Biodiversity and Conservation of Neotropical Montane Forests

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Patterns of Diversity and Floristic Composition in Neotropical Montane Forests

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ABSTRACT

Gentry, Alwyn H. (Missouri Botanical Garden, St. Louis, Missouri 63166, U.S.A.). Patterns of diversity and floristic composition in Neotropical montane forests. Biodiversity and Conservation of Neotropical Montane Forests. 103–126. 1995.—Data for plants ≥2.5 cm dbh in 0.1-ha samples of Neotropical montane forests above 800 m elevation are compared. The available data set comes from 36 tropical Andean sites representing 17 departments in four countries as well as 17 Central American and Mexican sites. Diversity of Andean forests decreases linearly with altitude above 1500 m; up to 1500 m Andean forests are as diverse as lowland tropical forests. Central American montane forests, like lowland equivalents, are generally less diverse than are similar South American forests. Up to 1500 m, Andean forests are floristically similar to lowland Amazonian forests; above 1500 m they are composed of a very different set of predominantly Laurasian families and genera. Different Andean forests at similar elevations are remarkably similar in their floristic composition at the family and generic levels. Lauraceae has the most species of all the woody families in virtually all Andean forests between 1500 m and 2900 m elevation, followed by Melastomataceae and Rubiaceae. At high altitudes near the timberline Compositae and Ericaceae have the most species of the woody flora. Central American montane forests are floristically distinct in the greater prevalence of Laurasian families and genera.

RESUMEN

Gentry, Alwyn H. (Missouri Botanical Garden, St. Louis, Missouri 63166, U.S.A.). Patterns of diversity and floristic composition In Neotropical montane forests. Biodiversity and Conservation of Neotropical Montane Forests. 103–126. 1995.—Se comparan datos para plantas con un diámetro a la altura del pecho ≥2,5 cm en muestras de 0,1 ha de bosques montanos neotropicales por encima de los 800 m de altitud. Los datos disponibles provienen de 36 localidades andinas que representan 17 departamentos en cuatro países así como también 17 localidades de América Central y Mexico. La diversidad de los bosques andinos disminuye linealmente con la altitud por encima de los 1500 m; hasta los 1500 m los bosques andinos son tan diversos como los bosques tropicales de tierras bajas. Los bosques montanos de América Central, al igual que sus equivalentes de tierras bajas, son generalmente menos diversos que bosques similares de Sur América. Hasta los 1500 m los bosques andinos son similares florísticamente a los bosques amazónicos de tierras bajas; por encima de los 1500 m están compuestos de un conjunto muy diferente de familias y géneros predominantemente Lauràsicos. Distintos bosques andinos a elevaciones similares son marcadamente parecidos en su composición florística a nivel de familias y de géneros. Lauraceae es la familia de plantas leñosas más rica en especies en virtualmente todos los bosques andinos entre los 1500 y 2900 m de elevación, seguida por Melastomataceae y Rubiaceae. A altitudes elevadas cerca del límite superior del bosque, Compositae y Ericaceae pasan a ser los elementos de la flora leñosa más ricos en especies. Los bosques montanos de América Central son florísticamente diferentes en la mayor prevalencia de familias y géneros Laurásicos.

Al Gentry died in a plane crash in Ecuador on 3 August 1993. This paper is essentially his first draft, slightly edited and revised by Rosa Ortiz-Gentry, Oliver Phillips, and Brad Boyle. Tables II and III were compiled by Sally Adkins, and the figures were drawn by Flemming Nørgaard and John Myers.

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Introduction

Neotropical montane forests are among the most poorly known and most threatened of all tropical forest vegetations. In Colombia, for example, various estimates suggest that less than 10% (Henderson et al., 1991) of Andean forests remain intact, or perhaps even less than 5% (Carrizosa, 1990) for high-altitude upper montane forests. In Ecuador almost nothing is left of natural forests of the central valley, and of the forests on the western Andean slope only 4% remain (Dodson & Gentry, 1991).

For a variety of reasons, related to their complex topography and a biogeographical history featuring continual altitudinal migration of vegetation zones in response to changing climate, these ecosystems today present a kaleidoscopic array of distinctive biological communities, typically characterized by unusually high complements of endemic species. Partly because of their inaccessibility due to steep terrain, partly because of the world's focus on the plight of tropical lowland rain forests, and partly because so many of their species are poorly known taxonomically, they have received surprisingly little scientific attention until quite recently. There is now, however, a growing literature on the floristics of northern Andean and montane Central American forests (for summaries see Cleef et al., 1984; Gentry, 1989; Frahm & Gradstein, 1991; Rangel, 1991; Gentry, 1992; and chapters in this volume). The recent increase of interest in these forests has been fueled by the severity of the deforestation crisis.

This review of the patterns of diversity and floristics of Neotropical montane forests is based mostly on samples of plants ≥2.5 cm dbh (≥2.5 cm maximum diam. for lianas) in 0.1-ha samples (Gentry, 1982a). It also includes some data sets used in other analyses (Gentry, 1988, 1992; and others). All of the Mexican and montane Central American data are presented here for the first time as are 10 of the 36 Andean samples. Of 10 samples from lowland Central America, four are previously unpublished. While there is much overlap between the Andean data presented here and a similar overview of the Andean forests that focused on Peru, included in a recent volume on the biogeography and conservation of that country (Gentry, 1992), this analysis includes a greater altitudinal range of sites with a lower altitude cutoff at 800 m rather than 1000 m elevation. The present analysis used a somewhat different altitudinal grouping of sample sites to take advantage of the additional data. This paper also includes a substantial comparison of montane forest data with lowland forest data.

Methods

Sites were selected essentially serendipitously as part of an attempt to sample as complete a representation of the forested Neotropics as possible. Most of the montane sample data were collected incidental to programs of floristic inventory or monographic studies. Many sample sites are field stations where well-preserved montane forests are readily accessible. Other sites, especially in extensively deforested regions, were discovered by checking out rumors of mature forest patches in isolated cordilleras, often involving hikes of many hours or even days. Once an appropriately undisturbed area of forest was located, a study site was selected, on the basis of topography and physiognomy so as to sample the least precipitous and most completely closed canopy forest available. No attempt was made to sample at specific altitudes; the availability of accessible forest determined the area to be sampled at a particular locality.

At each study site a series of 10 transects, 2 × 50 m, was laid out, usually either roughly perpendicular to a trail or parallel to the elevational contours of a ridge. Terrain determined the plot layout, and no attempt was made to follow a predetermined geometric pattern. The transects were generally placed end to end in a more or less zigzag pattern inside a total sample patch of relatively homogeneous forest typically 1–2 ha in size. Each transect was defined by a 50 m long center line along which all plants ≥2.5 cm dbh and within 1 m of the line were censused. Trees, treelets, and even overgrown herbs were included, depending on whether the midpoint of their base was inside the sample area; lianas (measured at point of greatest diameter) were included if they had any roots within the plot. Hemiepiphytes and stranglers were included if they reached 2.5 cm diam. within 1.5 m of the ground (i.e., at or below breast height), and they were measured at their thickest diameter below breast height. This sampling scheme is now widely replicated as an appropriate Rapid Inventory Methodology (e.g., Lott et al., 1987; Cuadros, 1990; Peixoto & Gentry, 1990; RAP Report, 1991, 1992; Keel et al., 1993; Palacios et al., 1994).

Each plant was identified to family or genus and sorted by morphospecies. Each taxon (or, in taxonomically difficult groups, each individual) was vouchered for future specific identification. Species richness and family richness were calculated for each site as simply the number of species (identified species plus unique morphospecies) or number of families (following traditional family concepts; e.g., Gentry, 1993a).

At a few sites, the full 10 transects could not be completed for logistic reasons. Those sites are included in Table I with the actual sample area indi-

TABLE I

Mexican, Central American, and Andean 0.1-ha sample sites in montane forests and southern Central American lowlands (below 800 m elev.)

Site	Grid coor.	Alt. (m)	Est. ppt. (mm)	Holdridge Life zone	Reference
Mexico					
Sierra Juarez, Oaxaca	17°36′N 96°29′W	2250	5000	bp-MB	Rzedowski & Palacios, 1977
Benito Juarez, Chiapas	15°20′N 92°15′W	2100	600?	bs-MB?	—
Las Joyas (Manantlan), Jalisco	19°35′N 104°18′W	1950	1727	bmh-MB	
Quince Ocotes (Manantlan), Jalisco	19°44′N 104°14′W	1800	—	—	—
Sierra Juarez, Oaxaca	17°37′N 96°22′W	1750	5500	bp-MB	—
Motozintla, Chiapas	15°20′N 92°21′W	1600	741	bs-MB	—
Sierra Juarez, Oaxaca	17°35′N 96°21′W	1255	5700	bp-PM	—
Bosque de Guadalupe, Veracruz	19°30′N 96°57′W	1225	1514	bh-MB	—
Nicaragua					
Cerro el Pichaco	13°00′N	1400	2000	bh-MB	—
Costa Rica					
Parque Nacional Braulio Carrillo, Heredia	10°08′N 84°06′W	2775	3000	bpM	Hartshorn & Peralta, 1988
Parque Nacional Braulio Carrillo, Heredia	10°08′N 84°06′W	2750	3000	bpM	Hartshorn & Peralta, 1988
Parque Nacional Braulio Carrillo, Heredia	10°08′N 84°07′W	2750	3000	bpM	Hartshorn & Peralta, 1988
Parque Nacional Braulio Carrillo, Heredia	10°10′N 84°07′W	2225	3260	bpMB	Hartshorn & Peralta, 1988
Parque Nacional Braulio Carrillo, Heredia	10°11′N 84°06′W	2000	3450	bpMB	Hartshorn & Peralta, 1988
Parque Nacional Braulio Carrillo, Heredia	10°11′N 84°06′W	1990	3450	bpMB	Hartshorn & Peralta, 1988
Finca Motillones	—	1750	—	—	—
Parque Nacional Braulio Carrillo, Heredia	— —	1730	4000	bpMB	
Monteverde, Alajuela	10°20′N	1550	2500	bmhMB	—
Costa Rica (lowland)					
Magsasay (Parque Nacional Braulio Carrillo)	10°24′N 84°03′W	150	4015	bmht	Hartshorn & Peralta, 1988
Parque Nacional Carara	—	140	3500	bht	—
Guanacaste (upland)	10°30′N 85°10′W	100	1600	bst	—
Guanacaste (gallery forest)	10°30′N 85°10′W	100	1600	bst	—
La Selva	10°24′N 83°03′W	40	4015	bmht	Hartshorn & Peralta, 1988

(continued)

TABLE I (*continued*)

Site	Grid coor.	Alt. (m)	Est. ppt. (mm)	Holdridge Life zone	Reference
Sirena, Parque Nacional Corcovado	08°30′N 83°35′W	30	3800	bmht	—
Rancho Quemado, Peninsula de Osa	08°43′N 83°36′W	300	—	—	—
Panama (Lowland)					
Pipeline Road	09°10′N 79°45′W	300	3000	bhT	—
Madden Forest	09°66′N 79°36′W	50	2433	bhT	—
Curundu	08°59′N 79°33′W	20	1830	bhT (or bsT, transition to bh)	
Colombia					
Neusa, Cundinamarca (500 m^2)	05°11′N 74°06′W	3050	1000?	bhM	Carrizosa, pers. comm.
Sabana Rubia, Cesar	—	2900	2500	bmhMB	—
Carpanta (Dunning), Cundinamarca	04°34′N 73°41′W	2850	2800	bmhMB	Repizzo, 1993
Alto de Sapa, Antioquia	—	2670	3000	bmhMB	—
Ucumari, Risaraldas	04°45′N 75°30′W	2620	2500	bmhMB	—
Cerro Kennedy, Magdalena	11°05′N 74°01′W	2550	3000	bmhMB	—
Cerro Espejo, Guajira	10°28′N 72°50′W	2500	2500	bmhMB	—
Carpanta (Siete Cuerales), Cundinamarca	04°34′N 73°41′W	2370	2849	bmhMB	Repizzo, 1993
Finca Meherenberg, Huila	02°16′N 76°12′W	2290	2292	bmhMB	Rangel & Espejo, 1989
Cedral, Risaraldas	04°45′N 75°33′W	2140	2500?	bmhMB	—
Finca Zíngara, Valle (600 m^2)	03°32′N 76°35′W	1990	1647	bmhMB	Giraldo, 1990
Farallones de Cali, Valle	03°30′N 76°35′W	1950	1800	bmhMB	—
Hacienda Himalaya, Valle (400 m^2)	03°38′N 76°33′W	1860	2000	bmhMB	—
La Planada, Nariño	01°10′N 77°58′W	1800	4300	bmhPM	—
Alto de Cuevas, Antioquia	06°40′N 76°30′W	1710	4000	bpMB	—
Campano, Magdalena	—	1690	—	—	—
Antadó, Antioquia	—	1560	3800	bmhPM	—
Alto de Mira, Magdalena	10°55′N 73°50′W	1200	2500	bmhPM	—
Murri, Antioquia	06°35′N 76°50′W	960	4200	bpPM	—
Ecuador					
Pasochoa, Pichincha (400 m^2)	00°28′S 78°46′W	3010	1490	bhM	Valencia & Jorgensen, 1992

