NEOTROPICAL FLORISTIC DIVERSITY: PHYTOGEOGRAPHICAL CONNECTIONS BETWEEN CENTRAL AND SOUTH AMERICA, PLEISTOCENE CLIMATIC FLUCTUATIONS, OR AN ACCIDENT OF THE ANDEAN OROGENY?[1,2]

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The interchange of plant species between North and South America has been a major factor in determining the Neotropical phytogeographical patterns observed today. Although this has long been realized, recent historical geological evidence as well as increasing knowledge of today's distributional patterns now makes possible a more thorough analysis of how these patterns originated. This paper briefly reviews the geological background, summarizes the composition of the extant Neotropical flora, points out the striking ecological consistency of many taxa and life forms, and suggests how some of the present phytogeographical patterns have developed from the interplay of these factors.

GEOLOGICAL BACKGROUND

Several major geological events have had profound effects on the evolution and distribution of the Latin American flora. One of the most significant of these was the separation of South America from Africa that began only 127 million years BP (Rabinowitz, 1976; McKenna, 1981) with contact or near-contact present until 80–90 million years BP (Raven & Axelrod, 1974; McKenna, 1981). During most of the first third of angiosperm evolution, a time during which many of the modern orders and families of plants arose, South America was a part of the West Gondwanaland cradle of the angiosperms (Raven & Axelrod, 1974). However, during virtually all of the Tertiary and much of the Cretaceous South America was an island continent, at least from the perspective of tropical plants, and most of the evolution of its rich and varied flora took place in isolation following separation from Africa. Thus, such characteristic and ecologically important trop-

ical American angiosperm families as Bromeliaceae, Humiriaceae, Cactaceae, and Caryocaraceae, had ample time to evolve and radiate in South America.

Although the history of the separation of South America from Africa is clear, the tectonics of the earlier separation of North America from the Gondwanan land mass is still uncertain (see Coney, this symposium). Apparently North America (including the Central American peninsula) separated from Africa-South America in Jurassic time, well before the origin of the angiosperms (Lillegraven et al., 1979). However, by late Cretaceous a chain of volcanic islands (Nicoya Complex) had developed connecting Central America with Ecuador (Dengo, 1975; Lillegraven et al., 1979). New geological evidence (Dickinson & Coney, 1980) suggests that a connection between nuclear Central America and South America was reestablished in Late Cretaceous as both major American land masses moved westward more or less in tandem.

How much of the late Cretaceous connection between Central and South America was above sea level is not known, although it probably consisted mostly of an interrupted island arc. Further complicating the picture, much of northwestern South America was submerged during most of the Cretaceous (Irving, 1975). Both the low coastal range of western Colombia and southern Darien and the northern Andean Cordillera Occidental were originally island arcs associated with westward movement of the South American plate during upper Mesozoic time (Zeil, 1979: 193). McKenna (1981) has suggested that the present Pacific coast of northern South America may have resulted from accretion during the early Tertiary of left-behind fragments of the south end of the Central American volcanic arc. According to McKenna (1981) some of the islands of this arc may have remained above water, separated from North America only by sequential opening and closing of water gaps, until colliding with South America and providing a plausible scenario for "Noah's Arc" dispersal of hystricognath rodents between North and South America, a model consistent with the discovery by Juteau et al. (1977) that much of the west coast of Ecuador is formed from a block of originally oceanic crust.

There was a general regression of epicontinental seas from northwestern South America at the end of the Cretaceous (Harrington, 1962; Lillegraven et al., 1979) concomitant with a late Cretaceous orogeny that gave rise to the forerunner of the Colombian Cordillera Occidental (Irving, 1975). More than 160 km was added to the northwestern South American continental margin during Late Cretaceous time. The Greater Antilles, then far to the south of their present position and in part submerged, presumably also constituted part of some kind of late Cretaceous inter-American connection as suggested by Malfait and Dinkelman (1972) and discussed in the context of biogeography by Tedford (1974) and Rosen (1974). (See Pregill (1981) for a different interpretation but much of the geology on which it is based (Perfit & Heezen, 1978) has apparently been superseded (Dickinson & Coney, 1980; Coney, this symposium).) According to this interpretation, the continued westward movement of South America and the slightly southwestward movement of North America led to decoupling faults that separated the proto-Antilles from both land masses. A new subduction zone then formed to their northeast as the proto-Antilles moved northeastward. Continued westward movement of South America and southwestward movement of North America led to

pinching off of a segment of the Pacific plate as the Caribbean plate, with relatively eastward displacement of the whole Caribbean region relative to South America. Probably nuclear Central America south of the Motagua fault also moved eastward with the Caribbean plate from an original position more directly south of Mexico, closing part of the gap between North and South America (Dickinson & Coney, 1980). In the late Teritary, formation of the Central American trench and an associated new epoch of volcanism again led to uplift of islands in the region between South America and nuclear Central America. These islands eventually coalesced into today's lower Central America with substantial land connection across the Isthmus of Panama established in the Pliocene apparently only about 3 million years ago (Keigwin, 1978; Marshall et al., 1982).

Although closing of the Isthmus of Panama between North and South America was clearly one of the most important "changing Cenozoic barriers" for the Latin American biota, the presence of a previous, albeit interrupted, late Cretaceous connection would have provided shorter water gaps between the continents fairly early and thus may modify our concept of the phytogeographical importance of this late event. In late Cretaceous time many modern families and genera of plants were extant in West Gondwanaland and in a position to take advantage of island stepping-stones between South and North America.

Thus most of the cases of exclusively or predominantly American families like Cactaceae with strongly differentiated components in both tropical North and South America, which Raven and Axelrod (1974) accounted for by chance relatively long distance dispersal at various times during the early Cenozoic, may reflect instead more or less direct late Cretaceous migration between the two continents, presumably mostly via island hopping. Similarly, the dichotomous composition of the West Indian flora, with both strong southern and northern affinities, would be expected as the result of an original stocking of a proto-Antillean region located between North and South America as emphasized by Rosen (1974), although his arguments for direct land connections do not accord with the geological evidence (Coney, this symposium). This dichotomy may have been even stronger in the early Tertiary to judge from the presence of now locally extinct otherwise exclusively South American taxa like *Aetanthus* (although there may be identification problems in separating this from the generalized northern *Loranthus* pollen type that was already present in Europe in the Eocene, according to Muller, 1981) and *Catostemma* in the Oligocene of Puerto Rico (Graham & Jarzen, 1969) along with northern elements like *Fagus, Hauya, Engelhardtia, Liquidambar*, and *Nyssa*, which have never been able to reach South America.

That the interrupted link between North and South America was completely ruptured at the beginning of the Tertiary, as the proto-Antilles began their northward movement, means that only those very old taxa already extant in the Cretaceous would have had the opportunity for more or less direct inter-American island hopping prior to the Pliocene formation of the Isthmus of Panama. In general, the flora of the early Tertiary of what is now temperate North America seems to have been more like the modern tropical American flora than it is today. However, it is very difficult to judge to what extent the apparent affinities of Paleocene and early Eocene North American and South American floras might

represent shared descent from hypothetical common wide-ranging middle Cretaceous early angiosperm stocks, or whether they suggest an independent, relatively direct floristic interchange between South America and tropical North America subsequent to the separation of Africa and South America. The difficulty of floristic interpretation is compounded by the serious taxonomic errors in identification of fossil floras that are now known to have characterized much early paleobotanical work (cf. Graham, 1972: 8; Dilcher, 1974; Hickey & Wolfe, 1975). As summarized by Leopold and MacGinitie (1972), the floristic affinities of the Rocky Mountain region, the only part of then biotically tripartite North America in potentially direct contact with nuclear Central America, show successive changes through the early Tertiary. They find the generalized Paleocene flora difficult to relate to that of any extant phytogeographic region, but suggest that the mesic early Eocene flora was primarily related to the southeast Asian subtropical and warm-temperate mixed mesophytic forest, the middle and late Eocene floras to those of the subhumid Central American tropics, the Oligocene flora to the live oak forests of the highlands of northern Mexico, and a final shift to modern Cordilleran conifer forests in the Miocene (Leopold & MacGinitie, 1972). Presumably most of the genera shared with South America during the latest Cretaceous and earliest Tertiary reflect wide-ranging Cretaceous common ancestors (cf. Raven & Axelrod, 1974), while the subhumid middle and late Eocene flora analyzed as characteristically and autochthonously tropical American in origin would have to represent either an old uniquely tropical North American flora (which later must have spread to South America to account for the overwhelmingly pan-American distributions of most of those genera today) or early floristic interchange with South America. Contrary to the Central American[4] distributional centers suggested for such genera as *Ocotea, Beilschmiedia, Cedrela, Luehea, Oreopanax,* and *Swartzia* by Leopold and MacGinitie (1972), all are better represented today in South America than in Central America with the possible exception of *Cedrela* (three of the eight species only in Central America, and two others also occurring there). Even three of the four genera—*Homalium, Bernoullia, Beilschmiedia,* and *Engelhardtia*—related to Rocky Mountain fossil forms and suggested as endemic to Central America in their American ranges, are as well or better represented in South America. Unfortunately the Tertiary fossil record from Central America and South America is inadequate to show when such genera achieved their modern pan-neotropical distributions, but phytogeographic and ecological evidence suggests that it was long before establishment of the Panamanian land bridge. Many of these plants have wind-dispersed or mammal-dispersed seeds or fruits and are unlikely candidates for long distance dispersal (Gentry, 1982a), which would be consistent with having achieved their present distributions via a relatively direct inter-American migration route, presumably prior to the Eocene.

Although some South American floristic elements evidently reached Central America early, perhaps via island hopping along the late Cretaceous Antillean connection, the Tertiary floras of South America and North America remained

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[4] Central America is used throughout this paper in a broad sense to include Mexico.

fundamentally different (Germeraad et al., 1968). For example Graham's (1973, 1982) analysis of the Paraje Solo formation suggests that in the Miocene the southern Veracruz lowlands had only a few scattered representatives of the South American-derived tropical forest which now characterizes the region, while a basically North American plant community, similar to the deciduous forest of the eastern United States and today restricted to intermediate elevations, was well represented. Pollen of ten of the fourteen arborescent genera that would have been expected in similar deposits in the southeastern United States is present. While redeposition of pollen from plants growing at higher altitudes could have affected these results (Axelrod, pers. comm.), it is clear that the eastern deciduous forest elements were at least present in the region. In contrast, the Paleocene pollen flora of Colombia contained exclusively such lowland tropical elements as Annonaceae, Bombacaceae, Melastomataceae, Araceae, and several genera of palms: *Mauritia, Astrocaryum,* and several pollen genera (Hammen & Garcia, 1966).

Further south in Central America, in then recently emerged Panama, only three of the temperate North American genera—*Alnus, Juglans,* and *Myrica*—are present in the Miocene Gatun formation and none of them are present in earlier Panamanian deposits (Graham, 1973). These same three genera appear in the South American palynological record only subsequent to closing of the Isthmian connection in latest Pliocene and Pleistocene times. The many widespread South American families and genera that today barely enter Central America in eastern Panama provide evidence that the Tertiary barrier to northward migration was equally effective. As might be expected, none of the South American taxa that barely enter Central America are represented in the West Indies either. To summarize, the water gap between North and South America separated two very distinct Cenozoic floras in the two continents despite a probable early opportunity for relatively direct island hopping across the proto-Antillean chain. However, the opportunity for limited late Cretaceous migration between South and North America would readily account for the many characteristically Gondwanan taxa with distinctive and strongly differentiated Central American derivatives (see below).

The second Cenozoic geological event with major phytogeographical importance for the Neotropics was the uplift of the Andes. Although the Andean orogeny was certainly more complicated than often supposed (Zeil, 1979), the general picture of major uplift of the already extant southern and central Andes in the Mid-Cenozoic and of the northern Andes more recently seems well established. The Colombian Cordillera Central is older and existed already in the Cretaceous (Zeil, 1979: 109) but probably was eroded down to a low range of hills prior to the recent orogeny. Most of the uplift of the northern Andes took place only in the last five million or so years, during Pliocene and Pleistocene times (Hammen, 1974; Flenley, 1979). The Andes are unique: by far the most extensive mountain range in the world's tropics.

