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Patterns of Tree Species Richness in Rain Forests of the Middle Caquetá Area, Colombia, NW Amazonia¹

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ABSTRACT

Tree species, genus, and family richness (DBH $\geq$ 10 cm) is recorded in 95 plots of 0.1 ha, situated in most physiographic units in the middle Caquetá area, east of Araracuara, in the Amazon lowlands of Colombia.

A positive correlation is present between forest canopy height and tree species density. Highest tree taxon density is recorded in upland (non-flooded) plots with well-drained soils. Lowest tree taxon density is found in poorly drained swamps, while plots on podzolized ("white sand") soils show intermediate levels. In well-drained flood plains tree taxon density is lower in comparison with well-drained uplands, but this difference becomes smaller when stem densities are taken into account. Patterns of cumulative numbers of tree taxa in series of plots combined are similar. The results suggest that general patterns of tree taxon richness are mostly related to habitat hostility and environmental stress factors.

Fluvial dynamics, between plot soil heterogeneity and beta diversity, play only a subordinate role in the maintenance of the high tree species diversity in the well-drained uplands. Here, tree species density in proportion to stem density is slightly higher in forests on the less nutrient poor, more clayey and reddish soils with thinner humus forms compared to forests on very poor, loamy, and yellowish soils with thicker humus forms. These results may be explained in terms of habitat hostility (stress) or forest dynamics. Gap phase dynamics could be important in maintaining high levels of tree species alpha diversity in well-drained upland forests. Extinction of tree species related to cyclic forest disappearances on a regional scale has probably been relatively unimportant.

RESUMEN

Se analizaron la riqueza de especies, generos y familias de los árboles (DAP $\geq$ 10 cm) en 95 parcelas de 0.1 ha, ubicadas en la mayoría de las unidades fisiográficas de la cuenca media del Río Caquetá, al este de Araracuara, en las tierras bajas de la Amazonia Colombiana.

Se presenta una correlación positiva entre la altura del dosel superior y la densidad de especies arbóreas. La densidad de taxa arbóreas más alta se encuentra en bosques de tierra firme (no inundados por los ríos) sobre suelos bien drenados. La densidad de taxa arbóreas más baja se encuentra en bosques de pantanos mal drenados, mientras parcelas sobre suelos podzolizados muestran densidades intermedias. En suelos bien drenados de las llanuras de inundación por los ríos la densidad de taxa arbóreas es más baja que en suelos bien drenados de tierra firme. Sin embargo, esta diferencia se disminuye si se toma en cuenta las densidades de los troncos. Los patrones de las cantidades acumulativas de taxa arbóreas en series de parcelas combinadas son similares. Los resultados sugieren que los patrones generales de la riqueza de taxa arbóreas se correlacionan más que todo con la hostilidad de los hábitats y con factores de estres ambiental.

La dinámica fluvial, la heterogenidad edáfica entre las parcelas y la diversidad beta juegan sólo un papel subordinado en el mantenimiento de la diversidad de especies arbóreas alta, en bosques sobre suelos bien drenados de tierra firme. Aquí, la densidad de especies arbóreas en proporción a la densidad de los troncos es un poco mayor en los bosques sobre suelos menos pobres en nutrientes, más arcillosos y más rojos con formas de humus más delgadas en comparación con los bosques sobre suelos muy pobres en nutrientes, francos y amarillentos con formas de humus más gruesas. Estos resultados se podrían explicar en términos de hostilidad de los hábitats (estres) o la dinámica de los bosques. La dinámica en fases de los claros podría ser importante en el mantenimiento de los niveles altos de la diversidad alfa de las especies arbóreas. Es probable que la extinción de las especies arbóreas en las áreas de tierra firme relacionada con las desapariciones cíclicas de los bosques de escala regional ha sido relativamente insignificante.

Key words: *alpha diversity; beta diversity; forest dynamics; environment; habitat; soil; stress.*

NORTHWESTERN AMAZONIAN RAIN FORESTS are among the most tree species rich of the world (Gentry

1988a, b; Neill *et al.* 1993; Valencia *et al.* 1994). This phenomenon must be explained by characteristics of the area in relation to speciation, biogeographical dispersal, extinction, and specific processes leading to an effective maintenance of high tree

¹ Received 25 July 1994, revision accepted 20 February 1995.

species richness. Three processes of maintenance of tree species richness are particularly mentioned in relation to upper Amazonia.

Fluvial dynamics are seen as responsible for large scale forest disturbances leading to levels of tree species turnover that would favor maintenance of high tree species diversity (*e.g.*, Colinvaux *et al.* 1985, Räsänen *et al.* 1987). Higher productivity and species turnover on the Andean-origin nutrient rich soils in the area would, under the condition of aseasonal high rainfall, contribute to the maintenance of high tree species alpha diversities in upper Amazonia (Gentry 1988a). Indeed, recently, higher stem turnovers in tropical forests have been positively correlated to tree species richness, at least on a worldwide scale (Phillips *et al.* 1994). Finally, soil differentiation and beta diversity, related to habitat specialization of tree species (*e.g.*, Gentry 1981, 1988a), may lead to a high regional forest diversity, which would subsidize alpha diversities by mass effects or source-sink dynamics (Shmida & Wilson 1985; Pulliam 1988; see also Schluter & Ricklefs 1993).

Within the context of an integrated forest and soil mapping project of the middle Caquetá area east of Araracuara in the Amazon lowlands of Colombia (Fig. 1), the number of tree species has been recorded in 95 plots of 0.1 ha distributed over most physiographic units in the area (survey report in Duivenvoorden & Lips 1993). In the present paper these data are presented in relation to flooding, drainage, and the presence of podzolized ("white sand") soils in the area. Tree species richness in well-drained upland areas is studied in more detail in relation to soil factors. The results will be discussed in the light of the abovementioned hypotheses, taking into account the distribution of the various land systems in the area. Tree compositional patterns in relation to environmental factors are described in Duivenvoorden (1995). A reconnaissance of near-total vascular plant species counts in various physiographic units near Araracuara is given by Duivenvoorden (1994).

