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ALTITUDINAL CHANGES OF FOREST DIVERSITY AND COMPOSITION IN THE RAMAL DE GUARAMACAL IN THE VENEZUELAN ANDES

CAMBIOS ALTITUDINALES EN LA DIVERSIDAD Y COMPOSICIÓN DE LOS BOSQUES EN EL RAMAL DE G UARAMACAL EN LOS ANDES DE VENEZUELA

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ABSTRACT

Qualitative and quantitative data on forest floristic composition, structure and diversity were collected from eleven 0.1 ha (20 x 50 m) plots between 1830 and 2580 m to determine how forests change with increasing altitude on the northern slope of Cruz Carrillo National Park (Guaramacal) in the Andes of Trujillo and Portuguesa states, Venezuela. A total of 4,521 individuals ≥ 2.5 cm d.b.h. was recorded, comprising 213 morphospecies, 124 genera, and 59 families of vascular plants. There included 171 species of trees, 7 tree ferns, 5 hemiepiphytes, 3 large herbs, 22 lianas, 4 palms and one climbing terrestrial herb. The most species-rich family was Lauraceae (26 species), followed by Rubiaceae (21), Melastomataceae (16), Myrtaceae (10), Euphorbiaceae (8), and Asteraceae (7). Floristic diversity increased from 1830 to 2350 m but decreased above that. Forest stature decreased at higher elevation, and density of small individuals increased. Analysis of floristic composition using Bray-Curtis cluster analysis and distribution pattern of the most important species (Importance Value Index) indicate altitudinal changes that suggest the presence of two vegetation zones separated by a transitional forest type.

Keywords: altitudinal zonation, floristic composition, diversity, forest structure, montane forests.

RESUMEN

Con el fin de evaluar el efecto de la altitud sobre los bosques de la vertiente norte del Parque Nacional Cruz Carrillo (Guaramacal), estados Trujillo y Portuguesa, Venezuela, se recolectaron datos cuantitativos y cualitativos sobre composición florística, estructura y diversidad en once parcelas de 0,1 ha (20 x 50 m) ubicadas entre 1830 y 2580 m. Se registró un total de 4.521 individuos = 2,5 cm d.a.p., comprendiendo 213 morfospecies, 124 géneros, y 59 familias de plantas vasculares. Entre ellas se encontraron 171 especies de árboles, 8 helechos arborescentes, 5 hemiepífitas, 3 hierbas altas, 22 lianas, 4 palmas y una trepadora terrestre. La familia con mayor riqueza de especies fue Lauraceae (26 species), seguido por Rubiaceae (21), Melastomataceae (16), Myrtaceae (10), Euphorbiaceae (8) y Asteraceae (7). La diversidad florística aumentó desde 1830 hasta 2350 m y disminuyó a partir de ahí. A mayor altitud la estatura del bosque disminuyó y la densidad de individuos pequeños aumentó. El análisis de la composición florística usando análisis de agrupamiento de Bray-Curtis y el patrón de distribución de las especies más importantes (Indice de Valor de Importancia) indicó cambios altitudinales que sugieren la existencia de dos zonas de vegetación separadas por una zona de transición.

Palabras clave : zonificación altitudinal, composición florística, diversidad, estructura, bosques montanos.

INTRODUCTION

On tropical mountains, the elevational limits of forest formations can vary with latitude or in response to local or regional peculiarities in topography or climate (Grubb and Whitmore 1966, Monasterio and Reyes 1980, van der Hammen and Cleef 1986, van der Hammen 1995). In the tropical Andes, the distribution of vegetation types and their qualitative and quantitative composition are thought to be determined largely by gradients of temperature, rainfall, and relative humidity (van der Hammen and Cleef 1986, van der Hammen 1995). Gradients of temperature have pronounced effects on patterns of vegetation zonation, especially on the limits of the tree line (Troll 1973, Rundel 1994).

Previous quantitative studies addressing the altitudinal variations in floristic diversity, forest structure, and composition in tropical mountains (e.g. Veillon 1965, Gentry 1988b, 1995, Kitayama 1992, Kappelle *et al.* 1995, Lieberman *et al.* 1996, Boyle 1996, Vasquez and Givnish 1998) differ greatly in their scope, sampling methods, and analytical techniques. Whereas studies based mostly on purely physiognomic and floristic criteria (Cuatrecasas 1958, van der Hammen 1974) found clear altitudinal zonation and more or less discrete vegetation belts in the northern Andes, quantitative studies in other tropical mountain areas have been less conclusive about zonation (Nakashizucha *et al.* 1992, Kappelle *et al.*1995, Lieberman *et al.* 1996, Vásquez and Givnish 1998).

Gentry (1988b, 1992, 1995) used numerous 0.1 ha samples of plants = 2.5 cm dbh in Neotropical montane forests to analyze patterns of diversity and floristic composition along elevational gradients. He found that diversity decreased linearly with elevation from above 1500 m to near the treeline (3000 m), and that floristic composition changed in predictable ways with increasing altitude. Lauraceae, then Melastomataceae and Rubiaceae were the most species-rich families between 1500 and 2900 m in most Andean forest sites (Gentry 1995).

In the northeastern Andes of Venezuela, there are lower offshoots of the main cordillera that show both a clear depression of the treeline and obvious differences in moisture between opposing slopes. One such example is the Ramal de Guaramacal, which lies within a national park (Cruz Carrillo National Park) and is not subject to strong human intervention (Ortega *et al.* 1987, Figure 1). With a single road traversing the park up its drier northwestern (Andes-facing) slope and then down the moister southeastern (llanos-facing) slope, the area offers an excellent opportunity to sample the vegetation across an elevational gradient.

This study examines the diversity, structure and composition of the montane forests on the northeastern slopes of Ramal de Guaramacal, Trujillo state, Venezuela. Two main questions are addressed: (1) Does species diversity of woody plants decrease linearly with increasing elevation? and (2) Are clear transitions in forest composition apparent over a short elevational gradient?. This study is part of a broader program to document the vegetation and flora of Cruz Carrillo National Park, conducted jointly by the Universidad de los Llanos in Guanare, Venezuela and the National Museum of Natural History of the Smithsonian Institution, Washington, DC. (Dorr *et al.* 2000). The program aims to classify and map the vegetation of the park in addition to conducting an in-depth floristic analysis.

STUDY SITE

Cruz Carrillo National Park is located at the northeastern end of the Cordillera Oriental of the Andes. It encompasses the Ramal of Guaramacal, which lies to the southeast of Boconó, in Trujillo and Portuguesa states, Venezuela (Figure 1). The park lies at 9° 05'-21' N latitude, 70° 00'-20' W longitude, and covers an area of approximately 21,466 hectares. It covers an altitudinal range on the northern slope of 1800 to 3200 m.

The climate of the region is characterized by a dry season from November to March and a rainy season from April to October, with maximum precipitation in June and July (Rangel 1989, Reaud-Thomas 1989). Mean annual temperature varies from 17.7°C at 1560 m to an estimated 4.5° C at 3200 m in the Páramo de Guaramacal (Rangel 1989). Detailed information about climate, geology and soils of the study area is presented in Cuello (1999).