(*continued*)

TABLE I (*continued*)

Site	Grid coor.	Alt. (m)	Est. ppt. (mm)	Holdridge Life zone	Reference
Maquipucuna, Pichincha	00°07′N 78°37′W	1600		bpPM	Miranda, pers. comm.
Huamani, Napo	00°40′S 77°40′W	1150	1668		Jørgensen, 1992
Peru					
El Pargo, Cajamarca (600 m^2)	06°30′S 79°03′W	3000	1200	bh-MT	—
Cerro Aypate, Piura	04°35′S 79°32′W	2740	1800	bmh-MT	—
Montaña de Cuyas, Piura	04°32′S 79°44′W	2450	1600	bhm-MBT	—
Chorro Blanco, Cajamarca (400 m^2)	06°10′S 78°45′W	2410	1800	bmh-MT	—
Cutervo, Cajamarca	06°10′S 78°40′W	2230	1800	bh-MBT	Brack & Vilchez, 1974
Venceremos, Amazonas	05°45′S 77°40′W	1850	4200	bp-MBT	—
Chirinos, Cajamarca	05°25′S 78°53′W	1750	1800	bhMBT	—
La Genoa, Junin	11°05′S 75°25′W	1160	2010	bmhPT	Reynel & León, 1989
Rio Candamo, Puno	13°30′S 69°50′W	800	4000	bpS	—
Bolivia					
Sacramento, La Paz	16°15′S 67°45′W	2450	2200	bmh MBST	—
Calabatea, La Paz (500 m^2)	14°59′S 68°30′W	1540	2200	bmh MBST	—
Incahuara, La Paz	15°55′S 67°40′W	1540	4000	pbST	—
Argentina					
Salta, Salta	24°40′S 65°30′W	1300	712	—	—
Parque el Rey, Salta	24°45′S 64°40′W	1000	1500	—	Brown et al., 1985

cated. They are included in the floristic analyses but not in the diversity calculations (except for three very high-altitude sites where samples of 400–500 m^2 are adequate to include all the woody species in a low-diversity forest).

For each site the average altitude of the study plot was determined with an altimeter. Where available, rainfall and temperature data were taken from the literature or field station records. Where precipitation records were not directly available, rainfall was estimated by plotting each site on a Holdridge Life Zone map and extrapolating the site's position on the life zone nomagram (Holdridge, 1967) from its position with respect to neighboring life zones.

Each site is also classified geographically as to Mexico, southern Central America (Costa Rica), northern Andes (Colombia and Ecuador), central Andes (Peru and Bolivia), and southern Andes (Argentina). The lone Nicaraguan site was not classified geographically. Multiple regressions of species richness versus altitude and precipitation were carried out for the entire data set and for different subsets of the

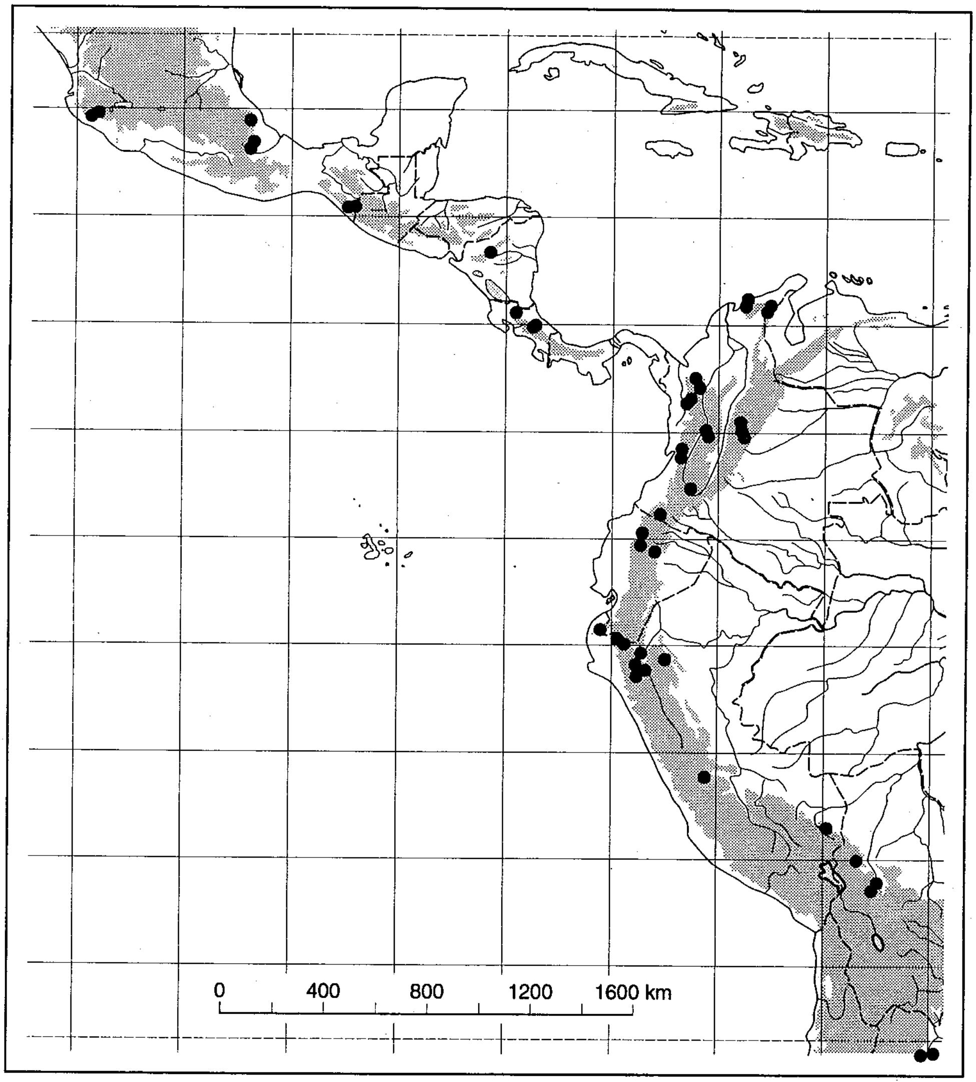

FIGURE 1. Neotropical montane forest sites for 0.1-ha samples from which data for species ≥2.5 cm diam. were sampled. Details for each site are given in Table I.

data, to analyze the relative importance of different environmental factors in predicting species richness. The resulting regression equations were compared using Kruskal-Wallis and Wilcoxon rank sum tests (Hollander & Wolfe, 1973).

Results

The sampled montane forests (Table I, Fig. 1) span the altitudinal gradient of Neotropical forests from 800 m to over 3000 m and extend latitudinally from the north margin of the tropics at 20°N latitude in Mexico to the subtropics in Argentina near 25°S latitude. In the Andes, they include 19 sites in Colombia (eight from the Cordillera Occidental; three from the Cordillera Central; five from the Cordillera Oriental, including two from Serrania de Perija; and three from the isolated Sierra Nevada de Santa Marta), three in Ecuador, seven of nine in Peru, three in Bolivia, and two in northern Argentina. In Central America, they include eight samples in Mexico (from the states of Jalisco, Chiapas, Oaxaca, and Veracruz), one from Nicaragua, and eight from Costa Rica. Andean samples include data sets from five sites from 800 to 1200 m, five sites from 1500 to 1700 m, seven sites from 1700 to 2000 m, seven sites from 2000 to 2500 m, seven sites from 2500 to 2900 m, and three sites from above 3000 m altitude. Central American

TABLE II

Diversity data for Mexican, Central American, and Andean montane forest above 800 m elevation, based on 0.1-ha samples

			No. of species				No. of individuals				
Site	Av. elev. (m)	No. of families (+ indet.)	Total*	Lianas (+ hemi-ep. and str.)	Trees ≥2.5 cm dbh	Trees ≥10 cm dbh (+ lianas)	Total*	Lianas (+ hemi-ep. and str.)	Trees ≥2.5 cm ≤10 cm dbh	Trees ≥10 cm dbh (+ lianas)	Trees ≥2.5 cm dbh
Mexico											
Sierra Juarez, Oaxaca	2250	26	44	5(+2)	37	—	390	47(+6)	—	—	337
Benito Juarez, Chiapas	2100	21	ca. 30	1	29	17	233	1	181	51	232
Las Joyas, Jalisco	1950	25(+1)	35	8(+2)	25	18(+2)	198	22(+2)	121	53(+2)	174
Quince Ocotes, Jalisco	1800	33	44	5	39	22	246	—	—	—	—
Sierra Juarez, Oaxaca	1750	27(+5)	56	5(+3)	48	—	347	8(+4)	—	—	335
Motozintia, Chiapas	1600	9	12	0	12	—	107	0	—	—	107
Sierra Juarez, Oaxaca	1255	24(+3)	ca. 50	5(+6)	39	—	397	30(+23)	—	—	344
Bosque de Guadalupe, Veracruz	1225	26	ca. 40	7	33	16(+2)	306	55	186	65(+2)	251
Nicaragua											
Cerro el Picacho	1400	20	ca. 65	6(+6)	53	22	213	15	133	65	198
Costa Rica											
P. N. Braulio Carrillo	2775	17	24	0(+5)	19	—	188	9(+28)	—	—	160
P. N. Braulio Carrillo	2750	19	28	1(+4)	23	—	243	1(+29)	—	—	213
P. N. Braulio Carrillo	2750	25(+1)	39	4(+5)	30	—	239	5(+32)	—	—	202
P. N. Braulio Carrillo	2225	34	66	3(+11)	52	—	439	5(+52)	—	—	382
P. N. Braulio Carrillo	2000	35(+2)	68	6(+8)	54	—	356	8(+14)	—	—	334
P. N. Braulio Carrillo	1900	36	69	5(+13)	51	—	358	10(+29)	—	—	319
Monteverde	1550	52(+1)	ca. 127	16(+11)	100	—	—	—	—	—	data lost
Finca Motillones	1750	39	87	5(+16)	66	—	273	15(+37)	—	—	221
Colombia											
Murri, Antioquia	960	54	ca. 175	28(+29)	118	49	324	42(+49)	163	70	233
Alto de Mira, Magdalena	1200	38	ca. 82	14(+12)	56	38(+2)	316	16(+52)	139	116(+3)	248
Antadó, Antioquia	1560	55	ca. 160	24(+28)	ca. 108	57(+1)	388	43(+49)	194	102(+1)	296
Campano, Magdalena	1690	44	ca. 104	16(+10)	78	86(+2)	405	66(+15)	236	89(+2)	324
Alto de Cuevas, Antioquia	1710	49	x. 119	ca. 14(+24)	ca. 81	36(+5)	363	27(+52)	181	103(+4)	284
La Planada, Nariño	1800	40	121	8(+27)	89	47(+1)	433	20(+81)	252	80(+1)	332
Hacienda Himalaya, Valle (400 m^2)	1860	39(+)	81	18(+10)	54	29(+)	441	46(+11)	280	ca. 103(+1)	383
Finca Zíngara, Valle (600 m2)	1990	39(+)	(118)	10(+14)	(94)	[37(+1)]	357	42(+27)	182	ca. 105(+1)	287
Farallones de Cali, Valle	1950	54(+1)	134	19(+9)	106	35(+1)	302	32(+9)	201	60(+2)	261
Cedral, Risaradas	2140	43(+1)	ca. 120	22(+9)	89	ca. 47 (+1)	531	46(+20)	341	124(+1)	465
Finca Meerenberg, Huila	2290	43	107	14(+5)	88	45	364	51(+10)	215	88(+)	303
Carpanta (Siete Cuerales), Cundinamarca	2370	36	ca. 75	5(+5)	65	32	354	27(+9)	223	95(+6)	318
Cerro Espejo, Guajira	2500	46	78	20	58	50	406	87	177	142	319
Cerro Kennedy, Magdalena	2550	35	57	8	49	30	326	41	168	117	285
Ucumari, Risaraldas	2620	445	98	12(+5)	85	49	562	42(+122)	283	115	398