STUDY SITE

The middle Caquetá area (0°25'–1°30'S, 72°30'–70°40'W) receives an average annual precipitation of slightly above 3000 mm (Fig. 1). Its current climate can be classified as Af (Köppen 1936). In terms of Holdridge *et al.* (1971), the area is part of the humid tropical forest zone (BhT). At Araracuara, the annual rainfall departs from the average yearly rainfall (between-year rainfall variability;

see Ashton 1992) are small (between 1–11% in the period of 1985–1990). The area is almost entirely covered by mature rain forests, not visibly disturbed by recent human intervention. Population density is far below 0.2 person/km².

At its western and northwestern margin the area is bordered by a plateau of about 300 m above sea level (130–150 m above the low water level of the Caquetá River) built up of Palaeozoic sandstone. By far the largest part of the area consists of a dissected sedimentary plain of about 250 m above sea level, with steeply sloped valleys, which are generally between 30–60 m deep. This plain is mostly built up by non- to slightly consolidated, clayey to sandy, Miocene sediments, which are deposited in fluvial and lacustrine environments, the latter with influxes of brackish water (Pebas Formation; Lips & Duivenvoorden 1991, Hoorn 1993). The Caquetá River is by far the largest river in the area and the only one with its catchment in the Andes. The flood plains of the Caquetá River and the local (*i.e.*, Amazonian) rivers comprise 14 percent of the area. Two non-flooded fluvial terrace systems of the Caquetá River were recognized: low terraces and high terraces of 10–15 and 25–55 m above the low level of the Caquetá River, respectively. The flood plain of the Caquetá River is from Late Glacial to Holocene age (from 13,000 years BP up to the present), whereas the low terraces of the Caquetá River are deposited in the middle Pleniglacial period (about 65,000–26,000 years BP; Van der Hammen *et al.* 1992).

Soils (mineral soil profiles and humus forms) in the area are extensively described in Duivenvoorden and Lips (1993), where morphological and chemical properties are listed. Soils are basically subdivided according to physiographic position in flood plains or uplands (the latter not flooded by river water, but sometimes poorly drained and inundated due to high phreatic water levels), drainage (poorly drained "swamp" soils versus well-drained soils, the latter with drainage class ≥ 2 according to FAO 1977), and the presence of features of podzolization (*i.e.*, "white sand" soils, generally waterlogged, covering less than about 5 percent of the uplands, and confined to sandstone outcrops, and non-dissected high terraces of the Caquetá River and the Tertiary sedimentary plain). Moderately fertile soils, with base saturation above 50 percent, are only found in the frequently inundated flood plain of the Caquetá River. In all other flood plain and upland systems, soils are strongly leached and chemically moderately to extremely poor.

Two groups of well-drained upland soils have

FIGURE 1. Location of the middle Caquetá area in Colombian Amazonia, together with a Walter diagram from Araracuara (Duivenvoorden & Lips 1993). The upper map shows the approximate position of the 0.1 ha sample plots.

been recognized (Duivenvoorden & Lips 1993). Soils pertaining to the first group classify as Alisol and Acrisol (FAO 1988) and Paleudult or (rarely) Hapludult (SSS 1990), and are mostly developed in Andean-origin deposits of the low terraces of the Caquetá River and sediments of the Tertiary Pebas formation. They are characterized by fine textured, reddish B horizons and contain relatively high total major nutrient concentrations (Table 1). Soils pertaining to the second group classify as Acrisol and Ferralsol (FAO 1988), or as Kandiudult, Paleudult, Kanhapludult, Hapludult, or (one plot only) Hap-

lohumult (SSS 1990), and are mostly developed on Guiana shield derived medium to coarse textured Tertiary deposits or on Palaeozoic sandstone outcrops. These soils are characterized by medium textured, yellowish B horizons within 100 cm depth and show very low total major nutrient concentrations (Table 1). In the well-drained uplands total necromass and fine root content of ectorganic horizons ranges from 490–5240 and 28–1520 g/m², respectively. Relatively thin humus forms with few fine roots are mostly associated with soils of the so-called Ali-Acrisol group, whereas relatively thick

TABLE 1. *Total nutrient concentrations at volume weighted standardized depths of 0–20 cm and 50–100 cm within the two groups of well-drained upland soils recognized in the middle Caquetá area; N represents the number of analyzed profiles. Ca, Mg, K, Na, and P content determined after dry combustion at 500°C and destruction with 48% HF and 4N H₂SO₄; N according to Kjeldahl.*

	cm	Ali-Acrisol group			Acric-Ferralsol group		
		Mean ± standard error g·kg ⁻¹	Range	N	Mean ± standard error g·kg ⁻¹	Range	N
Ca	0–20	0.12 ± 0.02	0.08–0.17	6	0.06 ± 0.01	0.03–0.12	9
	50–100	0.13 ± 0.01	0.08–0.19	7	0.07 ± 0.01	0.04–0.11	9
Mg	0–20	1.66 ± 0.23	1.23–2.74	6	0.21 ± 0.06	0.03–0.64	9
	50–100	2.9 ± 0.46	1.74–5.28	7	0.34 ± 0.08	0.08–0.82	9
K	0–20	5.4 ± 0.79	2.78–7.96	7	0.27 ± 0.04	0.13–0.47	9
	50–100	8.7 ± 1.24	4.29–14.44	7	0.49 ± 0.07	0.14–0.77	9
Na	0–20	0.61 ± 0.09	0.36–0.98	7	0.10 ± 0.02	0.03–0.23	9
	50–100	0.81 ± 0.12	0.46–1.30	7	0.16 ± 0.03	0.05–0.30	9
P	0–20	0.27 ± 0.03	0.17–0.40	7	0.12 ± 0.01	0.06–0.18	9
	50–100	0.28 ± 0.03	0.19–0.36	7	0.14 ± 0.01	0.10–0.20	9
N	0–20	2.2 ± 0.33	1.32–4.03	7	1.04 ± 0.21	0.40–2.30	9
	50–100	0.91 ± 0.08	0.72–1.28	7	0.38 ± 0.04	0.26–0.66	9

and well-rooted humus forms are mostly found on soils of the so-called Acric-Ferralsol group.

