Density and diversity of plants in relation to soil nutrient reserves in well-drained upland forests in the north-western Amazon basin

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The authors have studied diversity of plants with DBH ≥2.5 cm in series of spatially distributed 0.1-ha plots in well-drained upland forests in the western Amazon basin in Colombia, Ecuador, and Northern Peru. Rainfall, lithology, flooding, topography and soil drainage were fairly constant and we expected to find similar levels of plant diversity. Indeed, on a species-to-area basis the three forest areas were equally diverse. Average diversity varied between 170 and 182 species/0.1 ha, while maximum diversity ranged between 203 and 213 species/0.1 ha. However, on a species-to-individual basis, the Colombian upland forests were distinctly less diverse, due to substantially higher plot densities of plants in the smaller size classes. It is hypothesized that this is caused by a comparatively low mortality of understory plants in the Colombian upland forests due to low soil nutrient reserves (Ca, Mg, P, N) in that area.

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Introduction

Between regions, at distances well over hundreds of kilometres, rainfall and lithology are important determinants of plant diversity of lowland Neotropical forests. At smaller, local scales, flooding, topography, and soil drainage are among the factors thought to control plant diversity. In this paper we present the results of a comparative study of diversity of woody plants with DBH ≥ 2.5.cm, recorded in widely distributed, small plots at three sites in the north-western Amazon basin. Since Gentry (1988) described the high tree species richness of rain forests around Iquitos in Peru (Fig. 1), more or less equally high diversities were recorded from Amazonian sites in Ecuador (*e.g.* Valencia *et al.* 1994) and Colombia (mainly the middle Caquetá area; *e.g.* Duivenvoorden 1996). Large areas of the Amazon basin in Ecuador, northern Peru en Colombia are still covered by non-fragmented 'virgin' lowland rain forests. The whole area has negligible altitudinal gradients and a largely uniform geomorphology (Dumont *et al.* 1990), comprised mostly by more or less dissected sedimentary plains. Furthermore, the area receives everywhere a yearly rainfall of about 3000 mm with a low seasonality (all months show an average precipitation above 100 mm) (Lips & Duivenvoorden 2001). A similar humid rainfall regime prevailed in Pleistocene and Holocene climatic history (*e.g.* Colinvaux *et al.* 2000; Hooghiemstra & van der Hammen 1998; Lips & Duivenvoorden 1994). Because all these important environmental factors show relatively little regional variation, there is no *a priori* reason to expect any substantial difference in woody plant species richness in the north-western Amazon basin.

Methods

The study was carried out in three different areas in the north-western Amazon basin: the Metá area, forming part of the middle Caquetá basin in Colombia; the Yasuní area in Ecuador; and the Ampiyacu area pertaining to the Maynas Province in Peru (Fig. 1). All areas are Humid Tropical Forest (bh-T) in the life zone system of Holdridge *et al.* (1971).

