Wetland and upland forest ecosystems in Peruvian Amazonia: Plant species diversity in the light of some geological and botanical evidence

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ABSTRACT

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Recent hypotheses have suggested fluvial disturbance resulting from long-term sub-Andean tectonics as a source of high species diversity in western Amazonia, a region presented as a mosaic of fossil and current floodplains produced by vast lateral river migrations. In such a system, wetland forests would be a center of high diversity. These hypotheses are discussed. On the one hand, an analysis of the differential tectonic effects of faulting and folding on the two western Amazonian morphostructural units clearly indicates that areas affected by fluvial dynamics are limited to well-defined depressions, the tendency of which is subsidence or entrenchment. Most uplands have not been affected by fluvial dynamics since the Pleistocene. On the other hand, botanical surveys show that the respective wetland and upland floras are very distinct, and that upland-forest species diversity is clearly greater than that of wetland forests. Several arguments suggest that the disturbance of forests on vast areas and severe ecological constraints (e.g., flooding) lead to reduced plant-species diversity. The great age and stability of upland forests, and the rather constant ecological conditions in the understory (including gap-phase regeneration) are still convincing explanations of their high species diversity.

INTRODUCTION

Haffer's (1969) refuge theory has favoured an interdisciplinary approach to understanding high species diversity of Amazonian forests. This theory supposes a dryer climate during the Pleistocene, and the development of savannahs throughout the basin with a consequent fragmentation and reduction of forests to refuge areas. Amazonian forests would have reached their current extension during the Holocene. Paleoclimatic data (Tricart, 1974; Colinvaux, 1979; Ab'Saber, 1982), however, did not irrefutably establish the occurrence of vast savannahs during the Pleistocene. In particular, the inter-

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pretation of feldspar found in equatorial Atlantic sediments as an indicator of a dryer climate (Damuth and Fairbridge, 1970) was refuted by Milliman and Barretto (1975).

The weakness of paleoclimatic arguments led to the consideration of the effects of past and present river dynamics. Campbell and Frailey (1984) suggested, from analyses of sub-Andean Quaternary sediments in Madre de Dios (Peru), the occurrence of catastrophic flooding in the late Pleistocene due to the melting of Andean glaciers. The result of such flooding would have been the fragmentation of western Amazonia into a mosaic of flooded and unflooded forests. The present high diversity of western Amazonian forests would reflect a 'supersaturated equilibrium' resulting from the colonization of Holocene flooded areas by species from unperturbed upland forests. Colinvaux et al. (1985) also connect the high diversity of Amazonian forests to ecological instability, and Salo et al. (1986) pointed out the effect on vegetation of river meandering and lateral migration. From a study in Madre de Dios, Salo and Kalliola (1989) defined a successional series from new sediment deposits colonized by pioneer species to upland forests. Räsänen et al. (1987) attributed the occurrence of lateral river migrations in vast areas throughout the Amazon basin to long-term Andean tectonics, and they described the Amazon basin as a complex mosaic of fossil and modern floodplains. These authors suggested that the high species diversity of Amazonian forests results from the constant ecological instability resulting from the long-term fluvial disturbance.

Some new geological, geomorphological, and botanical data lead us to re-evaluate these hypotheses. The variation observed in the upper Tertiary and Quaternary terranes and the differential effects of Plio-Quaternary tectonics tend to limit the lateral migations of the river more than to extend them. Moreover, plant species richness is generally higher in upland forests than in the wetland forest ecosystems which are frequently perturbed by fluvial dynamics.

TECTONICS, MORPHOLOGY, AND FLUVIAL DYNAMICS

Two morphostructural units constitute the Amazonian region of Peru (Fig. 1). One, lying in the central and southern part of eastern Peru, depends on Andean tectonics; the morphology is rough. The other covers the northern part of eastern Peru and depends on the Guayanan-Brazilian Craton tectonics; the morphology is smooth. Altitudes of both units are less than 500 m above sea level.