METHODS

FIELD SAMPLING.—In land units previously mapped on aerial photographs, soils were described by augering down to 1.20 m. At sites with homogeneous soils and physiognomically homogeneous forests stands, rectangular plots were delimited by compass, tape and stakes, working from a random starting point. In terms of Oldeman (1990) the forest in the plots consisted of (parts of) eco-units in late aggradation to late biostatic phases. Open gaps, with exceptionally low aerial covers of tree crowns, due to recent falls of upper canopy trees or land slides, were not included in the plots. The long side of the plots was parallel to the contour levels. Most plots measured 20 × 50 m, but in some cases were 16 × 66.6 m, or 10 × 100 m (one plot only). Slope angle was measured with an Abney level. The distance between two adjacent plots was never less, and generally far more than 250 m.

In the plots canopy height was estimated and all trees (DBH ≥ 10 cm; DBH = stem diameter at 1.30 m or directly above stilt or tabular roots extending above 1.30 m) were marked by a slash, and numbered. Of these trees, DBH was measured and total height, height of first branch or ramification, and maximum and minimum crown diameters were estimated, using a 6 m calibrated stake. Botanical samples were made of all marked trees, with exception of few very common species.

A total number of 94 plots, well-distributed over the middle Caquetá area (Fig. 1), were sampled in this way, of which 39 were in well-drained upland areas. In one additional upland plot tree species composition and stem density were recorded, without further data.

Afterwards, crown cover, defined as the vertical projection of the crown including holes divided by the plot area, and crown volume was calculated assuming an ellipsoid crown model (Bongers & Popma 1988). Upper canopy height was calculated as the average height of the smallest group of largest trees (DBH ≥ 10 cm) with a cumulative crown cover exceeding 75 percent of the plot area. Estimated canopy height was used in few plots of low forests, where cumulative crown cover remained below 75 percent. Methodologies of field sampling and laboratory analyses of mineral soils and humus forms are given in Duivenvoorden and Lips (1993), and will not be reproduced here.

DATA ELABORATION.—Tree taxon richness is presented as the number of species per 0.1 ha (tree taxon density; Magurran 1988), as the number of tree taxa in proportion to stem density per 0.1 ha ("proportional tree taxon richness"), or as the cumulative number of tree taxa recorded in series of plots combined ("tree taxon pool").

Statistical procedures were performed using SYSTAT (1992). Differences in tree taxon density between physiographic categories (Fig. 3) were compared by ANOVA and Tukey-Kramer HSD pairwise mean comparison tests. Information on the

TABLE 2. Forest structure and tree taxon density recorded in plots of 0.1 ha in land systems of the middle Caquetá area, arranged according to flooding, drainage, and the presence of podzolized ("white sand") soils. Values represent averages $\pm$ standard error with range in parentheses.

