



# Anthropogenic change in subtropical dry forest during a century of settlement in Jaiquí Picado, Santiago Province, Dominican Republic

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## Abstract

**Aim** The dry forests of the tropics have received little scholarly attention relative to their significance and their rate of disappearance. This study aimed to characterize the structure and composition of two intermingled Antillean subtropical dry forest types and shed light upon their origins, development, and possible future conditions.

**Location** Jaiquí Picado, Santiago Province, Dominican Republic (19° 26' N, 70° 54' W).

**Methods** Biophysical data from quadrat sampling of vegetation, soils, and site characteristics were subjected to cluster analysis, means comparisons, discriminant analysis, and linear regression. Extensive interviews with local land users provided information on early forests as well as present and historical land use practices.

**Results** Spatial patterning of the area's two main forest types relates closely to past land use but not to any observed differences in the physical characteristics of their sites. 'Old-growth' stands found on land never placed in cultivation resemble the forests encountered by late-nineteenth-century settlers of the area in their wealth of woody plant taxa and relative abundance of endemic and other native species. In the 'scrub' stands growing on land abandoned from grazing, fully 70% of stems belong to one native (*Acacia macracantha* Willd.) and two exotic (*Haematoxylon campechianum* L. and *Prosopis juliflora* (Sw.) DC.) woody legumes that contribute to the markedly greater representation of deciduous and thorn-bearing individuals in this type. The two forest types do not differ significantly in average bole dimensions, but the canopies of scrub stands are concentrated in a narrower layer, their understories are more open, and they contain more multiple stems of apparent sprout origin. A chronosequence of scrub stands covering a range in age of three decades indicates a moderate increment in species diversity over time and gradual disappearance of some of the more abundant invasive shrubs; but such stands continue to be dominated throughout this period by the same three scrub trees, while most species characteristic of old-growth forests, including many of the least abundant, fail to appear among the regeneration in their understories.

**Main conclusions** Antillean forests classified as thorn scrub may include a form of 'disclimax' created through past land use activities in areas once bearing more diverse tropical dry forest. Whether they will ever develop into stands similar to the previous forests is uncertain, given the present state of fragmentation and other processes taking place within these ecosystems.

## Keywords

Tropical dry forest, species diversity – woody plants, anthropogenic change, vegetation succession, plant community dynamics, Caribbean, Hispaniola

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## Resumen

En una zona seca de la República Dominicana, coexisten extensiones de 'breña', o 'monte de espinas', entremezcladas con fragmentos de un bosque subtropical seco de mayor diversidad, formando patrones espaciales que no pueden ser atribuidos a ninguna diferencia aparente entre las condiciones físicas de los sitios. Se aplicó una variedad de métodos, incluyendo el muestreo de parcelas de vegetación y suelos así como entrevistas con los residentes locales, para caracterizar estos dos tipos de bosque e investigar su posible origen. Los rodales del bosque maduro, los cuales se encuentran en terrenos nunca cultivados, se asemejan en su riqueza de especies leñosas y la abundancia de especies endémicas y nativas a los bosques encontrados por los pobladores que llegaron al área a finales del siglo diecinueve. En la breña que nace en terrenos abandonados del pastoreo, el 70% de los tallos pertenece a tres especies leguminosas leñosas – una nativa (*Acacia macracantha* Willd.) y dos exóticas (*Haematoxylon campechianum* L. y *Prosopis juliflora* (Sw.) DC.) – que contribuyen a una representación notablemente mayor de árboles caducifolios y espinosos en esta vegetación. Los dos tipos de bosque no difieren significativamente en las dimensiones medias de sus troncos, pero el dosel del monte espinoso se concentra en un estrato más angosto; su sotobosque se mantiene más abierto; y contiene una proporción mayor de tallos múltiples aparentemente nacidos de rebrotes. La comparación de una secuencia de rodales de monte espinoso, cuyas edades cubren un rango de tres décadas, indica que la diversidad de especies leñosas aumenta paulatinamente durante tal periodo y que se van desapareciendo algunos de los arbustos invasivos más abundantes; pero el monte sigue dominado por los mismos tres árboles espinosos, y la mayoría de las especies características del bosque maduro, incluyendo muchas de las más escasas, no llegan a aparecer entre la regeneración en su sotobosque. Entre los bosques antillanos ahora clasificados como 'monte espinoso' puede haberse incluido una especie de 'disclímax' ocasionado por las actividades humanas en terrenos anteriormente cubiertos de un bosque seco más diverso; el desarrollo futuro de estos montes – en particular su posibilidad de aproximarse a la composición de los bosques maduros – es aún impredecible.

## Términos clave

Bosque seco tropical, diversidad – especies leñosas, cambios antropogénicos, sucesión vegetacional, comunidades ecológicas – dinámica, Antillas, Isla Española.

## INTRODUCTION

The native dry forests of tropical and subtropical latitudes are known to be species-rich but imperilled ecosystems (Kepler & Kepler, 1970; Janzen, 1988a; 1988c; Redford *et al.*, 1990; Lerda *et al.*, 1991; Mares, 1992; Mooney *et al.*, 1995). Although dry forests constitute the potential vegetation of a greater proportion of the tropics than moist, wet, or rain forests (Brown & Lugo, 1982), ecological research has neglected them in comparison with the forests of the humid zones, in part because relatively little of their original area remains wooded (Walter, 1973: 65; Janzen, 1988c; Murphy & Lugo, 1990, 1995; Prance, 1991). European occupation of the American tropics brought severe deforestation, followed by persistent cash cropping and pasturage, to the regions of dry forest (Parsons, 1965; NRC, 1980; Murphy & Lugo, 1986a); long-term successional dynamics of these heavily disturbed communities are still poorly understood (Murphy *et al.*, 1995). As tropical dry forests become increasingly fragmented and their species

ever more threatened, evidence regarding prior vegetation and the processes of change will become less available even as it acquires greater importance for the conservation and informed management of the remaining fragments.

In the Dominican Republic, Subtropical Dry Forest is the second most extensive life zone (Holdridge, 1967) occupying 20% of the country's land area in four main sections (OEA, 1967 I: 18). The vegetation of this life zone has been decimated, however, leaving only an estimated 1.4–2.3% of the national territory or some 1000 km<sup>2</sup> in closed dry forest cover according to surveys already dated (OEA, 1967 I: 172; Hartshorn *et al.*, 1981: 19); still less persists in neighbouring Haiti (FAO, 1993). Even within the forested areas, only negligible remnants of dry forest vegetation exist that have not been greatly altered by human activities (OEA, 1967 I: 19; Palmer, 1976: 206; DVS, 1990:17; Hager & Zanoni, 1993). Factors combining to make the fate of this ecosystem a cause for concern include the critical current pace of deforestation in the Dominican Republic (Grainger, 1993); the relatively high incidence of endemism

among Hispaniolan plant species generally (36%; Liogier, 1984) and Antillean dry forest species (over one third; Gentry, 1992); the characteristic vulnerability of island biota (Elton, 1958; Carlquist, 1965); the occurrence of rare and threatened fauna in Dominican dry forest habitats (DVS, 1990: 131); and the economic significance of a number of the island's disappearing dry forest trees (Hartshorn *et al.*, 1981: 20–21). Baseline data on these forests are wanting, and published records of their species composition are few, primarily qualitative, and temporally restricted (references in Hager & Zanoni, 1993). The present project sought to characterize in some detail the dry forest vegetation in one area of the island and to determine the effects of historical land uses upon its structure and composition.

Change in vegetation is most reliably studied by direct observation over time, particularly in areas where dendrological dating is not feasible (Miles, 1979). Because long-term formal research was not initiated in tropical dry forests prior to the alterations that have taken place, the understanding of past change rests heavily upon interpretation of existing biological evidence. The historical documentation that has enriched numerous studies of temperate vegetation (e.g. Peterken, 1976; Sharpe *et al.*, 1987) is unavailable for many tropical areas. Nonetheless, direct observations of appreciable extent and acuity often exist in the unrecorded experience of rural communities dependent upon local forest resources. In the present study, vegetation of varied ages and past treatments was sampled directly and considered in the light of published research as well as detailed interviews with local residents.

## STUDY AREA

Jaiquí Picado is a village in the foothills of the Cordillera Central just south of the western Cibao Valley of the Río Yaque del Norte in the province of Santiago, Dominican Republic (Fig. 1, insert). The locality has undergone the array of land uses typical of its region yet retains sufficient forest cover to have been considered for inclusion in a proposed (Plan Sierra, 1992a) charcoal production zone. Factors contributing to the selection of Jaiquí Picado as a study site included a relatively short history of postcolonial settlement familiar to current residents; continuing economic dependence upon forest products; the reported existence of patches of dry forest never clear-felled or placed in cultivation; and the community's expressed interest and willingness to participate in a forest study (Roth, 1997).

The boundaries of Jaiquí Picado have never been mapped officially but are estimated to encompass some 16–18 km<sup>2</sup> of highly dissected terrain ranging in elevation from 280 to 520 m above sea level. The settled portion is concentrated on a narrow east-to-west-running ridge at 450–500 masl from which drainage in both directions eventually joins the Río Yaque del Norte, principally via the Río Amina. Much of the landscape consists of the steep slopes of narrow ephemeral drainage channels that open into small upland valleys. The bedrock is principally middle-Miocene limestone classified as the upper Gurabo formation (Blesch, 1967; E. Marcano F., pers. comm. 1993). Soil associations have not been determined for the area,

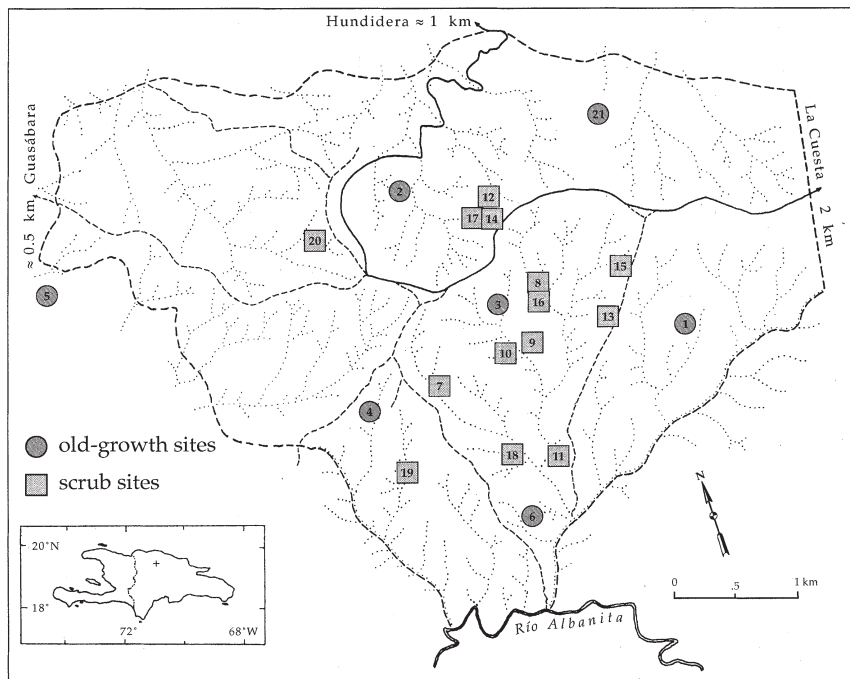
which national soil studies have characterized only as 'rough hilly land' with shallow, often rocky, friable sandy or clay loams developed in calcareous substrates and highly susceptible to erosion (OEA, 1967 III: 121; Pretell & Soto, 1967; Pretell, 1967). Tests performed for an earlier study (González J., 1980: 16, Mercedes U., 1980: 29, Mercedes U., 1984: 5) found local soils to be shallow, basic, medium-textured, low in phosphorus, and averaging 4% in organic matter content.

Mean annual temperature in Jaiquí Picado is estimated to be between 25 and 26 C and the annual precipitation somewhat below 1000 mm, placing it in the Subtropical Dry Forest life zone (Montanari, 1967a; Tasaico, 1967; ONE, 1984, 1987). Precipitation in the area shows a generally bimodal pattern with 6–7 dry months/y (Montanari, 1967b), but quantity and distribution of rainfall vary widely from year to year as is common in dry zones, with years of extreme drought having potentially determinant effects upon the biota (Murphy & Lugo, 1986a, 1995; Medina & Cuevas, 1990). The vegetation has been variously mapped as 'dry-region hardwood' (Woodward, 1910), 'part evergreen to mostly deciduous' (Durland, 1922), 'subxerophytic' (Ciferri, 1936), and 'arid-region thorn' (Chardón, 1976) forest types, and described in broad terms as a low, shrubby, and thorny xerophytic woodland of variable density composed mainly of Leguminous and Cactaceous species (Freeman, 1967). A recent classification (Hager & Zanoni, 1993) provides greater taxonomic and physiognomic differentiation among the country's dry and semideciduous forests while emphasising their highly altered condition. The present landscape of Jaiquí Picado exhibits a mosaic of forested patches of varying sizes and ages interspersed with pasture areas and active agricultural plots.

## METHODS

Two complementary approaches – field sampling of woody vegetation and extensive interviews with local residents – contributed interactively to this study. Initial interviews were conducted during lengthy landscape traverses with individuals considered to be especially familiar with the natural and human history of the area. A broadly shared recognition of two principal forest types was evident from these discussions, and a list of tracts of each type was later assembled through widespread questioning. Meanwhile, the population was censused in collaboration with community leaders and a more structured survey was developed that included a range of subjects involving history, ecology, and use of forest resources. This latter interview was conducted in June–October 1993, and June 1994, with each of seventy-six randomly chosen participants, together representing 54% of the 1993 adult population of Jaiquí Picado (Roth, 1997).