The higher reaches of Guaramacal have remained relatively free from human intervention until recently, when an access road was constructed for a communication antenna and access to coffee plantations. However, forests in the park are still relatively undisturbed and are well preserved compared to the surrounding areas.

Preliminary studies by Ortega *et al.* (1987) and Cuello (1999) described the vegetation of Guaramacal as consisting mostly of montane cloud forests, which they divided into Subandean (lower montane) forests and Andean (upper montane) forests, following Cuatrecasas (1958) and van der Hammen (1989). The montane cloud forests on the northern slope of Guaramacal are dense, of medium height (10-25 m), with many epiphytes, and extend from about 1800 to 2600 m. From 2600 to about 2800 m, a transitional vegetation occurs (elfin forest mixing with shrubs), giving way to open "páramo" vegetation (subpáramo according to Cuatrecasas 1986), which is found from 2800 m to the highest ridges at 3200 m (Ortega *et al.* 1987,

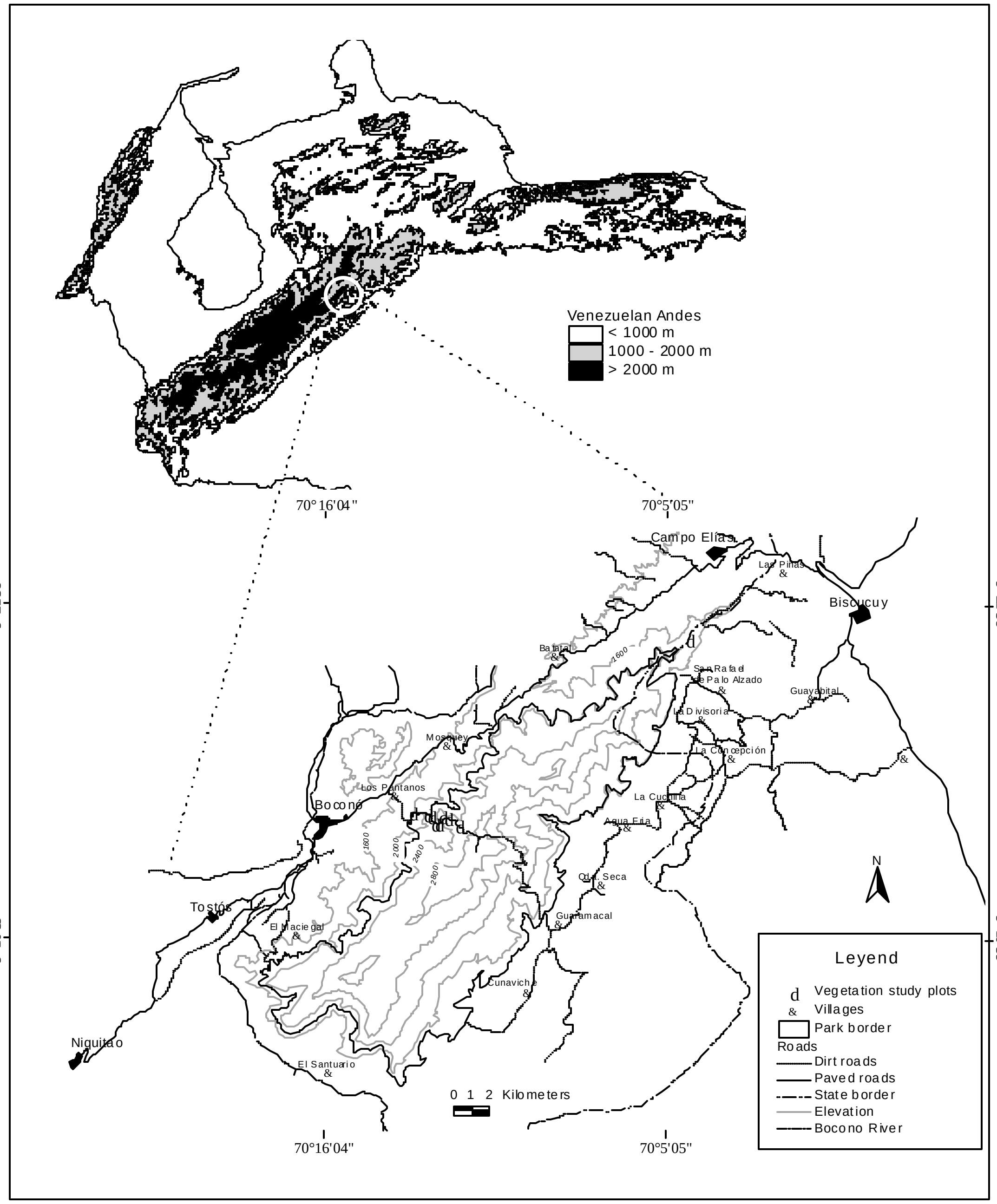

Figure 1. Study site, Cruz Carrillo National Park in the Ramal of Guaramacal, Trujillo state, Venezuela.

Cuello 1999). The ecotone between the montane forest and the open páramo vegetation is usually quite abrupt throughout most of the high Venezuelan Andes, but Guaramacal (particularly on the northern slopes) appears to be different since there is a more gradual transition from forest to páramo, and it is hard to distinguish a definite treeline (Ortega *et al.* 1987).

Table 1. Diversity measures for each elevation plot on the northern slope of Guaramacal.

Elev.	Num fam.	Num. Gen.	Num. species	Mean species per family	Mean indiv. per species	Shannon index H'	Evenness E	Fisher's alpha	Rarefaction of species number (182 individuals)
1830	28	46	53	1.89	7.54	3.21	0.81	16.38	39.77
1850	22	29	35	1.59	5.20	3.03	0.85	12.88	34.95
1960	17	32	40	2.47	8.52	3.08	0.83	11.53	34.47
2070	25	38	46	1.84	9.69	3.02	0.79	12.87	35.56
2100	19	31	35	1.84	11.46	2.34	0.66	9.22	27.95
2170	23	33	41	1.78	7.71	2.93	0.79	12.56	34.23
2300	23	41	49	2.13	7.69	3.08	0.79	15.02	37.52
2350	31	44	60	1.93	7.98	3.35	0.82	18.11	43.55
2400	34	43	59	1.74	9.27	3.26	0.80	16.79	40.95
2480	25	31	36	1.44	16.72	3.00	0.84	8.40	27.78
2580	20	24	32	1.60	12.84	2.98	0.87	8.09	29.35

SAMPLING METHODS

This study sampled plants with dbh = 2.5 cm in 0.1 ha (20 x 50 m) plots. This method uses a single, wider rectangular shape for the plot and differs from the 0.1 ha transect method of Gentry, which uses ten 2 x 50 m lines laid out one after the other without any specific compass direction (Gentry 1982, 1988a). I adopted this method to avoid confusing local diversity with beta diversity caused by traversing different microhabitats, an inherent problem of long, narrow sample shapes (Condit *et al.* 1996, Boyle 1996). Eleven sample plots were situated at 1830, 1850, 1960, 2070, 2100, 2170, 2300, 2350, 2400, 2480 and 2580 m on the northern slope of Guaramacal. All plots were placed relatively close to the road that traverses the park, with exception of the lowest one (1830 m) which had to be established outside the north-eastern border of the park to be able to locate it in undisturbed forest (Figure 1). Selection of study sites was determined by topography and physiognomy in order to sample mature forest on accessible slopes.

