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Forest recovery in abandoned agricultural lands in a karst region of the Dominican Republic

L. W. Rivera[1], J. K. Zimmerman[2,3] & T. M. Aide[1]
[1]*Department of Biology, University of Puerto Rico, San Juan, Puerto Rico;* [2]*Institute for Tropical Ecosystems Studies, University of Puerto Rico, San Juan, Puerto Rico 00936-3682 (e-mail: jzimmer@sunceer.upr.clu.edu)*

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Abstract

This study documents the status of forest vegetation in the karst region of Los Haitises National Park, Dominican Republic, following the abandonment of pastures ($\leq$ 5 years), young ($\leq$ 5 years) '*conucos*' (mixed plantings), old (7–30 years) *conucos*, and cacao plantations ($>$ 25 years). We compared these sites to vegetation characteristics of patches of forest in karst valleys ('old forest'–too old to know their exact land use) and on mogote tops with no recent history of human disturbance. The youngest sites date to when squatters were removed from Los Haitises National Park. Forest structure (density, basal area, and species richness of woody plants $\geq$ 1 cm DBH) were all significantly affected by land use. Density was highest in intermediate-aged valley sites (old *conucos*) and *mogote* tops, while both basal area and species richness tended to increase with age of abandonment. Although cacao plantations had been abandoned for more than 25 years the species diversity was low, due to continued regeneration of this persistent crop. Abandoned pastures had the greatest nonwoody biomass and were dominated by the fern *Nephrolepis multiflora* which had completely replaced pasture grasses. An ordination of the woody plant communities separated the *mogote* tops from valleys, emphasizing the strong control that topography has on the forest community in moist and wet tropical forests on karst substrates. Valley sites were arranged in the ordination in order of their age, suggesting a successional sequence converging on the composition of the 'old forest' sites.

Introduction

Human activities have destroyed much of the world's tropical forests, and rates of deforestation are still high (Burgess 1993; Saxena & Nautiyal 1997). The causes of tropical deforestation are multifaceted but are driven by population growth, politics, and patterns of economic development (Paulson 1994; Ruder & Roper 1996). However, these factors can change, permitting forest recovery. In Puerto Rico, for example, total forest area was reduced to 6% by the late 1940s, but economic changes caused the abandonment of agricultural lands, and forest cover increased to approximately 33% by 1985 (Birdsey & Weaver 1987). Although the Brazilian Amazon has had high rates of deforestation, large areas used for agriculture and grazing have been abandoned and are in secondary succession (Skole et al. 1994). Secondary forests have many valuable ecological characteristics and their wise management could mitigate socioeconomic factors leading to the destruction of mature forests (Brown & Lugo 1990; 1994). Secondary forests can be important sources of firewood, pulp, valuable timber species, habitat for shade-requiring crops and habitat for many native plant and animal species (Weaver & Birdsey 1986; Finegan 1992; Del Amo & Ramos 1993).

Moist and wet tropical forests associated with karst topography occur in all of the Greater Antilles and parts of Central America (Kelly et al. 1988). In moist and wet climates, karst develops a unique physiognomy marked by steep haystack-shaped hills or '*mogotes*' separated by valleys where alluvium collects. Compared with other Caribbean forest types, these forests have high species diversity and endemism (Furley & Newey 1979; Chinea 1980; Furley 1987; Kelly et al. 1988; Zanoni et al. 1990; Borhidi 1991). High species diversity results, in part, because the contrasting edaphic conditions of the mogote tops (exposed with poor, rocky soils) an valley bottoms (protected, with deep, moist organic soils) result in distinct plant communities (Chinea 1980). Although the topography is very rough, deforestation has greatly affected these forests (Murphy 1916; Rivera & Aide 1998; Zanoni et al. 1990; Borhidi 1991; Brothers 1997). Deforestation (i.e. pastures, mixed cropping or '*conucos*', and timber extraction) is mainly restricted to the valleys between *mogotes*, but the steep slopes and *mogote* tops are also affected by fires, and cutting for wood and charcoal production.

In the Dominican Republic, the largest area of karst topography occurs in Los Haitises National Park (LHNP; Figure 1). Although human occupation of the area pre-dates the arrival of European settlers (as indicated by the presence of Amerindian petroglyphs), widespread human settlement of the park did not begin until the 1960s (Brothers 1997). Los Haitises National Park was established in 1976, but park boundaries were not controlled until 1992. Forests in karst valleys were almost entirely cleared and the remaining forest was mostly restricted to steep slopes and tops of *mogotes*. In 1992, most of the inhabitants and livestock were removed from the park and park boundaries were patrolled (Brothers 1997).

The unique nature of these habitats and the high diversity and endemism of plant species justify special efforts in determining the impact of past human land use history on forest recovery as a first step in developing management schemes. The goal of the study was to determine the effects of previous land use and time since abandonment on the structure and composition in the karst forest of LHNP, Dominican Republic. We addressed the following questions: (1) How do the different types of land use affect forest regeneration in terms of density, basal area, diversity, and species composition? and (2) What are the implications of these patterns for the future management of the park? To answer these questions we sampled the vegetation in 28 sites that varied in time since abandonment and land use history.