A total of 80 plots, each 0.1-ha, were established, 30 in Metá and 25 in both Yasuní and Ampiyacu. Field work was planned using aerial photographs (Duivenvoorden 2001) and satellite images of Landsat TM (Tuomisto & Ruokolainen 2001). During walks through the forests, soils and terrain units were described rapidly, and forests were visually examined to identify sites with homogeneous soils and physiognomically uniform forest stands. In these stands, rectangular plots (mostly 20 × 50 m) were delimited by compass, tape measures and stakes, working from a random starting point, with the restriction that the long side of the plot was parallel to contour lines. Plots were made in forests that lacked signs of human intervention. The only exceptions to this were some swamp plots in the floodplain of the Ampiyacu river in Peru, where few palms had been cut recently to harvest fruits from *Mauritia flexuosa*. Plots were established with a mini-
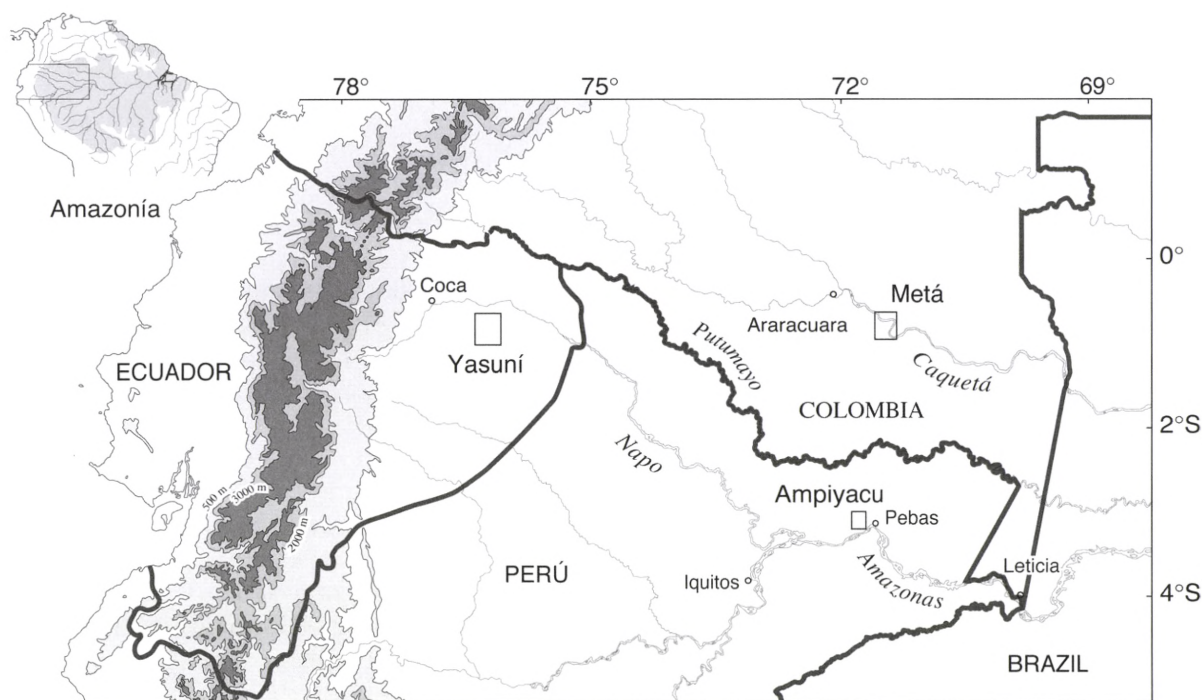
Fig. 1. Location of the three study sites in the north-western Amazon basin (more details can be found in Duivenvoorden *et al.* 2001).

mum between-plot distance of 500 m and their geographical positions were mapped with GPS. The extent (total area encompassed by the network of plots) was largest in Yasuní and smallest in Ampiyacu (Table 1). Plots were subdivided into subplots of 10 × 10 m, in which all vascular plant individuals with DBH ≥2.5 cm (DBH = diameter at 1.30 m height) were numbered and measured with a tape measure. The height of the trees was estimated using long poles as a reference. Field work took place in 1997 and 1998.

Botanical collections were made of all vascular plant species (DBH ≥2.5 cm) found in each plot. Identification took place at the herbaria COAH, QCA, QCNE, AMAZ, USM, MO, NY and AAU (abbreviations according to Holmgren *et al.* 1990). The nomenclature of families and genera followed Mabberley (1989). Specimens that could not be identified to species

were clustered into morpho-species on the basis of simultaneous morphological comparisons with all other specimens. Hereafter the term species refers to both morpho-species and botanical species.

In the central part of each plot, a soil augering was done to 1.20 m depth to describe the mineral soil horizons (in terms of colour, mottling, horizon boundaries, presence of concretions, and texture) and to define soil drainage (in classes of FAO 1977). At each augering a soil sample was taken at a depth of 65-75 cm. For analyses, soil samples were dried at temperatures below 40°C, crumbled and passed through a 2-mm sieve. Total content of Ca, Mg, K, Na, and P was determined by means of atomic emission spectrometry of a subsample of 100-200 mg from the sieved fraction, that had been digested in a solution of 48% HF and 2M H_2SO_4 (after Lim & Jackson 1982). Total

content of C and N was determined for the sieved fraction by means of a Carlo Erba 1106 elemental analyser. Soil analyses were done at the soil laboratory of Institute for Biodiversity and Ecosystem Dynamics of the Universiteit van Amsterdam.