(*continued*)

TABLE II (*continued*)

			No. of species				No. of individuals				
Site	Av. elev. (m)	No. of families (+ indet.)	Total*	Lianas (+ hemi-ep. and str.)	Trees ≥2.5 cm dbh	Trees ≥10 cm dbh (+ lianas)	Total*	Lianas (+ hemi-ep. and str.)	Trees ≥2.5 cm ≤10 cm dbh	Trees ≥10 cm dbh (+ lianas)	Trees ≥2.5 cm dbh
Alto de Sapa, Antioquia	2670	28	ca. 63	10(+)	49	21(+1)	386	57(+10)	241	78(+1)	319
Carpanta (Dunning) Cundinamarca	2850	23	ca. 46	11(+3)	34	30	280	61(+)	128	91(+9)	219
Sabana Rubia, Cesar	2900	31(+1)	ca. 51	9(+2)	40	25	343	17(+3)	242	81	323
Neusa, Cunamarca ($500 m^2$)	3050	19	ca. 35	ca. 11	ca. 24	7(+1)	478	56	278	144(+2)	422
Ecuador											
Huamani, Napo	1150	56	151	27(+22)	102	47	389	58(+45)	200	86	286
Maquipucuna, Pichincha	1600	49	ca. 123	12(+26)	85	49(+2)	438	18(+106)	234	80(+3)	314
Pasochoa, Pichincha ($400 m^2$)	3010	21	ca. 35	ca. 14	ca. 21	8(+)	552	237	190	125	315
Peru											
Rio Candamo, Puno	800	65	±232	36(+10)	184	65(+1)	443	51(+25)	300	67	367
La Genoa, Junin	1160	43	106	24(+5)	77	42(+6)	347	58(+8)	95	86(+8)	256
Chirinos, Cajamarca	1750	38(+1)	97(+)	15(+9)	73	ca. 39(+2)	389	37(+14)	263	75(+2)	338
Venceremos, Amazonas	1850	46(+1)	159	16(+14)	129	62(+3)	514	32(+28)	346	108(+3)	450
Cutervo, Cajamarca	2330	42	ca. 96	13(+9)	76	36(+2)	469	52(+38)	294	86(+2)	370
Chorro Blanco, Cajamarca	2410	ca. 20	ca. 42	—	—	—	396	52	217	127	344
Montaña de Cuyas, Piura	2450	31	66	19(+3)	44	24(+1)	357	79(+20)	188	70(+2)	278
Cerro Aypate, Piura	2740	28	51	14(+1)	107	26(+1)	390	40(+1)	243	106(+1)	349
El Pargo, Cajamarca ($600 m^2$)	3000	20	ca. 36	ca. 7	ca. 29	15(+1)	366	33	200	133(+1)	333
Bolivia											
Calabatea La Paz ($500 m^2$)	1540	48(+)	110(+)	17(+9)	93	33(+)	532	52(+4)	352	102	476
Incahuara, La Paz	1540	44	147	11(+6)	130	57(+1)	523	25(+14)	391	93(+1)	484
Sacramento, La Paz	2450	33	91	16(+3)	72	34	572	85(+20)	374	93	467
Argentina											
Parque el Rey, Salta	1000	27	40	10	30	20(+11)	188	44	95	49(+11)	144
Salta, Salta	1300	14	25	3	22	11	197	4	138	55	193

Note: Geographic information for each site is given in Table I.
*Total number of species and individuals recorded at each site composed of lianas plus trees ≥ 2.5 cm dbh.

samples include three from 2700 to 2800 m, four from 2000 to 2500 m, five from 1700 to 2000 m, and five from 1200 to 1600 m altitude. Comparative data from Neotropical lowland samples are given in Gentry, 1988.

Diversity

The Andean samples show remarkable consistency in patterns of diversity (Table II, Fig. 2) and floristic composition at the family level (Table III, see also Fig. 5). Within each geographic region (Mexico, southern Central America, northern Andes, central Andes, and southern Andes) the same pattern of diversity versus elevation is apparent. However, there were significant differences in diversity among Andean, Costa Rican, and Mexican montane forests (Kruskal-Wallis test: $\chi^2 = 13.21, n = 45, p < 0.01$) and between Andean and Mexican montane forests (Wilcoxon rank sum test: $z = 3.29, n = 36, p < 0.01$); Andean forests were the most diverse. The difference between Andean and Costa Rican forests is almost

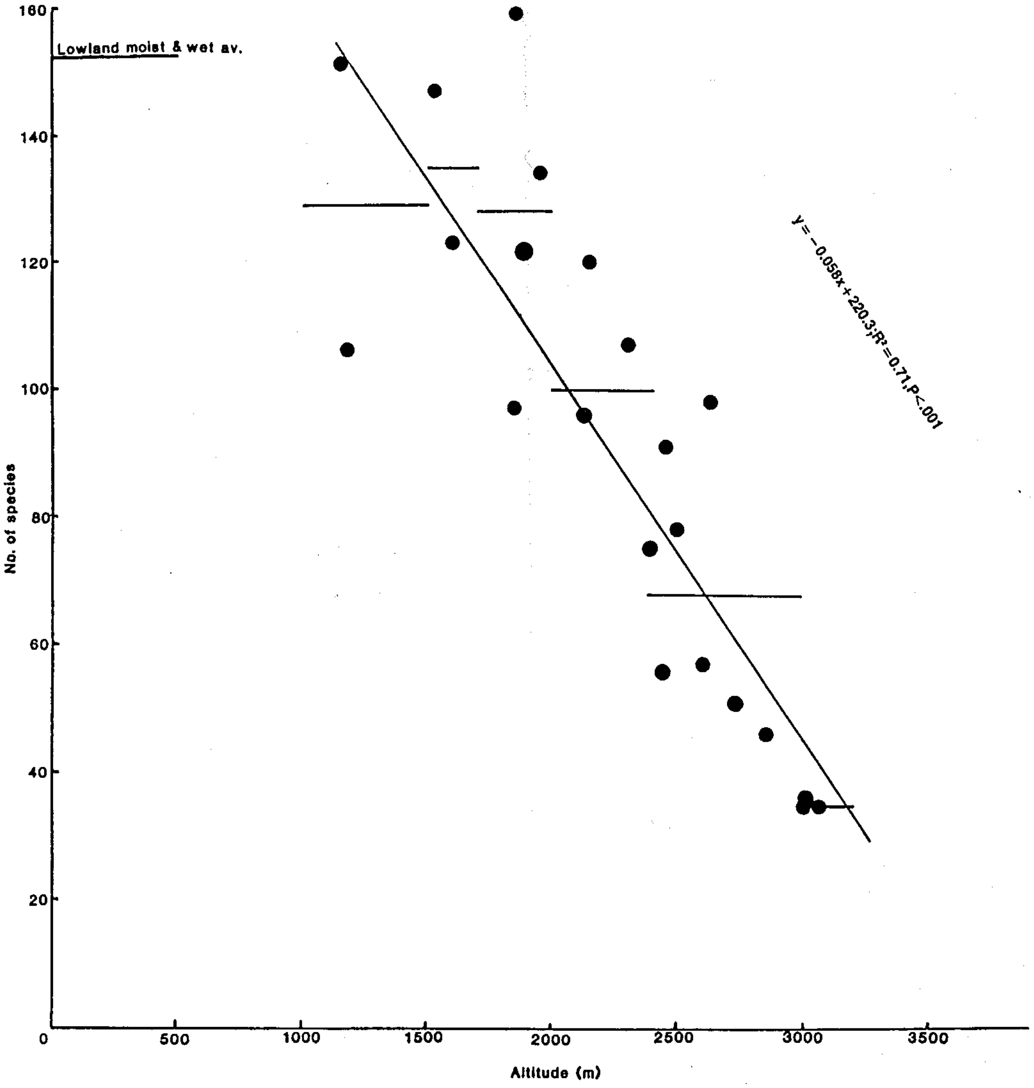

FIGURE 2. Andean diversity vs. altitude regression line for number of species (≥2.5 cm diam.) in 0.1-ha samples.

significant (Wilcoxon rank sum test: $z = 1.86$, $n = 36$, $p < 0.07$). Costa Rican forests are more diverse than Mexican forests, and in general there is no change in diversity with latitude among Andean forests until south of the tropic of Capricorn in Argentina.

Diversity of woody plants in the montane Neotropics is generally unremarkable compared with that in lowland tropical forests, and high-altitude forests are consistently depauperate. Up to about 1500 m elevation there is little difference in diversity between Andean foothill (x = ca. 160 species) and lowland Amazonian forests (x = ca. 180 species) or between lowland Central American (x = ca. 130 species) and premontane Central American (x = ca. 100 species) (Fig. 3). In every geographical region the montane forests poorest in species are those nearest the timberline, while those nearest the base of the mountains are richest.

Above 1500 m elevation there is a linear decrease in species richness with altitude (Fig. 2). This relationship is highly significant in Andean forests (no. of species = 260.1 – [0.073 × elev.]; $r^2 = 0.87$, $n = 24$, $p = 0.0001$) and southern Central American montane forests (no. of species = 209.8 – [0.066 × elev.]; $r^2 = 0.90$, $n = 8$, $p < 0.0001$). It is also apparent, but not significant, in Mexican montane forests (no. of species = 68.6 – [0.017 × elev.]; $r^2 = 0.11$, $n = 8$, $p < 0.43$).

Family diversity also decreases generally with al-

TABLE III

Thirty most prevalent Andean families with species ≥2.5 cm diam. arranged by site.