Methods

Los Haitises National Park is located near the north coast of Dominican Republic and south of Samaná Bay (Figure 1). The average annual rainfall in the region is approximately 2000 mm (Zanoni et al. 1990). The limestone parent material was formed during the Miocene (Zanoni et al. 1990). The topographic features of the karst region are sinkholes, caves, cliffs, karst valleys (long and narrow valleys) and mogotes (Kelly et al. 1988; Zanoni et al. 1990). The original vegetation of LHNP is classified as subtropical broadleaf forest with strong differences in vegetation composition between the karst valleys and the *mogotes* (Zanoni et al. 1990). The vegetation of LHNP includes at least 670 native plant species, of which 32 species are thought to be confined to the park (Zanoni et al. 1990).

Study sites were located in three areas readily accessible by road or from the sea: Trepada Alta (TA), Caño Hondo (CH), and Los Naranjos (LN) (Figure 1). Interviews with park guards were used to determine the land use history of each site (A. Flecker, Cornell University, pers. comm.). In consultation with park guards, sites were chosen to represent the variation in forest age and land use within each of the three study areas. Sites were chosen using guard's specific knowledge of previous land use and not the current status of vegetation. *Mogote* tops were largely chosen for their accessibility, and all were covered by closed forest.

In valleys, we surveyed 5 pasture sites, 13 *conucos* (mixed plantings of root crops, citrus, and other crops), and 2 former cacao plantations, 2 sites of unknown prior use (termed 'old forest' because they are too old to know their exact land use). In addition, we sampled 6 *mogote* tops. All pasture sites were abandoned at the time settlers were removed ($\leq$ 5 years) and all cacao plantations, and old forests had been abandoned for a much longer time ($>$ 25 years). Lacking any evidence of human disturbance (e.g., wood extraction), we assumed that the *mogote* tops we sampled had been free of human disturbance for $>$ 25 years. There was sufficient variation in time since abandonment in *conucos* to justify dividing these sites into two groups ('young', $\leq$ 5 years, and 'old' $>$ 5 years). Although we observed some evidence of selective logging in *mogote* tops (e.g. *Manilkara bidentata* [A. DC.] Chev.), these sites showed little evidence of human impact. The two 'old forest' sites were identified by park guards as having had little human use in recent times. However, the presence of cultivated

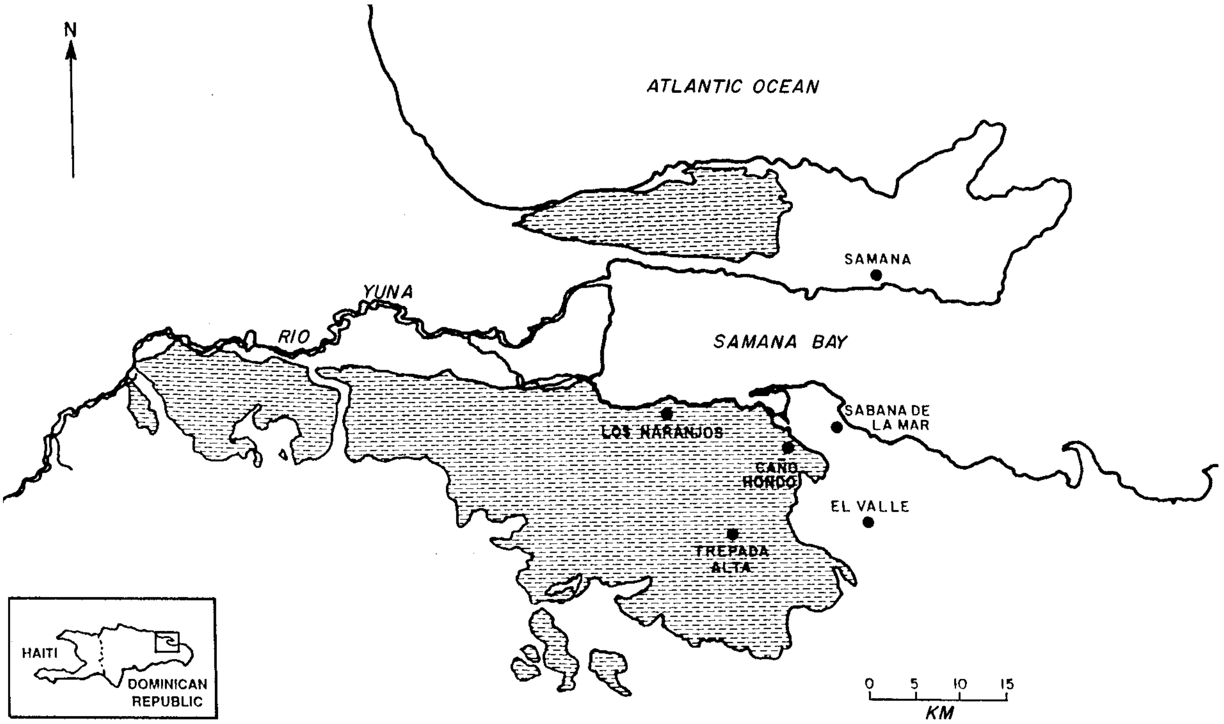

Figure 1. Location of study areas in northeastern Dominican Republic (inset). Stippled areas denote location of karst topography (haystack hills or *mogotes*). The portion south of Samaná Bay coincides largely with Los Haitises National Park. Vegetation was sampled in Los Naranjos, Caño Hondo, and Trepada Alta.

plants (e.g. breadfruit, citrus, and avocado) indicated past human influence.

