

Tree species richness of upper Amazonian forests

(Amazonia/rain forest/diversity)

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ABSTRACT Upper Amazonian data for tree species richness in 1-hectare plots are reported. All plants ≥ 10 cm diameter were censused and identified in six plots in Amazonian Peru and one on the Venezuela–Brazil border. The two plots from the everwet forests near Iquitos, Peru, are the most species-rich in the world, with ≈ 300 species ≥ 10 cm diameter in single hectares; all of the Peruvian plots are among the most species-rich ever reported. Contrary to accepted opinion, upper Amazonian forest, and perhaps Central African ones, have as many or more tree species as comparable Asian forests. Very high tree species richness seems to be a general property of mature lowland evergreen forests on fertile to moderately infertile soils on all three continents.

That Southeast Asian rain forests are the world's richest in tree species has been widely noted in both scientific and popular literature (1–5). This impression stems from the fact that hectare parcels of Southeast Asian forests typically have included 120–200 species of trees ≥ 10 cm diameter at breast height (dbh), whereas similar samples of African and neotropical forests generally have 60–120 tree species (figure 1.5 in ref. 1). Trees are one of the few kinds of organisms that show this pattern, which contrasts markedly with α -diversity figures for birds (6–9), reptiles and amphibians (10, 11), butterflies (ref. 12; G. Lamas, personal communication), and bats (G. Creighton and L. Emmons, personal communications), where neotropical communities have more species or nonflying mammals (ref. 13; L. Emmons, personal communication), where community species richness is similar in similar forests from continent to continent. Even for plants, other kinds of comparisons at a much larger scale show many more species in the Neotropics as a whole than in Southeast Asia or Africa (14, 15).

Two serious problems in the extant data base confound intercontinental comparisons of tree species richness. The first is the major intersite variation in tree species richness on a given continent. Although the Asian tree plots span the full gamut of habitat types from poor soil, relatively low diversity, heath or kerangas forests to high diversity, continually moist rain forests on relatively fertile soils, all the equivalent neotropical and African data sets have been until recently from sites anticipated to be at the low end of the tropical diversity gradient (16). In the Neotropics, this has been further confounded by reliance on local tree identifiers or "materos" who always lump together under the same vernacular name many species of large taxonomically complex genera such as *Inga*, *Eschweilera*, *Protium*, or *Iryanthera*.

Thus, the neotropical species richness values for trees with which Whitmore (1) compared the Asian data were mostly for intrinsically relatively low diversity forests in special habitats [seasonally inundated igapó, white sand caatinga or campinarana (17, 18)] or from Central American forests (e.g., see ref. 19), which are comparatively depauperate in tree

species for biogeographical reasons (cf. ref. 15). Many relatively low-diversity neotropical data sets (17, 20–22) relied heavily on "matero" identifications. Apparently the only Amazonian terra firme site for which a complete botanical inventory of trees with species numbers calculated by herbarium comparison of vouchers has been published is a Central Amazonian plot near Manaus (23). This plot had as many tree species in a hectare (ha) as many comparable Southeast Asian plots despite using 15 cm rather than 10 cm dbh as the lower diameter cutoff. Moreover, the Manaus site has a pronounced dry season and relatively low annual precipitation (≈ 2000 mm), factors expected to correlate with relatively low species richness (16, 24, 25).

This paper reports values for tree species diversities in standardized sample plots in upper Amazonia, an area with generally better soils, higher annual precipitation, and a weaker dry season than the few Amazonian sites for which tree plot data were previously available. All of these sites are in or near areas proposed as Pleistocene refugia, unlike many of the previously sampled areas (26). In six 1-ha plots in Amazonian Peru and one in the upper Rio Negro drainage on the Brazil–Venezuela border, all plants ≥ 10 cm dbh were identified. Complete species lists, stand characteristics, and intersite floristic comparisons will be reported elsewhere (27). Each tree in these plots is permanently marked with an aluminum tag and voucher specimens are deposited in the herbaria of the Missouri Botanical Garden, Universidad Nacional de San Marcos, and Universidad Nacional de Amazonia Peruana. Each plot was laid out in closed-canopy mature forest on flat or slightly undulating terrain. The plots were selected to be homogeneous except for a small streamlet passing near or through five of the plots. Such rivulets are a potential complicating factor, but they are so omnipresent in Amazonia that it is difficult to locate a square hectare plot that does not intersect one. Therefore, I have assumed that, along with tree falls and poorly drained patches, they constitute an unavoidable part of the microgeographic within-site variation of a hectare of Amazonian forest. Slight intrasite differences in soil fertility are associated with these microtopographic differences on the local soil catena at some sites; however, these differences are trivial when compared to the major between-site differences in soil nutrients (25, 27).

