

Vegetation-environment relationships in forest ecosystems of the Cordillera Central, Dominican Republic¹

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SHERMAN, R. E., P. H. MARTIN, AND T. J. FAHEY (Department of Natural Resources, Cornell University, Ithaca, NY 14853) Vegetation-environment relationships in forest ecosystems of the Cordillera Central, Dominican Republic. *J. Torrey. Bot. Soc.* 132: 293–310. 2005.—We examined forest vegetation-environment relationships in the central mountain range of Hispaniola to improve general understanding of tropical montane forests. Forest inventory data were collected in 1999 and 2000 from 245 plots established in the Armando Bermúdez and Carmen Ramírez National Parks, Dominican Republic, over an elevation range of 1,100–3,075 m. Average tree density (≥ 10 cm dbh), basal area, and dbh were highly variable across the elevation gradient; species richness declined significantly with elevation; and the canopy height of broadleaved stands declined whereas the height of stands dominated by the endemic pine, *Pinus occidentalis* Sw., was relatively constant across the elevation gradient. Four major forest associations were identified using TWINSpan: a low elevation broadleaved forest; a pine-broadleaved mixed forest; a mid-elevation cloud forest; and a largely monospecific pine forest that extends from the cloud forests to the summits of the highest peaks and dominates the leeward slopes of the mountains. Species composition varied continuously along the elevation gradient up to 2,250 m; however, above 2,250 m there was an abrupt shift from cloud forest to monospecific pine forests. Temperature, humidity, and fire history appear to regulate the position of this boundary, probably reflecting the position of the trade wind inversion. Ordination and logistic regression indicated that disturbance history and topo-edaphic factors influenced individual species distributions.

Key words: cloud forests, disturbance, diversity, Dominican Republic, gradient analysis, logistic regression, pine forests, trade wind inversion, tropical montane forests.

Tropical montane forests are among the most fragile and highly threatened of all tropical forest ecosystems (Gentry 1995, Hamilton et al. 1995, Henderson 1991, Bruijnzeel 2001). Compared to lowland tropical rainforests, montane forests have received little attention until recently, and, hence, our understanding of these ecosystems is limited. The many important services provided by tropical montane forests, such as watershed protection, erosion control, and stable hydrologic flows, have been widely acknowledged (Peñafiel 1995); however, the rich biological diversity of tropical montane forests is not as well documented or appreciated (Churchill et al. 1995). Although there has been a rapid growth in the number of floristic surveys con-

ducted in neotropical montane forests (Gentry 1989, Gentry 1995, Kappelle and Zamora 1995, Wolf 1993), quantitative studies are few, and our understanding of the controls on plant species distributions and community patterns in these complex mountain landscapes remains limited (Lieberman et al. 1996).

A general understanding of the patterns of forest structure, composition, and diversity across tropical montane landscapes has emerged as a result of qualitative and quantitative surveys in a variety of geographical settings. Changes in temperature and moisture along the elevation gradient dominate the environmental controls on tropical mountain vegetation distribution in ways that are analogous to temperate zone mountains (Whittaker 1967), as originally proposed by Holdridge (1967) in the life-zone concept. The environmental changes that accompany the elevation gradient vary among mountain ranges within the tropical belt, owing to such influences as latitude, continental versus island locations, and broad atmospheric circulation patterns; nevertheless, a general scheme of elevational changes in humid tropical montane vegetation can be described (Webster 1995): lowland broadleaved forest grades into a lower montane broadleaved forest that gives way to stunted forest in the zone of maximum cloudiness (“cloud forest”), with non-forest vegeta-

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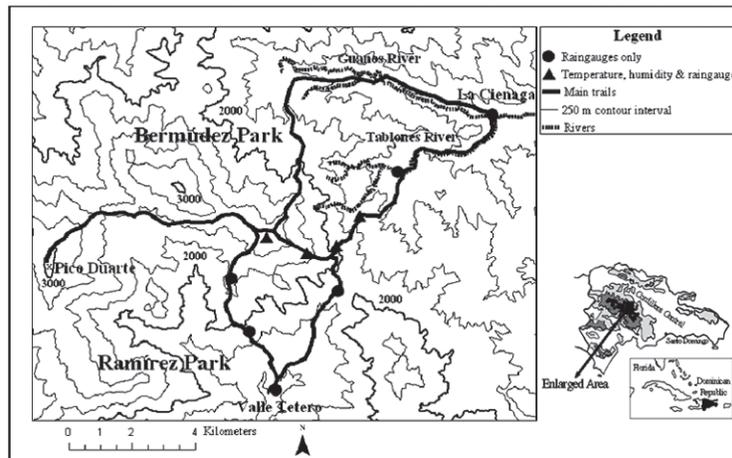


FIG. 1. Map of the study area in the Cordillera Central of the Dominican Republic.

tion above where either temperature or other environmental factors limit forest development. The particular patterns of these changes (e.g. elevation ranges, abruptness of transitions) appear to vary among mountain systems with climate and the floristics of the regions. Moreover, local, secondary controls on vegetation distribution resulting from soils, topography, and disturbance history clearly play a role in regulating tropical montane forest patterns (Svenning 2001, Weaver 1991, Aiba and Kitayama 1999, Takyu et al. 2002, Tanner 1977), although fewer studies have attempted to quantify these controls. Analysis of forest vegetation patterns in a wide variety of tropical mountains is needed to improve understanding of ecological patterns and processes in these important ecosystems.

Within the Caribbean region, montane forests occur on many of the larger islands, especially in the Greater Antilles. In particular, the Cordillera Central on the island of Hispaniola has extensive areas above 1,000 m supporting a diverse assemblage of primary forests with high complements of endemics (Anonymous 2000). The most distinctive feature of the montane forest vegetation of Hispaniola is the extent and importance of the endemic pine species, *Pinus occidentalis* Swartz, which dominates the forest to varying degrees throughout the entire extent of the Cordillera Central (Hartshorn et al. 1981, Holdridge 1942). This unique ecoregion is considered a high conservation priority both nationally and regionally because of its distinct biodiversity and hydrologic benefit (Anonymous 2000, Dinerstein et al. 1995). Although floristic studies have been conducted in the region (How-

ard 1973, Judd 1987, Zanoni 1990), quantitative studies are lacking. The objective of the present study was to quantify the distribution and abundance of woody vegetation across the complex mountain landscape of the Cordillera Central of the Dominican Republic and thereby to contribute to a broader understanding of vegetation-environment relationships in tropical montane forests. We hypothesized that the distribution of forest associations and tree species would change gradually with climate along the elevation gradient and that local variations in distribution and abundance would depend upon topographic variation as well as the influence of disturbance history in the form of fire (Horn et al. 2001, May 2000) and hurricanes (Boose et al. 1994).

Materials and Methods. **STUDY AREA DESCRIPTION.** This study was conducted in the 766 km² Armando Bermúdez National Park and adjacent 764 km² Carmen Ramírez National Park of the Dominican Republic (19° 02' N, 71° 05' W) (Fig. 1). These two parks are located in the northwest trending central mountain range of Hispaniola and span an elevation range from 1,000 to 3,098 m. The two parks were created in 1956 and 1958, respectively, before any major logging or farming activities occurred and most of the area consists of virgin forests. Our study focused on the deeply dissected slopes to the east of Pico Duarte, where the range of undisturbed forest is from 1,200 m upward. The study area encompassed approximately 85 km² extending from the community of La Ciénaga de Manabá at the park entrance at 1,100 m elevation

to the top of Pico Duarte, the highest point in the Caribbean at 3,098 m, and included both the windward northeastern slope and the leeward, southwestern slope of the massif (Fig. 1). Climatic patterns on the island reflect the influence of the prevailing northeast trade winds, so that precipitation is about 45% greater on the northeastern slopes of the mountains (Horst 1992). May and June are the wettest months and January to March the driest. Freezing temperatures occur above 2,100 m, particularly during the winter months (Pedersen 1953). The geology of these mountains is complex, dominated by Cretaceous volcanic, metamorphic and plutonic rocks (Lewis 1980).

VEGETATION SAMPLING AND ENVIRONMENTAL MEASUREMENTS. We quantified temperature and moisture in our study site at a series of stations distributed along the elevation gradient (Fig. 1). Precipitation was measured at seven locations using recording rain gauges (Rainew Tipping Bucket Rain Gauge, RainWise Inc.) positioned in large openings over a two-year period (1999–2001). Rain gauges were serviced at bi-weekly intervals over the period of measurements. Air temperature and relative humidity were measured at four stations (Fig. 1) over almost 2 yr (June 2001–April 2003) using HOBO H8 Pro RH/Temperature data loggers (Onset Computer Corporation, Bourne, MA). Finally, we estimated the elevation of the cloud base on the northeastern flank of the massif twice daily (1100 h and 1600 h) over a one and a half year period (April 1999–September 2000) by visual reconnaissance from a viewpoint at La Ciénaga de Manabá.

Forest inventory data were collected in 1999 and 2000 from 245 permanent plots that were located along several hiking trails and rivers (Fig. 1) by pacing randomly selected distances between plots. Each plot was then sited off the trail by a randomly selected number of paces in a random compass direction. Circular plots, either 0.1 ha or 0.05 ha in size (depending on tree density, species diversity, and topography), were established at each location. Within each plot, all trees ≥ 10 cm dbh (diameter at breast height) were measured to the nearest 0.1 cm, tagged, and identified in the field by common name with the help of a local guide (Francisco Peralta). Understory woody plants < 10 cm dbh were identified and enumerated in a 1 m wide plot through the diameter positioned along the plot's aspect. Personnel at the National Botanical Garden in

Santo Domingo, Dominican Republic identified specimens of all woody plants encountered in the field to species or genus level. Voucher specimens are housed at the herbarium of this Botanical Garden.