Morphostructural Unit I: Andean tectonics

The evenness of eastern Andean foothill morphology was broken during the Eocene (Benjamin et al., 1987; Sébrier et al., 1988), and transformed into an
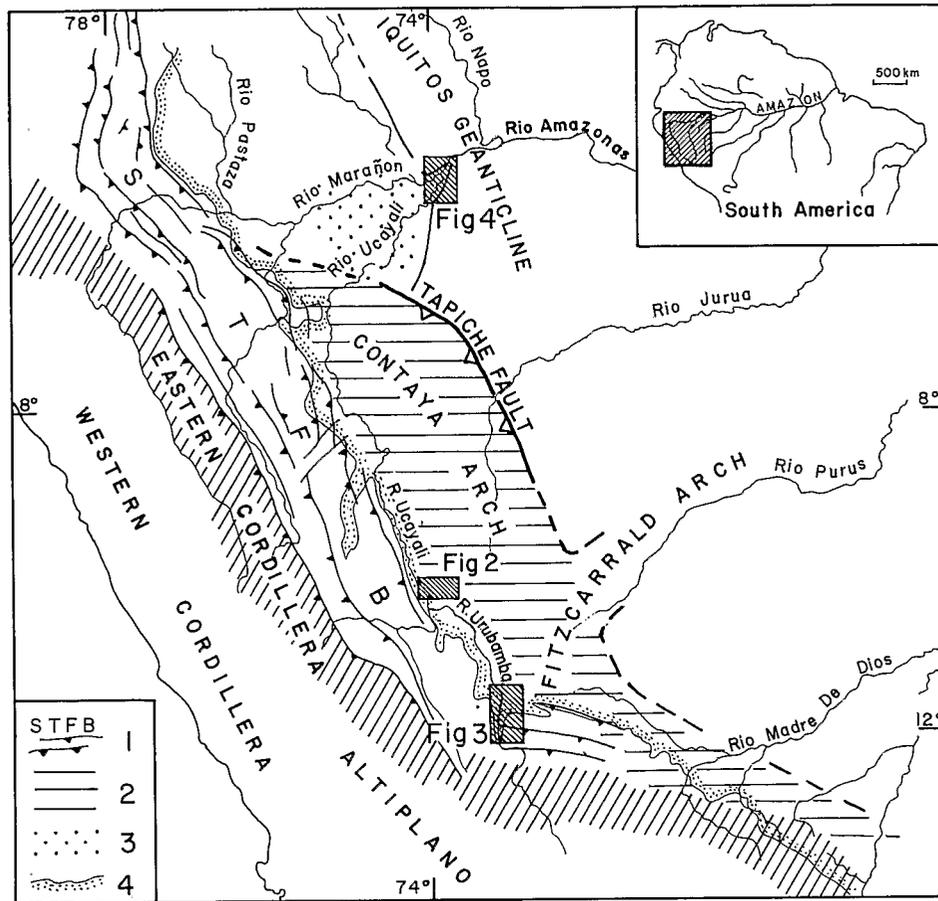
Fig. 1. Structural scheme of the Andes. 1: sub-Andean thrust and fold belt; 2: uplifted Amazonian regions; 3: areas of major subsidence; 4: 500-m altitude limit.

Appalachian relief with up to 1000 m between valley bottoms and hill tops (Dumont and Arana, 1987; Fornari et al., 1987; Argollo and Servant, 1989). The filling-in of the valleys is contemporaneous with the fluvial deposits found at the upper Tertiary series on the Andean piedmont (Buffetaut and Hoffstetter, 1977; Frailey, 1986; Fornari et al., 1987). During the late Miocene and Pliocene periods, sub-Andean terranes were strongly deformed; Miocene layers were tilted (Atalaya region) or folded (Camisea anticlines). The current morphology of the Contaya and Fitzcarrald arches results from the new working of previously formed faults (Rüegg and Fyfe, 1950; Oppenheim, 1975; Laurent, 1985). Then, valleys up to 200 m in depth were scoured in these upper Tertiary layers. They were partially filled with fluvial deposits during the lower Pleistocene (J.F. Dumont, unpublished data). Quarternary con-

glomerates were deposited in stepped terraces, the uppermost lying to 60 m above the current level of the river beds scoured in the Tertiary basement and early Pleistocene sediments.

