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Geographical Gradients
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CHANGES IN PLANT COMMUNITY DIVERSITY AND FLORISTIC COMPOSITION ON ENVIRONMENTAL AND GEOGRAPHICAL GRADIENTS[1,2]

Alwyn H. Gentry[3]

ABSTRACT

Trends in community composition and diversity of neotropical forests as measured by a series of samples of (1) plants ≥ 2.5 cm dbh in 0.1 ha, (2) plants over 10 cm dbh in 1-ha plots, and (3) complete local florulas are analyzed as a function of various environmental parameters. These trends are also compared with those found in similar data sets from other continents. Altogether the basic 0.1-ha data sets are reported for 87 sites in 25 countries on six continents and several islands. New data from ten 1-ha tree plots in upper Amazonia are also compared with each other and with similar data from the literature. Some noteworthy trends include: (1) Lowland neotropical plant species richness is generally far more tightly correlated with precipitation than with edaphic factors. (2) The nearly linear increase of lowland neotropical plant species richness with precipitation reaches an asymptote (community saturation?) at about 4,000 mm of annual rainfall. (3) Although the species represented in adjacent forest types on different substrates may change dramatically, diversity tends to change relatively little in upper Amazonia. (4) The species present at different sites are very different but the families represented and their diversities are highly predictable from environmental parameters. (5) On an altitudinal gradient in the tropical Andes there is a sharp, essentially linear decrease in diversity from 1,500 m to near the upper limit of forest above 3,000 m. (6) There is no indication of a "mid-elevation bulge" in diversity, at least not in the sampled habit groups. (7) Even near timberline, montane tropical forests are as diverse as the most diverse temperate forests. (8) Moist subtropical forests are markedly less diverse than their inner-tropical equivalents, but dry subtropical forests in Mexico are apparently richer in species than inner-tropical dry forests. (9) Central African forests are about as species rich as neotropical forests with similar amounts of precipitation, but forests in tropical West Africa are relatively depauperate. (10) Tropical Australasian forests are no more diverse than equivalent neotropical forests; the world's highest tree species diversity is in upper Amazonia, not Southeast Asia. (11) Contrary to accepted opinion, equivalent forests on the three continents are similar in plant species richness and (with a very few notable exceptions) floristic composition but are markedly different in structure. The predictability of the floristic compositions and diversities of tropical forest plant communities seems strong, albeit circumstantial, evidence that these communities are at ecological and perhaps evolutionary equilibrium, despite indications that certain aspects of their diversity are generated and maintained stochastically.

Comparisons of the species richness (or other facets) of different forests or different vegetation types are often difficult because of the dissimilarity of the available data. In tropical Asia there is a wealth of data for trees in large sample areas (Ashton, 1964, in press; Whitmore, 1984; Proctor et al., 1983; Kartawinata et al., 1981) but few published data on nontrees. In the Neotropics there are several local florulas (Croat, 1978; Dodson & Gentry, 1978; Janzen & Liesner, 1980; Dodson et al., 1985), but until recently there have been no tree-plot data from high diversity regions based on reliable identifications. Africa has far more extensive coverage by regional and country-wide floras but no local florulas nor large-plot data from high-diversity regions.

Recently, a series of 0.1-ha samples of many of the world's most diverse extra-tropical plant communities has been accumulating (e.g., Naveh & Whittaker, 1979; Cowling, 1983; Peet & Christensen, 1980; Rice & Westoby, 1983; Eiten, 1978). Elsewhere we

have reported the first comparable data set for tropical forests (Gentry & Dodson, 1987a, b). A standardized sampling technique that includes only plants ≥ 2.5 cm in diameter in 0.1 ha has also been developed and applied to a series of tropical forests (Gentry, 1982b, 1986b; Lott et al., 1987; Stallings et al., in press; Lorence & Sussman, 1988); the methodology for obtaining these 0.1-ha samples, each the sum of ten 2 × 50 m belt transects, is discussed in detail elsewhere (Gentry, 1982b, in prep.). The primary data set on which this paper is based are these 0.1-ha samples, which are now available for 38 lowland neotropical sites, 11 montane neotropical sites, and 13 subtropical and 9 temperate-zone sites in the Americas. Similar data sets are available from 6 sites in tropical Africa, 3 sites in tropical Australasia, 2 sites in Europe, and from several tropical islands: New Caledonia, Madagascar, Mauritius, Jamaica (Tables 1, 2; Fig. 1). Supplementary data are taken from local florulas in the Neotropics (Dodson & Gentry, 1978, 1988; Croat, 1978;

FIGURE 1.   *Locations of study sites. Dots = 0.1-ha samples (see Tables 1, 2). Arrows = local florulas. For location of 1-ha tree plots see Gentry, 1988.*

Janzen & Liesner, 1980; Dodson et al., 1985; Hammel, pers. comm. (La Selva, Costa Rica)) and from the Makokou region of northwestern Gabon (Halle, 1964, 1965; Halle & Le Thomas, 1967, 1970; Florence & Hladik, 1980; Hladik & Halle, 1973; Hladik & Gentry, in prep.). A supplemental data set is provided by a series of 1-ha tree plots in various parts of the Neotropics (Gentry, 1988; Prance et al., 1976; Campbell et al., 1986; see also Gentry, 1982b) and Paleotropics (e.g., Ashton, 1964, 1977, in press; Gartlan et al., 1986).

Here I first review how the species richness of plant communities changes on five different environmental gradients: latitudinal, precipitational, edaphic, altitudinal, and intercontinental. Observations on a few noteworthy trends in forest structure are also included. Second, I analyze some patterns of floristic change along the same environmental gradients. Finally, I use these analyses to examine briefly the question of why some plant communities have so many more species than others.

In all of these analyses I will use number of species as the simplest and most appropriate measure of diversity, as suggested by Whittaker (1977). Shannon-Wiener H' values are reported in Tables 1 and 2, but are

so tightly correlated ($R^2 = 0.93$) with the absolute number of species that their use would add little to the analysis. Moreover, the wet-forest H' values of 7 to 8 are far above the levels at which H' has been statistically analyzed (cf. May, 1975).

TEMPERATE-TROPICAL PATTERNS

Figure 2 summarizes the latitudinal trends in species richness, based on the 74 lowland (= < 1,000 m) 0.1-ha sites for which comparable samples are available. It is well known that tropical forests are generally far richer than temperate forests in species (e.g., see Richards, 1952; MacArthur, 1972). Figure 2 indicates that for vascular plants species-rich tropical forests are typically an order of magnitude more diverse. Also apparent in Figure 2 are several much less well-known corollaries to the general latitudinal diversity gradient. 1) The difference in species richness between different tropical forests is far greater than the difference between temperate zone and species-poor tropical forests. Whereas the temperate forest samples have 15–25 species and tropical dry forest ones mostly 50–60 species, the samples of moist and wet tropical forests average about 150 species and pluvial forests over 250 species (Gentry,

TABLE 1. *Site characteristics for 0.1-ha samples.*

Site	Grid Coordinates	Altitude (m)	Precipitation (mm)	Number of Families	Number of Species	H′	Reference
Temperate North America							
Burling Tract, Virginia	38°55′N 77°10′W	30	1,053	12	21	3.54	Givnish et al., unpubl.
Northwest Branch, Maryland	39°02′N 77°02′W	20	1,060	14	20	3.22	—
Tyson Reserve, Missouri (oak woods)	38°30′N 90°31′W	150	932	12	23	3.26	Zimmerman & Wagner, 1979
Tyson Reserve, Missouri (chert glade)	38°30′N 90°31′W	150	932	11	25	3.68	Zimmerman & Wagner, 1979
Babler State Park, Missouri	38°32′N 90°40′W	150	930	13	21	3.61	—
Cuivre River State Park, Missouri	39°01′N 91°00′W	140	930	15	26	3.46	—
Valley View Glades, Missouri	38°15′N 90°37′W	225	930	14	22	3.68	—
Indian Cave State Park, Nebraska	40°30′N 95°43′W	320	900	12	23	3.74	Tate, 1969
Great Smoky Mountains National Park, Tennessee/ N.C.					21–30 (upper 5%)		White, 1983
Europe							
Süderhackstedt, West Germany	54°N 11°E	20	695	10	15	2.19	Walter & Lieth, 1960
Allacher Lohe, West Germany	48°04′N 11°30′E	530	866	11	20	3.41	Walter & Lieth, 1960
Temperate and Subtropical South America							
Rio Jejui-mi, Paraguay	24°42′S 55°30′W	150	1,800	31	85	5.40	S. Keel & V. Vera, pers. comm.
Parque El Rey, Argentina	24°45′S 64°40′W	1,000	1,500	27	40	4.18	Brown et al., 1985
Salta, Argentina	24°40′S 65°30′W	1,300	712	16	25	3.41	Walter & Lieth, 1960
Arroyo Riachuelo, Corrientes, Argentina	27°30′S 58°50′W	60	1,200	27	47	4.46	Walter & Lieth, 1960
Alto de Mirador, Chile	40°14′S 73°18′W	800	4,000	13	16	3.45	Ramírez & Riveros, 1975
Bosque de San Martín, Chile	39°30′S 73°10′W	30	2,316	14	18	3.25	Riveros & Ramírez, 1978
Puyehue National Park, Chile	40°43′S 72°18′W	500	3,000	13	16	2.41	Muñoz, 1980
"Subtropical" Central America							
Chamela, Mexico	19°30′N 105°03′W	50	733	37	92	5.76	Lott et al., 1987

TABLE 1. *Continued.*

Site	Grid Coordinates	Altitude (m)	Precipitation (mm)	Number of Families	Number of Species	H'	Reference
Chamela, Mexico	19°30'N 105°03'W	50	733	34	83	5.42	Lott et al., 1987
Chamela, Mexico	19°30'N 105°03'W	50	733	46	105	5.9	Lott et al., 1987
Los Tuxtlas, Mexico	18°35'N 95°08'W	200	4,953	40	108–109	4.52	Lot-Helgueras, 1976
Cerro Olumo, Nicaragua	12°18'N 85°24'W	750	2,000	36	97–98	5.8	—
Cerro El Picacho, Nicaragua	13°00'N 85°55'W	1,400	2,000	39	65	5.22	—
Lowland Neotropics (12°N to 12°S, ≤ 1,000 m)							
Corcovado, Costa Rica	8°30'N 83°35'W	30	3,800	46	132	6.56	Hartshorn, 1983
Guanacaste (upland) Costa Rica (700 m²)	10°30'N ≈ 85°10'W	100	1,600	21+	53[a]		Hartshorn, 1983
Guanacaste (gallery), Costa Rica (800 m²)	10°30'N ≈ 85°10'W	50	1,600	33+	68[a]		Hartshorn, 1983
Curundu, Panama	8°59'N 79°33'W	20	1,830	42	90	5.78	Gentry, 1982b
Madden Forest, Panama	9°66'N 79°36'W	50	2,433	45	126	6.34	Gentry, 1982b
Pipeline Road, Panama	9°10'N 79°45'W	300	3,000	58	167	6.77	Gentry & Emmons, 1987
Galerazamba, Colombia	10°48'N 75°15'W	10	500	21	55	5.05	—
Tayrona, Colombia	11°20'N 74°02'W	50	1,500	31	65	5.36	—
Bosque de la Cueva, Colombia	11°05'N 73°28'W	360	2,000	36	93	5.5	—
Tutunendo, Colombia	5°46'N 76°35'W	90	9,000	53	258	7.57	Gentry, 1986b
Bajo Calima, Colombia	3°55'N 77°02'W	100	7,470	58	265	7.74	Gentry, 1986b
Boca de Uchire, Venezuela	10°09'N 65°25'W	150	1,200	20	66	5.16	Gentry, 1982b
Blohm Ranch, Venezuela	8°34'N 67°35'W	100	1,400	31	68	5.38	Troth, 1979
Estación Biológico de los Llanos, Venezuela (500 m²)	8°56'N 67°25'W	100	1,312	21+	59[a]		Gentry, 1982b
Cerro Neblina, Venezuela (No. 1)	0°50'N 66°11'W	140	3,000	31	97	5.33	
Cerro Neblina, Venezuela (No. 2)	0°50'N 66°11'W	140	3,000	26	83	4.95	
Río Palenque, Ecuador (No. 1)	0°34'S 79°20'W	200	2,980	50	119	6.15	Dodson & Gentry, 1978