	Site*																																		
Family	N	PO	EP	SR	C	CK	CA	AS	U	CE	MC	S	CB	CSC	CU	M	CD	FZ	FC	HH	V	LP	CH	AC	CM	MA	AN	IN	CL	AM	LG	HU	MU	RC	TSSR†	AV‡
Lauraceae	3	–	2	4	2	8	5	5	10	10	5	7	8	8	16	11	12	10	12	2	29	5	13	5	8	11	10	24	6	4	6	8	6	4	274	8.2
			–	=		≡	–	=	≡	≡	–	–	≡	≡	≡	≡	≡	–	≡		≡		≡		–	≡	–	≡				=				
Melastomataceae	3	3	3	3	3	3	3	10	9	3	3	15	5	5	8	10	10	11	10	7	7	10	2	6	4	7	15	18	12	8	1	4	13	5	239	7.0
		=	=	–				≡	=	–		≡	≡		=	=	=	=	=	=		≡				–	≡	=	≡	≡			–			
Rubiaceae	1	1	1	–	–	2	–	5	6	1	1	10	3	8	8	8	5	14	10	4	20	8	10	10	12	6	11	12	12	5	4	6	13	11	229	6.7
								=	–			=		≡	≡	–		≡	=		=		=	≡	≡		=	–	≡				–			
Moraceae	–	–	–	–	–	–	1	–	2	1	1	1	–	–	1	7	4	4	7	8	8	10	3	7	12	9	9	6	5	4	14	6	14	14	158	4.6
																				≡		≡		=	≡	=					≡		≡	≡		
Compositae	7	6	8	7	2	2	6	3	5	9	6	7	2	7	4	7	8	1	1	1	4	2	7	3	1	4	2	3	3	2	3	1	1	1	136	4.0
	≡	≡	≡	≡			=			=	=	–		–									–													
Leguminosae	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2	2	4	4	5	6	7	2	2	5	3	–	5	9	5	11	20	14	14	133	3.9
																				=									–		=	≡	≡	≡		
Guttiferae	1	–	1	1	4	1	–	4	2	1	1	–	1	1	2	4	4	4	7	3	9	5	4	3	4	4	9	3	2	4	2	7	5	7	111	3.3
					–																–											–				
Ferns	–	–	–	–	5	2	–	5	1	1	–	4	1	4	5	5	2	3	5	3	1	7	3	5	1	7	8	7	3	7	–	3	4	6	108	3.2
					≡			=																		–				=						
Araceae	–	–	–	–	1	–	1	1	3	1	2	1	–	1	4	4	9	2	3	2	3	10	2	8	1	7	5	1	3	2	–	5	9	3	94	2.8
																	–					≡		=		–										
Euphorbiaceae	–	–	–	–	–	2	–	–	2	–	–	3	3	3	3	2	2	5	9	2	6	4	4	6	3	3	3	8	3	2	4	6	4	–	92	2.7
Palmae	–	–	–	–	1	2	–	2	3	1	–	1	–	–	3	3	5	1	3	2	2	6	1	6	1	2	4	5	3	7	2	2	9	5	82	2.5
																														=						
Myrtaceae	1	–	–	2	–	3	3	–	1	3	2	2	1	4	2	2	2	6	1	1	2	5	3	1	3	5	–	7	2	1	3	3	–	12	81	2.4
						=				–																								–		
Myrsinaceae	4	1	2	1	5	2	2	1	3	3	1	4	–	5	3	4	1	3	2	3	2	3	0	2	2	3	2	3	2	–	2	1	2	2	76	2.2
	=		–		≡					–																										
Solanaceae	–	–	–	2	–	–	8	–	5	2	8	0	–	2	2	4	8	–	2	1	2	1	2	3	3	1	2	–	2	2	1	3	2	2	70	2.1
							≡				≡																									
Araliaceae	1	1	1	2	1	1	1	2	5	2	1	3	1	?	1	1	3	5	1	1	4	4	4	3	1	4	3	3	1	1	1	1	3	1	68	2.0
Piperaceae	–	2	–	–	1	–	2	2	1	1	1	–	1	2	4	1	6	1	4	2	1	1	1	5	2	4	1	4	2	2	1	4	4	1	64	1.9
Ericaceae	4	2	1	2	3	1	–	3	1	–	1	3	4	3	2	3	1	2	–	2	3	5	–	3	–	2	3	1	–	2	–	3	1	–	61	1.8
	=												–																							
Annonaceae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2	2	4	4	6	2	1	–	–	–	4	6	1	–	1	7	8	5	55	1.6
Meliaceae	–	–	–	1	–	–	1	–	3	2	2	1	–	1	1	2	2	–	1	1	4	3	–	2	2	2	1	–	–	–	2	3	5	7	49	1.4
Sapindaceae	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	1	1	3	3	1	2	2	3	1	3	1	2	2	7	6	4	2	46	1.4
Bignoniaceae	–	–	–	–	–	–	1	–	–	–	1	–	–	–	1	–	3	–	2	–	1	–	1	2	2	–	4	1	4	4	5	2	3	5	42	1.2
Cyclanthaceae	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	2	–	2	4	2	2	1	4	3	1	1	1	–	3	5	3	34	1.0
Monimiaceae	–	–	1	–	1	–	–	–	2	–	1	3	–	–	1	2	2	1	–	1	2	–	–	2	2	–	–	4	1	1	–	1	2	4	34	1.0
Flacourtiaceae	–	1	–	–	–	–	–	–	1	–	–	–	–	–	2	2	1	1	–	–	3	2	3	2	1	2	1	–	1	–	3	–	1	5	32	0.9
Sapotaceae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	–	–	1	2	–	5	4	4	1	–	3	2	7	32	0.9
Cunoniaceae	1	–	2	2	2	1	–	1	2	1	–	2	1	2	4	2	–	–	1	2	1	–	–	1	–	1	–	1	–	1	–	1	–	–	30	0.9
Apocynaceae	–	–	≡	–	–	–	1	–	1	–	–	–	–	1	–	–	–	–	2	–	1	–	3	–	3	–	2	–	2	1	3	2	3	5	30	0.9
Sabiaceae	–	–	–	1	–	1	1	–	4	2	1	2	–	1	3	1	–	–	1	1	–	–	–	1	–	1	3	–	–	–	–	1	1	1	27	0.8
Aquifoliaceae	–	1	–	1	3	4	1	3	2	2	–	2	–	1	–	–	1	2	–	–	–	–	–	–	1	1	1	1	–	–	–	–	–	–	27	0.8
Bombacaceae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	1	1	–	3	1	2	–	–	3	–	–	3	1	2	3	3	26	0.8

Note: ≡ largest families, = second largest families, – third to tenth largest families.

*N, Neusa (Colombia); PO, Pasochoa (Ecuador); EP, El Pargo (Peru); SR, Sabana Rubia (Colombia); C, Carpanta (Colombia); CK, Cerro Kennedy (Colombia); CA, Cerro Aypate (Peru); AS, Alto de Sapa (Colombia); U, Ucumari (Colombia); CE, Cerro Espejo (Colombia); MC, Montaña de Cuyas (Peru); S, Sacramento (Bolivia); CB, Chorro Blanco (Peru); CSC, Carpanta Siete Cuerales (Colombia); CU, Cutervo (Peru); M, Finca Meherenberg (Colombia); CD, Cedral (Colombia); FZ, Finca Zíngara (Colombia); FC, Farallones de Cali (Colombia); HH, Hacienda Himalaya (Colombia); V, Venceremos (Peru); LP, La Planada (Colombia); CH, Chirinos (Peru); AC, Alto de Cuevas Colombia); CM, Campano (Colombia); MA, Maquipucuna (Ecuador); AN, Antadó (Colombia); IN, Incahuara (Bolivia); CL, Calabatea (Bolivia); AM, Alto de Mira (Colombia); LG, La Genoa (Peru); HU, Huamani (Ecuador); MU, Murri (Colombia); RC, Rio Candamo (Peru).

†Total species-site records.

‡Average number of species.

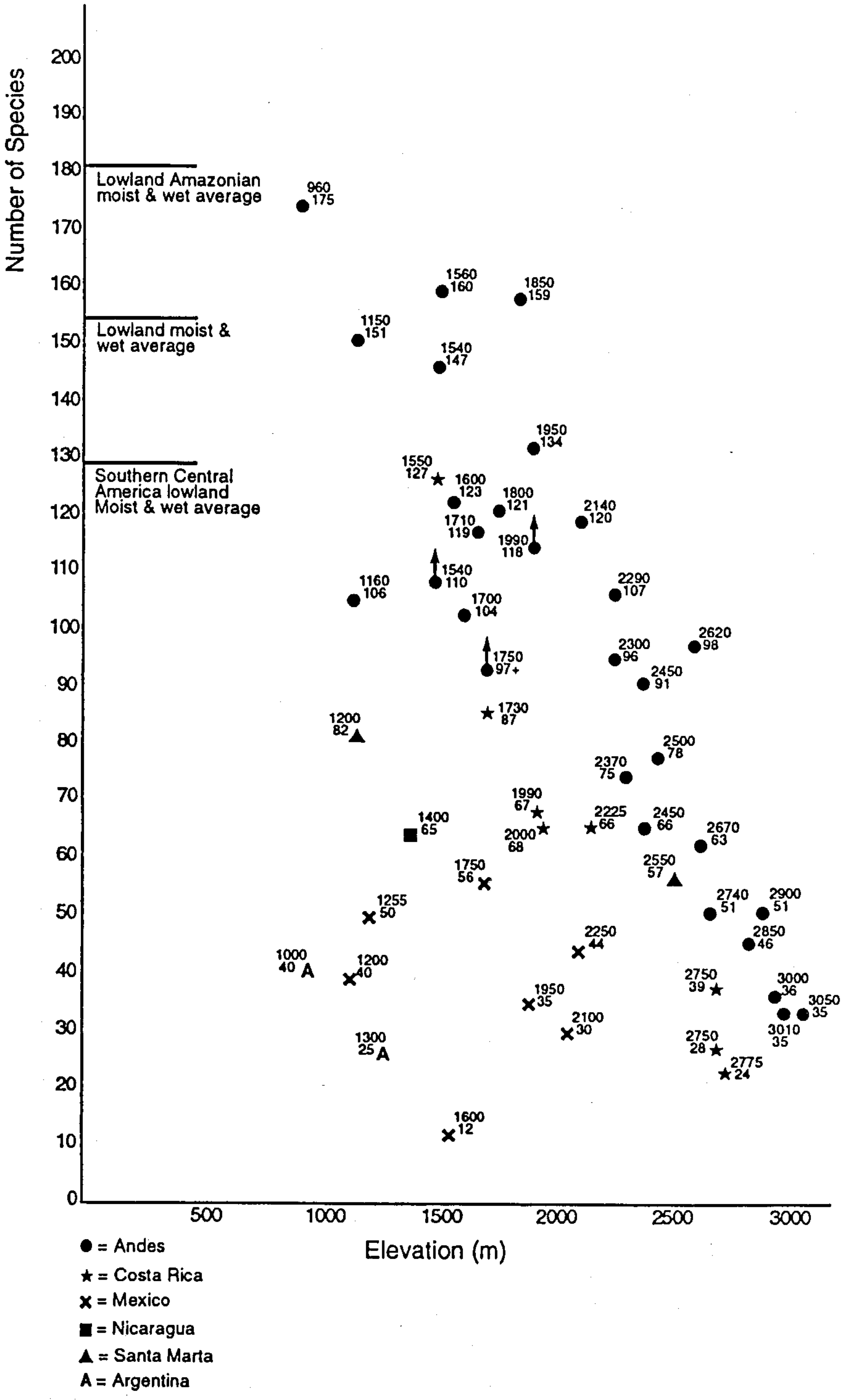

FIGURE 3. Neotropical diversity vs. altitude for numbers of species (≥2.5 cm diam.) in 0.1-ha samples.

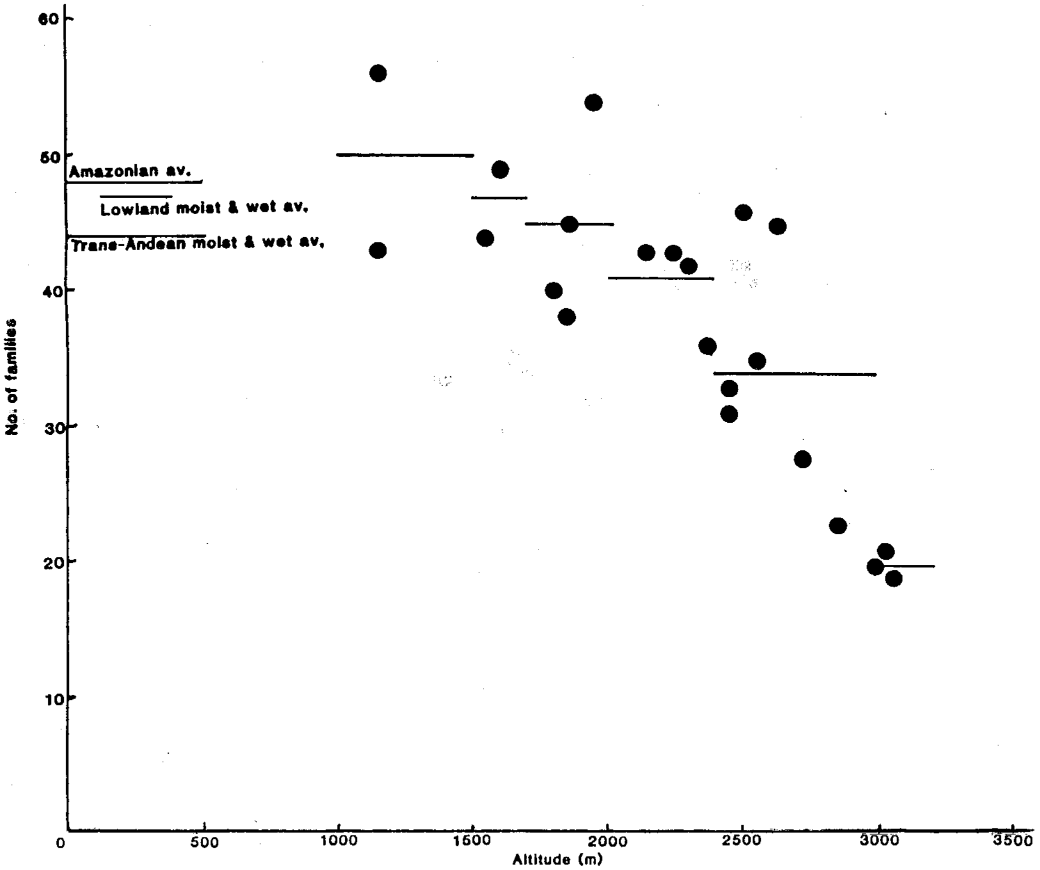

FIGURE 4. Familial diversity vs. altitude in Neotropical montane forests. Numbers of families with species ≥2.5 cm diam. in 0.1-ha samples.

titude although less sharply than species richness, and only above 2000 m (Fig. 4). Thus higher altitude forests have somewhat fewer families and conspicuously fewer species per family. There may be a slight increase in family diversity around 1000–1500 m, where sites average 50 families per 0.1-ha sample. Presumably this increase is due to the tendency for exclusively montane, basically Laurasian families to overlap with largely Gondwanan tropical lowland families at this elevation. Above 1500 m only montane families and genera are present. Below 1000 m the flora is composed almost exclusively of lowland tropical families (Gentry, 1992).