Each site was permanently marked with pvc tubes. In each site, we identified and measured every woody stem (lianas not included) $\geq$ 1 cm in diameter at breast height (dbh) in 4 parallel transects (1 $\times$ 50 m; 200 m^2) and all trees $\geq$ 10.0 cm dbh in two 500 m^2(10 $\times$ 50 m^2) plots which included the transects. On narrow *mogote* tops, transects were combined into two transects 2 $\times$ 50 m and included in a single 10 $\times$ 50 m plot to sample larger ($\geq$ 10 dbh) trees (total area = 500 m^2). Data were collected during January 1997. Calculations of basal area and tree density were based on the combined samples from transects and plots. Species richness was calculated using data only from the transects in order that it be expressed on an equal-area basis. Importance values were calculated as the average of relative density and relative basal area. The importance values for each species in each site were analyzed using Nonmetric Multidimensional Scaling (MDS; McCune & Mefford 1997). MDS is a non-parametric technique and the interpretation of the results is less complicated in comparison with other ordination techniques (Clarke 1993). Species Indicator Analysis, described by Dufrene & Legendre (1997), was used to indicate which species were unique to particular land uses. Dufrene & Legendre (1997) describe the advantages of this over other classification methods. Inferential statistics were used to confirm trends in the data. The results must be interpreted with caution because selection of study sites was not random. Biomass of non-woody vegetation was estimated for each site by sampling two quadrats (50 $\times$ 50 cm) in each of the four transects. Non-woody biomass samples were separated into ferns, herbs, grasses, and vines. Plant nomenclature followed Liogier (1981–1995). Voucher specimens were deposited in the herbarium of the National Botanical Garden in Santo Domingo, Dominican Republic (JBSD).

Results

The structure of vegetation differed markedly among the differing land uses. Tree density was significantly different among the land uses (ANOVA $F = 5.8, .P = 0.0015$; Figure 2a). Mean density was highest in *mogote* tops (7658 stems ha^{-1}) and lowest in the

Table 1. Mean importance value of the ten top species for each land use sampled in Los Haitises National Park, Dominican Republic.

Species	Family	Pasture	Young Conuco	Old Conuco	Cacao	Old Forest	Mogote top
Piper aduncum L.	Piperaceae	42.6	27.6				
Psidium guajava L.	Myrtaceae	24.7	4.8				
Hura crepitans L.	Euphorbiaceae	4.4		2.1			
Inga vera Wilid.	Leguminosae	4.2	2.4	10.4	12.9	4.8	
Cupania americana L.	Sapindaceae	3.7					
Lantana camara L.	Verbenaceae	3.1	3.9				
Lepianthes spp.	Piperaceae	2.4	3.1				
Piper laeteviride Ekman ex Trelease	Piperaceae	2.1		16.8		13.3	
Cecropia schreberiana Miq.	Moraceae	1.7	6	4.4	5.2	3.7	
Hamelia patens Jacq.	Rubiaceae	1.1					
Triumfetta spp.	Malvaceae		13.5				
Citrus spp.	Rutaceae		7.4				
Cocos nucifera L.	Palmae		4.7				
Piper jacquemontianum (Kunth) DC.	Piperaceae		2.3	7.8	5	8.4	
Spondias mombin L.	Anacardiaceae			8.1	9.7		
Guarea guidonia (L.) Steumer	Meliaceae			6.2	9.5	26.2	
Musa spp.	Musaceae			6			
Roystonea borinquena O.F. Cook	Palmae			3.2			
Theobroma cacao L.	Sterculiaceae			1.7	33.5		
Psychotria pubescens Sw.	Rubiaceae				6.6	8.6	
Dendropanax arboreus (I.) Decne. & Planch	Araliaceae				4.9		
Urera baccifera (I.) Wedd.	Urticaceae				2.7		
Zanthoxylum martinicense (Lam.) DC.	Rutaceae				2.5	6.8	
Artocarpus altilis (S. Park.) Fosb.	Moraceae					7.9	
Ocotea membranacea (Sw.) Howard	Lauraceae					2.7	
Ocotea coriacea (Sw.) Britton	Lauraceae				1.6	1.6	14.2
Bombacopsis emarginata (A. Rich.) A. Robyns	Bombacaceae						9.7
Prunus myrtifolia (L.) Urban	Rosaceae						5.4
Coccoloba diversifolia Jacq.	Polygonaceae						5.4
Cinnamodendron ekmanii Sleumer.	Lauraceae						4.7
Calophyllum calaba L.	Guttiferae						4.1
Pseudolmedia spuria (Sw.) Ghseb.	Moraceae						3.3
Lonchocarpus latifolius (Wilid.) DC.	Leguminosae						3.2
Ziziphus rhodoxylon Urb.	Rhamnaceae						1.6
Clusia minor L.	Guttiferae						1.6

old forest (3510 stems ha^{-1}) and cacao (3575 stems ha^{-1}) sites. A post-hoc comparison among means (Tukey-Kramer test, Statistix for Windows Analytical Software, 1996) grouped pastures, young *conuco*, cacao, and forest sites, which all had relatively low densities. The densities in old *conuco* sites (6630 stems ha^{-1}) were intermediate and were not significantly different from any of the other land uses.