TABLE 1. *Continued.*

Site	Grid Coordinates	Altitude (m)	Precipitation (mm)	Number of Families	Number of Species	H'	Reference
Río Palenque, Ecuador (No. 2)	0°34'S 79°20'W	200	2,980	43	121	6.18	Dodson & Gentry, 1978
Centinela, Ecuador	0°34'S 79°18'W	550	3,000	55	140	4.78	Gentry, 1986b
Jauneche, Ecuador	1°16'S 79°42'W	60	1,855	38	96	5.39	Dodson et al., 1985
Capeira, Ecuador	2°00'S 79°58'W	50	804	26	60	5.41	Dodson & Gentry, 1988
INPA, Manaus, Brazil	3°S 60°W	75	1,995	34	101		Gentry, 1978
Mocambo, Belem, Brazil	1°30'S 47°59'W	30	2,760	39	131	6.42	Pires & Prance, 1977
Linhares, Espirito Santo, Brazil	19°18'S 40°04'W	50	1,403	53+	ca. 212	7.4	Peixoto & Gentry, in prep.
Jacarepagua, Rio de Janeiro, Brazil	23°05'S 43°25'W	200	1,500	45+	ca. 160		
Tarapoto, Peru	6°40'S 76°20'W	500	1,400	38	97	5.96	—
Sucursari, Peru	3°15'S 72°55'W	140	3,500	46+	ca. 240ª	7.46	—
Yanamono, Peru (upland) (No. 1)	3°28'S 72°50'W	140	3,500	50	212	7.49	Gentry & Emmons, 1987
Yanamono, Peru (upland) (No. 2)	3°28'S 72°50'W	140	3,500	50	225	7.59	Gentry & Emmons, 1987
Yanamono, Peru (tahuampa)	3°28'S 72°50'W	130	3,500	51	163	6.67	
Mishana, Peru (floodplain)	3°47'S 73°30'W	130	3,500	58	249	7.63	Gentry & Emmons, 1987
Mishana, Peru (tahuampa)	3°47'S 73°30'W	130	3,500	40	168	6.44	
Mishana, Peru (upland white sand)	3°47'S 73°30'W	140	3,500	46	196	7.21	Gentry & Emmons, 1987
Bosque von Humboldt, Peru	8°50'S 75°00'W	270	2,500	44	154	6.37	
Cabeza de Mono, Peru	10°20'S 75°18'W	320	3,500(+)	42	147	6.82	Gentry, 1988
Cocha Cashu, Peru	11°51'S 71°19'W	400	2,000	49	162	6.78	Gentry & Terborgh, in press
Tambopata, Peru (lateritic terra firme)	12°50'S 69°17'W	260	2,000	48	149	6.7	Erwin, 1985
Tambopata, Peru (sandy terra firme)	12°50'S 69°17'W	260	2,000	43	130	6.44	Erwin, 1985
Africa							
Makokou, Gabon (No. 1)	0°34'N 12°52'E	500	1,755	39	135	6.44	Hladik, 1978
Makokou, Gabon (No. 2)	0°34'N 12°52'E	500	1,755	32	116	6.25	Hladik, 1978

TABLE 1. *Continued.*

Site	Grid Coordinates	Altitude (m)	Precipitation (mm)	Number of Families	Number of Species	H'	Reference
Omo Forest, Nigeria	7°N 5°E	50	1,800	29	73	4.42	Richards, 1939
Oban Forest, Nigeria (200 m²)	5°10'N 8°28'E	50	4,000	?	(53++)		
Mt. Cameroon, Cameroon	4°N 9°E	230	8,000	37	129	6.31	Richards, 1963
Korup National Park, Cameroon	5°N 8°31'E	50	5,460	43	139	6.34	Gartlan et al., 1986
Belinga, Gabon (500 m²)	1°N 14°E	750	1,800	26(+)	115		Aubreville, 1967
Perinet, Madagascar	18°55'S 48°25'E	950	1,200	52+	ca. 199		
Australia							
Davies River State Park, Queensland	17°05'S 145°34'E	800	2,300	41	115	6.29	Connell et al., 1984
Asia							
Semengoh Forest, Sarawak	1°50'N 110°05'E	20	4,000	47	243	7.39	Walter & Lieth, 1960
Bako National Park, Sarawak	1°52'N 110°06'E	30	4,000	39	143	6.5	Ashton, in press
Tropical Islands							
Rivière des Pirogues, New Caledonia	22°10'S 166°50'E	360	2,200	47	151	6.31	
Round Hill, Jamaica	17°50'N 77°15'W	40	1,200	31	58	3.96 (4.47)	Kapos, 1982
Brise Fer, Mauritius	20°30'S 57°30'E	600	2,400	26	61		Lorence & Sussman, 1988

[a] Extrapolated from number of species in sample of < 1,000 m².

1986b). 2) The latitudinal decrease in species richness seems to be asymmetrical about the equator; in the Southern Hemisphere it begins near the Tropic of Capricorn, but in the north it begins well inside the Tropic of Cancer, apparently near 12°N latitude. 3) Temperate zone forests are very similar in species richness of woody plants, compared with the massive differences in species richness between temperate and tropical forests or between different tropical forests. Temperate zone forests are so massively depauperate that even if boreal forests with two or three species ≥ 2.5 cm dbh in 0.1 ha were included in Figure 2, they would not significantly change it, even though the reported values are for some of the reputedly richest temperate zone forests.

4) Species-poor tropical forests with single-species dominance are generally still much more diverse than any temperate-zone forest. 5) South temperate forests, at least in Chile, where data sets are available, have fewer species than temperate forests in North America, contrary to the popular perception of the "rich" Valdivian forest; a major reason for this difference is that Valdivian forests do not have sympatric congeners like the up to seven *Quercus* and four *Carya* species typical of 0.1-ha samples of eastern North American forests. 6) Subtropical dry forests can have more species than do full-tropical dry forests, even though wet or moist forests usually have fewer species in the subtropics than in the inner tropics.

TABLE 2. *Site characteristics for 0.1-ha samples from upland Neotropics (≥ 1,000 m, 12°N to 12°S).
Parentheses indicate sites too incompletely sampled for a meaningful estimate of number of species in 0.1 ha.*

Site	Grid Coordinates	Median Altitude (m)	Number of Families	Number of Species	H'
(Monteverde, Costa Rica (200 m²))	10°48'N 84°50'W	1,550	(33+)	(61+)	
Cerro Kennedy, Colombia (500 m²)	11°05'N 74°01'W	2,600	26	50[a]	4.92
(Cuchillo de San Antonio, Colombia (200 m²))	10°58'N 73°30'W	1,710	(15+)	(24+)	
Finca Zungara, Colombia (600 m²)	3°32'N 76°35'W	1,990	37+	100[a]	
Farallones de Cali, Colombia	3°30'N 76°35'W	1,950	55	134–135	6.48
Finca Mehrenberg, Colombia	2°16'N 76°12'W	2,290	40	107	4.46
La Planada, Colombia	1°10'N 77°58'W	1,800	38	116	5.14
Pasochoa, Ecuador (400 m²)	0°28'S 78°25'W	3,010	21	28[a]	3.03
Venceremos, Peru	5°45'S 77°40'W	1,850	46	159	6.65
Incahuara, Bolivia	15°55'S 67°35'W	1,540	45	130	6.71
Sacramento, Bolivia	16°18'S 67°48'W	2,450	32	93	4.89

[a] Extrapolated from number of species in sample of < 1,000 m².

There are also latitudinal differences in forest structure. In general, tropical forests, far from being open and cathedral-like, are denser than temperate forests. This difference is almost entirely due to small-diameter plants, lianas, and trees less than 10 cm dbh (also see Gentry, 1982b). Biomass (as extrapolated from basal area) is roughly equivalent among different tropical forests ($\bar{X}$ = 34.9 m²/ha, N = 36 (excluding Africa; $\bar{X}$ = 70.7 m²/ha, N = 6)) and north temperate deciduous forests ($\bar{X}$ = 29.6 m²/ha, N = 5) but markedly greater in the Valdivian forests ($\bar{X}$ = 155.7 m²/ha, N = 3) as well as in their north temperate equivalent, the northwestern coniferous forests (Waring & Franklin, 1979).

DIVERSITY VS. PRECIPITATION

In the Neotropics, plant species richness is strongly correlated with absolute annual precipitation (Gentry, 1982b). However, this relationship is more complex than originally suggested (Gentry, 1982b), and the correlation may not exist at all in the Paleotropics. In tropical Asia, high rainfall areas such as Mt. Cherrapunji, Assam, often have relatively low plant species richness (Ashton, in press). In tropical Africa, two high rainfall sites (> 5,000 mm per year) in southwestern Cameroon (Korup, Mt. Cameroon) have only marginally more species in 0.1-ha samples than do samples from northeastern Gabon that receive < 2,000 mm of annual rainfall. Moreover, a more monsoonal climate site in Nigeria (Omo Forest) had many fewer species than the Gabon sites despite having similar precipitation values. Thus, it seems likely that the generalization that diversity increases linearly with precipitation (Gentry, 1982b) applies only in the special case of the Neotropics, where total annual rainfall and strength of
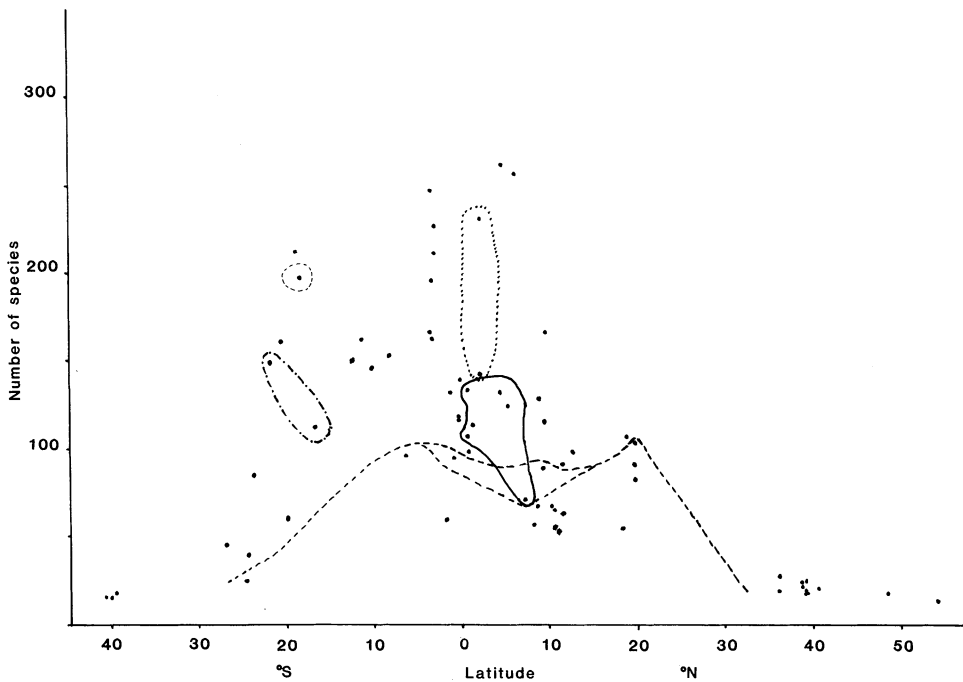
FIGURE 2. Species richness of 1,000 m² samples of lowland (< 1,000 m) forest as a function of latitude. Closed line encloses continental African points; dotted line encloses Asian points; dash-dot line encloses Australian and New Caledonian samples; other tropical and subtropical points all neotropical except anomalously high diversity Madagascar point at 19°S, (circled). Dashed line separates dry forest (bottom) from moist and wet forest (top) with three intermediate sites (moist forest physiognomy despite relatively strong dry season) indicated by alternate lines.

the dry season are strongly correlated. A potential test of the relative importance of distribution and amount of precipitation comes from a single 0.1-ha site in coastal Brazil (Linhares), which has the unusual (for the Neotropics) condition of low, evenly distributed annual rainfall. Although analysis of the Linhares diversity data is not completed (Peixoto & Gentry, in prep.) and the site is thus not included in Figure 3, it is obvious that its estimated 212 species in 0.1 ha are far more than would be expected from its 1,400 mm of annual precipitation.

While the many additional 0.1-ha samples now available from the lowland Neotropics generally strengthen the previously reported relationship between neotropical plant species richness and precipitation (Gentry, 1982b), additional data sets at the upper end of the precipitation scale strongly indicate that the relationship becomes nonlinear, reaching a marked asymptote at around 4,000–4,500

mm of annual precipitation (Fig. 3). The relationship is significantly curvilinear ($F = 4.299$, $P < 0.05$). From 4,000 mm to near the wettest place in the world (Tutunendo, Colombia) there is little or no change in the species richness of neotropical plant communities as measured by the 0.1-ha sampling protocol. The regularity of species richness patterns, and especially the apparent lid on community richness suggested by this asymptote, seem strong circumstantial evidence of the kind that zoologists (e.g., MacArthur, 1965, 1969) have construed as representing niche saturation and community equilibrium.

It is also possible that part of the apparent lid on plant community richness merely reflects the intrinsic limitations of the sampling technique. Figure 4 compares the accumulation of species with sample area for several representative sites. In low-diversity forests the species area curves level off below 500 m² indicating that most of the species present
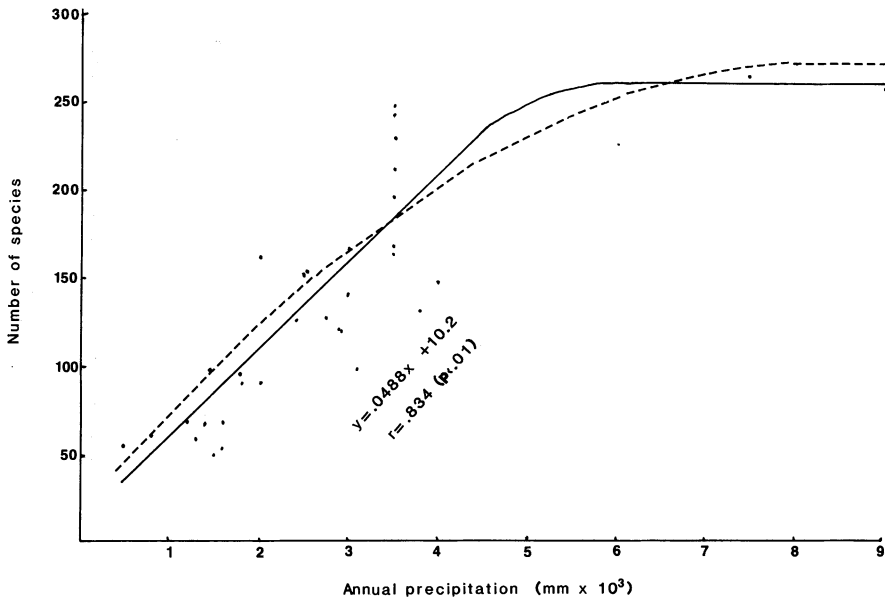
FIGURE 3. *Numbers of species in 0.1-ha samples of lowland neotropical forest vs. annual precipitation. Solid line = straight line regression for sites with < 5,000 mm annual precipitation with visually estimated asymptote. Dashed line = computer generated curve:* $y = 12.37 + 0.0613x - 0.000003598x^2$. *The curve is displaced slightly upward from the data points, since questionable morphospecies and lost specimens are treated as distinct species by the computer while the data points represent best estimates of species numbers. Data from Table 1 with subtropical sites excluded.*

in a given community have been sampled, but in species-rich vegetations the species–area curves show little sign of leveling off. To what extent a larger sampling area might reveal significant diversity differences between the different high rainfall sites remains unknown.