The classification of the region's land cover used on existing aerial photomosaics (Plan Sierra, 1992b) proved too crude to guide a vegetation sampling design, and its typology corresponded only superficially with the abovementioned forest categories. Instead, sampling was carried out within virtually all designated tracts (hereafter referred to as 'sites') of the two forest types, availing itself of information furnished by residents in distinguishing stand types and ages. The sites



**Figure 1** Approximate location of old-growth and scrub forest sampling sites in Jaiquí Picado. Cover types could not be mapped with sufficient accuracy to be represented here; the few existing old-growth fragments are mostly included among the labelled sampling sites, however, whilst a shifting mosaic of stages ranging from crops and pasture through scrub forest occupies the remaining area not immediately adjacent to roads. Tentative limits of Jaiquí Picado: - - - - -; principal road: ————; secondary unpaved roads: - - - - -; intermittent drainage: ·········; permanent stream: =====. Inset: Location of Jaiquí Picado ( $19^{\circ} 26' N$ ,  $70^{\circ} 54' W$ ) within the Dominican Republic on the island of Hispaniola.

were widespread within Jaiquí Picado (Fig. 1) and, other than any constraints imposed by the spatial patterning of the categories themselves, conformed to no apparent bias in selection.

Forested sites were sampled in August–November 1993, and June 1994, using  $200\text{ m}^2$  inventory plots ( $20\text{ m} \times 10\text{ m}$  rectangles projected planimetrically), orientated with long edges parallel to the slope to capture maximal within-site variability. The plots were located randomly within sites but without replacement in the sense that any overlapping positions were discarded, and plot numbers were adjusted to site size to keep sampling effort reasonably even. All woody plants rooted within each forested plot and  $\geq 1.5\text{ m}$  tall were identified to species or assigned morphospecies designations, with specimens taken for later determination or confirmation; voucher specimens are held by the author at the University of Kentucky, Lexington, KY, U.S.A. The height of each such individual was measured vertically to the nearest  $0.5\text{ m}$  with a marked pole or hypsometer. Bole diameter at  $1.3\text{ m}$  above ground (d.b.h.) was measured to the nearest centimetre with diameter tape or calliper for each separate stem at that level. Woody species having individuals  $< 1.5\text{ m}$  tall were noted where present, but their abundance was not quantified. Species abundance data were subjected to cluster analysis as an independent test of the type designations of sites, and species-area curves and diversity indices were developed for the two types. Botanical nomenclature follows the works of Liogier (1982, 1983, 1985, 1986, 1989, 1994, 1995, 1996).

Site history, including age of existing vegetation, was established as thoroughly as possible through inquiries made

of local residents. Slope inclination angle and azimuth, appearance of understory and substrate, and physical evidence of past or present land use were recorded at each plot. Predominant leaf size (adapting Raunkiaer's 1934) ranking to include intermediate gradations), percentage cover, and depth of the litter were averaged for each plot from measures made at one random location in each vertical third of the plot. A composite soil sample consisting of a trowelful to a depth of  $15\text{ cm}$  or impeding hard layer from each of the three sections was also taken from a random subset of the plots at all but one site. Soil samples were subjected to analysis of texture (sieving, sedimentation, and pipette techniques; Klute, 1986; SSIS, 1991), organic matter content (loss on ignition at  $460\text{ C}$ ; Klute, 1986), pH (electrode; NEC-67, 1991), and chemical constituents (ICAP spectrometry using Morgan extractant solution; NEC-67, 1991). Individual means tests and discriminant analysis were used to ascertain differences in these site characteristics between the forest types, and evidence regarding developmental trends was sought through linear regression of a number of stand and site characteristics on stand age.

In addition to the forested sites, five overgrown pastures of varying ages since last brush clearing were sampled in June of 1994 using five randomly placed  $100\text{ m}^2$  ( $5.64\text{-m}$  radius) circular plots per site. Each individual woody plant rooted within a given plot was identified as described above and its height measured in decimetres using marked poles; because most plants did not reach  $1.3\text{ m}$  in height, d.b.h. data were not recorded. Site history, slope, and aspect were noted for these plots, but grass cover precluded comparable measurements of other site characteristics, and soil samples were not taken.

## RESULTS AND DISCUSSION

### Forest typology

The woody vegetation type most readily apparent in Jaiquí Picado broadly fits descriptions of tropical thorn forest or woodland (Schimper, 1903: 363, Beard, 1944), or thorn bush (Walter, 1973: 35). It consists primarily of spine-bearing leguminous trees forming a single-layered low canopy of thin, spreading crowns with compound leaves and leptophyllous leaflets (Fig. 2a). Local residents refer to this vegetation as *breña* or scrub forest, a term used interchangeably with *monte de espinas* (thorn woodland). Distinguished from this scrub forest is *monte de hojas* (broad-leaved woodland), also called *monte viejo* (old or mature woodland) and *monte virgen* (referring to forest on sites not known to have been cultivated, although some amount of cutting has invariably taken place). This old-growth forest (Fig. 2b) is viewed as more developed than scrub forest in both structure and species composition due to less severe types and intensities of past disturbance. Although informants sometimes related particular species to physical characteristics of their sites, the forest categories recognized by participants in all initial interviews were described as reflecting stand origin and perhaps age rather than environmental differences.

The vegetation sampling described above was conducted in all old-growth and scrub forest sites indicated by informants and for which, in the latter case, sufficient information was obtained to permit a reasonable estimate of the year of latest cultivation. Thirty-one plots within seven sites were inventoried in old-growth forest; fifty-seven plots were located in fourteen scrub forest sites ranging in age from 2 to 29 y since abandonment from agriculture (Table 1a; Fig. 1). Scrub forest stands older than this were not encountered, as the more mature secondary growth is continually eliminated through repeated cutting for charcoal and crop production. Although the old-growth plots amounted to only half the aggregate area of scrub forest plots, sampling was relatively more intensive in old-growth forest, considering that the estimated land area with scrub forest cover is more than four times that with old growth.

Based on species abundance data from the twenty-one sites (Roth, 1997: Appendix I), matrices were developed using the association indices of Bray & Curtis (1957) and Morisita & Horn (Horn, 1966); these were subjected to an array of hierarchical clustering algorithms to determine whether the two forest types distinguished by known historical treatment sorted objectively into botanical associations based solely upon their species composition. Using either index together with single, complete, group average, or weighted-average linkage procedures (Baev & Penev, 1995), the results were consistent: old-growth sites grouped as one loose cluster, with the two most homogeneous stands joined at some distance from the rest, while scrub sites were related more closely among themselves as a distinct major cluster (Fig. 3). If historically defined forest types do not correlate with some underlying environmental distinction, this correspondence between historical and species-based typologies suggests that the existing differences in species

composition are due to processes somehow associated with past agricultural activities, and that the lands now bearing scrub forest stands may once have had vegetation similar to the present old-growth forests.

Several lines of evidence lend further support to this inference. First, analysis of the physical characteristics of the sites failed to uncover variation that would appear capable of explaining independently the observed differences in forest cover. Individual attributes of sites bearing old-growth forest are juxtaposed with those of scrub forest sites in Table 2 along with particulars of the tests used for comparison. Within the moderate sample sizes, and therefore somewhat limited statistical power, available, only five of these site variables showed significant differences between the two groupings. In each of these cases the plausible mechanisms of causality are either indirect – via agricultural influences – or opposite to directions that might imply environmental determination of forest type. For example, litter depth and leaf(let) size in the litter were significantly greater for old-growth forests, but these can be considered consequences of forest cover rather than independent characteristics of the sites themselves. Old-growth forest sites also averaged double the percentage slope of the scrub sites sampled and their soils were significantly more sandy; these traits tend to limit available soil moisture, which in a drought-prone climate might be expected to restrict, rather than increase (below) the structural development and potential species numbers in forests. Instead, these two factors have evidently ‘caused’ old-growth forest cover indirectly via land users who have refrained from cultivation or pasturage on some of the steepest, most erodible slopes. Of all measured chemical constituents of the soils, only copper showed a significant difference between forest types, but this may also be related to land use for agriculture. The only apparent explanation for the more than trebled average concentration of this element under scrub forests is the past application of cupriferous fungicides – widely used to control various pathogens of the leading local cash crop, tobacco (Schumann, 1991: 45, 153–155, and pers. comm. 1996; W. Nesmith, pers. comm. 1997) – in areas once cultivated. For none of the remaining variables in Table 2 were differences evident between sites bearing old-growth and those with scrub forest, either singly or in combinations sought through discriminant analysis (Hotelling’s  $\tau^2 = 150.53$ ;  $F = 8.36$ ;  $P = 0.27$ ).

Further evidence for the prior existence of old-growth forest where scrub forest now stands is the abrupt juxtaposition of occasional patches of the two forest types abutting with straight or fenced borders and sharing common topographic positions. In the only case where a site difference between such patches was noted, it was a virtually complete cover of small boulders that had prevented cultivation on the side now bearing old-growth forest.

Direct reports of historical processes observed by residents of Jaiquí Picado lend additional support to the notion that scrub forests are a recent development closely related to human activities. Post-Colombian settlement of Jaiquí Picado began in the late nineteenth century, prior to which the area is described as having been *montería*, or wilderness, uninhabited although visited regularly by hunters. Parents of the oldest



**Figure 2** Photographic views of the two principal forest types in Jaiquí Picado, Dominican Republic, illustrating the structure characteristic of each: (a) legume-dominated scrub forest on a site abandoned from farming 31 y previously; (b) mixed-species old-growth forest on land never known to have been placed in cultivation.

present residents were among the area's eventual agricultural settlers, and members of the second generation of this settlement had no trouble recalling the forests that were felled. The nine oldest residents interviewed were born between 1904 and 1920. Each tree they named as characteristic of the earlier forests is presented in Table 3a in order of its frequency of mention among these nine respondents, together with its abundance

within samples of the two forest types. Only three of the forty-two trees mentioned were encountered more often in scrub forest sample plots, which encompassed nearly twice the total area of the old-growth plots. Fully two-thirds (twenty-eight) of these species were found exclusively or in substantially higher numbers in old-growth forest. Four of the listed species were not recorded in any of the sample plots although they

**Table 1** (a) Total numbers of individuals, species, and higher taxa of woody plants found in given areas of old-growth forest and scrub forest samples, Jaiquí Picado, Dominican Republic. (b–e) Common indices for different components of species diversity of the two forest types; discussion of and equations for these indices may be found in Pielou (1975), Magurran (1988), Ludwig & Reynolds (1988), and Baev & Penev (1995).

	Old-growth forest	Scrub forest
a. Totals for community samples:		
Number of sites	7	14
Number of 200 m <sup>2</sup> plots	31	57
Aggregate sampling area (m <sup>2</sup> )	6200	11400
Individuals (N)	2122	1611
Species (S)	105	56
Genera	85	49
Families	40	27
Mean number of species per 200 m <sup>2</sup> plot	16	6
Expected number of species in 6200 m <sup>2</sup>	105	45
b. Indices of species richness:		
Margalef (R1)	13.58	7.45
Menhinick (R2)	2.28	1.40
c. Indices of heterogeneity:		
Fisher's log series ( $\alpha$ )	23.20	11.30
Hill (N1, expH')	36.00	8.64
Shannon and Wiener (H')	3.58	2.16
d. Indices of evenness:		
Hill (N2/N1, E')	0.58	0.46
Pielou (J', E1)	0.77	0.54
e. Indices of dominance:		
Berger-Parker (Nmax/N)	0.13	0.46
Simpson ( $\lambda$ , N2 <sup>-1</sup> )	0.05	0.25

were seen during reconnaissance walks. Three others – *Guarea guidonia* (L.) Sleumer, *Tetragastris balsamifera* (Sw.) Kuntze, and *Calophyllum calaba* L. – have evidently disappeared from Jaiquí Picado. These extirpated species, together with the uncommon *Ceiba pentandra* (L.) Gaertn. – all regarded as primarily characteristic of river banks by respondents familiar with them as well as by independent botanical sources (Hager & Zanoni, 1993) – were the only species remembered from the former vegetation that were described as being restricted to a particular topographic position. If the other species were cut mainly from lands to be cultivated, they undoubtedly once grew on sites now occupied by scrub forest.