A third event of major phytogeographic importance was the advent of Pleistocene climatic fluctuations associated with glacial advances and retreats at higher latitudes. In the montane tropics these climatic oscillations took the form of an altitudinal lowering and compression of vegetational zones, as elegantly docu-

mented by van der Hammen (1974) and his associates from the palynological record in the Colombian Cordillera Oriental. In the lowland tropics temperature changes associated with glacial advances were minimal but changes in precipitation were pronounced. The cycles of glacial advance and retreat were associated in the tropical lowlands with alternating dry and wet periods respectively. Contrary to early suggestions (e.g., Haffer, 1970), the wet periods of the tropics were not the same as the well known pluvial periods of arid temperate and subtropical deserts that accompanied glacial advances. Instead, tropical wet periods were perhaps 180° out of phase with the temperate-subtropical pluvial periods; as if the glacial advances tied up so much of the water of the earth's normal atmospheric circulation that not enough was left for "normal" tropical rainfall. As a result of these cyclical changes in precipitation the lowland neotropical forests were periodically reduced in extent to scattered pockets, chiefly around the periphery of Amazonia during dry periods (Haffer, 1969, 1978; Simpson, 1971; Prance, 1973, this symposium; Simpson & Haffer, 1978).

The biological significance of this dynamic model, very different from the popular conception of the stable "forest primaeval," is that it provides optimal conditions for speciation, as populations of tropical forest species repeatedly fragment and recoalesce (see papers in Prance, 1982). Some problems with the Pleistocene refuge model have been noted. For example, have long-lived trees and lianas had adequate time to speciate so profusely in the relatively short time and few generations available since the beginning of the Pleistocene? Moreover the distributional patterns that have been cited as evidence for former refugia—species pairs in many unrelated taxa coming together at coincident contact zones—could also result from in situ speciation along environmental gradients. Nevertheless the Pleistocene refuge model has been widely accepted by biogeographers as a general explanation accounting for much tropical speciation. Not only did forest species successfully survive dry periods in these habitat islands, but the repeated cycles of multiple range fragmentation could potentially have multiplied their numbers. In other words, the Neotropics have many species because of the multiplicative effect of its more numerous refugia; Africa has few because it generally lacked such refugia.

FLORISTIC BACKGROUND

One of the outstanding features of the Neotropical flora is its extreme richness in species. Thus Raven's (1976) estimate for number of Neotropical plant species was 90,000, three times as high as his estimate for tropical Africa plus Madagascar and 2½ times the estimate for tropical Australasia. Prance (1977) and other authors have generally accepted Raven's estimates. Other recent, perhaps slightly higher, estimates for continental floristic diversity are available for the Palaeotropics—30,000 species for continental tropical Africa alone (Brennan, 1979) and 25,000–30,000 species for the Flora Malesiana region (Jacobs, 1974). Nevertheless it seems clear that the estimated number of plant species for the Neotropics is much higher than for the entire Palaeotropical region. Prance (pers. comm.) estimates 30,000 species for Amazonian Brazil alone and the best available estimate for Central America is 18,000 to 20,000 (Gentry, 1978) and an (overlapping) one for Mexico is 14,000 to 20,000 (Rzedowski, 1965, 1978).

While it is generally appreciated that Africa is floristically relatively depau-
perate (Richards, 1973; Brennan, 1979), many studying the flora of Southeast
Asia (Whitmore, 1975; Ashton, 1964, 1977) have suggested that the dipterocarp
forests of that region are the world's richest, citing samples of number of tree
species over 10 cm dbh as evidence. Actually, Prance et al.'s (1976) recent sample
of 179 tree species ≥15 cm dbh in a hectare of forest near Manaus is as diverse
as most of the Southeast Asian forests. If individual Southeast Asian forests have
as many or more tree species as their neotropical equivalents, can the Neotropics
really have as many more species as suggested by Raven's estimates?

The available estimations of Neotropical floristic diversity are very tentative.
In order to assess more accurately whether the Neotropics are really as incredibly
species rich as suggested by Raven's estimates, I decided to try to count the
number of species directly. First, I compiled a list of all Neotropical seed plant
genera based on the available regional floras and familial monographs, supple-
mented by a search through the entire Missouri Botanical Garden herbarium for
additional generic names from the region. Although a few small local genera were
probably missed, the resulting list of over 4,200 Neotropical genera seems rea-
sonably complete. Second, I estimated the number of Neotropical species in each
genus, using recent monographs such as the Flora Neotropica series, when treat-
ments were available, and the figures supplied by Willis's Dictionary (Airy Shaw,
1973) in most other cases. A few additional data sources on species numbers were
used for some groups—Compositae were taken from Heywood et al. (1977), Le-
guminosae mostly from Polhill and Raven (1981), Orchidaceae from Dressler
(1981), Solanaceae from D'Arcy (1979), Verbenaceae and Eriocaulaceae from
Moldenke (1980), Gramineae (mostly Davidse, pers. comm.), and Bignoniaceae,
Sabiaceae, and Buxaceae from my own data. The Willis figures for species num-
bers are directly useful only for genera restricted to the Neotropics and in the
few cases where species numbers for a genus are given by geographical region.
The resultant data set accounted for over 3,660 genera with almost 65,000 Neo-
tropical species.

Unfortunately, the other 533 non-monographed non-endemic Neotropical gen-
era include a total of 60,000 species based on the Willis figures. These genera fall
into two main groups—large pantropical genera like *Piper* or *Eugenia,* or basically
Laurasian herbs that range south into the montane Neotropics. About 20,000 of
these species fall into pantropical genera that tend to be well represented in the
Neotropics suggesting that a third to a half (i.e., 7,000–10,000) of them are Neo-
tropical. The remaining 40,000+ species are either in cosmopolitan genera (e.g.,
Ipomoea) or are basically temperate zone genera with relatively poor Neotropical
representation (e.g., *Astragalus, Draba, Carex, Gentiana*). Perhaps only 10–15%
of the total species of these genera are Neotropical, implying an overall total of
at least 76,000 Neotropical species.

However, there is another serious problem in compiling such an estimate. The
Neotropics are generally much more poorly known floristically than other parts
of the world and very many Neotropical plant species remain undescribed. In
regions like the western Colombian Chocó, probably a quarter of all plant species
are strictly endemic and in many groups like Araceae or Ericaceae almost none
of the endemic species have been described (Gentry, 1982a). A well-documented

example comes from the Río Palenque field station in western Ecuador where, in the process of writing a local florula (Dodson & Gentry, 1978), 61 new species were discovered in a minuscule 1.7 km² area; subsequent collections and re-evaluation of tentatively identified problem taxa now brings the total to almost 100 species described from Río Palenque. Such figures suggest that there must be at least 10,000 undescribed neotropical plant species that would elevate the total number of neotropical seed plant species to 86,000 or more.

We may conclude that Raven's original estimate of 90,000 neotropical species was fairly accurate. That the neotropics as a whole are extraordinarily richer in plant species than other parts of the world seems established beyond any serious doubt.

The Neotropical flora generally shows very strong pantropical connections. That pantropical distributions predominate among tropical families is well known (e.g., Good, 1974). However, these phytogeographic similarities are even stronger than generally realized, especially at the generic level and especially with Africa. For example, 30% of the genera that occur at Makokou, Gabon, are also found in the Neotropics and many more African genera are more like some Neotropical genus than like other African ones (Hladik & Hallé, 1973; Gentry, in prep.). Statistical comparisons of percentages of genera in common between different tropical areas (e.g., Thorne, 1973) are especially misleading since the important genera tend to be shared while small segregate genera contribute disproportionately to the differences. The picture is also confused by taxonomic parochialism on the part of workers on different continents.

The relevant point of these pantropical floristic similarities in the context of this analysis is that the peculiarities that distinguish the present Neotropical flora have arisen despite a common floristic stock shared at least with Africa (i.e., West Gondwanaland) and to a large extent with tropical Asia as well. In this context it is almost irrelevant whether this intercontinental commonality was derived from dispersal events or continental movements. The question to be addressed here is why this shared floristic stock has given rise to so many more species in the Neotropics.

ENDEMIC FAMILIES

The greater diversity in the Neotropics results in part from a conspicuously larger and more ecologically important complement of endemic families. Even retaining traditional broad familial delimitations, there are at least 38 endemic or essentially endemic (i.e., with one or two African species, most of whose ancestors probably arrived relatively recently via long distance dispersal) Neotropical families with a total of 5,690 species (Table 1). Thirteen of these families have over 50 species as compared to only three endemic palaeotropical families with more than 50 species—Dipterocarpaceae[5] (580 spp.), Pandanaceae (700 spp.), and Nepenthaceae (68 spp.). Six essentially endemic Neotropical families have over a hundred species, and two—Bromeliaceae and Cactaceae—have about 2,000

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[5] The discovery of a primitive dipterocarp in South America (Maguire & Ashton, 1977) does not change the status of the family by the definition of "essentially endemic" used here.

TABLE 1.   Endemic Neotropical families (in some cases with a single African species or a single monotypic or ditypic African genus presumably recently arrived by long-distance dispersal).

1) *Tropical forest taxa**

Bromeliaceae (46 genera/2, 108 species (plus 1 sp. in Africa))
Caricaceae (3/29 (plus one ditypic African genus))
Caryocaraceae (2/24)
Cyclanthaceae (11/178)
Dialypetalanthaceae (1/1)
Duckeodendraceae (1/1)
Humiriaceae (8/46 (plus 1 sp. in Africa))
Lacistemmaceae (2/14) (included in Flacourtiaceae in Flora Neotropica)
Marcgraviaceae (4/125)
Quiinaceae (4/53)
Rapateaceae (15/79 (plus 1 monotypic African genus))
Vochysiaceae (7/182 (plus 1 ditypic African genus))

Trigoniaceae/*Trigonia* (1/24)
Bignoniaceae/Bignonieae (46/359)
Lecythidaceae/Lecythidoideae (300)

2) *Taxa of dry and/or Andean parts of South America (a few reaching North America)*

Brunelliaceae (1/51)
Calyceraceae (4/46)
Columelliaceae (1/4)
Gomortegaceae (temp.) (1/1)
Malesherbiaceae (1/27)
Myzodendraceae (temp.) (1/11)
Nolanaceae (1/18)
Tovariaceae (1/2) (included in Capparidaceae in Flora of Panama)
Tropaeolaceae (2/92)

3) *Taxa of dry parts of tropical North America*

Crossosomataceae (1/4)
Fouqueriaceae (2/8)
Garryaceae (1/18)
Lennoaceae (3/8) (1 rare species on the dry Caribbean coast of northern Colombia)
Theophrastaceae (5/110) (a few species of *Jacquinia* and *Clavija* in South America)

4) *Taxa of dry tropical/subtropical parts of both continents*

Cactaceae (62/2,000) (a widespread species also in Africa and Ceylon with at least 1 derivative in Madagascar)
Julianaceae (2/5) (but probably an artificial group)
Koeberliniaceae (1/1)
Krameriaceae (1/15)
Loasaceae (12/266 (plus 1 in Africa)) (several small genera in Mexico and SW U.S.)
Martyniaceae (3/13)

5) *Miscellaneous (aquatics or semiaquatics and Guayanan edaphic specialists)*

Cannaceae (1/55)
Cyrillaceae (3/13) (?) (in Europe in Eocene; mostly West Indian)
Mayacaceae (1/9 (also 1 in Africa))
Saccifoliaceae (1/1)
Sarraceniaceae (?) (3/17) (only 1 genus (6 spp.) in tropics)
Tepuianthaceae (1/5)
Thurniaceae (1/3)

* I have followed traditional familial limits. Rhabdodendraceae (2 species) was treated as a distinct family in Flora Neotropica. The other families listed by Prance (1978) as endemic are segregates (e.g., Peridiscaceae), erroneously listed (Pontederiaceae), or both (Heliconiaceae).

species each. Unlike most of their Palaeotropical counterparts, many of the Neo-tropical-restricted families are ecologically important. Bromeliaceae is one of the major epiphyte families; Cactaceae dominate many dry regions. Families like Caryocaraceae, Humiriaceae, and Vochysiaceae are important canopy trees of lowland tropical forests. To these may be added such speciose endemic groups as tribe Bignonieae of Bignoniaceae (Gentry, 1980a), which is the predominant group of Neotropical lianas; subfamily Lecythidoideae (Lecythidaceae; Prance & Mori, 1979), which is one of the predominant taxa of canopy trees of Ama-zonian forests; or subtribes Pleurothallidinae, Maxillarinae, and Oncidinae of the Orchidaceae, which together comprise nearly 5,000 species of Neotropical epi-phytes (Dodson, pers. comm.).