	Plots	Height upper canopy m	Stems no./0.1 ha	Basal area m ² /0.1 ha	Trees DBH $\geq$ 10 cm			Families
					Crown volume 1000 m ³ /0.1 ha	Species	Genera no./0.1 ha	
Well-drained flood plains	23	22 $\pm$ 1.4 (7-37)	67 $\pm$ 5.5 (8-136)	3.0 $\pm$ 0.33 (0.2-8.9)	8 $\pm$ 1.2 (0.3-29.2)	27 $\pm$ 2.4 (5-54)	21 $\pm$ 1.8 (4-40)	15 $\pm$ 1.1 (4-26)
Frequently inundated flood plain Caquetá River	8	23 $\pm$ 2.6 (14-37)	73 $\pm$ 12.5 (41-136)	3.6 $\pm$ 0.83 (1.7-8.9)	11 $\pm$ 2.7 (5.4-29.2)	25 $\pm$ 3.7 (7-41)	20 $\pm$ 2.7 (7-30)	15 $\pm$ 1.7 (6-20)
Rarely inundated flood plain Caquetá River	5	23 $\pm$ 2.3 (19-30)	62 $\pm$ 5.0 (46-74)	2.9 $\pm$ 0.24 (2.2-3.6)	7 $\pm$ 1.0 (5.1-10.6)	32 $\pm$ 4.1 (18-41)	25 $\pm$ 3.7 (13-35)	18 $\pm$ 1.5 (13-21)
Flood plains clear and black water Amazonian rivers	10	20 $\pm$ 2.1 (7-28)	66 $\pm$ 7.9 (8-103)	2.6 $\pm$ 0.37 (0.2-4.5)	7 $\pm$ 1.3 (0.3-13.6)	27 $\pm$ 4.3 (5-54)	21 $\pm$ 3.1 (4-40)	15 $\pm$ 1.9 (4-26)
Well-drained uplands	40 ^a	25 $\pm$ 0.6 (17-33)	72 $\pm$ 2.4 (53-127)	3.2 $\pm$ 0.09 (1.9-4.8)	8 $\pm$ 0.4 (3.3-14.7)	38 $\pm$ 1.4 (18-57)	26 $\pm$ 1.1 (12-46)	19 $\pm$ 0.5 (11-24)
Low terraces Caquetá River	9 ^a	25 $\pm$ 1.4 (20-32)	71 $\pm$ 3.9 (58-95)	3.4 $\pm$ 0.25 (2.4-4.8)	8 $\pm$ 1.0 (3.9-13.6)	37 $\pm$ 2.5 (28-51)	25 $\pm$ 2.1 (19-40)	19 $\pm$ 0.9 (14-23)
High terraces Caquetá River	10	24 $\pm$ 1.0 (18-29)	63 $\pm$ 2.6 (53-78)	3.1 $\pm$ 0.17 (2.2-3.9)	7 $\pm$ 0.6 (4.9-10.5)	35 $\pm$ 2.9 (18-55)	25 $\pm$ 2.4 (15-40)	18 $\pm$ 1.2 (12-24)
River terraces Amazonian rivers	4	26 $\pm$ 3.1 (20-33)	61 $\pm$ 4.8 (53-73)	3.0 $\pm$ 0.21 (2.7-3.4)	9 $\pm$ 2.3 (5.2-14.7)	37 $\pm$ 2.0 (31-40)	25 $\pm$ 2.7 (18-31)	20 $\pm$ 2.1 (15-24)
Tertiary sedimentary plain	13	26 $\pm$ 1.1 (17-32)	83 $\pm$ 5.2 (64-127)	3.3 $\pm$ 0.18 (1.9-4.5)	9 $\pm$ 0.7 (3.3-12.7)	42 $\pm$ 2.8 (22-57)	29 $\pm$ 2.4 (12-46)	19 $\pm$ 1.0 (11-24)
Sandstone plateaus	4	25 $\pm$ 1.9 (19-27)	69 $\pm$ 1.1 (66-71)	3.1 $\pm$ 0.20 (2.8-3.6)	7 $\pm$ 0.9 (4.8-8.9)	42 $\pm$ 3.2 (33-48)	27 $\pm$ 2.1 (21-31)	20 $\pm$ 1.8 (16-23)
Poorly drained flood plains	14	14 $\pm$ 1.9 (6-31)	95 $\pm$ 19.6 (12-297)	2.3 $\pm$ 0.35 (0.7-4.5)	3 $\pm$ 0.6 (0.2-8.2)	15 $\pm$ 2.4 (4-38)	13 $\pm$ 2.0 (4-32)	11 $\pm$ 1.1 (4-18)
Flood plain Caquetá River	7	16 $\pm$ 3.4 (6-31)	101 $\pm$ 35.1 (12-297)	2.7 $\pm$ 0.61 (0.7-4.5)	3 $\pm$ 1.0 (0.2-8.2)	12 $\pm$ 2.3 (4-21)	11 $\pm$ 2.1 (4-20)	9 $\pm$ 1.3 (4-14)
Flood plains clear and black water Amazonian rivers	7	13 $\pm$ 1.6 (8-20)	89 $\pm$ 20.4 (42-195)	2.0 $\pm$ 0.36 (0.7-3.2)	3 $\pm$ 0.8 (0.9-6.3)	18 $\pm$ 4.0 (6-38)	15 $\pm$ 3.3 (5-32)	12 $\pm$ 1.7 (5-18)
Poorly drained uplands								
Low terraces Caquetá River	8	17 $\pm$ 1.9 (6-24)	85 $\pm$ 15.5 (13-168)	2.5 $\pm$ 0.37 (0.2-3.7)	5 $\pm$ 1.1 (0.2-10.7)	17 $\pm$ 2.9 (4-27)	15 $\pm$ 2.4 (4-21)	11 $\pm$ 1.4 (4-15)
Upland podzolized soils	10	14 $\pm$ 2.0 (8-23)	79 $\pm$ 8.4 (41-116)	1.9 $\pm$ 0.35 (0.6-3.7)	4 $\pm$ 0.8 (0.8-7.6)	23 $\pm$ 4.4 (7-44)	20 $\pm$ 3.6 (6-38)	13 $\pm$ 2.0 (5-25)
High terraces	3	13 $\pm$ 4.6 (8-22)	60 $\pm$ 10.9 (44-81)	1.5 $\pm$ 0.62 (0.6-2.6)	3 $\pm$ 1.5 (0.9-5.7)	23 $\pm$ 11.0 (7-44)	20 $\pm$ 9.5 (6-38)	14 $\pm$ 5.9 (5-25)
Tertiary sedimentary plain	2	13 $\pm$ 0.3 (12-13)	114 $\pm$ 2.0 (112-116)	2.0 $\pm$ 0.46 (1.5-2.4)	3 $\pm$ 0.1 (2.9-3.1)	12 $\pm$ 3.5 (8-15)	11 $\pm$ 4.5 (6-15)	8 $\pm$ 3.0 (5-11)
Sandstone plateaus	5	16 $\pm$ 3.2 (8-23)	76 $\pm$ 10.2 (41-104)	2.2 $\pm$ 0.60 (0.7-3.7)	5 $\pm$ 1.4 (0.8-7.6)	28 $\pm$ 5.4 (15-42)	23 $\pm$ 4.2 (14-33)	15 $\pm$ 1.9 (11-21)

^a Height upper canopy, crown volume, and basal area based on 1 plot less than indicated.

FIGURE 2. Correlation of upper canopy height with tree taxon density (left) and tree taxon density in proportion to stem density (right) in the middle Caquetá area (trees DBH ≥ 10 cm).

forest structure and the humus forms was condensed by using first components derived from principal components analyses (PCA) of standardized variables listed in Table 4. Slope and geographic longitude were defined in two classes: slope class = 0 if slope = 0°, otherwise slope class = 1, and longitude class = 0 for plots located east of 71°30', and class = 1 for plots west of 71°30' (Fig. 1). In the calculation of the Spearman rank correlation (Table 6), the original values of slopes and longitude

were entered, and two mineral soil classes were conceived as ranks (see text). Prior to ANOVA, linear correlation and regression, PCA and independent *t*-tests, data were inspected for homogeneity of variance, additivity, and normality and, if necessary, log transformed. Residuals were examined for normality and outliers. Plot distances (Tables 3 and 5) were calculated on the basis of approximate plot positions using the Geodistances module in R package (Legendre & Vaudor 1991).

FIGURE 3. Tree taxon density in various physiographic categories in the middle Caquetá area. Lines show maximum values. Vertical bars and lines are averages and standard errors of N plots, shown in legend. Results of Tukey-Kramer comparison tests between physiographic categories are shown by characters in parentheses.

RESULTS

GENERAL DATA SET.—A total of 1077 tree species ($\text{DBH} \geq 10$ cm), 271 genera, and 60 families were sampled (Leguminosae as one family and Cecropiaceae separated from Moraceae; Mabberley 1989).

To date, 525 tree species (48%) have been identified (see list in Duivenvoorden & Lips 1993). A general overview of tree taxon densities and selected forest structure properties in the land systems in the middle Caquetá area (arranged according to flooding and drainage) is given in Table 2.