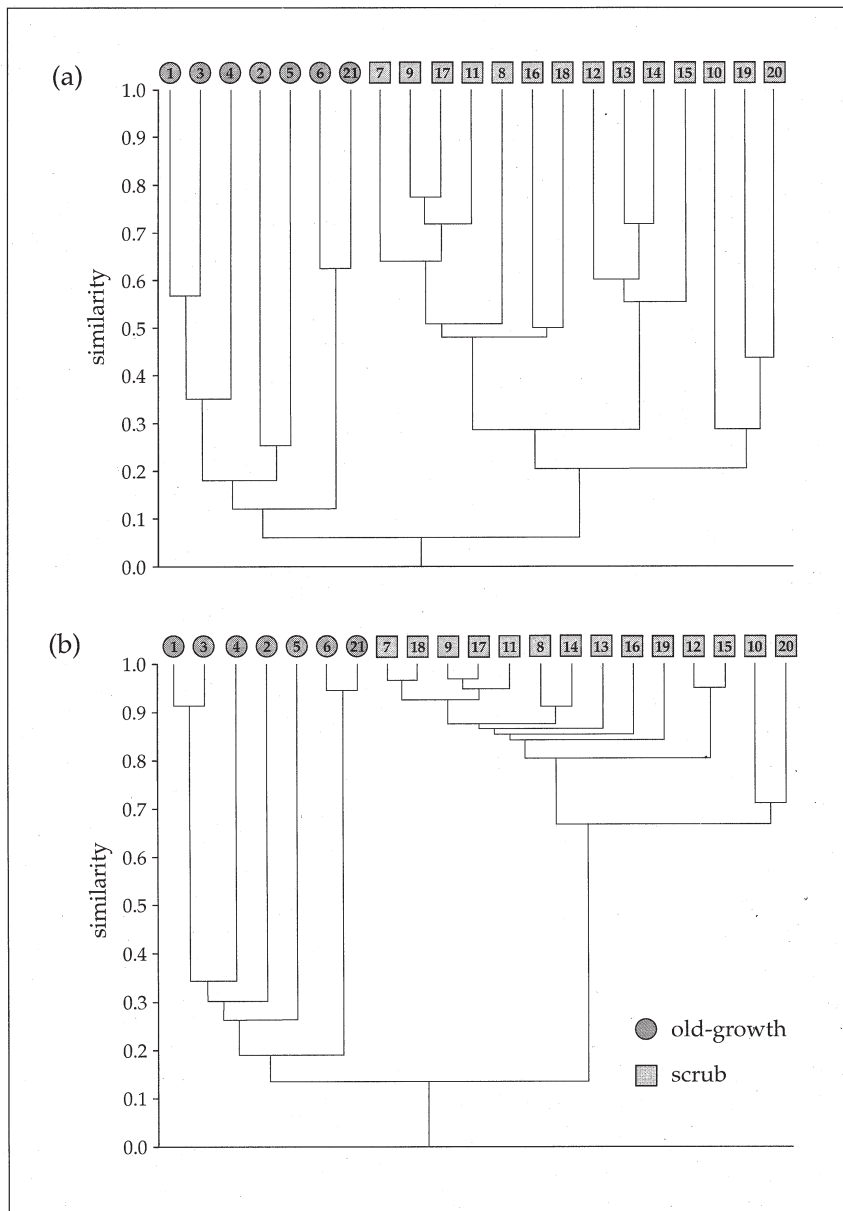
Conversely, the same people reported without exception that the three leguminous species now dominating scrub forests – *Acacia macracantha* Willd., *Haematoxylon campechianum* L., and *Prosopis juliflora* (Sw.) DC., in descending order of present abundance – were virtually absent from the earlier forests, regardless of site (Table 3b). The status of these trees as recent invaders was unsuspected by most members of younger generations in Jaiquí Picado, but their elders could remember the approximate times of appearance of the scrub species, the sequence coinciding precisely among respondents. *A. macracantha* – the only one of these three species native to Hispaniola – was said to have been always present but quite rare until it began spreading about 1920, followed closely by *H. campechianum*, which appeared around 1925; *P. juliflora* was unknown in Jaiquí Picado before perhaps 1930 and remained uncommon there until the 1950s. These three species now grow throughout the landscape and, based on the present study, constitute an estimated 50% of individual trees and 61% of the basal area of all woody vegetation within Jaiquí Picado.

The old-growth and scrub forests differentiated by residents

of Jaiquí Picado can thus be taken as botanically distinguishable entities whose spatial distribution there reflects anthropogenic influences over the last 100 y rather than climatic zonation or differences in any of the edaphic or topographic variables considered. This may help to explain the reported difficulty of distinguishing between subtropical dry forest and subtropical thorn woodland when the former has been intensively utilized (e.g. Knudson *et al.*, 1988: 16). It also recommends re-examination of those classifications of Hispaniolan vegetation in which dry forest and scrub are demarcated as natural zones corresponding broadly with physical parameters of their sites or regions (Antonini, 1968: Fig. 7; Palmer, 1976: Fig. 9). Although drier parts of the island may have borne a variant of thorn woodland prior to European contact, the boundaries between present stands of *breña* and *monte de hojas* are unlikely markers of its original limits. Conversion to scrub forest apparently began centuries ago along some of the wider valley floors first taken for intensive herding. Though probably not unique, the remnant old-growth dry forest stands in Jaiquí Picado appear to be unusually intact fragments left dispersed among the highly altered scrub forest patches that are far more common today (Hager & Zanoni, 1993). Comparison of the species composition and structure of these two forest types in Jaiquí Picado reveals the character and magnitude of the effects of historical land use upon the vegetation.

#### Species composition of scrub v. old-growth forests

Species counts from samples are listed by site for each forest type and the species ordered according to total sampled abundance per type in Appendices Ia & Ib of Roth (1997); Table 1a summarizes these species and area data from samples



**Figure 3** Cluster diagrams based on species abundance matrices of old-growth and scrub forest woody plant samples, Jaiquí Picado, Dominican Republic, illustrating the range of groupings formed using different association indices and hierarchical clustering algorithms: (a) Weighted average linkage using index of Bray & Curtis (1957); (b) Single linkage using association index of Morisita & Horn (1966).

of the two forest types. The difference in richness of woody plant taxa is quite pronounced: within a plot area just over one-half that of scrub forest ( $6200 \text{ m}^2$  v.  $11,400 \text{ m}^2$ ), old-growth forest contains nearly twice the number (105 v. 56) of species, 1.7 times as many genera, and 1.5 times as many families. Given that the relationship of cumulative species number to sampling area is generally curvilinear within a given vegetation type, a rarefaction technique (Hurlbert, 1971; Baev & Penev, 1995) was employed to estimate the number of species to be expected in an area of scrub forest as small as that of the combined old-growth sample plots: the corresponding total thereby decreases to forty-five (Fig. 4; Table 1), or well below one-half of the species richness of old growth. At the scale of individual  $200 \text{ m}^2$  sample plots, old growth averages sixteen

species per plot, in contrast with six species per scrub plot (Mann–Whitney  $U = 2195$ ;  $n_1 = 31$ ,  $n_2 = 57$ ;  $P < 0.001$ ).

Comparison of these values with published species enumerations for other tropical dry forests is hampered by discrepancies in the areas surveyed as well as the sizes and types of plant counted, but the plotting of species-area values from a number of such studies in relation to the rarefaction curves for Jaiquí Picado (Fig. 4) facilitates such comparison across moderate differences in area. Among the data points shown in Fig. 4, only those from studies restricting counts to trees  $>10 \text{ cm d.b.h.}$  (open circles) are found below the species-area curve for scrub forest in Jaiquí Picado, where woody individuals as small as  $2.5 \text{ cm d.b.h.}$  were included in the samples. Most of the species-area values based on a comparably



**Table 2** Averages for site and soil characteristics of plots bearing old-growth *v.* scrub forest, Jaiquí Picado, Dominican Republic.

Site characteristics:	Mean [median] for:		Test statistic: <sup>1</sup>	Value	d.f. [n <sub>1</sub> , n <sub>2</sub> ]	P	Significance at 0.05 level
	Old-growth sites	Scrub sites					
<b>Topography</b>							
Slope (%)	71	36	<i>U</i>	1888.5	31, 57	<0.0001	*
Aspect: deviation from S ( ° )	101.3	91.6	<i>t</i>	0.398	18	0.6951	n.s.
Aspect: deviation from E ( ° )	108.5	115.5	<i>U</i>	56.5	6, 14	0.6207	n.s.
<b>Surface cover</b>							
Litter depth (cm)	2.5	1	<i>U</i>	2029	31, 57	<0.0001	*
Litter cover (%)	80	65	<i>U</i>	844.5	19, 57	0.1772	n.s.
Leaf size in litter (rank) <sup>2</sup>	5	3	<i>U</i>	1974.5	31, 57	<0.0001	*
<b>Physical soil characteristics<sup>3</sup></b>							
Air-dried sample density (g/cc)	0.988	1.105	<i>t</i>	-0.822	21	0.4206	n.s.
Sand in mineral fraction (%)	39.8	22.4	<i>t</i>	3.94	18	0.0010	*
Clay in mineral fraction (%)	19.0	26.3	<i>t</i>	-1.46	18	0.1624	n.s.
Organic matter (%)	11.5	11	<i>U</i>	73	6, 14	0.4329	n.s.
<b>Chemical soil characteristics<sup>3</sup></b>							
pH	7.65	7.7	<i>U</i>	57	6, 17	0.3092	n.s.
CEC (meq/100g)	126.6	113.6	<i>t</i>	0.786	21	0.4404	n.s.
<b>Extractable ions (ppm)</b>							
NH <sub>4</sub>	7	5	<i>U</i>	96.5	6, 17	0.0912	n.s.
NO <sub>3</sub>	33	38	<i>t</i>	-0.69	21	0.4979	n.s.
P	8.5	8	<i>U</i>	89	6, 17	0.2476	n.s.
K	143	205	<i>t</i>	-2.03	21	0.0548	n.s.
Ca	23844	22107	<i>t</i>	0.506	21	0.6178	n.s.
Mg	620	529	<i>t</i>	1.91	21	0.0695	n.s.
B	1.35	1.09	<i>t</i>	1.4	21	0.1757	n.s.
Mn	3.42	2.82	<i>t</i>	1.08	21	0.2919	n.s.
Zn	1	1	<i>U</i>	75.5	6, 17	0.8313	n.s.
Cu	0.2	0.665	<i>t</i>	-5.61	21	<0.0001	*
Fe	2.35	2.2	<i>U</i>	71.5	6, 17	1.0000	n.s.
Al	6.5	6	<i>U</i>	79.5	6, 17	0.6236	n.s.

<sup>1</sup> Mann-Whitney rank sum (*U*) tests were used in place of Student's *t*-tests for the ordinal leaf size rankings and all variables whose sampled data did not meet the assumption of normality; in these cases medians are reported in place of means and numbers per group in place of d.f.

<sup>2</sup> Ranks used for average surface area of leaves or leaflets in litter, with upper size limits in mm<sup>2</sup> and names assigned by Raunkiaer (1934) to the odd-numbered rankings, are: Rank 1, to 25 mm<sup>2</sup> (leptophyll); Rank 2, to 75 mm<sup>2</sup>; Rank 3, to 225 mm<sup>2</sup> (nanophyll); Rank 4, to 675 mm<sup>2</sup>; Rank 5, to 2025 mm<sup>2</sup> (microphyll); Rank 6, to 6075 mm<sup>2</sup>; Rank 7, to 18225 mm<sup>2</sup> (mesophyll).

<sup>3</sup> Physical characteristics of soils were determined by the author at the Soil Laboratory of the Department of Plant and Soil Sciences, Stockbridge Hall, University of Massachusetts, Amherst, MA; chemical tests were performed by the Cooperative Extension Soil and Plant Tissue Testing Laboratory of the West Experiment Station, University of Massachusetts, Amherst, MA. References for procedures are cited in text.

wide range of diameters (closed circles), among them a dry forest in the southern Dominican Republic (García & Alba, 1989) and one in Jamaica (Gentry, 1988), lie closer to the curve for old-growth forest. Of these, only the data from Guánica, Puerto Rico (Murphy & Lugo, 1986b), approximated the rarefied value for scrub forest. The low diversity in Guánica seems noteworthy given that the Puerto Rican forest shows a closer overlap in species composition as well as a more similar distribution of species abundances to old-growth than to scrub forests of Jaiquí Picado. Although the dry forest in Guánica has held protected status for over 60 y and was once viewed as virtually pristine (Ewel & Whitmore, 1973: 20), parts have been subjected to occasional removal of trees for timber and charcoal, cultivation of crops, browsing by feral goats and pastured livestock, and planting of introduced trees (Lugo *et al.*, 1978; Wadsworth, 1990). Human influences are considered to

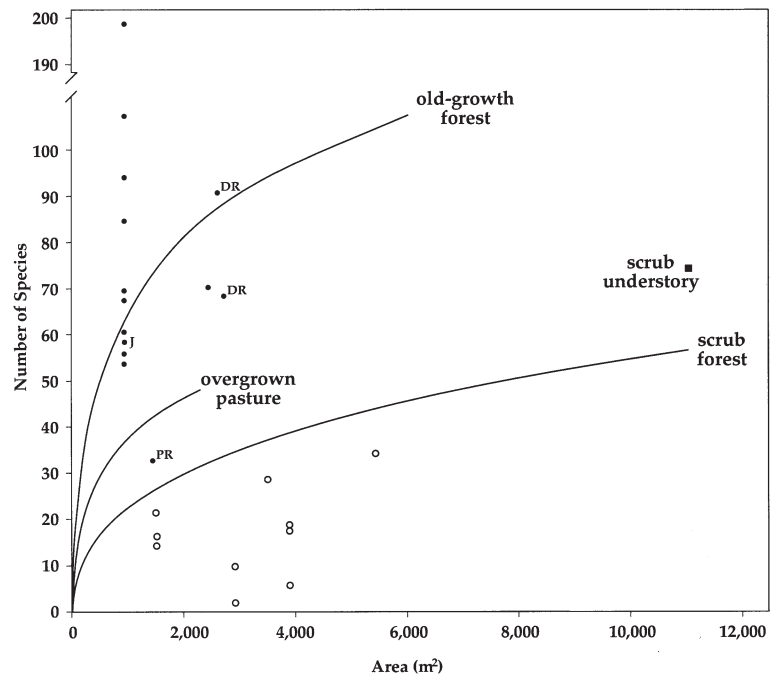
account in part for the limited structural development and species numbers of the Guánica forest (Murphy & Lugo, 1990; Murphy *et al.*, 1995), as appears to be the case for the scrub stands in Jaiquí Picado, though the contrasts between these forests should also prove instructive. The entire flora of Puerto Rico amounts to only 60% of the number of species on Hispaniola (Liogier, 1982: 13), a difference possibly associated with the relative size of the islands (MacArthur & Wilson, 1967).