Each 0.1 ha plot was 20 x 50 m and was divided into ten 10 x 10 m grid squares which were used to calculate the species frequency in each plot. Within each plot, all rooted individuals – trees, shrubs, lianas, tall and thick-stem or climbing terrestrial herbs and hemiepiphytes– = 2.5 cm dbh (diameter at breast height, 1.3 m from the base of the trunk, or lower for shrubs and thick-stem herbs) were recorded, labeled with numbered aluminum tags and their dbh and height recorded. The 2.5 cm dbh minimum size was chosen to include most of the small woody understory species, as well as lianas and hemiepiphytes, and to make these samples comparable with Gentry’s (1982, 1988a) data. Height was estimated using a 2 m clipper pole as a reference. Multistemmed species were counted as single individuals, but all stems were recorded for calculation of basal area. The same criterion was applied to multiple aerial roots of hemiepiphytes such as *Clusia*.

Individuals were assigned to morphospecies, and a voucher sample for each morphospecies was collected for each plot. In ambiguous species, multiple vouchers were collected. Later, morphospecies were matched for all plots. Because voucher samples from plots were mostly sterile, general collections of fertile specimens outside the plots were also made. Identifications were made by the author with the help of specialists at the Universidad de los Llanos in Guanare, Venezuela, at the Missouri Botanical Garden, and at the Smithsonian Institution. Some specimens were also sent to relevant specialists in other herbaria for identification (see Acknowledgements).

DATA ANALYSIS

Numbers of species, genera, and families were determined and compared for each site along elevation and for the total area surveyed. Species richness per site (N), Shannon diversity index (H'), Pielou's Evenness (E), and Fisher's alpha index (a) (Fisher *et al.* 1943) were calculated (Magurran 1988). The calculations were performed using the software program BioDap (Clay and Thomas, 1996). Because recent work using tree populations suggests that species accumulate more predictably as a function of individuals counted than as a function of area (Condit *et al.* 1996), and considering the variation in number of individuals for comparison among plots, species-individual curves and rarefaction of species numbers were used to check whether local diversity was adequately measured and to calculate the number of species expected in each sample if all samples contained equivalent numbers of individuals (Lieberman *et al.* 1996). The number of species

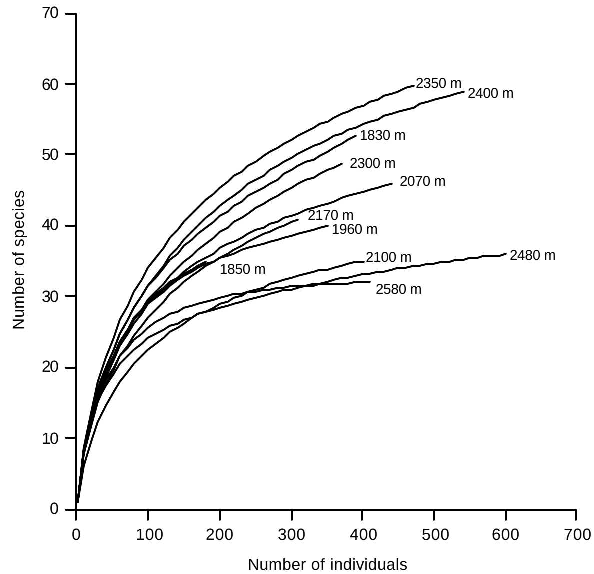

Figure 2. Species individuals accumulation curves for eleven 0.1 ha plots on the northern slope of Guaramacal.

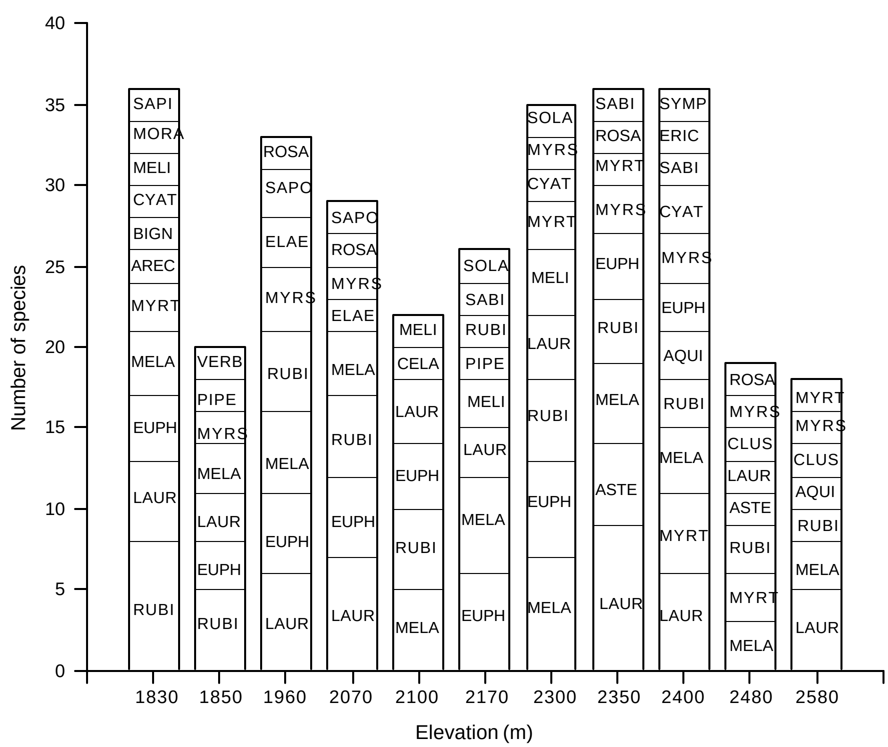

Figure 3. Number of species in the most diverse plant families (families with more than 2 species) at each elevation on the northern slope of Guaramacal. Family names are represented by their initial four letters.

Table 2. Forest structure for plots on the northern slope of Guaramacal, Venezuela.