It is noteworthy that many of the endemic families listed in Table 1 are taxa of dry, more or less subtropical habitats. The only endemic tropical North Amer-ican families—Crossosomataceae, Fouqueriaceae, Garryaceae, Koeberliniaceae (disjunct to Paraguay), and Lennoaceae (also local in extreme northern Colom-bia)—are dry area specialists. Although endemic, basically South American fam-ilies are more diversified ecologically, many of them, including Malesherbiaceae, Nolanaceae, and amphicontinental Cactaceae, Martyniaceae, Julianaceae, Kra-meriaceae, and Loasaceae are predominantly plants of dry areas.

Although these endemic taxa make an appreciable contribution to Neotropical species richness, the question of *why* families that evolved in the Neotropics have speciated more profusely than their Palaeotropical equivalents has not yet been addressed.

LAURASIAN TAXA

The phytogeographical significance of the new developments in plate tectonics was first brought into focus by Raven and Axelrod (1974). One of the major thrusts of the Raven-Axelrod synthesis was the fundamental difference between the floras of the northern or Laurasian continents and those of the now widely separated southern continents that were clustered together at the time of origin of the angiosperms. Even before plate tectonics became generally accepted, it had been realized that the high altitude South American flora was largely derived from north temperate sources and that the Panamanian isthmus had been a critical barrier to the southward migration of many northern taxa. One of the contribu-tions of the Raven and Axelrod synthesis was pointing out the remarkable degree to which many plant families, even those shared by both North and South Amer-ica, can be unambiguously referred either to the Gondwanaland or to the Laur-asian floras on account of their general distributional patterns and the fossil rec-ord. They listed 51 basically Gondwanaland plant families (or equivalent units) that probably spread from South America to North America in the middle to late Cenozoic as the Isthmian barrier decreased, and an additional 54 families (or equivalents) whose original presence in North America was probably older but whose major presence there probably resulted from mid- to late-Cenozoic migra-tion from South America. Similarly a list of 29 Laurasian families (or equivalents) whose major arrival in South America probably coincided with building of the Isthmus of Panama in late Miocene to Pliocene was suggested, nine of them qualified as perhaps already having had a prior presence in South America; 11

TABLE 2. Laurasian elements of the Neotropical flora. Numbers indicate Neotropical genera with known species numbers/species in those genera (+ Neotropical genera for which species estimates are unavailable/total species in those genera).

†Aceraceae	1/5		(Krameriaceae)	1/15	
Actinidiaceae	1/80		Labiatae (?)	14/489	(+13/1,594)
*Aquifoliaceae	1/150		†Lennoaceae	4/8	
Aristolochiaceae	3/182		Liliaceae	23/167	(+15/1,217)
†Balsaminaceae	1/2		*Lythraceae (?)	16/361	
*Basellaceae	3/7		Magnoliaceae		(+2/130)
Bataceae	1/1		Myricaceae		(+1/35)
Berberidaceae	1/24	(+1/450)	†(Nyssaceae)	1/1	
Betulaceae	3/5		Oleaceae	8/52	
Boraginaceae (?)	11/96	(+14/1,020)	Orobanchaceae	1/2	(+1/140)
Buxaceae	3/42		Papaveraceae	1/1	(+3/120)
Callitrichaceae (?)		(+1/25)	†Pinaceae	4/40	
Caprifoliaceae	1/2	(+4/458)	Plantaginaceae	1/1	(+1/265)
Caryophyllaceae	6/77	(+15/1,389)	†Platanaceae	1/7	
*Celastraceae	16/102	(+4/361)	Plumbaginaceae	2/7	
*Chloranthaceae	1/40		Polemoniaceae	4/33	(+5/276)
Cistaceae		(+3/120)	Primulaceae	2/4	(+2/210)
			Pyrolaceae	1/1	(+3/33)
Clethraceae	1/38		Rafflesiaceae	4/29	
Cornaceae	2/8	(+1/6)	Ranunculaceae	3/14	(+7/1,097)
Crassulaceae	3/25	(+4/515)	*Rhamnaceae	23/168	
†Crossosomataceae	1/4		Rosaceae	16/95	(+15/2,279)
Cruciferae	19/93	(+16/1,304)	*Sabiaceae (?)	2/47	
Cyrillaceae	2/13		Salicaceae	2/30	
Droseraceae	1/20		Saxifragaceae	12/85	(+5/730)
Empetraceae	1/1		Scrophulariaceae	70/853	(+4/185)
Ephedraceae (?)		(+1/40)	Staphyleaceae	2/5	(+1/30)
Fagaceae	4/164		Styraceae	1/3	(+1/130)
†Fouqueriaceae	2/8		Symplocaceae	1/160	
†(Garryaceae)	1/18		*Theaceae	7/84	(+2/130)
Gentianaceae	19/494		Theophrastaceae	3/107	
Geraniaceae	4/42	(+2/490)	Typhaceae		(+1/10)
†Hamamelidaceae	3/5		*Ulmaceae	6/17	(+2/110)
Hippocastanaceae	2/3		Umbelliferae	48/480	
Hydrophyllaceae	2/46	(+3/230)	Valerianaceae	5/44	(+1/200)
†Illiciaceae	1/1		*Vitaceae	2/3	(+3/505)
Juglandaceae	4/18		Total	416/5,229	(+157/15,834)

† = does not reach South America.
* = listed as moving from South America to North America by Raven and Axelrod (1974).

other predominantly Laurasian families were suggested as probable earlier arrivals in South America. As thus interpreted, the modern flora of tropical America is of remarkably bipolar composition, with the great majority of its plant families having clearly Laurasian or clearly Gondwanan affinities. From this perspective, one might anticipate that the Neogene mixture of two different floristic elements via the Central American isthmus could have had a major effect on increasing floristic diversity, perhaps almost doubling the resultant flora of each of the two major neotropical regions. Although such floristic interchange also occurred in the Palaeotropics, it was less direct, interrupted by large expanses of desert in North Africa and a persistent water barrier between the Sunda and Sahul shelves in Australasia.

However, my analysis (Tables 2–6) suggests that adding together of Laurasian

TABLE 3.   Summary of transect data for plants over 1″ dbh in a 1,000 m² sample of lowland wet forest at Los Tuxtlas, Veracruz (precipitation of 4,100 mm a year) (Gentry, in prep.).

	No. Spp.	No. Ind.		No. Spp.	No. Ind.
Gondwanan Families					
			Palmae	4	113
Acanthaceae	1	1	Piperaceae	4	6
Anacardiaceae	1	2	Polygonaceae	2	2
Annonaceae	2	5	Rubiaceae	4	12
Apocynaceae	3	5	Sapindaceae	4	5
Araceae	3	3	Sapotaceae	3	8
Araliaceae	1	2	Solanaceae	3	5
Bignoniaceae	4	9	Tiliaceae	2	3
Bombacaceae	1	1	Urticaceae[a]	3	22
Capparidaceae	1	2	Violaceae	3	10
Caricaceae	1	2	Total	97	321
Compositae	2	3			
Convolvulaceae	1	1	*Laurasian Families*		
Dilleniaceae	2	7	Celastraceae	2	3
Euphorbiaceae	4	10	Rhamniaceae	1	2
Flacourtiaceae	2	2	Staphyleaceae	1	2
Hippocrateaceae	2	8	Ulmaceae	1	1
Lauraceae	5	9	Total	5	8
Leguminosae	7	12			
Malpighiaceae	4	7	*Unassigned Families*		
Meliaceae	5	6	Malvaceae[b]	1	1
Menispermaceae	1	1	Verbenaceae	2	2
Monimiaceae	1	3	indet. (cf. *Fraxinus*)	1	1
Moraceae	7	24	Total	4	4
Musaceae	1	7			
Myrtaceae	3	3			

Total: 106 species, including 29 liana species. For a similar 1,000 m² sample in a South American or southern Central American forest with 4,100 mm of rain 170 species over 2.5 cm diam. would be expected (based on the regression of species numbers versus precipitation calculated from the 19 sites of Gentry, 1981, 1982, and in prep.). The Veracruz diversity is significantly lower than the expected inner tropical value (R. Perozzi, pers. comm.). Note the overwhelming preponderance of Gondwana-derived families.

[a] Assignment as "Gondwanan" tentative.
[b] The Los Tuxtlas genus is *Robinsonella*, an exclusively Central American (= tropical Laurasian?) genus, and the family may be fundamentally Laurasian in origin.

and Gondwanan elements has not greatly increased overall Neotropical floristic diversity. There are over 10 times as many Gondwanan-derived as Laurasian-derived Neotropical species. The northward migrating Gondwanan taxa have so overwhelmed the corresponding southward migrating Laurasian taxa numerically that the latter's contributions to the total Neotropical flora have generally been relatively insignificant. This pattern is especially prevalent in the tropical lowlands of Central America, which must once have been populated by a tropical Laurasian floristic equivalent of the endemic Central American herpetofauna (Savage, 1966), mammalian fauna (Patterson & Pascual, 1972) or avifauna (e.g., Cracraft, 1973) (see Raven & Axelrod, 1974: 625–626). Graham (1976, 1982) has shown that a few South American taxa such as *Dichapetalum, Casearia, Laetia, Symphonia, Gustavia,* and *Byttneria* had already reached Veracruz, Mexico by Miocene times. Yet the Paraje Solo palynoflora was dominated by temperate North American

TABLE 4. Amazonian-centered Gondwanan families. Numbers indicate Neotropical genera with known species numbers/neotropical species in those genera (+ Neotropical genera for which species estimates are unavailable/total species in those genera).

Anacardiaceae (?)	15/133	(+2/257)	(Lacistemaceae)	2/14	
Annonaceae	28/555	(+3/250)	Lauraceae	11/700	(+4/870)
Apocynaceae	64/687	(+2/125)	Lecythidaceae	11/275	
Bignoniaceae	72/631		Leguminosae	216/2,980	(+48/8,189)
Bixaceae	1/5		Loganiaceae	12/136	(+2/106)
Bombacaceae	20/187		Malpighiaceae	44/801	
Burseraceae (?)	5/102	(+2/120)	Meliaceae	8/125	
Caryocaraceae	2/24		Menispermaceae	17/142	(+1/30)
Chrysobalanaceae	8/334		Moraceae	23/408	
Cochlospermaceae	2/8		Myristicaceae	5/81	
Combretaceae	7/97		Ochnaceae	9/67	(+1/300)
Connaraceae	4/57	(+1/100)	Olacaceae	13/87	
Convolvulaceae	21/1,000		Palmae	52/1,110	(+3/42)
(Dialypetalanthaceae)	1/1		Polygalaceae	6/183	(+3/630)
Dichapetalaceae	3/43		Quiinaceae	4/53	
Dilleniaceae	5/60		Rhizophoraceae	5/24	
(Duckeodendraceae)	1/1		Sapindaceae	27/438	(+5/490)
Ebenaceae	2/82		Sapotaceae	9/208	(+3/234)
Elaeocarpaceae	4/7	(+2/125)	Simaroubaceae	11/106	
Euphorbiaceae	92/2,607		Sterculiaceae (?)	14/293	(+2/360)
Flacourtiaceae	28/267		Tiliaceae	20/139	
Gnetaceae	1/6		Trigoniaceae	1/24	
Hernandiaceae	3/22		Turneraceae (?)	1/60	(+2/26)
Hippocrateaceae	12/114		Violaceae	11/98	(+2/650)
Humiriaceae	8/46		Vochysiaceae	7/182	
Icacinaceae	13/56		Total	961/15,866	(+88/12,904)

elements. Similarly an Oligocene site in Puerto Rico (Graham & Jarzen, 1969) was characterized by the presence, although at reduced levels, of several of the same north temperate genera that today are disjunct in the midaltitude "bosque caducifolia" of Mexico: *Liquidambar, Fagus, Nyssa* as well as such other Laurasian taxa as *Myrica, Engelhardtia,* and *Hauya*. These taxa led Graham and Jarzen to emphasize prior, more direct migration between Mexico and the Greater Antilles. Nevertheless a number of tropical South American taxa that must have arrived over water were present.