Although diversity of Andean forests is very strongly correlated with elevation (Fig. 2), it shows a less significant correlation with precipitation ($r^2 = 0.36, p < 0.05$) or distance from the equator. Latitude does have a significant effect on species richness, but only if the subtropical sites in Mexico and Argentina are included.

Including estimated precipitation in the regression of Andean species richness versus elevation does not significantly increase the fit of the model. In fact, elevation alone explains 87% of the variance in Andean species richness at elevations above 1500 m. Too few sites are available from Mexico and Central America to statistically evaluate how differences in precipitation affect the diversity-elevation regression there. However, there is some correlation of species richness with precipitation in subtropical montane sites. The lowest diversity of all sample sites is for the driest Mexican montane forest sampled, at Motozintla, Chiapas. Excluding the highest altitude near-timberline Costa Rican site, the second lowest diversity value in the data set is for the Argentinean dry forest at Salta (25 species), whereas a moist Argentinean forest at Parque El Rey has 40 species, comparable to Mexican forests at similar elevations and altitudes. I have no montane dry forest data from nearer the equator, where scrubby nonforest formations occur in drier areas. While it is likely that montane dry forests once existed in the equatorial Andes, I know

TABLE IV

Diversity data for lowland Central American forests, based on 0.1-ha samples below 800 m elev.

			No. of species				No. of individuals				
Site	Av. elev. (m)	No. of families (+ indet.)	Total*	Lianas (+ hemiep. and str.)	Trees ≥2.5 cm dbh	Trees ≥10 cm dbh (+ lianas)	Total*	Lianas (+ hemiep. and str.)	Trees ≥2.5 cm ≤10 cm dbh	Trees ≥10 cm dbh (+ lianas)	Trees ≥2.5 cm dbh
Costa Rica											
Parque Nacional Carara	140	51	ca. 149	24(+5)	120	59(+5)	345	48(+7)	204	86(+6)	290
Guanacaste (upland) (800 m²)	100	ca. 30	ca. 61	8	53	18	331	77	217	37	254
Guanacaste (Gallery forest) (800 m²)	100	ca. 40	ca. 63	8	55	22	164	19	115	30	145
La Selva	40	47	ca. 130	26(+5)	99	39(+4)	328	51(+11)	194	72(+5)	266
Magsasay (Parque Nacional Braulio Carrillo)	150	51	141	29(+6)	106	33(+4)	371	52(+14)	239	66(+5)	305
Sirena, Parque Nacional Corcovado	30	46	130	34(+5)	ca. 91	44(+4)	291	54(+)	155	82(+4)	237
Rancho Quemado, Peninsula de Osa	300	46	ca. 120	ca. 13(+5)	102	54(+4)	264	29(+6)	157	72(+4)	229
Panama											
Curundú	20	42	90	20	70	29	282	60	169	53	222
Madden Forest	50	44	131	31	100	36	324	70	172	82	254
Pipeline Road	300	58	167	38	130	39	393	117	207	69	276

*Totals based on lianas plus trees ≥2.5 cm dbh.

of no remaining example that might be censused to establish its diversity or floristic characters.

To what extent the decreasing diversity farther north at similar elevations in montane Central American is due to more subtropical ecological conditions and to what extent to different biogeographical histories (cf., Gentry, 1982b, see also discussion below) remains undetermined. At any rate the trend of decreased diversity in Central America is paralleled in lowland forests, where the average for eight southern Central American lowland forest 0.1-ha samples is only 132 species (Table IV), as compared with an average of 183 species for a comparable series of 24 Amazonian moist and wet forest sites (Gentry, 1993b).

Sierra Nevada de Santa Marta

Another interesting anomaly in the diversity data is the Sierra Nevada de Santa Marta in northern Colombia, which generally has fewer species per sample than other Andean sites (Fig. 3). At least three theories might account for this pattern: geographical isolation, human impact, and effect of climatic changes. As a geographical montane outlier, the Sierra Nevada de Santa Marta might be expected to have fewer species vis à vis island biogeographical theory.

This gratifying concordance with ecological theory is confounded by the fact that most of the Sierra Nevada de Santa Marta, including areas forested today, has a long history of pre-Columbian habitation, with most of today's forest growing over archaeological ruins, at least at lower elevations. Perhaps human disturbance rather than geographical isolation has led to less diverse plant communities in the Sierra Nevada. It is noteworthy that the most anomalously low-diversity Sierra Nevada de Santa Marta sample, from Alto de Mira, is from a low-elevation site. Progressively higher altitude samples are closer to the standard Andean diversity regression, with the Cerro Kennedy sample from 2550 m only marginally below the regression line. Such a pattern might be expected if a history of human use concentrated at lower elevations were the factor responsible for the low diversity, but not if geological isolation, which should be increasingly severe at high altitudes, were responsible.

It is perhaps relevant that a lowland 0.1-ha sample from 360 m elevation at Bosque del Cueva on the northeast flank of the Sierra Nevada is one of the lowest diversity sites in my entire lowland Neotropical moist and wet forest data set (Gentry, 1988).

Subsequent to our sampling of this forest, selected because it was the best-developed forest we could find in the region, it was discovered to lie over significant archaeological remains, which have since been excavated (H. Cuadros, pers. comm.).

Unfortunately for the human disturbance hypothesis, there is another potential explanation of the low diversity of the Sierra Nevada de Santa Marta moist forests. The massif is located at 11°N latitude, well into the subequatorial dry zone, and is completely surrounded by a large area of dry and arid vegetation. During Pleistocene glacial advances, this dry vegetation probably expanded, restricting the orographically moist island surrounding the Sierra to the higher slopes, at the same time that greater cold and glacial advance forced montane formations lower. A plausible result would be local extinction of many lowland moist forest elements and a relatively depauperate modern moist forest vegetation. Perhaps relevant to this hypothesis, dry forest 0.1-ha samples near the base of the Sierra Nevada de Santa Marta (Tayrona: Gentry, 1988, in press) do not show any depression in species richness, unlike their moist forest equivalents.

Although reasons for such diversity patterns as decreased species richness in Central America montane forests and the Sierra Nevada de Santa Marta remain to be worked out, the patterns clearly exist, documented here apparently for the first time.

Floristic Composition: Andes

Andean montane forests are composed of a distinctive group of taxa that overlap little with those of lowland tropical forest (Gentry, 1992). Lower-elevation Andean forests up to about 1500 m, however, are floristically similar to lowland Amazonian or trans-Andean forests, with Leguminosae the largest family and Bignoniaceae the largest of the lianas. These premontane forests are especially similar floristically to lowland forests on relatively rich soils (Gentry, 1992; Fig. 5), where Moraceae is typically the second largest family, with strangler figs often especially prominent just as they are in lower-elevation Andean forests. Rubiaceae, Palmae, Sapindaceae, Annonaceae, Meliaceae, and Sapotaceae are other large families in both premontane forests and lowland forests on good soils.

Some relatively minor floristic differences between premontane and lowland forests are also apparent. Guttiferae, especially hemiepiphytic *Clusia,* is better represented (*Clusia* is the third most prevalent genus, with 2.6 species per sample) in the premontane forests. Melastomataceae and Piperaceae are also more prevalent in premontane forests, at least as forest trees and treelets, measured by these samples. Tree ferns and hemiepiphytic aroid and cyclanth climbers are more generally prevalent than in lowland forest, and these groups become even more prominent in mid-elevation forests between 1500 and 1700 m.

There are also floristic differences at lower taxonomic levels. For example, most sampled montane legumes are species of *Inga* as contrasted to the rich array of legume genera represented in lowland forest samples. *Inga* is the second most species-rich Andean genus overall (Table V) and the highest-elevation legume genus, reaching 2370 m; four to nine *Inga* species per sample are represented at most sites below 2000 m. *Inga* is the largest premontane genus, averaging 7.8 species per sample below 1500 m. Other lowland legume genera are sporadically represented in the premontane samples, but only eight of them occur above 1540 m and only two legume genera besides *Inga* (*Pithecellobium, Dussia*) occur above 1860 m.

Above 1500 m elevation, mid-elevation Andean forests are much more distinctive floristically (Gentry, 1992; Fig. 5, Table III). Mid-elevation (roughly 1500–2500 m) and upper elevation (2500–2900 m) Andean forests are composed mostly of a very different suite of plant families than are the premontane or lowland tropical forests.

Lauraceae is by far the most prevalent and characteristic component of these forests; it is the most species-rich family in 13 of the 24 samples between 1540 and 2550 m and second or third in most of the others. Apart from two very incomplete samples, the only exceptions are the very wet forests of the western slopes of Colombian western cordillera, where Melastomataceae or Rubiaceae or both are the most species-rich families (tied with Moraceae at La Planada). Overall, Lauraceae average 8.2 species per sample, far more than any other family.

Melastomataceae and Rubiaceae follow Lauraceae as the most species-rich families in the mid-elevation Andean samples, averaging 7.0 and 6.7 species per sample, respectively, over the entire data set. Both families are generally in the top three or four families in these samples. Rubiaceae tend to be slightly more prevalent at lower elevations (average, 9.9 species per sample below 2000 m vs. 8.2 for Melastomataceae), Melastomataceae at higher ones (average 5.7 species per sample vs. 4.1 between 2000 and 2900 m). Although both of these families are predominantly shrubs and small trees, both also include important Andean canopy genera. In Rubiaceae, these include *Cinchona* (especially 2000–2500 m: 0.6 species per

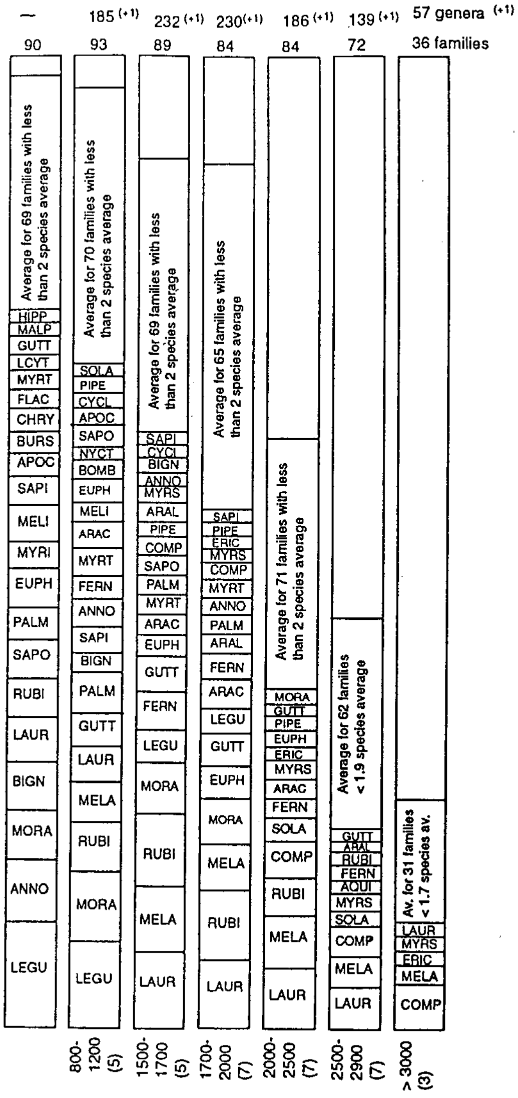

FIGURE 5. Floristics of Andean montane forests, with relative importance of families at different elevations, based on samples of species ≥2.5 cm diam. in 0.1-ha sample plots. Sample plots are described in Table I. At bottom of bars: elevation (m) and (number of sites); at top, number of genera and families present in each elevational range.

sample), *Elaeagia*, (especially 1500–1700 m: 1.0 species per sample), *Guettarda* (especially 1700–2000 m: 0.7 species per sample), and *Ladenbergia* (especially 1500–1700 m: 0.6 species per sample).