Elev.	Height (m)			Diameter (cm)		Number of individual and percentages per diameter class diameter classes (cm)												Basal area	Total #
	Max.	Mean	Canopy	Max.	Mean	2.5-5		5.1-10		10.1-20		20.1-30		30.1-50		>50			
						# ind.	%	*# ind.*	%	*# ind.*	%	*# ind.*	%	*# ind.*	%	*# ind.*	%	m2	indiv.
1830	24	7.3	10-20	64	9.2	*157*	39.25	*136*	34.00	*68*	17.00	*27*	6.75	*10*	2.50	*2*	0.50	4.94	400
1850	19	6.5	10-15	70.5	11.9	*68*	37.36	*53*	29.12	*30*	16.48	*17*	9.34	*7*	3.85	*7*	3.85	4.57	182
1960	20	8.0	10-15	38.2	7.2	*141*	39.39	*169*	47.21	*34*	9.50	*11*	3.07	*3*	0.84	*0*	0.00	2.66	358
2070	24	7.6	10-18	114.6	7.9	*227*	51.01	*141*	31.69	*51*	11.46	*10*	2.25	*11*	2.47	*5*	1.12	6.64	445
2100	18	6.5	10-15	62.1	7.1	*213*	51.95	*136*	33.17	*41*	10.00	*11*	2.68	*8*	1.95	*1*	0.24	3.31	410
2170	26	9.4	10-20	90	9.3	*140*	44.30	*91*	28.80	*59*	18.67	*9*	2.85	*12*	3.80	*5*	1.58	4.99	316
2300	21	7.1	8-15	111.4	10.5	*137*	36.34	*144*	38.20	*53*	14.06	*17*	4.51	*16*	4.24	*10*	2.65	8.57	377
2350	22	8.1	8-15	60	7.9	*235*	49.06	*154*	32.15	*53*	11.06	*19*	3.97	*15*	3.13	*3*	0.63	5.19	479
2450	19	6.5	6-15	108.2	8.3	*277*	49.91	*170*	30.63	*62*	11.17	*24*	4.32	*16*	2.88	*6*	1.08	6.91	555
2480	23	7.0	6-14	127.3	6.3	*344*	57.05	*175*	29.02	*70*	11.61	*8*	1.33	*5*	0.83	*1*	0.17	4.59	603
2580	19	8.6	6-14	69	9.4	*165*	40.15	*116*	28.22	*90*	21.90	*25*	6.08	*13*	3.16	*2*	0.49	5.67	411
Totals					**x=7.92**	***2104***		***1485***		***611***		***178***		***116***		***42***		**58.04**	4536

accumulating with increasing number of individuals was calculated using Biodiversity Profesional Beta (BioDiversity 1997 NHM & SAMSEN).

The Bray-Curtis index (Bray and Curtis 1957) or Sørensen cuantitative similarity index (Magurran 1988) and Importance Value Index [IVI (Curtis and McIntosh 1951)] were used to analyze changes in floristic composition with elevation.

RESULTS

Floristic diversity

4521 individuals were recorded in the eleven 0.1 ha plots. They were determined to belong to 213 morphospecies, in 124 genera and 59 families, based on the analysis of 601 voucher specimens. The morphospecies included 8 ferns, one gymnosperm (*Podocarpus oleifolius* var. *macrostachyus)* and 204 flowering plants. About 88% of the morphospecies were identified to species. Of the remaining 26 morphospecies, 15 (7%) were identified to genus, 7 (3%) to family, and 4 (2%) were undetermined (no vouchers could be collected). Species determinations and corresponding vouchers are listed in Appendix 1.

Table 1 summarizes the diversity measures for each of the eleven plots. The number of species per plot varied from 32 to 60, with an average of 40.5. Floristic diversity in terms of species richness, family and genera richness, as well as diversity indices such as Shannon, Fisher's alpha, and rarefaction of species number showed a general trend in relation to elevation of initially decreasing slightly in diversity to mid elevation (2100 m), and then increasing diversity to 2350-2480 m, to finally decrease again at the highest site. At 2100 m it is found the lowest evenness due to the high dominance of a single species (*Croizatia brevipetiolata*, see Appendix 1).

The number of families and genera followed the same pattern as species richness, with the maximum number of families at 2400 (34), and the maximum number of genera at 2350 m (44).

Rarefaction of species for 182 individuals (the lower number of individuals found in a plot) indicated close values of diversity for the plots between 1830 and 2070 m (35-37.2), a minimum diversity at 2100 m, then an increase in diversity to a maximum of 44.2 at 2400 m, and a decrease in diversity above that altitude.

Accumulation curves show the change in species richness with increasing numbers of individuals. Species accumulation curves for most plots were still increasing at 0.1 ha, indicating that local species richness was undersampled (Figure 2). Only the curve from 2580 m appear to be approaching an asymptote.

The plant families that contributed most to overall species richness were Lauraceae, Rubiaceae, Melastomataceae, and Myrtaceae (see

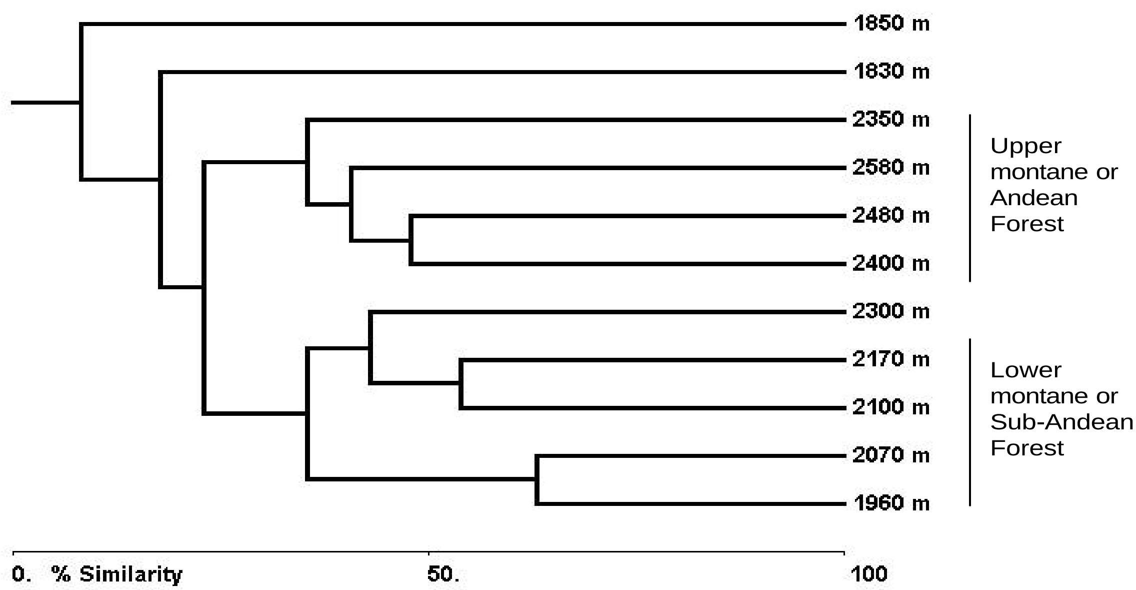

Figure 4. Bray-Curtis cluster analysis (Single link) for the eleven elevational plots on northern slope of Guaramacal.

Appendix). However, there were differences among elevations (Figure 3). Lauraceae was well represented in all plots, but was the most diverse at middle elevation (1960 and 2070 m) and at high elevations (2400 and 2580 m). Melastomataceae increased from 3 species at low elevation to 7 species at 2300 m, but then decreased to 3 species at higher elevation plots. The number of species in the Rubiaceae decreased with elevation from 8 species at 1830 m, it was constant with 5 species from 1850 to 2300 m, but decreased to 2 species at 2580 m. Euphorbiaceae were well represented at low elevation with 4 to 6 species from 1830 to 2300 m, but decreased in diversity at higher elevations.

Forest structure

Table 2 summarizes the structural parameters of the different elevational plots. The number of individuals per plot varied from 182 to 602, with an average density of 378. Density increased with altitude up to 2480 m and then decreased at the highest elevation. The canopy height was variable within plots, but generally decreased with altitude. Taller, emergent trees were found at every altitude. Maximum and mean diameter was variable among plots, with the highest diameter individual (127.3 cm) found at 2480 m. The highest mean diameter (11.9 cm) was found at 1850 m, and the average mean diameter among plots was 7.92 cm.