One-way ANOVA followed by Tukey-Kramer HSD tests, ANCOVA, correlation analyses, and regression were performed in JMP 3.1. In AN(C)OVA and regression residuals showed normal distributions. Between-plots distances were calculated using the Geographic Distances Module in R-package (Casgrain & Legendre 2000).

Results

The 0.1-ha sample plots in the well-drained upland forests in the three pilot areas did not differ substantially in the number of vascular plant species per unit area (Table 1). The species-area curve of Metá even seemed to rise towards a slightly higher position than that of Yasuní (Fig. 2D). However, the Metá plots contained significantly more trees and lianas than the plots in the other two areas (Table 1), which resulted in a steeper inclination of the Metá line in the individual-area plot (Fig. 2C). On a species-to-individual basis, therefore, as quantified by Fisher's alpha (Fisher et al. 1943; Condit et al. 1996) and visualized in the species-individual plot (Fig. 2B), the diversity in Metá was lower than in Ampiyacu and Yasuní. The accumulation graphs of individuals to area (Fig. 2C) and species to individuals (Fig. 2B) suggested that the diversity in Ampiyacu was somewhat above that in Yasuní. However, according to the Tukey-Kramer HSD tests the differences in density and diversity between these two sites were not significant.

The higher density in the Metá area was mostly attributed to the larger number of

Table 1. Density, species richness, Fisher's alpha, and basal area for woody plants (DBH ≥2.5 cm), and between-plot distance in well-drained upland forests at three study sites in the north-western Amazon basin. Numbers given are averages ± one standard deviation of n 0.1-ha plots. The F-ratio and probability are from one-way ANOVA between sites. Lower-case letters denote results of Tukey-Kramer HSD tests.

	Species	Individuals	Fisher's alpha	Basal area (m^2)	Distance (km)	n
Metá	173 ± 18.8	436 ± 68.7 a	108 ± 18.7 a	3.9 ± 0.91	17.8 ± 10.2	15
Yasuní	174 ± 15.3	360 ± 43.7 b	140 ± 27.0 b	4.8 ± 1.52	3.2 ± 2.0	10
Ampiyacu	185 ± 21.2	349 ± 27.2 b	161 ± 31.4 b	4.8 ± 0.47	27.7 ± 20.5	6
F-ratio	1.0	7.9	11.3	2.3		
Probability	0.37	0.002	0.0003	0.12		

Table 2. Plant density divided by diameter classes in well-drained upland forests at three study sites in the north-western Amazon basin. Numbers given are averages ± one standard deviation of n 0.1-ha plots. The F-ratio and probability are from one-way ANOVA between sites. Lower-case letters denote results of Tukey-Kramer HSD tests.

	2.5<5 cm	5<10 cm	10<20 cm	20<40 cm	40<60 cm	≥60 cm	n
Metá	237 ± 41.0 a	119 ± 21.9 a	54 ± 13.7	21 ± 3.1	2.7 ± 2.3	1.5 ± 1.1	15
Yasuní	196 ± 37.9 b	89 ± 13.7 b	44 ± 10.0	25 ± 9.3	4.9 ± 2.8	2.4 ± 2.2	10
Ampiyacu	183 ± 17.9 b	90 ± 11.1 b	48 ± 4.2	21 ± 2.7	4.7 ± 1.5	2.0 ± 1.4	6
F-ratio	6.4	10.6	2.5	1.4	3.1	1.0	
Probability	0.005	0.0004	0.098	0.27	0.06	0.37	

small trees with DBH <10 cm (Table 2). The average basal area did not differ significantly between the three sites (Table 1). However, the basal area accumulated over individuals was clearly lowest in Metá (Fig. 2A), probably due to the greater contribution of the big trees in Yasuní and Ampiyacu (Table 2). ANCOVA was done to test if the site differences in density could be accounted for by the basal area of trees and lianas. Several analyses were done including as covariate the ln-transformed basal area from all plants (DBH ≥ 2.5 cm) or from subsets of plants with DBH ≥ 10 cm, DBH ≥ 20 cm, and DBH ≥ 40 cm (untrans-formed), while testing the site effect on plant density of all plants (DBH ≥ 2.5 cm) or a subset of slender plants (2.5 cm $\leq$ DBH <10 cm). In all these ANCOVA, the explained variation (R^2) hardly increased when basal area was included as covariate (the highest increase was from 36% to 38% for the density of all plants, and from 41% to 44% for the subset of plants with 2.5 cm $\leq$ DBH < 10 cm). Also, the effect of basal area was never significant (probabilities remained above 0.25).