In each plot, the heights of two to four dominant trees were measured using a digital hypsometer. At the center of each plot, the location and elevation were recorded using a GPS; slope was measured in each cardinal direction from the plot center with a digital hypsometer; and aspect was measured using a compass. The average slope was calculated for each plot, and each plot's convexity or concavity was measured using the terrain shape index (McNab 1989); negative values represent convex-shaped and positive values concave-shaped terrain. We converted aspect into two uncorrelated measures of aspect, Eastness and Southness (Pereira and Itami 1991). The conversion formulas were: Eastness = $\sin(\pi * \text{aspect} / 180)$, where aspect was the slope aspect measured in degrees, and Southness = $\cos(\pi * (\text{aspect} + 180) / 180)$. The range for both values was -1 to $+1$: the maximum value for Eastness occurred on sites with a measured aspect of 90° and the maximum value for Southness occurred on sites with an aspect of 180° .

Four 2 cm diameter soil cores were extracted to a mineral soil depth of 15 cm at three randomly chosen locations in each plot. Soil samples were separated by organic and mineral horizons, the depth of the organic soil horizon recorded, and sub-samples pooled in the field. In the laboratory, soil samples were oven dried and organic soil pH measured in a 10:1 water:soil suspension and mineral soil pH measured in a 2:1 suspension. Finally, evidence of past disturbance was recorded in each plot in the form of fire scars (on pine trees) and charcoal in the soil, wind damage (uprooted or snapped-off trees), and standing dead stems.

DATA ANALYSIS. The basal area, density, and importance value (relative basal area + relative density)/2 were calculated for all live stems ≥ 10 cm dbh of each species, and the density and relative density of each species in the understory were calculated. These woody vegetation data were analyzed using classification and ordination techniques to identify major plant community assemblages and to link community patterns to environmental variables. To distinguish stands in different successional stages, the understory vegetation data were analyzed simultaneously with the overstory data by doubling the relative

density of understory vegetation so that values ranged from 0–200, the same as for importance values of overstory trees. Overstory and understory occurrences of the same species were treated as separate variables. Two-way Indicator Species Analysis (TWINSPAN), a hierarchical classification program, was applied to the floristic data to combine plots with similar vegetation characteristics into forest associations (Hill 1979). The data were ordinated using both detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMDS). The DCA ordination is a reciprocal averaging technique that simultaneously ranks plots based on similarities in species composition and ranks species based on the plots in which they occur (McGarigal et al. 2000). The resulting axes thus maximize correlations between species and plots and provide an index that characterizes the floristic nature of the samples (Lieberman et al. 1996). The NMDS ordination is a non-parametric multivariate technique that has been shown to be robust for ordination of vegetation community data (Minchin 1987, Clarke 1993). Correlations between the NMDS ordination axes and each environmental variable, and between the ordination axes and each species were used to illustrate the direction of increase for each variable in ordination space (Motzkin et al. 1999). The Bray-Curtis index, a robust measure of ecological distance (Clarke 1993), was used to calculate dissimilarity in species composition among sites. The output from the DCA ordination was used as the starting values for NMDS (Motzkin et al. 1999). The NMDS ordinations were rotated onto their principal components so that Axis I corresponded to the axis of maximum variation (Clarke 1993). All classification and ordination procedures were performed using PC-ORD (McCune & Mefford 1999).

The relationship between plot-level environmental factors and the distribution of individual species was investigated using a combination of logistic regression and generalized additive models (GAMs), a non-parametric analogue of logistic regression (Austin & Meyers 1996, Wisser et al. 1998). The GAMs were used for exploratory purposes to identify the response curve shape (e.g. linear, polynomial, etc.) between environmental variables and tree species. The following environmental parameters were used to predict the probability of a species' occurrence: Elevation, Eastness, Southness, Steepness (average slope), Terrain Site Index (TSI),

organic soil pH, and mineral soil pH. In addition, wind and fire disturbance, both binomial variables, were used in the logistic regression models. Each species was modeled within its own elevation range to reduce the influence of absences resulting from non-environmental factors (Austin and Meyers 1996; Wisser et al. 1998). Both general linear models and general additive models were computed using a binomial model with the logit link function in S-PLUS (Crawley 2002).

Results. CLIMATE PARAMETERS. Average night time temperature declined steadily with elevation at a rate of $6.2\text{ }^{\circ}\text{C km}^{-1}$ from 529 m, in the mountain town of Jarabacoa (from Horst 1992), to 1,865 m elevation. From 1,865–2,765, the rate of decrease was much lower ($3.2\text{ }^{\circ}\text{C km}^{-1}$). Atmospheric humidity, presented as the percentage of measurements that exceeded 90% relative humidity, declined gradually from 1,500–2,300 m and more abruptly above 2,300 m (Fig. 2a). Precipitation also declined slightly along the elevation gradient above 1,500 m on the windward side of the mountain, averaging $1,820 \pm 37$ mm across all sites, and it was substantially lower on the leeward slope (mean = 1,387 mm) (Fig. 2b). The elevation of the cloud base that developed on most afternoons throughout the year showed a pronounced peak in the frequency between 1,800 and 2,300 m elevation (Fig. 2c).

CLASSIFICATION OF VEGETATION. The vegetation was classified into eight major forest associations (third division of TWINSPAN) that varied in species composition and abundance: 1) secondary riparian forests; 2) low elevation broadleaved forests; 3) low elevation broadleaved-pine mixed forests; 4) cloud forests; and 5) four pine-dominated forest community types that occurred predominantly at higher elevation or on the leeward slope of the massif (Table 1).

Secondary Riparian Forests. These forests occurred along the lower river valleys below 1,300 m elevation that were cleared prior to the establishment of the national parks. These forests are distinct due to the dominance of two introduced species: *Inga vera* Willd., a species native to the island but not the mountains, and *Syzygium jambos* (L.) Alston, a non-native species. Epiphytes were not common but the abundance of vines and lianas was high in these forests (Martin et al. 2004).

Low-elevation Broadleaved Forests. This forest association occurred from 1,130 m to as

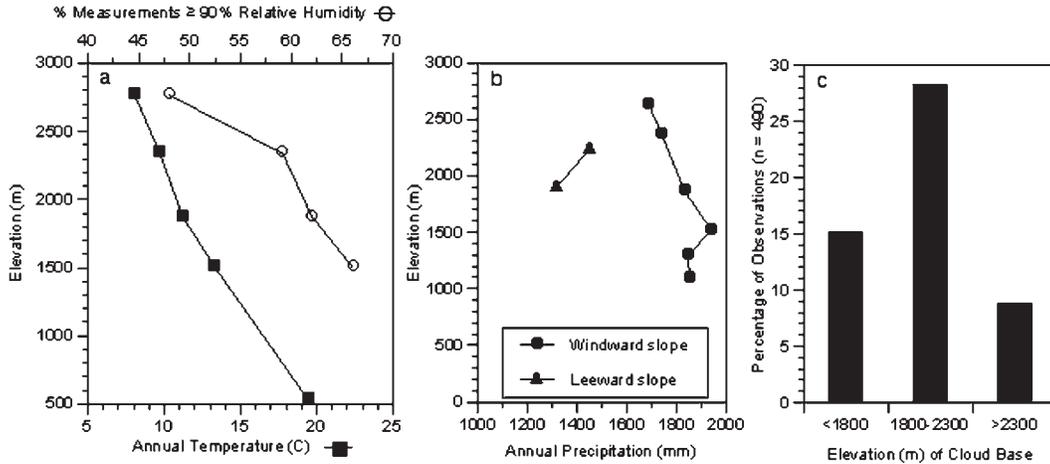


FIG. 2. Climate data collected along an elevational gradient in the Cordillera Central, Dominican Republic. (a) annual mean night temperature and relative humidity (percentage of measurements $\geq 90\%$ relative humidity); (b) precipitation measured on the windward and leeward side of the mountain; and (c) elevation of the cloud base measured daily in the afternoon.

high as 2,100 m but was the dominant community type between 1,200–1,500 m elevation. These forests were characterized by high species diversity in both the overstory and understory, a tall canopy stature, and a high abundance of epiphytes, vines, and lianas.

Pine-broadleaved Mixed Forests. In this forest association, *Pinus occidentalis* was always a dominant species (average importance value = 62%) but it shared dominance with a variety of broadleaved species. These forests occurred over a wide range of elevations, from 1,120–2,200 m. All plots showed evidence of past fire disturbance in the form of fire scars on pine trees or charcoal in the soil. *Brunellia comocladifolia* H. & B. and *Clusia chusoides* (Griseb.) D'Arcy, both early successional species (Francis and Lowe 2000), were common. The understory was a diverse mix of trees and shrubs; however, no pine regeneration was evident in these successional stands.

Cloud Forests. These forests were characterized by high species diversity and a low canopy stature. Two subgroups were identified, one occurring in ravines and depressions at lower elevations (1,550–1,800 m) and the other on northeastern slopes of the mountains between 1,900–2,200 m. Cyatheaceae, an arborescent fern family, was an important component of both sub-groups. Both wind and fire disturbance were observed in some of these plots. The understory was made up of a diverse mix of broadleaved species of trees and shrubs.

Pine Forests. Four categories of pine-dominated stands, where pine importance value exceeded 135%, were distinguished on the basis of associated woody plant species. *Pine I* occurred predominantly between 1,950–2,100 m elevation and was distinguished by high abundance of several early successional species (Cyatheaceae, *Garrya fadyenii* Hooker, and *Brunellia comocladifolia* H & B. in the overstory, and *G. fadyenii*, *Rubus eggersii* Rydb., *Baccharis myrsinites* (Lam.), and *Dittha maestrensis* Borhidi in the understory (Kappelle & Zamora 1995, May 2000)). Several cloud forest species occurred at low density in the understory, including *Podocarpus aristulatus* Parl., *Guettarda rotundifolia* Urb., and *Ilex repanda* Griseb. *Pine II* occurred between 2,050–2,300 m elevation on east-facing ridges and had an understory of shrubs (*Miconia selleana* Urb. & Ekman, *Weinmannia pinnata* L., and *Myrsine coriacea* (Sw.) R. Br.) and seedlings of *P. occidentalis*, *G. fadyenii*, and Cyatheaceae and some other cloud forest tree species. *Pine III* was a broad class of nearly monospecific pine stands that occurred from 1,460–2,600 m elevation. The understory consisted of pine saplings and a suite of shrubs whose composition varied with elevation and included *Myrsine coriacea*, *Myrica picardae* Krug & Urb., *Hypericum picnophyllum* Urb., *Lyonia* sp., *Senecio fuertisii* Urb., *Gaultheria domingensis* Urb., *Weinmannia pinnata*, *Tetrazygia* sp., and *Ilex* sp. Finally, *Pine IV* was monospecific stands at the highest elevations (above 2,400 m) and on

Table 1. List of dominant species and their importance values in each forest association identified by TWINSpan (see text for further description of each association).