Tree species, genus, and family density show a strong positive relationship with forest height (Fig. 2 left). In proportion to stem density, largely similar patterns are observed (Fig. 2 right). In some very low forests tree taxon density in proportion to stem density increases artificially because of the diminishing number of stems above the 10 cm diameter cut off.

Tree species density in well-drained upland plots is highest in the area (Fig. 3 left). In 5 well-drained upland plots over 50 tree species were sampled, with a maximum of 57 tree species in one plot set up in hilly terrain built up by the Tertiary Pebas formation. Average tree species density in well-drained uplands is about 28 percent higher than in well-drained flood plains. In proportion to stem density this difference becomes smaller (Fig. 3 right). Lowest tree species density is found in poorly drained (swamp) forests and forests on podzolized soils, also when stem density is taken into account. Forests on podzolized soils tend to be tree species richer per unit area than swamp forests, but these differences lack significance. Genera and family density patterns generally follow the species patterns.

Apart from the family-area curve of the well-drained uplands, which levels off after a cumulative area sampled of about 2.5 ha, slopes of tree taxon-area curves do not decline substantially (Fig. 4). This suggests that insufficient plots have been sampled to estimate the total tree taxon pool size in the various physiographic categories.

The dispersed distribution of the plots in the middle Caquetá area can be deduced from Figure 1, but also from the average between plot distance of all possible plot pairs, and from the standard deviation of all possible between plot-pair distances (Table 3). Plots in all physiographic categories are more or less equally distributed over the area. On the basis of equal cumulative sample sizes of 1.0 ha (0.8 ha for the upland swamps) the tree taxon pools of the poorly drained plots and the plots on podzolized soils remain far below that of well-drained plots, regardless of slightly different total stem densities. The well-drained uplands show higher tree taxon pools than the well-drained flood plains but this may be partly related to the higher total stem densities and between plot distances.

WELL-DRAINED UPLANDS.—Tree species richness is examined in relation to the two groups of well-drained uplands soils recognized in the area (Duivenvoorden & Lips 1993), and to the humus forms in the well-drained uplands (represented by the PCA component which largely reflects necromass and fine

FIGURE 4. Tree taxon-area curves in various physiographic categories in the middle Caquetá area. Curves are calculated on basis of one random sequence of the 0.1 ha sample plots.

root content; Table 4). Plots on both upland mineral soil groups hardly differ with respect to tree species density (t -test, $t = 0.70$, $P = 0.49$; Table 5). However, in proportion to stem density a higher species density is found on soils of the Ali-Acrisol group (t -test, $t = 2.4$, $P = 0.020$). When cumulative stem and species numbers are calculated, more tree species but substantially less tree stems are found on soils of the Ali-Acrisol group in comparison to the other mineral soil group (based on an equal total number of 19 plots).

Tree species density is not correlated with the humus form PCA component (Pearson $r = -0.20$, $P = 0.22$; plot not shown). Proportional tree species density, however, shows a significant negative linear regression with the humus form component ($F = 8.3$, $P = 0.006$; Fig. 5A). One plot (marked by an arrow in Fig. 5A) is reported as outlier. This plot is from a low terrace of the Caquetá River, but its soil has a number of properties typical for the rarely inundated flood plain (lack of reddish B ho-

TABLE 3. Cumulative amount of tree taxa (DBH ≥ 10 cm) in series of plots of 0.1 ha in the middle Caquetá area.

Physiographic category	N ^a	Distance between plot pairs (km)		Cumulative amount of tree stems	Cumulative number of taxa		
		Average	SD		Species	Genera	Families
Well-drained flood plains	23	70	55	1550	346	159	47
	10 ^b	71 $\pm$ 10	55 $\pm$ 4	682 $\pm$ 67	197 $\pm$ 13	110 $\pm$ 6	39 $\pm$ 2
Well-drained uplands	40	83	59	2874	668	203	55
	23 ^b	83 $\pm$ 4	58 $\pm$ 3	1641 $\pm$ 48	471 $\pm$ 21	166 $\pm$ 7	51 $\pm$ 2
	10 ^b	82 $\pm$ 9	57 $\pm$ 6	720 $\pm$ 47	252 $\pm$ 21	115 $\pm$ 10	43 $\pm$ 3
Poorly drained flood plains	14	96	72	1331	141	88	36
	10 ^b	98 $\pm$ 56	72 $\pm$ 4	874 $\pm$ 120	108 $\pm$ 11	73 $\pm$ 5	33 $\pm$ 1
Poorly drained uplands	8	70	48	680	90	61	26
Upland podzolized soils	10	95	66	788	154	92	38

^a Cumulative number of 0.1 ha plots.^b Values in these rows represent means and standard deviations derived from 100 random samples of *N* plots.

rizon, relative high total elemental concentrations, clay skins, and a very thin humus form profile). This outlying plot may be misclassified or transitional between flood plain and upland. If it is removed, the regression shows an even better fit ($F = 15.1$, $P < 0.001$). Multiple regression between proportional tree species density and mineral soil and humus form component simultaneously yields a significant fit ($F = 4.7$, $P = 0.015$), which improves when the same outlying plot is removed ($F = 8.2$, $P = 0.001$).

Other factors may contribute to higher stem

density and proportional tree species densities as well, and may complement or even substitute the soil factors entirely. Three of these possible factors have been considered: presence of slopes, forest structural development (represented by a PCA component which is largely correlated with upper canopy height and cumulative crown volume; Table 4) and the longitudinal position of the plots. Spearman rank correlations (Table 6) indicate that the two soil variables are slightly associated with plot distribution. Furthermore, they show that the humus form component is negatively associated with the nutrient status of the mineral soil, which confirms that necromass and fine root content of humus forms on soils of the Acric-Ferralsol group are generally higher than on soils of the Ali-Acrisol group. Soil factors seem hardly correlated with the forest structural PCA component. This is further illustrated by series of forest profiles, selected to depict the variation of aboveground forest development in each of the two well-drained upland soil groups (Fig. 6).

