

Tropical tree α -diversity: Results from a worldwide network of large plots

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We assembled data on the diversity of tree species, genera, families, and orders in 13 large-scale forest inventory plots across the tropics. Each plot included at least 16 ha where every individual ≥ 1 cm in stem diameter was censused, providing a much more thorough measure of α -diversity than the typical 0.1- or 1-ha inventories. Amazonian and Southeast Asian plots had more than 1000 tree species, double the highest prior estimate of α -diversity. Not all plots were so diverse, though, and there was 16-fold variation in species richness across the sites. By subsampling the larger plots, we evaluated species richness at smaller scales and found that it generally predicted richness in the larger plots quite well. There were exceptions, however. African plots had low diversity in single hectares, but reasonably high diversity in 20 ha. This can be attributed to the high degree of dominance in African plots: a few abundant species occupied a higher proportion of the forest than in other plots. Finally, based on the recent APG phylogeny, we evaluated diversity at higher taxonomic levels, and found that plots that were richest in species were also richer in genera, families, orders, species per genus, and genera per family. High richness at all taxonomic levels in the most diverse forests demonstrates that at least some of the variation in tropical forest diversity is ancient. However, high species-genus ratios in the richest forests also suggest that recent speciation has contributed to the variation in diversity across tropical forests.

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Introduction

Tropical forests are known for high α -diversity, with hundreds of tree species found on single hectares. This diversity hinders the understanding of diversity, though, because small plots are poor at uncovering the rare species. Single hectares are filled with singletons – species occurring only once – and clearly miss many local species. The Center for Tropical Forest Science has sought to remedy this by much larger-scale studies at a few key sites (Condit 1995, 1998, Ashton 1998). These large plots are expensive and labour-consuming, and cannot be done in many places, but they provide a window into the details of tropical tree diversity. Here we present a comparison of

species abundance and diversity at 13 sites where large inventories are complete. We focus on two basic issues. First, how well to the typical small inventories, 0.1 or 1 ha, represent α -diversity at a site? By how much do they underestimate local diversity? Given the underestimate, can they be used to predict patterns of diversity across sites? This is crucial to studies of variation in diversity, since all are based on small plot inventories (Gentry 1992, Phillips *et al.* 1994, ter Steege *et al.* 2000). Second, how do forests compare in diversity at higher taxonomic levels? Few studies have considered this topic before (Enquist *et al.* 2002), but recommendations to utilize criteria based on phylogeny, not just species, for assessing conservation needs are now surfacing (Webb *et al.* 2002,

Mace *et al.* 2003). Moreover, hypotheses about evolutionary patterns and the origin of diversity depend on deep phylogenetic divisions (Richardson *et al.* 2001, Bermingham & Dick 2001, Enquist *et al.* 2002).

Methods

Large plot inventories are now completed at 13 sites on three different continents. At each site, all individuals ≥ 1 cm in diameter (or dbh, diameter-breast-height) were mapped, measured, and identified to species over at least 16 ha. Two of the sites are in the Congo, 40 km apart; all others are widely separated (Table 1). Each of the two Congo sites includes two subplots of 500 x 200 m, with a 500 m gap between, but we treat these as single plots of 20 ha. All other plots are contiguous rectangles (1040 x 500, 1000 x 500, 500 x 500, 400 x 400, or 320 x 500 m). Details of census methods are described in Condit (1998). Sites were deliberately chosen to span major biogeographic and climatic realms; however, all but one are < 500 m elevation (the La Planada site in Colombia is 1800 m ASL).

Species, genus, and family richness were tallied in complete plots and in subquadrats within plots. In all cases, tallies of different taxa in a subquadrat were carried out by randomly choosing a pair of coordinates x and y , then considering a rectangular region whose lower-left corner was x, y (lower-left was based on general plot orientation; in most but not all plots, lower-left meant southwest). Unless otherwise specified, subquadrats were square with dimensions of 5, 10, 20, 25, 50, 100, or 200 m. Random quadrats were placed 100 times, and the mean and standard deviation of counts of individuals and taxa (species, genera, families, orders) were tallied.