Dominant species	Average importance value (%)
Secondary riparian forests	
<i>Tabebuia berterii</i> (DC.) Britton	31
<i>Syzygium jambos</i> (L.) Alston	27
<i>Pinus occidentalis</i> Sw.	20
<i>Inga vera</i> Willd.	20
<i>Ocotea leucoxyloides</i> (Sw.) Mez.	17
<i>Prunus occidentalis</i> Sw.	12
Low-elevation broadleaved forests	
<i>Tabebuia berterii</i> (DC.) Britton	27
<i>Prestoea montana</i> (Graham) Nicholson	27
<i>Pinus occidentalis</i> Sw.	15
<i>Turpina occidentalis</i> (Sw.) G. Don	13
<i>Meliosma impressa</i> Krug & Urb.	11
<i>Nectandra coriacea</i> (Sw.) Grisbach	11
<i>Ocotea leucoxyloides</i> (Sw.) Mez.	10
<i>Brunellia comocladifolia</i> H. & B.	7
<i>Alchornea latifolia</i> Sw.	6
<i>Pera brumelifolia</i> Griseb.	5
<i>Prunus occidentalis</i> Sw.	5
<i>Didymopanax tremulus</i> Krug & Urb.	5
Pine-broadleaf mixed forests	
<i>Pinus occidentalis</i> Sw.	62
Cyatheaceae	19
<i>Brunellia comocladifolia</i> H. & B.	15
<i>Clusia clusioides</i> (Griseb.) D'Arcy	13
<i>Lyonia</i> sp.	13
<i>Tabebuia berterii</i> (DC.) Britton	7
<i>Torrolbasia cunefolia</i> (C. Wr.) Krug & Urb.	7
<i>Didymopanax tremulus</i> Krug & Urb.	6
<i>Rondeletia ochracea</i> Urb. & Ekman	5
<i>Ilex impressa</i> Loes. & Ekman	5
<i>Ocotea wrightii</i> (Meissn.) Mez.	5
Cloud forests	
Cyatheaceae	57
<i>Brunellia comocladifolia</i> H. & B.	20
<i>Pinus occidentalis</i> Sw.	15
<i>Garrya fadyenii</i> Hooker	13
<i>Podocarpus aristulatus</i> Parl.	11
<i>Guettarda rotundifolia</i> Urb.	8
<i>Ilex repanda</i> Griseb.	6
<i>Ocotea wrightii</i> (Meissn.) Mez.	6
<i>Torrolbasia cunefolia</i> (C. Wr.) Krug & Urb.	6
<i>Tabebuia vinosa</i> A.H. Gentry	5
<i>Ocotea cicatricosa</i> C.K. Allen	5
Pine-dominated forests	
Pine I	
<i>Pinus occidentalis</i> Sw.	137
Cyatheaceae	24
<i>Brunellia comocladifolia</i> H. & B.	14
<i>Garrya fadyenii</i> Hooker	12

Table 1. Continued.

Dominant species	Average importance value (%)
Pine II	
<i>P. occidentalis</i> Sw.	175
Cyatheaceae	15
Pine III	
<i>P. occidentalis</i> Sw.	192
Pine IV	
<i>P. occidentalis</i> Sw.	199

the dry leeward slope between 2,000 and 2,600 m. Tree density was low, the canopy open and the sparse understory comprised of *Pinus occidentalis*, *Myrica picardae*, *Lyonia* spp., and the bunch grasses, *Danthonia domingensis* Hack. & Pilger and *Agrostis hiemalis* (Walt.) B.S.P. (Zanoni 1990).

FOREST STRUCTURAL CHARACTERISTICS. Altogether 11,379 live stems ≥ 10 cm dbh were recorded. A total of 166 species of woody plants (including palms and tree ferns) representing 57 plant families were recorded (Appendix). Of these, 45 species were classified as treelets (non-canopy trees ≤ 25 cm dbh) and 43 species as shrubs (< 10 cm dbh).

Tree density (≥ 10 cm dbh) averaged 667 stems/ha and ranged from 60–2,045 stems \cdot ha $^{-1}$ across all plots (Fig. 3a). Basal area averaged 24.3 m 2 \cdot ha $^{-1}$ and ranged from 3 to 74 m 2 \cdot ha $^{-1}$ (Fig. 3b). Basal area and density varied widely both within and among forest associations across the study area. Maximum values of stand density and standing dead stems occurred at mid-elevations (1,900–2,200 m) (Fig. 3c). Canopy height declined linearly with elevation in the broadleaved-dominated stands whereas the canopy height of pine-dominated stands (pine importance value $\geq 135\%$) showed no clear pattern (Figure 3e) except for a decline at the highest elevations. The height-to-diameter ratio for pine trees was constant across the elevation gradient for this species ($R^2 = 0.002$) indicating the growth form of this species did not change with elevation.

Species richness of woody plants declined significantly ($R^2 = 0.54$; $P < 0.001$) with increasing elevation (Fig. 3d). Taxonomic richness at the genus and family level also declined with elevation. Genus richness was only slightly greater than family richness as several families were represented by only one genus, and the

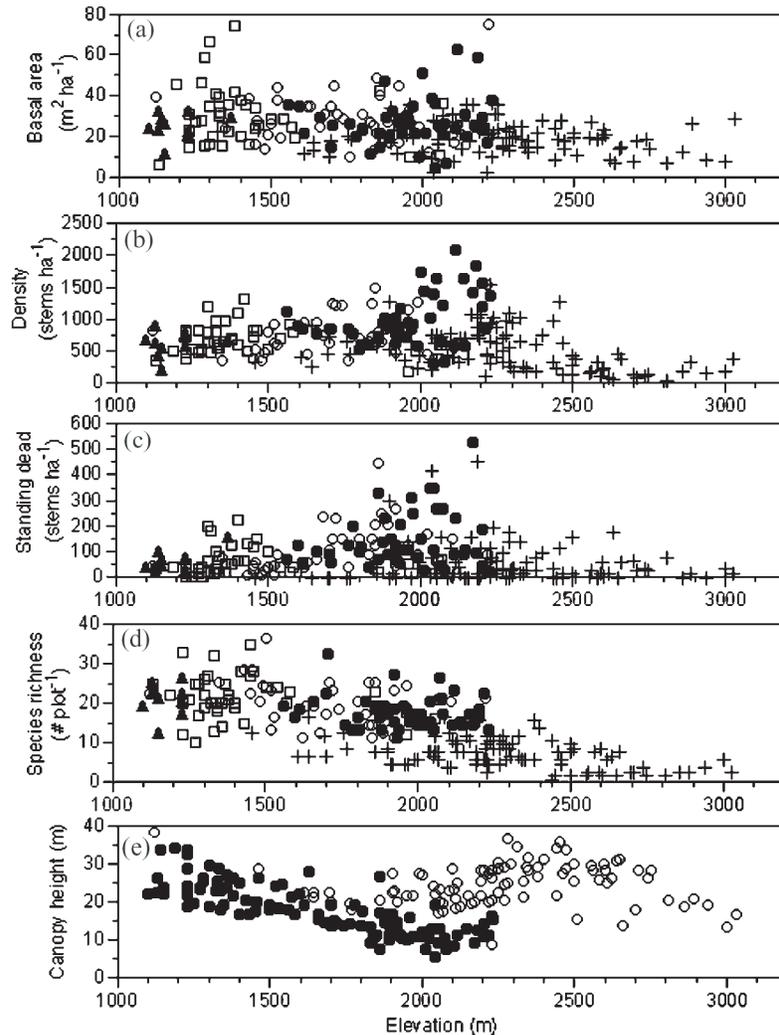


FIG. 3. Changes in (a) basal area, (b) density of live stems, (c) density of standing dead trees, (d) species richness, and (e) canopy height measured in plots across an elevation gradient in the Cordillera Central, Dominican Republic. In figures (a)–(e), symbols represent the major forest associations identified by TWINSPLAN: (\blacktriangle) secondary riparian forest; (\square) low elevation broadleaved forest; (\circ) pine-broadleaved mixed forest; (\bullet) cloud forest; (+) pine stands; in figure (e), symbols represent broadleaved forests (\bullet) and pine forests (\circ).

number of species per family declined gradually with elevation. When calculated by 200 m elevation intervals, species and family richness were relatively constant from 1,100–2,100 m, (averaging 85 species and 40 families), but above 2,300 m elevation the number of species and families decreased sharply, especially for the tree stratum, averaging only 19 species from 9 families of which only 6 species occurred in the overstory. Diversity was significantly higher in broadleaved forests than pine-dominated stands, but both forest types showed significant linear declines with increasing elevation.

ORDINATION OF VEGETATION. The first axis of the DCA ordination had a relatively high eigenvalue (0.692) and explained 66% of the total sample variance. Axis 1 could be interpreted primarily as an elevational gradient (temperature, humidity and precipitation) as elevation explained 83% of the variation of this ordination axis. The second and third ordination axes did not have much explanatory power.