There was also a significant difference in basal area among the land uses (ANOVA F 6.8, $P = 0.0006$; Figure 2b). Basal area was highest in the *mogote* tops (mean = 34.7 m^2 ha^{-1})and forest (mean = 44.4 m^2 ha^{-1}) sites and lowest in pastures (mean = 5.5 m^2 ha^{-1}) and young *conucos* (mean = 6.6 m^2 ha^{-1}). Old *conuco* (mean = 23.6 m^2 ha^{-1}) and cacao (mean = 26.7 m^2 ha^{-1}) sites had intermediate basal area. The post-hoc test distinguished pastures and young *conuco* from old forest and *mogote* tops, but old *conuco* and cacao sites were not statistically different from the other two groups.

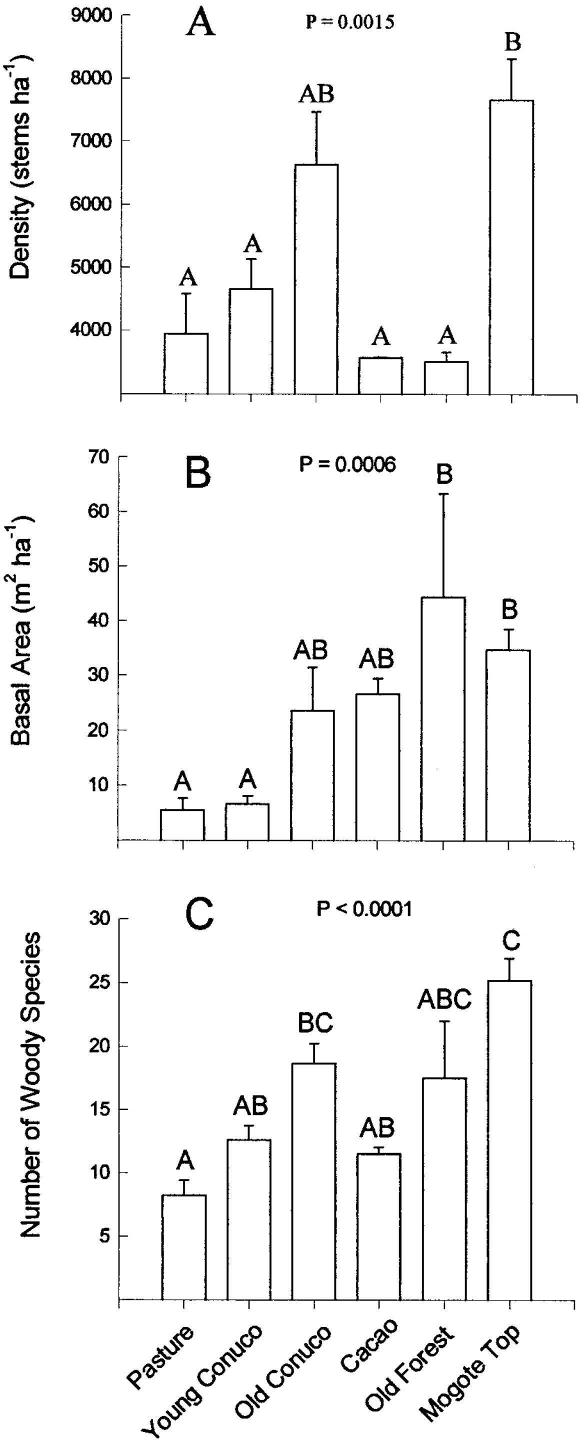

Figure 2. Effect of land use on mean (A) density (stems ha^{-2}), (B) basal area (m^2 ha^{-1}) and (C) number of woody species (sampled area = 200 m^2) for stems $\geq$ 1 cm dbh. Land uses with different letters were significantly different ($P < 0.05$; Tukey–Kramer test).

The distribution of stem diameters also differed markedly among land uses (Figure 3; test of independence on summed counts per diameter class, $\chi^2 = 10,547$; $P < 0.0001$). Pastures and young *conucos* were dominated by many small stems < 4 cm dbh, mostly shrubs and a few large trees. The other land uses contained many more trees $\geq$ 8 cm dbh, with the *mogote* tops exhibiting a relatively large number of intermediate-sized trees (2–16 cm dbh) (test of independence excluding pastures and young *conucos*, $\chi^2 = 5304.4$, $P < 0.0001$).

Total biomass of nonwoody vegetation was significantly higher in pasture sites in comparison with all other land uses (ANOVA F = 7.1, $P = 0.0004$, Figure 4). Mean biomass of nonwoody vegetation was 385 g m^{-2} in the pastures and ranged from 47 g m^{-2} in cacao to 179 g m^{-2} in young *conuco*. The higher biomass in the pasture was due to a significantly higher biomass of ferns in comparison with the other land uses (ANOVA F = 6.9, $P = 0.0005$). The dominant species of fern in pasture sites was *Nephrolepis multiflora* (Roxburgh) Jarret ex Morton, which usually completely covered the abandoned pastures with the exception of patches of shrubs and occasional, isolated larger trees. Graminoids were completely absent in pasture sites presumably due to the shading of *N. multiflora*. There were no significant differences in graminoid (not shown), vine, or herb biomass among the different land uses.