As the Isthmian connection closed, additional South American taxa moved north to completely dominate the Central American lowlands. Most of this invasion has been so recent that even at the specific level there has been little differentiation. Thus, in groups like tribes Tecomeae and Bignonieae of Bignoniaceae, virtually all of the species that reach northern Central America are indistinguishable from South American taxa (compare Gentry, 1982c with Gentry, 1973). There are only one species of Tecomeae and seven of Bignonieae in Guatemala that are not also in Colombia and Venezuela. Perhaps this northward migration is still taking place. At any rate, there is a clear northward decrease in the number of species of many Neotropical families (Gentry, 1982a). It seems likely that, in general, individual tropical lowland forests in northern Central America may be less diverse than their southern equivalents, as suggested by Sarukhan (1968). Toledo (1982) has shown that within Mexico tree species rich-

TABLE 5. Andean-centered Gondwanaland groups. Numbers indicate neotropical genera with known species numbers/Neotropical species in those genera (+ Neotropical genera for which species estimates are unavailable/total species in those genera).

5a. Northern Andes

Acanthaceae	61/1,493		Loranthaceae	16/592	(+1/15)
Araceae	38/1,386		Marantaceae	10/270	(+1/11)
Araliaceae	5/197	(3/356)	Marcgraviaceae	4/125	
Balanophoraceae	7/15		Melastomataceae	85/3,153	
Begoniaceae	1/600		Monimiaceae	8/246	
Bromeliaceae	46/2,108		Musaceae	2/82	
Brunelliaceae	1/51		Myrsinaceae	12/311	(+2/600)
Campanulaceae	9/568	(+7/712)	Nyctaginaceae ?	27/277	(+3/160)
Cannaceae	1/55		Orchidaceae	306/8,266	
Caricaceae	3/29		Oxalidaceae	1/8	(+2/870)
Columelliaceae	1/4		Passifloraceae	4/362	
Compositae	502/3,864	(+87/7,202)	Piperaceae	4/25	(+2/3,000)
Cyclanthaceae	11/178		Rubiaceae	147/2,906	(+21/2,545)
*Ericaceae	37/731		Tovariaceae	1/2	
Gesneriaceae	40/917		Tropaeolaceae	2/92	
Guttiferae	21/232	(+3/590)	Urticaceae ?	7/88	(+6/653)
Haloragidaceae	1/1	(+3/58)	Zingiberaceae	4/111	
			Total	1,425/29,345	(+141/16,772)

5b. Southern Andes/South Temperate

†Aetoxicaceae	1/1		Loasaceae	12/266	
†Araucariaceae	1/2		†Malesherbiaceae	1/27	
Calyceraceae	4/46		Myrtaceae	24/1,254	(+2/1,100)
Coriariaceae	1/1		†Myzodendraceae	1/11	
Cunoniaceae	3/12	(+1/170)	†Nolanaceae	1/18	
Cupressaceae	3/5		*Onagraceae	14/275	
†Epacridaceae	1/1		Podocarpaceae	1/37	
†Eucryphaceae	1/1		Portulacaceae	5/8	(+5/422)
†Frankeniaceae	3/8		Proteaceae	3/92	
†Gomortegaceae	1/1		†Restionaceae	1/1	
Hydnoraceae	1/6		Santalaceae	7/43	
Iridaceae	34/188	(+1/100)	Solanaceae	66/1,861	(+1/8)
Juncaceae	6/49		Winteraceae	1/1	
†Lardizabalaceae	2/3				
			Total	199/4,218	(+10/1,800)

† = does not reach Central America.

* = listed as moving from North America to South America by Raven and Axelrod (1974).

ness of the lowland tropical rain forest decreases dramatically northward. My data from a 1,000 m² sample of rich lowland rain forest in Veracruz also show fewer species than would be expected in a similar vegetation further south (Table 3). However, this pattern is shown only by lowland moist forest species: Mexican dry areas contrast in being very diverse, even in ultimately southern-derived taxa, with many endemic species (cf., Rzedowski, 1978: 75).

The relatively depauperate condition of lowland Central American forests may also have a much more recent origin and be due largely to Pleistocene climatic fluctuations. While drought has been considered the major effect of Pleistocene glaciation on the lowland tropics, Central America, at the margin of the tropics, may have been more affected by the concomitant general lowering of the temperature; many sensitive inner tropical taxa may have been eliminated or "con-

TABLE 6. Miscellaneous taxa. Numbers indicate neotropical genera with known species numbers/Neotropical species in those genera (+ Neotropical genera for which species estimates are unavailable/total species in those genera).

Guayana-centered groups		
Burmanniaceae	13/51	
Dipterocarpaceae	1/1	
Mayacaceae ?	1/9	
Podostemataceae	19/151	
Rapateaceae ?	15/79	
Saccifoliaceae	1/1	
Sarraceniaceae ?	1/6	
Tepuianthaceae	1/1	
Triuridaceae	4/12	
Total	56/311	
Dry-area Gondwanan groups		
Cactaceae	60/2,000	
Capparidaceae	10/40	(+4/416)
Erythroxylaceae	1/180	
Koeberliniaceae	1/1	
Martyniaceae	3/13	
Velloziaceae	4/229	
Zygophyllaceae	12/62	
Total	91/2,525	(+4/416)
Unassigned		
Aizoaceae	2/4	(+4/90)
Alismataceae	2/61	
Amaranthaceae	7/188	(+7/535)
Amaryllidaceae	26/799	(+3/210)
Asclepiadaceae	46/932	(+3/280)
Butomaceae	2/7	
Canellaceae	3/11	

Ceratophyllaceae	1/2	
Chenopodiaceae	10/34	(2/14)
Commelinaceae	17/163	
Cucurbitaceae	55/311	
Cyperaceae	8/88	(+18/3,738)
Dioscoreaceae	1/15	(+1/600)
Elatinaceae		(+2/45)
Eriocaulaceae	12/868	
Goodeniaceae	1/1	
Gramineae	127/838	(+80/4,692)
Haemodoraceae	1/2	
Hydrocharitaceae	8/20	
Juncaginaceae	2/5	
Lemnaceae	4/12	
Lentibulariaceae	3/116	
Linaceae ?	3/20	(+1/230)
Malvaceae	50/860	
Myoporaceae	1/1	
Najadaceae	1/8	
Nymphaeaceae	5/27	
Phytolaccaceae	13/78	(+2/38)
Polygonaceae	10/203	(+5/724)
Pontederiaceae	4/21	
Potamogetonaceae	5/42	
Rutaceae	36/233	(+4/313)
Taccaceae		(+1/30)
Thymelaeaceae	7/71	(+1/10)
Verbenaceae	40/1,143	
Xyridaceae	2/21	(+1/250)
Total	516/7,206	(+135/11,799)

fined southward'' by the slightly lower temperatures during glacial advances (Axelrod, pers. comm.). This may have been the ultimate fate of the tropical North American flora that is known to have inhabited even much of the southern and central United States during the Eocene and would be consistent with such patterns as the modern diversity of Sabiaceae, known to have been widespread in Tertiary North American tropical floras, which is greater in Panama and Costa Rica than it is in northern Central America (Gentry, 1981).

The northward movement of lowland tropical Gondwanan elements has had no significant counterpart of southward moving tropical Laurasian taxa. The most clearly Laurasian families to have noteworthy complements of species in lowland South American forests are Aristolochiaceae and Vitaceae, each with a single vine genus with numerous species in South America (*Aristolochia, Cissus*); not surprisingly, both are also well represented in the West Indies. Four other tropical lowland families of probable Laurasian derivation are characterized by affinity for dry areas and a strong representation both in the West Indies and in northern Central America. Three of these—Buxaceae, Boraginaceae, and Rhamnaceae—are proportionately better represented in temperate North America than in the Neotropics. In their dry area preference, these groups are reminiscent of the

endemic tropical Laurasian families previously noted. However, representatives of all of these families have penetrated into lowland South America. In the case of Buxaceae, penetration of South America is minimal (contrary to the distribution shown in Heywood, 1978) and restricted to a few limestone outcrops in northern Venezuela (*Styloceras* goes south in the Andes but may not be closely related; Gentry & Foster, 1981). Theophrastaceae has more recorded species in Peru than farther north but is a more predominant vegetational element and has greater generic diversity in Central America and the West Indies. One genus, *Clavija*, which links Theophrastaceae to Myrsinaceae, occurs in lowland tropical forests but is poorly represented in Amazonia and may have only a single species reaching coastal Brazil. Only two genera (*Cordia, Tournefortia*) of the twenty-four genera of Boraginaceae that reach the Neotropics penetrate the lowland tropical forests to any extent. Although Rhamnaceae were listed as basically Gondwanan by Raven and Axelrod (1974), the pattern shown by *Rhamnus* (Johnston & Johnston, 1978) seems typical of the group and points to a northern ancestry. As in Boraginaceae, the penetration of the family into lowland Neotropical forests is minimal (monotypic *Ampelozizyphus* and a few species of *Gouania* and *Colubrina*), although it is better represented in drier parts of South America.

While the lowland tropical South American flora would be almost imperceptibly changed if all of these putatively tropical Laurasian groups (a total of perhaps a few hundred species in all of lowland tropical South America) were eliminated, Laurasian taxa are much more important in Neotropical montane floras. In fact, there seems to be a basic dichotomy between the Laurasian-derived upland and Gondwanan-derived lowland neotropical floras. In Central American upland forests Laurasian elements clearly predominate ecologically with families like Pinaceae, Fagaceae, Juglandaceae, Magnoliaceae, Theaceae, and Ulmaceae especially important as canopy members of the temperate montane forests. These northern taxa gradually decrease southward so that families like Hamamelidaceae and Pinaceae do not cross the Río San Juan lowlands and are not present south of northern Nicaragua, while Garryaceae and many important genera of other families (e.g., *Ulmus, Celastrus*, most Juglandaceae) reach only upland Panama.

Even in South America, Laurasian elements tend to prevail in montane forests, ecologically, if not always in numbers of species. Many of these species are wind-pollinated and thus especially well represented in the fossil record. Consequently we may be reasonably confident that the palynological documentation of their recent arrival in South America is meaningful. Such knowledge of the history of Andean forests relies almost totally on the work of van der Hammen and his associates (summary in van der Hammen, 1974). The first montane elements to arrive at the Palynological sites in the Cordillera Oriental at the Sabana de Bogota were *Hedyosmum* and *Myrica*, as the Cordillera was uplifted during the Pliocene. By the beginning of the Pleistocene, the principal upheaval of the region was completed. During the earliest Pleistocene glacial advance the palynoflora of this region suggested a primitive and depauperate paramo vegetation including such ultimately northern-derived elements as *Aragoa* (Scrophulariaceae), *Hypericum* (Hypericaceae), Umbelliferae, *Plantago, Polylepis* (Rosaceae; perhaps southern), *Valeriana*, and Ranunculaceae. During the Pleistocene the palynoflora fluctuated

FIGURE 1.   Typical Amazon-centered distribution of a taxon of canopy trees, Moraceae tribe Olmedieae. Tribal distribution with species diversity isohyets plotted from the data of Berg (1972: fig. 1). Note the concentration of species in (wetter) western Amazonia in the area of the Colombia/Brazil/Peru frontier. Additional collecting in poorly known northern Amazonian Peru and adjacent Colombia will probably extend the high diversity region westward.

with the changing altitudinal zonation of the vegetation brought about by climatic changes between glacial and interglacial periods. Both the paramo and montane forest floras were gradually enriched during the Pleistocene. In the lower Pleistocene, such additional northern elements as *Geranium, Gentiana, Lysipomia, Juglans,* and (perhaps southern) Urticaceae appear in the pollen record, along with southern taxa like *Gunnera* and phytogeographically problematical *Styloceras* (see Gentry & Foster, 1981). *Alnus* first arrived at the end of the lower Pleistocene and became dominant during the middle Pleistocene. *Quercus* first appeared approximately 250,000 years ago at the end of the Middle Pleistocene and thereafter increased progressively in importance. Although some southern taxa like *Weinmannia* also arrived in the Cordillera Oriental during the Pleistocene, northern elements prevailed and the present northern Andean forests are still dominated by Laurasian taxa.