The strong relationship of species richness to precipitation in neotropical forests is fur-

ther supported by preliminary data from 1-ha tree plots in upper Amazonia (Gentry, 1988). In these samples only trees and large lianas ≥ 10 cm in diameter were censused (Fig. 5). The two most species-rich sites are from the everwet high rainfall (3,000–4,000 mm) Iquitos area of northern Amazonian Peru, where diversity reaches almost ridiculous ex-

FIGURE 4. *Species–area curve for 100 m² subsamples of representative high- and low-diversity 0.1-ha samples.*

FIGURE 5.   *Density of trees and large lianas in 1-ha Amazonian plots. Black = lianas; hatched = trees >
30 cm dbh; white = trees 10–30 cm dbh.*

FIGURE 6.   *Number of species in 1-ha Amazonian tree plots (plants ≥ 10 cm dbh). Black area = lianas ≥
10 cm greatest diameter.*

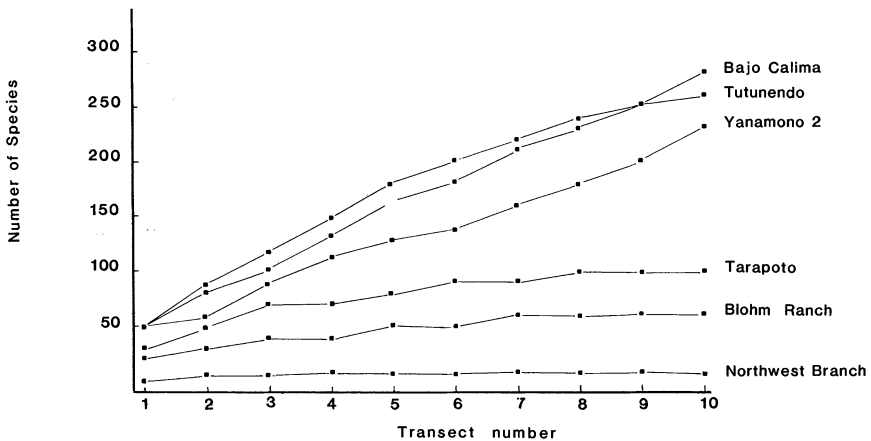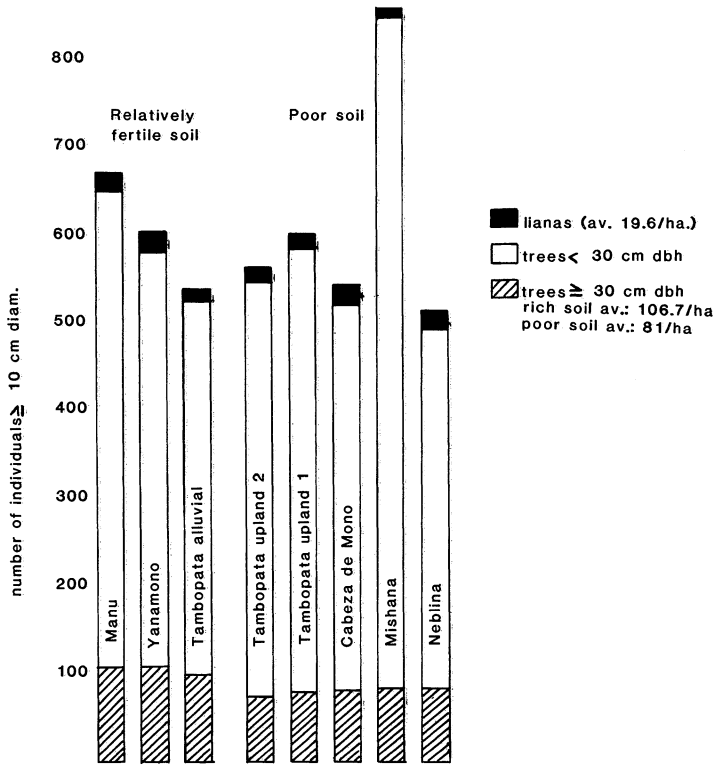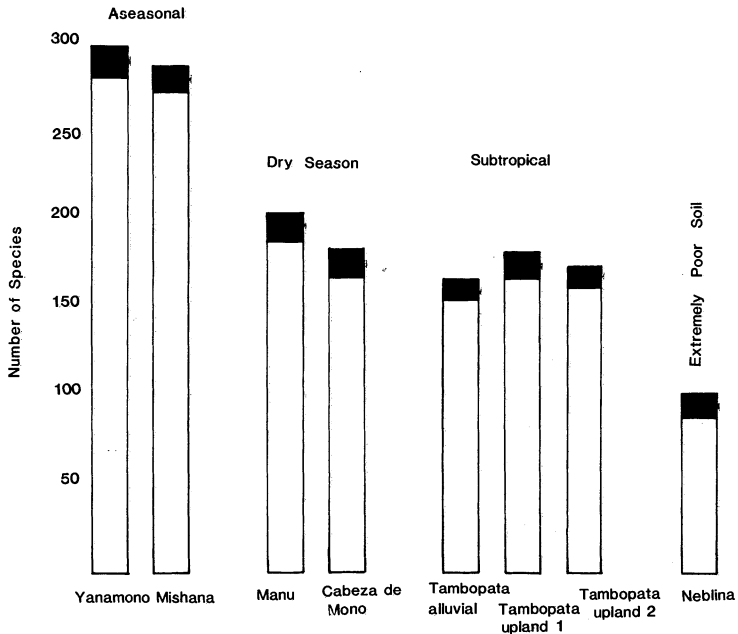tremes (Fig. 6). At Yanamono there are 300 species $\geq$ 10 cm in diameter out of the 606 individual plants in a hectare plot! The other 1-ha plots in Amazonian Peru are in areas with generally greater dry season stress and less overall precipitation. Two sites between 10° and 12°S latitude have about 200 species $\geq$ 10 cm dbh, while several 1-ha plots in different habitat types at Tambopata Reserve in southeastern Madre de Dios (12°50'S) have between 153 and 181 species. Thus tree species richness also appears to be greatest in aseasonal high rainfall areas, at least within Amazonia.

Epiphyte diversity likewise increases in wetter areas. While epiphytes can be well represented in areas with high atmospheric humidity but relatively low rainfall, our data indicate that absolute precipitation is generally a remarkably good predictor of epiphyte diversity (Gentry & Dodson, 1987b). We have data sets from a series of local florulas in western Ecuador and southern Central America; epiphytes vary from 9–24 species (2–4% of the total flora) in dry-forest sites to 72–216 species (12–16% of the total flora) in moist-forest sites to 238–368 species (23–24% of the total flora) in wet-forest sites (Gentry & Dodson, 1987a, b). For a series of 1,000 m² samples in which all plant species were identified and tabulated in three western Ecuadorian forests, 3 epiphytes constituted 2% of the species in a dry forest, 13 epiphytes constituted 8% of the species in a moist forest, and 127 epiphytes constituted 35% of the species in a wet forest (Gentry & Dodson, 1987b). The wet forest at Rio Palenque is so diverse in plant species that, even excluding tree species, it has more species of herbs (including herbaceous epiphytes) or of shrubs in 0.1 ha than any nontropical plant community in the world (Gentry & Dodson, 1987a).

DIVERSITY VS. SOIL NUTRIENTS

There has been much recent interest in the relationships between tropical soil nutrient levels and plant community richness (Ashton,

1977, in press; Gartlan et al., 1986). These authors suggest that phosphorus, magnesium, and potassium are among the nutrients whose levels are most strongly correlated with tropical plant community diversity. Nevertheless, at least in the Neotropics, soil nutrients are far less important than biogeographic factors or precipitation in determining plant species richness (Gentry, 1982b; Stark et al., submitted ms.). Multiple regression of a series of 31 lowland neotropical sites for which we have both soil and species richness data for 0.1-ha samples produced the equation: Species Richness = 84.48 + 0.025(mean annual precipitation) − 0.100(extractable soil K). $R^2 = 0.76$, N = 31 (Stark et al., submitted ms.).

Thus our data indicate that the nutrient most closely correlated with neotropical species richness is K. The importance of K agrees with what Ashton (1977, in press) found for a large series of tree plots in Borneo, Gartlan et al. (1986) also found available K to be highly and significantly correlated with floristic diversity in a series of sites in Cameroon. Our data contrast with those of Ashton (1977, in press) and Gartlan et al. (1986) in that we do not find phosphorus to be strongly correlated with diversity. This may be due in part to different techniques of nutrient extraction (ammonium acetate vs. HCl). It is also related to the fact that the most species-rich 0.1-ha sample (Bajo Calima, Colombia) comes from a peculiar white clay soil with 0 phosphorus as measured by our technique.

Whereas Ashton's (in press) data sets indicate greatest diversity at intermediate nutrient values, a "humped" nutrient/diversity curve that fits the model proposed by Tilman (1982, 1984), I see no indication in my data of a general decrease in diversity on richer soils in the Neotropics. Quite the contrary, the most species-rich tree plot in the world at Yanamono, Peru, is on relatively rich soil (Gentry, 1988; Stark et al., submitted ms.); further south, in an area with a strong dry season, the 0.1-ha Cocha Cashu sample on unusually rich alluvial soil is farther above the precipitation–diversity regression line than
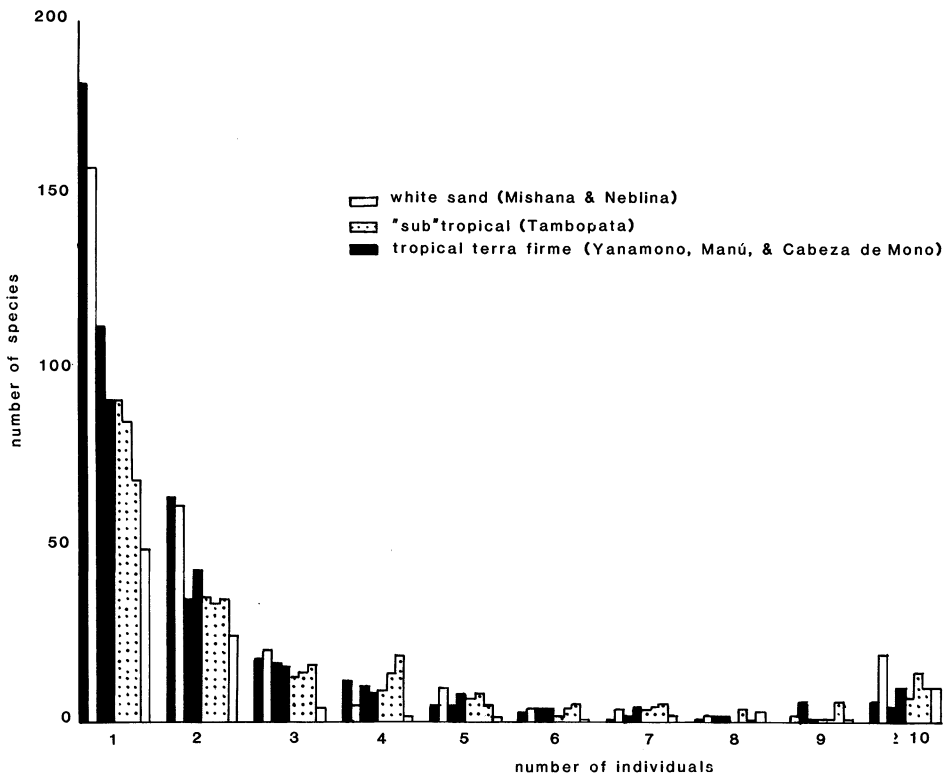
FIGURE 7. *Number of individuals/species in 1-ha Amazonian tree plots (plants ≥ 10 cm diam.).*

any other site (Gentry, 1985a). My data do fit well with Ashton's along the low nutrient end of the diversity–soil nutrient gradient, where there is a general increase in species richness from nutrient-poor to intermediate sites, contrary to the suggestions of Huston (1979, 1980).

Another way of comparing the effects of soil fertility on diversity is by comparing otherwise approximately matched site pairs on fertile and poor soils. The series of six tree plots in Amazonian Peru fall into three natural groups based on latitude and strength of the dry season (Gentry, 1988). Of the two plots in the everwet Iquitos area, one on rich soil has (marginally) more species than a nearby site on white sand; on a species per individual basis the difference would be much stronger (Figs. 7, 8). Of two sites from central Peru, the one on rich alluvial soil (Manú Park) has more species than one on poor soil (Iscozacin). Several plots at Tambopata south of the Hold-

ridge system tropical–subtropical demarcation have fewer species than the full-tropical ones on either rich or poor soils. Moreover, the site with the most nutrient-poor soil of all, Cerro Neblina, on pure white sand, has many fewer species than do any of the other sites. Thus the Amazonian tree plot data generally support the idea that relatively rich soil correlates with relative richness in tree species.