Important canopy Melastomataceae include *Axinaea*, *Merriania*, and *Miconia*. *Bucquetia* is one of the most dominant canopy species in one of the highest-altitude forests (Neusa); a *Miconia* is the third commonest species ≥10 cm dbh in another (Sabana Rubia). Both families also include important Andean genera of hemiepiphytes such as *Blackea* and *Topobea* in Melastomataceae and *Hillia* and *Cosmibuena* in Rubiaceae. In addition, many shrubby Melastomataceae, belonging to at least nine genera, and Rubiaceae, belonging to at least 14 genera, are represented in the Andean forest samples. *Miconia* is the most species-rich genus in both Andean and Central American montane forests (Tables V and VI), and *Psychotria* and *Palicourea* are among the dozen most species-rich Andean genera. *Tibouchina* (Melastomataceae) is especially important in mid-elevation successional vegetation. Both families also occur in lowland forests, but they are less prevalent there, at least as trees and hemiepiphytes.

The fourth most species-rich family in middle elevation forests between 1500 and 2000 m is Moraceae, mostly represented by *Ficus*, which is the seventh largest genus in the Andean samples overall. Although 18 other genera of Moraceae are included in Andean samples from above 800 m, most occur below 1500(–1700) m. Only *Morus*, included in nine samples from 1640–2740 m, is exclusively Andean. *Cecropia* occurs sporadically in samples up to 2450 m, *Clarisia* to 2140 m, *Helicostylis* and *Pseudolmedia* to 1950 m, and *Naucleopsis*, *Sorocea*, and *Coussapoa* to (1850–)1860 m.

The other most important families in mid-elevation Andean forests include ferns, Guttiferae, Euphorbiaceae, Palmae and mostly hemiepiphytic Araceae, plus Leguminosae (mostly *Inga*). The ferns are mostly *Cyathea*, which is equal to *Miconia* as the most species-rich genus in the 1700–2000 m elevation samples (3.3 species per sample) and is second only to *Miconia* in the 1500–1700 m samples (3.6 species per sample). Seven basically lowland genera of Guttiferae are represented in the 1500–1700 m elevation samples. All but *Symphonia* reach up to 1750 m (and four extend above 2000 m). *Clusia* is the most prevalent, occurring in all but five of the 19 samples between 1500 and 2500 m; it is most prevalent from 1700 to 2000 m, where it averages 2.6 species per sample, and is the fifth most species-rich genus. Euphorbiaceae has 11 genera represented in mid-altitude samples, all reaching to at least 1750 m, with *Alchornea*, *Croton*, *Hieronyma*, and *Richeria* extending above 2000 m. By far the most important mid-elevation euphorb genera are *Hieronyma* and *Alchornea*. The former is represented in 17 of 19

TABLE V

Most prevalent Andean genera, as average number of species ≥2.5 cm diam. at different elevational ranges, based on 34 0.1-ha samples

Genus	Altitude range (m)‡						
	>3000	2500–3000	2000–2500	1700–2000	1500–1700	800–1500	≥800
Saurauia (Actinidiaceae)	0.3	0.6	0.4	1.3	0.2	0.2	3.0
Guatteria (Annonaceae)	—	—	0.3	1.6	1.0	1.4	4.3
Ilex (Aquifoliaceae)	0.3	2.3	0.6	0.3	0.8	—	4.3
Anthurium (Araceae)†	—	1.0	2.3	2.0	1.6	0.6	7.5
Philodendron†	—	—	0.4	1.6	0.8	1.6	4.4
Dendropanax (Araliaceae)	—	0.1	0.3	0.6	0.8	0.8	2.6
Oreopanax	1.0	1.1	0.5	1.3	0.8	—	4.7
Schefflera	—	0.7	0.5	1.3	0.8	0.6	3.9
Quararibea (Bombacaceae)	—	—	—	0.6	0.4	1.6	2.6
Cordia (Boraginaceae)	—	0.4	—	0.4	0.2	1.2	2.2
Brunellia (Brunelliaceae)	—	0.4	0.7	0.1	—	—	1.2
Protium (Burseraceae)	—	—	—	0.1	0.4	1.4	1.9
Hedyosum (Chloranthaceae)	0.7	1.0	1.1	0.3	0.6	0.2	3.1
Eupatorium (Compositae)	1.0	—	—	—	—	—	1.0
*Liabum**	1.0	0.1	0.7	—	—	—	1.8
*Mikania**	1.3	1.4	2.0	1.3	1.4	0.6	8.0
Weinmannia (Cunoniaceae)	1.0	1.3	1.6	0.4	0.4	0.4	5.1
Asplundia Cyclanthaceae)†	—	—	0.1	1.4	1.6	1.8	4.9
Sloanea (Elaeocarpaceae)	—	—	0.1	0.3	1.0	1.6	3.0
Ericaceae ind.†	1.0	1.4	2.3	1.0	1.0	1.2	7.9
Alchornea (Euphorbiaceae)	—	—	1.0	1.3	1.0	0.6	3.9
Hieronyma	—	0.3	1.1	1.9	1.0	0.4	4.7
Cyathea (Fern)	—	1.3	2.0	3.3	3.6	2.0	12.2
Casearia (Flacourtiaceae)	0.3	0.1	0.4	0.7	0.8	8.8	3.1
Clusia (Guttiferae)	0.7	1.6	1.0	2.6	1.6	2.6	10.1
Tovomita	—	0.1	0.3	1.1	0.8	0.8	3.1
Ocotea (Lauraceae)	0.7	2.6	2.8	2.0	1.2	2.4	11.7
Persea	0.7	0.3	2.1	0.7	0.8	0.2	4.8
Lauraceae ind.	0.3	3.0	3.0	4.7	7.2	2.2	20.4
Inga (Leguminosae)	—	—	0.6	3.1	3.4	7.8	14.9
Marcgravia (Marcgraviaceae)†	—	—	0.3	0.4	1.0	1.0	3.0
Clidemia (Melastomataceae)	—	—	—	—	1.8	0.2	1.0
Miconia	2.0	3.1	4.6	3.3	5.2	3.8	22.0
Topobaea†	—	0.1	0.1	0.9	1.2	1.2	3.5
Guarea (Meliaceae)	—	0.1	0.3	0.7	0.6	2.4	4.3
Mollinedia Monimiaceae)	—	—	0.7	0.4	0.8	0.4	2.3
Siparuna	0.3	0.4	0.6	0.4	0.6	1.2	3.5
Brosimum (Moraceae)	—	—	—	—	—	1.2	1.2
Cecropia	—	—	0.4	1.1	1.0	1.2	3.7
Ficus†	—	0.1	1.1	2.7	3.4	1.6	8.9
Pourouma	—	—	—	—	0.8	1.0	1.8
Myrsine (Myrsinaceae)	1.3	1.3	1.0	—	0.6	—	4.2
Eugenia (Myrtaceae)	—	0.3	0.1	1.3	0.8	0.4	2.9
Myrcia (Myricaceae)	—	0.1	0.7	0.7	1.6	0.6	3.7
Neea (Nyctaginaceae)	—	—	—	0.1	0.4	2.8	3.3
Heisteria (Olacaceae)	—	—	—	0.1	0.2	1.2	1.5
Chamaedorea (Palmae)	—	—	0.3	0.6	—	1.2	2.1
Geonoma	—	0.6	0.6	0.9	1.0	0.8	3.9
Piper (Piperaceae)	0.7	1.0	2.1	2.1	2.4	2.0	10.3
Elaeagia (Rubiaceae)	—	0.1	0.7	0.6	1.0	0.2	2.6
Faramea	—	0.1	0.4	1.9	1.0	0.6	4.0
Palicourea	0.7	0.9	1.7	1.1	1.2	0.6	5.2
Psychotria	0.3	0.3	1.3	3.0	2.2	1.0	8.4
Meliosma (Sabiaceae)	—	1.3	1.1	0.4	0.8	0.6	4.2
Paullinia (Sapindaceae)	—	0.1	—	0.9	1.4	2.6	5.0
Pouteria (Sapotaceae)	—	—	—	0.1	2.4	1.6	4.1

(*continued*)

TABLE V *(continued)*

Genus	Altitude range (m)‡						
	>3000	2500–3000	2000–2500	1700–2000	1500–1700	800–1500	≥800
Hydrangea (Saxifragaceae)†	—	0.1	0.4	1.0	0.6	0.4	2.5
Solanum (Solanaceae)	—	1.3	1.3	0.6	0.8	1.0	4.8
Symplocos (Symplocaceae)	0.3	1.1	0.4	—	0.2	0.2	2.2
Cissus (Vitaceae)*	—	0.6	0.6	0.3	0.6	1.0	3.1

*Lianas.
†Hemiepiphytes and stranglers.
‡— = Genus absent at elevational range.

samples between 1500 and 2000 m elevation, averaging 1.3 species per sample, and the latter occurs in 13 of the 19 samples and averages 1.1 species per sample. Palmae has 10 mostly lowland genera reaching mid-elevation samples, six of them above 2000 m. Two sampled palm genera (*Dictyocaryum*, *Ceroxylon*) are exclusively montane, the latter occurring in samples up to 2670 m and exceeded in elevation only by *Geonoma* (sampled up to 2850 m). Five hemiepiphytic Araceae genera (along with terrestrial *Xanthosoma*) are included in mid-elevation genera, but only three are of any significance. The most frequent is *Anthurium*, which was included in all but six of the 27 samples between 1500 and 3000 m; it is

TABLE VI

Most prevalent genera in Central American and Mexican montane forests, based on 0.1-ha samples, as average number of species per genus per samples in each elevational range

Genus	Altitude range (m)‡					
	>2500	2000–2500	>2000	1700–2000	1200–1600	>1200
Ilex (Aquifoliaceae)	1.0	1.5	2.5	0.6	0.4	3.5
Anthurium (Araceae)†	1.0	0.3	1.3	0.6	0.2	2.1
Dendropanax (Araliaceae)	1.0	1.5	2.5	1.4	1.0	4.9
Oreopanax	1.3	1.5	2.6	1.0	1,0	4.8
Schefflera†	1.0	0.8	1.8	0.6	—	2.4
Viburnum (Caprifoliaceae)	1.0	0.8	1.8	0.6	0.2	2.6
Clethra (Clethraceae)	1.0	0.8	1.8	0.2	0.4	2.4
Weinmannia (Cunoniaceae)	1.7	1.3	3.0	0.4	0.4	3.8
Cavendishia (Ericaceae)*	1.0	0.5	1.5	0.4	0.4	2.3
Ericaceae ind.*	1.0	—	1.0	0.2	—	1.2
Quercus (Fagaceae)	—	2.3	2.3	1.2	1.8	5.3
Cyathea (Fern)	1.0	1.0	2.0	1.6	0.8	4.4
Clusia (Guttiferae)†	—	0.8	0.8	1.4	1.4	3.6
Ocotea	0.7	1.0	1.7	1.4	1.6	4.7
Cinnamomum (Lauraceae)	—	0.8	0.8	1.0	1.2	3.0
Lauraceae ind.	—	0.8	0.8	1.6	1.4	3.8
Miconia (Melastomataceae)	2.7	4.0	6.7	2.8	1.2	10.7
Guarea (Meliaceae)	—	0.3	0.3	1.0	0.8	2.1
Ardisia (Myrsinaceae)	1.3	1.5	2.8	1.4	0.6	4.8
Myrsine	0.3	1.0	1.3	0.2	—	1.5
Geonoma (Palmae)	—	0.8	0.8	1.0	0.4	2.2
Piper (Piperaceae)	1.0	0.3	1.3	0.6	0.8	2.7
Psychotria (Rubiaceae)	—	1.0	1.0	0.2	1.8	3.0
Rondeletia	—	1.0	1.0	0.8	0.2	2.0
Escallonia (Saxifragaceae)	1.0	—	1.0	—	—	1.0
Solanum (Solanaceae)	1.0	—	1.0	0.6	0.2	1.8
Ticodendron (Ticodendraceae)	—	0.8	0.8	0.4	0.2	1.4
Drimys (Winteraceae)	1.0	0.5	1.5	0.2	—	1.7

*Lianas.
†Hemiphytes and stranglers.
‡— = Genus absent at given elevational range.

the third most species-rich genus (2.3 species per sample) between 2000 and 2500 m and occurs in samples up to 2850 m. *Philodendron* is included in 13 mid-elevation samples up to 2290 m but is much smaller than *Anthurium* in these samples. *Rhodospatha* occurs in five of six samples between 1500 and 1710 m, averaging 1 species per sample, but it was not sampled at higher altitudes.