Soil concentrations of cations, P, and N were substantially lower in Metá than in the other two sites (Table 3). The well-drained upland
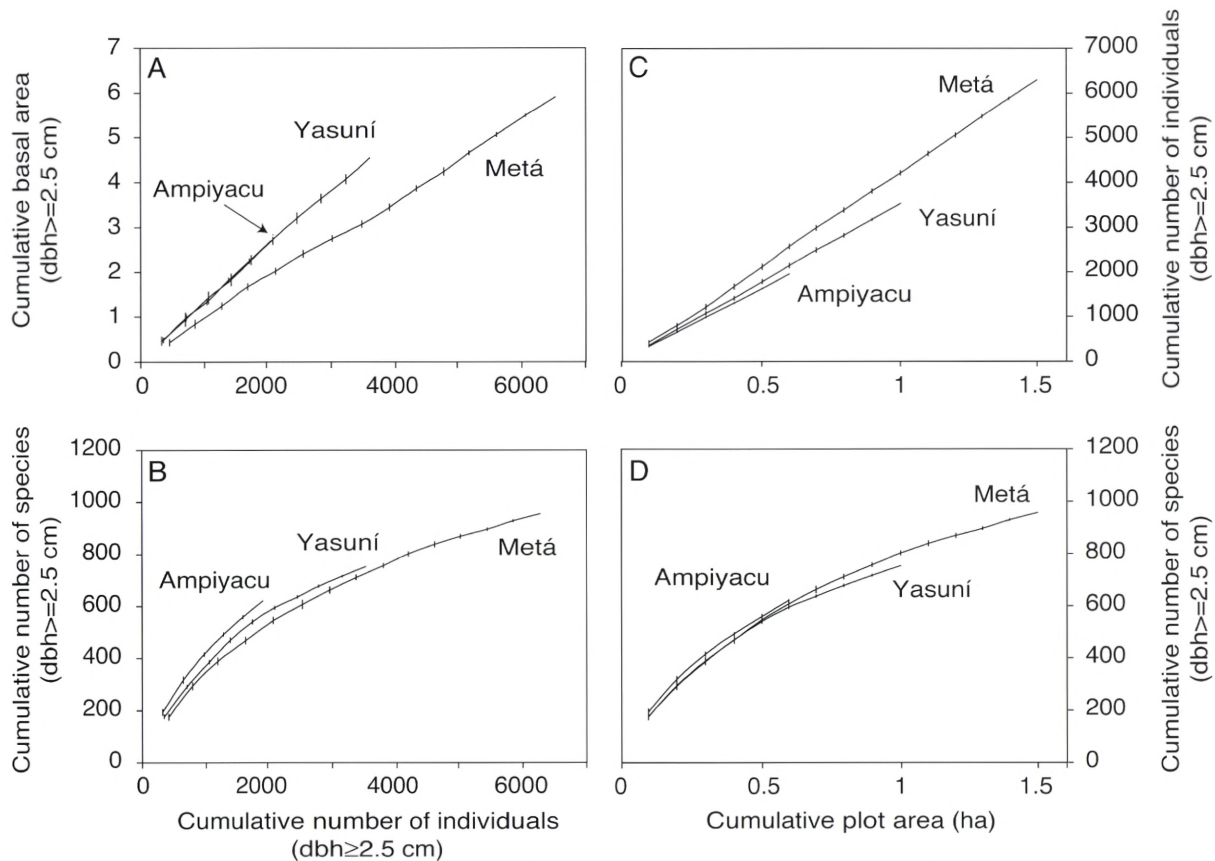

Fig. 2. Accumulation curves of basal area, density, and species (DBH$\geq$2.5 cm) recorded in 0.1-ha well-drained upland plots in each of three study sites in the north-western Amazon basin. Curves are drawn through averages derived from 10 random plot sequences. Bars represent one standard deviation.