The highest proportion of individuals was found within the two lowest diameter classes (<10 cm). Only the plots at 1960 and 2300 m had a higher number of individual in the second diameter class (5–10 cm dbh). The number of individuals <10 cm dbh generally increased with elevation up to 2480 m, and the highest number of large trees was found at 2300 m. Basal area increased from 2100 m up to 2300 m then decreased at higher elevation.

Species life forms are presented in Table 3 and Appendix 1. Density and number of tree species was higher at 2400 m and then decreased at 2580 m. Palms were very common at lower elevation, but rare above 2170 m. Tree ferns were common at 1830 m, and increased between 2170 and 2480 m, but decreased at higher elevation. Lianas were densest and most diverse at 2350 m. Of the total species recorded in the northern slope 171 species are trees, seven are tree ferns, three are hemiepiphytes, three are large herbs (including one fern), 22 are lianas (including 3 undetermined morphospecies), four are palms and one a climbing terrestrial herb.

Floristic composition

Along the elevational gradient, the highest

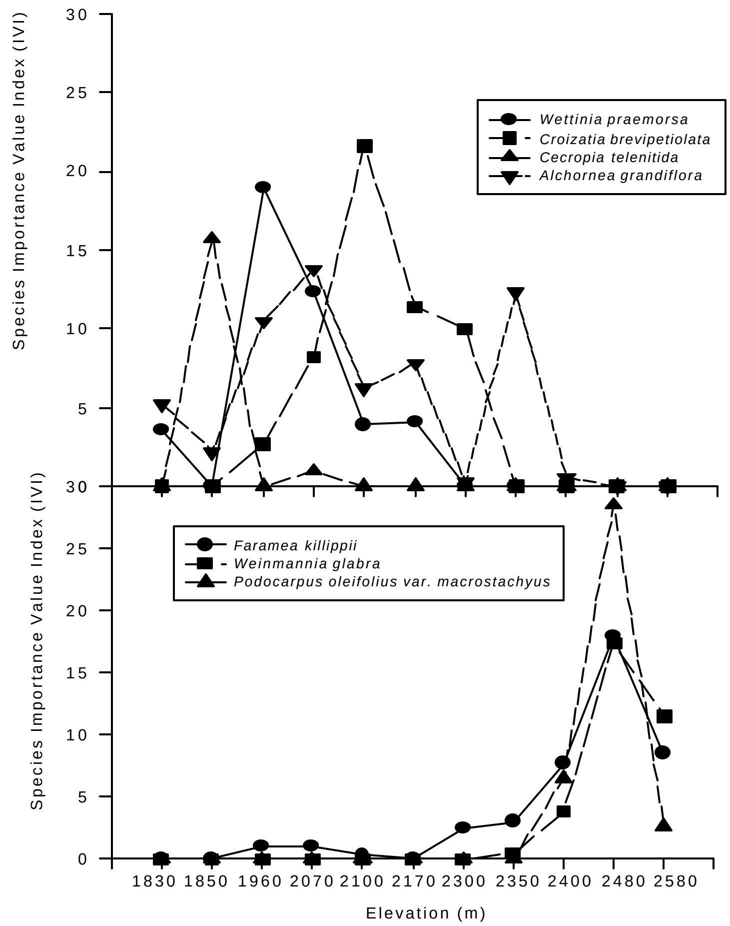

Figure 5. Importance value index ([relative density + relative frequency + relative dominance]/3) of the most dominant species for each elevation. Top: widespread species, bottom: upper montane species.

similarity in floristic composition was found between the plots at 1960 and 2070 m, 2100 and 2170 m, and 2350 and 2400 m (Figure 4). Two clear groupings are seen, with plots at 2350 m and above showing high levels of similarity between each other, and plots at 2170 m and below also showing high levels of similarity. The plot at 2300 m is intermediate, but is more similar to those below it than to those above.

DISCUSSION

On the northern slope of Guaramacal the pattern of floristic diversity does not follow the prediction of decreasing diversity with increasing altitude as suggested by Gentry (1982, 1988b, 1995). From 1830 m to 2580 m, diversity initially decreases as elevation increases up to 2100 m, thereafter increases with elevation until about 2350 m, where it start to decline again. This pattern is likely to be correlated with precipitation, since moisture availability seems to increase with elevation from the dry interandean Boconó valley to the top of the mountain (Cuello and Barbera 1999), however there is not available local climate data to test this pattern. Low diversity of tropical dry forest compared to moist forest is well documented (Gentry 1995).

Givnish (1998) suggested that in dry areas diversity should initially increase with elevation due to the increased availability of moisture and then decline, but this would be the first empirical evidence in the Andes in support of this hypothesis. The diversity peak at 2350-2400 m on the northern slope was notable and is worth examining in future work. Such an increase in diversity has been found in other montane forests at elevations around 2400

Table 3. Life form distribution among individuals ≥ 2.5 cm dbh in eleven 0.1-ha plots on the northern slope of Guaramacal, Venezuela

Elev.	Trees	Palms	Tree ferns	Lianas	Hemi-epiphytes	Tall herbs and climbings	Total individuals
Percentages of individuals							
1830	51.25	23.75	13.75	3.50	0.00	7.75	400
1850	99.45	0.00	0.00	0.00	0.55	0.00	182
1960	75.70	22.35	0.00	1.96	0.00	0.00	358
2070	73.48	19.10	2.02	4.94	0.45	0.00	445
2100	95.85	3.41	0.00	0.73	0.00	0.00	410
2170	91.78	4.43	0.95	2.53	0.32	0.00	316
2300	96.82	0.00	2.65	0.00	0.53	0.00	377
2350	86.01	1.04	1.88	5.22	5.22	0.63	479
2400	86.13	0.00	9.19	1.26	3.24	0.18	555
2480	74.96	0.00	8.46	0.66	5.14	10.78	603
2580	81.51	0.49	1.22	1.22	10.46	5.11	411
Percentages of species							
1830	79.25	5.71	3.77	11.32	0.00	1.89	53
1850	97.14	0.00	0.00	0.00	2.86	0.00	35
1960	95.00	2.17	0.00	2.50	0.00	0.00	40
2070	86.96	2.86	2.17	6.52	2.17	0.00	46
2100	88.57	2.44	0.00	8.57	0.00	0.00	35
2170	85.37	2.04	2.44	7.32	2.44	0.00	41
2300	93.88	0.00	4.08	0.00	2.04	0.00	49
2350	81.67	1.69	1.67	11.67	1.67	1.67	60
2400	89.83	0.00	3.39	3.39	1.69	1.69	59
2480	80.56	0.00	5.56	5.56	5.56	2.78	36
2580	75.00	3.13	3.13	6.25	9.38	3.13	32

m (Veillón 1965, Kappelle *et al.* 1995, Kapelle 1996, Rangel 1995). It should be pointed out that in these studies showing diversity peaks at intermediate elevations, their elevational intervals were relatively short (i.e., ca. 50 m in Veillon 1965; 100 m in Kappelle *et al.* 1995) compared to those studies that support the linear decreasing trend in diversity with elevation (Gentry 1995, Lieberman *et al.* 1996, Boyle 1996), which were either based on single samples from different sites (Gentry 1995) or based on samples taken at greater intervals (300 m in Lieberman *et al.* 1996; 500 m in Boyle 1996). The scale of these studies may have overlooked this kind of local variation. Although the existence of high diversity in transitional zones between subandean and Andean forests was documented by Ulloa and Jørgensen (1992) in the Ecuadorian Andes and by Rangel (1995) in the Colombian Andes, these diversity peaks have not been widely recognized due to the limited amount of quantitative sampling in montane forests on different slope exposures.