Although much less diverse, upper montane forests between 2500 and 3000 m are not very different in floristic composition from mid-elevation forests. Lauraceae (mostly *Ocotea*, the second most species-rich genus at this elevation, with at least 2.6 species per sample) remains the dominant family, followed by Melastomataceae (mostly *Miconia* the largest genus, with 3.1 species per sample). Compositae, barely represented below 2000 m, becomes the third most species-rich family, represented by 10 genera, with scandent *Mikania* (1.4 species per sample) by far the most prevalent.

Solanaceae, Myrsinaceae, Aquifoliaceae, and Araliaceae show a similar pattern to Compositae, all becoming significant above 2000 m, and joining the three above-mentioned families with ferns, Rubiaceae, and Guttiferae as the 10 most species-rich high Andean families between 2500 and 3000 m. Five genera of Solanaceae are included in samples from upper montane forests below 3000 m, with *Solanum* (1.3 species per sample) and *Cestrum* (0.6 species per sample) being the most frequent. In the relatively dry cloud forests around Ayabaca, in Peru's Piura Department, Solanaceae are especially well represented and edge out Lauraceae as the most species-rich family. Four genera of Myrsinaceae are included in these samples, with *Myrsine*, rare below 2000 m, the most important, occurring in six of seven samples and averaging 1.3 species per sample. *Ilex*, the single regional genus of Aquifoliaceae, is far better represented in upper montane forests than elsewhere. It is second only to *Miconia* and *Ocotea*, being represented in all samples and averaging 2.3 species per sample. All three montane genera of Araliaceae occur in the 2500–3000 m samples, with *Oreopanax* (1.1 species per sample) and *Schefflera* (0.7 species per sample) constituting important components of high montane forests.

At the highest elevations, near timberline above 3000 m, Andean forests again change drastically in floristic composition. Compositae, represented by eight genera and averaging 7 species per sample in my three highest altitude samples, is the most species-rich family; liana genera (*Mikania*, *Jungia*, *Bidens*, *Liabum*) are especially well represented. Compositae species can also be dominant in the highest-altitude forests: for example, *Paragynoxys* with 69 trees ≥ 2.5 cm dbh at Sabana Rubia. Lauraceae and Melastomataceae are often the dominant trees in timberline forest but are represented by fewer species. The only Lauraceae included in the timberline forest samples are *Ocotea* and *Persea*, each averaging 0.7 species per sample. Melastomataceae genera sampled include *Axinaea*, *Bucquetia*, and *Tibouchina* as well as *Miconia*, the last mentioned being the most species-rich genus above 3000 m. Ericaceae (2.3 species per sample), mostly scandent, are more prevalent in sampled forest above 3000 m than at lower elevations and tie with Myrsinaceae as the third most species-rich family: Myrsinaceae, represented by *Myrsine* and *Geissanthus*, is proportionally more important in the highest-elevation forests than at other elevations. The other most important (1.0 species per sample) highest-elevation genera in these samples are *Oreopanax* and *Weinmannia*, followed by *Hedyosmum*, *Virburnum*, *Vallea*, *Clusia*, *Gaiadendron*, *Myrica*, *Piper*, *Hesperomeles*, and *Palicourea*, and scandent *Muehlenbeckia*, each averaging 0.7 species per sample.

Of these timberline elements, especially noteworthy are *Gaiadendron*, an arborescent Lorathaceae root parasite; Rosaceae, hardly represented at lower altitude, with *Prunus* and *Polylepis*, as well as *Hesperomeles* included in these samples; and the strong representation of such putatively Laurasian families as Chloranthaceae, Caprifoliaceae, and Myricaceae. *Polylepis*, a well-known Andean genus, is most noticeable for its near-absence from the sampled forests, being represented by a single individual in the El Pargo sample; *Polylepis* occurs mostly in nearly monospecific stands at altitudes higher than any sampled here.

To summarize Andean floristics, a progressively smaller suite of families and genera make up Andean forests at increasing altitudes. Up to 1500 m the familial composition is similar to lowland forests. From 1500 to 3000 m, Lauraceae is generally the most species-rich family, followed by Melastomataceae and Rubiaceae. Above 3000 m, Compositae dominates, followed by Melastomataceae, Ericaceae, and Mysinaceae.

Central American Montane Floristics

As noted above, Central American forests are significantly less diverse than their Andean equivalents. They also have significant floristic differences, although most of their constituent families are shared. The most species-rich families and genera of Central American montane forest samples are indicated in Tables VI and VII. Of the 28 most important (averaging ≥0.6 species per sample) Central American families (Table VII) all are represented in the Andean

TABLE VII

Floristic composition in Central American montane forests above 1200 m elevation, as number of species ≥2.5 cm diam. per family in 0.1-ha samples

	Site*																		
Family	BC1	BC2	BC3	SJ1	BC	B	BC4	BC5	M1	M2	SJ2	FM	MO	MT	EP	SJ3	G	TSSR†	AV‡
Melastomataceae	2	4	3	1	6	1	11	11	2	1	2	7	—	ca. 9	1	2	—	63	3.8
Lauraceae	—	1	1	6	4	—	2	2	2	4	11	4	—	ca. 8	5	9	2	61	3.6
Rubiaceae	—	—	1	2	5	3	5	—	—	1	4	8	—	12	3	5	3	52	3.1
Araliaceae	3	3	4	5	5	3	2	3	2	2	3	5	3	—	1	3	3	50	2.9
Compositae	—	—	4	3	4	1	1	3	2	1	2	2	2	5	3	1	—	34	2.0
Myrsinaceae	2	1	2	1	5	2	4	4	2	1	—	3	—	1	2	—	—	30	1.8
Ericaceae	3	2	3	—	4	—	3	1	—	—	—	5	1	2	—	2	—	26	1.5
Fagaceae	—	—	—	2	2	4	1	1	2	3	—	—	4	—	1	—	4	24	1.4
Ferns	1	1	1	1	1	—	1	1	—	—	3	2	—	3	2	3	2	24	1.4
Myrtaceae	—	—	—	1	1	—	1	1	—	—	3	2	—	ca. 8	2	3	2	24	1.4
Guttiferae	—	—	—	—	2	1	1	3	—	1	1	3	—	3	2	3	—	20	1.2
Meliaceae	—	—	—	—	1	1	2	2	1	2	—	3	—	5	2	—	1	20	1.2
Palmae	—	—	—	—	1	—	3	3	—	—	—	5	—	4	3	—	1	19	1.1
Celastraceae	—	—	—	2	2	—	1	—	3	1	2	—	—	4	2	—	2	19	1.2
Solanaceae	1	3	3	1	—	—	—	—	2	1	1	—	—	4	2	—	—	18	1.1
Leguminosae	—	—	—	—	—	—	—	—	—	2	1	1	5	4	3	—	2	18	1.1
Euphorbiaceae	—	—	—	1	2	—	4	2	1	1	1	4	—	—	1	1	—	18	1.1
Cunoniaceae	2	2	1	1	2	—	2	1	—	—	1	—	—	1	—	1	—	14	0.8
Aquifoliaceae	1	1	1	4	1	—	1	—	—	—	2	1	—	—	—	1	1	14	0.8
Araceae	1	1	1	—	1	—	1	2	—	—	2	3	—	1	—	1	—	14	0.8
Piperaceae	1	1	1	—	—	—	1	1	1	—	—	1	—	2–3	1	—	2	12	0.7
Moraceae	—	—	—	—	—	—	—	—	—	1	2	1	—	3	—	1	—	12	0.7
Symplocaceae	—	—	2	—	2	1	2	—	—	1	1	1	—	2	—	1	—	11	0.6
Vitaceae	—	—	—	1	1	—	1	1	1	—	—	2	—	1	—	1	2	11	0.6
Rosaceae	—	—	1	1	1	—	—	—	—	1	2	1	—	2	—	1	—	10	0.6
Caprifoliaceae	1	1	1	—	1	1	1	1	1	1	—	—	—	—	—	1	—	10	0.6
Sabiaceae	—	—	—	1	—	—	1	—	1	1	1	1	—	2	1	—	1	10	0.6
Saxifragaceae	1	1	1	1	—	1	—	2	—	—	—	1	—	1	1	—	—	10	0.6

Note: — = Family absent from site.

* BC1, Braulio Carrillo (2775 m); BC2, Braulio Carrillo (2750 m); BC3, Braulio Carrillo (2750 m); SJ1, Sierra Juarez (2250 m); BC, Braulio Carrillo (2225 m); B, Benito (2100 m); BC 4, Braulio Carrillo (2000 m); BC5, Braulio Carrillo (1990 m); M1, Manantlan, Las Joyas (1950 m); M2, Manantlan, Quince Ocotes (1800 m); SJ2, Sierra Juarez (1750 m); FM, Finca Motillones (1730 m); MO, Monteverde (1850 m); MT, Motozintla (1600 m); EP, El Picacho (1400 m); SJ3, Sierra Juarez (1255 m); G, Guadaloupe (1200 m).

†Total species-site records.

‡Average number of species per site (17 sites).

samples. Similarly of the most prevalent Central American genera (with ≥1.0 species per sample for sites in at least one elevational range) (Table VI) all but *Rondeletia* are also represented in the Andean samples. Furthermore, the most species-rich families in the two regions are generally the same. Lauraceae and Melastomataceae are the most species-rich families in both data sets, although their order is reversed. Rubiaceae is third in both data sets. Araliaceae, Compositae, Mysinaceae, and Ericaceae—the next most prevalent Central American families—are all prominent on the equivalent Andean list. Similarly, *Miconia* is the largest genus in both regions, and genera such as *Ilex*, *Anthurium*, *Oreopanax*, *Weinmannia*, *Cyathea*, *Ocotea*, *Geonoma*, *Piper*, *Psychotria*, and *Solanum* feature prominently on both lists of genera. None of the important Andean genera of Table V are absent from Central American montane forests. We might conclude from such data that the Andean and Central American montane forests are very similar floristically.

Moreover, the more diverse Andean forests include no significant family not also represented in the montane Central American samples. Although 33 families occur in the Andean samples but not in the Central American or Mexican ones (as in Table VIII), all are minor (average ≥0.5 species per plot) and most are very minor (1–4 records in entire sample), chiefly representing taxa in peripheral areas (either lowland taxa rarely getting above 800 m, or herbaceous taxa rarely large enough to enter the sample, or weedy taxa rarely entering closed-canopy forests). Twenty-four of the 33 families are very minor—as judged by only 1–4 records in the entire data set (Table VIII), and Begoniaceae has only five records and Voshysiaceae six. Of the eight families with six or more Andean records that are not recorded in Central American montane forest samples, six are tropical lowland families that rarely exceed 800 m in elevation—Chrysobalanaceae, Lecythidaceae, Myristicaceae, Olacaceae, Violaceae, and Vochysiaceae.