Not only is scrub forest in Jaiquí Picado relatively poor in species; in addition, the distribution of individuals among these species shows considerable skew. The three prominent tree species referred to earlier encompass 70% of all individuals found within this type; this same percentage of woody individuals in old-growth forest includes a minimum of fifteen species. At the level of individual stands, the most abundant

**Table 3** (a) Woody plant species mentioned by oldest residents of Jaiquí Picado, Dominican Republic, as characteristic of the forests cleared for cultivation by their parents, together with the abundance of each of these species found in the old-growth and scrub forest samples of the present study. Botanical designations could be established with certainty in all but three cases in which the local common name identifies a tree only to genus level and two cases in which a single name may refer to two unrelated species; the abundances noted for these exceptions are sums of the values for all species included in the common name. (b) The three predominant tree species in scrub forests of Jaiquí Picado, Dominican Republic, with their present abundances in sample plots and the number among the nine oldest residents who mentioned each species as having been nonexistent or very rare in preagricultural forests. Vernacular names listed for these three species are universal in Jaiquí Picado but may differ or be interchanged even over relatively short distances within the Dominican Republic and hence, as is true of all common names reported herein, are relevant only to the present study.

	According to (number out of nine oldest respondents)	Species	Abundance in samples of	
			Old-growth (total no. in 6200 m <sup>2</sup> )	Scrub forest (total no. in 11400 m <sup>2</sup> )
(a) Trees characterising early forests in Jaiquí Picado (local names)				
jaiquí	9	<i>Bumelia salicifolia</i> (L.) Sw.	6	0
uvero	8	<i>Coccoloba diversifolia</i> Jacq.	28	0
cigua, c. blanca, c. prieta	8	<i>Ocotea coriacea</i> (Sw.) Britton/ <i>Drypetes alba</i> Poit.	189	1
caoba	8	<i>Swietenia mahagoni</i> (L.) Jacq.	0	0
ciguamo	7	<i>Krugiodendron ferreum</i> (Vahl) Urb.	58	0
caya	7	<i>Mastichodendron foetidissimum</i> (Jacq.) Cronq.	22	1
candelón	6	<i>Acacia scleroxyla</i> Tussac	55	4
pinillo	6	<i>Zanthoxylum flavum</i> Vahl	5	3
almácigo	5	<i>Bursera simaruba</i> (L.) Sarg.	79	7
roble, roble blanco	5	<i>Catalpa longissima</i> (Jacq.) Dum.-Cours.	2	1
palo amarillo	3	<i>Chlorophora tinctoria</i> (L.) Gaud.	3	0
guayacán	3	<i>Guaiacum officinale</i> L.	12	0
guácima	3	<i>Guazuma ulmifolia</i> Lam.	0	38
guaconejo	2	<i>Amyris</i> sp(p).	70	1
canela	2	<i>Canella winterana</i> (L.) Gaertn.	10	4
guacimilla	2	<i>Cordia alliodora</i> (R. & P.) Oken	1	1
yaya	2	<i>Oxandra lanceolata</i> (Sw.) Baill.	68	0
cacheo	2	<i>Pseudophoenix vinifera</i> (Mart.) Becc.	1	0
aguacero	1	<i>Adelia ricinella</i> L./ <i>Bumelia obovata</i> (Lam.) A. DC.	14	6
caimoní	1	<i>Ardisia obovata</i> Desv. ex Ham.	10	0
algodón blanco	1	<i>Ateleia microcarpa</i> (Pers.) D. Dietr.	2	0
mara	1	<i>Calophyllum calaba</i> L.	0	0
ceiba	1	<i>Ceiba pentandra</i> (L.) Gaertn.	1	0
guano	1	<i>Coccoloba tinctoria</i> sp.	1	0
palo amargo	1	<i>Colubrina elliptica</i> (Sw.) Brizicky & Stern	89	5
roble prieto	1	<i>Ehretia tinifolia</i> L.	3	30
airraján	1	<i>Eugenia ligustrina</i> (Sw.) Willd.	14	0
escobón	1	<i>Eugenia</i> sp(p).	274	3
higo	1	<i>Ficus</i> sp(p).	1	0
palo de burro	1	<i>Guapira domingensis</i> (Heimerl) Alain	9	0
cabirma	1	<i>Guarea guidonia</i> (L.) Sleumer	0	0
canelilla	1	<i>Myrcianthes fragrans</i> (Sw.) McVaugh	91	0
aniseto	1	<i>Piper amalago</i> L.	3	0
crevajacha	1	<i>Polygala penaea</i> L.	3	0
almendro	1	<i>Prunus myrtifolia</i> (L.) Urb.	1	0
córbano	1	<i>Pseudalbizzia berteriana</i> (Balbis) Britton & Rose	1	35
palo de leche	1	<i>Rauwolfia nitida</i> Jacq.	0	0
palma	1	<i>Roystonea hispaniolana</i> Bailey	0	0
saúco	1	<i>Tecoma stans</i> (L.) Humb., Bonpl., & Kunth	0	0
amacey	1	<i>Tetragastris balsamifera</i> (Sw.) Kuntze	0	0
memiso	1	<i>Trema micrantha</i> (L.) Blume	28	0
pino de teta, pino macho	1	<i>Zanthoxylum</i> sp(p).	3	5
(b) Trees newly common in Jaiquí Picado (local names)				
aroma	9	<i>Acacia macracantha</i> (Humb. & Bonpl.) ex Willd.	22	734
campeche	9	<i>Haematoxylon campechianum</i> L.	14	294
cambrón	9	<i>Prosopis juliflora</i> (Sw.) DC.	11	106

**Figure 4** Curves of expected number of woody plant species vs. sampling area, developed using a rarefaction method (Hurlbert, 1971; Baev & Penev, 1995) from samples of old-growth and scrub forests as well as overgrown pastures in Jaiquí Picado, Dominican Republic. ■ = Woody plant species in total sampled area of scrub forest understory, Jaiquí Picado. ● = Plots of species vs. area for woody plants  $\geq 2.5$  cm d.b.h. (the same minimum diameter used in the present study) in tropical dry forests elsewhere, as reported in García & Alba (1989); Murphy & Lugo (1986b); Gentry (1988); Lott *et al.* (1987); and Sussman & Rakotozafy (1994). ○ = Species-area plots for woody plants  $> 10$  cm d.b.h. in tropical dry forests elsewhere, as reported in Murphy & Lugo (1990) and Sawyer & Lindsey (1971). Data corresponding to other Antillean locations are those from Azua, Dominican Republic (DR); Round Hill, Jamaica (J), and Guánica, Puerto Rico (PR).



species were highly consistent among the fourteen scrub sites sampled, whereas the trees most common in old-growth samples varied substantially from site to site. Several common indices of species richness, evenness, and their amalgamation as 'heterogeneity' are shown for each forest type in Table 1b-e; though these indices for scrub forest were necessarily calculated from full data sets prior to rarefaction, every index of species diversity and/or evenness calculated for the old-growth forest assumes close to double the value for the scrub forest type, while scrub forest shows higher values of all quantities expressing concentration of dominance. Although comparisons across methodologies must be viewed with caution, the uneven species composition of these Dominican scrub forests seems particularly manifest in the light of Martijena & Bullock's (1994) contrast of monospecific-dominant with mixed dry forests at the same latitude in western Mexico. The inverse Simpson index of scrub forest in Jaiquí Picado ( $\lambda^{-1}=4$ ) is identical with the value that these authors report for monodominant forests of *Celaenodendron mexicanum* Standley, whereas this evenness index for old-growth forests in Jaiquí Picado ( $\lambda^{-1}=21$ ) substantially exceeds that of the mixed forests in the Mexican study ( $\lambda^{-1}=13$ ).

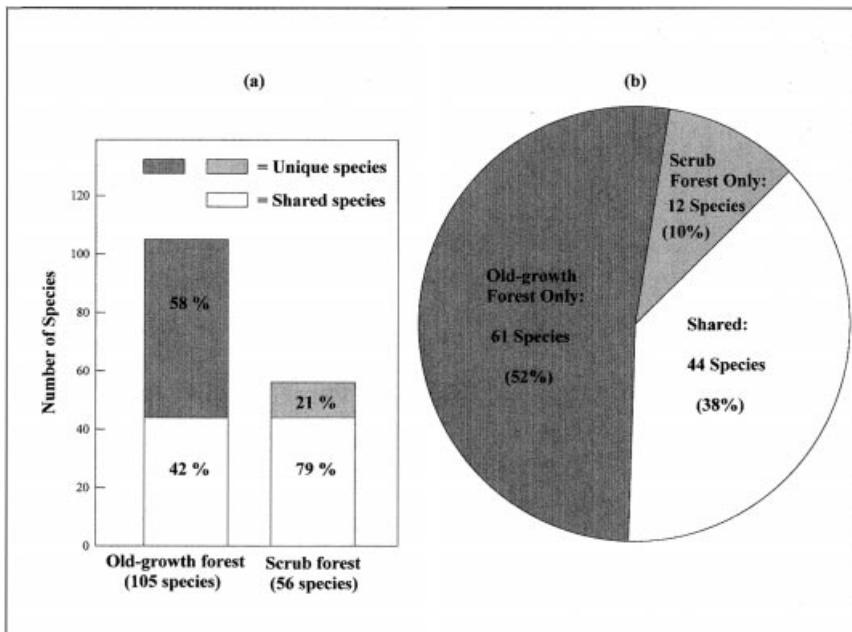
Comparison of the numbers of woody plant species exclusive to each of the two designated forest types in Jaiquí Picado further accentuates this difference in botanical richness. Over half of the old-growth species were absent from scrub, whereas only one-fifth of scrub species were not encountered in old-growth plots (Fig. 5a). Expressed as a proportion of all species recorded in samples, only 10% of the aggregate species list was found only in scrub forest, whereas 52% of the total was restricted to old growth (Fig. 5b); collections and observations made outside of the inventoried plots suggest that the difference would increase with further sampling. The high species density

within the small remaining area of old-growth forest, together with the large proportion of species restricted to this forest type, underscore the significance of the old-growth patches as local concentrations of biological diversity.

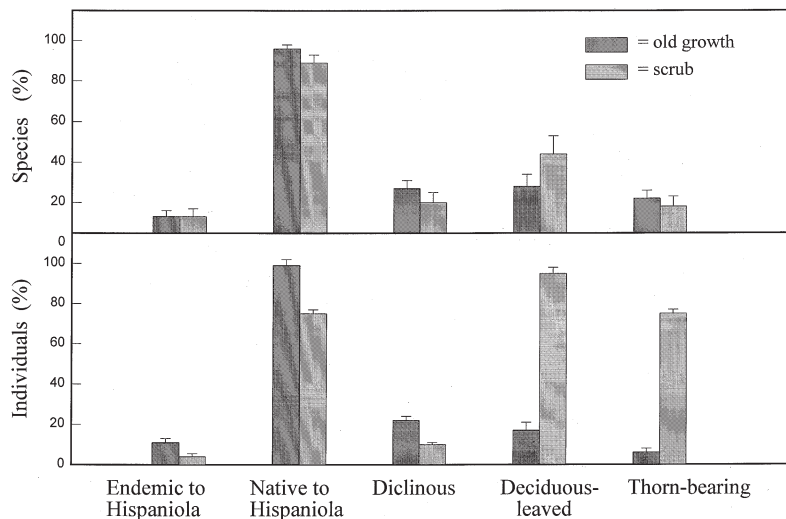
#### Species characteristics in the two forest types

Beyond their taxonomic composition, scrub and old-growth forests differ conspicuously in certain ecological and distributional characteristics of their constituent species. A few such features that could be determined for most or all of the 106 identified species and seven additional genera in the samples are noted in Appendices 1a & 1b of Roth (1997); their prevalence among species and individuals of the two forest types is illustrated in Fig. 6.

Depletion of native species is one common aspect of altered vegetation; the elimination of narrowly endemic elements is of particular note. Some tropical dry forests have high rates of endemism (Gentry, 1995), and tropical islands often have unusual concentrations of endemic species (Gentry, 1986). The forest samples from Jaiquí Picado included a total of sixteen woody plant species considered endemic to Hispaniola. Old-growth forest samples contained twice the number of endemic species found in scrub forests and more than three times their density by area, although due to the diminished species richness of scrub forest the percentage of endemic species in the two forest types did not differ; the same was true of native species (Fig. 6a). When the abundance of each species is taken into account (Fig. 6b), the differences are highly significant statistically: scrub forests had a markedly lower proportion and density of individual endemics and, due in large part to the abundances of *H. campechianum* and *P. juliflora*, the proportional presence of native woody plants was distinctly



**Figure 5** Unique and shared woody plant species in old-growth and scrub forest samples, Jaiquí Picado, Dominican Republic (a) as percentages of species found in each forest type and (b) as percentages of all species found in forest samples.