Species abundances are crucial to understanding diversity estimates, since rare species are easily missed in inventories. Complete

abundance distributions from all plots were compared with histograms. To more precisely compare the proportion of rare species, abundances were recalculated in exactly 20 ha from all plots larger than 20 ha, and the proportion of species with < 0.3 individuals per ha was used as a rare species count. In the 25-52 ha plots, the standard deviation and confidence limits for this proportion were calculated from 100 random subquadrats of 20 ha; in 50 ha plots, subquadrats were 1000 x 200 m (close to the shape of the Congo plots), whereas in 25 ha plots, the subquadrats were 500 x 400 m. (In larger plots, we compared 1000 x 200 m and 500 x 400 m subquadrats and found little difference in the percentage of rare species.) In the Congo, confidence limits were not available, since each site had only a 20 ha sample.

Generic, family, and order designations for each species were based on the classification of APG II (the Angiosperm Phylogeny Group 2003). This is based on the most recent evidence available and attempts to reflect angiosperm phylogeny as closely as possible. Across all 13 plots, there were 1080 genera, and we were able to place nearly all of them in APG II. In cases where we could not place a genus, we did not assign a family unless we were certain that it belonged to a group unaltered by the APG classification. There remain unidentified morphospecies in most of the plots – trees that could be consistently distinguished from other known species, but are not matched (yet) to herbarium specimens. Most of these morphospecies have been assigned generic designations, and thus can be classified, but 10% of all species at the plot in Thailand, 8% in Ecuador, and 6% in Cameroon could not be assigned genera (all other plots had $< 4\%$ unassigned). Estimates of genus, family, and order richness at these sites are biased downward, but probably by $< 5\%$ (since many of the unassigned species are likely to be in already tallied genera).

Table 1. Large tropical forest plots associated with the Center for Tropical Forest Science. Those marked with an asterisk were < 25 ha, and data for those sites are based on the full 16 or 20 ha. Main references for each plot are footnoted.

	plot size (ha)	mm annual precipitation (dry season in mo.)	species per ha ≥ 10 cm dbh	species in full plot ≥ 10 cm dbh	species per ha ≥ 1 cm dbh	species in full plot ≥ 1 cm dbh
Lambir, Borneo, Malaysia ¹	52	2664 (0)	245.7	1008	618.1	1179
Huai Khae Khaeng, Thailand ²	50	1476 (6)	65.6	217	101.8	259
Mudumalai, India ³	50	1206 (6)	22.0	63	25.6	72
Pasoh, Peninsular Malaysia ⁴	50	1788 (0)	207.3	678	496.5	814
Sinharaja, Sri Lanka	25	5074 (0)	71.2	167	142.7	205
Palanan, Philippines	16	3218 (4)	98.9	262	201.6	335
Barro Colorado, Panama ⁵	50	2551 (3)	90.7	227	168.0	301
La Planada, Colombia	25	4087 (0)	85.0	172	150.1	219
Yasuni, Ecuador ⁶	25	3081 (0)	253.6	820	665.2	1104
Luquillo, Puerto Rico ⁷	16	3548 (0)	42.2	87	77.6	140
Korup, Cameroon	50	5272 (3)	85.4	307	235.1	494
Ituri, D.R. Congo ⁸ :						
Lenda (monodominant)	20	1674 (2)	49.1	211	166.0	365
Edoro (mixed)	20	1785 (2)	67.0	212	172.2	380

1. Lee *et al.* (2002)
2. Bunyavejchewin *et al.* (2001)
3. Sukumar *et al.* (1992)
4. Manokaran *et al.* (1992), Condit *et al.* (1996b, 1999)
5. Hubbell and Foster (1983), Condit *et al.* (1996a, 1999)
6. Romoleroux *et al.* (1997), Valencia *et al.* (2004)
7. Zimmerman *et al.* (1994), Thompson *et al.* (2002)
8. Makana *et al.* (1998)

Total diversity

Previous studies have found 300 or even 500 species of trees in small plots of forest (Phillips *et al.* 1994, Valencia *et al.* 1994). Our largest plots show that these are substantial underestimates of true α -diversity: more than 800 species of trees ≥ 10 cm dbh were found within 25 ha squares in the Lambir plot in Borneo and the Yasuni plot in Ecuador (Table 1). Both sites had ≥ 1100 species of trees plus treelets ≥ 1 cm dbh. The Yasuni plot had over 350 species of understory treelets on 9 ha of topographically homogeneous ridge-top (Valencia *et al.* 2004). Diversity was broadly associated with climate: the three richest sites had no dry season, while the poorest site was also the driest (Table 1).