Table 3. Average ± one standard deviation of total concentrations of different elements, measured at 70 cm soil depth in well-drained upland forests at three study sites in the north-western Amazon basin, in n 0.1-ha plots. The F-ratio and probability are from one-way ANOVA between sites. Lower-case letters denote results of Tukey-Kramer HSD tests.

	Ca	Mg	K	Na	P	C	N	n
			mg. kg^{-1}			%		
Metá	67 ± 22.9 ab	728 ± 488.7 a	2058 ± 1468 a	216 ± 156.0 ab	166 ± 42.7 a	0.44 ± 0.11	0.05 ± 0.02 ab	15
Yasuní	791 ± 1902 c	3940 ± 1939 b	6500 ± 2547 b	1857 ± 1570 c	305 ± 74.5 b	0.47 ± 0.15	0.07 ± 0.02 c	10
Ampiyacu	102 ± 30.0 bc	3088 ± 976.1 b	8270 ± 2806 b	588 ± 114.1 bc	351 ± 319.1 b	0.56 ± 0.08	0.06 ± 0.01 bc	6
F-ratio	8.8	32.5	15.5	4.9	9.9	1.6	6.8	
Probability	0.001	<0.0001	<0.0001	0.016	0.0006	0.22	0.004	

Table 4. Pearson correlation coefficient between ln-transformed total concentrations of different elements measured at 70 cm soil depth and density, species richness, Fisher's alpha, and ln-tranformed basal area for woody plants (DBH ≥2.5 cm) in well-drained upland forests at three study sites in the north-western Amazon basin.

	lnMg	lnK	lnNa	lnP	lnC	lnN	Species	Density	Fisher's	ln Basal area
lnCa	0.69	0.51	0.49	0.47	0.17	0.50	-0.01	-0.51	0.42	0.04
lnMg		0.93	0.69	0.67	0.23	0.74	0.07	-0.76	0.60	0.18
lnK			0.75	0.65	0.23	0.64	0.21	-0.72	0.66	0.14
lnNa				0.47	0.21	0.42	0.15	-0.42	0.43	0.06
lnP					0.23	0.54	0.18	-0.38	0.42	0.22
lnC						0.35	-0.03	-0.29	0.23	0.03
lnN							-0.15	-0.64	0.37	-0.03
Species								0.26	0.69	0.15
Density									-0.47	-0.02
Fisher's										0.08

soils in Yasuní and Ampiyacu did not differ for these elements. C content was roughly similar in all three areas. The contents of the cations, P, and N were highly correlated (Table 4).

Each of the individual soil variables showed a low degree of correlation with species richness (Table 4). However, plant density was clearly negatively correlated to all soil variables, especially to Mg, K, and N (Table 4, Fig. 3). Hence, Fisher's alpha was positively correlated to the soil variables, mostly with Mg and K (Table 4, Fig. 3). Multiple regression of species richness against the entire set of ln-transformed soil chemical variables did not yield a significant result (F-ratio = 1.2, p = 0.36). Both density (F-ratio = 7.2, p = 0.0001) and Fisher's alpha (F-ratio = 3.4, p = 0.01) were significantly regressed against this same set. However, in these two analyses the partial regression coefficients were not significant (p >0.05), apart from the coefficient for ln-transformed K concentrations on Fisher's alpha (p = 0.02). Including basal area (from all plants or from the same subsets as used in the ANCOVA test of the site effect) as covariate in these multiple regressions hardly changed the results (with or without basal area R^2 remained about 68% for density, and 51% for Fisher's alpha, and the probabilities of the basal area effect were above 0.60).