**Figure 6** Percentages of woody plant species and individuals having stated distributional and ecological characteristics in samples of old-growth vs. scrub forests, Jaiquí Picado, Dominican Republic. Species counted as native to the island include endemics; other terms are explained in text. (Bar extensions indicate +1 SE.)

reduced as well. This substantial displacement of native trees and shrubs by naturalized post-Colombian introductions signifies that scrub forest as described herein is not only new to Jaiquí Picado but could never have existed as a forest type in Hispaniola prior to the sixteenth century.

Trees dependent upon outcrossing may also be undergoing differential exclusion from scrub. Species having physiological barriers to self-fertilization, and thereby requiring multiple propagules for establishment of new populations, are at a relative disadvantage for island colonization; but the prevalence of such barriers in older oceanic island floras suggests that outcrossing, primarily through dioecy, eventually takes on selective advantage within the circumscribed populations of islands (Carlquist, 1974; Ehrendorfer, 1979). Although insufficient data on dichogamy (asynchronous maturation of

stigma and anthers), self-incompatibility, and other types of functional dioecy were found for the flora of Jaiquí Picado to permit their consideration here, information on the various forms of dicliny (possession of unisexual flowers) provides a minimal indication of the tendency toward outcrossing for the species in each forest type. If the native portion of the old-growth forest samples can be considered an approximation of the original vegetation of Jaiquí Picado, dioecious species constituted 16% and diclinous ones collectively 28% of that flora. Scrub forest vegetation differs from this in a direction that could lead to an augmenting trend. Scrub forest samples produced only eleven diclinous species compared to the twenty-eight found in old-growth forest (Fig. 6a), although again given the difference in total species numbers the proportional representation was not significantly different. Among

individuals, 22% of the composition of old-growth forest belonged to diclinous species, in highly significant contrast to 10% of the trees in scrub forest (Fig. 6b). On the one hand, members of diclinous species have not been proportionately successful establishing themselves in the scrub forest type; on the other hand, the considerable fragmentation of present old-growth forest, together with its probable effects on pollinators, may be isolating members of less abundant species such that the lack of self-fertilization would once again constitute a disadvantage. Diclinous species in Jaiquí Picado include primarily uncommon ones, unlike the situation reported by Hubbell (1979) in Costa Rican dry forests, as indicated by the fact that they comprise only 22% of the individuals of old-growth forest while representing 27% of its species; the corresponding ratio is still lower for diclinous species in scrub forest.

Because the occurrence of deciduousness and thorns is often specified in descriptions of dry forest types, and recognition of these traits is expressed in the local distinction between *monte de espinas* and *monte de hojas*, it is of interest to compare old-growth and scrub forests with regard to these characteristics as well. Published information on foliage type was found for two-thirds of the species, which it seems reasonable to assume is a random subset of the flora in regard to this trait; all thorn-bearing species were readily identifiable as such, although further separation by type and size of spines would be more meaningful ecologically. Samples of old-growth forest had somewhat higher numbers of both deciduous and thorn-bearing species than scrub forest samples, with the lower percentage of the former and higher percentage of the latter not significant in either case (Fig. 6a). Here again, however, the concentration of scrub forest individuals in a few similar species contributes to pronounced differences in the vegetation as proportionally constituted: 95% of the individual trees classified in scrub forest samples were deciduous as contrasted with only 17% of those in old-growth forest, and 75% of scrub forest trees had thorns as opposed to 6% of individuals in old-growth plots (Fig. 6b).

These features lend the scrub forest vegetation a spare and uninviting appearance captured in many of its popular and botanical designations. Both have been attributed directly or indirectly to drought (Schimper, 1903), although an understanding of any selective advantages would require more detailed consideration of the array of morphological and physiological traits coexisting within this same climate, together with past and newly existing faunal influences. Walter (1973) and Medina & Cuevas (1990) discuss the costs and benefits of deciduousness vs. the evergreen sclerophyll condition also exhibited by many of the old-growth trees and shrubs in Jaiquí Picado; their relative advantages are undoubtedly influenced by factors such as rooting depth, site exposure, and canopy position; and selection within present scrub areas must favour rapid early growth, sprouting ability, and juvenile defence against large introduced herbivores. Janzen (1988a) reported that Costa Rican secondary growth shows greater deciduousness than the forests it replaces, attributing this difference to the predominance in early regeneration of fast-growing species, which are typically deciduous. As properties

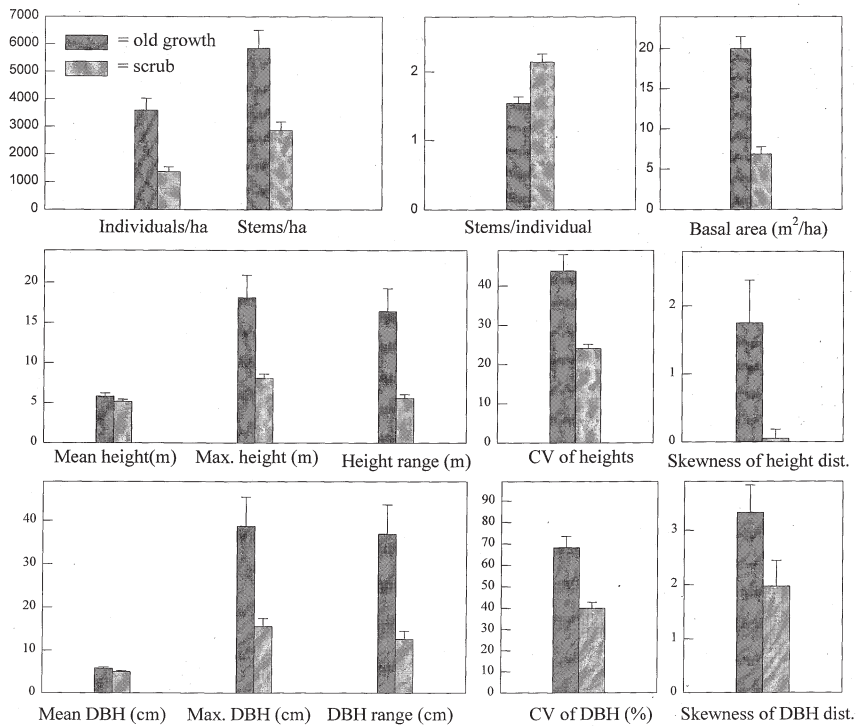
of the present forest cover, thorns and a variety of leafing characteristics have unquestionable ecological effects of their own, including those mediated by human actions. For example, farmers use type and depth of leaf litter as an indication of the readiness of a given plot of land for cultivation; and, although aware of the damage wrought by fire on exposed slopes, they justify broadcast burning of slash from the scrub forest they clear for agriculture based on the necessity of ridding prospective farm plots of scattered fallen branchlets with their dangerous thorns (Roth, 1997).

Prevalence of thorns in the scrub forests of Jaiquí Picado does not stem from a proliferation of cacti such as those characterizing the vegetation of some drier areas of the Dominican Republic (Ekman, 1930; Ciferri, 1936; García & Alba, 1989; Hager & Zanoni, 1993). Two Cactaceae species with a total of only six individuals were found in scrub forest samples, as compared with three individuals of a single species recorded in old growth; doubling within such low values is not statistically significant, and the ecological importance of this life-form in either community appears minimal. Whether more cacti might have prospered among second growth without its invading leguminous trees or the repeated clearing of brush from maintained pastures is uncertain.

Woody vines also show comparably low representations in scrub and old-growth forests, although herbaceous ones – not recorded in these samples – appeared to be more abundant in some scrub plots. Only twenty-four woody vines within four species were noted in scrub forest samples and thirty-seven individuals representing seven vine species were found in old-growth ones; proportions of neither species nor individuals differed significantly between the two forest types.

The ability to sprout from roots or cut stems would seem especially important where browsing, pasture clearing, and harvesting of wood have been concentrated. In dry forests cut at Guánica, Puerto Rico, 62% of individuals in two-year-old regeneration were of sprout origin (Murphy & Lugo, 1986b) and half the woody plants found in 13-year-old regrowth were from sprouts (Dunevitz, 1985: 56). Sprouting ability is not mentioned in most descriptions of Dominican species and therefore could not be quantified for comparison between the two forest types as in Fig. 6; nor was field designation of sprout vs. seed origin of individual stems attempted, given that not all clumping can be attributed with certainty to sprout origin (Howard & Zanoni, 1989). However, the average number of stems per apparent individual in scrub forest was 40% higher than that in old-growth forest (Fig. 7). Residents were questioned about the sprouting ability of the species with which they were familiar, and although many could not recall ever having seen certain species felled, or qualified their responses according to age and condition of the stumps when cut, substantial agreement existed regarding the trees least capable of vegetative regeneration: these were ones largely restricted to the old-growth forests. Of the twenty-six species most commonly reported as unable to sprout, five were not encountered in field samples, eighteen were found exclusively or more abundantly in old growth, and only three appeared more often in the scrub forest samples.

Species recorded during traverses or mentioned by local



**Figure 7** Average stand characteristics of sampled old-growth and scrub forests, Jaiquí Picado, Dominican Republic. CV = coefficient of variation. (Bar extensions indicate +1 SE.)

residents, but not encountered in sample plots, were excluded from the above comparisons because their characteristics cannot adequately be related to community type. Those with the most restricted numbers and distributions, however, were associated primarily with old-growth patches. It is noteworthy that the three trees mentioned above that are thought to have disappeared from Jaiquí Picado in recent decades possess features found to be more prevalent in old-growth vegetation: all are native, evergreen, and thornless; two of the three have diclinous flowering; and at least one is regarded as incapable of sprouting. Among the species missed in sampling were several endemics, at least one of which, *Antirhea heteroneura* Urb. & Ekman (Rubiaceae) is considered to be quite rare (R. G. García, pers. comm. 1993). Although insignificant numerically, the disappearing old-growth species may have important consequences for the organisms with which they interact (Gilbert, 1980; Terborgh, 1986; Smythe, 1987).

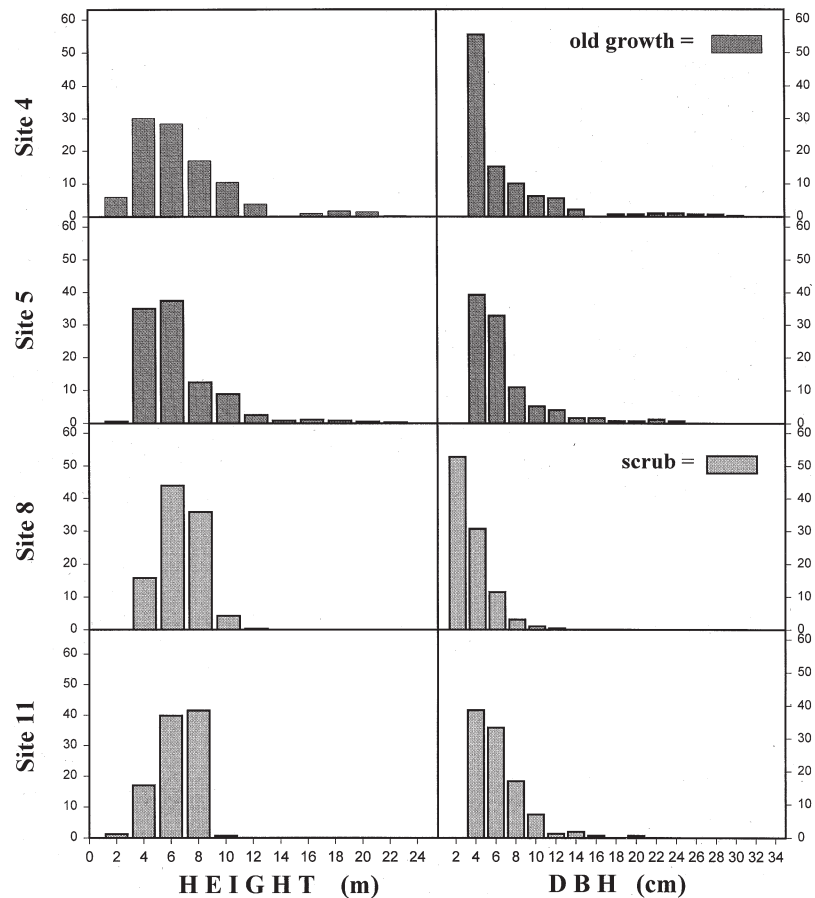
### Structure of scrub v. old-growth forests

Given the differing origins and composition of old-growth and scrub forests, marked differences might be expected in their structure as well. Younger forests on a given site tend to have trees of shorter stature and smaller average girth. In young even-aged stands arising after disturbance, especially those dominated by a single species, the diameter – and even more so the height – distribution of trees is also typically narrower and more normal than that found in older forests (Smith, 1962). Aggregate basal area usually shows a monotonic, albeit decelerating, increase with age; but competition among trees in developing forests leads to a reduction in the density of

individuals or stems per hectare over time, except where successively more tolerant species come to occupy lower strata (Spurr & Barnes, 1980; Peterken, 1996).