A total of 162 woody plant species was observed in the 28 study sites (total area sampled was 26000 m^2 for trees $\geq$ 10.0 cm dbh, and 5600 m^2 for trees 1.0–9.99 cm dbh). Nineteen species (11.7%) were introduced from outside of the Hispaniola. The total number of species and of unique species associated with each land use varied greatly: pastures (25 spp.; 2 spp.), young *conuco* (43 spp.; 7 spp.), old *conuco* (56 spp.; 8 spp.), cacao (19 spp,; 0 sp.), old forest (29 spp.; 4 spp.), and *mogote* tops (106 spp.; 83 spp.).

Considering only those data collected from the four 50 m transects in each site, species number for trees $\geq$ 1 cm dbh was significantly different among land uses (ANOVA F = 15.1, $P < 0.0001$; Figure 2c). Pasture sites had the lowest species diversity (mean = 8.2 species per 200 m^2 and *mogote* tops had the highest (mean = 25.2 species). A post-hoc comparison of means indicated that woody plant species diversity was significantly lower in pasture sites than in old *conuco* and *mogote* tops, and significantly lower in young *conuco* and cacao than on *mogote* tops (Figure 2c).

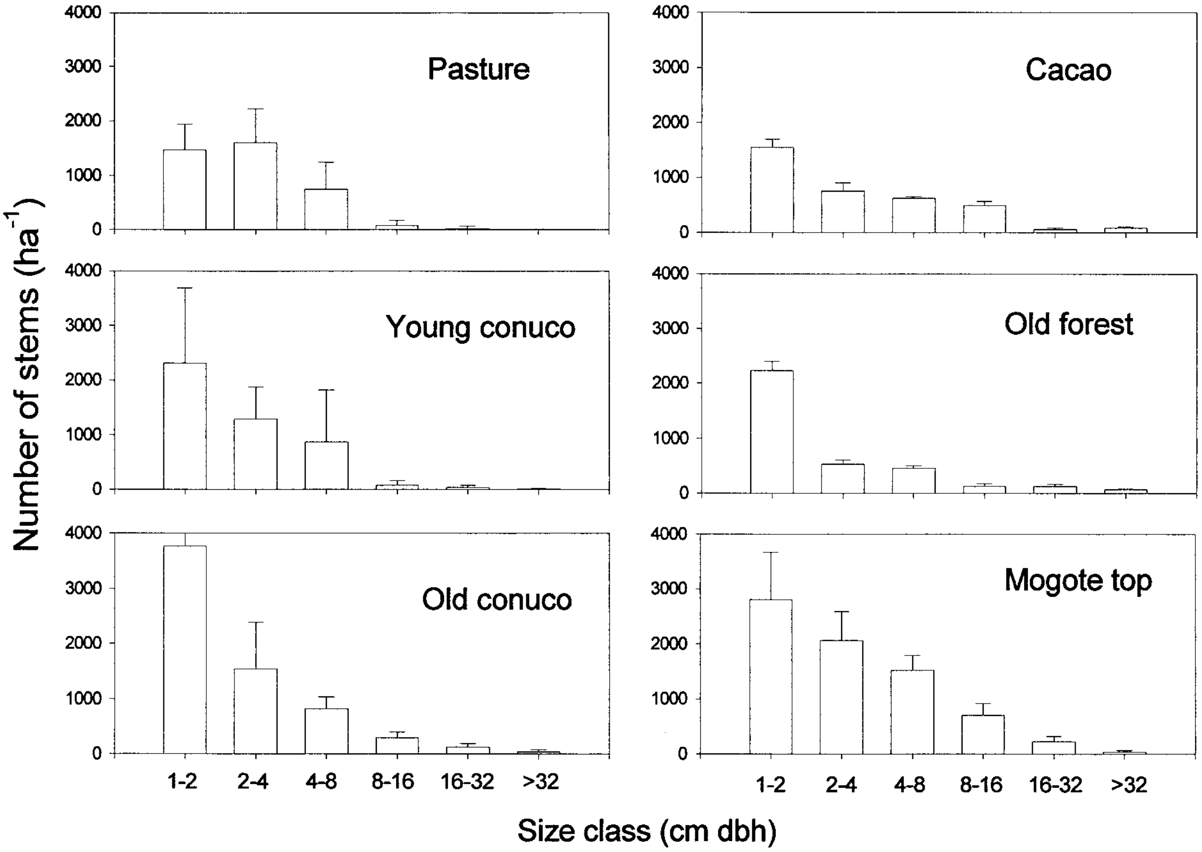

Figure 3. Mean number of woody stems (± SE) in different size classes in each land use.

Ordination of woody species clearly separated *mogote* tops from the rest of the land uses indicating their distinctive species composition (Figure 5; Table 1). There were two other distinct groups: (1) pastures and young *conucos* and (2) cacao plantations, old *conucos*, and older areas whose previous use was unknown (old forest). The age given for one young *conuco* may be incorrect, since its floristic composition falls among the old *conucos* (Figure 5). Removing *mogotes* from the ordination did not produce any further differences among the remaining land uses.