If a value of ≤ 100 ppm for ammonium acetate extractable calcium is taken as a rough indicator of nutrient-poor soils (25, 28), the six Peruvian sites sort into three geographical pairs with members differentiated by differences in soil fertility. Two sites are in the aseasonal Iquitos area near 04° S latitude: the Mishana tree plot is on white sand, and the Yanamono one is on relatively rich alluvial terrace lateritic soil. Two of the sites lie between 10° and 12° S latitude in areas with marked, but not extreme, dry seasons: the Cabeza de Mono plot is on a relatively infertile sandy old river terrace; the Cocha Cashu one on rich alluvium. The final two sites are on the Rfo Tambopata at 12°50' S, south of the Holdridge system tropical–subtropical demarcation (29): one is on

Abbreviations: dbh, diameter at breast height; ha, hectare.

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sandy upland terra firme, and the other is on rich alluvium. The site on the Venezuela–Brazil border, near the base of Cerro Neblina, is on highly leached ultrapoor white sand. The sites and their soils are more completely described elsewhere (25, 27, 30).

The four full-tropical Peruvian plots all include more species ≥ 10 cm dbh/ha than previously reported for any neotropical site. The two plots in the continually moist Iquitos area both include almost 300 species ≥ 10 cm dbh/ha, far exceeding any other known site in the world. Even the Cerro Neblina forest has more species ≥ 10 cm dbh/ha than most previously reported neotropical values. All of the upper Amazonian plots are as rich as or richer than the Manaus site (23) in species (Table 1). Thus, the single high-diversity figure published for the Neotropics, previously considered something of an anomaly in the context of the data summarized in Fig. 1, is more typical of neotropical forests than the relatively low-diversity plots collated by Whitmore (1).

Although comparable data for 1-ha plots in the diverse forests of Central Africa are not available, data for plants ≥ 10 cm dbh extracted from 0.1-ha sample plots at Makokou, Gabon, include as many species as do similar size subplots of most of the neotropical hectares (Fig. 2). Moreover, there are at least 389 tree species potentially ≥ 10 cm dbh at Makokou (35), suggesting that the number of species ≥ 10 cm dbh/ha may well be as great as in many Southeast Asian and neotropical sites. Such high values are probably typical of Central African forests, since 0.1-ha plots near Korup National Park, Cameroun, and on the lower slopes of Mt. Cameroun have, respectively, 38 and 43 species ≥ 10 cm dbh and 0.64-ha plots at Korup have up to 138 species ≥ 10 cm dbh (Fig. 2).

I conclude that the everwet forests of upper Amazonia may be the world's richest in tree species. The dipterocarp forests of Southeast Asia, although remarkably diverse, are not as exceptional as has been supposed; rather, their high diversity of trees in small sample plots is shared with some South American forests and possibly some Central African forests as well. Indeed, it is hard to imagine a more diverse forest than at Yanamono where there are only twice as many individuals ≥ 10 cm dbh as species in a 1-ha patch of forest (Table 1), with 63% of the species represented by single individuals and only 15% of the species represented by more than two individuals. In the first 50 trees sampled at Yanamono, only two species were repeated; there were 58 species in the 65 individuals in the first 0.1-ha subplot and 90 species in the 115 individuals in the first 0.2-ha sampled.