Diversity in single hectares vs. large plots

Single hectares from the 13 plots included a wide range of species diversity of trees ≥ 10 cm dbh, from a mean of 22 in southern India to 254 in Amazonian Ecuador (Table 1). Expanding plots to 25 or 50 ha greatly increased species counts, and including smaller trees (1–10 cm dbh) increased counts further (Table 1). Across plots, the magnitude of the augmentation was consistent: for instance, in Thailand, Sri Lanka, India, and Panama, the increase in species from 1 ha (≥ 10 cm dbh) to 25 or 50 ha (≥ 1 cm dbh) was very close to 3-fold; at the very diverse sites in Malaysia and Ecuador, it was closer to 4-fold. The consistency of this increase suggests that small plots are a valid way to judge patterns of relative diversity (Gentry 1992, ter Steege *et al.* 2000), but that they substantially underestimate α -diversity.

The plots in Africa, especially the monodominant sites in the Congo, deviated most from this pattern: the increase in species count from

a single hectare to the larger plot was 5- to 7-fold. The contrast is clear when comparing, for instance, the Congo monodominant site with the Panama site. A single hectare in the former had barely half the species ≥ 10 cm dbh as a single hectare in Panama, yet 20 ha in the Congo had more species than 50 ha in Panama among trees ≥ 1 cm dbh.

The standard deviation in diversity was low, always substantially below the mean. As a result, given the large size of the plots, confidence intervals in diversity estimates were very narrow, usually $< 5\%$ of the mean (Appendices 1–3).

Species accumulation

Species-area curves illustrate the increase in diversity from small to large plots in all forests at once (Fig. 1). To the extent that all the curves in Fig. 1 have the same shape, small plots accurately assess relative diversity differences among forests (but underestimate total α -diversity). Indeed, species-area curves from all plots were quite similar in general form, roughly parallel to one another (Condit *et al.* 1996b). Nearly all differences between plots in diversity at all plot sizes were statistically significant (confidence limits were omitted from Fig. 1 to avoid clutter, but are given in Appendices 1–3).

The species-area curves were not precisely parallel, however, and in cases where they intersected, small plots are misleading. The two dashed green curves in Fig. 1 represent the two 20-ha plots in the Congo; both curves started well below the Sri Lanka and Panama curves but intersected them and rose higher. The plot in Thailand also had a curve intersecting those from several other plots. Differences in shape of the curves are most likely due to differences in abundance distributions (He & Legendre 2002).