Inspection of the dominant species in each land use (Table 1) indicates the major differences in species composition between land uses. Pastures were dominated by the shrubs *Piper aduncum* L. (Importance Value, I.V. = 42.6%) and P̂sidium guajava L. (I.V. = 24.7% Table 1). Young *conucos* were dominated by *P. aduncum* (I.V. = 27.6) and *Triumfetta* spp. (I.V. = 13.5%). Old *conucos* were dominated by *Piper laeteviride* Ekman ex Trelease (I.V. = 16.8%) and *Inga vera* Willd. (I.V. = 10.4). Abandoned cacao plantations were dominated by cacao (*Theobroma cacao* L.; I.V. = 35.5%) and *I. vera* (I.V. = 12.9%). *Inga vera* had been used as a shade tree for cacao plantations. Old forest sites were dominated by *Guarea guidonia* (L.) Sleumer (I.V. = 26.2%) and *P. laeteviride* (I.V. = 13.3%). Finally, *mogote tops*, the most diverse sites, were dominated by *Ocotea coriacea* (Sw.) Britton (I.V. = 14.2%) and *Bombacopsis emarginata* (A. Rich) A. Robyns (I.V. = 9.7%).

Pearson correlations between MDS axis scores and species' importance values indicated that Axis 1, which distinguished *mogote* tops from the remaining sites, gave high positive weighting to *B. emarginata* (*r* = 0.660), *Cinamodendron ekmanii* Urb. (*r* = 0.617), *Coccoloba diversifolia* Jacq. (*r* = 0.669), *Exothea paniculata* (Juss.) Radlk. (*r* = 0.597), *O. coriacea* (*r* = 0.709), and *Sideroxylon domingense* Urb. (*r* = 0.679). These five species were all confined to *mogote* tops and were often dominant species (highest importance value; Table 1). Axis 2 gave high

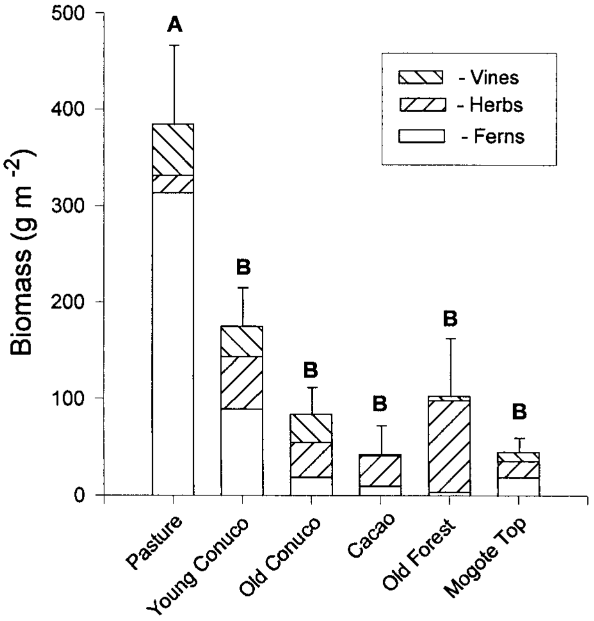

Figure 4. Mean biomass of nonwoody plants for each land use. Land uses with different letters were significantly different ($P < 0.05$; Tukey–Kramer Test).

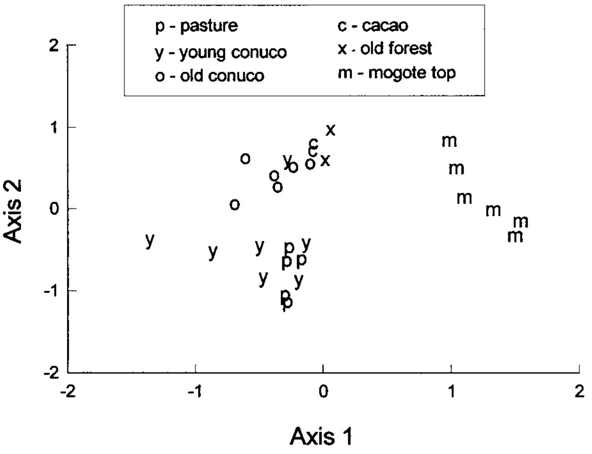

Figure 5. Ordination analysis (Nonmetric Multidimensional Scaling) based on importance values of woody species occurring in each land use.

positive correlation to *Psychotria pubescens* Sw. $r = 0.599$) and a negative correlation to *Piper aduncum* $r = -0.795$) and separated recently abandoned areas (pastures and young *conucos*) from older ones (old *conucos*, cacao plantations, and old forest).

To further identify differences in species composition among land uses, we used Indicator Species analysis to identify unique species within each land use. Twenty-four of the 162 species (14.8%) had indicator values $\geq$ 50%, indicating the occurrence of these species was concentrated in a particular land use (Table 2). *Piper aduncum* (indicator value = 60%) and *Psidium guajava* (81%) were the major indicator species for the pasture sites, where they were also dominant species (Table 1). Young and old *conucos* each had only one species with an indicator value $\geq$ 50%, *Triumfetta* spp. (68%) and *Spondias mombin* L. (62%), respectively. These were common species in both land uses, but not the dominant species (Table 1). *Theobroma cacao* has a high indicator species value in abandoned cacao (91%) where it dominated strongly (Table 1). The major indicator species for the old forest sites were: *Eugenia domingensis* Berg. (89%), *Euphorbiaceae* (50%), *Ocotea membranacea* (Sw.) Howard (81%), *Ocotea* spp. (50%), *Psychotria pubescens* (51%), *Psychotria* sp. (50%), and *Quararibea turbinata* (Sw.) Poir. (50%). Only one of these species, *O. membranacea*, was among the most common species in the old forests (Table 1). *Mogote* tops were the group with the highest number of indicator species (12) and *Coccoloba diversifolia* and *Prunus myrtifolia* (L.) had the maximum indicator value (100%), indicating that they occurred only on *mogote* tops. Five of these species were also the most common species on *mogote* tops (Table 1).