The floristic composition of the montane forests of Guaramacal generally agrees with the altitudinal trends of family dominance found between 1700 and 2400 m in the northern Andes (Gentry 1988b; 1992), where Lauraceae (=2.5 cm dbh; 0.1 ha samples) was the most species-rich family, followed by Melastomataceae and Rubiaceae.

Forest zonation

Even though the forests studied covered a relatively short elevational range (1830–2580 m) throughout which some of the main canopy species were present (i.e., *Alchornea grandiflora, Billia columbiana, Clusia trochiformis, Hyeronima moritziana, Meliosma tachirensis, Prunus moritziana,* and *Tetrorchidium rubrivenium*), it was possible to distinguish two vegetation zones using the similarity indices and analysis of the distribution patterns of the seven species with the highest importance values (Cuello 1997; Figure 5). The upper zone was distinguished by the presence of *Weinmannia glabra* and *Podocarpus oleifolius* and the high density of *Faramea killipii*. Although there was a great number of wide-ranging species in this altitudinal range, there was also a group of species only found in those high-elevation plots. Those species (*Brunellia integrifolia, Byrsonima karstenii, Gaiadendron punctatum, Ilex myricoides, Podocarpus oleifolius* var. *macrostachyus, Symbolanthus calygonus, Symploccos rigidissima, S. bogotensis, Ternstroemia acrodantha*, and *Weinmannia glabra* and others) belong to the group of species characteristic of the Andean (upper) montane forest (van der Hammen and Cleef 1983a, b). The placement of the 2300 m plot and its floristic similarities with the plot both above and below suggest that it is best considered a transition zone between lower montane forest and upper montane forest (Subandean and Andean forests according to van der Hammen 1989).

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Appendix 1. List of vascular plants, habits (H: a=tree, l=liana, p=palm, ha= tree fern, he=hemiepiphyte, hg=tall herbs), vouchers identified from the study plots and number of individuals of each species at each plot altitude. All vouchers were collected by Cuello *et al.* and are deposited at PORT, MO, VEN and US.

FAMILY	SPECIES	H	Voucher	Number of individuals at each plot altitude										
				1830	1850	1960	2070	2100	2170	2300	2350	2400	2480	2580
Acanthaceae	*Mendoncia tovarensis* (Klotzsch & Karsten ex Nees) Leonard	l	1800	5										
	Ruellia tubiflora Kunth. var. *tetrastichantha* (Lindau) Leon	a	1038							1				
Actinidiaceae	*Saurauia tomentosa* (Kunth) Spreng.	a	1190		11									
	Saurauia yasicae Loes	a	1143							2		1		
Annonaceae	*Rollinia mucosa* (Jacq.) Baill.	a	1814	1										
Aquifoliaceae	"Ilex sp.1"	a	1189		1									
	Ilex laurina Kunth.	a	1147									2	8	12
	Ilex myricoides Kunth.	a	1140									5		16
	Ilex truxillensis Turcz. subsp. *bullatissima* Cuatrec.	a	1120									3		
Araliaceae	*Dendropanax arboreus* (L.) Dcne. & Planch.	a	1787	5		1	4							
	Schefflera ferruginea (Willd. ex Roem. & Schult.) Harms	a	1083								1	1	15	6
Arecaceae	*Geonoma jussieuana* Mart.	p	2105								5			
	Geonoma orbigniana Mart.	p	1950											2
	Geonoma undata Klotzsch	p	1731	58										
	Wettinia praemorsa (Willd.) Wess. Boer	p	915	20		80	86	14	14					
Asteraceae	"Bejuco compuesta 2"	l	2082								1			
	Ageratina neriifolia (B.L. Rob.) R.M. King & H. Rob.	a	2079								1			
	Critoniopsis paradoxa (Sch. Bip.) V.M. Badillo	a	1110									10	55	
	Mikania banisteriae DC.	l	2010				15	1						
	Mikania nigropunctulata Hieron	l	2068								4			
	Mikania stuebelii Hieron	l	2075								4			
	Pentacalia vicelliptica (Cuatrec.) Cuatrec.	l	2085								1			
Bignoniaceae	*Schlegelia spruceana* K. Schum.	l	1816	1										
	Tabebuia guayacan (Seem.) Hemsl.	a	1790	3							1			
Bromeliaceae	*Gregia aristeguietae* L. B. Smith	hg	2080								3			
Brunelliaceae	*Brunellia* cf. *integrifolia* Szyszyll.	a	1936								6	3	10	
Burseraceae	*Protium tovarense* Pittier	a	1778	6										
Caprifoliaceae	*Viburnum tinoides* L.f. var. *venezuelensis* (Killip & A. C. Smith) Steyerm.	l	1919										2	
Caricaceae	*Vasconcella microcarpa* (Jacq.) A. DC. subsp. *pilifera* (V.M. Badillo) V.M. Badillo	a	1201		2									
Celastraceae	*Celastrus liebmanii* Standl.	l	1011					1						
	Perrottetia quinduensis Kunth	a	1003					4	26					
Chloranthaceae	*Hedyosmum* cf. *gentryi* D'Arcy & Liesneri	a	1813	5			6							
	Hedyosmum crenatum Occhioni	a	1115								43	28	70	9
	Hedyosmum cuatrecazanum Occhioni	a	989					16	31	9				
	Hedyosmum racemosum (Ruiz & Pav.) G. Don	a	s/n			1								