Andean tectonic and fluvial dynamics in Morphostructural Unit I

Both Quaternary faulting and erosional topography due to folding tectonics limit the lateral migrations of the main rivers. Near Atalaya, the 5–10-km-wide floodplain is bounded by the sub-Andean foothills to the west, and by the western edge of the Contaya arch to the east. This latter was uplifted by Quaternary faulting. ^{14}C dating of two terraces (13 850 $+480/-360$ YBP; 7990 $+750/-550$ YBP) shows that the entrenchments occurred during the late Pleistocene and early Holocene respectively, after upper Tertiary tilting of the basement (Fig. 2). Since then, the Ucayali River has flowed within its valley. Folding tectonics have produced a general uplifting and a correlative entrenchment of the river as a result. The Urubamba River runs S–N, according to fossil stream directions observed in late Miocene terranes, and cuts across the upper Tertiary Camisea folded structures (Fig. 3; see Heim, 1948),
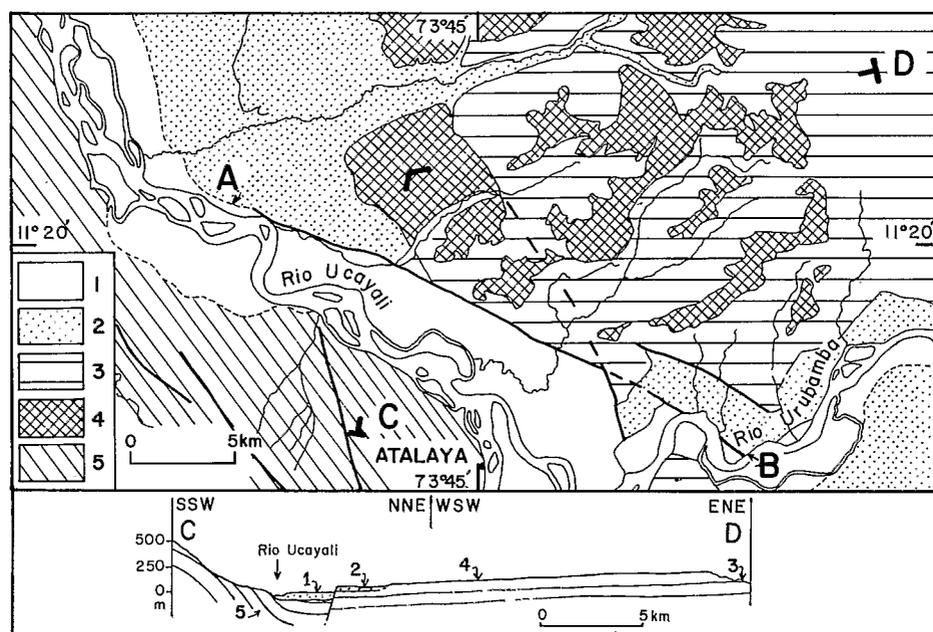
Fig. 2. Morphostructural scheme of Atalaya region (see Fig. 1). 1: Ucayali River floodplain; 2: unflooded Quaternary terraces (A: 13 850 $+480/-460$ years YBP; B: 8520 $+440/-420$ years YBP); 3: erosional morphology on upper Tertiary deposits; 4: tilted-back slope of the Contaya Arch; 5: upper Mesozoic and Tertiary sedimentary basement. C–D: section location.
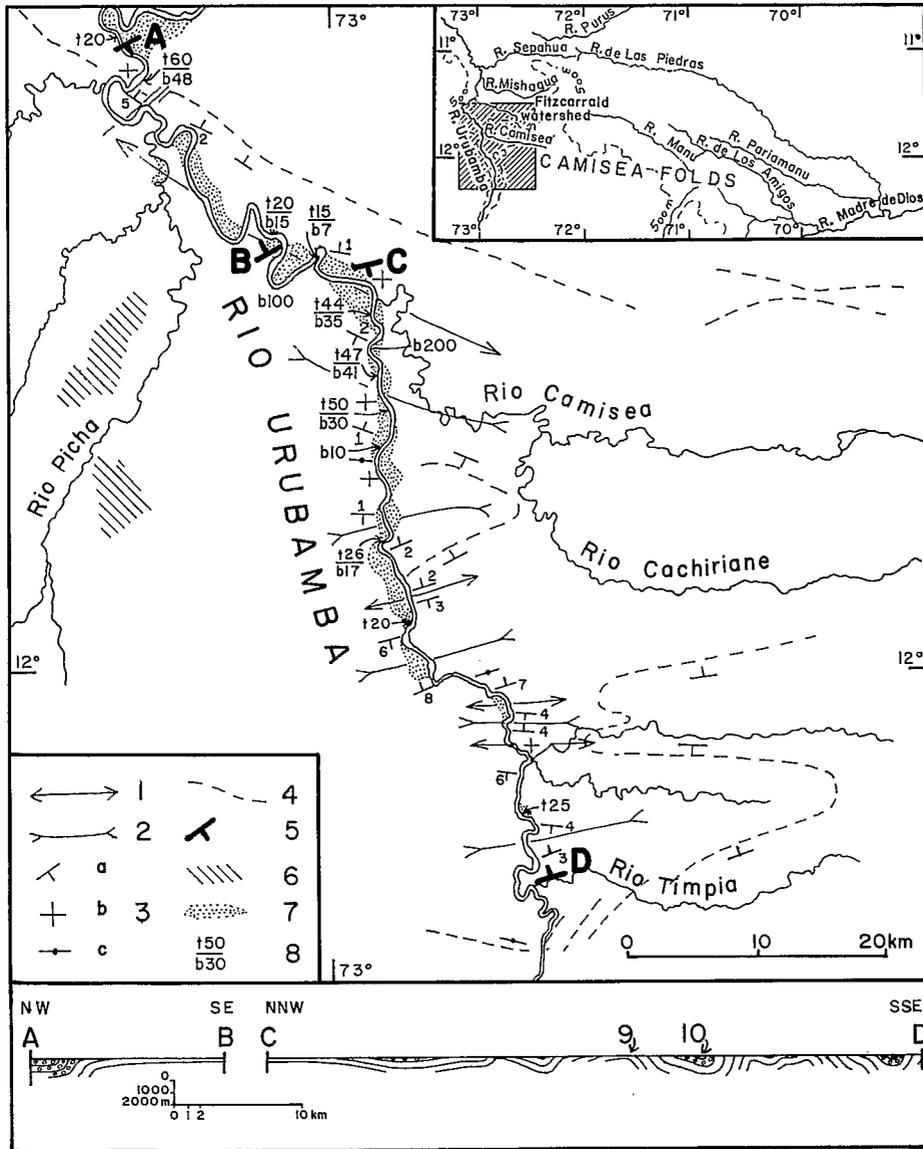
Fig. 3. Morphostructural scheme of the Urubamba valley. 1: anticline; 2: syncline; 3. a – dip: 1 = 10°, 2 = 20°; 3 = 30°, etc.; b – horizontal stratum; c – vertical stratum; 4: main structural lines of erosion-resistant layers; 5: section location; 6: high erosional surface; 7: flooded area; 8: t50/b30: terrace level (50 m)/basement level (30 m) inferred from low-water level; 9: Tertiary silty layers; 10: upper Tertiary conglomerate.