Especially noteworthy in the context of the relative importance of soil nutrients and precipitation as determinants of species richness is the series of 0.1-ha samples from different substrates in the Iquitos area (Table 3). All of the sites have the high species richness (168–212 species) that would be expected (Gentry, 1982b) in a region with high rainfall and no dry season. While samples from the forests subjectively judged likely to be subjected to greater stress (i.e., seasonally inundated tahuampa or white-sand campinarana) have slightly lower species richness, all

% of species with number of individuals

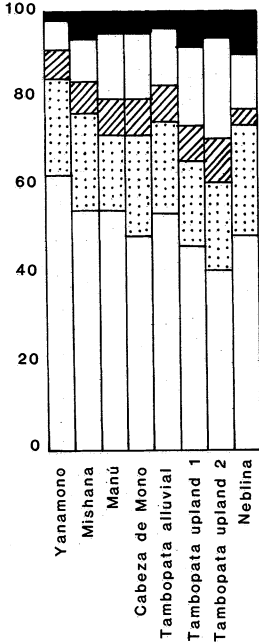FIGURE 8. *Percent of species with different numbers of individuals in Amazonian tree plots (plants ≥ 10 cm diam.). Lower white bar = 1 individual; dotted bar = 2 individuals; hatched bar = 3 individuals; black bar = 10 or more individuals. Note that an average across all plots of 50% of the species are represented by single individuals.*

sites are very diverse compared with moisture-stressed sites with a strong dry season or low annual precipitation.

I conclude that the species richness of neotropical plant communities generally increases with soil fertility and with precipitation, when such broader-scale biogeographic factors as latitude and altitude are controlled. This relationship would predict that the highest neotropical α-diversities should be found in upper Amazonia, where the soils are relatively rich, compared with those of comparably high rainfall areas of the Guayana Shield. My data for 0.1-ha samples and for 1-ha tree plots both appear to fit this prediction. Moreover, many other kinds of organisms, including birds, reptiles and amphibians, butterflies, and bats, appear to show excactly the same pattern of greatest diversity in areas with relatively fertile soils near the base of the Andes, suggesting that this relationship is a general biogeographic trend (Gentry, 1988). It is possible that increased productivity on the generally richer soils of this region makes possible finer niche partitioning and specialization in otherwise marginal habitats (cf. Emmons, 1984; Gentry & Emmons, 1987).

Even though the effect of soil nutrients on α-diversity may be relatively minor, soil nutrients undoubtedly do play a major role in contributing to the high overall diversity of Amazonian forests through their effect on β-diversity (e.g., Gentry, 1981, 1986a, c). Much of upper Amazonia, probably more than any other part of the lowland Neotropics, constitutes a conspicuous habitat mosaic, with very different sets of plant species occurring in adjacent communities on different substrates (Salo et al., 1986; Gentry, 1986a, c). Table 3 shows how little overlap in species there is between different, more or less equally diverse plant communities on different substrates in the Iquitos area. Only 3–24 species

TABLE 3. *Number of species shared by 1,000 m² samples of Iquitos area forest types.*

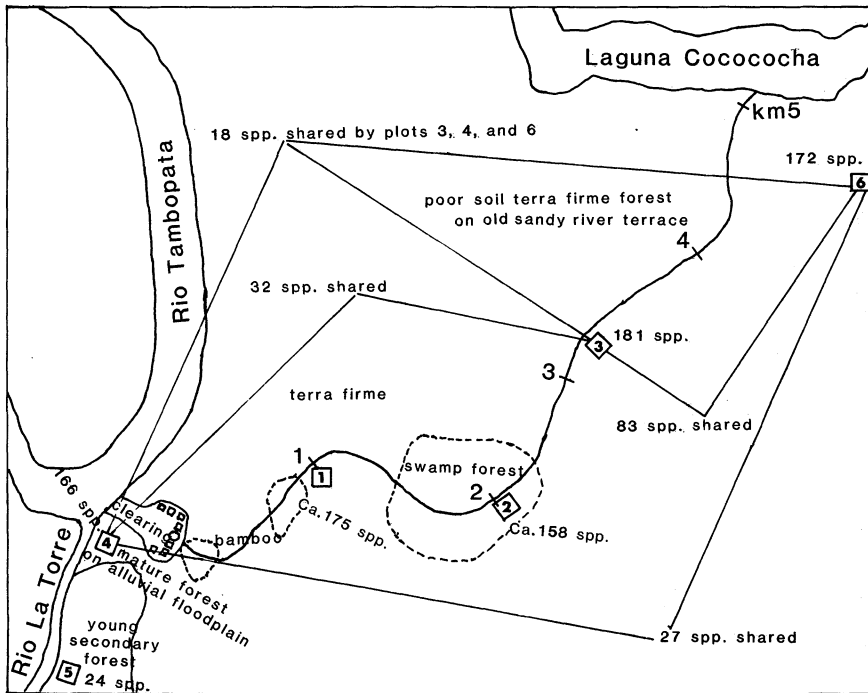|	Yanamono No. 1	Yanamono No. 2	Yanamono Tahuampa	Mishana Lowland	Mishana Campinarana	Mishana Tahuampa
Yanamono						
Terra firme No. 1	212	91	20	24	12	14
Terra firme No. 2		230	20–21	19	9	8
White-water tahuampa			163	9	5	ca. 19
Mishana						
Lowland noninundated				249	55	17
Campinarana (white sand)					196	3
Black-water tahuampa						168

FIGURE 9. *Location of 1-ha tree plots in the Tambopata Wildlife Reserve, Madre de Dios, Peru. Indicated species numbers for plots 2 and 5 are approximate since sampling is not yet complete. Plot 1 data in part based on field identifications of Gary Hartshorn (pers. comm.), and the actual number of species will undoubtedly be higher as well. Shared species indicated only for plots (3, 4, 6) completely sampled and identified by me.*

out of the ca. 200 species sampled for any habitat are shared by a different adjacent habitat. The one exception is the Mishana white-sand and floodplain samples (55 species overlap), but these two vegetation types have similar substrates and are not very well differentiated. While some of this lack of overlap might be due to inadequacy of the sampling technique in such diverse plant communities, a repeat sample of the same forest at Yanamono gave a much greater, almost 50% overlap in species; in other species-rich moist and wet forests similar repeat samples of the same vegetation always give the same ca. 50% overlap in sampled species (Gentry, 1982b), contrasting strongly with the ≤ 20% overlaps between different communities. Similarly, for two 1-ha tree plots on terra firme forest on poor sandy soil at Tambopata, 83 species (46% of the 181 species in plot 1 and 48% of the 172 species in plot 2) were shared with the other plot, for a coefficient of association of 44%. Only 16–18% of the species

of either poor soil plot were shared with a nearby tree plot on rich alluvial soil (coefficients of correlation of 10–11%) (Fig. 9). Incompletely analyzed data for additional plots in other forest types at Tambopata indicate that they, too, will show little overlap in species with sandy soil or alluvial forests. The uniquely high species richness of the Tambopata reserve for such well-known groups as birds (Donahue et al., in press) and butterflies (Lamas, 1985) has been suggested as largely due to the reserve's habitat diversity, a conclusion that clearly accords with the botanical evidence.

Thus the high species richness of woody plants in Amazonia as compared with the rest of the Neotropics (Gentry, 1982a) is largely β-diversity due to habitat specialization. Typically, related species may fill similar niches in forests on different upper Amazonian substrates (Gentry, 1981, 1986c). Dramatic differences in specific composition, though not intracommunity diversity, accompany spe-

Decrease in diversity with altitude
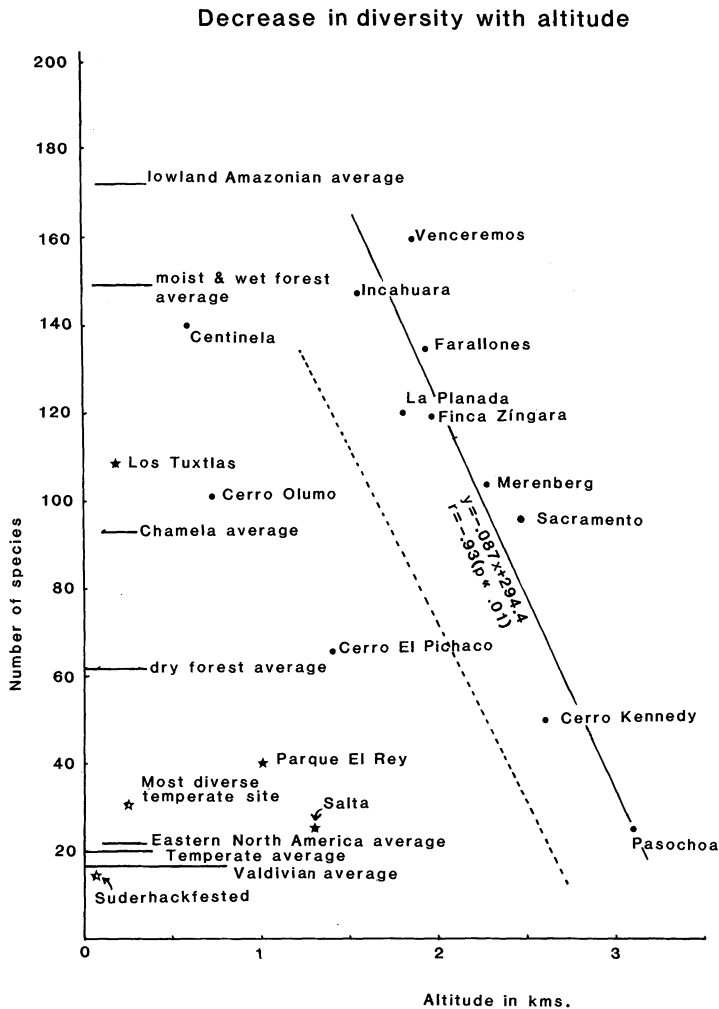
FIGURE 10. *Species richness of 0.1-ha samples vs. altitude. Points to right of dashed line and the calculated regression are for Andean sites. Comparative data from other selected sites to left of dashed line. Stars are for individual temperate and subtropical sites: Süderhackfestedt is in Germany; Salta and Parque El Rey are in northwest Argentina; Los Tuxtlas is in Veracruz, Mexico; Cerro Olumo and Cerro El Pichaco are in Nicaragua; Centinela is an isolated ridge west of the Andean Cordillera Occidental in Ecuador. Average species richness for other site-series indicated by lines spanning appropriate altitudinal range; Chamela is western Mexican dry forest. Several of the Andean values are preliminary, being based only on field identifications with herbarium comparison of vouchers still pending or on samples of less than 1,000 m² (see Table 2).*

cializations for different edaphic conditions, often related to different soil-nutrient availability in different Amazonian habitats.

ALTITUDINAL TRENDS

Eleven sites in tropical forests between 1,500 and 3,100 m altitude, mostly in the Andes, are included in Table 2. Although the available data set for upland sites is very incomplete, the trend of decreasing diversity with increasing altitude is clear. At least within the Andes, this inverse correlation is linear (Fig. 10), but the relatively low diversity of two Central American lower montane sites suggests that the extra-Andean decrease in diversity with altitude may not follow the same rules; certainly Central American montane forests have very different floristic compositions as well. Although there has been much
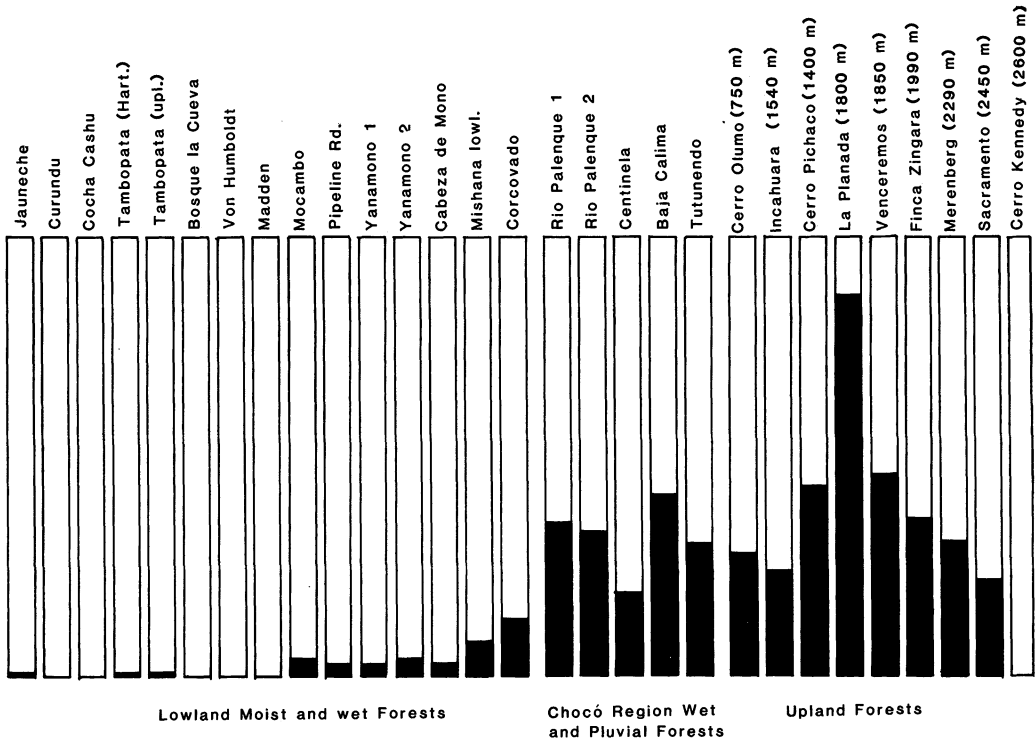
FIGURE 11.   *Percent of hemiepiphytes (black portion of bar) in sampled climbers for 0.1-ha samples of upland forests (in altitudinal sequence) compared with lowland Chocó area and non-Chocó area samples. Note apparent peak in hemiepiphytes at 1,800 m.*

speculation in the literature about a "mid-altitude bulge" in diversity (Janzen, 1973; Janzen et al., 1976; Scott, 1976; Gentry & Dodson, 1987b), there is no hint of such a phenomenon in the data of Figure 10. Instead, there seems to be a constant rate of decreasing species richness in moist Andean forests from the lowland tropics to near tree line. Unfortunately, no sites have been sampled from the Andean foothill region between 600 and 1,500 m, making it difficult to judge at what altitude the decrease in diversity begins. Clearly there is no altitudinal effect up to at least 500 m (Cocha Cashu, Peru; see Gentry, 1985a). Since samples from sites at 1,700 m would be near the average value for lowland wet- and moist-forest sites (Fig. 10), we can assume that there is little or no decrease in diversity up to that altitude.