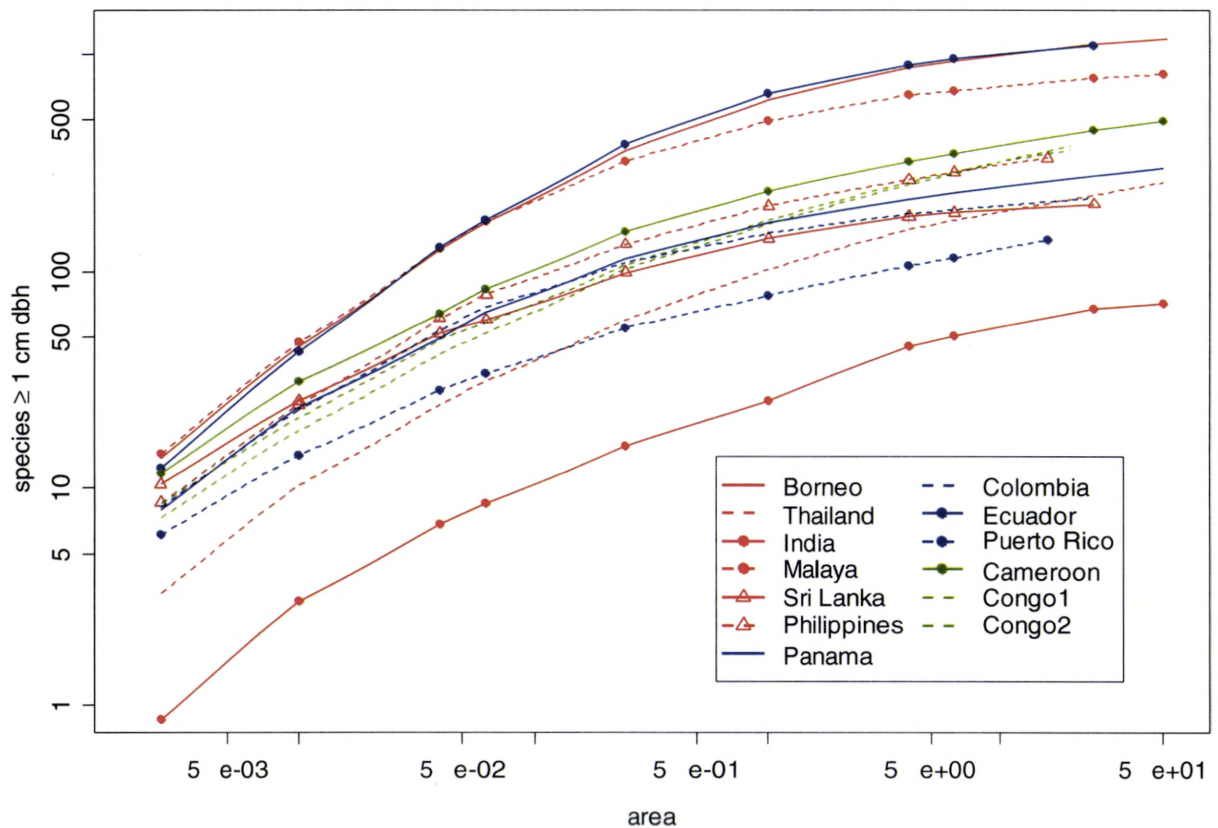


Fig. 1. Species accumulation as a function of the area of successfully larger square subquadrats within tropical forest plots. Asian sites are indicated in red, American in blue, and African in green.

Abundance distributions

Large plots provide detailed descriptions of species-abundance distributions because large number of individuals are sampled over many species. That abundance distributions from different forests had similar shapes led Hubbell (2001) to derive a general theory relating species accumulation to species abundance. In

eight plots, species-abundance distributions were similar and nearly log-normal (Fig. 2A). All deviated in the same way, with a left skewness that indicates more rare species than common. Hubbell's (2001) neutral model predicts this skewness, but McGill (2003) argued that the log-normal is still the best description.

Five other plots had abundance distributions that were quite different, having more rare

Fig. 2. Species abundance distributions in large tropical forest plots. The vertical axis shows the fraction of species in the entire plot falling in various abundance categories. The horizontal axis gives density of individuals ≥ 1 cm dbh per ha, on a logarithmic scale; bin size increases exponentially with abundance, as usual in log-transformed abundance distributions. The 13 different plots are split into two groups to make it easier to see individual lines. The division was post-hoc, based on similarity in form: A) eight plots which had symmetrical, nearly log-normal abundance distributions; B) five which had wider and flatter distributions. Asian sites are indicated in red, American in blue, and African in green. →