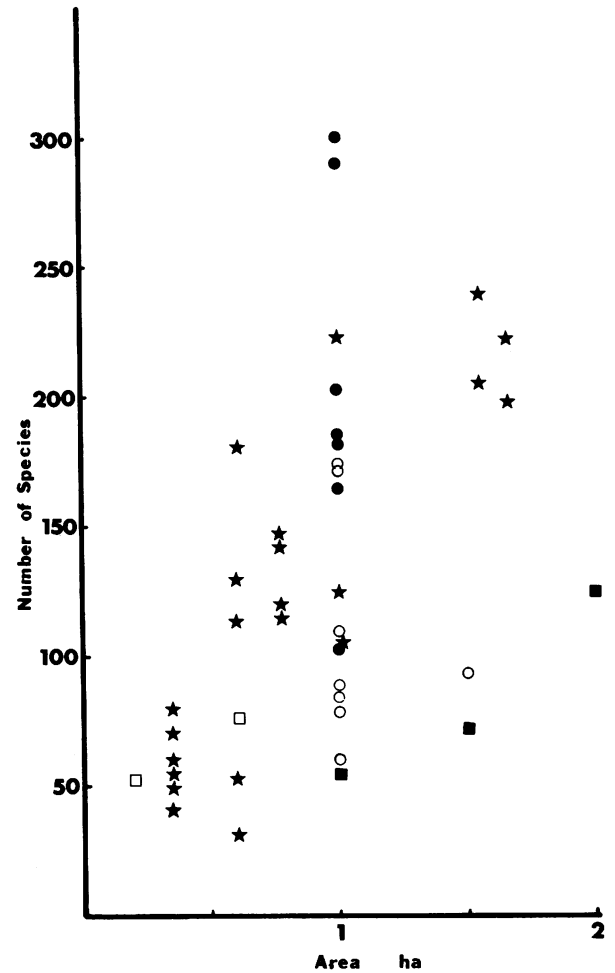


FIG. 1. Number of species ≥ 10 cm diameter on small plots in homogenous mixed-species tropical lowland rain forest. Stars, Southeast Asia; circles, Neotropics; squares, Africa. Solid circles are from Table 1; left open square, combination of two noncontiguous 0.1-ha transect samples at Makokou, Gabon; right open square, average number of species on 0.64-ha plots at Korup, Cameroun (34); other data are from Whitmore (figure 1.5 in ref. 1).

Moreover, many of the site's common species were not included in the sample, suggesting that the local tree species

Table 1. Number of species and stems in contiguous 1-ha plots in upper Amazonia

Site	Coordinates	Total	No. of individuals			Total species	No. of species				
			Trees ≥ 10 cm dbh	Lianas	Trees ≥ 30 cm dbh		Trees ≥ 10 cm dbh	Lianas	Trees ≥ 30 cm dbh	Families	Legumes
Yanamono	3°16' S, 72°54' W	606	580	26	110	300	283	17	81	58	42–43
Mishana	3°47' S, 73°30' W	858	842	16	83	289	275	14	54	50	37–38
Cocha											
Cashu	11°45' S, 71°30' W	673	650	23	110	204	189	15	68	48	26–27
Cabeza de Mono	10°20' S, 75°18' W	544	520	24	81	185	169	16	49–50	40	30–31
Tambopata alluvial	12°49' S, 69°43' W	540	526	14	100	165	155	10	54	41	22
Tambopata terra firme	12°49' S, 69°43' W	602	585	17	80	181	168	13	51–52	42	25–26
Neblina base camp	0°50' N, 66°10' W	513	493	20	84	102	89	13	24	32	22

Data are for trees ≥ 10 cm dbh and lianas ≥ 10 cm greatest diameter. Sites are all in Amazonian Peru, except Neblina base camp on Venezuela–Brazil border; all sites are between 140 and 400 m altitude. Species numbers in some families are based in part on "morphospecies"; in a few cases morphospecies limits are unclear or a voucher specimen has been lost. The limiting values for total number of species at each site are 294–303 (Yanamono), 285–291 (Mishana), 201–204 (Cocha Cashu), 185–190 (Cabeza de Mono), 165–170 (Tambopata alluvial), 179–186 (Tambopata terra firme), 101–103 (Neblina base camp). In each case, the most likely value for number of species in the plot is given.