The NMDS ordination clearly distinguished five major forest community types: the secondary riparian forest stands, broadleaved forest plots, pine-broadleaved mixed forests, cloud for-

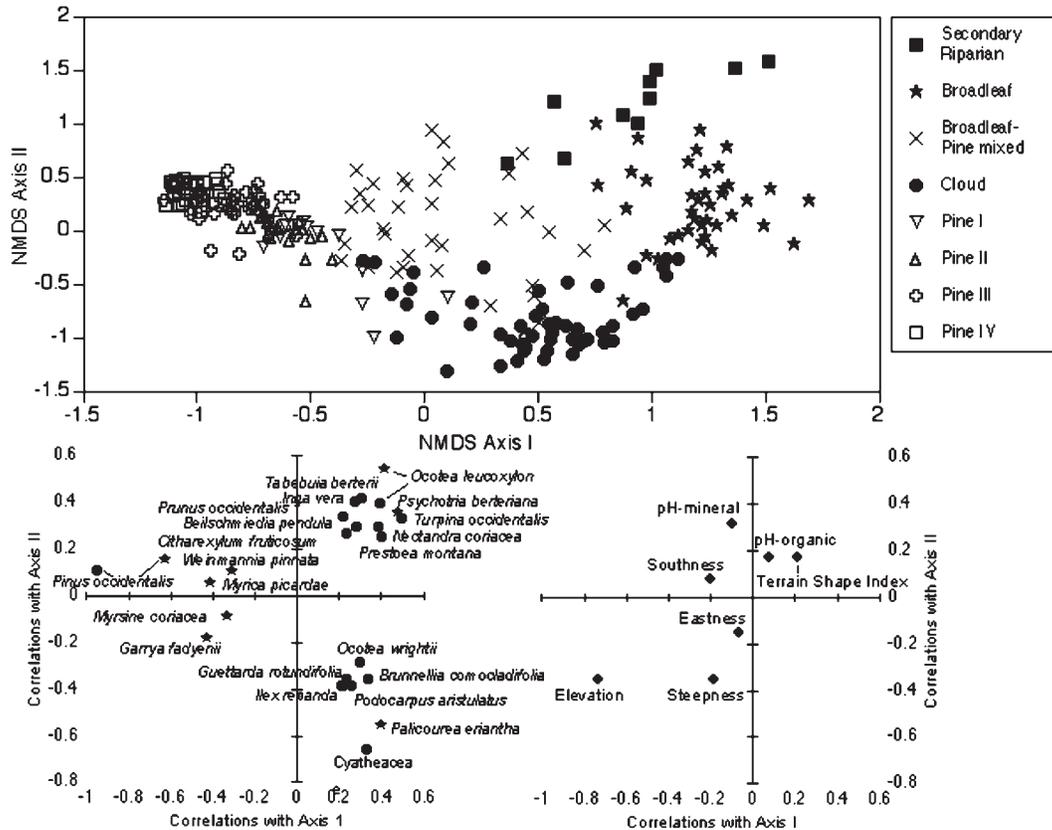


FIG. 4. (a) Ordination of 245 forest plots from the Cordillera Central, Dominican Republic by non-metric multidimensional scaling based on species importance values. Community types identified by TWINSpan are superimposed on the ordination plot. (b) Scatter plot of correlation coefficients between axis scores and the most influential species; circles represent trees (≥ 10 cm dbh) and stars are understory species. (c) Correlations between axes and environmental factors.

ests and pine-dominated stands (Fig. 4a). The ordination grouped all the pine-dominated stands into one community type. The species with the highest correlations with the NMDS axis scores are plotted to illustrate their position in ordination space (Fig. 4b). Plots with negative values along Axis 1 (i.e., pine plots) were strongly correlated with higher elevations (Fig. 4c). Pine plots also were positively correlated with Southness and Steepness and negatively correlated with the topographic slope index (i.e., less common on concave topography).

ENVIRONMENTAL PREDICTORS OF DISTRIBUTIONS OF DOMINANT TREE SPECIES. Predictive models were developed for seven dominant or distinctive species (Table 2). Different sets of environmental and disturbance parameters were significant predictors of the presence/absence of the various species, but elevation was a strong predictor of all species. *Pinus occidentalis* Sw. had

a 100% probability of occurrence at elevations above 2,500 m, a minimum probability of occurrence at approximately 1,400 m, and a secondary abundance peak at lower elevations. Past fire disturbance was a strong predictor of *P. occidentalis*, and an interaction between Southness and elevation helped to predict the occurrence of pine on leeward slopes. *Brunellia comocladifolia* H. & B. was most common at elevations between 1,500 to 2,000 m on steep, windward slopes with no history of fire and low mineral soil pH. *Prestoea montana* (Graham) Nicholson peaked between 1,300–1,500 m elevation on north facing slopes in concave-shaped topography. *Garrya fadyenii* Hooker was favored on wind-disturbed sites located on windward slopes between 1,700–2,100 m elevation where there had been no history of fire. *Didymopanax tremulus* Krug and Urb. occurred especially on ridges with two peaks of abundance at 1,350–

Table 2. Summaries of predictive models for selected species from the Cordillera Central of the Dominican Republic. Predictor variables are presented in order of significance. The shape of the response curve is given; for linear responses, the nature of the relationship (+ or -) is indicated. N is the number of plots in which a species occurred out of the total number of plots analyzed within that species elevational range. McFadden's ρ^2 indicates the degree to which the model explains species presence or absence; ρ^2 gives much lower values than the more familiar R^2 of least-squared regression. Levels of significance are as follows: *** = $P \leq 0.001$; ** = $P \leq 0.01$; * = $P \leq 0.05$.

Species	Significant environmental parameters	Response	N	ρ^2
<i>Pinus occidentalis</i>	Fire***	binomial (+)	163/227	0.29
	Elevation***	bimodal		
	Southness \times Elevation**	Interaction		
<i>Brunellia comocladifolia</i>	Elevation*	unimodal	107/181	0.26
	Steepness*	linear (+)		
	Eastness*	linear (+)		
	Southness*	linear (-)		
	pH-mineral*	unimodal		
	Fire*	binomial (-)		
<i>Prestoeamontana</i>	Elevation***	unimodal	41/114	0.42
	Fire**	binomial (-)		
	Southness*	linear (-)		
	TSI*	linear (+)		
<i>Garrya fadyenii</i>	Eastness**	log (+)	69/205	0.17
	Elevation**	unimodal		
	Wind*	binomial (+)		
	Fire*	binomial (-)		
<i>Didymopanax tremulus</i>	TSI**	linear (-)	37/145	0.16
	Elevation*	bimodal		
<i>Podocarpus aristulatus</i>	Fire**	binomial (-)	34/170	0.25
	Elevation*	unimodal		
	Southness*	linear (-)		
<i>Prunus occidentalis</i>	Steepness***	linear (-)	25/93	0.25
	Elevation**	linear (-)		
	TSI**	unimodal		
	Fire*	binomial (-)		

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1,550 m and 1,750–1,900 m elevation. *Podocarpus aristulatus* Parl. occurred predominantly between 1,900–2,200 m on north-facing slopes in the absence of fire. *Prunus occidentalis* Sw. was most likely to occur on flat terrain (low steepness, TSI = 0) at low elevation (1,100–1,400 m) on sites with no history of fire.

Discussion. On tropical mountains, the distribution and abundance of plant species and the structure, composition, and physiognomy of the plant community are correlated with the elevation gradient; however, the cause of these correlations is not entirely clear. A variety of climatic factors change along the elevation gradient and localized variation in other environmental factors (e.g., soil, topography) and in disturbance regimes is superimposed on the climatic gradient. The response of woody plant distributions to these complex influences has not been examined extensively in tropical mountains (Tanner 1977, Hartshorn and Peralta 1988, Weaver 1991, Aiba and Kitayama 1999, Sven-

ning 2001, Kimura and Simbolon 2002, Takyu et al. 2002). The Cordillera Central of Hispaniola (Dominican Republic) was previously classified by Hartshorn et al. (1981) as encompassing three Holdridge life-zones (lower and upper montane wet and lower montane moist forest). Our survey provides a more detailed view that helps to clarify the nature of tropical montane forest dynamics.

On the northeastern slope of the mountains, rainfall varied by only 13% across the elevation gradient, and the only prominent spatial variation in precipitation was associated with a rain-shadow effect on the leeward (southwest) side of the mountains (Figure 2b). Other climatic features varied in ways that indicated the influence of the trade wind inversion (TWI), a synoptic subsidence inversion whose base is frequently observed between 1,900–2,300 m in the Caribbean (Schubert et al. 1995). For example, air temperature declined at about the usual surface-air lapse rate ($-6.4 \text{ }^\circ\text{C km}^{-1}$; Orvis et al. 1997) up to about 1,800 m and more slowly above

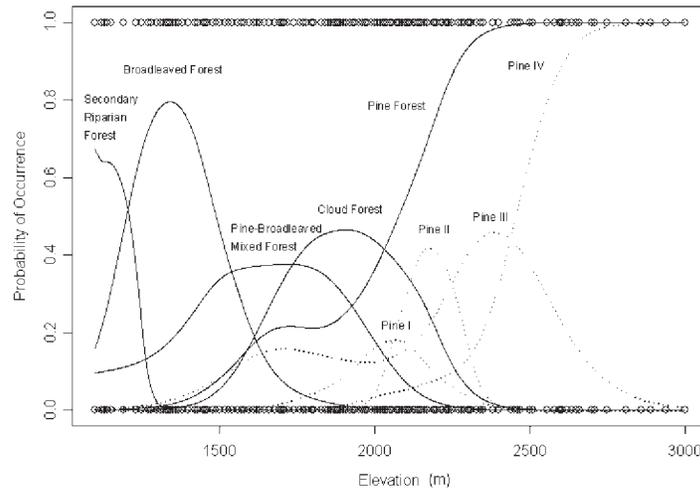


FIG. 5. Probability response curves of forest community types as a function of elevation. Curves are based on non-parametric logistic regressions.