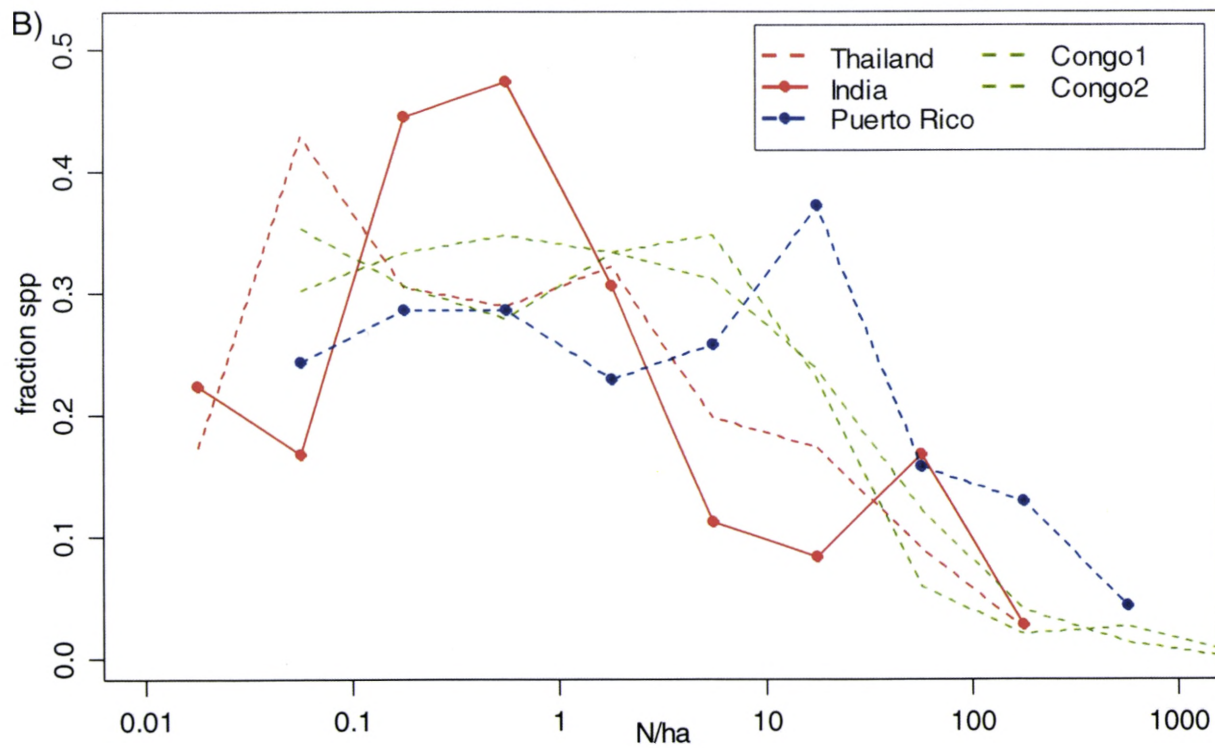
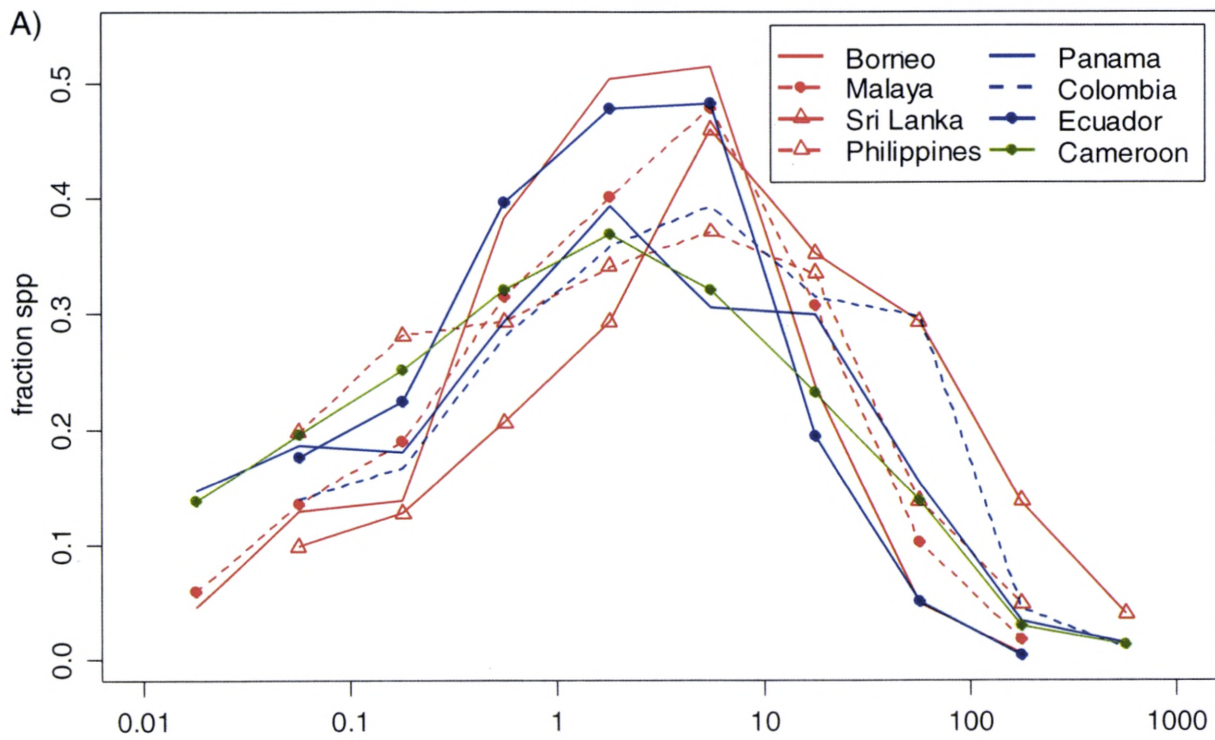