as well as across a vast, bulged, Quaternary terrace to the north near Shepahua. Minor rivers drain the Camisea folded structures flowing westwards (Urubamba tributaries: Camisea, Shepahua, Mishagua) and eastwards (Madre de Dios tributaries: Manu, Los Amigos, Pariamanu, Las Piedras).

Morphostructural Unit II: subsident basin on Guayanan–Brazilian craton

The vast Marañon sedimentary basin lies between the Andean foothills uplifted along the sub-Andean thrust and fold belt (Ham and Herrera, 1961; Mégard, 1984) to the west, and the positively epeirogenic Guayanan–Brazilian craton to the east. The Marañon basin started subsiding during the Jurassic about 170×10^6 YBP (Steinmann, 1930; Rosensweig, 1953; Sanz, 1974). Then, the basin spread westward to the current Andean region which has not yet been uplifted. Andean uplifting began about $55–45 \times 10^6$ YBP (Benjamin et al., 1987; Sébrier et al., 1988), and led to the formation of an intracontinental basin. This basin has subsided, as shown by the great thickness of the sediment deposit – 5000 m, of which 1300 m have been deposited since the upper Tertiary (Sanz, 1974). A negative epeirogenesis in relation to Andean tectonics and uplifting affected the Iquitos geanticline during the Tertiary, as shown by a 500–600-m-thick sediment deposit (Sanz, 1974; Soto, 1979; Laurent, 1985). Epeirogenesis was positive again during the Quaternary and constrained the main rivers, forcing them to converge and flow into the Amazon River. Currently, the Iquitos geanticline uplands are 30 m higher than the floodplain. They are very distinct, however, from the Marañon basin wetlands which are subsiding. The western limit of the Iquitos geanticline (NNS–SSE) is parallel to and superimposed upon an important network of faults in the basement (Laurent, 1985). The Ucayali flows into the Marañon within a depression (Fig. 4) between two uplifted blocks (horst), respectively located northward (Nauta) and southward (Jenaro Herrera). Both blocks belong to the Iquitos geanticline. These faulting tectonics are corroborated by the occurrence of normal faults in upper Tertiary–early Quaternary terraces (Dumont et al., 1988).

Subsidence, tectonics, and fluvial dynamics in Morphostructural Unit II

Tectonic constraints on fluvial dynamics are very weak in the central part of the subsiding Marañon basin. Main river courses are approximately perpendicular to Andean belt directions. Floodplain widths reach up to 100 km. Mean channels are unstable; meanders laterally migrate up to 20–30 m each year (Campo Serra, 1980; Lamotte, unpublished data). Interfluves are irregularly inundated by rainfall and by the river at the time of highest flooding. This is the case with the lands lying between the Marañon and the Ucayali, an area of more than 25 000 km^2 (Villajero, 1988) which extends to about
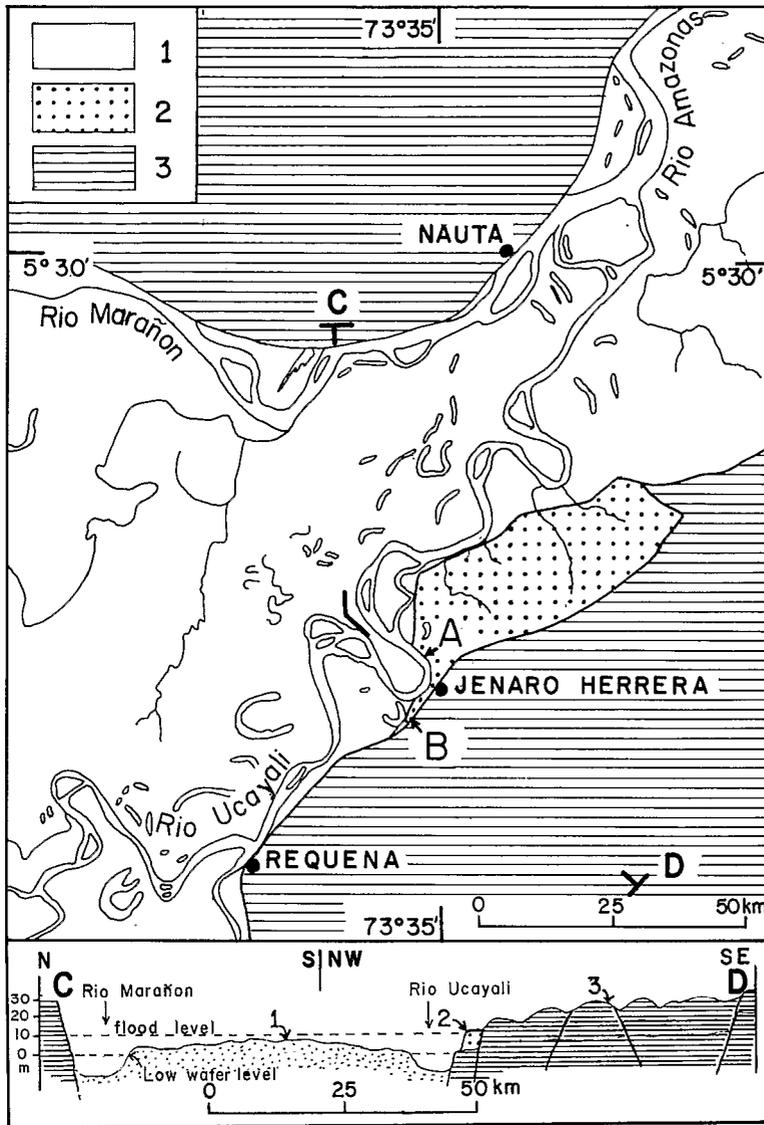
Fig. 4. Morphostructural scheme of Marañon–Ucayali subsidence area. 1: flooded area; 2: Quaternary terraces (A: 13 850 +480/−460 years YBP; B: 32 750 +3520/−2440 years YBP); 3: uplifted upper Tertiary Iquitos geanticline.