Discussion

In LHNP, human impact has been concentrated in the valleys. The tops of the *mogotes* have been disturbed less due to poor soils and difficult access; thus much of their plant diversity remains. In valleys between *mogotes*, where agriculture was concentrated, land use and age of abandonment are confounded. Although abandoned *conucos* ranged in age $\leq$ 5 years to $>$ 5 years, all pasture sites had been abandoned for less than 5 years and cacao sites had been abandoned for more than 25 years. The lack of parallel chronosequences does not allow us to speculate on variation in successional trajectories among land uses. Rather, our results present a snapshot in time showing how variation in human land use patterns affect forest structure and composition in a tropical karst landscape.

The study sites do not represent a chronosequence, but the relationship between forest structure and age of abandonment showed trends similar to other studies. With the exception of the *mogote* tops, the major effect is an increase in density of woody stems from the youngest sites, pastures ($\leq$ 5 years and young *conuco* ($\leq$ 5 years), to a peak in the old *conucos*,

Table 2. Species indicator analysis based on relative abundance of each species in each land use. (Land uses: P = pasture, YC = young conuco, OC = old conuco, C = cacao, OF = old forest, and M = *mogote* top).

	Land use					
Species	P	YC	OC	C	OF	M
Psidium guajava L.	81	13	0	0	0	0
Piper aduncum L.	60	31	3	0	0	0
Triumfetta spp.	1	68	0	0	0	0
Spondias mombin L.	0	5	62	10	0	1
Theobroma cacao L.	0	1	4	91	0	0
Psychotria pubescens Sw.	0	0	4	38	51	1
Ocotea membranacea (Sw.) Howard	0	0	3	0	81	1
Eugenia domingensis Berg.	0	0	0	4	89	0
Psychotria sp.	0	0	0	0	50	0
Euphorbiaceae	0	0	0	0	50	0
Ocotea sp.	0	0	0	0	50	0
Quararibea turbinata (Sw.) Poir.	0	0	0	0	50	0
Ocotea coriacea (Sw.) Britton	0	0	0	0	9	76
Coccoloba diversifolia Jacq.	0	0	0	0	0	100
Prunus myrtifolia (L.) Urban	0	0	0	0	0	100
Cinnamodendron ekmanii Slumer	0	0	0	0	0	67
Sideroxylon domingense Urb.	0	0	0	0	0	67
Bombacopsis emarginata (A. Rich.) A. Robyns	0	0	0	0	0	67
Calophyllum calaba L.	1	2	0	0	0	56
Exothea paniculata (Juss.) Radik.	0	0	0	0	0	50
Plumeria magna Zanoni & Mejia	0	0	0	0	0	50
Pimenta racemosa (Mill.) J. W. Moore	0	0	0	0	0	50
Clusia rosea Jacq.	0	0	0	0	0	50
Allophyllus cominia (L.) Sw.	0	0	0	0	0	50

and then a decrease in the older cacao and old forest sites. This pattern of increased densities during the first 20 to 30 years, followed by thinning, has also been observed in other studies of secondary forests (Brown & Lugo 1994; Aide et al. 1995, 1996). Time since abandonment was also a good predictor of basal area, increasing from approximately 5 m^2 ha^{-1} in pastures and young *conucos* to 22 m^2 ha^{-1} in the intermediate-aged old *conucos* and cacao plantations to approximately 45 m^2 ha^{-1} in the old forest sites. Changes in species richness with age paralleled that of basal area, except that cacao plantations had lower than expected number of species given the age of these sites. The large number of cacao seedlings and saplings in abandoned plantations suggests that this species will continue to dominate these sites for many years (Rivera, pers. obs.).

Areas of differing land use in LHNP had distinct assemblage of species, as has been observed on other studies of tropical secondary forests (Zimmerman et al. 1995; Rivera & Aide 1998). The greatest distinction was between *mogote* tops and valley sites. *Mogote* tops contained the greatest number of indicator species, demonstrating their unique species composition. In relatively undisturbed areas of Puerto Rico there are strong differences in the communities of woody species between *mogote* tops and valleys (Chinea 1980), thus the difference in species composition observed in LHNP probably also results from the difference in topographic position, albeit reinforced by differences in human disturbance.

Pasture sites were dominated by ferns, primarily *Nephrolepis multiflora*, and contained few woody species. The almost complete lack of grasses was surprising considering that the pastures had been abandoned for $<$ 5 years. In nonkarst (Aide et al. 1995) and karst (Rivera & Aide 1998) regions of Puerto Rico ferns are also important colonisers of abandoned pastures and they can persist in sites that have been abandoned for over 15 years. The woody vegetation in abandoned pastures was sparse and *Piper aduncum* and *Psidium guajava*, an introduced fruit tree probably native to continental tropical America (Little et al. 1977), were the most common species. The slow appearance of woody species in abandoned pastures has been attributed to poor dispersal of seeds into pastures (Fleming & Heithaus 1981; McDonnell & Stiles 1983) and competition for light, or barrier to seed germination created by the high biomass of ferns and herbaceous vegetation (Aide et al. 1995).