Although there is no increase in diversity at middle elevations, there are some noteworthy physiognomic changes. One of the

most striking is the increase in sampled hemi-epiphytes around 1,800 m (Fig. 11). However, since increased numbers of hemi-epiphytic species (and individuals) are concomitant with decreased numbers of free-climbing liana species and individuals, there is no net change in community diversity. Also noteworthy is the relative abundance of hemi-epiphytic climbers in wet lowland sites in the Chocó area, a typical example of the tendency of the forests of this region to have features and taxa more characteristic of upland forests (Fig. 11; Gentry, 1986b). At higher altitudes free-climbing lianas take over again, so that at 2,500 m and above, hemiepiphytes have completely dropped out.

Even near the tree line above 3,000 m, Andean forests are more species rich than are temperate forests. Our highest-altitude sample, from 3,010 m at Pasochoa in the Ecuadorian Andes, has 25 species compared with only 21–30 species in the richest 5% of

TABLE 4. *Representation of different habits in local florulas (from Gentry & Dodson, 1987b).*

Habit	Capeira		Santa Rosa		Jauneche		Barro Colorado	
	Number	%	Number	%.	Number	%	Number	%
Epiphyte (including stranglers)	8	2	19	3	72	12	216	16
Parasites + saprophytes	4	1	6	1	4	1	12	1
Climbers	112	24	115	18	136	22	258	20
Trees ≥ 10 cm dbh	69	15	142	21	112	19	290	22
Terrestrial herbs, shrubs, treelets	270	58	381	58	280	47	540	41
Total species	463		667		604		1,316	

[a] Data from B. Hammel (pers. comm.).

some 312 Great Smokies Mountains samples (White, pers. comm.) and 15–26 ($\bar{X} = 20.5$) for the 13 other temperate-zone forests listed in Table 1.

SOME INTERCONTINENTAL DIVERSITY TRENDS

At a continental level, the Neotropics have many more species of plants than do either the Asian or Australasian tropics (Raven, 1976; Prance, 1977; Gentry, 1982a). Elsewhere, I have suggested that the "excess" neotropical species are mostly in herbaceous, epiphytic, and shrub taxa that have speciated explosively along the lower slope of the Andes and in southern Central America. To what extent, if any, does higher α-diversity of neotropical forests contribute to the continental pattern?

While I have relatively few comparable paleotropical data sets, a few general trends seem evident. One surprising indication from the available African data is that Central African forests ($\bar{X} = 127$ spp., N = 5) may be as diverse in species ≥ 2.5 cm dbh as their neotropical equivalents ($\bar{X} = 105$ spp., N = 9) for sites with 1,600–2,000 mm of precipitation. Even though the two high-rainfall sites in Cameroon do not show the increases in species richness that might be expected in the Neotropics, they are still very diverse, and the drier Gabon samples actually have more species than would be expected for similar rainfall values in the Neotropics. Moreover, one of the high rainfall sites with anomalously low diversity (Mt. Cameroon) is on the slopes of an active volcano, and the other (Korup)

is on an unusually poor, highly leached skeletal soil (Thomas, pers. comm.).

West African forests, including Nigeria's Omo Forest in my data set and the Ghana forests studied by Hall & Swaine (1981), may be poorer in species for historical reasons since there are suggestions that most West African forests may have been extensively altered by Bantu populations prior to the first European colonization (Keay, 1953; Jones, 1956). Even though my anomalously low diversity Omo Forest site was in a plot of protected forest considered to be climax (though surrounded by a mosaic of other plots subjected to varying degrees of degradation historically) (G. Pilz, pers. comm.), a number of its constituent species, such as *Pausinystalia macroceras*, *Spathodea campanulata*, *Markhamia lutea*, and *Musanga cecropioides*, seem more characteristic of late secondary than of primary forest.

Nor is the high diversity of Central African forests restricted to woody plants. Data comparable to a complete local florula are available for one African forest site at Makokou, Gabon (Hladik & Halle, 1973; Florence & Hladik, 1980; Hladik & Gentry, in prep.). Comparison of these data with local florulas from the Neotropics indicates that Makokou is not only as species rich as equivalent neotropical local florulas, but it also has a similar habit composition (Table 4; Gentry & Dodson, 1987b). Similarly, data from 1-ha tree plots indicate that African forests may be almost as rich in tree species as comparable neotropical and Southeast Asian forests (Gartlan et al., 1986; Thomas, pers. comm.: 138

TABLE 4. *Continued.*

Río Palenque		La Selva[a]		Makokou	
Number	%	Number	%	Number	%
238	23	368	25	66+	6+
6	1	8	1	9	1
171	16	182	12	259	23
165	16	310	21	389	34
475	45	622	42	418	37
1,055		1,490		1,140	

spp. in 0.64 ha on transect S, Korup National Park, Cameroon; Gentry, in press).

On the other hand, it is noteworthy that my single Madagascar site is richer in species than any of the continental African sites, which might be anticipated from the now widely accepted hypothesis that Africa's low continent-wide plant (and bird) species richness stems largely from extinctions associated with climatic deterioration during the Pleistocene or late Tertiary, whereas Madagascar was protected by being an island (Raven & Axelrod, 1974; Axelrod & Raven, 1978).

Quite the opposite of Africa, Asian forests have been widely thought to have more tree species than neotropical forests (e.g., Ashton, 1977; Whitmore, 1984). This conclusion was based on comparison of extant neotropical data for 1-ha tree plots with similar Asian data sets. However, the previously available neotropical tree plots were all from areas that would be anticipated on biogeographical or ecological grounds to have species-poor forests (Gentry, 1988). Hectare plots in upper Amazonia consistently have more tree species than in most Asian forests (Gentry, 1988), and the most species-rich 1-ha plots are in upper Amazonia. Indeed, these plots are so diverse—up to 300 species out of 606 individuals ≥ 10 cm diameter at Yanamono, Peru—that it is hard to imagine how a forest could be much more diverse.

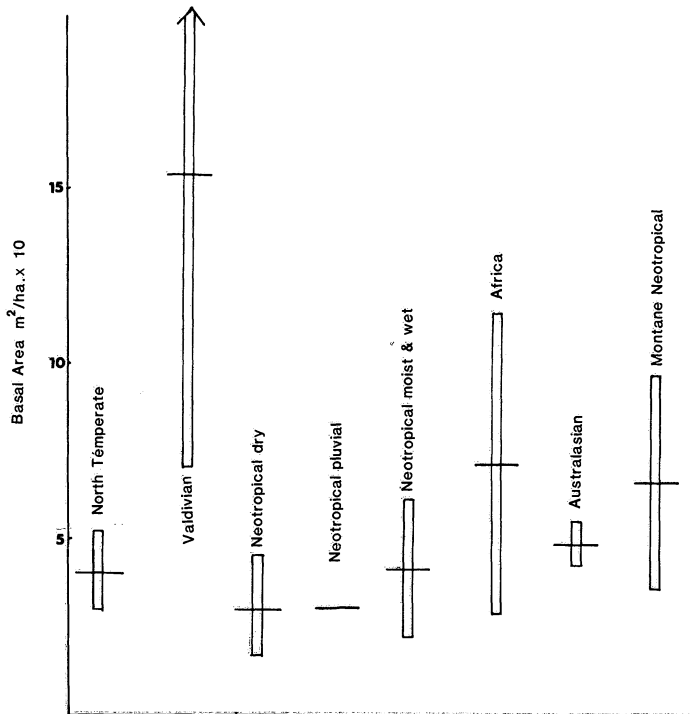I conclude that plant community diversity, at least of woody plants in plots of 1 ha or

FIGURE 12. *Basal areas for 0.1-ha samples of some different forest types. Line = average basal area for forest type; bar = ± 1 s.d.*

% of species

| | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 | 100 |

Yanamono — Leg, Mor, Eup, Myr, Lau, Sap, Ann, Mel, Rub, Bur, Fla, Ste, 46 other families

Tambopata upl. 1 — Leg, Mor, Lau, Ann, Sap, Me, Myr, Rub, Chr, Ela, Eup, Pal, 30 other families

Tambopata upl. 2 — Leg, Mor, Lau, Ann, Sap, Me, Bur, Eup, Hip, Myr, Pal, Rub, 34 other families

Tambopata alluv. — Leg, Mor, Lau, Ann, Sap, Eup, Mel, Myr, Nyc, Pal, 31 other families

Cocha Cashu — Leg, Mor, Ann, Lau, Sap, Mel, Bom, Eup, Myr, Sap, 37 other families

Cabeza de Mono — Leg, Lau, Sap, Bur, Eup, Ann, Chr, Lec, Myr, Apo, Ela, Mor, 28 other families

Mishana — Leg, Lau, Sap, Euf, Ann, Mor, Bur, Myr, Apo, Chr, Myt, Rub, 31 other families

Neblina — Leg, Bur, Mor, Lau, Eup, Sap, Ann, Mal, Pal, Sap, 21 other families

Xingu (3 ha.) — Leg, Mor, Myt, Lau, Lec, Eup, Mel, Sap, Bom, Apo, Chr, Ana, Ann, Bor, Nyc, Pal, 23 other families

Korup — Leg, Rub, Ann, Eup, Ebe, Fla, Ola, Ste, Me, Irv, Lau, Mel, Scy, Ver, 12 other families

Makokou (200 m²) — Leg, Eup, Bur, Hip, Ann, Ola, Apo, Com, Lau, Myr, Rub, Sap, Sap, 10 other families

Kuala Belalong — Dip, Eup, Leg, Myt, Gut, Mel, Sap, Ana, Mor, Rub, Ste, Lau, Myr, Ann, Bur, 37 other families

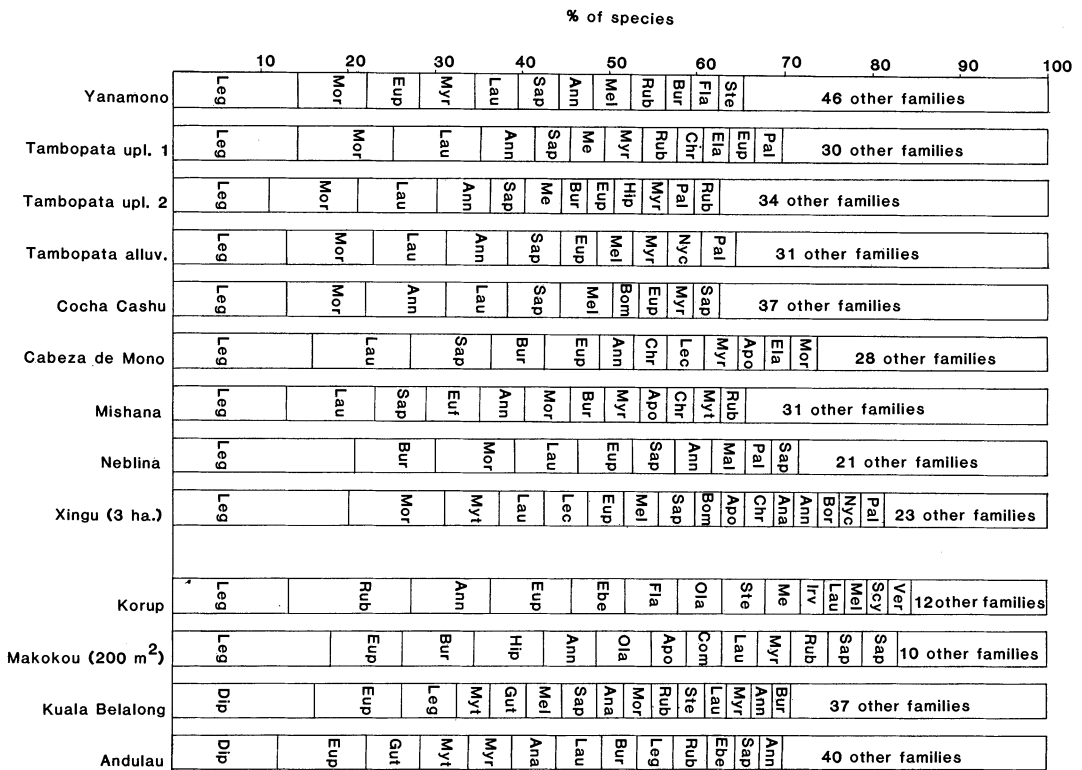Andulau — Dip, Eup, Gut, Myt, Myr, Ana, Lau, Bur, Leg, Rub, Ebe, Sap, Ann, 40 other families

FIGURE 13. *Familial compositions of some tropical forest tree plots (plants ≥ 10 cm dbh) in Amazonia (Yanamono to Xingu), Central Africa (Korup and Makokou), and Southeast Asia (Kuala Belalong, Andulau). South American sites are from original data except Xingu (Campbell et al., 1986); Korup is from D. Thomas (pers. comm.); the Makokou data are the total for the ≥ 10 cm dbh subset for the two 0.1-ha plots listed in Table 1 combined. The two Asian sites are from Ashton (1964): the data are for a total sample area of 20 ha at each site, composited from 50 individual acre plots on different types of terrain. The other data are for 1-ha plots except as otherwise noted. Family codes are the first letters of the familial names, self-evident except me = Melastomataceae, mel = Meliaceae, sap = Sapotaceae (the second, if present, = Sapindaceae), myr = Myristicaceae, myt = Myrtaceae. Note that Leguminosae, the dominant family in all neotropical and African tree plots, is just as speciose as is Dipterocarpaceae in Southeast Asia. Also note that, except for dipterocarps, the forests on all three continents are mostly composed of species belonging to the same few woody families.*

less, has a similar range of variation according to local environmental conditions in all three of the world's main tropical regions; what happens at larger spatial scales remains an open question.