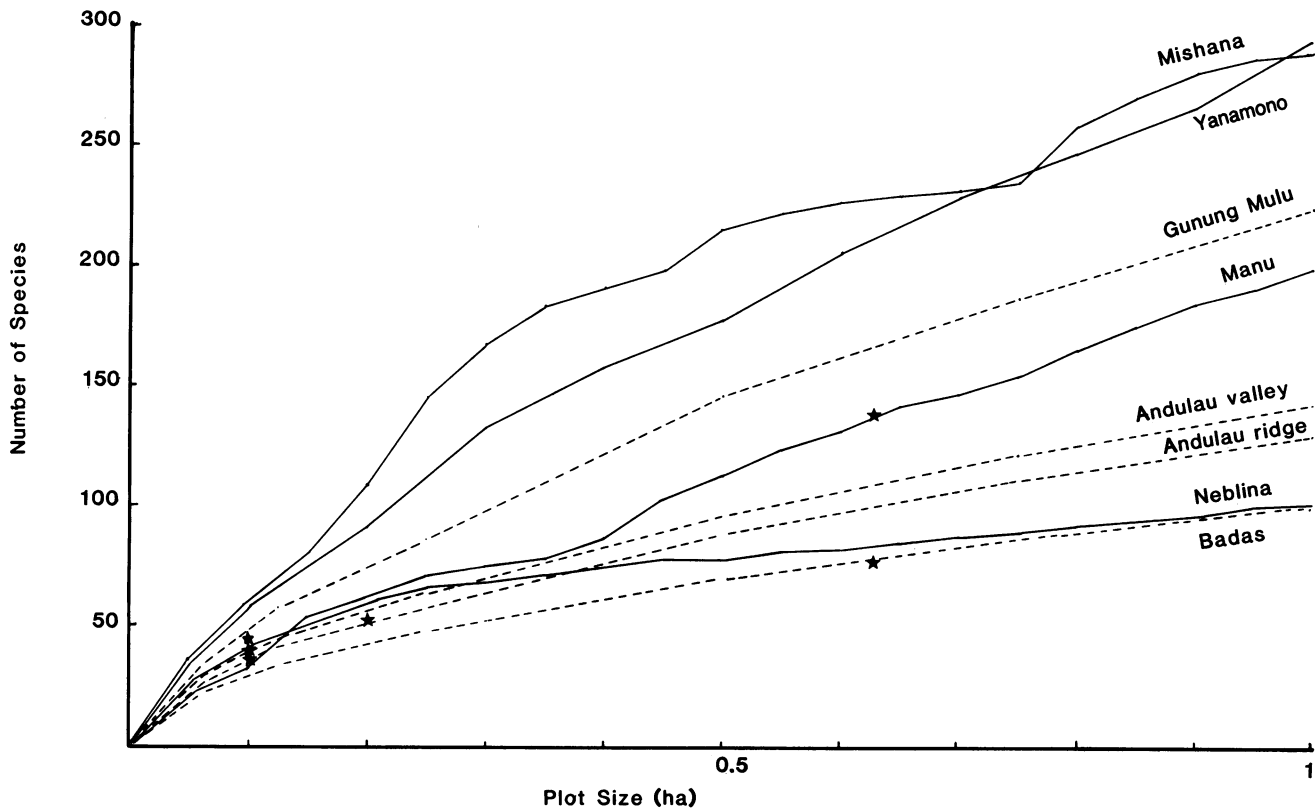


FIG. 2. Species area curves for plants ≥ 10 cm dbh in subplots of some 1-ha tree plots. Solid lines, neotropical sites reported here; dashed lines, Asian sites; the Gunung Mulu data are from ref. 32, and the Andulau and Badas data are from ref. 33. Stars, Central African sites; the 0.1-ha values are, from top to bottom, Mt. Cameroun, Korup, Makokou; the 0.2-ha value is Makokou; the lower 0.64-ha value is the average for 135 plots at Korup (34), and the higher one indicates the highest individual plot value (D. Thomas, personal communication).

richness would continue to increase rapidly with increasing plot size.

Upper Amazonian forests may generally have the most diverse floral and faunal assemblages in the world. The Cocha Cashu site in Manu National Park has the world's largest published inventory of birds (9). The Tambopata site has even more bird species (36), and the highest known butterfly diversity in the world (12). The world's largest local inventory of mammals is from Balta, Peru (A. Gardner, personal communication), the most diverse reptilian fauna is from the Iquitos area (37, 38), and the most diverse amphibian fauna is from Santa Cecilia, Ecuador (31). The new data presented here suggest that, instead of being a striking anomaly, patterns of tree species richness parallel those of birds, butterflies, reptiles and amphibians, and mammals, with the world's greatest local concentrations of species in the relatively moist and fertile forests near the base of the Andes. Whether these patterns relate more to the effects of hypothesized Pleistocene refugia or to modern ecology, as well as the degree to which they may prove to be replicated in other geographical regions, remain unclear. From a planetary perspective, the emerging generality that diversity may be uniquely concentrated in upper Amazonia suggests that special focus on preserving remnants of these rapidly disappearing ecosystems is of the utmost conservational importance.

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