FAMILY	SPECIES	H	Voucher	Number of individuals at each plot altitude										
				1830	1850	1960	2070	2100	2170	2300	2350	2400	2480	2580
Clethraceae	*Clethra fagifolia* Kunth var. *fagifolia*	a	1059							1	3	6	18	7
Clusiaceae	"Clusia sp."	he	1934										18	
	Clusia alata Triana & Planch.	he	1215		1								13	
	Clusia cerroana Steyerm.	he	1967				2							4
	Clusia pseudo-mangle Planch. & Triana	he	1970						1					11
	Clusia trochiformis Vesque	he	1017							2	25	18		30
Cunnoniaceae	*Weinmannia* aff. *balbisiana* Kunth	a	2106								10			
	Weinmannia glabra L.f.	a	1116								1	8	21	37
	Weinmannia sorbifolia Kunth	a	1195		1									
Cyatheaceae	"Alsophila sp."	ha	1765	49										
	"Sphaeropteris sp."	ha	1051							2				
	Cyathea caracasana (Klotzsch) Domin	ha	1938									48	43	
	Cyathea fulva (Mart. & Gal.) Fee	ha	2011				9		3	8	9			
	Cyathea kalbreyeri (Baker) Domin	ha	1763	9										
	Cyathea pauciflora (Kuhn) Lellinger	ha	1157									3		5
Cyclanthaceae	*Asplundia vagans* Harling	ht	1803	34										
Dicksoniaceae	*Dicksonia sellowiana* Hook.	ha	1921										8	
Elaeocarpaceae	*Sloanea* aff. *guianensis* Aubl.	a	1775	2		25	8							
	Sloanea laurifolia (Benth.) Benth.	a	937			6								
	Sloanea rufa Planch. Ex Benth.	a	2003			1	2							
Ericaceae	*Diogenesia tetrandra* (A. C. Jm.) Sleumer	l	2118								5			
	Psammisia hookeriana Klotzsch.	l	1125					1			10	1		
	Themistoclesia dependens (Benth.) A. C. Smith	l	1974									6		3
Euphorbiaceae	*Acalypha macrostachya* Jacq.	a	1177		25									
	Alchornea grandiflora Muell. Arg.	a	927	10	5	20	11	5	4	1	24	1		
	Croizatia brevipetiolata (Secco) Dorr	a	956			14	74	188	71	78				
	Hyeronima cf. *oblonga* (Tul.) Mull. Arg.	a	953			3	10		2	6	2	3		
	Hyeronima moritziana (M. Arg.) Pax & Hoffmann	a	948	3		1	1		1	5	2	2		
	Mabea occidentalis Benth.	a	1519	18										
	Sapium stylare Mull. Arg.	a	2029					12	14	1				
	Tetrorchidium rubrivenium Poepp.	a	1196	8	1	1	1	1	5	5	7			
Fabaceae	*Dussia coriacea* (Sw.) Roem. & Schult.	a	2053				5	2	4					
	Machaerium cf. *floribundum* Benth.	l	1807	1										
Flacourtiaceae	*Casearia tachirensis* Sleumer	a	2032				4	3	23	3				
Gentianiaceae	*Symbolanthus calygonus* (R. & P.) Griseb	a	2122								1	10		
Gesneriaceae	*Besleria pendula* Hanst.	a	942			18	20						3	
	Drymonia crassa C.V. Morton	l	2048						1					
Hippocrateaceae	*Salacia* aff. *cordata* (Miers.) Mennega	l	1786	1										
Icacinaceae	*Calatola venezuelana* Pittier	a	1005	11				1						
	Citronella costaricensis (Donn. Sm.) R.A. Howard	a	1165						3	1		1	2	
Lauraceae	"Lauraceae 1"	a	1084								1	2		4
	"Laurel grande cf. Nectandra"	a	2026						3					

FAMILY	SPECIES	H	Voucher	Number of individuals at each plot altitude										
				1830	1850	1960	2070	2100	2170	2300	2350	2400	2480	2580
	"Laurel hediondo"	a	1817	1										
	"Ocotea sp. A"	a	1044							10				
	"Persea sp.1"	a	1963											12
	"Persea sp.3"	a	1770	1										
	Aiouea dubia (Kunth.) Mez	a	926			2	9			1	2	2	2	
	Aniba cf. *cinnamomiflora* C.K. Allen	a	1780	5		22	20	2						
	Beilschmiedia tovarensis (Meissn.) Sa. Nishida	a	1987			5	2	5	2	9	11			
	cf. *Persea peruviana* Nees	a	976					2						
	Ocotea aff. *karsteniana* Mez	a	1123				2				1	6	11	
	Ocotea aff. *puberula* (Rich.) Nees	a	922			15	9							
	Ocotea aff. *tarapotana* (Meissn.) Mez	a	1799	1										
	Ocotea auriculata Lasser	a	1178		3									
	Ocotea floribunda (Sw.) Mez	a	1010					1		8	4	11		
	Ocotea jelski Mez	a	1137									1		6
	Ocotea leucoxylon (Sw.) de Lanessen, s.l.	a	2110								8	5		
	Ocotea macropoda (Kunth) Mez	a	1791	5										
	Ocotea rubrinervis Mez	a	2000				1							
	Ocotea sericea Kunth	a	2076								2			
	Ocotea smithiana O. C. Schmidt	a	1197		1	1								
	Ocotea terciopelo C. K. Allen	a	2083								2			
	Ocotea vaginans (Meissn.) Mez	a	1989				1		1		22			
	Persea aff. *mutisii* Kunth	a	1928										9	14
	Persea meridensis Kopp.	a	943			3	3				1			
	Pleurothyrium costanense van der Werff	a	1188		1									
Loranthaceae	*Gaiadendron punctatum* (R. & P.) G. Don	a	1121								1	1		
Malpighiaceae	*Bunchosia armeniaca* (Cav.) DC.	a	1181		6									
	Byrsonima karstenii W. R. Anderson	a	1131									6		
Melastomataceae	"Miconia sp. A"	a	999		3			3						
	"Miconia sp."	a	03-09-334							5				
	Anaectocalyx bracteosa (Naud.) Triana	a	1112								14	34	48	15
	Blakea schlimii (Naud.) Triana	l	944	1		7	7		6					
	Henriettella cf. *verrucosa* Triana	a	1769	7										
	Meriania grandidens Triana	a	2002				17	2	2	9				
	Meriania macrophylla (Benth.) Triana	a	1997				1	17	9					
	Miconia tovarensis Cogn.	a	1278			7								
	Miconia cf. *dolichopoda* Naud.	a	1174		1				6		2			
	Miconia cf. *minutiflora* (Bonpl.) DC.	a	960			1		6	5					
	Miconia lonchophylla Naud.	a	1043	7						1	4			
	Miconia lucida Naud.	a	932			9	7							
	Miconia mesmeana Gleason subsp. *longipetiolata* Wurdack	a	1948							2				2
	Miconia theaezans (Bonpl.) Cogn., s.l.	a	1151	1	3			12	12	1		3		8
	Miconia tinifolia Naud.	a	1106							3	3	13	14	
	Miconia ulmarioides Naud.	a	1119							3	34	37	19	