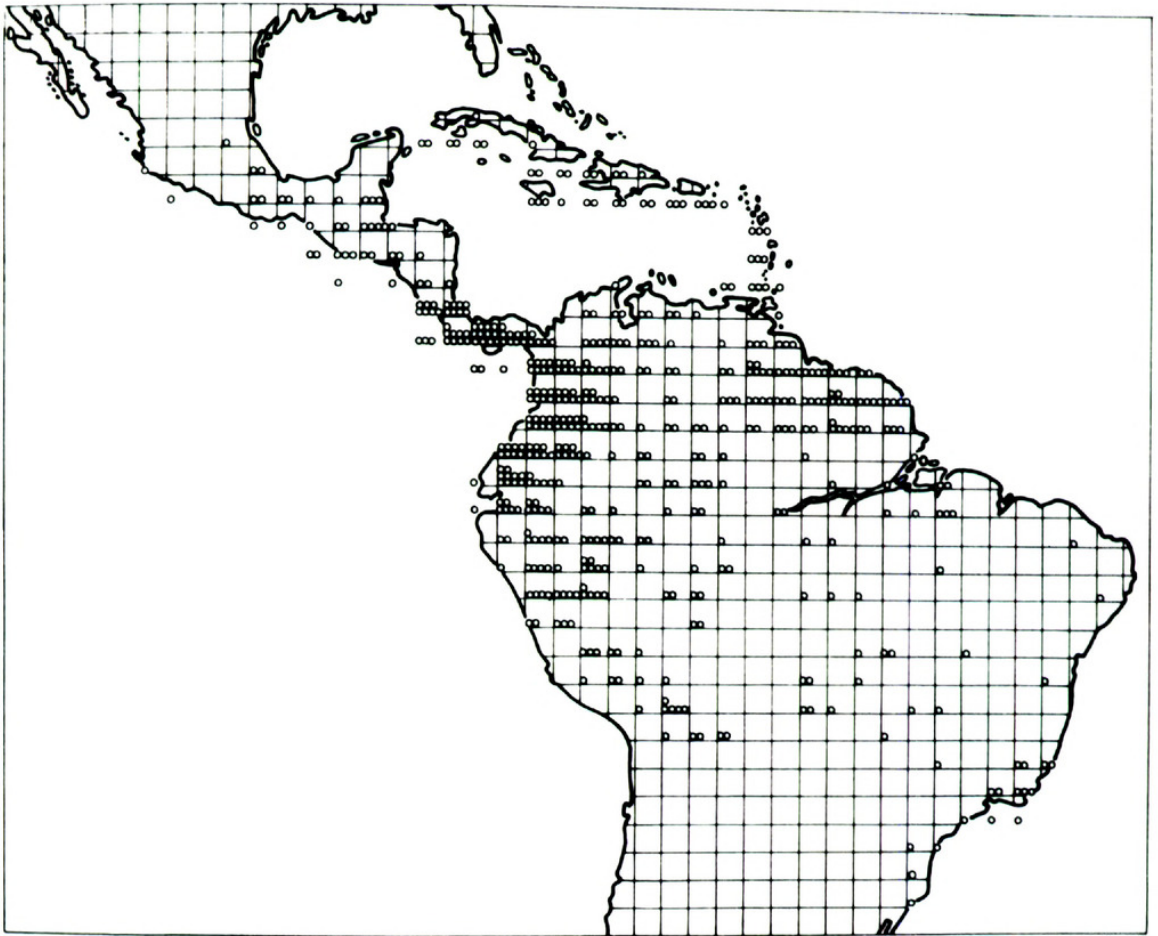Even today such northern families as Myricaceae, Juglandaceae, Betulaceae,

FIGURE 2.   Extra-Amazonian or Andean-centered distribution of a taxon of "palmetto" (Zingiberaceae: subfamily Zingiberoideae; Maas, 1977: fig. 5; number of species per grid square).

Fagaceae, Magnoliaceae, Berberidaceae, Hippocastanaceae, Cyrillaceae, Clethraceae, Cornaceae, Oleaceae, and Caprifoliaceae are present in tropical South America almost entirely in the upland Andes. Within the Andes, there is a decrease in representation of these families farther south. For example, *Quercus,* the absolute dominant of most Colombian lower montane forests, does not occur in Ecuador. Other woody families like Salicaceae, Ulmaceae, Theaceae, Celastraceae, Aquifoliaceae, Sabiaceae, and Staphyleaceae, have one or two widespread species (or genera) that have become widespread in the tropical lowlands (respectively: *Salix humboldtiana, Trema micrantha* and *Celtis iguanea, Ternstroemia, Gouepia, Ilex inundata, Ophiocaryon, Turpinia occidentalis*). Interestingly, the lowland representatives of such taxa are often restricted in Amazonia to ecologically impoverished extreme sites such as seasonally inundated streamsides (*Salix, Ilex, Ophiocaryon duckei, Ampelozizyphus* (Rhamnaceae)), white sand substrates (many *Ternstroemia* and *Ophiocaryon*), or second growth (*Trema, Celtis*). Similarly, the only Amazonian species of south temperate *Podocarpus* is restricted to white sand (*Gentry et al. 28871* (MO) from near Iquitos, apparently an undescribed species).

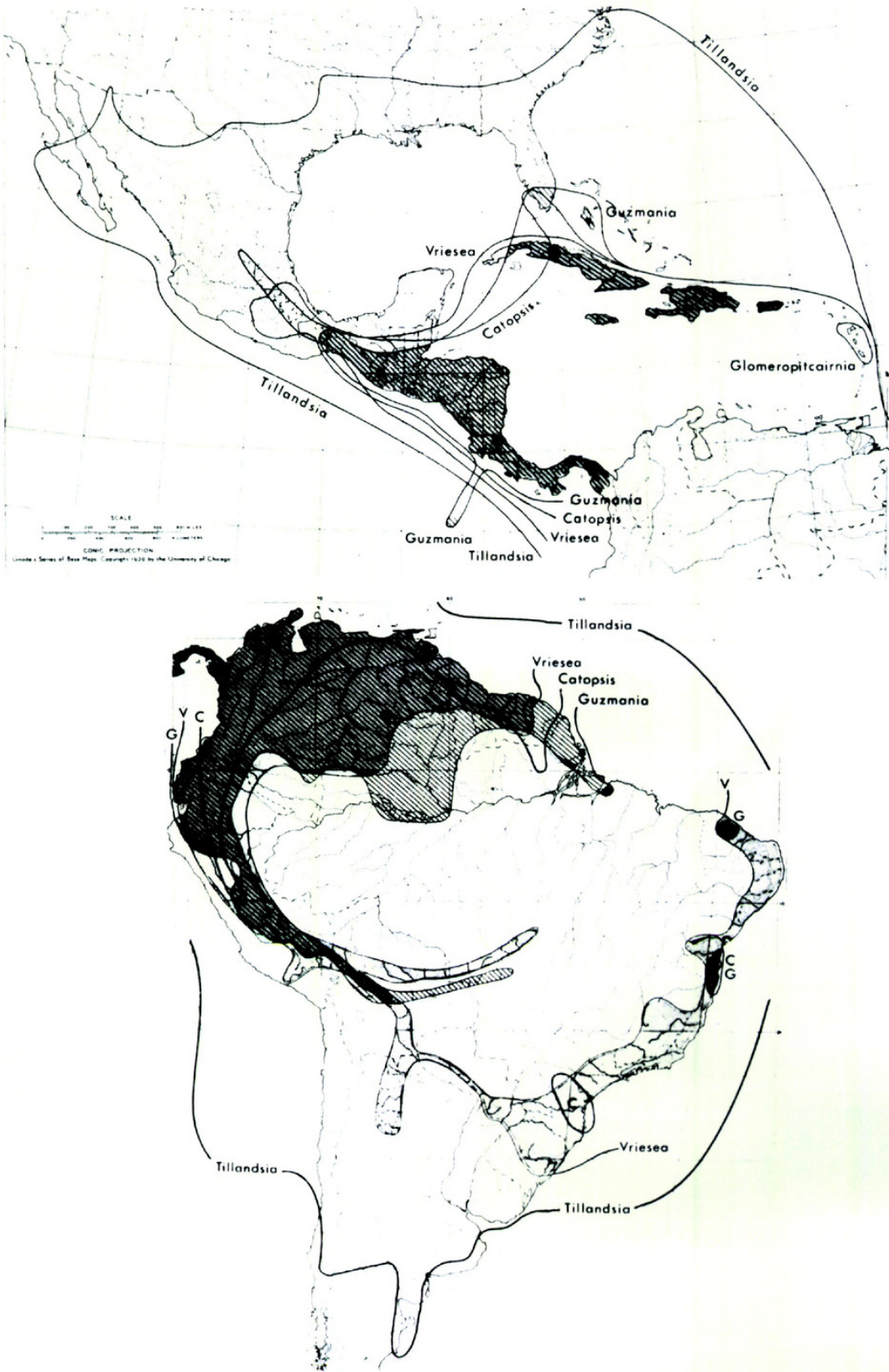Predominantly herbaceous Laurasian families have a greater tendency to be

FIGURE 3.   Extra-Amazonian or Andean-centered distribution of a predominantly epiphytic tax-on (Bromeliaceae, subfamily Tillandsioideae; Smith & Downs, 1977: fig. 213).
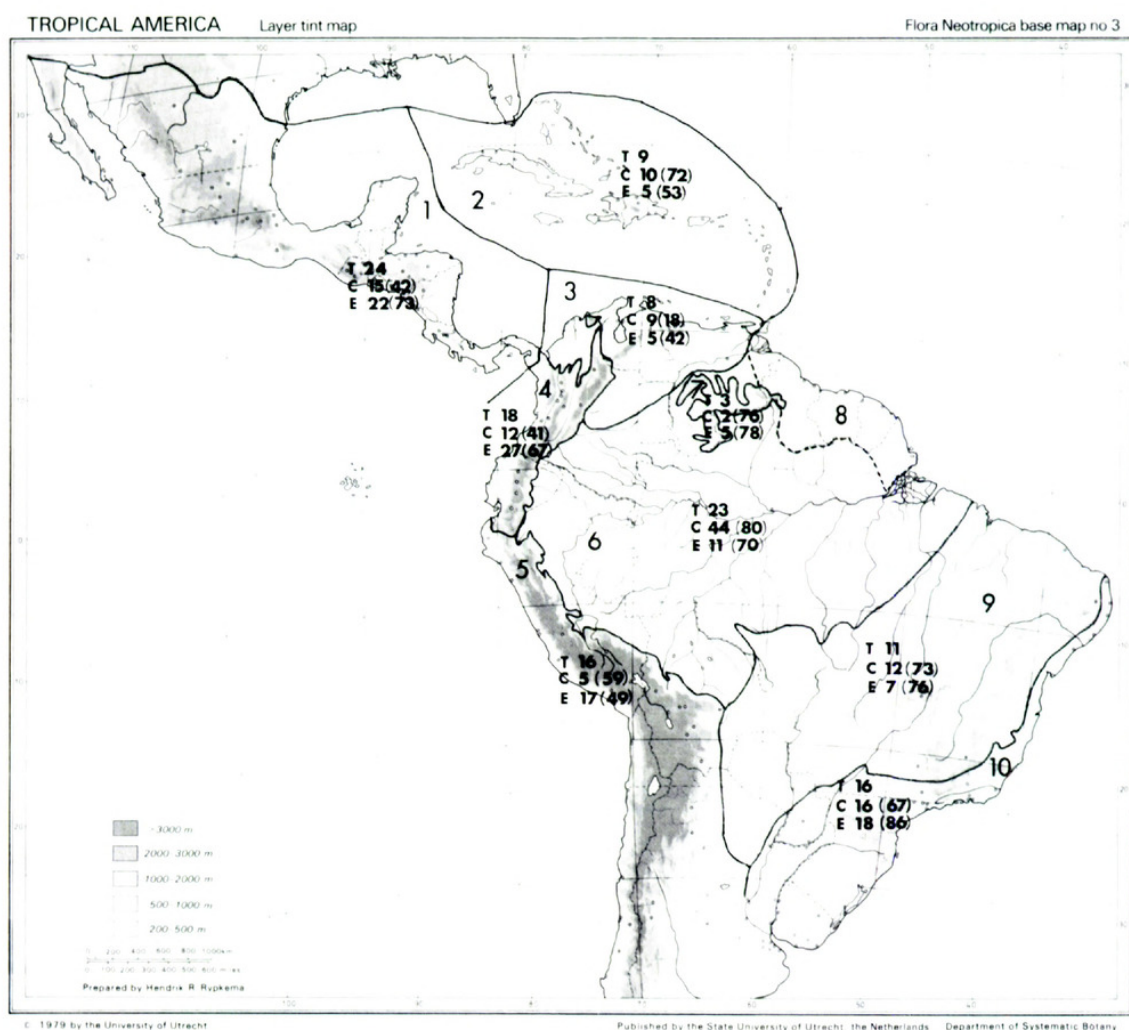
FIGURE 4. Neotropical phytogeographic regions. 1. Mexico and Central America. 2. West In-
dies. 3. Northern Venezuela-Colombia. 4. Northern Andes. 5. Southern Andes. 6. Amazonia (western
border defined by 500 m contour). 7. Guayana Highlands (over 500 m). 8. Guiana subregion (included
as part of Amazonia except for species not found elsewhere in Amazonia). 9. Cerrado and associated
dry areas. 10. Coastal Brazil. Small numbers indicate percent of monographed species occurring in
or endemic to each region. T = Percent of total sample of 8,117 recently monographed species oc-
curring in that region. C = Canopy trees and lianas: percent of the species of taxa characterized by
habit occurring in each region (percent of region's species of that habit group which are endemic to
the region in parentheses). E = Epiphytes and palmettos: percent of the species of taxa characterized
by habit occurring in each region (percent of region's species of that habit group which are endemic
to the region in parentheses). See Tables 7, 8, 9 for complete data.