After partialling out the effects of slope, forest structure, and plot distribution by means of multiple regression, residual proportional tree species density remains larger on soils of the Ali-Acrisol group (t -test, $t = 2.8$, $P = 0.008$), and continues to show significant regressions with the humus form component ($F = 5.3$, $P = 0.027$; again with better fit after removal of the same outlying plot: $F = 9.9$, $P = 0.003$; see Fig. 5B), or with the humus form component and the mineral soil combined ($F = 4.2$, $P = 0.027$; or $F = 6.7$, $P = 0.003$ after removal of the same outlying plot).

TABLE 4. The contribution of forest structure and humus form variables to the first axis of PCA of 39 well-drained upland plots in the middle Caquetá area. The first axis of the PCA of the forest structure variables explained 95% of the variance. The first axis of the PCA of the humus form variables explained 66%.

	Loadings first PCA axis
Forest structure variables	
Height upper canopy	0.95
Crown volume (trees DBH ≥ 10 cm)	0.94
Basal area (trees DBH ≥ 10 cm)	0.63
Humus form variables ^a	
Necromass L horizon	0.41
Necromass F + H horizons (ash-free)	0.95
Fine root ($\varnothing \leq 5$ mm) mass F + H horizons	0.95

^a All log transformed.

TABLE 5. *Tree species density and cumulative amount of tree species (DBH $\geq$ 10 cm) recorded in plots of 0.1 ha in the well-drained uplands from the middle Caquetá area; values represent average $\pm$ standard deviation (calculated if possible); N = number of plots.*

	Well-drained upland soil groups	
	Ali-Acrisol	Acric-Ferralsol
Number 0.1 ha ⁻¹		
Tree species	39 $\pm$ 8.3 (N = 21)	37 $\pm$ 9.2 (N = 19)
Tree species in proportion to stem density	0.58 $\pm$ 0.091 (N = 21)	0.50 $\pm$ 0.104 (N = 19)
Cumulative number in 19 plots of 0.1 ha		
Tree species	431 $\pm$ 9 ^a	379
Stems	1307 $\pm$ 18 ^a	1430
Average distance between all possible plot pairs (km)	83 $\pm$ 2.6 ^a	80
Standard deviation of distance between all possible plot pairs (km)	59 $\pm$ 1.5 ^a	58

^a Values represent average $\pm$ standard deviation derived from 100 random samples taken from 21 plots.

DISCUSSION

ENVIRONMENTAL STRESS FACTORS AND GENERAL PATTERNS OF TREE SPECIES DENSITY.—Tree species, genus, and family density in mature forests of the middle Caquetá area is predictably influenced by physiography and environmental factors. Environmental hostility may limit the influx of tree species and weaken competitive abilities of poorly adapted species. It may, furthermore, influence the mode of canopy impacts and the size of eco-units (Oldeman 1983), leading to structurally less complex forests with a lower niche availability (Terborgh 1992). Upper canopy height of mature forests reflects the degree of environmental hostility and this explains the strong general correlation between forest height and tree taxon density.

Permanent water logging in soils is a main factor limiting tree taxon alpha diversity in the middle Caquetá area. The paucity of tree taxa in Neotropical lowland swamp forests is, of course, well-known (*e.g.*, Richards 1952, Hart 1990), although systematic inventories are rare (Lieberman *et al.* 1985; see also Kahn & Granville 1992). Low oxygen availability leading to reduced nutrient uptakes, lower decomposition rates, higher nutrient immobilization, and stronger acidification may impose severe stress to tree species in swamps (Junk 1982, 1989). Uniform conditions imposed by the superficial water layer may further reduce niche differentiation.

Forests on podzolized soils may suffer from highly variable moisture conditions or nutrient stress due to extremely low elemental concentrations and high acidity in the mineral horizons (despite higher elemental concentrations in the humus forms as-

sociated with these soils; J. M. Lips, pers. comm.; Whitmore 1989). Systematic inventories from Amazonian "white sand" forests are scarce, but seem to reveal the tendency of comparatively intermediate tree taxon diversities (Takeuchi 1961; Anderson *et al.* 1975; Prance 1978; Gentry 1986, 1988a). Both swamp and "white sand" forests may also be particularly vulnerable to catastrophic climatic events, which may have led to relatively high extinction rates in comparison to well-drained forests (Ashton 1992).

The absence of the abovementioned stress factors is a principal condition for the maintenance of high tree taxon alpha diversities in the well-drained forests in the middle Caquetá area. The negative influence of flooding upon tree species densities corresponds to trends observed elsewhere in Amazonia (*e.g.*, Campbell *et al.* 1986, Balslev *et al.* 1987; see also Dumont *et al.* 1990).

The tree densities above 50 species/0.1 ha in several well-drained upland plots are comparable to the high level of 55–60 species found by Gentry (1988b) in the first 0.1 ha samples of the very tree species-rich Mishana and Yanamono plots near Iquitos. This suggests that the world's highest levels of tree species densities are not confined only to the Amazon basins of northern Peru (Gentry 1988b) or Ecuador (Neill *et al.* 1993, Valencia *et al.* 1994), but may be found in well-drained upland forests from the middle Caquetá area as well (see also Duivenvoorden 1994).

Subjectiveness in the morphocategorization, sampling bias by not including larger gaps in the plots, and the dispersed distribution of the plots hampers the comparison between tree species den-

FIGURE 5. Correlation of humus form PCA component with tree species density in proportion to stem density (upper diagram), and residual tree species density in proportion to stem density after singling out effects of slope, forest structure PCA component, and plot distribution (lower diagram), in well-drained uplands from the middle Caquetá area (trees DBH $\geq$ 10 cm). Arrows point at outliers (see text for explanation).

sities in the series of 10 plots combined with forest inventories based on single plots or transects (*e.g.*, Campbell *et al.* 1986). The fact that larger gaps were avoided in the plot siting implies that average

tree taxon densities in the various physiographic categories may be slightly overestimated. This overestimation may vary among the physiographic categories, depending upon the abundance of gaps which have not been recorded.