Structural characteristics of the sampled forest patches are summarised in Fig. 7. Mean stem dimensions, and especially their combined basal area per hectare, are generally greater for the old-growth samples from Jaiquí Picado than the values cited for other Dominican dry forests in the few detailed inventories that have been reported (Luciano & Checo, 1986; Hernández & Disla, 1987; Knudson *et al.*, 1988; García Brito, 1992). Mean height and diameter of trees sampled in old-growth forests exceed the corresponding average dimensions found in scrub, but the observed differences are not statistically significant. Similar average heights despite different stand ages and origins accord poorly with results of earlier studies (Brown & Lugo, 1990) and suggest that the old-growth stands may have had some of their larger trees culled or that the trees in scrub forests grow relatively quickly to a level at which height growth in the old-growth stands has tended to level off. The latter possibility concurs with several farmers' explanations and with the widespread recognition of the low average stature of mature dry forests (Ewel, 1977); but the cut stumps that were found within every site, and that dominated sample densities in a few scrub plots, indicate that human activities cannot be discounted among the influences shaping these forests' structure.

Frequency distributions of the height and diameter of trees, as exemplified in Fig. 8, better illustrate the structural differences to be found between the two forest types. Scrub stands show rather more concentrated size distributions than do old-growth ones, in which small numbers of very large trees



**Figure 8** Relative frequency distributions for height and diameter of woody stems in old-growth and scrub forest types, Jaiquí Picado, Dominican Republic, at four sites having near-average tree sizes and densities for their types: (a) old-growth site 4: mean height = 6.3 m; mean d.b.h. = 5.5 cm; density 3613 individuals/ha with 5875 stems/ha; (b) old-growth site 5: mean height = 6.0 m; mean d.b.h. = 6.6 cm; density 3640 individuals/ha with 4450 stems/ha; (c) scrub forest site 8: mean height = 5.8 m; mean d.b.h. = 4.9 cm; density 2213 individuals/ha with 4328 stems/ha; (d) scrub forest site 11: mean height = 5.8 m; mean d.b.h. = 5.1 cm; density 1425 individuals/ha with 2908 stems/ha.

and large numbers of small ones contribute to the 'inverse-J'-shaped curve associated with balanced uneven-aged forests (Smith, 1962). This contrast is expressed in Fig. 7 by the markedly greater maxima, and hence ranges, of both height and d.b.h. in old-growth stands and the significantly greater positive skew in their height and diameter distributions than in those for scrub stands. Even eliminating the disproportionate influence of the few largest trees through the use of standard deviation, relativised as coefficient of variation, as an indication of the bulk of each distribution, the spread of both height and diameter is distinctly wider in the old-growth forests (Fig. 7).

Mean sizes of woody plants, then, are presently inadequate to differentiate the structure of these forest types. The canopy of old-growth forests is less restricted to a single stratum, having instead a scattering of tall trees and increasing numbers of smaller ones that combine to lower the average height of the stand while augmenting its total basal area (Fig. 7). The multilayered effect this produces within the old-growth forests, together with the fact that their stand densities are significantly greater (Fig. 7) and their individual crowns often deeper, contributes to the more pronounced shade noticeable beneath them. Scrub forest canopies do not reach as high, but their relative dearth of smaller trees and shrubs also leaves them with a more open understory. The smallest diameter classes within the scrub forests depicted in Fig. 8 are largely composed

of multiple stems or low branches, of which scrub forests have a significantly higher ratio per tree (Fig. 7). The more intense heat and light under scrub forests may inhibit establishment of shade-adapted species in the lower strata, or conversely, these environmental conditions may be viewed as resulting from the absence of understory species due to other factors such as grazing, poor dissemination, root competition, or conceivably allelopathy; more thorough knowledge of the particular interactions involved would be of help in predicting future dynamics of these stands.

According to descriptions provided by older residents of Jaiquí Picado, the structure of the original *montería* of the area was still further developed in the direction of the present old-growth forests, influenced in part by many large specimens of the species in Table 3a. These accounts were often quite specific in relating the names, sizes, and remembered locations of particular trees. Most people gestured with outstretched arms to indicate the girth of stumps once commonly encountered, and a former sawyer described beams 'squared off at up to 30 inches' whose removal he had witnessed (all quotations from Roth, 1997). Felled boles of some trees 'bridged entire ravines, from one side to the other.' A number of respondents recalled that 'as many as four men had to keep at a single trunk with axes' to cut down the larger ones. Very few trunks of comparable size presently exist in Jaiquí Picado.

Elders' accounts of early forests did not concentrate solely on the size of the tallest trees; several elaborated that there were 'trunks of all sizes', 'from smallest to largest – whatever you pleased', with 'plenty of smaller shrubs beneath' and 'little trees of the same kinds as the large ones, that sprouted from their fruit', indicating that the wide frequency distributions existed then as well. Nearly all mentioned the preponderance of 'shady, leafy trees like the ones in old growth – none of these thorny ones.' Allusion to the deep, cool shade beneath these forests was another common feature of people's descriptions; and the thick litter layer beneath them and their 'black' soils were cited by many as reasons for bountiful first crops. Another recurring element in these descriptions was their reference to the large quantities of dead trunks and branches to be found on the forest floor, enough so that plentiful fuel could be obtained without resorting to the cutting of live wood. Seasoned firewood is a rarity now in Jaiquí Picado, where locally produced charcoal is presently kept for use in the absence of fossil cooking fuel. The presence of rotting logs has been taken as a sign of primary vegetation in Puerto Rican forests (Wadsworth, 1950); in Jaiquí Picado, substantial quantities of dead wood were recorded only on the old-growth site most remote from settlement.

### Processes affecting forest change

If the differences in structure and composition between old-growth and scrub forests can be associated in some way with prior cultivation, the specific causes and processes involved in the incursion of scrub forest are nevertheless far from obvious. Activities historically associated with farming in Jaiquí Picado have included forest clearing and fragmentation; various degrees of stump removal, ploughing, and burning; planting of mixed subsistence or cash crops for relatively short periods, often followed by sowing of exotic pasture grasses and/or periodic brush removal; grazing by introduced livestock; and gradual abandonment to a forest fallow. These have been interspersed with selective removal of woody species for timber or other uses; virtual clearfelling, usually of scrub species, for charcoal production; hunting of native wildlife; release and wild proliferation of various exotic ungulates; and intentional or accidental release of alien plants and predators. Efforts to distinguish the differential effects of these influences are hindered by their multiplicity, the difficulty of obtaining reliable land-use histories of sufficient detail and chronological extent, and the lack of localized baseline data to characterize prior vegetation. One recent study (Molina, 1998) utilizes sequential aerial photographic coverage, direct sampling of forested plots, and interviews with local informants to ascertain the effects of a number of previous land uses in a Puerto Rican dry forest. The activities associated with the past century of human settlement in Jaiquí Picado, however, have often succeeded each other in variously repeating and not entirely predictable permutations on a given parcel of land, such that a univariate demarcation of influences is unlikely to be applicable.

Historical accounts helpful in sorting out these influences are detailed elsewhere (Roth, 1997); overall they indicate that the openings created for early agriculture did not, in themselves,

lead to the substantial reduction in floral diversity characteristic of scrub. The eventual diffusion of scrub growth over abandoned cropland responded instead to a synergism among the clearings maintained for grazing, a number of aggressive native and introduced thorn trees, cattle as the vectors for these trees' seeds, and the inhospitable conditions offered by pastures for the regeneration of old-growth forest species. Widespread charcoal production, which is often assumed responsible for dry forest degradation in the Dominican Republic, postdated these changes and was confined for the most part to the already low-diversity scrub stands. Meanwhile, selective commercial extraction of timber trees contributed to botanical impoverishment within standing old-growth forest.

### Present trends: will scrub become old-growth?

The substantial reduction and fragmentation of old-growth dry forest and the marked loss of species that has accompanied the spread of scrub cover raise questions about the possibility of reversing these trends. In particular, it seems pertinent to inquire whether present scrub forest, left to develop on its own, might eventually approach the composition of old-growth forest through spontaneous successional processes. The likelihood of any present stands being left unharvested for the requisite period is a different, if closely related, consideration that will be affected largely by political and economic circumstances (Roth, 1997).

Like the perturbations themselves, the factors that influence forest regeneration following disturbance are also multiple and interacting (Hewetson, 1956; Sousa, 1984; Murphy & Lugo, 1986a; Janzen, 1988b). Prognoses depend on the extent and severity of the alterations that have taken place as well as the characteristics used to gauge forest recuperation. Thus, Ewel (1977, 1980) characterized tropical dry forests as relatively resilient because the regenerating stands in dry forests he studied were approaching their (substantially lower) mature heights at a rate faster than that of second-growth tropical moist forests, and others (Murphy *et al.*, 1983) have noted similar relative gains in biomass and a rapid early increase in the percentage cover of dry forest regeneration. Structural development in successional dry forests nonetheless appears to be far slower than that of moist forests when measured on absolute scales (Lugo *et al.*, 1981); Janzen (1988a) predicted that a minimum of 100–1000 y would be necessary for the newly regenerating vegetation of tropical dry forest zones in Costa Rica to approximate the structure of the previously existing forests. In regard to biological diversity, Brown & Lugo (1990) projected that the species richness of mature tropical forests would be attainable after some 80 y of regrowth, based on rapid rates of species accumulation documented in dry and other tropical secondary forests, but they also recognized that the species composition of early successional vegetation seldom reproduces that of old growth. In plots of 13-y-old dry forest regeneration in Puerto Rico, Dunevitz (1985: 91) encountered 59% of the tree species found in nearby mature forest plots, but the harvesting treatment applied to her cut plots did not include the periods of agriculture and grazing



that commonly follow dry forest clearing in the Dominican Republic.

Studies of the long-term fate of old-growth species in tropical dry forest regeneration are wanting, and indications from other ecosystems differ widely. Birdsey & Weaver (1982), for example, reported the understory of secondary moist forests in Puerto Rico to have become rich in native species typical of old growth. In contrast, research with herbaceous plants in temperate forests spanning more than 300 y in age (Peterken & Game, 1984) demonstrates that successional forests may remain poor indefinitely in species characteristic of old-growth woodland; the failure of such plants to become re-established is attributed to isolation in time and space from seed sources and to alterations in soil properties following cultivation.

Both of these latter processes are relevant also to tropical dry forests. Although seedlings were found to reproduce the species abundance of adult tree populations within one Dominican old-growth dry forest (Burgos & Diloné, 1986), and isolated leguminous scrub trees elsewhere have been shown to serve as eventual foci for substantial seed deposition by the birds using these trees or their epiphytes (Archer *et al.*, 1988; Nadkarni, 1988), species seeding into abandoned crop and pasture lands are likely to include a greatly restricted subset of the surrounding vegetation. Furthermore, seedling recruitment into scrub may prove ineffective despite adequate seed input (Hernández & Disla, 1987; Castilleja, 1988). Moisture, shade, porosity, organic matter content, and other seedbed characteristics affected by land management are probable influences, as is the nutritional state of the soil. Above-ground stores of nitrogen, phosphorus, and organic matter virtually disappear from some tropical dry forests with the burning that normally accompanies swidden agriculture (Kauffman *et al.*, 1993); and erosion, especially as aggravated by mechanical clearing for intensive agriculture, can greatly compromise the potential for site recuperation (Maass *et al.*, 1988). Sprouts often account for the bulk of stems appearing in early regeneration of dry secondary forests (Murphy *et al.*, 1983; Dunevitz, 1985: 56), and differential sprouting ability can interact with methods of swidden farming to influence succession in forest fallows (Nyerges, 1989). Competition, either from prolific sprouters or from fast-growing species dispersed by livestock during a pasture stage, has the potential to impede the establishment of populations of later arrivals.

Results of regression analyses of site and stand characteristics on scrub stand age in Jaiquí Picado are presented in Table 4. Tests were performed only on those characteristics that differed significantly and meaningfully between scrub and old-growth forests (Tables 1 and 2; Fig. 7), in order to explore the hypothesis that these features of scrub forests begin to approximate the old-growth values as the scrub stands increase in age. This approach carries the assumptions and caveats common to all studies of succession that create presumed chronosequences based on simultaneous, spatially distinct samples (Miles, 1979: 20).

Of the two site characteristics examined, litter depth increases significantly although quite slowly with age of secondary growth, while leaf(let) size in the litter does not show an increase with stand development, reflecting the continued

dominance of the canopy by compound-leaved legumes. Maximum stand height and the range of tree heights increase gradually with age, indicating some raising and deepening of the canopy. These same parameters of tree diameter do not change linearly with time, although basal area shows a highly significant increase with stand age, due perhaps to increasing stem density as well as modest growth in average diameter. The stand characteristic exhibiting the strongest linear relation with age is the mean number of woody species per plot, suggesting a moderate increase in diversity through time. Extrapolation well beyond the observed ranges using the generated regression equation would project a time span of 69 y for scrub forests to accumulate the average species density of old-growth forest (sixteen species per 200 m<sup>2</sup> sample plot); however, the assumption of a continuing linear increase that is implicit in such predictions has no empirical justification.