weedy and their patterns are not so well marked. Nevertheless, except for a few
weeds, families like Crassulaceae, Caryophyllaceae, Ranunculaceae, Cruciferae,
Saxifragaceae, Rosaceae (s.s.), Plumbaginaceae, Geraniaceae, Callitrichaceae,
Balsaminaceae, Umbelliferae, Primulaceae, Gentianaceae, Polemoniaceae, Hy-
drophyllaceae, Scrophulariaceae, Orobanchaceae, and Plantaginaceae are much
better represented in the montane Neotropics than in the lowlands.

    For both trees and herbs there is a strong dichotomy between the noticeable
presence of Laurasian taxa in montane forests and their virtual absence in the
lowlands.

Most of the Laurasian taxa, especially the woody ones, have speciated rather little in the Andes (see Gentry, 1982a). Presumably this reflects in part their recent arrival. As a result, the impressive list of 72 Laurasian-derived Neotropical families in Table 2 accounts for a very small percentage (<10%) of the total Neotropical flora and virtually none of that of the lowland tropics.

GONDWANAN TAXA

The major components of the Neotropical flora are Gondwanaland-derived groups (Tables 4–6). However, there is a fundamental phytogeographic difference within this group, for these autochthonous South American families fall consistently into two major distributional groups. Many of these families are centered in Amazonia (Table 4; Fig. 1) and may be referred to as Amazonian-centered. Most of the remainder are fundamentally and contrastingly extra-Amazonian with very poor representation in Amazonia and usually have their distributional centers in the Andes, especially the northern Andes (Table 5; Figs. 2, 3). These taxa may conveniently be termed Andean-centered taxa although their main diversity is reached in the lowlands near the base of the mountains and in middle elevation cloud forests rather than in the high mountains themselves.

I first became aware of these two striking patterns in the field. In order to document them, I extracted and compiled distributional data for recently monographed Neotropical families and large genera, beginning with the Flora Neotropica monographs, but also including as many other Flora Neotropica-caliber revisions of major taxa as I could find in major systematic botany journals for the last ten to twenty years. This yielded a data set of 8,117 monographed species. Subdividing the Neotropics into the nine phytogeographic regions shown in Figure 4, and counting the number of monographed species occurring in each region provided the data summarized in Tables 7 and 8. The great majority (71% or almost 5,800 species) of monographed species belong to families that are either clearly Amazonian-centered (3,052 spp.) or clearly northern-Andean-centered (2,715 spp.). The component families of each of these major phytogeographical groups not only show strikingly concordant distributional patterns but also amazing consistency ecologically. The Amazonian-centered taxa are overwhelmingly canopy trees and lianas; the extra-Amazonian ones are chiefly shrubs, epiphytes, and palmettos.

AMAZONIAN-CENTERED TAXA

The Amazonian-centered taxa include 38% of the total data set of monographed species. These families have an average of almost half (44%) of their species in Amazonia. Virtually all of these taxa are predominantly canopy trees and lianas; moreover, almost all canopy trees and lianas of the Neotropical lowlands belong to these Amazonian-centered groups. These taxa are conspicuously under-represented in the Andes; on the average only 12% of their species occur in the northern Andean region and only 5% in the Southern Andes. They are well represented in the coastal Brazil region (16% of their species), which constitutes a distinct secondary center for most of them; however, not a single one of these monographed major taxa has as many species in coastal Brazil as in Amazonia,

TABLE 7. Number of species and endemism in monographed taxa by predominant habit group and geographical distribution. Number of endemic species for each region in parentheses.

Habit[1]	Amazonia	Coastal Brazil	Cerrado & Caatinga	North. Andes	South. Andes	Central America & Mexico	North. Venezuela & Colombia	West Indies	Guayana Highland	Lowland Guiana[2]
Canopy trees and lianas	1,334 (1,072)	482 (322)	373 (272)	373 (154)	144 (85)	453 (189)	280 (56)	312 (226)	55 (42)	177 (57)
Epiphytes and palmettos	292 (205)	498 (426)	184 (140)	723 (481)	469 (231)	607 (443)	142 (59)	130 (69)	140 (109)	57 (38)
Herbs and shrubs	60 (16)	140 (76)	167 (103)	128 (51)	437 (231)	559 (319)	107 (9)	151 (41)	—	4 (2)
Vines[3]	75 (40)	74 (40)	45 (18)	126 (73)	78 (40)	132 (65)	47 (11)	55 (30)	1 (1)	9 (9)
Montane trees[4]	7 (5)	12 (8)	3 (1)	71 (47)	57 (39)	98 (84)	22 (7)	27 (20)	8 (6)	—
Arid area trees	—	2 (1)	17 (12)	4 (1)	47 (37)	37 (30)	8 (3)	9 (4)	—	—
Miscellaneous[5]	61 (52)	80 (67)	143 (130)	29 (12)	31 (20)	48 (35)	22 (8)	38 (34)	13 (10)	47 (43)
Total (8,117)	1,829 (1,390)	1,288 (940)	932 (676)	1,454 (819)	1,263 (683)	1,934 (1,165)	628 (153)	722 (424)	217 (168)	294 (149)
Percent of species occurring in region	23%	16%	11%	18%	16%	24%	8%	9%	3%	4%
% Endemism[6] (total = 6,567/8,117 = 81%)	76%	73%	73%	56%	54%	60%	24%	59%	77%	—
Total endemism[7]	17%	12%	8%	10%	8%	14%	2%	5%	2%	2%

[1] Predominant habit of monographed taxon.
[2] Figures for Guianas subregion include only those species that occur in the lowland Guianas but not also in Amazonia.
[3] Distribution primarily reflects pattern of single large family—Passifloraceae (363 spp.).
[4] Betulaceae, Brunelliaceae, Clethraceae, Juglandaceae, Polylepis, Podocarpaceae, Rhamnus, Colubrina, Sabiaceae. Rhamnaceous taxa include many Mexican desert shrubs.
[5] Parasites, aquatics, Velloziaceae, Proteaceae.
[6] Endemic species in region as percent of total monographed species in that region.
[7] Endemic species in region as percent of total species in all monographed taxa.

TABLE 8. Percent distribution of monographed taxa by predominant habit group and geographical distribution.

Habit[1]	Total Spp.	Percent of Species[3]									
		Amaz.	Coast. Braz.	Cerrado & Caatinga	North. Andes	South. Andes	Central Amer. & Mexico	N. Venezuela & Colombia	West Indies	Guayana Highland	(Guianas)[2]
Canopy trees and lianas	3,052	44	16	12	12	5	15	9	10	2	(6)
Epiphytes and palmettos	2,715	11	18	7	27	17	22	5	5	5	(2)
Herbs and shrubs	1,034	6	14	16	12	42	54	10	15	—	—
Vines[4]	459	16	16	10	27	17	29	10	12	—	(2)
Montane trees[5]	256	3	5	1	28	27	38	9	11	3	—
Arid area trees	105	—	2	16	4	45	35	8	9	—	—
Others (parasities, aquatics, Velloz., Proteac.)	496	12	16	29	6	6	10	4	8	3	(9)
Total	8,117										

[1] Predominant habit of monographed taxon.
[2] Figures for Guianas subregion include only those species that occur in the lowland Guianas but not also in Amazonia.
[3] Percents total to more than 100% since widespread species are counted in each region in which they occur.
[4] Distribution primarily reflects patterns of single large family—Passifloraceae (363 spp.).
[5] Betulaceae, Brunelliaceae, Clethraceae, Juglandaceae, Polylepis, Podocarpaceae, Rhamnus, Colubrina, Sabiaceae. Rhamnaceous taxa include many Mexican desert shrubs.

not even Dilleniaceae, whose strong representation in the coastal region was emphasized by Kubitzki (1975). Many of the Amazonian-centered families have derivative species in the cerrado and associated dry areas of the Brazilian shield (12% of the species); in almost every case the cerrado species are shrubs or subshrubs in taxa that are otherwise trees or lianas. These groups are markedly poor in the West Indies (10% of the species on the average, with a dispropor-tionate part of that total due to the evolutionary explosion of a single otherwise small section of *Tabebuia*).

The Amazonian-centered taxa are poorly represented in Central America (only 15% of their species), which is rather surprising since they make up nearly all of the moist and wet forest canopy of the Central American lowlands, just as in Amazonia. Most of the species of these taxa that do reach Central America are not endemic; rather, they are mostly those few Amazonian species that happen to have unusually wide ranges. Thus, only 6% of the 3,000 monographed species of Amazonian-centered taxa are endemic to Central America. This contrasts with 80% endemism in Amazonia, where 35% of all the species of these taxa are endemic. Within Central America there is a marked decrease in the representation of Amazonian-centered taxa from south to north. Most of these families have several species reaching eastern Panama, noticeably fewer reaching western Pan-ama and Costa Rica, and none crossing the Holdridge system tropical/subtropical delimitation at 12°N latitude in Nicaragua (exactly the same latitude as the di-versity-reducing Isthmus of Kra in Malaysia!). Those Amazonian-centered fam-ilies that do extend farther into Central America typically have only one or two species north of Nicaragua (see Gentry, 1982a, for specific examples of these patterns). Nevertheless, the relatively few Amazonian-centered taxa that reach northern Central America continue to constitute virtually all of the lowland forest canopy (Table 3 and Gentry, in prep.).

An interesting subsidiary pattern is shown in Central America by several of these taxa. Several of the groups have a distinct secondary radiation in northern Central America. A good example is provided by Bignoniaceae with tribe Cres-centieae having three genera and 35 species almost exclusively in Central America (Gentry, 1979, 1980a). Although derived from the fundamentally South American tribe Tecomeae, Crescentieae are so distinct from that group in such important features as indehiscent fruits and bat-pollinated flowers that they have sometimes been treated as a distinct family (see Gentry, 1974a). Clearly Crescentieae reflect a long history of differentiation in Central America subsequent to an initial col-onization by South American Tecomeae stock. Yet most other Central American Bignoniaceae are undifferentiated from their South American progenitors even at the species level.

It is tempting to think of such patterns as reflecting a two pulse migration: (1) early colonization by island hopping across the proto-Antilles at the end of the Cretaceous with subsequent major differentiation and (2) a major migration sub-sequent to closing of the Isthmus of Panama that was too recent to permit much generic, or even specific, differentiation.