Fig. 3. Scatter plots of density and Fisher's alpha index of plants with DBH ≥ 2.5 cm against total concentration of selected elements recorded at 70 cm soil depth in 0.1-ha plots, marked according to each of three study sites in the north-western Amazon basin.
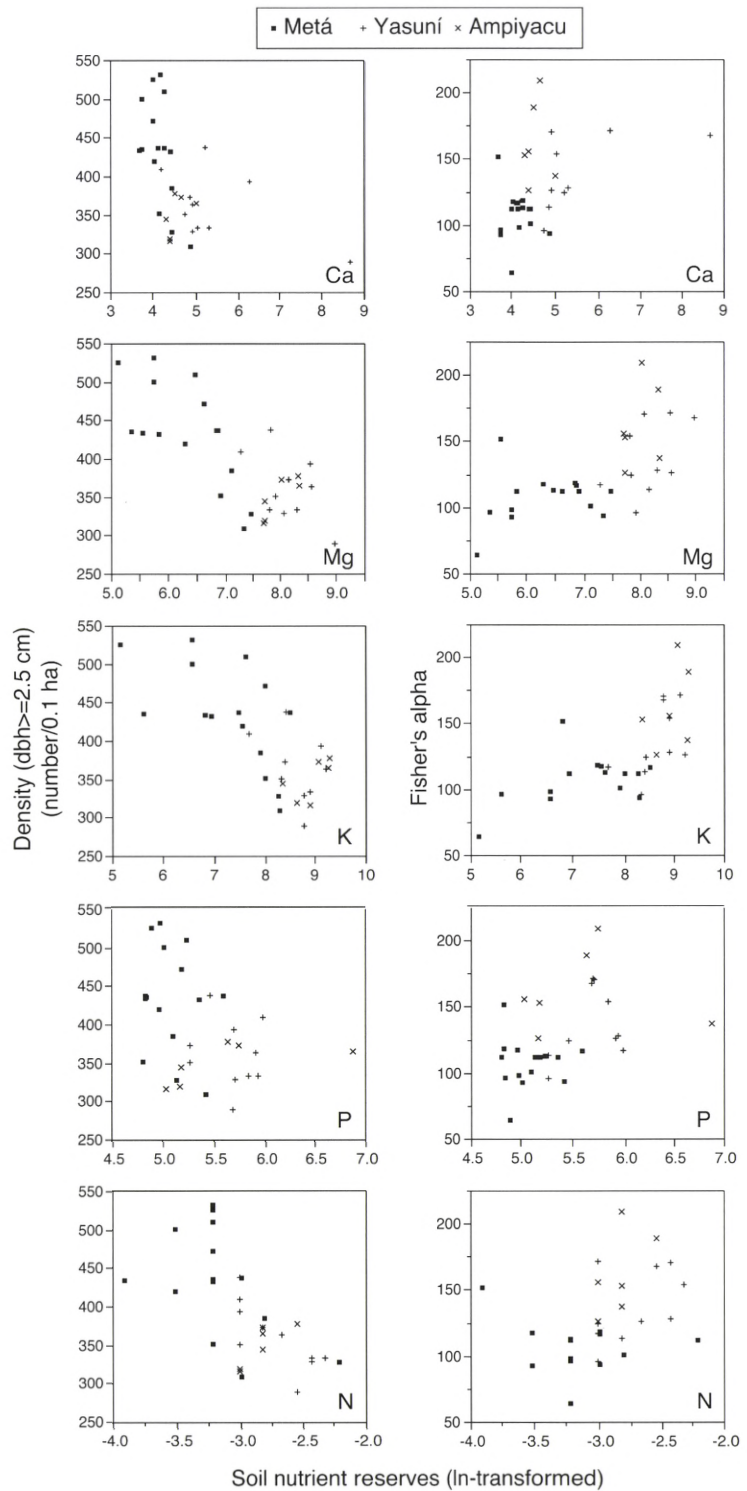
Discussion