200 km above the river confluence. Through this interfluve, Marañon water is drained toward the Ucayali basin (V. Benavides, personal communication, 1987). Crossing the Iquitos geanticline, the Marañon and Ucayali rivers follow the northern and southern uplifted blocks, respectively. Straight segments of mean channels suggest the occurrence of faults. Meandering is dissymetric,

with a single channel outward and several channels inward within the depression. Such a pattern may result from Quaternary distensional tectonics.

Folding and faulting tectonics in fluvial dynamics

Folding tectonics determine the morphology of uplifted regions such as the sub-Andean morphostructural unit. Main rivers are generally entrenched and flow from the Andes toward the Amazon basin, inside deep canyons through the sub-Andean thrust and fold belt. Faulting tectonics are considered less important than folding tectonics in Andean geodynamics. In the subsiding areas such as the Marañon basin, however, faulting tectonics play a major role in limiting wetlands and uplands (Sternberg, 1950, 1955), as well as on meandering patterns (Sternberg, 1957; Tricart, 1977). The limits between wetlands and uplands within the Iquitos geanticline clearly result from faulting tectonics.

Räsänen et al.'s (1987) model, which attributes the western Amazonian landscape to fluvial perturbance produced by long-term sub-Andean tectonics, did not take into account the differential effects of folding and faulting tectonics on morphology. In particular, the effects of faulting tectonics in delimiting wetlands and uplands, and their effect on river meandering and lateral migration, were not considered. The amplitude of lateral river migrations – the whole of Peruvian Amazonia is presented as a mosaic of fossil/current floodplains – is exaggerated. On the contrary, folding tectonics (which lead to river entrenchment) and faulting tectonics (which canalize rivers) both contribute to limiting lateral river migrations.

WETLAND AND UPLAND FOREST ECOSYSTEMS: TWO FLORISTIC SETS

Wetlands support several forest ecosystems (Prance, 1979; Encarnación, 1985): forests on irregularly or periodically flooded alluvial soils along whitewater rivers; forests periodically flooded by blackwater rivers; permanently flooded swamp forests in depressions on clayey substratum; and forests on waterlogged soils in upland valleys irregularly flooded by rainfall. A few floristic inventories have been made in order to compare wetland forests on inundated (fluvisol, histosol) or waterlogged soils (gleysol) and upland forests on well-drained soils (acrisol, luvisol). Gentry (1986, p. 110) concluded, from 0.1-ha plots surveyed near Iquitos, that the number of species common to wetland and upland forests is very low. In Ecuadorean Amazonia, Balslev et al. (1987) listed 60 species (18%) common to adjacent unflooded and floodplain forests of a total of 333 species recorded. Pires (1979) found 345 species on 15 ha surveyed, including wetlands (várzea and igapó forests) and uplands, with an overlap of 83 species (24%). The palm community in most wetland forests clearly differs from that of upland forests by its species rich-

ness and vertical distribution (De Granville, 1976; Kahn and de Castro, 1985; Kahn, 1986a). Most species found in seasonal swamp forests in upland valleys are encountered in all wetland forests (Kahn and Mejia, 1990a, this volume), and they are occasionally found as adult plants in upland forests (Kahn et al., 1988; Kahn and Mejia, 1990b). Although there are few data, a clear difference between the species compositions of wetland (including seasonal swamp forests in upland valleys) and upland forests can be shown. The lack of floristic similarity also suggests that the limits between wetlands and uplands were established a long time ago. Each floristic set would have evolved separately as a result.