($-3.2\text{ }^{\circ}\text{C km}^{-1}$) in the same manner as observed in Hawaii (Giambelluca and Nullet 1991). Atmospheric humidity declined sharply above 2,300 m, and the elevation of the cloud base that developed on most afternoons throughout the year showed a pronounced peak in frequency between 1,800 and 2,300 m elevation (Fig. 2c). Hence, the zone of maximum humidity and cloudiness, about 1,800–2,300 m, coincides roughly with the range of elevation of the base of the TWI. Finally, it is worth noting that chronic wind speeds throughout the study area are low, even at the highest elevations, although destructive winds are associated with hurricanes that are common in the Caribbean region (Horst 1992, Reading 1990).

To illustrate the elevational patterns of forest change, the probability distribution of each forest association was plotted (Fig. 5). Although each forest association showed a peak in frequency along the elevation gradient, the boundaries overlapped considerably and the vegetation did not form distinct vegetation zones. The DCA ordination provided additional evidence that species composition varied continuously over most of the gradient, as reflected in the ordination plot scores of Axis I (Fig. 6) (Lieberman et al. 1996); however, at about 2,250 m, there was an abrupt shift in the ordination scores indicating a discontinuity in the floristic composition at this elevation that reflected the shift from a diverse, broadleaved forest to a mono-

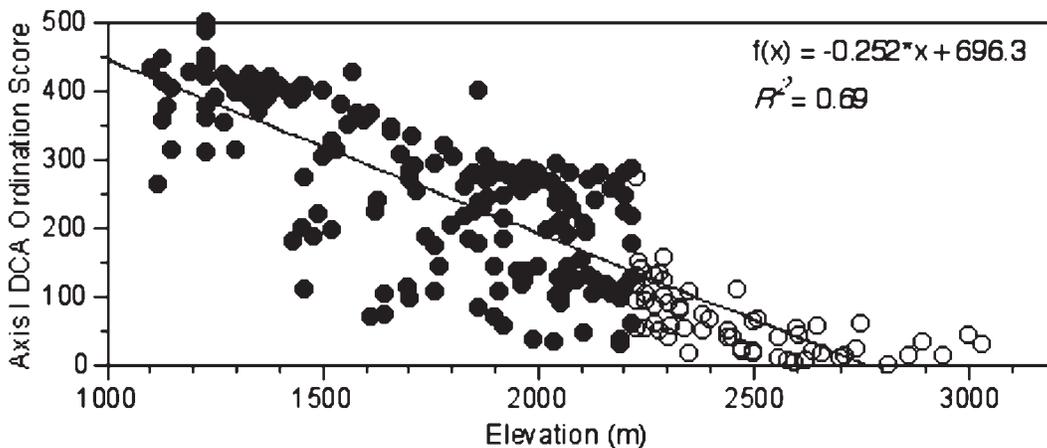


FIG. 6. Axis 1 sample scores from detrended correspondence analysis ordination in relation to plot elevation. Symbols represent plots < 2350 m elevation (●) and plots > 2350 m (○).

specific pine forest. The DCA axis scores also clearly showed the large variation in the species composition among plots within an elevation zone, especially below 2,250 m. This was due to the wide variety of habitats sampled within each elevation zone and the corresponding variation in topo-edaphic factors that influenced individual species distributions (Fig. 6).

The role of local variation in topography, soils and disturbance history in shaping forest patterns in the Cordillera Central was evident from both the community-level NMDS ordination and the logistic regression models of individual species distributions. Like others (Tanner 1977, Weaver 1991, Takyu et al. 2002), we observed that topographic variables (slope angle and convexity) significantly influenced community and species patterns (Table 2). Most prominent in our study site were the high abundance of *Prestoea montana* on concave topography (supporting the observation of Weaver (1991) in Puerto Rico) and of *Didymopanax tremulus* on wind exposed ridges (supporting observations by Hager and Zandoni 1993) in Hispaniola. Mineral soil pH also was a significant environmental factor associated with the distribution of woody vegetation. Fire was the most prominent disturbance agent that influenced vegetation distribution, but hurricanes also apparently have played a significant role; evidence of severe windthrow was clearly associated with the distribution of two dominant woody taxa, *Garrya fadyenii* and Cyatheaceae (Table 2). Disturbance by landslides and severe floods also accompanies hurricanes; for example, extensive areas were disturbed by both of these agents in and near our study site by Hurricane George in 1998. Their influence on forest distributions was clear. For example, we commonly observed seedlings of *P. occidentalis* on fresh alluvium and colluvium. Unfortunately, we were unable to identify the history of these disturbances in our sample plots, and future research is needed to further explore these influences.

The exact nature of the vegetation-environment interactions that regulate species distributions along the elevation gradient in the Cordillera Central remains uncertain. Kitayama and Mueller-Dombois (1994a) reasoned that three elevation-related climatic factors sorted vegetation types in Hawaii: 1) the lower limit of the cloud zone; 2) the decrease in precipitation and humidity above the base of the TWI; and 3) the lower limit of ground frost. In our study area, the cloud base most frequently coincided with

the elevation range at which the cloud forest association became prominent; however, this association was observed at lower elevations in ravines and topographic depressions, suggesting more complex controls that may be related to moisture, fertility, or protection from disturbance by fire.

The upper elevation limit of the cloud forest association also may involve a complex and possibly unique set of environmental controls. Three features may coincide with the rather abrupt transition from broadleaved cloud forest to pine forest and the elevation limit of many angiosperm trees at about 2,300 m: 1) the position of the TWI; 2) the common occurrence of ground-frost; and 3) the recurrence of fire disturbance. We cannot conclusively demonstrate how these features interact. In Hawaii, Kitayama and Mueller-Dombois (1994b) suggested that distinct vegetation boundaries were associated with the first two of these features, with treeline set by water deficits associated with the TWI and alpine desert scrub above the frost line. In the Cordillera Central, the endemic pine, *Pinus occidentalis*, apparently is well adapted to both drought and frost as it is the only arborescent species at these upper elevations. Furthermore, a variety of adaptations to fire disturbance clearly favor this species in locations where fire is ubiquitous (Darrow and Zandoni 1993), and fires are more likely to spread through pine-dominated stands than broadleaved forests (Kalisz and Stone 1984). The abundance of *P. occidentalis* in our study area was strongly associated with historical fires. We recorded high frequencies of fire disturbance in drier sites above the TWI and on the leeward, south and west slope of the massif (Martin and Fahey, pers. obs.). Although our survey observations do not demonstrate conclusively that temperature, humidity, and fire frequency interact to regulate the position of the cloud forest-pine forest boundary, the coincidence of these features is suggestive of such interactions.

We observed a gradual decline of canopy height along the elevation gradient (Figure 3), consistent with numerous observations in other tropical montane forests and tentatively ascribed to a variety of environmental stresses (Brujinzeel and Veneklaas 1998). However, in the Cordillera Central, stunting in the elevational range of the cloud forest zone was confined to the broadleaved tree species whereas the height of *P. occidentalis* remained nearly constant across most of the mountain transect. Clearly,

the environmental stresses that restrict height growth, and perhaps elevational limits of the broadleaved forest species, do not strongly influence the growth of the pine. Comparative studies of physiology and productivity of pine and broadleaved trees across this elevation gradient could help to reveal the controls on tree growth in cloud forests.

The position and role of *Pinus occidentalis* in forest patterns and dynamics in the Cordillera Central appears to be exceptional for humid montane tropical forests. Like many pines of mountainous regions, *P. occidentalis* has a very wide elevation range in Hispaniola, from 200–3,100 m (Darrow and Zanoni 1993), and hence spans several life zones. The local abundance of the species varies markedly, but in many areas throughout the Cordillera Central it strongly dominates the landscape where recurring fires favor pine over competing vegetation. Below about 2,300 m in our study area, *P. occidentalis* commonly occurs in mixed stands with various broadleaved trees; however, it shows little or no reproduction in these stands and is clearly a seral stage following fires that probably recur on fire-prone landscape positions. Fires occur naturally following lightning strikes in the dry season, but some anecdotal accounts suggest recent expansion of pine abundance owing to human-caused fires (Klotz and Torres 1991 [cited in Dobler et al. 1995]). Other catastrophic disturbances, like landslides and floods, also may favor pine regeneration, although the relative abundance is lower than following fires. In contrast, windthrow, which does not remove the sapling layer, favors the growth and recruitment of species already established in the understory which are predominantly broadleaved tree species. Above 2,300 m, and on the drier leeward flank of the Cordillera Central, *P. occidentalis* appears to be capable of self-replacement, probably because of a more open canopy and the lack of broadleaved tree reproduction.

The montane forests of eastern and southern Mexico and eastern Guatemala present an interesting comparison with the compositional patterns observed in Hispaniola. Climatic conditions are similar in that trade winds from the Gulf of Mexico strongly influence the weather patterns, the mountains are subject to hurricanes from the Caribbean, and polar air masses cause freezing conditions in the highlands during the winter (Davis et al. 1997). Vegetation patterns also are similar: lower montane wet and moist forests give way to cloud forests at mid-eleva-

tion that are replaced by pine and oak forests at higher elevations. Pines are distributed throughout the elevation range of the mountains occurring as an early successional species at the lower elevations following disturbance by fires and is a climax tree species in the colder, drier sites of the highlands (Rzedowski 1978).

Previous quantitative surveys in neotropical montane forests have documented declining richness of plant species and families with increasing elevation (Gentry 1988). Tallied at the plot level, species richness in our study area also declined gradually with elevation (Fig. 3); however, when tallied by 200 m elevation zones, species richness was nearly constant to 2,100 m, above which it declined sharply. The same combination of the TWI, ground frost, and recurring fires may contribute to this diversity pattern. The observation that species richness was relatively constant within 200 m intervals up to 2,100 m emphasizes the influence of microhabitats in species distributions. For example, *Podocarpus aristulatus*, a species characteristic of the cloud forest that typically grows between 1,900–2,200 m, was found growing in an isolated site at 1,300 m elevation. Clearly the forest patterns in the Cordillera Central are strongly influenced by topographic factors and disturbance history that are superimposed on the elevation gradient.