The woody regeneration appearing in overgrown pastures – those spared the usual periodic machete-weeding for spans of two to four years – and beneath scrub forests shows ambiguous patterns as well. Altogether, seedlings of eighty-three woody species were found in samples of the two types of regeneration. Of these, eleven species were encountered only in pasture samples, thirty-four were found only in understories of scrub plots, and thirty-eight occurred in both types of site. The 47% greater total number of woody species found in scrub undergrowth samples than in pasture samples was recorded on an area 356% larger, rendering questionable the apparently greater diversity of scrub understory; graphs of the species-area data (Fig. 4) indicate that within a comparable sampling area, the diversity of woody pasture ingrowth could plausibly equal that of scrub understory. The regeneration invading pastures and scrub understories also presented similarities in species composition. Considering collectively the woody species in all overstory samples and regeneration plots, a significant positive association was found between those appearing in scrub understories and those growing into abandoned pastures (Yates-corrected  $\chi^2 = 15.2$ , 1 d.f.,  $P < 0.0001$ ). This seems surprising given the differing availability of light and water to be expected within these two cover types. However, much of the present scrub vegetation has developed through an overgrown pasture stage, and regeneration noted beneath these forests may include young offspring of trees that grew up in prior pastures and whose seedlings are destined to succumb in the understory conditions. Also, continued grazing beneath much present scrub as well as in overgrown pasture exerts a common influence upon the lower strata of both. Extended interviews with a number of people who tend livestock showed wide agreement concerning the woody species that they knew cattle or goats to browse, and several of these, including the once common *Mastichodendron foetidissimum* (Jacq.) Cronq. and *Bumelia salicifolia* (L.) Sw., were absent from pasture samples and quite rare in scrub undergrowth.

The rate of accumulation of pasture-invading species with increasing sample size, at least within the small areas of pasture sampled (Fig. 4), indicates a species richness intermediate between that of old-growth and scrub forest types. To the extent that it includes potential canopy or understory species, this would suggest that if spared pasture clearing, and perhaps

Regression on age of:	$r^2$	$P$	Linear equation (if $P < 0.05$ )
<b>Stand density</b>			
Woody individuals (#/ha)	0.247	0.0707	n.s.
Woody stems (#/ha)	0.412	0.0133	$C = 1402 + (104 \times A)$
Basal area (m <sup>2</sup> /ha)	0.485	0.0057	$C = 2.21 + (0.302 \times A)$
<b>Stand structure</b>			
Maximum tree height (m)	0.474	0.0064	$C = 5.11 + (0.182 \times A)$
Range of tree heights (m)	0.362	0.0229	$C = 3.33 + (0.141 \times A)$
C.V. of tree heights (%)	0.276	0.0538	n.s.
Maximum DBH (cm)	0.026	0.5808	n.s.
Range of DBH (cm)	0.026	0.5808	n.s.
C.V. of DBH (%)	0.157	0.161	n.s.
Sprout ratio (stems/individ.)	0.158	0.1589	n.s.
<b>Litter</b>			
Depth (cm)	0.635	0.0004	$C = 0.433 + (0.0575 \times A)$
Leaf(let) size (index)	0.0125	0.7039	n.s.
<b>Woody plant diversity</b>			
Species/200 m <sup>2</sup>	0.561	0.002	$C = 2.49 + (0.202 \times A)$

**Table 4** Linear regressions of site and stand characteristics (C) on age since abandonment from agriculture (A), based on fourteen scrub forest sites, Jaiquí Picado, Dominican Republic.

sporadic grazing as well, abandoned pastures might develop into forests more diverse than existing scrub. The understories of scrub forests also appear to be richer in species than their overstories (Fig. 4). However, forty-nine (43%) of the 113 woody species found in either old-growth or scrub forest were not encountered in scrub understory or pasture ingrowth, while both types of regeneration consisted for the most part of species found abundantly as adults in scrub forest. The regeneration under scrub forests thus chiefly reproduces scrub overstory, with most species characteristic of old-growth forest failing to appear there. Based on the 132 woody species recorded in all types of sample, a significant positive association exists between the species found in scrub overstory and those in scrub understory (Yates-corrected  $\chi^2 = 19.6$ , 1 d.f.,  $P < 0.0001$ ), while the questionably significant relationship between species in old-growth overstory and those in scrub understory is negative ( $\chi^2 = 4.59$ , 1 d.f.,  $P < 0.0322$ ). Forty of the old-growth forest species not encountered in scrub overstory were also absent from scrub and pasture regeneration; approximately half of these, including six endemics, were among the rarest species in old growth.

Within the 27-y span of ages considered, then, scrub forest vegetation appears to undergo a moderate increase in vertical structure, basal area, and litter thickness over time as well as a slow but distinct accretion in the number of woody species reaching breast height. Some of the more weedy shrubs invading pastures, such as *Cestrum diurnum* L., *Hamelia patens* Jacq., and *Samyda dodecandra* Jacq., tend to disappear from scrub forest with age; yet ingrowth of a considerable number of the species more characteristic of mature forests – including *Ocotea coriacea* (Sw.) Britton, *Maytenus domingensis* Krug & Urb., *Myrcianthes fragrans* (Sw.) McVaugh, *Amyris* spp. P. Browne, *Oxandra lanceolata* (Sw.) Baill., *Krugiodendron ferreum* (Vahl) Urb., *Savia sessiliflora* (Sw.) Willd., *Phyllostylon brasiliensis* Benth. & Hooker, *Coccoloba diversifolia* Jacq., *Gymnanthes lucida* Sw., *Thouinia trifoliata* Poit., *Mastichodendron foetidissimum*, *Schaefferia frutescens* Jacq., *Guapira*

*brevipetiolata* (Heimerl) Alain, *Eugenia ligustrina* (Sw.) Willd., *Erythroxylum rotundifolium* Lunan, *Guaiaicum officinale* L., *Guaiaicum sanctum* L., *Ardisia obovata* Ham., and *Bumelia salicifolia* – is found sporadically if at all. The same three scrub species – *Acacia macracantha*, *Haematoxylon campechianum*, and *Prosopis juliflora*, in descending order of abundance – continue to dominate the scrub overstory throughout this period, and the least abundant old-growth species generally fail to appear in the natural regeneration within three decades of abandonment from cultivation.

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#### REFERENCES

- Antonini, G.A. (1968) *Processes and patterns of landscape change in the Linea Noroeste, Dominican Republic*. PhD Dissertation, Columbia University, New York.

- Archer, S., Scifres, C., Bascham, C.R. & Maggio, R. (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol. Monogr.* **58**, 111–127.
- Baev, P.V. & Penev, L.D. (1995) *BIODIV: program for calculating biological diversity parameters, similarity, niche overlap, and cluster analysis, Version 5.1*. Pensoft, Sofia, Bulgaria.
- Beard, J.S. (1944) Climax vegetation in tropical America. *Ecology*, **25**, 127–158.
- Birdsey, R.A. & Weaver, P.L. (1982) *The forest resources of Puerto Rico*. U. S. Department of Agriculture Forest Service Resource Bulletin SO-85, Southern Forest Experiment Station, New Orleans, LA.
- Blesch, R.R. (1967) *Mapa geológico preliminar, República Dominicana, escala 1: 250,000*. Unión Panamericana, Organización de los Estados Americanos, Washington, D. C.
- Bray, J.R. & Curtis, J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* **27**, 325–349.
- Brown, S. & Lugo, A.E. (1982) The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica*, **14**, 161–187.
- Brown, S. & Lugo, A.E. (1990) Tropical secondary forests. *J. trop. Ecol.* **6**, 1–32.
- Burgos Morillo, J. F. & Diloné Germosén, F. N. (1986) *Identificación de la importancia e incidencia de las malezas en el bosque seco y sus influencias competitivas en los árboles existentes*. Tesis de Ingeniero Agrónomo, Concentración en Recursos Forestales, Instituto Superior de Agricultura, Universidad Católica Madre y Maestra, Santiago de los Caballeros, República Dominicana.
- Carlquist, S. (1965) *Island life: a natural history of the islands of the world*. The Natural History Press, Garden City, NY.
- Carlquist, S. (1974) *Island biology*. Columbia University Press, New York.
- Castilleja, G. (1988) Seed germination and seedling establishment in a subtropical dry forest. *TRI News* 4–6. Yale School of Forestry and Environmental Studies, New Haven, CT.
- Chardón, C.E. (1976) [1939] Reconocimiento de los recursos forestales de la República Dominicana. *Reconocimiento de los recursos naturales de la República Dominicana*, pp. 279–303. Editora de Santo Domingo, Santo Domingo, República Dominicana.
- Ciferri, R. (1936) Studio geobotanico dell'isola Hispaniola (Antille). *Atti Ist. bot. Univ. Pavia*, Serie IV, VIII, 1–336.
- Dunevitz, V.L. (1985) *Regrowth of clearcut subtropical dry forests: mechanisms of recovery and quantification of resilience*. M.S. Thesis, Michigan State University, East Lansing, MI.
- Durland, W.D. (1922) The forests of the Dominican Republic. *Geogr. Rev.* **12**, 206–222.
- DVS (1990) *La diversidad biológica en la República Dominicana*. (Reporte preparado con apoyo del Servicio Alemán de Cooperación Social-técnica – DED – y el Fondo Mundial para la Vida Silvestre – WWF.) Departamento de Vida Silvestre, Subsecretariado de Recursos Naturales, Secretariado de Estado de Agricultura, Santo Domingo, República Dominicana.
- Ehrendorfer, F. (1979) Reproductive biology in island plants. *Plants and islands* (ed. by D. Bramwell), pp. 293–306. Academic Press, London.
- Ekman, E.L. (1930) Excursión botánica al nord-oeste de la República Dominicana. *Estación Agronómica de Moca* [Departamento de Agricultura, Santo Domingo, República Dominicana ], Serie B, **17**, 1–16.
- Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.
- Ewel, J.J. (1977) Differences between wet and dry successional tropical ecosystems. *Geo-Eco-Trop.* **1**, 103–117.
- Ewel, J.J. (1980) Tropical succession: manifold routes to maturity. *Biotropica*, **12**(Suppl.), 2–7.
- Ewel, J.J. & Whitmore, J.L. (1973) *The ecological life zones of Puerto Rico and the U. S. Virgin Islands*. Forest Service Research Paper ITF-18, U. S. Department of Agriculture/Forest Service, Institute of Tropical Forestry, Río Piedras, PR.
- FAO (1993) *FAO production yearbook 1992*. Food and Agriculture Organization of the United Nations, Rome.
- Freeman, P.H. (1967) *Mapa: uso actual de la tierra y tipos de vegetación, República Dominicana, escala 1: 250,000*. Unión Panamericana, Organización de los Estados Americanos, Washington, D. C.
- García Brito, P. (1992) *Inventario forestal del bosque del suroeste*. Informe del proyecto 'Manejo Natural del Bosque Seco' del Instituto para el Desarrollo del Suroeste (INDESUR) ya la Sociedad Alemana de Cooperación Técnica (GTZ). Santo Domingo, República Dominicana.
- García, R.G. & Alba V., N. (1989) Estudio ecoflorístico comparativo del bosque seco subtropical de Azua y Monte Cristi, República Dominicana. *Moscsoa*, **5**, 55–84.
- Gentry, A.H. (1986) Endemism in tropical versus temperate plant communities. *Conservation biology: the science of scarcity and diversity* (ed. by M. E. Soulé), pp. 153–181. Sinauer Associates, Sunderland, MA.
- Gentry, A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographic gradients. *Ann. Mo. Bot. Gdns*, **75**, 1–34.
- Gentry, A.H. (1992) Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos*, **63**, 19–28.
- Gentry, A.H. (1995) Diversity and floristic composition of neotropical dry forests. *Seasonally dry tropical forests* (ed. by S. H. Bullock, H. A. Mooney and E. Medina), pp. 146–194. Cambridge University Press, Cambridge.
- Gilbert, L.E. (1980) Food web organization and the conservation of tropical biodiversity. *Conservation biology: an evolutionary-ecological perspective* (ed. by M. E. Soulé and B. A. Wilcox), pp. 11–33. Sinauer Associates, Sunderland, MA.
- González J., C.E. (1980) *Estudio de un área de bosque seco con fines de planificar el manejo de recursos energéticos*. Tesis de grado, Instituto Superior de Agricultura, Universidad Católica Madre y Maestra, Santiago, República Dominicana.
- Grainger, A. (1993) *Controlling tropical deforestation*. Earthscan Publications, London.
- Hager, J. & Zanoni, T.A. (1993) La vegetación natural de la República Dominicana: una nueva clasificación. *Moscsoa*, **7**, 39–81.
- Hartshorn, G., Antonini, A., DuBois, R., Harcharik, D., Heckadon, S., Newton, H., Quesada, C., Shores, J. & Staples, G. (1981) *The Dominican Republic: country environmental profile, a field study*. JRB Associates, McLean, VA.
- Hernández, J.M. & Disla, M.T. (1987) *Estudios básicos para el desarrollo de un plan de manejo del bosque seco dominicano*. Informe Especial no. 4, Proyecto de Desarrollo de Madera como Combustible, Instituto Superior de Agricultura, Santiago, República Dominicana.
- Hewetson, C.E. (1956) Discussion on the 'climax' concept in relation to the tropical rain and deciduous forest. *Emp. For. Rev.* **35**, 274–291.
- Holdridge, L.R. (1967) *Life zone ecology*. Tropical Science Center, San José, Costa Rica.
- Horn, H.S. (1966) Measurement of overlap in comparative ecological studies. *Am. Nat.* **100**, 419–424.
- Howard, R.A. & Zanoni, T.A. (1989) Two atypical examples of seed distribution in the Dominican Republic. *Moscsoa*, **5**, 216–225.
- Hubbell, S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, **203**, 1299–1309.
- Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–586.