ANDEAN-CENTERED TAXA

The second major Neotropical phytogeographic pattern, contrastingly extra-Amazonian, may be referred to conveniently as Andean-centered and is almost

the mirror image of that shown by the Amazonian-centered taxa. In those regions where Amazonian-centered taxa are well represented, Andean-centered taxa are poorly represented and vice versa. Families with this pattern have their distributional centers in the northern Andes, where over a fourth (27%) of their species occur, and are also well represented in the southern Andes (17% of their species) (Table 8). These groups are predominantly epiphytic (Araceae, Araliaceae, Bromeliaceae, Cyclanthaceae, Ericaceae, Gesneriaceae, Guttiferae, Piperaceae/*Peperomia*, Orchidaceae, etc.), understory shrubs (Acanthaceae, Caricaceae, Melastomataceae, Monimiaceae, Myrsinaceae, Piperaceae, Rubiaceae, Solanaceae), and coarse palmetto-type monocots (Musaceae, Marantaceae, Zingiberaceae). These groups are not only conspicuously under-represented in Amazonia (11% of their species), they are also poorly represented in the dry cerrado-caatinga region (7% of their species). Like the Amazonian-centered group, they are well represented in the coastal Brazil region (18% of their species) and poorly represented in northern Venezuela and the West Indies.

Unlike their Amazonian-centered counterparts, the Andean-centered taxa are very well represented in Central America, especially Costa Rica and Panama, where 22% of their species occur. Southern Central America is clearly a major secondary center of speciation for most of these groups. Although some of these groups actually appear to have more species in Costa Rica or Panama than in the northern Andes, this may be mostly an artifact of the much poorer floristic data base from northwest South America. In any event, these groups account for most of the incredible floristic diversity of the Choco region (Gentry, 1982a). The Andean-centered taxa show very pronounced endemism in Central America, with 73% of the Central American species endemic. This is in strong contrast to the low (42%) Central American endemism of Amazonian-centered taxa (Table 9). Clearly both Central America and western South America have been major evolutionary centers for these groups.

Although representation of these taxa is highest in mountainous phytogeographic regions, it should be re-emphasized that high species diversities do not occur at high altitudes but rather in the wet lowland and premontane cloud forests along the base and lower slopes of the mountains.

These two dominant phytogeographic patterns—Amazonian-centered trees and lianas and Andean-centered palmettos, shrubs, and epiphytes—together account for the great majority (71% of my sample) of Neotropical plant species. Together these families, all basically Gondwanan, absolutely dominate the lowland neotropical flora, both in Central and South America. Thus any explanation of the patterns of evolutionary diversification in these taxa will largely explain the richness of the Neotropical flora.

DRY-AREA-CENTERED TAXA

A few subsidiary distributional patterns need to be mentioned. One is that of taxa with distributional centers in dry areas and poor representation both in Amazonia and the moist Andes. Three good examples are Capparidaceae, Cactaceae, and Zygophyllaceae. Amaranthaceae and possibly Chenopodiaceae, the latter often specialized for the highly alkaline conditions typical of deserts, are also better represented in dry than in wet areas. Dry-area-centered taxa tend to be largely shrubs and herbs although some well known tree genera like *Prosopis*

TABLE 9. Relative endemism of phytogeographic regions. Percent of those species occurring in each region that are endemic.

Habit[1]	Total % Endemic to 1 Reg.	Amaz.	Coast. Brazil	Cerrado & Caatinga	North. Andes	South. Andes	Central Amer. & Mexico	N. Venezuela & Colombia	West Indies	Guayana Highland
Canopy trees and lianas	81	80	67	73	41	59	42	18	72	76
Epiphytes and palmettos	81	70	86	76	67	49	73	42	53	78
Herbs and shrubs	82	27	54	62	40	53	57	8	27	—
Vines[2]	71	53	54	40	58	51	49	23	55	100
Montane trees[3]	85	71	67	33	66	68	86	32	74	75
Arid area trees	84	—	50	71	25	79	81	38	44	—

[1] Predominant habit of monographed taxon.
[2] Distribution primarily reflects patterns of single large family—Passifloraceae (363 spp.).
[3] Betulaceae, Brunelliaceae, Clethraceae, Juglandaceae, *Polylepis*, Podocarpaceae, *Rhamnus*, *Colubrina*, Sabiaceae. Rhamnaceous taxa include many Mexican desert shrubs.

and *Bulnesia* also show this pattern. These groups are best represented in the southern Andean region (42% of their species), here including part of the monte, and the Central American region (54% of their species), especially Mexico and northern Central America. Not surprisingly, taxa adapted to dry areas are also relatively well represented in the northern Venezuelan-Colombian region and the dry cerrado-chaco-caatinga region of the Brazilian shield.

Although representation of these taxa is about as strong in the Southern Andean region as in the Central American region, endemism is slightly greater in Central America (57% vs. 53% of the region's species) and even more pronounced in the cerrado region (62%). Rzedowski (1962, 1978) has pointed out that endemism in Mexico is most striking among dry area taxa even though species of lowland tropical forests dominate the country's flora in terms of absolute numbers. Despite the high endemism, taxa ultimately derived from the south strongly predominate in the Mexican dry area flora, in contrast to the north temperate-derived dry area flora of the United States deserts (Rzedowski, 1973). Such patterns, especially the prevalence of a preponderance of well-marked endemic families like Fouqueriaceae, Lennoaceae, Crossosomataceae, Malesherbiaceae, and Cactaceae in dry areas, have been cited (e.g., Rzedowski, 1962, 1978) as evidence of a long evolutionary history of dry taxa, implying the uninterrupted persistence of dry areas at least through most of the Cenozoic. Axelrod (1979) suggests that much of the early evolution and differentiation of dry area taxa may have been in edaphically dry areas with taxa spreading as dry climates expanded in the late Tertiary and Quaternary times. Whether originally edaphically restricted or not, the strong differentiation of many of these groups in Mexico and northern Central America implies that some of their ancestors may well have arrived via late Cretaceous island hopping (cf. Bignoniaceae, tribe Crescentieae above, most of whose members are specialized for such edaphically dry substrates as limestone outcrops and seasonally inundated savannahs).

It should be noted that, although amphitropical range disjunctions of dry area taxa are frequent, many of these surely reflect recent long distance dispersal (Raven, 1963), rather than the ancient patterns emphasized above. Moreover, although many of these dry area taxa might seem to be autochthonously Mexican and northern Central American based on their preponderance of species there, most of them are either clearly of Gondwanan affinities or presumably so by phytogeographic analogy. Thus the high species numbers of dry area adapted shrub and herb taxa in Mexico and adjacent regions are probably mostly a secondary phenomenon resulting from active evolutionary diversification in response to the increasingly dry climatic regimes of the Pliocene and Pleistocene, rather than necessarily due to ancient arrival or autochthonous origin. Genera disjunct between Chile and California, for example, are all prime candidates for long distance dispersal (Carlquist, 1982). Even some amphitropical dry-area shrubs like *Larrea* are now generally believed to result from relatively recent long distance dispersal rather than ancient distributions (Wells & Hunziker, 1976). Clearly range disjunctions of dry area plants must be interpreted on an individual basis.

While these dry area taxa are a significant and interesting component of the Neotropical flora, they are relatively unimportant in terms of overall Neotropical species richness, just as Rzedowski (1962) noted for Mexico.

MISCELLANEOUS SUBSIDIARY PATTERNS

A few other Neotropical phytogeographical patterns merit special note. Coastal Brazil is noteworthy for the concentration of often primitive species in a restricted area (e.g., Kubitzki, 1975; Soderstrom & Calderon, 1974) and some of the archaic taxa of coastal Brazil—e.g., primitive Dilleniaceae (Kubitzki, 1975), Bambuseae (Soderstrom & Calderon, 1974), *Perianthomega* (intermediate between the two main tribes of Bignoniaceae and perhaps close to the ancestral stock of the neotropical Bignonieae), a *Cecropia* with the simply spicate female inflorescence of African *Musanga* (Berg, pers. comm.)—may date from the Cretaceous separation of South America and Africa. Nevertheless no family has its distributional center in coastal Brazil. The same families that are well represented there are invariably better represented either in Amazonia or the Andes. However, both the recently uplifted Andes and most of Amazonia, which was underwater into the Pleistocene, are relatively recent entities geologically speaking, and the apparent prevalence of unspecialized taxa in Coastal Brazil may suggest the importance of this region as a source area for other phytogeographic regions.

Another rather isolated lowland area noted for its endemism (Gentry, 1982a) is the Chocó region of Pacific coastal Colombia and adjacent Ecuador. This rich, perhumid, but geologically young, region is an important subset of what is here termed the Northern Andean region. The floristic significance of the Chocó area is almost entirely at the species level although it does have a few endemic genera like *Trianaeopiper* (Piperaceae) and *Cremosperma* (Gesneriaceae). No family has its chief center of distribution in Chocó other than as part of the Northern Andean region.

Finally the Guiana Region, and especially the Guayana Highlands, are well known as areas of high endemism and much phytogeographic interest (Maguire, 1970). Geologically this area is very old, and the plants of the tepui summits have had the potential for very long periods of evolution in isolation. Nevertheless, exchange between summit flora and the lowland forest flora that ascends the tepui slopes has apparently been much more extensive than once thought (compare Steyermark, 1979, and Maguire, 1970). Even many of the species of the summits are shared with the lowlands, which are in turn no more than a northern phytogeographic subset of Amazonia. To be sure, there are a few strikingly distinct endemic species and genera in the region that might be recognized as distinct families—Saccifoliaceae (close to Gentianaceae), and Tepuianthaceae (close to Rutaceae). More intriguing are several non-endemic families that are found in the Neotropics only in the Guayana region. These include Sarraceniaceae (disjunct from North America), Tetrameristaceae (two monotypic genera, the other in Asia), and Dipterocarpaceae (see Maguire & Ashton, 1978; the opposing view that *Pakaraimea* is closer to Tiliaceae (Kostermans, 1978) is based on weak evidence and is phytogeographically irrelevant since the South American taxon clearly belongs to the Dipterocarpaceae ancestral plexus, no matter where the taxonomic limits are drawn). Such patterns suggest ancient survivals, not active evolutionary diversification.

A very few small families do have their centers of Neotropical diversification in the Guayana area. The only generally accepted families that seem to show this

pattern are Burmanniaceae, Podostemaceae, Triuridaceae, Mayacaceae, Thurniaceae, and Rapateaceae. Together they account for a total of not more than some 300 species. All are specialized for unusual life styles, as saprophytes, aquatics, or semiaquatics. In general the overall floristic significance of the Guayana area, and especially the Guayana Highlands, now seems very much less than earlier believed. If the 3% of my data set of monographed species that occur in the Guayana Highlands is any indication, the total flora of that region is minuscule indeed, even when allowance is made for the relatively small area of upland Guayana. On the other hand, the famed high endemism of the Guayana highlands, although much less than the 90% suggested by Maguire (1970), is somewhat supported by my data set. The 77% endemic species of the Guayana Highlands is slightly higher than the similar figure for any other phytogeographic region (Table 7).

Two other regions that are surprisingly depauperate in plant species as judged from this data set are the West Indies and the northern Venezuela/Colombia region, with respectively 9% and 8% of the total of monographed species. The 59% endemism value for the West Indies is almost identical to the 60% overall specific endemism of Central America, but the 24% figure for northern Venezuela/Colombia is by far the lowest such figure for any of these phytogeographical regions. In this light it is clear how Steyermark (1979) was able to achieve such a fine scale in delimiting centers of endemism in Venezuela, some centers based on as few as two species. With such low total endemism, even a few endemic species become noteworthy.

FLORISTIC SUMMARY

To summarize Neotropical floristic patterns, we have two major dichotomies. The first is between the basically Laurasian montane flora and basically Gondwanan lowland flora. The second, within the predominant latter group, is between a large group of families with Amazonian distributional centers, and a second important group that has distributional centers in the Andes, especially the northern Andes, and tends to be poorly represented in Amazonia. It is now clear that the Laurasian/Gondwanan dichotomy results from the separation of North and South America through most of Cenozoic time. The fundamental dichotomy between Amazonian- and Northern Andean-centered families, although equally clear cut, has not previously been generally recognized.

Virtually all lianas and canopy trees of the lowland Neotropics belong to Amazonian-centered taxa. Canopy trees of montane forests come from both Laurasian and Gondwanan groups with a gradation in the relative importance of the two from north to south. Epiphytes, understory shrubs, and palmettos mostly belong to Gondwanan groups with northern Andean distributional centers. Many Neotropical herbs are from widespread predominantly north temperate groups; like Gondwana-derived herb taxa they have extra-Amazonian distributional patterns. Vines (as opposed to lianas) are represented in both Laurasian and Gondwanan groups; however, it is noteworthy that the only representatives of clearly Laurasian families to extensively invade the lowland Neotropics are vines (*Aristolochia, Cissus, Gouania*) mainly occurring in forest edge situations rather than

mature forest. Shrubs are best represented in dry areas and typically show an amphitropical pattern with distributional centers both in northern Central America and the southern Andean region.