We sampled a wide variety of habitats within each elevation zone to capture the complex, topographic variation of the landscape that can strongly influence the local abundance of species. In contrast, previous studies of tropical montane forests attempted to minimize the complexity of the environmental gradient by sampling similar physiographic positions along the elevational gradient (Gentry 1995, Lieberman et al. 1996, Mueller-Dombois et al. 1981). Moreover, replication of plots within elevation zones was not feasible in previous studies because the high species diversity demanded very large sample plots (Lieberman et al. 1996). Because species richness at our site was only moderately high, we were able to sample with smaller plots that allowed us to assess the influence of small-scale variation in the environment on forest composition and structure across the elevation gradient. With regard to disturbance, the frequency of catastrophic disturbance in our study area, in the form of fires and severe hurricanes, is probably much higher than most other tropical montane forest regions. This disturbance history clearly has influenced the distribution and abundance of pine (fire) as well as *Brunellia como-*

cladifolia H. & B., *Garrya fadyenii* Hooker, and Cyatheaceae, all of which are favored by wind disturbance but negatively associated with fire. These influences are probably less important where small gaps are the principal mechanism of canopy turnover in tropical montane regions where hurricanes and natural fires are uncommon. In contrast, it seems likely that topographic factors, like slope angle, topographic slope index, and soil chemistry, probably commonly influence tree species distributions in most montane tropical forests (Tanner 1977, Takyu et al. 1999, Aiba and Kitayama 2002). More quantitative studies in a variety of tropical montane settings are needed to better understand how natural disturbance and complex environmental gradients interact to regulate the distinctive tree distribution patterns observed on Hispaniola and in other tropical forests.

Literature Cited

- ANONYMOUS. 2000. Madre de las Aguas Conservation Area, Dominican Republic, The Nature Conservancy. 8 p.
- AIBA, S. AND K. KITAYAMA. 1999. Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecol.* 140: 139–157.
- AUSTIN, M. P. AND J. A. MEYERS. 1996. Current approaches to modeling the environmental niche of eucalypts: implication for management of forest biodiversity. *For. Ecol. Manage.* 85: 95–106.
- BOOSE, E. R., D. R. FOSTER, AND M. RLUET. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecol. Monog.* 64: 369–400.
- BRUIJNZEEL, L. A. 2001. Hydrology of tropical montane cloud forests: A reassessment. *Land Use Water Resour. Res.* 1: 1–18.
- BRUIJNZEEL, L. A. AND E. J. VENEKLAAS. 1998. Climatic conditions and tropical montane forest productivity: The fog has not lifted yet. *Ecology* 79: 3–9.
- CHURCHILL, S. P., H. BALSLEV, E. FORERO, AND J. L. LUTEYN. 1995. Introduction, p. xi–xiv. In S. P. Churchill, H. Balslev, E. Forero and J. L. Luteyn [eds.], *Biodiversity and Conservation of Neotropical Montane Forests*. The New York Botanical Garden, Bronx, NY.
- CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Austr. J. Ecol.* 18: 117–143.
- CRAWLEY, M. J. 2002. *Statistical Computing: An Introduction to Data Analysis using S-Plus*. John Wiley and Sons, Inc., West Sussex, England. 761 p.
- DARROW, W. K. AND T. A. ZANONI. 1993. El pino de La Española (*Pinus occidentalis* Swartz): un pino subtropical poco conocido de potencial económico. *Moscosoa* 7: 15–37.
- DAVIS, S. D., V. H. HEYWOOD, O. HERRERA-MACBRYDE, J. VILLA-LOBOS, AND A. C. HAMILTON. 1997. Centres of Plant Diversity: A Guide and Strategy for their Conservation. Volume 3, The Americas. The World Wide Fund for Nature and IUCN-The World Conservation Union, IUCN Publications Unit, Cambridge, UK. 562 p.
- DINERSTEIN, E., D. M. OLSON, D. J. GRAHAM, A. L. WEBSTER, S. A. PRIMM, M. P. BOOKBINDER AND G. LEDEC. 1995. *A Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean*. The World Bank, Washington DC. 129 p.
- DOBLER, G., L. E. PERALTO, L. T. DEBORD AND J. G. TORRES. 1995. *Investigación y Manejo de Especies Maderables de Uso Común en la Sierra: una guía técnica*, Plan Sierra. Servicio Alemán de Cooperación Social-Técnica, Santiago, Dominican Republic.
- GENTRY, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75: 1–34.
- GENTRY, A. H. 1989. Northwest South America (Colombia, Ecuador, and Peru), p. 392–400. In D. Campbell and H. D. Hammond [eds.], *Floristic Inventory of Tropical Forests*. New York Botanical Garden, Bronx, NY.
- GENTRY, A. H. 1995. Patterns of diversity and floristic composition in neotropical montane forests, pp. 103–126. In S. P. Churchill, H. Balslev, E. Forero and J. L. Luteyn [eds.], *Biodiversity and Conservation of Neotropical Montane Forests*, The New York Botanical Garden, Bronx, NY.
- GIAMBELLUCA, T. W. AND D. NULLET. 1991. Influence of the trade-wind inversion in the climate of a leeward mountain slope in Hawaii. *Climate Res.* 1: 207–216.
- HAGER, J. AND T. A. ZANONI. 1993. La vegetación natural de la República Dominicana: Una nueva clasificación. *Moscosoa* 7: 39–81.
- HAMILTON, L. S., J. O. JUVIK, AND F. N. SCATENA. 1995. The Puerto Rico Tropical Cloud Forest Symposium: Introduction and Workshop Synthesis. In L. S. Hamilton, J. O. Juvik and F. N. Scatena [eds.], *Tropical Montane Cloud Forests*. Springer-Verlag, New York, NY.
- HARTSHORN, G., G. ANTONINI, R. DUBOIS, D. HARTSHORN, S. HECKADON, H. NEWTON, C. QUESADA, J. SHORES, AND G. STAPLES. 1981. The Dominican Republic, Country Environmental Profile: A Field Study. JRB Associates, McClean, WV.
- HARTSHORN, G. AND R. PERALTA. 1988. Preliminary description of primary forests along the La Selva-Volcan Barva altitudinal transect, Costa Rica, p. 281–295. In F. Almeda and C. Pringle [eds.], *Tropical Forests: Diversity and Conservation*. Academy of Sciences and Pacific Division, American Association for the Advancement of Science, San Francisco, CA.
- HENDERSON, A., S. P. CHURCHILL, AND J. L. LUTEYN. 1991. Neotropical plant diversity. *Nature* 351: 21–22.
- HILL, M. O. 1979. TWINSPLAN: A fortran program for arranging multivariate data. Cornell Ecology Programs, Cornell University, Ithaca, NY.
- HOLDRIDGE, L. R. 1942. The pine forests of Haiti. *Caribbean Forester* 4: 16–21.
- HOLDRIDGE, L. R. 1967. *Life Zone Ecology*. San Jose, Costa Rica, Tropical Science Center.
- HORN, S. P., L. M. KENNEDY, AND K. H. ORVIS. 2001. Vegetation recovery following a high elevation fire in the Dominican Republic. *Biotropica* 33: 701–708.