The final three families with some significance in the Andean samples but not represented in the montane Central American samples are Passifloraceae, whose Central American montane representatives are more uniformly herbaceous; Polygalaceae, which has the significant shrubby montane genus *Monnina* poorly represented in Central America; and, paradoxically, the Laurasian family Ulmaceae (with only six Andean records), clearly a collection artifact.

In contrast, several important Central American families are not represented in the Andean samples (Table VIII). Two of those families sampled only in montane Central America are dry-area lowland taxa that entered the driest Mexican sample (Agavaceae, Cactaceae). Two others, Ebenaceae and Ochnaceae, are lowland families, the presence of which only in Central American samples represents random noise; each has a single species at a single site. However, the other five families represented in Central American but not Andean sites are Laurasian families clearly more prevalent in Central America. They are Hammamelidaceae, Oleaceae, Pinaceae, Ticodendraceae, and Umbelliferae. Each has several sampled species or genera or is represented in several different samples.

Fagaceae, the eighth most species-rich family in the Central American data, is especially instructive. *Quercus*, averaging 5.3 species per sample, is the second largest Central American genus. Although *Quercus* reaches the Andes, where it is recorded as present, even dominant, in several Colombian forests, it does not reach the border of Ecuador and is represented by a single species. Clearly, Fagaceae is a much more important floristic element in montane Central America than it is in the Andes, despite its absence from the families listed in Table VIII.

Celastraceae is a similar case. Although represented by four genera in the Andean samples, it is rarely encountered, averaging only 0.5 species per sample. *Zinowiewia* was sampled only in Colombia, and *Perrottetia* mostly in Colombia. Only *Maytenus* and *Celastrus* are fairly widespread in the Andes. In contrast, Celastraceae is represented by seven genera and an average of 1.1 species per sample in Central America. Three of the Central America genera (*Euonymus*, *Quetzalia*, *Wimmeria*) are absent from the Andes. Celastraceae has an obviously Laurasian distribution.

At the generic level as well, there are some striking differences in representation in montane Central America and the Andes. Of the top 25 Central American genera, *Rondeletia* is entirely absent from the Andean samples, and *Ardisia* (0.2 vs. 4.6 species per sample) and *Clethra* (0.2 vs. 2.4) are much more poorly represented. *Ticodendron*, along with its whole family, Ticodendraceae, is unknown from South America but is one of the commonest species between 1500 and 2000 m in some samples from Mexico and Costa Rica.

Thus, even on the basis of these data alone, the Laurasian phytogeographic affinities of many Central American montane taxa are apparent. The floristic distinctness of Central America is accentuated if Mexico and nuclear Central America are considered separately from southern Central America. Even within Central America, the floristic difference between Mexico or nuclear Central American sites dominated by Laurasian taxa and southern Central American ones, with a floristic composition more like that of the Andes, is apparent (Table IX). Of the 96 families represented in the Central American samples, 21 are found only in Mexico and 25 only in Costa Rica. However, the Costa Rican families and genera not included in the Mexican samples are all widespread in both South and Central America, except *Myrrhiodendron*, a highly atypical woody umbellifer. In contrast, the Mexican samples include many Laurasian families and genera that do not reach farther south than the margins of nuclear Central America in Nicaragua (Table X). Laurasian families not sampled in Costa Rica include Betulaceae (*Alnus*, *Carpinus*, *Ostrya*), Hammamelidaceae (*Matudaea*, *Liquidambar*), Myricaceae (*Myrica*), Oleaceae (*Fraxinus*, *Ligustrum*), Pinaceae (*Pinus*), Ranunculaceae (*Clematis*), and Styracaceae (*Styrax*). Representatives of several of these Laurasian families are dominant in various nuclear Central American and Mexican sites, including *Oreomunnea* at 1750 m in the Sierra Juarez, *Quetzalia* at 2250 m in the Sierra Juarez, *Myrica* at Benito, *Matudea* at Manantlan/Quince Ocotes, *Carpinus* and *Liquidambar* at Guadeloupe, *Zinowiewia* at Manantlan/Las Joyas, *Quercus* and *Pinus* at Motozintla, and *Alfaroa* at El Picacho. Although a few of these Laurasian elements do have a minor representation in the Andes, especially in the northern Andes, genera such as *Carpinus*, *Ostrya*, *Liquidambar*, *Fraxinus*, and *Pinus* are shared with the deciduous forests of eastern North America but are entirely lacking in South America.

At higher elevations than any sampled here, this

TABLE VIII

Familial differences between montane forests of the Andes and Central America (including Mexico), based on 0.1-ha samples and including species ≥2.5 cm diam.

In Andes but not Central America

Family	No. of species
Basellaceae	2
Begoniaceae	5
Berberidaceae	2
Blromeliaceae	2
Buxaceae	4
Capparidaceae	1
Caricaceae	2
Caryocaraceae	1
Chrysobalanaceae	12
Coriariaceae	1
Cornaceae	1
Dilleniaceae	4
Erythroxylaceae	1
Gentianaceae	3
Humiriaceae	1
Lacistemataceae	3
Lecythidaceae	14
Linaceae	2
Myristicaceae	18
Olacaceae	8
Opiliaceae	1
Orchidaceae	1
Papaveraceae	2
Passifloraceae	8
Polygalaceae	17
Quiinaceae	3
Santalaceae	2
Sterculiaceae	4
Ulmaceae	6
Valerianaceae	4
Violaceae	12
Vochysiaceae	5
Zingiberaceae	4

In Central America but not Andes

Family	No. of species*
Agavaceae	1
Cactaceae	—
Ebenaceae	1
Hamamelidaceae	—
Ochnaceae	1
Oleaceae	—
Pinaceae	—
Ticodendraceae	—
Umbelliferae	—

*— = Data not added by author.

difference is even more pronounced, with high-elevation Mexican forests generally dominated by a few species of gymnosperms, especially species of *Pinus* and *Abies* (Rzedowski, 1981). The diversity of higher-elevation Mexican montane forests is apparently intermediate between eastern North America forests and tropical cloud forests.

Conclusion

Montane Neotropical forests, like lowland forests, are put together in decidedly nonrandom ways. Diversity decreases linearly with elevation from above 1500 m to near treeline. Mexican montane forests are less diverse than southern Central American ones, which are in turn less diverse than Andean forests. Subtropical Andean forests in Argentina are also relatively depauperate (Brown et al., 1985). The isolated Sierra Nevada de Santa Marta has relatively low diversity, but this situation may be due to anthropogenic influence rather than isolation.

Montane forest floristic composition changes in predictable ways with increasing altitude. In the Andes, premontane forests between 800 and 1500 m have a floristic composition similar to lowland tropical forests, with Leguminosae and Moraceae as the dominant tree families and Bignoniaceae and Sapindaceae as the dominant lianas. In mid-elevation forests between 1500 and 2500 m, Lauraceae is the dominant family, followed by Melastomataceae, Rubiaceae, and Moraceae. Upper montane forests between 2500 and 3000 m are similar in floristic composition to mid-elevation forests, with Lauraceae

TABLE IX

Familial and generic differences between montane forests of Mexico and Central America, based on 0.1-ha samples and including species ≥2.5 cm diam.

In Mexico but not Costa Rica		In Costa Rica but not Mexico	
Family	Genus	Family	Genus
Agavaceae	*Agave*	Acanthaceae	*Justicia*
Anacardiaceae	*Toxicodendron*	Annonaceae	*Guatteria*
Asclepiadaceae	*Marsdenia*	Apocynaceae	*Tabernaemontana*
Betulaceae	*Alnus, Carpinus, Ostrya*	Bignoniaceae	*Amphitecna*
Burseraceae	*Bursera*	Bombacaceae	*Quararibea*
Cactaceae	*Opuntia*	Boraginaceae	*Cordia, Tournefortia*
Connaraceae	(ind.)	Brunelliaceae	*Brunellia*
Convolvulaceae	*Ipomoea*	Combretaceae	*Combretum*
Hamamelidaceae	*Liquidambar, Matudaea*	Dichapetalaceae	*Dichapetalum*
Hippocrateaceae	*Salacia*	Ebenaceae	*Diospyros*
Loganiaceae	*Buddleja*	Gesneriaceae	*Besleria, Drymonia*
Menispermaceae	*Abuta*	Gramineae	*Chusquea*
Myricaceae	*Myrica*	Icacinaceae	*Calatola*
Ochnaceae	*Ouratea*	Loranthaceae	*Gaiadendron*
Oleaceae	*Fraxinus, Ligustrum*	Malvaceae	*Hampea, Malvaviscus*
Onagraceae	*Fuchsia*	Marcgraviaceae	*Marcgravia*
Pinaceae	*Pinus*	Musaceae	*Heliconia*
Podocarpaceae	*Podocarpus*	Nyctaginaceae	*Neea*
Ranunculaceae	*Clematis*	Palmae	*Prestoea, Chamaedorea, Geonoma*
Styracaceae	*Styrax*	Polygonaceae	*Muehlenbeckia*
Thymelaeaceae	*Daphnopsis*	Proteaceae	*Panopsis*
		Sapotaceae	*Pouteria*
		Umbelliferae	*Myrrhidendron*
		Urticaceae	*Urera*
		Winteraceae	*Drimys*

and Melastomataceae the most species-rich families, but Compositae becomes the third most important family, and Solanaceae, Myrsinaceae, Aquifoliaceae, and Araliaceae are more diverse. Near the treeline above 3000 m the floristic composition is very distinct, with Compositae and Melastomataceae the most diverse families, followed by Ericaceae and Myrsinaceae.

Southern Central American montane forests are generally dominated by the same taxa as Andean forests, but with an admixture of Laurasian elements such as Fagaceae and Ticodendraceae. Nuclear Central American mid-elevation forests from Mexico to northern Nicaragua are floristically very different, being dominated by Laurasian families and genera, many of which do not reach farther south.

While montane Neotropical forests at similar elevation are floristically similar at the level of genus and family, at least from Costa Rica to Bolivia, the species composition of different montane forests is very different. Montane floras have generally higher levels of endemism than lowland tropical floras. Their greater endemism combined with their ongoing devastation by humans, makes the preservation of the small tracts that remain one of the world's highest conservation priorities.

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TABLE X

Families with greatest species-richness differences between montane forests of Mexico and Central America

More prevalent in Mexican samples				More prevalent in Costa Rican samples				More prevalent in Nicaraguan sample	
Family	MAV	CRAV	D	Family	CRAV	MAV	D	Family	No. of species
Lauraceae	4.3	2.8	1.5	Melastomataceae	6.4	1.3	5.1	Leguminosae	3
Fagaceae	2.4	0.5	1.9	Ericaceae	3.0	0.1	2.9	Bignoniaceae	2
Theaceae	1.4	0.1	1.3	Palmae	2.0	0	2.0	Juglandaceae	2
Betulaceae	0.8	0.0	0.8	Myrsinaceae	2.8	0.9	1.9	Acanthaceae	2
Leguminosae	1.3	0.6	0.7	Compositae	2.8	1.1	1.6	Sapotaceae	2
				Rubiaceae	3.9	2.3	1.6	Urticaceae	2
				Fern	2.1	0.8	1.3	Verbenaceae	2
				Meliaceae	1.6	0.6	1.0		
				Araliaceae	3.5	2.6	0.9		
				Araceae	1.4	0.5	0.9		
				Cunoniaceae	1.3	0.4	0.9		
				Euphorbiaceae	1.5	0.6	0.9		
				Solanaceae	1.4	0.6	0.8		
				Winteraceae	0.8	0.0	0.8		
				Myrtaceae	2.0	1.3	0.7		
				Guttiferae	1.5	0.8	0.7		

Note: MAV = Mexican average; CRAV = Costa Rican average; D = Differences.

tance of W. Stevens and A. Grijalva; and Mexican data with E. Jardel (Manantlan) and Linares-Williams (Veracruz). Jim Miller kindly provided the Chiapas data, and Brad Boyle the Oaxaca data and most of the Costa Rican data. I especially thank Rosa Ortiz for her help with processing the data on which this analysis is based and Rick Clinebell for his assistance with statistical analysis.

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