"Forests on swampy ground are always poorer in species than those on terra firme" (Richards, 1969, p. 151). All species inventories in wetland forests present a lower species richness per unit area than do those in upland forests. Balslev et al. (1987) estimated a species richness of 228 species per ha in an upland forest and 149 species per ha in an irregularly flooded forest. Species richness is lower in periodically flooded forests (i.e., where ecological constraints are higher) than in occasionally flooded sites: 60 species on 1 ha in an igapó forest (flooded by blackwater) near Belém (Black et al., 1950), and 40 species on 0.5 ha in a várzea forest (flooded by whitewater) along the Rio Xingú (Campbell et al., 1986). These three surveys took into account only trees greater than 10 cm D_{bh}. Pires (1979) listed 224, 196, and 180 species (trees over 30 cm D_{bh} on three 5-ha plots located respectively in upland and, várzea, and igapó forests. Gentry (1986) found 196 to 249 species in 0.1-ha plots in unflooded areas and 163–168 species in two 0.1-ha plots in flooded forests, near Iquitos. Rodrigues' (1961) and Revilla's (1981) data, respectively from an island on clayey, 2-month-annually flooded soil, and from an igapó near Manaus, also show a lower species richness in wetland forests in comparison with upland forests in the same region (Prance et al., 1976). Understory palm species are clearly less well represented in a seasonal swamp forest (3 species per 0.12 ha) than in the neighbouring upland forest (14 and 17 species per 0.12 ha) in central Amazonia (Kahn and de Castro, 1985). Such a difference in palm species richness between wetlands and uplands is also true in Peruvian forests (Kahn and Mejia, 1990).

INSTABILITY OR STABILITY OF ECOLOGICAL CONDITIONS AS THE SOURCE OF DIVERSITY IN TROPICAL RAIN FORESTS?

All Amazonian forest ecosystems are not equally rich. The richest ecosystems are uncontestably the upland (terra firme) forests (Black et al., 1950; Pires et al., 1953; Lechthaler, 1956; Prance et al., 1976; Gentry, 1982, 1986; Boom, 1986; Campbell et al., 1986; Balslev et al., 1987; Gentry and Dodson, 1987). Salo et al. (1986) partially explain the high between habitat species diversity (β-type) by perturbance due to fluvial dynamics. All disturbances

of forest ecosystems (treefall gaps, storms, fluvial dynamics, and deforestation for timber extracting, shifting cultivation, industrial plantations, or pastures) lead to a succession which tends to restore the floristic and structural characteristics of the former ecosystem. Frequent disturbance favours the installation of highly competitive woody pioneer species on vast areas. For instance, in Malaya, *Macaranga* spp. invade open areas, and speciation is observed (Whitmore, 1969; Whitmore and Airy Shaw, 1971); in the Ivory Coast, *Macaranga barteri, Ma. hurifolia, Musanga cecropioides, Trema guineensis,* and the introduced *Cecropia peltata* follow human activity and cover newly deforested areas (Alexandre, 1978; De Namur and Guillaumet, 1978; Kahn and de Namur, 1978; Kahn, 1982). Within the genus *Cecropia,* wetland and upland species are distinct (Berg, 1978). This shows that fluvial dynamics, as a disturbance factor, has led to speciation. *Cecropia* spp. tend to form almost monospecific stands (Salo et al., 1986; Lamotte, 1990, this volume), however, and such speciation therefore does not contribute to increasing species richness. "Pioneer habitats are numerically common, but their diversity is limited by environmental severity" (Pickett, 1976, p. 113). In the later phases of primary and secondary successions, species richness is progressively restored by the installation of shade-tolerant species under the pioneer tree canopy. This increase in diversity depends on the proximity of species-rich forests from which seeds are produced and disseminated. Disturbance due to fluvial dynamics, as well as to human deforestation of upland forests, destroys species-rich ecosystems, and can only contribute to specializing pioneer species even more. The severe ecological conditions imposed by flooding produce increased competition which maintains a highly-specialized wetland flora and a lower diversity as a result. "Forests on sites which are in any way unfavourable tend to have fewer species than those growing under more optimal conditions" (Richards, 1969, p. 151). On the one hand, fluvial dynamics destroys the most species-rich ecosystems, while on the other, high diversity tends to be restored on newly emergent lands. There are no obvious reasons for species diversity (β-type) to increase overall. Such an approach cannot explain the very high diversity within upland forests. For instance, most species of the highly diversified palm genera *Bactris* and *Geonoma* occur in upland forest understory (Kahn et al., 1988; Kahn and Mejia, 1990b); only a few species are found in wetland forests (Kahn and de Castro, 1985; Kahn and Mejia, 1990a).