- Janzen, D.H. (1988a) Guanacaste National Park: tropical ecological and biocultural restoration. *Rehabilitating damaged ecosystems* (ed. by J. Cairns, Jr.), pp. 143–192. CRC Press, Boston, MA.
- Janzen, D.H. (1988b) Management of habitat fragments in a tropical dry forest: growth. *Ann. Mo. Bot. Gdns*, **75**, 105–116.
- Janzen, D.H. (1988c) Tropical dry forests: the most endangered major tropical ecosystem. *Biodiversity* (ed. by E. O. Wilson), pp. 130–137. National Academy Press, Washington, D. C.
- Kauffman, J.B., Sanford, R. L. Jr, Cummings, D.L., Salcedo, J.H. & Sampiao, E.N.S.B. (1993) Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. *Ecology*, **74**, 140–151.
- Kepler, C.B. & Kepler, A.K. (1970) Preliminary comparison of bird species diversity and density in Luquillo and Guánica forests. *A tropical rain forest* (ed. by H. T. Odum and R. F. Pigeon), pp. E183–E191. Office of Information Services, U. S. Atomic Energy Commission, Oakridge, TN.
- Klute, A. (ed.) (1986) *Methods of soil analysis, Part I: physical and mineralogical methods*, 2nd edn. American Society of Agronomy: Soil Science Society of America, Madison, WI.
- Knudson, D.M., Chaney, W.R. & Reynoso, F.A. (1988) *Fuelwood and charcoal research in the Dominican Republic*. Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN.
- Lerdau, M., Whitbeck, J. & Holbrook, N.M. (1991) Tropical deciduous forest: death of a biome. *Trends Ecol. Evol.* **6**, 201–202.
- Liogier, A.H. (1982, 1983, 1985, 1986, 1989, 1994, 1995, 1996) *La flora de la Española*, Vols I, II, III, IV, V, VI, VII, VIII. Universidad Central del Este, San Pedro de Macoris, República Dominicana.
- Liogier, A.H. (1984) La flora de la Española: sus principales características. *Memoria de la segunda jornada científica: medio ambiente y recursos naturales*, pp. 184–195. Academia de Ciencias de la República Dominicana. Editorial CENAPEC, Santo Domingo, República Dominicana.
- Lott, E.J., Bullock, S.H. & Solís-Magallanes, J.A. (1987) Floristic diversity and structure of upland and arroyo forests of coastal Jalisco. *Biotropica*, **19**, 228–235.
- Luciano, L. & Checo, H. (1986) *Estudio sobre la producción tradicional de carbón vegetal y su impacto sobre el bosque seco nativo, región suroeste*. Informe Especial no. 2, Proyecto de Desarrollo de Madera como Combustible, Instituto Superior de Agricultura, Santiago, República Dominicana.
- Ludwig, J.A. & Reynolds, J.F. (1988) *Statistical ecology: a primer on methods and computing*. John Wiley & Sons, New York.
- Lugo, A.E., González-Liboy, J.A., Cintrón, B. & Dugger, K. (1978) Structure, productivity, and transpiration of a subtropical dry forest in Puerto Rico. *Biotropica*, **10**, 278–291.
- Lugo, A.E., Schmidt, R. & Brown, S. (1981) Tropical forests in the Caribbean. *Ambio*, **10**, 318–324.
- Maass, J. M., Jordan, C.F. & Sarukhan, J. (1988) Soil erosion and nutrient losses in seasonal tropical agroecosystems under various management techniques. *J. appl. Ecol.* **25**, 595–607.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Magurran, A.E. (1988) *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ.
- Mares, M.A. (1992) Neotropical mammals and the myth of Amazonian diversity. *Science*, **255**, 976–979.
- Martijena, N.E. & Bullock, S.H. (1994) Monospecific dominance of a tropical deciduous forest in México. *J. Biogeogr.* **21**, 63–74.
- Medina, E. & Cuevas, E. (1990) Propiedades fotosintéticas y eficiencia de uso de agua de plantas leñosas del bosque deciduo de Guánica: consideraciones generales y resultados preliminares. *Acta Científica*, **4**, 25–36.
- Mercedes U., J.R. (1980) *Estudio para un diseño de un sistema de manejo integrado en áreas de bosque seco en República Dominicana*. Tesis de grado, Instituto Superior de Agricultura, Universidad Católica Madre y Maestra, Santiago, República Dominicana.
- Mercedes U., J.R. (1984) *Estudio de un sistema de manejo agroforestal en el bosque seco de la República Dominicana*. Nota Técnica no. 10, Instituto Superior de Agricultura, Santiago, República Dominicana.
- Miles, J. (1979) *Vegetation dynamics*. Chapman & Hall, London.
- Molina, S.A. (1998) *Recovery of a Caribbean dry forest after abandonment of different land uses in Guánica, Puerto Rico*. PhD Dissertation, Universidad de Puerto Rico, Río Piedras, PR.
- Montanari, J.H. (1967a) *Mapa de isoyetas, República Dominicana, escala 1: 500,000*. Unión Panamericana, Organización de los Estados Americanos, Washington, D.C.
- Montanari, J.H. (1967b) *Mapa: datos hidrológicos y de gastos de agua, República Dominicana, escala 1: 250,000*. Unión Panamericana, Organización de los Estados Americanos, Washington, D. C.
- Mooney, H.A., Bullock, S.H. & Medina, E. (1995) Introduction. *Seasonally dry tropical forests* (ed. by S. H. Bullock, H. A. Mooney and E. Medina), pp. 1–8. Cambridge University Press, Cambridge.
- Murphy, P.G. & Lugo, A.E. (1986a) Ecology of tropical dry forest. *Ann. Rev. Ecol. Syst.* **17**, 67–88.
- Murphy, P.G. & Lugo, A.E. (1986b) Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica*, **18**, 89–96.
- Murphy, P.G. & Lugo, A.E. (1990) Dry forests of the tropics and subtropics: Guánica Forest in context. *Acta Científica*, **4**, 15–24.
- Murphy, P.G. & Lugo, A.E. (1995) Dry forests of Central America and the Caribbean. *Seasonally dry tropical forests* (ed. by S. H. Bullock, H. A. Mooney and E. Medina), pp. 9–34. Cambridge University Press, Cambridge.
- Murphy, P.G., Lugo, A.E. & Murphy, A.J. (1983) Seasonal dynamics and recovery of a Caribbean dry forest. *Bull. Ecol. Soc. Am.* **64**, 113.
- Murphy, P.G., Lugo, A.E., Murphy, A.J. & Nepstad, D.C. (1995) The dry forests of Puerto Rico's south coast. *Tropical forests: management and ecology* (ed. by A. E. Lugo and C. Lowe), pp. 178–209. Springer-Verlag, New York.
- Nadkarni, N.M. (1988) Tropical forest ecology from a canopy perspective. *Tropical rainforests: diversity and conservation* (ed. by F. Almeda and C. M. Pringle), pp. 189–208. California Academy of Sciences and Pacific Division, American Association for the Advancement of Science, San Francisco.
- NEC-67 (1991) *Recommended soil testing procedures for the north-eastern United States*. Northeast Coordinating Committee on Soil Testing (NEC-67) Bulletin no. 493. Agricultural Experiment Station, University of Delaware, Newark, DE.
- NRC (1980) *Research priorities in tropical biology*. National Research Council, National Academy of Sciences, Washington, D.C.
- Nyerges, A.E. (1989) Coppice swidden fallows in tropical deciduous forest: biological, technological, and sociocultural determinants of secondary forest successions. *Human Ecol.* **17**, 379–400.
- OEA (1967) *Reconocimiento y evaluación de los recursos naturales de la República Dominicana*. Unión Panamericana, Organización de los Estados Americanos, Washington, D. C.
- ONE (1984) *República Dominicana en cifras 1984*. Oficina Nacional de Estadística, Secretariado Técnico, Presidencia de la República, Santo Domingo, República Dominicana.
- ONE (1987) *República Dominicana en cifras 1987*. Oficina Nacional de Estadística, Secretariado Técnico, Presidencia de la República, Santo Domingo, República Dominicana.
- Palmer, E.C. (1976) *Land use and landscape change along the Dominican-Haitian borderlands*. PhD Dissertation, University of Florida, Gainesville, FL.
- Parsons, J.J. (1965) Cotton and cattle in the Pacific lowlands of Central America. *J. Interamerican Studies* **7**, 149–159.

- Peterken, G.F. (1976) Long-term changes in the woodlands of Rockingham forest and other areas. *J. Ecol.* **64**, 123–146.
- Peterken, G.F. (1996) *Natural woodland: ecology and conservation in northern temperate regions*. Cambridge University Press, Cambridge.
- Peterken, G.F. & Game, M. (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *J. Ecol.* **72**, 155–182.
- Pielou, E.C. (1975) *Ecological diversity*. John Wiley & Sons, New York.
- Plan Sierra (1992a) *Plan maestro, sector forestal: informe principal*. (Documento interno elaborado por Swedforest Consulting AB con financiamiento de la Agencia Sueca de Cooperación Internacional Técnica y Económica). Plan Sierra, San José de las Matas, República Dominicana.
- Plan Sierra (1992b) *Fotomapa: uso de la tierra 1991, escala 1:20,000; hojas 607431–2 y 607434–5. Plan maestro, sector forestal: acompañamiento*. (Preparado por Swedforest Consulting AB con la Swedish Space Corporation.) Plan Sierra, San José de las Matas, República Dominicana.
- Prance, G.T. (1991) Deforestation: a botanist's view. *Sustaining Earth: response to the environmental threat* (ed. by D. J. R. Angell, J. D. Comer and M. L. N. Wilkinson), pp. 52–59. St. Martins Press, New York.
- Pretell, O.F. (1967) *Mapa: capacidad productiva de la tierra, República Dominicana, escala 1:250,000*. Unión Panamericana, Organización de los Estados Americanos, Washington, D. C.
- Pretell, O.F. & Soto, G. (1967) *Mapa: asociaciones de suelos de la República Dominicana, escala 1:250,000*. Unión Panamericana, Organización de los Estados Americanos, Washington, D. C.
- Raunkiaer, C. (1934) The use of leaf size in biological plant geography. *The life forms of plants and statistical plant geography*, pp. 368–378. Clarendon Press, Oxford.
- Redford, K.H., Taber, A. & Simonetti, J.A. (1990) There is more to diversity than tropical rain forests. *Conserv. Biol.* **4**, 328–330.
- Roth, L.C. (1997) *Traditional knowledge and management of subtropical dry forest: a study of resource use, landscape change, and biodiversity in a rural area of the Dominican Republic*. PhD Dissertation, Clark University, Worcester, MA.
- Sawyer, J.O. & Lindsey, A.A. (1971) *Vegetation of the life zones in Costa Rica*. Monograph no. 2, Indiana Academy of Science, Indianapolis, IN.
- Schimper, A.F.W. (1903) *Plant-geography upon a physiological basis* (English translation by W. R. Fisher). Clarendon Press, Oxford.
- Schumann, G.L. (1991) *Plant diseases: their biology and social impact*. APS Press, St. Paul, MN.
- Sharpe, D.M., Guntenspergen, G.R., Dunn, C.P., Leitner, L.A. & Stearns, F. (1987) Vegetation dynamics in a southern Wisconsin agricultural landscape. *Landscape heterogeneity and disturbance* (ed. by M. G. Turner), pp. 137–155. Springer-Verlag, New York.
- Smith, D.M. (1962) *The practice of silviculture*, 7th edn. John Wiley & Sons, New York.
- Smythe, N. (1987) The importance of mammals in neotropical forest management. *Management of the forests of tropical America: prospects and technologies* (ed. by J. C. Figueroa Colón, F. H. Wadsworth and S. Branham), pp. 79–98. Institute of Tropical Forestry, Southern Forest Experiment Station, USDA/Forest Service, Río Piedras, PR.
- Sousa, W.P. (1984) The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.* **15**, 353–391.
- Spurr, S.H. & Barnes, B.V. (1980) *Forest ecology*, 3rd edn. John Wiley & Sons, New York.
- SSIS (1991) *Soil survey laboratory methods manual* (Soil survey investigations report, 42, Version 1.0, October, 1991). Soil Survey Investigations Staff, United States Department of Agriculture Soil Conservation Service, National Soil Survey Center, Lincoln, NE.
- Sussman, R.W. & Rakotozafy, A. (1994) Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. *Biotropica*, **26**, 241–254.
- Tasaico, H. (1967) *Mapa ecológico de la República Dominicana, escala 1:250,000*. Unión Panamericana, Organización de los Estados Americanos, Washington, D. C.
- Terborgh J. (1986) Keystone plant resources in the tropical forest. *Conservation biology: the science of scarcity and diversity* (ed. by M. E. Soulé), pp. 330–344. Sinauer Associates, Sunderland, MA.
- Wadsworth, F.H. (1950) Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. *Caribb. Forester*, **11**, 38–47.
- Wadsworth, F.H. (1990) Plantaciones forestales en el Bosque Estatal de Guánica. *Acta Científica*, **4**, 61–68.
- Walter, H. (1973) *Vegetation of the Earth in relation to climate and the eco-physiological conditions*. The English Universities Press, London.
- Woodward, K.W. (1910) *Informe sobre las condiciones forestales de la República Dominicana*. Imprenta La Cuna de América, Santo Domingo, República Dominicana.

## BIOSKETCH

Vegetation dynamics, with particular reference to human interaction with plants and landscapes, are a principal focus of interest for **Linda Roth**, who holds a master's degree in forest science and a doctorate in geography. Her prior work in this area has included investigation of the effects of hurricanes on mangrove ecosystem dynamics and management prospects as well as participation in conservation and educational projects in tropical and temperate America.

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