- HORST, O. H. 1992. Climate and the "encounter" in the Dominican Republic. *J. Geogr.* 91: 205–210.
- HOWARD, R. A. 1973. The vegetation of the Antilles, pp. 1–38. *In* A. Graham [ed.], *Vegetation and vegetational history of Northern Latin America*. Elsevier, Amsterdam, the Netherlands.
- JUDD, W. S. 1987. Floristic study of Morne La Visite and Pic Macaya National Parks, Haiti. *Bull. of the Florida State Museum* 32: 1–136.
- KALISZ, P. J. AND E. L. STONE. 1984. The Longleaf Pine Islands of the Ocala National Forest, Florida: A Soil Study. *Ecology* 65: 1743–1755.
- KAPPELLE, M. AND H. ZAMORA. 1995. Changes in woody species richness along an altitudinal gradient in Talamanca Montane *Quercus* forests, Costa Rica, pp. 135–148. *In* S.P. Churchill [ed.], *Biodiversity and Conservation of Neotropical Montane Forests*. The New York Botanical Garden, Bronx, NY.
- KIMURA, M. AND H. SIMBOLON. 2002. Allometry and life history of a forest understory palm, *Pinanga coronata* (Arecaceae), on Mount Halimum, West Java. *Ecol. Res.* 17: 323–338.
- KITAYAMA, K. AND D. MUELLER-DOMBOIS. 1994. An altitudinal transect analysis of the windward vegetation on Haleakala, a Hawaiian island mountain: (1) climate and soils. *Phytocoenologia* 24: 111–133.
- KITAYAMA, K. AND D. MUELLER-DOMBOIS. 1994. An altitudinal transect analysis of the windward vegetation on Haleakala, a Hawaiian island mountain: (2) vegetation zonation. *Phytocoenologia* 24: 135–154.
- LEWIS, J. F. 1980. Cenozoic tectonic evolution and sedimentation in Hispaniola. *Transactions of the 9th Caribbean Geology Conference, Santo Domingo* 1: 65–73.
- LIEBERMAN, D., M. LIEBERMAN, R. PERALTA, AND G. S. HARTSHORN. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *J. Ecol.* 84: 137–152.
- MARTIN, P. M., R. E. SHERMAN, AND T. J. FAHEY. 2004. Forty years of tropical forest recovery from agriculture: structure and floristics of secondary and old-growth riparian forests in the Dominican Republic. *Biotropica* 36: 297–317.
- MAY, T. 2000. Five years of post-fire vegetation succession in a Caribbean cloud forest (Cordillera Central, Dominican Republic). *Ecotropica* 6: 117–127.
- MCCUNE, B. AND M. J. MEFFORD. 1999. *PC-ORD. Multivariate Analysis of Ecological Data*. MjM Software Design. Gleneden Beach, OR. 300 p.
- MCGARIGAL, K., S. CUSHMAN, AND S. STRATFORD. 2000. *Multivariate Statistics for Wildlife and Ecology Research*. Springer-Verlag, New York, NY. 283 p.
- MCNAB, W. H. 1989. Terrain shape index: Quantifying effect of minor landforms on tree height. *For. Sci.* 35: 91–104.
- MINCHIN, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69: 89–107.
- MOTZKIN, G., P. WILSON, D. R. FOSER, AND A. ALLEN. 1999. Vegetation patterns in heterogeneous landscapes: The importance of history and environment. *J. Veg. Sci.* 10: 903–920.
- MUELLER-DOMBOIS, D. 1987. Forest dynamics in Hawaii. *Trends Ecol. Evol.* 7: 216–220.
- MUELLER-DOMBOIS, D., K. W. BRIDGES, AND H. L. CARSON. 1981. *Island Ecosystems: Biological Organization in Selected Hawaiian Communities*. Hutchinson Ross Publishing Company, Stroudsburg, PA. 583 p.
- ORVIS, K. H., G. M. CLARK, S. P. HORN, AND L. M. KENNEDY. 1997. Geomorphic traces of quaternary climates in the Cordillera Central, Dominican Republic. *Mountain Res. Develop.* 17: 323–331.
- PEDERSEN, A. 1953. Frost damage in the pine forest. *Caribbean Forester* 2(3–4): 93–96.
- PENAFIEL, S. R. 1995. Biological and hydrological values of forests in the Central Cordillera Mountains, Philippines, p. 266–273. *In* L. S. Hamilton, J. O. Juvik and F. N. Scatena [eds.], *Tropical Montane Cloud Forests*. Springer-Verlag, New York, NY.
- PEREIRA, J. M. C. AND R. M. ITAMI. 1991. GIS-based habitat modeling using logistic multiple regression: a study of the Mt. Graham red squirrel. *Photogrammetric Engineering and Remote Sensing* 57: 1475–1486.
- READING, A. J. 1990. Caribbean tropical storm activity over the past four centuries. *Int. J. Climatology* 10: 365–376.
- RZEDOWSKI, J. 1978. *Vegetación de México*. Editorial Lumisa, Arcos de Belén, Mexico.
- SCHUBERT, W. H., P. E. CIESIELSKI, C. LU, AND R. H. JOHNSON. 1995. Dynamical adjustment of the trade wind inversion layer. *Amer. Meteorological Soc.* 52: 2941–2952.
- SVENNING, J. C. 2001. Environmental heterogeneity, recruitment limitation and the mesoscale distribution of plants in a tropical montane rainforest (Maquipucuna, Ecuador). *J. Trop. Ecol.* 17: 97–113.
- TAKYU, M., S. AIBA, AND K. KITAYAMA. 2002. Effects of topography on tropical lower montane forests under different geological conditions on Mount Kinabalu, Borneo. *Plant Ecol.* 159: 35–49.
- TANNER, E. V. J. 1977. Four montane rain forests of Jamaica: A quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *J. Ecol.* 65: 883–918.
- WEAVER, P. L. 1991. Environmental gradients affect forest composition in the Luquillo Mountains of Puerto Rico. *Interciencia* 16: 142–151.
- WEBSTER, G. L. 1995. The Panorama of neotropical cloud forests, p. 53–77. *In* S. P. Churchill, H. Balslev, E. Forero and J. L. Luteyn [eds.], *Biodiversity and Conservation of Neotropical Montane Forests*. The New York Botanical Garden, Bronx, NY.
- WHITTAKER, R. H. 1967. Gradient analysis of vegetation. *Biological Review* 42: 207–264.
- WISER, S. K., R. K. PEET, AND P. S. WHITE. 1998. Prediction of rare-plant occurrence: A southern Appalachian example. *Ecol. Appl.* 8: 909–920.
- WOLF, J. H. D. 1993. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Ann. Missouri Bot. Garden* 80: 928–960.
- ZANONI, T. A. 1990. The flora and vegetation of Pico Duarte and Loma La Pelona, Dominican Republic: "The top of the Caribbean". *Mem. New York Bot. Garden* 64: 279–289.

Appendix

Woody plants, palms, and tree ferns collected in the Armando Bermúdez and Carmen Ramírez National Park of the Cordillera Central, Dominican Republic.

Aquifoliaceae (Theales)

- Ilex fuertesiana* Loes. Treelet; 1270–2220 m; common; endemic.
Ilex impressa Loes. & Ekman. Treelet (very common) to tree (uncommon); 1100–2300 m; endemic.
Ilex krugiana Loes. Treelet; occasional; native.
Ilex macfadyenii (Walp.) Rehder. Treelet; > 1900 m; occasional; native.
Ilex microwrightioides Loes. Treelet; 1130–2230 m; uncommon; endemic.
Ilex repanda Griseb. Treelet; 1300–2240 m; common; native.
Ilex tuerckheimii Loes. Shrub; common; endemic.

Araliaceae (Cornales)

- Didymopanax tremulus* Krug & Urb. Tree; 1190–2075; endemic.
Oreopanax capitatum (Jacq.) Decne. & Planch. Tree; 1120–2100 m; native.

Areaceae or Palmae (Arecales)

- Prestoea montana* (Graham) Nicholson. Palm; 1190–1960 m; occasional; native.

Asteraceae or Compositae (Asterales)

- Baccharis myrsinites* (Lam.) Pers. Treelet; 1100–2660 m; common; native.
Eupatorium illitium Urb. Shrub; 1230–2750 m; very common; endemic.
Eupatorium odoratum L. Shrub; 1100–1500 m; occasional; native.
Eupatorium puberulum Lam. Shrub; occasional; endemic.
Herodotia mikanioides Urb. & Ekman. Shrub; < 1,900 m; endemic.
Senecio fuestisii Urb. Shrub

Bignoniaceae (Bignoniales)

- Tabebuia berteroi* (DC.) Britton. Tree; 1100–1960; common; endemic.
Tabebuia bullata A.H. Gentry. Tree; 1450–2020 m; occasional; endemic.
Tabebuia vinosa A.H. Gentry. Tree; 1560–2380 m; common.

Boraginaceae (Solanales)

- Cordia picardea* Urb. Shrub; 1700–2100 m; occasional; endemic.

Brunelliaceae (Rosales)

- Brunellia comocladifolia* H. & B. Tree; 1120–2240 m; very common; native.

Buddlejaceae (Gentianales)

- Buddleja domingensis* Urb. Shrub; 1100–1900 m; occasional; endemic

Caesalpinaceae (Fabales)

- Chamaescrista glandulosa* var. *picardae* (Urb.) Irw. & Barneby. Shrub; 1239–2055; occasional; native.
Senna domingensis (Spreng.) H. S. Irwin & Barneby. Shrub; occasional; native.

Cecropiaceae (Urticales)

- Cecropia* sp. Treelet; < 1800 m; uncommon.

Celastraceae (Celastrales)

- Torrolbasia cuneifolia* (Wr.) Krug & Urb. Tree; 1230–2230 m; common; native.

Chloranthaceae (Piperales)

- Hedyosmum domingensis* Urb. Shrub; 1,200–1,900 m; native.

Clusiaceae (Theales)

- Clusia clusiodes* (Griseb.) D'Arcy. Parasitic tree; 1120–1990 m; common; native.

Cunoniaceae (Rosales)

- Weinmannia pinnata* L. Shrub (very common) to tree (uncommon); 1430–2660 m; native.

Cyatheaceae (Polypodiales)

- Alsophila* spp. Tree fern; 1150–2350 m; very common.
Cyathea spp. Tree fern; 1150–2350 m; very common.

Elaeocarpaceae (Malvales)

- Sloanea ilicifolia* Urb. Tree; 1110–2055 m; occasional; endemic.

Ericaceae (Ericales)

- Gaultheria domingensis* Urb. Shrub; 1230–2300 m; occasional; endemic.
Lyonia alainii Judd. Shrub; 1380–2300 m; common; endemic
Lyonia buchii Urb. Tree; 2300–3000 m; occasional; endemic.
Lyonia cf. *tinensis* Urb. Shrub; 1230–2020; occasional; endemic.
Lyonia heptamera Urb. Shrub; 2300–3098 m; occasional; endemic.
Lyonia truncata Urb. var. *montecristina* (Urb. & Ekman) Judd. Tree; < 1,400 m; occasional; endemic.

Euphorbiaceae (Euphorbiales)

- Alchornea latifolia* Sw. Tree; 1110–2055 m; occasional; native.
Chaetocarpus domingensis G. Proctor. Tree; 1600–1840 m; occasional; endemic.
Croton angustatus Urb. Tree; 1230–2510 m; common; native.

- Croton azuensis* Urb. Shrub; endemic.
Dittia maestrensis Borhidi. Treelet; 1130–2230 m; common; native.
Dittia myricoides Griseb. Treelet 1380–2200; occasional; native.
Pera bumelifolia Griseb. Tree; 1120–2070; common; native.
Phyllanthus sp. Treelet, uncommon.
Sapium buchii (Urb.) Urb. Tree; endemic.

Flacourtiaceae (Violales)

- Lunania ekmanii* Urb. Treelet; < 1500 m; uncommon; native.

Garryaceae (Cornales)

- Garrya fadyinii* Hooker. Treelet; 1230–3030 m; common; native.

Gesneriaceae (Bignoniales)

- Rhytidophyllum berterioanum* Mart. Treelet; uncommon; endemic.
Rhytidophyllum grandiflorum Xu & Skog. Treelet; uncommon.

Hypericaceae (Theales)

- Hypericum pycnophyllum* Urb. Shrub; < 1900 m; endemic.

Juglandaceae (Jugundales)

- Juglans jamaicensis* C. DC. Tree; < 1500 m; uncommon; native.

Labiatae or Lamiaceae (Lamiales)

- Salvia uncinata* Urban. Shrub; 1900–2700 m; endemic.
Satureja alpestris (Urb.) J. Jiménez. Shrub; 1800–3098 m; occasional; endemic.