Soils in the Metá plots showed distinctively lower reserves of cations, P and N, than soils from the other two sites. The nutrient reserves from the Metá soils resembled closely those found in other well-drained upland soils from the middle Caquetá area in Colombian Amazonia (compare Fig. 4.4 in Duivenvoorden & Lips 1995). Lips and Duivenvoorden (1996b) grouped such upland soils into a so-called Acri-Ferralsol group. Furthermore, they suggested that the low levels of the soil nutrient reserves were due to the highly weathered status of the soil parent material that could have originated from the Guayana shield area (Hoorn 1993, 1994). The same authors also report soil analyses from at least 7 well-drained upland soil profiles in the middle Caquetá basin with higher soil nutrient reserves, similar to those found in the Yasuní and Ampiyacu plots in the current study. These soils were grouped into the so-called Ali-Acrisol group and their high soil nutrient reserves were attributed to the Andean origin of the soil parent materials (Duivenvoorden & Lips 1995; Lips & Duivenvoorden 1996b). This shows that there is more variation in nutrient reserves in the well-drained upland soils in the middle Caquetá basin than indicated by our samples from the 15 plots in the Metá area studied here. In the middle Caquetá basin, just as in well-drained upland forests of lowland Borneo (Ashton 1989; see also Potts *et al.* 2002), threshold reserve levels of about 1200 ppm Mg and 200 ppm P (compare Table 3) mark significantly different routes of development of the humus profile, regarding morphological and chemical differences of the litter layer (ectorganic horizons) (Duivenvoorden & Lips 1995) and leaf litter fall (Lips & Duivenvoorden 1996a). Since the survey of the middle Caquetá basin in the late eighties, new data on nutrient reserves from several well-drained upland soil profiles

have become available, making it possible to illustrate more precisely the strong association between the accumulated litter on the forest floor and the nutrient status of the mineral soil (Fig. 4).

More trees were found per unit area in the small size classes in the Metá area. In the context of the entire Amazon basin, ter Steege *et al.* (2003) reported a comparatively high tree density in the north-western Amazon basin. They attributed this to the constantly high climatic moisture conditions, which would induce high shade tolerance among trees (Huston 1994; Givnish 1999). As rainfall in the Metá area is similar to rainfall at the other sites, climatic moisture cannot explain the higher understory density in the Metá plots.

The Metá area differed from the other areas regarding both soil fertility and tree density. Potentially, this difference may have an expla-
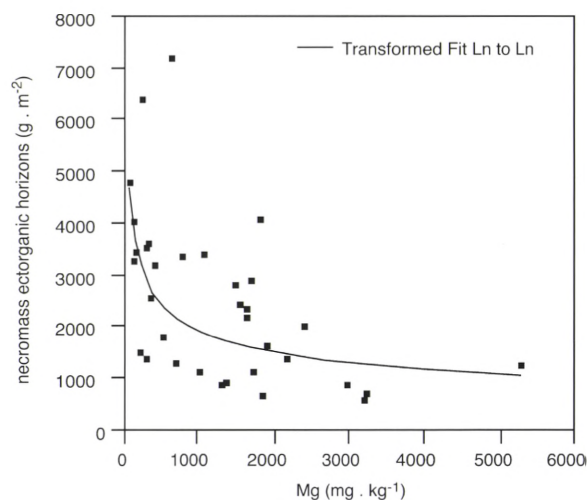

Fig. 4. Regression of necromass (dry weight) of ectorganic horizons against soil nutrient status as represented by the total concentration of Mg at 70 cm soil depth in well-drained upland soils in the middle Caquetá area, Colombian Amazonia. Details of field methods are in Duivenvoorden & Lips (1993, 1995). Linear least squares regression between ln-transformed variables is significant (F=17.3, p=0.0002).

nation with a distinct spatial component at a regional scale. For example, human disturbance by indigenous forest dwellers in the Holocene or the dynamics of climatic change may have been different in Metá compared to Yasuní or Ampiyacu. However, a regional spatial explanation is not strictly required as there is evidence that the relationship between treelet density and soil fertility (at mesic upland sites) also occurs *within* Colombian Amazonia (Fig. 5). In fact, the negative correlation between density and soil nutrient levels in tropical forests has also been reported at neotropical (Clinebell *et al.* 1995) and worldwide scale (Phillips *et al.* 1994).