Although tropical forest α-diversity may be similar on different continents, its structure is not. For example, lowland neotropical forests have fewer lianas than African forests and more lianas than Asian forests (Emmons & Gentry, 1983). Large palms as a major and characteristic canopy element of lowland terra firme forest seem largely restricted to the Neotropics (Gentry & Emmons, 1987), Madagascar (20 palms ≥ 10 cm dbh/ha at

Perinet), and a few other islands (e.g., New Caledonia: 20 palms ≥ 10 cm dbh/ha at Rivière des Pirogues). While stem densities of trees ≥ 10 cm dbh may be similar from continent to continent (Dawkins, 1959), tropical African forests tend to have more large trees and higher basal areas (and presumably biomasses) (70.7 m²/ha vs. 34.9 m²/ha) than do neotropical or Australasian forests (Fig. 12). On the other hand, Asian dipterocarp forests may have uniquely high densities of small polelike trees. Such structural differences, only beginning to be discovered, may be critical to forest organisms. For example, the intercontinental difference in liana density
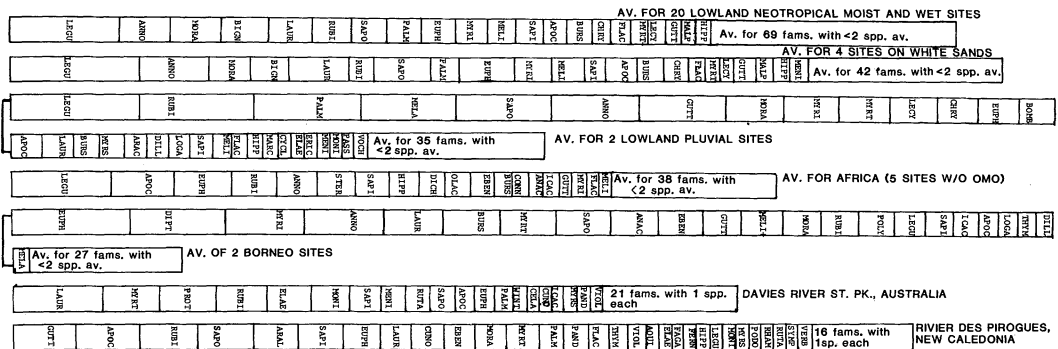
FIGURE 14. *Comparison of average number of species per family for 0.1-ha samples from subsets of different lowland neotropical forest types with equivalent paleotropical data. From top to bottom the columns represent: 1) average for 20 lowland neotropical moist and wet sites; 2) average for 4 neotropical sites on white sand; 3) average for 2 pluvial-forest sites in Chocó; 4) continuation of 3; 5) average for 5 central African sites (i.e., excluding Omo); 6) average for 2 Bornean sites; 7) continuation of 6; 8) Davies River State Park, Queensland, Australia; 9) Rivière des Pirogues, New Caledonia. Shortest column segments are two species tall.*

FLORISTICS

Neotropical plant communities are put together in decidedly nonrandom ways. Thus community-level frequency of different seed dispersal and pollination syndromes is generally predictable from environmental parameters (Gentry, 1982b, 1983). Similarly, the floristic composition of different plant communities is remarkably consistent, at least at the familial level. Legumes are virtually always the dominant family in neotropical and African lowland primary forests. The only neotropical exceptions are on extremely rich soils where Moraceae become very diverse and are occasionally as species-rich as Leguminosae in 0.1-ha plots (Gentry, 1986b, c). Of the 43 continental neotropical lowland 0.1-ha samples between 23.5°N and S latitudes, 39 had Leguminosae as the most species-rich family. The dominance of legumes in the Neotropics and Africa is equally apparent when only trees ≥ 10 cm dbh are considered (Fig. 13). Indeed, legumes contribute almost exactly as much to the diversity of neotropical and African forests as dipterocarps do in Southeast Asia. Similarly, in Af-

rica, on the rich volcanic soil of the Mt. Cameroon plot, several families, especially Rubiaceae, Apocynaceae, and Euphorbiaceae have more species than legumes, but this forest, on the lower slopes of an active volcano, may not be strictly primary.

The other families that contribute most to species richness of different plant communities are also predictable. In the Neotropics the same 11 families—Leguminosae, Lauraceae, Annonaceae, Rubiaceae, Moraceae, Myristicaceae, Sapotaceae, Meliaceae, Palmae, Euphorbiaceae, and Bignoniaceae—contribute about half (38%–73%; $\bar{X} = 52\%$) of the species richness to 0.1-ha samples of any lowland forest. At least eight of these families are always among the ten most species-rich families in any lowland neotropical moist or wet forest (Fig. 14; Gentry, 1987b). Similarly, in 0.1-ha samples of lowland neotropical dry forests, Bignoniaceae, the preeminent liana family, is always second only to Leguminosae in its contribution to species richness (Fig. 15).

Somewhat surprisingly, the dominant families in neotropical forests also tend to be the most speciose on other continents. Rubiaceae, Annonaceae, and Euphorbiaceae are always among the ten most species-rich families in Africa and Asia, just as they are in the Neotropics. The rest of the 11 most species-rich neotropical families (Lauraceae, Moraceae,
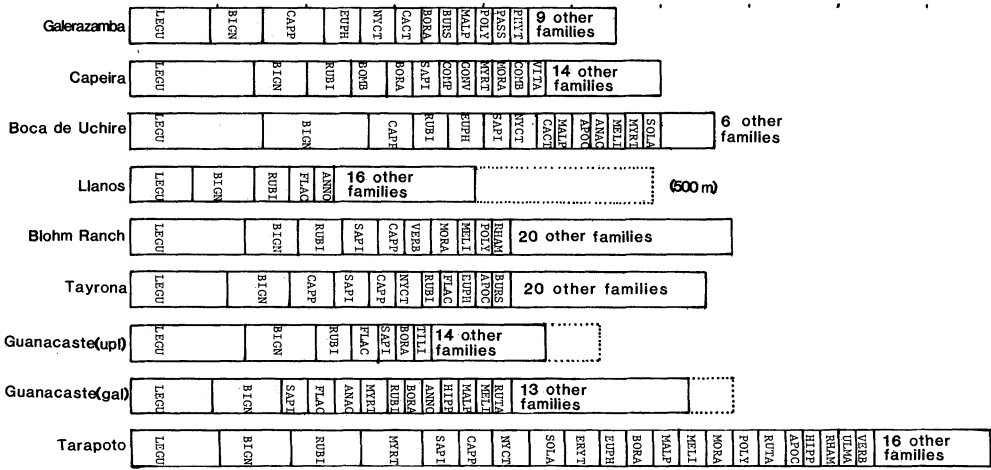
FIGURE 15. *Number of species per family for 0.1-ha samples of lowland neotropical dry forests. For three sites with sample areas of < 1,000 m²—Llanos, Guanacaste (upland) and Guanacaste (gallery), with 500 m², 700 m², and 800 m² of sample area, respectively—the actual values are inside the solid outlines with the anticipated number of species in 1,000 m² indicated by the dotted outline. Shortest column segments are two species tall.*

Sapotaceae, Palmae, Myristicaceae, Meliaceae, and Bignoniaceae) are all represented in at least some samples from both Africa and Asia and, except for Bignoniaceae and Palmae, are among the ten most species-rich families in at least one African or Asian sample. Thus, with the exception of the substitution of Dipterocarpaceae for Leguminosae as the most species-rich woody family in Southeast Asian forests, pantropical familial composition of lowland forests is remarkably similar.

Other minor differences include Ebenaceae (almost always present in Africa and Asia and among the ten most species-rich families in about half the samples from those continents but only occasionally represented in the neotropical samples, never by more than a single species), Olacaceae (usually represented on all continents but generally among the ten most species-rich families in Africa, never so in Asia or the Neotropics), and Sterculiaceae (always among the ten most species-rich families in Africa; represented by 1–3 species in almost all neotropical and Asian samples, although among the ten most species-rich families only in Cocha Cashu, Peru). Dichapetalaceae are almost always among the ten most species-rich families in African samples but

are only occasionally represented by one or two species in the Neotropics and are absent from my Asian samples. Apocynaceae and Sapindaceae almost always turn up in samples from any continent but are generally among the ten most species-rich families in Africa (always in the case of Apocynaceae) but only rarely elsewhere. Disproportionately represented in Asia, besides Dipterocarpaceae, are Myrtaceae (always among the most species-rich families vs. almost always present but only rarely among the most species-rich families in the Neotropics and represented by a single species in a single sample on continental Africa). Other noteworthy anomalies include 9 species of Proteaceae, 7 of Elaeocarpaceae, and 6 of Monimiaceae in the Queensland sample (these three families ranking 3rd, 5th, and 6th in diversity after Lauraceae, Myrtaceae, and Rubiaceae), 7 Araliaceae species and 5 of Cunoniaceae in the New Caledonia sample (ranking 5th and 8th, respectively, in familial diversity), and 8 and 3 species, respectively, of *Xanthophyllum* (Polygalaceae) at Semengoh and Bako, Borneo.

Put another way, all of the paleotropical forests sampled were constituted almost entirely of the same plant families encountered in equivalent samples of neotropical forests.

Although 13 families not represented in the Neotropics were included in the paleotropical samples, and although each African and Asian sample included 1–3 families not represented in the Neotropics, with two exceptions, the sum contribution of all of these to species richness of the Asian and African forests is negligible. The two exceptions are Dipterocarpaceae in tropical Asia and Pandanaceae in Madagascar (3 spp.), Queensland (2 spp.), and New Caledonia (4 spp.). Excluding these two families, an average of 2 species (and ca. 3 individuals) per sample was contributed to paleotropical community diversity by families not included in the equivalent neotropical samples. At this level New Caledonia was the most distinctive, with one species each of Balanopaceae, Epacridaceae, Oncothecaceae, and Pittosporaceae, plus 4 of Pandanaceae. The Madagascar sample included, besides 3 Pandanaceae, a species of Sarcolaenaceae and two of Pittosporaceae, the Queensland sample a species of Balanopaceae and 2 of Pandanaceae (plus one of the sometimes Cunoniaceae segregate Davidsoniaceae). In Africa, Ancistrocladaceae was represented by one individual at one site, Medusandraceae by one individual at one site, and Scytopetalaceae by two species at one site. Only in the latter case did an endemic family contribute significantly to a site's diversity, with *Ouabangia alata* the 5th most common species (13 individuals) at Korup and *Rhaptopetalum* cf. *coriaceum* represented by three individuals at the same site. It is perhaps worth noting that several of the endemic families included in the above total are somewhat dubious segregates—Pandaceae (from Euphorbiaceae), Irvingiaceae (from Simaroubaceae), and Ixonanthaceae (from Linaceae). Lowland tropical forests throughout the world are overwhelmingly made up of the same plant families, with the exception of the Dipterocarpaceae for Leguminosae substitution in Southeast Asia.

Even at the generic level, there are striking floristic similarities between the compositions of lowland tropical forests on different continents. The generic similarity is especially marked between Africa and South America.

An average of 30% (with extremes of 25% at Korup to 34% at Belinga) of the genera at the six continental African sites are neotropical genera, nearly all also included in the neotropical samples. When complete local floras are compared, generic concordance between tropical Africa and the Neotropics remains equally high. Thus 30% of the genera represented at Makokou Gabon also occur in the Neotropics. Both sets of figures would be much higher if such tenuously differentiated genera as *Pycnanthus* and *Virola* (Myristicaceae) or *Macrolobium* and its segregates (Leguminosae) were considered to be congeneric.

Generic overlap between tropical Asia and the Neotropics is less, averaging 23%, and between Australasia and the Neotropics intermediate (25% neotropical genera in the Queensland sample, 26% in the New Caledonia one). These relationships might be predictable from Cretaceous and Tertiary plate tectonic history and the timetable of Gondwanan breakup. In this light, it is especially interesting that about 36% of the genera sampled at Perinet, Madagascar, are shared with the Neotropics, the highest value for any paleotropical site.