Young *conucos* ($<$ 5 years since abandonment) lacked the thicket of ferns present in pastures, but otherwise had a similar suite of woody species. Species indicator analysis (Dufrene & Legendre 1997) demonstrated that the primary difference in woody species between pastures and young conucos was the dominance of young *conucos* by *Triumfetta* spp. and a lower density of *Psidium guajava*. Older *conucos* ($>$ 5 years post-abandonment) were dominated by the shrub *Piper laeteviride* and contained more large trees than young *conucos*. Abandoned cacao plantations were strongly dominated by persistent *Theobroma cacao* and were not dominated by *P. laeteviride*, but were otherwise similar in species composition to old *conucos*. Old forest sites were dominated by *Guarea guidonia* (which was also common in old *conucos* and cacao plantations) and *Piper laeteviride* and were the only sites where *Eugenia domingensis, Ocotea membranacea* and several other species occurred in high abundance.

Similarities in the species composition of pastures and young *conucos*, on the one hand, and old *conucos*, cacao, and old forest sites on the other, suggests a successional sequence converging on a composition similar to the old forest sites. The lack of older pasture sites prevents us from testing the idea that compositional differences between land uses will persist over time (i.e. parallel successional sequences) as suggested in our Puerto Rican studies (Rivera & Aide 1998; Zimmerman et al. 1995). Repeated sampling of the LHNP sites will be necessary to test this idea.

Management implications

These results suggest that if the sites are left alone, areas formerly in agriculture will become forested in a relatively short period of time. Our work in Puerto Rico in karst (Rivera & Aide 1998) and other areas (Aide et al. 1995; 1996; Zimmerman et al. 1995) indicates that pastures and young conuco sites will have a closed canopy and a high density of trees in approximately 20 years. The species richness in these sites should be similar to those of other land uses (approximately 20 tree and shrub spp. per 200 m^2) and it is likely that *G. guidonia* will be the dominant species. Management techniques could accelerate the recovery in the abandoned pastures and increase species diversity in cacao plantations. Pastures appear resistant to tree establishment due to dispersal limitation (Aide & Cavalier 1994) and high densities of herbaceous vegetation (Aide et al. 1995), particularly the fern *Nephrolepis multiflora*. The recovery process could be accelerated by planting fast-growing shrub and tree species that would shade out the ferns and attract dispersers of other native species. The species richness of cacao plantations was very low even though these area had been abandoned for $>$ 25 years. The shaded understory below the *T. cacao* canopy appears to restrict colonization to the most shade-tolerant species, as has been suggested for areas previously cultivated for shade coffee (Rivera & Aide 1998). The removal of *T. cacao* individuals could facilitate the colonization of native species in these areas.

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Appendix 1. Summary data of the forest characteristics at each of the study sites in three areas (TA, Trepada Alta; LN, Los Naranjos; CH, Caño Hondo, see Figure 1) in the karst zone of LHNP, Dominican Republic. No. of species are reported on an equal area basis using data from 1 × 50 m transects only. Basal area and density were calculated by combining data from transects (trees $\geq$ 1 cm dbh) and plots (trees $\geq$ 10 cm dbh). Plots totaled 1000 m^2 (except where noted*) and included the transect areas. (* a single plot of 500 m^2 was used to augment sample of larger ($\geq$ 10 cm dbh) trees).

Site	Land use	Age–Years	No. of species (200 m^2)	Basal area ($m^2 ha^{-1}$)	Density (stems ha^{-2})
TA1	Pasture	5	9	12.7	4950
TA5	Pasture	4	12	7.6	4840
TA12	Pasture	<3	6	2.4	4650
LN4	Pasture	<5	9	2.1	3750
LN5	Pasture	<5	5	2.9	1550
TA2	Young Conuco	5	13	10.2	4540
LN2	Young Conuco	1–3	12	7.9	5180
LN3	Young Conuco	2–3	11	1.8	2910
LN1O	Young Conuco	1–2	15	11.6	6380
TA7	Young Conuco	3	17	8.8	5580
CH4	Young Conuco	1–2	8	1.1	3270
CH2	Young Conuco	3	11	4.8	4760
TA4	Old Conuco	7–9	23	16.6	8590
CH3	Old Conuco	>10	19	20.2	7300
CH5	Old Conuco	>10	12	15.0	4200
CH8	Old Conuco	>15	20	12.9	9250
LN11	Old Conuco	>30	21	14.2	4900
TA13	Old Conuco	>15	17	62.8	5540
CH7	Cacao	>25	11	29.5	3580
CH6	Cacao	>30	12	23.9	3570
TA3	‘Old Forest’	>30	13	63.4	3360
LN9	‘Old Forest’	>30	22	25.4	3660
TA6	*Mogote* Top	>30	30	22.2*	7640*
TA8	*Mogote* Top	>30	25	49.7*	6950*
TA10	*Mogote* Top	>30	30	28.9*	9690*
LN6	*Mogote* Top	>30	21	33.6	6070
LN7	*Mogote* Top	>30	20	35.9	9480
LN8	*Mogote* Top	>30	25	38.0*	6120*

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