It might be argued that more fertile soils allow the presence of larger trees that reduce treelet densities by imposing restrictions on conditions of growth and settlement in the forest understory (for example, lower levels of photosynthetically active radiation). This application of the assemblage-level thinning hypothesis (Oksanen 1996; Gotelli & Colwell 2001) to tropical forests seems appropriate for the data here presented. The basal area and the number of big trees were relatively low in the Metá area (Table 1, Fig. 2A), which would explain the enhanced density of treelets and lianas in the small diameter classes. However, accounting for basal area in ANCOVA and regression hardly affected the way sites or soils explained density. This indicates that sites (or soils) might control the understory densities in a way that is independent from forest biomass. The ANCOVA test results should be interpreted with care. The lack of significance of the basal area effect might be attributed to the small number of sample plots which reduces the power of the ANCOVA. On the other hand, the overall numbers of big trees (which contribute mostly to basal area) were low due to the small plot sizes. This might enlarge the variance of the basal area estimates and reduce the chance of obtaining significant test results.
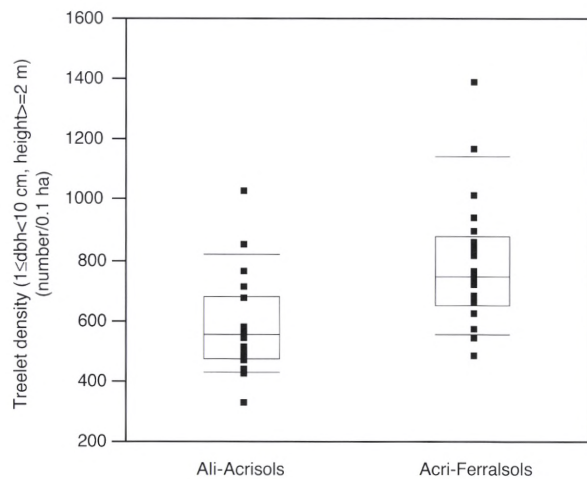

Fig. 5. Number of small trees ($1 \leq$ DBH < 10 cm; height ≥ 2 m) in plots of 0.1 ha on well-drained upland soils in the middle Casquetá area (Colombian Amazonia). Treelets were counted in subplots of 0.01 ha in each 0.1 ha plot. Ali-Acrisols represent soils with relatively high cation reserves and thin humus profiles and Acri-Ferralsols soils with relatively low cation reserves and thick humus profiles. Details of soils and field methods are in Duivenvoorden & Lips (1993, 1995). Treelet density differed significantly between the two soil groups (ANOVA F-ratio=13.6, p=0.0007), also after accounting for basal area of large trees in the plots.

Small and insignificant differences in steady-state levels of forest biomass along soil fertility gradients are predicted by theories of conservation (Jordan 1985) and closed cycling of nutrients in tropical forests (Burnham 1989). In the light of these, it might be hypothesized that the higher understory density around Metá is due to a greater longevity, better defense against herbivory, and lower mortality of the understory plants involved. Slower growth, tougher leaves with lower nutritional quality and higher levels of phenols and tannins, and better plant defences (including improved traits to attract predators of herbivores) are commonly believed to be an evolutionary response of plants to poor soils (Janzen 1974; Coley & Barone 1996). Lower soil fertility must lead to higher investments in roots at the

expense of photosynthetic tissue. This imposes relatively strong impacts of leaf herbivory and eventually results in a positive selection effect on plants that have well-defended leaves. In the tropics, this hypothesis has been initially confirmed along gradients of extremely nutrient-poor white-sand soils to mesic sites (with ultisols and oxisols) (McKey *et al.* 1978). The patterns of treelet density in well-drained upland forests along the ecotone of Ferralsols to Alisols in the north-western Amazon basin, suggest that these mechanisms also operate along ecotones in the mesic soil environment (excluding white sand soils). In line with this, it might be hypothesized that upland tree species that characteristically occur in and directly around the Guayana shield area have better plant defence mechanisms with associated reduced mortality rates than tree species that typically occur in Amazonian forests on less poor upland soils (for instance, in the lowland forests along the footslopes of the Andes). Lower plant mortalities and lower biomass turnover on less fertile soils reduce chances of nutrient loss and can therefore be seen a nutrient conservation mechanism in humid tropical forests (Vitousek & Sanford 1986). Some evidence for this link between forest dynamics and soil fertility is available. Phillips *et al.* (1994) reported a fairly strong negative association between forest 'dynamism' and soil quality. In Colombian Amazonia, Lips and Duivenvoorden (1996a) showed that litter turnover was lower on less fertile upland soils.

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