FLUVIAL DYNAMICS.—Upland systems, built up predominantly of Tertiary deposits, and, to a lesser extent, of Pleistocene terraces, cover at least 86 percent of the middle Caquetá area (Van der Hammen *et al.* 1992, Duivenvoorden & Lips 1993). These estimates are in line with those from the Colombian and northern Peruvian Amazon as a whole, where current flood plains cover only 9 percent and 12 percent, respectively (Proradam 1979, Salo *et al.* 1986). Fluvial dynamics (*e.g.*, lateral channel migration, river bank erosion, etc.) affect only a small proportion of the middle Caquetá area and do not influence the most tree species-rich forests in the area. This situation does not seem to differ much from (northern) Peruvian Amazonia, where areas affected by fluvial dynamics are limited within well-defined depressions, which tend to show entrenchment and subsidence (Dumont *et al.* 1990; compare Räsänen *et al.* 1987).

FOREST DYNAMICS OR STRESS AFFECTING TREE SPECIES DIVERSITY IN WELL-DRAINED UPLANDS.—In the well-drained uplands of the middle Caquetá area the average number of tree species in proportion to stem density and the cumulative number of tree species in series of plots combined is slightly higher on the less nutrient poor soils of the Ali-Acrisol group (with generally thin humus forms) compared to the very nutrient poor soils of the Acric-Ferralsol group (with generally thick humus forms).

Soils of the Acric-Ferralsol group (and associated thick humus forms) may induce more stress compared to the soils from the Ali-Acrisol group (and associated thinner humus forms). Total nutrient contents of these soils are much lower (Table 1). Higher fine root amounts and concentrations at the surface induce more competition for rooting space, and higher susceptibility to drought or attacks by fungi or insects. The thick humus forms may show

TABLE 6. Spearman rank correlation between factors influencing tree species richness (DBH $\geq$ 10 cm) in well-drained uplands of the middle Caquetá area (N = 39 plots).

	Humus form	Mineral soil	Slope	Longitude
Mineral soil	-0.62			
Slope	-0.15	-0.14		
Longitude	0.30	-0.25	-0.12	
Forest structure (PCA component)	0.13	-0.01	-0.18	0.14

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FIGURE 6. Schematic forest profiles from the well-drained uplands in the middle Caquetá area. Left: plots on soils from the Ali-Acrisol group. Right: plots on soils from the Acric-Ferralsol group. From above to below plots with lowest, near first quartile, median, near third quartile, and highest PCA structure component score (see Table 4). All plots from level sites. Profiles depict tree position, tree height, height of first branch, and average crown width in $50 \cdot 7.5$ m depth (trees DBH ≥ 10 cm; crown shape and position artificial; equal horizontal and vertical scales).

lower nutrient-turnovers due to lower decomposition rates.

Soil effects may also be related to a positive influence of higher forest dynamics upon tree species alpha diversity (Phillips *et al.* 1994). Assuming higher forest productivity on the less nutrient poor soils of the Ali-Acrisol group (as suggested by Gentry 1988a), it might be hypothesized that stem turnovers would be higher on these soils compared to the soils of the Acrid-Ferralsol group. In general, however, forest productivity may not be directly correlated to soil nutrient status due to highly efficient nutrient uptake and conserving mechanisms (*e.g.*, Jordan 1985). Different modes of gap and eco-unit formation (Oldeman 1983, Kapos *et al.* 1990, Jans *et al.* 1993) may also lead to other forest dynamics along soil gradients.

The patterns of tree species richness in the well-drained uplands from the middle Caquetá area are not in line with those observed in Costa Rica by Huston (1980), who, perhaps, did not sufficiently partial out interference of flooding, precipitation, temperature (altitude), and drainage. They confirm, however, the claims of Gentry (1988a) that higher tropical plant community diversity would be found on more fertile soils under conditions of sufficient and constant rain fall (see also Clinebell *et al.* 1995). The situation in the middle Caquetá area may also correspond to patterns of tree species richness in the uplands from Borneo, where tree species richness is correlated with soil nutrient content along the nutrient poor end of a soil gradient (Ashton 1989; P. S. Ashton, pers. comm.). In Borneo, however, tree species richness subsequently declines with increasing mineral soil P and Mg, which is explained by an increasing domination of the canopy by a guild of fast growing emergent species (P. S. Ashton, pers. comm.). The richest upland Borneo plots (on basalt), show total P concentrations at 70–80 cm depth beyond 800 ppm (Ashton & Hall 1992), far beyond the levels observed in the well-drained uplands from the middle Caquetá area (Table 1). Large emergent trees are rare in the well-drained uplands of the middle Caquetá area. As in San Carlos de Río Negro (Uhl *et al.* 1988) trees may die before they become large, and there may be genetic restrictions on size of mature trees, or on tree longevity. Perhaps large-sized trees are more inclined to fall over because of superficial rooting. While patterns in Borneo can be explained in terms of Tilman's hypothesis concerning nutrient mediated niche specificities (Tilman 1982, Ashton 1989, Tilman & Pacala 1993), such an interpretation is not really possible with the well-drained upland dataset from

the middle Caquetá area because a decline in tree species richness along the nutrient rich side of the soil gradient is not present. In this discussion, it should be realized that species richness among big trees is, somehow, a function of understory treelet diversity, which is very high in well-drained upland forests in the middle Caquetá area (Duivenvoorden 1994). More insight is required in mechanisms of dispersal, longevity, and competition for nutrient and light resources among understory treelets before Tilman's hypotheses can be seriously tested in relation to tree species diversity in tropical forests (see also Tilman 1994).

The overall rather poor structural aboveground development of the upland forests (as reflected by the schematic forest profiles; Fig. 6) suggests that gap-phase dynamics may provide a general important mechanism by which high tree species density may be maintained. Without systematic recording, gaps by uprooted trees or toppled trees, probably mostly due to strong wind gusts shortly before or after heavy rain, were commonly encountered during the field work. In the dissected uplands multiple treefall gaps by landslides affecting areas less than 200 m² (rarely larger, see also Etter & Botero 1990) are common. Large clearings created by wind perturbation were observed as well (in all land systems). Epiphyte loads, mentioned as factor-inducing tree or branch fall (Strong 1977), are generally small in the middle Caquetá area.