Why are upland forests so rich in species? Ecological stability and low competition was emphasized by Van Steenis (1969, p. 104): "In contrast to environments with ecologically severe conditions (drought, salt, cold)... where competition is strong, and the survival-level high,... the survival-level in the tropical rain forest lies very low, allowing above it a very large expanse for free form development, for a sort of free enterprise of nature where usefulness is irrevelant and all sorts of harmless adornments can develop". And this is

true with species richness as well as with growth forms (Hallé et al., 1978). The understory is certainly disturbed by treefalls (Denslow, 1980; Hartshorn, 1980; Whitmore, 1982; Brokaw, 1985), but the former ecological conditions are soon re-established by pioneer tree development (first homeostatic phase defined by Hallé et al. (1978)). The size and density of larger trees determine the frequency and size of gaps which influence the frequency and density of some life-forms, as discussed by Kahn (1986b). Such disturbances temporarily affect the size of understory species communities (Richards and Williamson, 1975; Kahn, 1987), but they do not change understory species composition within the ecosystem. The complexity of Far Eastern rain forests is explained in terms of "seasonal and geological stability" and "their great age" by Ashton (1969); Ashton (1977, p. 702) concluded that "in the uniform physical environment and predictable climate of lowland Malaya natural selection will be dominated by biotic factors". Flowering and fruiting patterns, and pollination (Snow, 1965; Janzen, 1967; Frankie, 1975; Stiles, 1975, 1978; Gentry, 1982) are considered to play an essential role in speciation within tropical rain forests. Slight climatic change may disturb these patterns and thus isolate populations. In this way, dryer Pleistocene periods as well as Holocene dryer periods (Soubiès, 1980; Servant et al., 1981), while they may not have fragmented forests into islands within vast savannah areas, may have isolated genetic refuge areas within a forest continuum.

CONCLUSION

Forest ecosystems of the Amazon basin are known to reach very high diversity. Floristic inventories show that species richness is clearly higher in upland than in wetland forests. The analysis of differential faulting and folding tectonic effects on the two western Amazonian morphostructural units clearly indicates that areas affected by fluvial dynamics are rather limited within well-defined depressions, the tendency of which is subsidence or entrenchment. Most upland forests have not been affected by fluvial dynamics since the Pleistocene; plant species diversity is highest in these 'terra firme' forests which cover vast areas. Fluvial dynamics by meandering lateral migrations destroy species-rich ecosystems (upland forests) and favour the installation of less-rich ecosystems (wetland forests). The great age and stability of upland forest ecosystems, and the rather constant ecological conditions (including gap-phase regeneration) in the understory which have been previously proposed (Ashton, 1969, 1977; Richards, 1969; Van Steenis, 1969; Hallé et al., 1978) are still the most convincing explanation of high species diversity within upland forests. In order to elaborate new hypotheses from interdisciplinary approaches, it will be necessary to obtain more botanical data from forest ecosystems chosen inside morphostructural units characterized by neotectonics, sedimentology, paleoclimatology and soil studies.

ACKNOWLEDGMENTS

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