EVOLUTIONARY IMPLICATIONS

These very distinctive phytogeographic patterns suggest radically different speciation patterns in different regions and among the different adaptive types. Especially noteworthy are the differences (1) between upland, largely Laurasian, taxa and lowland, predominantly Gondwanan, groups and (2) within the latter group between the predominant Amazonian-centered and Andean-centered groups.

One striking differential is in pollination ecology. Almost half of the families of Laurasian-derived trees are wind-pollinated whereas virtually none of the Gondwanan angiosperm families is. Many of the northern Andean-centered groups are largely, or even predominantly, hummingbird-pollinated (e.g., Acanthaceae, Bromeliaceae, Campanulaceae-Lobelioideae, Ericaceae, Gesneriaceae, Loranthaceae-Loranthoideae, Marcgraviaceae, Musaceae, Tropaeolaceae, Zingiberaceae) whereas this pollination system is rather uncommon in other groups (e.g., a few Gentianaceae, Labiatae, Lythraceae, Polemoniaceae, Scrophulariaceae among Laurasian taxa; some miscellaneous species of Apocynaceae, Bignoniaceae, Combretaceae, Convolvulaceae, and Leguminosae among Amazonian-centered taxa). Plants with rather conspicuous, often large, tubular flowers pollinated by specialized large and medium-sized bees mostly belong to Amazonian-centered families (Apocynaceae, Bignoniaceae (Gentry, 1974a, 1974b), Cochlospermaceae (Frankie & Baker, 1974), Lecythidaceae (Prance, 1976; Mori et al., 1978), many Leguminosae (Frankie & Baker, 1974; Frankie et al., 1982)), but are also found among other groups (e.g., Marantaceae, Orchidaceae, Passifloraceae, Zingiberaceae). Even some Laurasian groups that are mostly large-bee pollinated in the temperate zone tend to have Neotropical representatives with other pollination systems (e.g., Scrophulariaceae, most of whose Neotropical genera have tiny inconspicuous flowers). Taxa having mostly species with small generalist-pollinated flowers (sensu Frankie et al., 1974, 1983; Gentry, 1982b) are well represented in all phytogeographical groups and show no obvious trends.

A related difference between phytogeographical/habit groups lies in their probable modes of speciation. Woody Laurasian taxa, largely wind-pollinated, have speciated very little in South America, even in the Andes where they are ecologically dominant. Even in Central America these plants have produced relatively few species. Ecotypic differentiation is frequent in some groups, for example among oaks in Costa Rica where different sets of related species tend to be restricted to different Holdridge life zones (Burger, 1977, pers. comm.). The general pattern of little speciation in these taxa is consistent with expectations based on the long generation times of woody plants, coupled with the relatively recent arrival of most of the taxa in South America and even southern Central America. It is also consistent with models that emphasize the importance of plant-pollinator interactions in promoting speciation, a potential patently unavailable to wind-pollinated species.

The woody Amazonian-centered canopy trees and lianas are the groups that show biogeographic patterns consistent with classical zoological models of allo-

patric speciation. These are the taxa that have the kinds of distributions that have been interpreted as resulting from speciation and/or survival in Pleistocene forest refugia. For example, Prance (1973) selected entirely woody Amazonian-centered taxa (Caryocaraceae, Lecythidaceae, Chrysobalanaceae, and Dichapetalaceae) to demonstrate the kinds of correlated patterns of restricted distributions—allopatric among closely related species but replicated in unrelated groups—that fit the predictions of the Pleistocene refuge model of tropical forest speciation. It is not surprising that Forero (1976) and Lleras (1978), both working with taxa of woody lianas, noted similar patterns in their groups. In these taxa outcrossing is the rule (Bawa, 1974), chromosome numbers are frequently high ("palaeopolyploidy") and often stable in a genus or family (Goldblatt & Gentry, 1980; Ehrendorfer, 1970), and hybridization is rare or non-existent (Ehrendorfer, 1970; Ashton, 1969). Major shifts in mode of pollination may be rare while speciation leading to specialization in such marginal habitats as white sand "campinarana" forests or seasonally inundated "varzea" or "tahuampa" forests is a major evolutionary theme (Gentry, 1980b, 1982d, 1982e). In general, closely related species show allopatric distributions and speciation seems somehow orderly with relatively few species per genus (14 spp./genus on the average with only 19 genera having over 100 species) and community diversity perhaps approaching a regulated ecological equilibrium (Gentry, 1982b).

The epiphytes, understory shrubs, and palmettos that make up most of the northern Andean-centered taxa are characterized by what appears to have been explosive speciation and adaptive radiation, almost certainly much of it sympatric. Genera are typically large (20 species per genus on the average; at least 120 genera with over 100 species). While it is conceivable that microgeographic speciation could explain much of the high diversity of typical Andean-centered taxa, my (Gentry, 1982a) attempt to fit the Chocó flora to the expectations of the Pleistocene refuge model were distinctly equivocal with very many local endemics occurring scattered throughout the region and constituting veritable "species swarms" in large evolutionarily plastic genera like *Anthurium*, *Piper*, and *Cavendishia*. The same patterns are documented by monographs of specific Andean-centered taxa (e.g., Harling, 1958; Smith & Downs, 1974, 1977, 1979; Berry, 1980; Luteyn, 1983). Berry (1980 and in prep.) suggested from his analysis of speciation patterns in *Fuchsia* that speciation in this group might reflect "shifting balance" phenomena (Wright, 1977; Templeton, 1980) with major genetic reorganizations or genetic transilience (Templeton, 1980) optimized both by the small localized populations and the need for constant recolonization of a habitat partitioned by mountains, local rainshadows and other climatic effects, vertically shifting cyclically coalescing and separating vegetational zones, and frequent landslides, which regularly provide open areas for colonization. The relatively short generation times of these herbaceous or shrubby groups, as well as their typically rather specific pollination relationships, should provide ideal conditions for rapid evolutionary differentiation, even under stable climatic conditions. There is some evidence that speciation in these groups frequently involves such phenomena as polyploidy (e.g., *Psychotria*, Hamilton, pers. comm.), hybridization (e.g., *Fuchsia*, Berry, 1980) or cleistogamy (e.g., Marcgraviaceae, Bedell, pers. comm.), Microgeographic, perhaps even more or less sympatric, speciation is probably

the rule rather than the exception. Shifts in specific pollinators are a common mode of speciation and co-evolution giving rise to finer biotic tuning of precise plant-pollinator systems such as those in *Heliconia* (Stiles, 1975), Orchidaceae (Dodson, 1975), Ericaceae (Luteyn, pers. comm.) or *Fuchsia* (Berry, 1980) seems a major evolutionary theme. In such groups speciation would appear an altogether open-ended phenomenon without the slightest hint of any kind of ecological equilibrium or limits on species diversity.

The Neotropics are much richer in epiphytes than the Palaeotropics (Richards, 1973; Madison, 1977; Burger, 1980). However, the tendency has been to explain this difference as due to lack of extinction in the relatively (at least to Africa) constantly mesic Neotropics and to interpret high epiphyte diversity as reflecting a long history of mesic conditions (Burger, 1980). I propose that high diversity in epiphytes and other Northern Andean-centered groups results mostly from recent very dynamic speciation, almost the antithesis of the prevalent lack-of-extinction hypothesis. Rather than the flora of tropical Africa (and to a lesser extent Asia) being impoverished with respect to the Neotropics, the latter may be considered as uniquely and phenomenally enriched.

There is increasing circumstantial evidence that this kind of unusually rapid speciation, concentrated along the base and lower slopes of the northern Andes, has involved much co-evolutionary interaction and has not been restricted to plants. Thus Stiles (1981) has shown that there are over 400 species of flower-feeding birds in the Neotropics, including 315 species of hummingbirds alone, as compared to 100–150 flower-feeding species in each Palaeotropical realm. Moreover, the Neotropical flower-feeding birds are generally much more specialized and show much greater flower specificity than their Palaeotropical equivalents. Stiles (1981) suggested from these patterns that bird-flower coevolution probably began relatively earlier in the New World than elsewhere. However, in the context of the botanical patterns discussed in this paper, I would suggest instead that it is probable that bird-flower coevolution, in general, and hummingbird speciation, in particular, has been much more rapid in the Neotropics. Certainly hummingbirds are concentrated in tropical and premontane parts of the northern Andean region (134 species in Colombia, ca. 133 in Ecuador (Bleiweiss, pers. comm.), 97 in Venezuela, 118 in Peru (Parker et al., 1982), compared to 52 in Panama (Ridgely, 1978), 51 in Costa Rica, 37 in Guatemala (Land, 1970), 60 in Mexico; see Stiles, 1981, table 5, for ecological and altitudinal distributional patterns) exactly as are the Andean-centered, largely hummingbird-pollinated groups of plants.

Although the data for flower-visiting bats are less precise, the rather generalized distributional patterns shown by Koopman (1981), are clearly similar to those of flower-visiting birds and my Andean-centered plant taxa. The greatest concentrations of nectar-feeding bat species (13 species each) are in the northern Andean region and Central America.

It is not yet clear whether such patterns are more a cause or an effect of the apparent evolutionary explosion of plant taxa characteristic of the northern Andean region. However, Terborgh and Winters (1982) have shown that for birds in general, local endemism is strikingly concentrated on the western side of the northern Andes, and Keister et al. (1983) have suggested theoretical reasons why

the partitioned population structures prevalent in this geographical region should favor rapid coevolution. Moreover, Marshall et al. (1982) note a grossly similar pattern for mammals with formation of the Isthmian land bridge resulting in what they consider to have been a balanced exchange of equilibrium faunas between North and South America followed by a unique and unbalanced secondary diversification of the immigrant taxa in South America, apparently somehow associated with the Andes. Perhaps the accelerated rates of speciation here suggested for northwestern South American plants is part of a much more general phenomenon.

To summarize, the exceedingly dynamic, even explosive evolution that seems to characterize the northern-Andean-centered taxa has given rise to a very significant proportion of the total Neotropical flora. Almost half of all Neotropical plant species appear to belong to these groups of epiphytes, understory shrubs, and palmettos, all of which are much more poorly represented in the Palaeotropics. Thus the historical accident of the Andean uplift, with the concomitant opportunity for explosive speciation among certain taxa of Gondwanan plants having the evolutionary potential for exploiting epiphytic, palmetto, and understory shrub strategies, may largely explain the "excess" plant species diversity of the Neotropics. It is essentially this *approximately half* of the Neotropical flora that is missing in the Palaeotropics, although similar patterns on a smaller scale might be expected in New Guinea, which seems the closest Palaeotropical equivalent of the Andean cordilleras.

CONCLUSION

A rich angiosperm flora similar to that in the rest of the tropics evolved during the last half of the Cretaceous in South America but this flora has subsequently given rise to many more species in the Neotropics.

At the end of the Cretaceous there was a possibility for relatively direct floristic interchange between South America and tropical North America via island hopping along the proto-Antilles; many of the Neotropical groups, especially some of the dry area taxa that show strong differentiation in both regions, may reflect this early interchange.

Uplift of the Andes, mostly in Neogene time, led to an incredible burst of speciation in a number of Gondwanan families. A similar evolutionary explosion in the same taxa also took place in Costa Rica and Panama. The taxonomic groups that have undergone this evolutionary explosion have distributional centers in the northern Andean region and southern Central America, are poorly represented in Amazonia, and consist mostly of epiphytes, shrubs, and palmettos; their pollination systems suggest that coevolutionary relationships with hummingbirds, nectar-feeding bats, and perhaps such specialized bees as Euglossines, have played a prominent role in their evolution. The evolutionary phenomena associated with the Andean uplift account for almost half of the total Neotropical flora and are thus largely responsible for the excess floristic richness of the Neotropics.

Closing of the Panamanian isthmus in the Pliocene led to (1) southward migration of some Laurasian taxa into the Andes where they have become ecologically dominant despite undergoing little speciation, at least in woody taxa, and

(2) northward invasion of lowland Gondwanan taxa of canopy trees and lianas into Central America, leading to their ecological dominance in lowland tropical forests throughout the region, despite little significant speciation in Central America.

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