Finally, it is important to realize that, on a wider geographic scale, all upland soils of the middle Caquetá area have a poor to very poor nutrient status (Table 1). This is also illustrated by the very low nutrient concentrations in litterfall in three well-drained upland plots, pointing at high nutrient use efficiencies (J. M. Lips & J. F. Duivenvoorden, pers. obs.) comparable, for instance, to those observed in the San Carlos de Río Negro site in Venezuela.

TREE SPECIES BETA DIVERSITY IN WELL-DRAINED UPLANDS.—Soil or habitat differentiation (Salo *et al.* 1986) in combination with dense plant community packing and beta diversity (the extent of species replacement along an environmental gradient; Whittaker 1972), would be responsible for the high regional tree species-richness in upper Amazonia. This would induce the maintenance of high tree alpha diversity (*e.g.*, Gentry 1981, 1988a; Gentry & Ortiz 1993) by means of source-sink and mass effects (Shmida & Wilson 1985, Pulliam 1988).

Indeed, in the middle Caquetá area as in other parts of upper Amazonia, relatively rich soils developed in Andean-origin parent materials (includ-

ing the Tertiary Pebas formation) may be found together with extremely nutrient poor "white sand" soils (Gentry 1988a, Duivenvoorden & Lips 1993). However, the largest variation in soil nutrient contents is found in the recent flood plain of the Caquetá river. In the uplands from the middle Caquetá area only few ecologically meaningful soil groups were encountered (Duivenvoorden & Lips 1993). In other soil surveys (for instance around Araracuara; Mejía *et al.* 1981), or in Amazonian Peru (Sourdatt 1987) well-drained upland soil differentiation is not exceptionally large either.

The soil heterogeneity in well-drained upland from the middle Caquetá area explains forest community differentiation (Duivenvoorden & Lips 1993, Duivenvoorden 1995). However, in correspondence analyses of tree species data from the 39 plots only small gradient lengths were encountered (Duivenvoorden 1995), which indicate that most plots share species from a pool of dispersed tree species. Only rather general patterns of beta diversity imposed by soil specialists can be traced. Many tree species may be soil indifferent, differing in other aspects of their ecology (Whitmore 1989).

Supportive evidence that soil heterogeneity and beta diversity would be largely responsible for the high number of tree species in the uplands of the middle Caquetá area and for the maintenance of high tree species alpha diversity is, therefore, not available. Furthermore, the influence of soil or habitat diversity in the area as a whole by immigration of tree species from the flood plains, swamps or "white sand areas" to the well-drained uplands is probably limited as well due to the small extension of these azonal systems (Duivenvoorden & Lips 1993). The large number of tree species found in the well-drained uplands must, most of all, be explained by low extinction rates, regional immigration, or exceptionally high speciation rates.

SPECIATION, DISPERSAL, AND EXTINCTION.—Processes of speciation or phytogeographic dispersal (for instance the possible superimposition of Subandean and Amazonian floras) in upper Amazonia and their effects upon tree species richness are still poorly understood. Speciation has been brought into relation with plant-pollinator interactions (*e.g.*, Bawa 1990) and the high upper Amazonian bird diversity (Haffer 1993). Others have mentioned soil or habitat diversity (Gentry 1989; unlikely, at least in well-drained upland situations, see above), river barriers (Salo *et al.* 1986; not confirmed by actual plant distributions according to Gentry & Ortiz 1993; unlikely because headwater areas and me-

andering rivers, both common in upper Amazonia, favor migration of plant populations; Haffer 1993), and the high age-heterogeneity of fluvial terraces (Räsänen *et al.* 1990; unclear how this would favor allopatric speciation, and unlikely in the middle Caquetá area and NW Amazonia in general, where Pleistocene and Holocene deposits are not widely exposed and restricted to stepped terraces along the present river flood plains; Khobzi *et al.* 1980, Dumont *et al.* 1991, Duivenvoorden & Lips 1993) as possible factors influencing speciation in upper Amazonia.

The middle Caquetá area has been situated somewhat outside the principal Pleistocene refuge areas in upper Amazonia (Haffer 1969, Ab'Sáber 1982, Prance 1982, Whitmore & Prance 1987). Nevertheless, geomorphic evidence for climatically induced large-scale disappearance of the forests in the middle Caquetá area could not be found (Lips & Duivenvoorden 1994). It seems possible, therefore, that a part of the large tree species pool in the uplands from the middle Caquetá area is somehow "inherited" from the presumed high Tertiary forest diversity in lowland Amazonia (Van der Hammen 1992). Extinction of tree species in the upland areas related to cyclic forest disappearances on a regional scale has probably been relatively unimportant.

CONCLUSIONS.—The survey of tree species density in various physiographic units in the middle Caquetá area has shown that tree alpha diversities are lowest in swamps, intermediate of size in areas with podzolized soils, and highest in well-drained areas, particularly in well-drained upland areas. Patterns of genera and family alpha diversity, and of cumulative numbers of tree taxa in series of plots combined, are more or less similar. These general patterns are explained by different degrees of habitat hostility and associated stress phenomena, principally induced by flooding, water logging, and/or extremely low soil nutrient concentrations in podzolized soils.

The maximum tree species alpha diversity in the well-drained uplands is comparable to high levels found in Peruvian and Ecuadorian Amazonia. Well-drained upland soils cover over 86 percent of the area. Fluvial dynamics affect only small proportion of the land systems and should not be overrated as mechanism for maintaining high levels of tree species diversity (see also Dumont *et al.* 1990). Tree species density in proportion to stem density in the well-drained uplands is slightly higher on the less nutrient poor, more clayey and reddish soils with thinner humus forms. These results may be

explained in terms of habitat hostility (stress) or forest dynamics. Between plot soil heterogeneity and beta diversity contribute little to the maintenance of high tree species diversity in the well-drained uplands. Here gap-phase dynamics could be more important. Because geomorphic evidence for cyclic forest disappearances on a regional scale has not been found in the middle Caquetá area, extinction may have been relatively unimportant.

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