There are also consistent and predictable floristic changes along environmental gradients, at least in the Neotropics. On poorer soils families like Burseraceae, Lauraceae, and Sapotaceae become more prevalent, whereas on the richest soils palms and Moraceae are disproportionately speciose.

In neotropical areas with a strong dry season, floristic composition is likewise predictable. Leguminosae are always the most species-rich family, with Bignoniaceae, represented mostly by wind-dispersed lianas, always second (Fig. 15).

On an altitudinal gradient in the Andes, Lauraceae consistently replace Leguminosae as the most species-rich family at intermediate elevations (Fig. 16). Other families that contribute to the diversity of middle elevation forests are Rubiaceae, Melastomataceae, Euphorbiaceae, Moraceae, Guttiferae, tree ferns, (hemiepiphytic) Araceae, and Palmae. Fam-
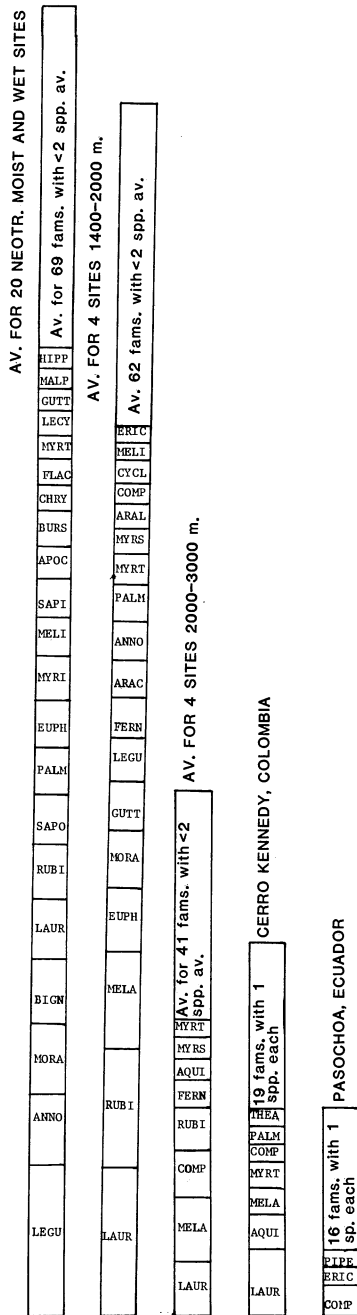
FIGURE 16. *Number of species per family for 0.1-ha samples at different altitudes in the Neotropics. From left to right columns are 1) average for 20 lowland neotropical moist- and wet-forest samples; 2) average for 4 sites between 1,400–2,000 m (Cerro Pichaco, Incahuara, Venceremos, Farrallones de Cali); 3) average for 4 sites at 2,000–3,000 m (Sacramento, Finca Mehrenberg, Cerro Kennedy, Finca Zungara); 4) Cerro Kennedy, Colombia (2,600 m, 500 m² of sample area);*

ilies like Bignoniaceae, Sapotaceae, Myristicaceae, Meliaceae, Sapindaceae, Burseraceae, and Chrysobalanaceae are especially noteworthy as absent or much more poorly represented than in lowland forests. At higher elevations (> 2,000 m), Melastomataceae, Compositae, Rubiaceae, and tree ferns become more prevalent, although of these only Compositae increase in absolute number of species. At even higher altitudes, Aquifoliaceae, Myrtaceae, and Theaceae become relatively more important, while near timberline Compositae and Ericaceae predominate.

Curiously, the site at 1,000 m altitude at Perinet, Madagascar, had virtually an identical familial composition to the middle-elevation neotropical site; in addition to Lauraceae being the most speciose family, Rubiaceae, Euphorbiaceae, Moraceae, and Guttiferae followed in species richness; the only substantial differences are a transposition of the roles of Melastomataceae (more species in the Andes) and Myrtaceae (more species at Perinet), the presence of several species of Monimiaceae and Oleaceae in Madagascar, and the frequency of hemiepiphytic Araceae in the Neotropics (Fig. 17). A Queensland, Australia, site from 850 m was also rather similar in familial composition to the Andean middle-elevation sites, again with Lauraceae dominating, closely followed by Rubiaceae, though with greater prevalence of such southern families as Proteaceae, Elaeocarpaceae, and Myrtaceae. Such strikingly repeated patterns in parts of the world so widely separated today can hardly be due to chance.

Many of the major latitudinal changes in floristic composition are well known, with families such as Fagaceae and Juglandaceae replacing the tropical taxa in North America (Fig. 18). Perhaps less emphasized are how remarkably similar in familial composition different eastern North American forests are. While species, and to some extent genera, do change from place to place, from a world

5) *Pasochoa, Ecuador (3,010 m, 200 m² of sample area). Site data from Table 2. Shortest column segments are two species tall.*
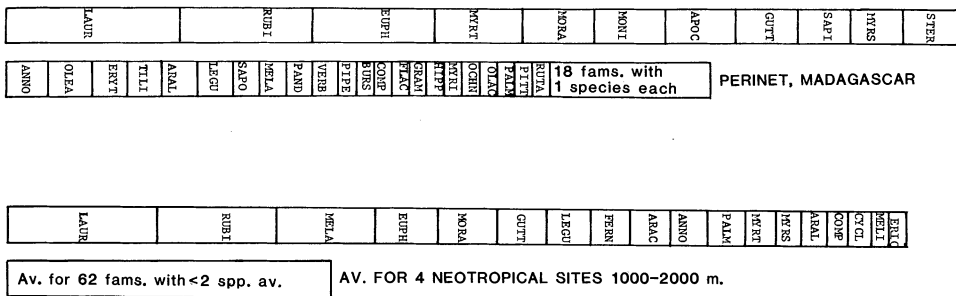
FIGURE 17. *Number of species per family for 0.1-ha sample at Perinet, Madagascar (950 m) (top two columns) compared with average for four mid-elevation neotropical sites (1,000–2,000 m) (bottom two columns). Note the remarkable similarity of familial composition. Perinet data based only on field identifications pending herbarium comparison of vouchers. Shortest column segments are two species tall.*

perspective the overall floristic composition of most of these forests is as similar as is their diversity. The contrastingly austral composition of the Valdivian flora is also well known. There are also floristic similarities between the austral and north temperate ones. For example, gymnosperms and Fagaceae become more prevalent in both north temperate and south temperate areas. One interesting and previously unremarked floristic difference between the Valdivian forests and their northern equivalents is that the former lack sympatric congeners. The difference in diversity between eastern North American and Valdivian forests (as well as between the North American forests and my two European samples) is almost entirely accounted for by this lack of sympatric species in genera like *Quercus* and *Carya*. Why Chilean *Nothofagus* species, unlike their northern cousins, should be almost entirely allopatric is unclear, but the effect of this pattern on the diversity of the south temperate forests is obvious.

DISCUSSION

To this point I have attempted to present a series of observations of changes in diversity and floristic composition on various gradients. I now focus briefly on some theoretical generalizations that would seem to derive from these data.

The overall message is that plant communities are put together in decidedly nonrandom ways. Diversity and floristic com-

position are highly predictable from environmental and geographical factors, with maximum plant community diversity occurring in full-tropical lowland areas with rich to intermediately infertile soils and high annual precipitation and/or little dry-season stress. Such patterns are often taken as evidence of niche saturation and community equilibrium (MacArthur, 1965, 1969; Cody, 1975; see also Whittaker, 1977).

Much of the controversy about equilibrium vs. nonequilibrium communities has focused on the role of niche specificity vs. stochastic generation or maintenance of diversity (e.g., Hubbell, 1984; Hubbell & Foster, 1986; Ashton, 1969; Connell, 1978). My data suggest that even though tropical forests contain many different plant species, they are far from random assemblages. Can these data and conclusions be reconciled with the very different ones of Hubbell (1979; Hubbell & Foster, 1986, 1987)? Below I will focus on several points that may be relevant to this debate.

From a somewhat different perspective, some authors (e.g., Federov, 1966) have argued that the exceedingly high diversity of tropical forests is too great to be accounted for by niche specificity; therefore, some kind of nonselective or stochastic mechanism must be invoked. However, it seems to me that it is stochastically most unlikely that the extreme species richness of forests like that at Yanamono, Peru, with 300 species out of 606 individuals in a hectare, would result
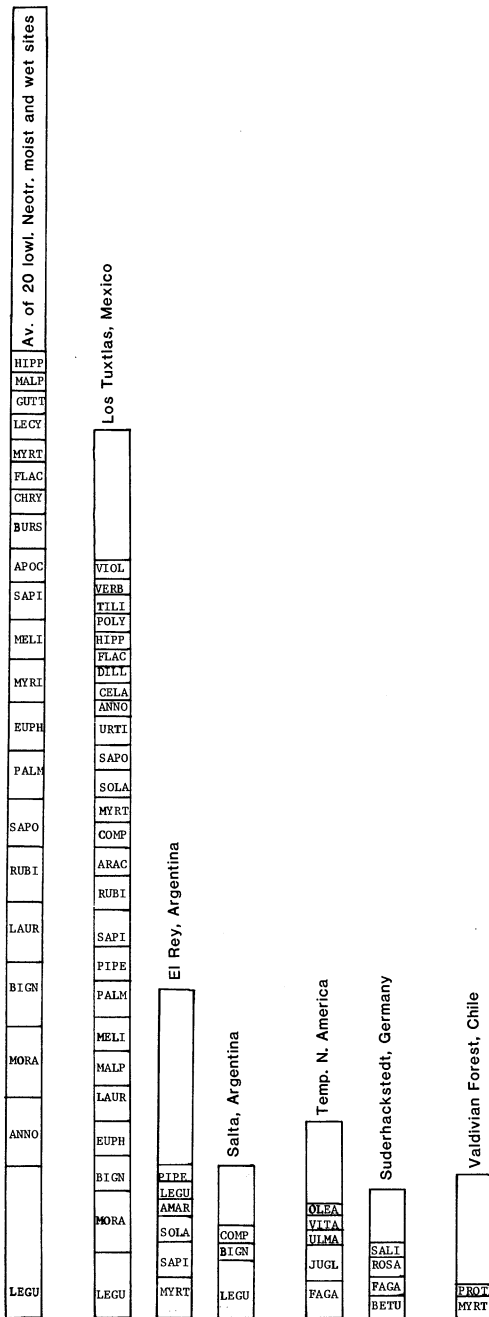
FIGURE 18. *Number of species per family for some 0.1-ha samples at different latitudes. From left to right, columns are: 1) average for 20 lowland neotropical moist- and wet-forest samples; 2) Los Tuxtlas, Mexico (wet forest, 18°35'N, 200 m alt.); 3) Parque El Rey, Argentina (moist forest, 24°45'S, 1,000 m alt.); 4) Salta, Argentina (dry forest, 24°40'S, 1,300 m); 5) average for seven temperate North American sites (28°15'N–39°2'N); 6) Suderhackstedt, Germany*

from random processes, unless there is a potential sample universe of many thousands of tree species. Forty-eight species are represented in the first 50 individuals sampled at Yanamono, and the 65 individuals in the first Yanamono 0.1-ha subplot constitute 58 species. Such high levels of diversity, far from indicating stochasticity, would seem to indicate very strong ecological pressures resulting in phenomenally low densities of the individual species (and high community diversity).

The striking regularities in the patterns discussed above clearly indicate that at some levels both community composition and diversity are highly predictable. How this relates to community equilibrium remains clouded, however, in part because of definitional problems. Hubbell & Foster (1986) defined an equilibrium community as one in which a particular combination of *species* maintains itself against outside perturbations, whereas the predictable diversities of different tropical forests with similar environments but different assemblages of species is more akin to the "equilibrium" theory of island biogeography (MacArthur & Wilson, 1967), considered by Hubbell as a nonequilibrium theory because of the taxonomic randomness involved. Many Amazonian forests are clearly richer in tree species than equivalent Central American forests (Gentry, 1988). They also have much greater habitat differentiation and β-diversity (Gentry, 1986a). Thus some of the higher diversity of the Amazonian forests may be due to the "mass effect" phenomenon of Shmida & Wilson (1985), with accidental immigrants adapted to other environments contributing significantly to the α-diversity of an individual Amazonian forest. Arguing along similar lines from the nonequilibrium viewpoint, Hubbell & Foster (1986) suggested that biogeographical pattern plays a major role in tropical forest α-diversity: if the regional diversity is greater, as it certainly is in Amazonia, more species, on the average,

←

(54°N); 7) average for three Valdivian, Chile, sites (39°30'S–40°43'S).

should occur in individual forests due purely to phenomena associated with patch dynamics and local immigrations. But there are also problems with such interpretations. That the families and genera represented in these different samples are so predictable strongly suggests that at least some kind of familial-specific niches may be involved. Moreover, the apparent partitioning of the species of each family into different sets of species specialized for different substrates in Amazonia seems strong circumstantial support for selectionist interpretations (Gentry, 1985b).

Data from several 1-ha tree plots in the Tambopata Reserve, Madre de Dios, Peru, can be used to document the effect of substrate specificity on species composition. Data are available from two completely identified 1-ha samples from similar poor-soil terra firme forest separated by about 1.5 km, a completely identified plot in mature forest on rich alluvial soil, and from as yet incompletely identified plots in young riverside secondary forest, in swamp forest, and in forest in a transitional area between the rich floodplain and poor-soil uplands (see Fig. 8). As is usually the case in species-rich tropical forests, most of the species sampled were represented by one or two individuals on a single plot and are inadequately sampled to draw any conclusions about habitat specificity. Table 5 lists the species that occur in all three completely sampled plots plus all species that are common (i.e., > 10 individuals) in at least one of the plots plus a few other selected species.

