	40	3	19	27.8	6333	May
6	C	≈ 1960	260	23	2	16	22.7	5150	May
7	C	≈ 1960	290	24	2	12	13.4	2550	Jun.
8	C	≈ 1960	290	30	3	17	26.1	3066	Jun.
9	C	≈ 1960	290	25	2	17	18.0	3400	Jun.
10	C	≈ 1960	300	23	2	11	22.5	1800	Jun.
11	C	≈ 1960	300	25	2	8	34.8	1000	Jun.
12	C	≈ 1960	310	21	2	12	34.8	1750	Jun.
13	C	≈ 1960	310	48	4	15	44.3	3075	Jul.
14	C	≈ 1960	270	30	3	13	50.9	3266	Jul.
15	C	≈ 1960	290	23	2	13	27.6	2100	Jul.
16	C	≈ 1960	310	25	2	15	21.1	2050	Jul.
17	P	≈ 1980	230	42	3	11	28.2	6633	Aug.
18	P	≈ 1960	120	22	2	24	34.6	4050	Aug.
19	P	≈ 1960	110	36	4	14	43.1	3400	Aug.
20	P	≈ 1960	110	35	2	19	47.5	9550	Aug.
21	P	≈ 1967	110	36	3	13	36.4	8900	Aug.
22	P	≈ 1967	110	50	3	22	12.5	6900	Aug.
23	P	≈ 1977	230	50	5	9	15.1	3500	Mar.
24	P	≈ 1977	300	19	2	14	28.3	2950	Dec.
25	P	≈ 1977	90	30	3	11	32.0	9133	Nov.
26	P	≈ 1977	90	50	4	17	39.3	7000	Nov.
27	P	≈ 1977	120	63	2	19	39.7	6200	Dec.

valleys had close seed sources. In addition to the seed source, dispersers also can play an important role in forest recovery. At least five species of bats (*Erophylla sezekorni*, *Brachyphylla cavernarum*, *Monophyllus redmani*, *Mormoops blainvillii*, and *Pteronotus parnellii*) have been reported from this area. Two of these bats species (*Ero. sezekorni*, *B. cavernarum*) are frugivores and seeds of *Piper* spp., *A. inermis*, *Cal. brasiliense*, *Solanum* spp., and *Cec. schreberiana* have been observed in two caves. The presence of many caves and bats is probably another important factor that has accelerated forest recovery in this area.

Forest has recovered in the karst region because deforestation occurred at a small spatial scale, seed sources were close to disturbed areas, and the disperser community (birds and bats) was able to remain in the area during the period of agriculture. Presently, the recovery process is being threatened by land use practices (e.g., roads and urbanization) that will permanently modify this unique ecosystem.

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