Lauraceae (Annonales)

- Beilschmieda pendula* (Sw.) Benth. & Hook. Tree; 1300–1960 m; occasional; native.
Ocotea cicatricosa C.K. Allen. Tree; 1370–2200 m; common; endemic.
Ocotea coriacea (Sw.) Britton. Tree; 1140–1860 m; common; native.
Ocotea floribunda (Sw.) Mez. Tree; 1100–1360 m; occasional; native.
Ocotea foeniculaceae Mez. Tree; 1450–1480 m; uncommon; native.
Ocotea leucoxydon (Sw.) Mez. Tree; 1100–1960; common; native.
Ocotea membranaceae (Sw.) R.A. Howard. Tree; 1100–1360 m; occasional; native.
Ocotea nemodaphne Mez. Tree; 1800–2200 m; uncommon; native.
Ocotea wrightii (Meissn.) Mez. Tree; 1270–2350 m; common; native.
Persea krugii Urb. Tree; common; native.
Persea oblongifolia Kopp. Tree; 1800–2200 m; uncommon; endemic.

Leguminosae or Fabaceae (Fabales)

- Inga vera* Willd. Tree; 1100–1920 m; common; native.
Pithecellobium sp. Tree; < 1500 m; uncommon.

Malpighiaceae (Geraniales)

- Byrsonima lucida* (Miller) L.C. Rich. Treelet; < 1800 m; occasional; native.

Melastomataceae (Myrtales)

- Clidemia fuertesii* Cogn. Shrub
Clidemia umbellata (Miller) L.O.Wms. Tree
Leandra lima (Desr.) W. Judd & Skean. Shrub
Heterotrichum umbellatum (Mill) Urb.
Meriania involucrata (Desr.) Naud. Shrub; endemic
Miconia desportesii Urb. Shrub
Miconia dielsiana Urb. Treelet; 1970–2330 m
Miconia dodecandra (Desr.) Cogn. Tree
Miconia krugii Cogn. Tree
Miconia punctata (Desr.) DC. Tree; 1130–2650 m; occasional; native.
Miconia selleana Urb. & Ekm. Treelet; 1970–2330 m; common; endemic.
Miconia viscidula Urb. & Cogn. Shrub; endemic
Ossaea scalpta (Venth.) DC. Shrub
Tetrazygia crotonifolia (Desr.) DC. Shrub; native
Tetrazygia longicollis Urb. & Cogn. Shrub
Tetrazygia urbanii (Cogn.) Croizat. Treelet; native.

Meliaceae (Sapindales)

- Cedrela odorata* L. Tree; 1100–1800 m; native; uncommon; native.
Guarea guidonea (L.) Sleumer. Tree; 1380–2270 m; uncommon; native.

Moraceae (Urticales)

- Ficus velutina* H. & B. Tree; < 1400 m; uncommon; native.

Myricaceae (Myricales)

- Myrica picardae* Krug & Urb. Tree; 1230–2660 m; common; endemic.

Myrsinaceae (Primulales)

- Myrsine coriacea* (Sw.) R. Br. Tree; 1120–2460 m; common; native.
Myrsine cf. magnolifolia Urb. & Ekman. Treelet; 1300–2100 m; occasional; endemic.
Myrsine nubicola Liogier. Tree; 1800–2300 m; occasional; endemic.
Wallenia apiculata Urb. Tree; 1500–2100 m; uncommon; endemic.

Myrtaceae (Myrtales)

- Calyptanthes limoncillo* Liogier. shrub; 1400–2000 m; occasional; endemic.
Eugenia domingensis Berg. Tree; < 1700 m; occasional; native.
Eugenia odorata Berg. Treelet; endemic.
Gomidesia lindeniana Berg. Tree; < 1800 m; common; native.

Myrcia deflexa (Poiret) DC. Tree; < 1800 m; occasional; native.

Myrcia splendens (Sw.) DC. Treelet; < 1800 m; occasional; native.

Pimenta racemosa var. *hispaniolensis* (Urb.) Landrum. Tree; 1830–2145 m; occasional; native.

Plinia sp. Tree; endemic.

Psidium guajava L. Treelet; < 1700 m; occasional; native.

Syzygium jambos (L.) Alston. Tree; < 1400 m; common; non-native.

Oleaceae (Oleales)

Chionanthus domingensis Lam. Tree; 1230–2055 m; occasional; native.

Haenianthus salicifolius Griseb. var. *obovatus* (Krug & Urb.) Knobl. Tree; <1700 m; occasional; native.

Onagraceae (Myrtales)

Fuchsia pringsheimii Urb. Shrub; 1320–2660 m; common; endemic

Fuchsia tryphylla L. Shrub; 1300–2100 m; endemic.

Papaveraceae (Berberidales)

Bocconia frutescens L. Treelet; < 1500 m; uncommon; native.

Pinaceae (Coniferales)

Pinus occidentalis Sw. Tree; 1100–3098 m; very common; endemic.

Piperaceae (Piperales)

Piper aduncum L. Treelet; < 1800 m; uncommon; native.

Piper amalago L. Treelet; < 1800 m; uncommon; native.

Piper rugosum Lam. Treelet; < 1800 m; uncommon; native.

Podocarpaceae (Coniferales)

Podocarpus aristulatus Parl. Tree; 1310–2290 m; cloud forest (common); endemic.

Polygalaceae (Geraniales)

Polygala fuertesii (Urb.) Blake. Treelet; endemic

Polygonaceae (Polygonales)

Coccoloba wrightii Lindau. Tree; 1370–1950; common; native.

Rhamnaceae (Rhamnales)

Rhamnus sphaerosperma Sw. Treelet; uncommon; native

Rosaceae (Rosales)

Prunus occidentalis Sw. Tree; 1130–1400 m; common; native.

Rubus eggessii Rydb. Shrub; 1800–2350 m; common; endemic

Rubiaceae (Gentianales)

Antirhea oligantha Urb. Treelet; endemic.

Chione seminervis Urb.&Ekm. Tree; 1800–2300 m; uncommon; native.

Guettarda cf. *mollis* DC. Treelet; < 2100 m; endemic.

Guettarda pungens Urb. Shrub; uncommon; native.

Guettarda rotundifolia Urb. Tree; 1800–2300 m; endemic.

Neolaugeria sp. Tree

Palicourea eriantha DC. Treelet; 1100–2660 m; very common; endemic

Psychotria berteriana DC. Shrub; 1100–2660 m; very common; native.

Psychotria dolicoctalia Urb. Treelet

Psychotria plumieri Urb. Treelet; < 1400 m; endemic.

Rondeletia conferta Urb.& Ekman. Treelet; < 1900 m; endemic.

Rondeletia ochracea Urb. Treelet; < 1700 m; endemic.

Scolosanthus liogieri Borhidi.

Stenostomum oliganthum (Urb.) Borhidi

Rutaceae (Sapindales)

Citrus aurantium L. Tree; 1100–1200 m; cultivated.

Citrus limeta L. Tree; 1200–1300 m; cultivated.

Citrus limon (L.) Burm. F. Treelet; 1100–1200 m; cultivated.

Zanthoxylum azuense (Urb. & Ekman) Jiménez. Shrub < 1900 m; endemic.

Sabiaceae (Sapindales)

Meliosma impressa Krug & Urb. Tree; 1140–2230 m; common; endemic.

Sapindaceae (Sapindales)

Allophylus crassinervis Radlk. Treelet; 1130–2200 m; occasional; native.

Cupania americana L. Tree; 1200–1300 m; uncommon; native.

Dodonaea angustifolia Lf. Tree; uncommon; non-native.

Sapotaceae (Ebenales)

Chrysophyllum oliviforme L. Shrub; < 1900 m; common; native.

Sideroxylon cubense (Griseb.) T. Pennington. Tree; native

Sideroxylon obovatum Lam. Native.

Solanaceae (Solanales)

Cestrum azuense Urb. & Ekman. Shrub; 1120–2750; very common; endemic

Cestrum coelophlebium O. E. Schulz. Shrub; 1120–2750; very common; endemic.

Cestrum inclusum Urb. Shrub; 1120–2250; very common; endemic.

Cestrum mononeurum Urb. & Ekman. Treelet; 1500–2200 m; endemic.

Cestrum tuerckheimii O. E. sch. Shrub; 2000–3098 m; endemic

Solanum crotonoides Lam. Shrub; 1270–2280 m; occasional; endemic.

Solanum nudum Humb. & Bonpl. Ex. Dunal. Shrub; 1100–2000 m; occasional; native.

Staphyleaceae (Rosales)

Turpina occidentalis (Sw.) G. Don. Tree; 1100–2055; common; endemic.

Styracaceae (Ebenales)

Styrax ochraceus Urb. Tree; rare; endemic.

Symplocaceae (Theales)

Symplocos domingensis Urb. Tree; endemic

Theaceae (Theales)

Cleyera bolleana (O.C. Schmidt) Kobuski. Treelet; 1800–2100 m; uncommon; endemic

Cleyera vaccinioides (O.C. Schmidt) Kobuski. Treelet; endemic.

Laplacea alpestris (Kn. & Urb.) Dyer. Treelet; endemic.

Laplacea cf. reticulataris Liogier. Tree; 1600–2100 m; endemic.

Laplacea cymatoneura Urb. Tree; endemic.

Laplacea portoricensis (Krug & Urb.) Dyer. Tree; native.

Ternstroemia buxifolia Ekman & Schmidt. Shrub; endemic.

Thymeliaceae (Euphorbiales)

Daphnopsis crassifolia (Poirot) Meissner. Treelet; 1350–2145 m; occasional; endemic.

Ulmaceae (Urticales)

Trema micrantha (L.) Blume. Tree; 1120–1860 m; occasional; native.

Urticaceae (Urticales)

Gyrotaenia myriocarpa Griseb. Treelet; < 1800 m; native.

Verbenaceae (Lamiales)

Citharexylum caudatum L. Tree; 1100–2055; common; native.

Citharexylum fruticosum L. Tree; 1100–2055; common; native.

Duranta arida Britton & Wilson. Shrub; 2000–2200 m; uncommon; endemic.