FAMILY	SPECIES	H	Voucher	Number of individuals at each plot altitude										
				1830	1850	1960	2070	2100	2170	2300	2350	2400	2480	2580
Meliaceae	*Guarea kunthiana* A. Juss.	a	1171	1	6				1	1				
	Ruagea glabra Triana & Planch.	a	928			3								
	Ruagea pubescens H. Karst.	a	1801	1			3	15	4	24		4		
	Trichilia hirta L.	a	1065							1				
	Trichilia septentrionalis C. DC.	a	1909					2	1	1			1	
Mimosaceae	*Inga quaternata* Poepp.	a	1179		2									
Moraceae	*Cecropia telenitida* Cuatrec.	a	1826	1	7		1							
	Ficus nymphaefolia P. Miller	a	1793	1										
	Ficus tonduzi Standl.	a	1198		3									
	Pseudolmedia rigida (Planch. & Karst.) Cuatrec. subsp. *rigida*	a	1825	1										
Myrsinaceae	*Cybianthus cuspidatus* Miq.	a	925			12				1				
	Cybianthus iteoides (Benth.) Agost.	a	1141			7	9					2		
	Cybianthus laurifolius (Mez) Agost.	a	1153								7	18	7	55
	Geissanthus fragans Mez	a	1199		7	4	8	16	2	2	1			
	Myrsine coriacea (Sw.) R. Br. ex Roem & Schult.	a	1107			1					4	4	15	5
	Parathesis venezuelana Mez	a	1182		4									
Myrtaceae	"Myrcianthes sp."	a	1023							3				
	"Myrtaceae-1"	a	04-02-112									1		
	"Myrtaceae2"	a	1774	2										
	"Myrtaceae-3"	a	04-06-267									1		
	Calyptranthes cf. *meridensis* Steyerm.	a	1104							5	2	51	24	11
	Eugenia albida Humb. & Bonpl.	a	1951				1				22			5
	Eugenia cf. *oerstediana* O. Berg.	a	1788	3										
	Eugenia cf. *tamaensis* Steyerm.	a	954			3				26		31	1	
	Eugenia moritziana H. Karst.	a	1173	9	4									
	Myrcia aff. *guianensis* (Aubl.) DC.	a	1925									3	4	
Piperaceae	"Piper sp."	a	2019						1					
	Piper aduncum L. var. *cordulatum* (C. DC.) Yunck.	a	1183		3									
	Piper longispicum C. DC. var. *glabratum* (Yunck.) Steyerm.	a	940	36	3	8	15	23	25	19	6	1		
Poaceae	*Arthrostylidium venezuelae* (Steud.) McClure	hg	1092									1		
	Rhipidocladum geminatum (McClure) McClure	hg	1240										64	21
Podocarpaceae	*Podocarpus oleifolius* D. Don ex Lambert var. *macrostachyus* (Parl.) J. Bunchholz & N. E. Gray	a	1126									4	1	10
Proteaceae	*Panopsis suaveolens* (H. Karst.) Pittier	a	1911								1	1	1	
Rosaceae	*Prunus* cf. *skutchii* Johnston	a	933			6								
	Prunus moritziana Koehne	a	1915			2	2		2	1	4	4	1	
Rubiaceae	"Palicourea sp".	a	1794	1										
	Coussarea moritziana (Benth.) Standl.	a	935	1		2	1			4		1		
	Dioicodendron dioicum (K. Schum. & Krause) Styerm.	a	1135							4	6	1		
	Elaeagia karstenii Standl.	a	2087								18			

FAMILY	SPECIES	H	Voucher	Number of individuals at each plot altitude										
				1830	1850	1960	2070	2100	2170	2300	2350	2400	2480	2580
	Elaeagia myriantha (Standl.) Hammel & C. M. Taylor	a	1192		1									
	Elaeagia ruiz-teranii Steyerm.	a	921			6	6	7		40			2	
	Faramea killippii Standl.	a	117			3	4	1		14	19	81	56	59
	Guettarda crispiflora Vahl. subsp. *discolor* (Rusby) Steyerm.	a	2055					1	3					
	Hippotis albiflora H. Karst.	a	1789	2										
	Palicourea angustifolia Kunth	a	1764	4		22	39							
	Palicourea apicata Kunth	a	2102								80		32	29
	Palicourea demissa Standl.	a	2049					13	14	21				
	Palicourea puberulenta Steyerm.	a	1109			8		10		24		29		
	Posoqueria coriacea M. Mart. & Galeotti subsp. *formosa*	a	1187	15	3									
	Psychotria longirostris (Rusby) Standl.	a	1200		3									
	Psychotria perijaensis Steyerm.	a	1172		24									
	Randia cf. *dioica* H. Karst.	a	1782	1										
	Rudgea nebulicola Steyerm.	a	1794	8										
	Simira erythroxylon (Willd.) Brem. var. *meridensis* Steyerm.	a	1176		3									
	Simira lezamae Steyerm.	a	1979				1							
	Tocoyena costanensis Steyerm. subsp. *andina* Steyerm.	a	1777	15										
Rutaceae	*Conchocarpus larensis* (Tamayo & Croizat) Kallunki & Pirani	a	1566	2										
	Zanthoxylum melanostictum Schltdl. & Cham.	a	929			5	10				12	8		
Sabiaceae	*Meliosma meridensis* Lasser	a	1086									3		
	Meliosma pittierana Steyerm.	a	1804	5					1					
	Meliosma tachirensis Steyerm. & Gentry	a	1080					3	4	4	1	1		
	Meliosma venezuelensis Steyerm.	a	2112								4	3		
Sapindaceae	*Allophylus* cf. *glabratus* (Kunth) Radlk	a	2018						1					
	Billia columbiana Planch. & Lindl. ex Triana & Planch.	a	947			4	4			1	2	3		
	Matayba camptoneura Radlk	a	1768	4			1							
	Paullinia cf. *latifolia* Benth. ex Radlk	l	1823	1										
Sapotaceae	cf. *Elaeoluma nuda* (Baehni) Aubr.	a	1087					4	1	1	4	1		
	Chrysophyllum cf. *cainito* L.	a	1984			10	1							
	Pouteria baehniana Monachino	a	1785	5		9	2							
Saxifragaceae	*Hydrangea* aff. *peruviana* Moricard	a	1180		5									
Simaroubaceae	"Picramnnia sp."	a	1802	1										
Smilacaceae	*Smilax kunthii* Killip & C. V. Morton	l	2071								1			
Solanaceae	"Markea sp."	a	2057								2			
	Cestrum darcyanum Benitez & N.W. Sawyer	a	2056						1					
	Sessea corymbiflora Gondot ex Rich. Taylor & R. Phillips	a	1053							1				
	Solanum aturense Humb. & Bonpl. ex Dunal	l	2034						1					
	Solanum confine Dunal	a	995							3				
Staphyleaceae	*Huertea glandulosa* Ruiz & Pav.	a	1194		2									

FAMILY	**SPECIES**	**H**	**Voucher**	**Number of individuals at each plot altitude**										
				1830	**1850**	**1960**	**2070**	**2100**	**2170**	**2300**	**2350**	**2400**	**2480**	**2580**
	Turpinia occidentalis (Sw.) G. Don	a	2024					5	2					
Symplocaceae	*Symplocos bogotensis* Brand.	a	1129								1	2		
	Symplocos rigidissima Brand.	a	1957									2		2
Theaceae	"Ternstroemia sp. A"	a	1917										1	
	"Ternstroemia sp.B"	a	1973											3
	Gordonia fruticosa (Schrader) H. Keng	a	1191		1					1				
	Ternstroemia acrodantha Kobuski & Steyerm.	a	1154									4		
Urticaceae	*Urera caracasana* (Jacq.) Griseb.	a	1175		26									
Verbenaceae	*Aegiphila floribunda* Moritz & Moldenke	a	1170		8									
	Aegiphila ternifolia (Kunth) Moldenke	a	1214		2			2	3	2				
Winteraceae	*Drymis granadensis* L.f.	a	1118								1	2	1	7
Indeterminada	Bejuco indet.	l	16-07-251											2
	Bejuco3	l	17-05-458										2	
	Indet.2	a	16-09-318											1
	Liana	l	19-08-495				1							
				400	182	358	446	401	316	377	479	547	602	413