At one extreme are 13 species that occur both in the two poor-soil plots and in the fertile-soil alluvial plot. These might be classed as ecologically insensitive; none of them occurs in the secondary forest, six of them (and possibly more) in the swamp plot, and most (perhaps all) of them on the intermediate plot. All of these are essentially uniformly dispersed with similar numbers of individuals in each hectare. *Bertholettia excelsa*, which has 1–2 large emergent trees per hectare throughout the Tambopata Reserve (except in secondary forest), is a good example of this pattern. Other good examples include the

subcanopy tree *Leonia glycicarpa*, which has 6–19 individuals per hectare, and the canopy tree *Symphonia globulifera* with 1–4 individuals per hectare, again excluding the second growth plot.

At the opposite extreme are the 21 habitat specialists listed in Table 5, locally common, but occurring in only a single habitat: good soil, poor soil, swamp, or second growth. The extreme case is *Lueheopsis hoehnei*, the absolute dominant in the swamp plot with 265 trees, but completely absent elsewhere; that this is only the second record of such a locally common species from Peru is instructive as to the state of Amazonian Peruvian floristic knowledge. Another example worth mentioning is *Sparrea schippii*, previously unreported from Peru (or indeed from Amazonia), which is the fourth most common species in the alluvial plot. The large number of species that are completely faithful to a single habitat (presumably also including many additional less common species not listed in Table 5) is a good example of the importance of niche specificity in maintaining overall Amazonian species diversity. Each community is rich in large part because it has many species uniquely adapted to a specific substrate.

Perhaps more interesting from the viewpoint of ecological theory are the other two distributional categories indicated in Table 5. The first are species that are common in one habitat but also have a few individuals in one or more of the other habitats. Some of these may represent cases of "mass effect" (Shmida & Wilson, 1985), with an occasional individual surviving but not reproducing outside its normal ecological range. The second pattern is species of the poor soil forest that are common in one of the two sample plots but absent from the other. These may be examples of "ecological equivalents" (Shmida & Wilson, 1985), where due to some accident of dispersal or establishment, a given species occurs at one site but not at another where it would be equally well adapted. The ecological equivalent hypothesis seems especially germane to *Cordia*, where *Cordia mexiana* and *C. panamensis* occur in one upland plot while *C.*

TABLE 5. *Differences in occurrence and abundance in different 1-ha tree plots of some common Tambopata species (all species occurring in all three complete plots or with 10 or more individuals in any one plot plus a few others). Plot 1 is relatively fertile terra firme; plot 2 is swamp forest; plots 3 and 6 are on poor sandy, upland terra firme; plot 4 is on rich alluvial soil; and plot 5 is in young riverside secondary forest.*

	Plot Number					
	1	2	3	4	5	6
Ecologically insensitive, ± uniformly dispersed						
Bertholettia excelsa	2	(1)	2	1	—	2
Eschweilera coriacea	6?	?	4	2	—	9
Glycidendron amazonica	1	(1)	1	2	—	1
Leonia glycicarpa	19	(1)	12	12	—	6
Lindackeria paludosa	4	(1)	10	1	—	4
Minquartia guianensis	1	—	3	1	—	2
Nectandra cissiflora	?	?	1	1	—	4
Neea divaricata	X	?	2	5	—	4
Ocotea rubrinervis	?	?	7	7	—	7
Oenocarpus mapora	1	(1)	4	3 (4)	—	3
Symphonia globulifera	1	(3)	3	3	—	4
Tapirira guianensis	1	—	—	1	—	2
Clarisia racemosa	1	—	3	2	—	2
Ecologically sensitive but widespread						
Amaioua corymbosa	1	(1?)	11	1	—	6
Euterpe precatoria	17	4	2	2	—	4
Iriartea deltoides	106	(15)	7	86	—	—
Iryanthera juruensis	5	(3)	19	5	—	22
Iryanthera laevis	17	(2)	13	2	—	31
Mabea	—	(1)	1?	11	—	—
Pourouma minor	18	(6)	17	1	—	44
Pseudolmedia laevis	14	(5)	4	7	—	1
Siparuna decipiens	13	3	8	1	—	9
Socratea exorrhiza	10	5	1	38	7+	2
Tetragastris altissima	1	(2+)	7	1	—	22
Ecologically restricted						
Cecropia membranacea	—	—	—	—	46+	—
Ficus insipida	—	—	—	—	13	—
Citharexylum poeppigii	—	—	—	—	9+	—
Sparrea schippii	—	—	—	17	—	—
Rinorea viridifolia	X	—	—	27	—	—
Astrocaryum murumuru	—	—	—	16	—	—
Myroxylon balsamum	1	?	—	6	—	—
Cordia lomatoloba	—	—	—	2	—	—
Cordia nodosa	X	—	—	1	—	—
Mauritia flexuosa	—	41	—	—	—	—
Lueheopsis hoehnei	—	265	—	—	—	—
Pithecellobium latifolium	—	12	—	—	1	—
Rouchera punctata	1	(2)	19	—	—	15
Virola sebifera	1	(1)	18	—	—	15
Ouratea	—	—	14	—	—	14
Euceraea nitida	—	(1)	6	—	—	8
Cedrelinga cateniformis	—	—	3	—	—	5
Cordia mexiana	—	—	10	—	—	—
Cordia panamensis	—	?	4	—	—	—
Cordia toqueve	—	?	—	—	—	4
Cordia ucayaliensis	—	—	—	—	—	7

TABLE 5. *Continued.*

	Plot Number					
	1	2	3	4	5	6
Major density differences not explainable by ecology						
Bixa arborea	—	—	15	—	—	—
Hevea guianensis	1	—	15	—	—	—
Pseudolmedia laevigata	1	—	23	—	—	4
Ocotea (*domatia*)	?	—	1	—	—	10
Arrabidaea tuberculata	—	—	—	—	—	4

X = present in Hartshorn plot but number of individuals not known.
? = presence or absence not known due to incomplete identifications (plot 1) or sampling not yet completed (plot 2).
( ) = species occurring in plot 2 only in corner on higher ground.

toqueve and *C. ucayaliensis* occur in the other. Both of the latter situations represent the pattern thought to be prevalent on Barro Colorado Island (Hubbell & Foster, 1986), with high diversity of a given community due in large part to nonequilibrium fluctuations in its species.

At a different level, my data on plant community composition also seem much less predictable and much more in accordance with the nondeterministic, nonequilibrium viewpoint. In the nine 1-ha tree plots that have been analyzed, there was not a single repetition of a most-dominant species. Although one (or a few) species is always much more common, there is a different "dominant" species in each plot. Even if the several most-dominant species in each plot are compared, there is little overlap. Considering only those species with 10 or more individuals per hectare in at least one tree plot generates a list of 54 species documented to be relatively common locally somewhere in upper Amazonia. But of these, only five species are abundant on two different plots. The shared abundant species include *Astrocaryum murumura*, common on all three rich-soil plots (Yanamono, Cocha Cashu, Tambopata alluvial), and *Hevea guianensis*, common on three poor-soil plots. The other shared abundant species are *Otoba parviflora* on two of the three rich-soil sites (Yanamono and Cocha Cashu) and *Iriartea deltoidea* on a different pair of rich-soil sites (Cocha Cashu and Tambopata alluvial). But even though the same species are

generally not abundant at different sites with similar ecology, they are usually *present*. If we take the three rich-soil tree plots as an example, all the abundant Tambopata alluvial-plot species are present in the Yanamono plot, and all the abundant Yanamono species, except *Otoba glycicarpa* and *Carapa guianensis*, are present at Tambopata. All of the abundant Cocha Cashu species are at Yanamono, and all but four of the abundant Yanamono species are at Cocha Cashu. If we compare the sandy-soil plots from Mishana and Cabeza de Mono, there is only one species abundant at both sites (*Hevea guianensis*), but all the common Cabeza de Mono species are present at Mishana, and most of the common Mishana species are at Cabeza de Mono. In contrast, only four species that are abundant at any poor-soil site are present at all in any rich-soil site, all at Yanamono, which has an intermediate level of soil fertility. The relevant point is that although the species present at a site may be predictable, the frequency of a particular species in different forests seems entirely unpredictable and is likely determined stochastically. This is similar to the concept that Shmida & Wilson (1985) have termed "ecological equivalency," i.e., the coexistence of species with effectively identical niche and habitat requirements for largely stochastic reasons. It is also the pattern that would be predicted by Hubbell's (1979; Hubbell & Foster, 1986) community drift theory. Indeed, Grubb (1986) generalized that the relatively sparse or rare

species that of necessity constitute the bulk of the species of species-rich communities should interact so infrequently with each other that niche differentiation becomes largely irrelevant.

The same conclusion arises from the 0.1-ha samples. There are almost always a few very common species in any sample. One of these is usually much more common than all the others; at 11 sites the most common species was between two and seven times more common than the second most common species. Yet the only repeat of a "most dominant" species among 25 moist- and wet-forest sites is *Catoblastus velutinus*, shared between Rio Palenque and immediately adjacent Centinela in western Ecuador. For 12 dry-forest sites there was not a single repeat of a "most dominant" species.

Even if all 213 species that are dominant or subdominant in any of these samples (i.e., among the most common 5–10 species) are considered, only 38 are repeated in two or more different samples; ten of these repeated common species (13 if Rio Palenque and Centinela are considered part of the same site) are in repeat samples of the same forest. Thus, only 24 species are abundant at more than one site. One species, *Socratea exorrhiza*, is abundant at four sites, and three species—*Jessenia bataua, Arrabidaea oxycarpa,* and *Arrabidaea pubescens*—are abundant at three sites. Ten of the 24 species abundant at more than one site are shared between different dry forests, twelve are shared between different moist forests (typically between Central America and Amazonia), and one (*Mansoa verrucifera*) is abundant in one dry-forest and in one moist-forest site.

A major part of the debate on whether tropical-forest ecosystems are at equilibrium or nonequilibrium may be a by-product of the scale of a particular study or the focus of a particular author. The "rare" species that "random walk" through a 50-ha plot on Barro Colorado Island are mostly common understory or second growth species that would be regarded as permanent and continuous members of the more comprehensive moist-forest

plant community that a biogeographer might define. The numerous microhabitat specialists suggested by a casual glance at a series of the Hubbell-Foster Barro Colorado Island distribution maps become nonspecialists if the relatively few individuals that occur away from a favored habitat are emphasized. I suspect that differences in taxonomic focus may also relate to the interpretational differences. Hubbell focused entirely on a particular combination of *species* in addressing the question of community equilibrium. My data suggest that while the species that make up different communities may be very inconstant from place to place, at the same time the different families (and perhaps genera) that contribute to community floristic diversity are very consistent. Perhaps the family is the basic unit on which selection for low population densities (and thus indirectly for high species richness) occurs. For example, many seed predators and leaf-eating insects are host-specific at the generic or familial, as well as the specific, level (Janzen, 1975, 1980, 1984). If family-specific predators and/or family-specific competition are added to the scenario of dynamic forests with some niche differentiation, an explanation pleasing to selectionists and nonselectionists alike could begin to take shape. As indicated in Table 1, the familial diversity of tropical moist and wet forests, unlike the species richness, is both high and remarkably constant. It is certainly within the realm of possibility that this is due to ca. 50 family-specific niches in a given forest, whereas the differing species richness of different forests could be largely stochastically generated by factors relating to higher turnover in the more species-rich sites on better soils and with higher productivities.

A different type of reconciliation, especially of the differences between upper Amazonian and Central American species richness, their causes, and the equilibrium status of the forests involved, might come from a different approach to the data. Hubbell & Foster (1986) emphasized that niche differentiation among Barro Colorado Island species seems to consist mostly of separation into

about a dozen generalized multi-species guilds based on degree of shade tolerance and preference for edaphic or topographic microsites. Indeed they suggest that *lack* of niche differentiation might make possible the co-occurrence of many potential competitors which are forced to share the same generalized niche. But by and large the lowland forests of Central America are composed of the same species that in Amazonia would be regarded as the most widespread and weediest species of their respective families or genera (Gentry, 1982a, 1986c). A relatively depauperate Central American forest made up of species adapted for weedy generalized strategies might have little in common with an upper Amazonian forest composed mostly of narrow-habitat specialists. Given a few million more years of evolution, perhaps Central American forests might seem much closer to ecological equilibrium than they do today.

It is no accident that many tropical biologists who have considered the question of why tropical forests are so rich in plant species have greatly modified their original views, no matter on which side of the equilibrium/non-equilibrium question they began (Ashton, 1969 vs. 1984; Hubbell, 1979 vs. Hubbell & Foster, in press; Gentry, 1982b vs. 1982a and Gentry & Dodson, 1987b). We still know so little about tropical forests that generalizations elude us. Almost certainly there are elements of truth on both sides of the question. Quite possibly different forests and the different taxa that make them up will often prove to be doing things quite differently. Although we have not yet reached anything like a consensus on how different factors, or even which factors, interact to determine diversity, it seems abundantly clear from the data presented here that there are discernible and surely deterministic patterns in the species richness of different plant communities. I conclude that which families, how many species, and possibly what individual species make up a tropical plant community are to a large extent deterministic and predictable from simple environmental parameters; how common the species are and how they are put together

into different communities may be completely random.

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