Table 2. Percent of rare species (those with ≤ 0.3 individuals per ha) at each of the plots, and relative abundance of the dominant species. Both are given as mean \pm 95% confidence limits, based on replicate 20-ha subquadrats. Confidence limits for Congo sites could not be calculated, since the plots were only 20 ha; for sites marked with an asterisk, the estimates are based on the full 16 ha, and also lack confidence limits.

<i>Plot</i>	% rare species	% dominance	dominant species
Lambir, Borneo, Malaysia	14.9 \pm 3.7	2.6 \pm 1.0	<i>Dryobalanops aromatic</i> Gaertner (Dipterocarp-)
Huai Khae Khaeng, Thailand	44.8 \pm 1.5	10.0 \pm 5.2	<i>Croton oblongifolius</i> Roxb. (Euphorbi-)
Mudumalai, India	41.7 \pm 4.8	22.8 \pm 6.5	<i>Kydia calycina</i> Roxb. (Malv-)
Pasoh, Peninsular Malaysia	19.2 \pm 3.5	2.7 \pm 0.3	<i>Xerospermum noronhianum</i> Blume (Sapind-)
Sinharaja, Sri Lanka	16.6 \pm 0.9	12.1 \pm 0.4	<i>Humboldtia laurifolia</i> M. Vahl (Fab-)
Palanan, Philippines *	37.9	5.6	<i>Nephtelium lappaceum</i> Poiret (Sapind-)
Barro Colorado, Panama	25.6 \pm 2.7	15.7 \pm 1.9	<i>Hybanthus prunifolius</i> Schulze-Menz (Viol-)
La Planada, Colombia	24.2 \pm 2.9	15.6 \pm 0.1	<i>Fareamea coffeoides</i> C.M. Taylor (Rubi-)
Yasuni, Ecuador	31.1 \pm 0.6	3.1 \pm 0.1	<i>Matisia oblongifolia</i> Poeppig & Endl. (Malv-)
Luquillo, Puerto Rico *	40.7	19.6	<i>Palicourea riparia</i> Benth. (Rubi-)
Korup, Cameroon	29.2 \pm 2.6	8.3 \pm 1.5	<i>Phyllobotryum spathulatum</i> Müll. Arg. (Salic-)
Ituri, D.R. Congo: Lenda (monodominant)	48.4	45.0	<i>Scaphopetalum dewevrei</i> Wildem. & Th.Dur. (Malv-)
Edoro (mixed)	52.2	41.8	<i>Scaphopetalum dewevrei</i>

species and no distinct mode of abundance (Fig. 2B). The Congo plots had the highest fraction of species with ≤ 0.3 individuals per ha: the percentage at both Congo plots exceeded the upper 95% confidence limit from all other plots (Table 2). The two plots in drier climates (Thailand and India) and the Puerto Rico plot also had high percentages of rare species. The India and Puerto Rico plots are the only two subjected to major human disturbance in the past century, and the latter suffers hurricane disturbance regularly (Zimmerman *et al.*

1994). Coupled with rarity, the Congo plots also had the most abundant species at any site (Table 2): *Scaphopetalum dewevrei* had a density of > 2000 treelets per ha, more than double the density of any other species in the 13 plots (it appears as the rightmost tail in Fig. 2B).

Monodominance

Species-area and species-abundance comparisons indicate that the Congo plots deviated in two ways from other plots: they had a steeper

increase in species richness from small to large samples (Table 1, Fig. 1), and they had more rare species as well as the most abundant species (Table 2, Fig. 2B). The latter reflects monodominance, where a single species occupies a high proportion of the trees in a forest; Congo plots had the highest degree of dominance among the 13 plots (Table 2). We suggest that monodominance is also responsible for the form of the species-area curve (He & Legendre 2002). High numbers of rare species mean that species counts from small plots are low, because rare species are inefficiently sampled; small plots thus represent true α -diversity poorly. Rare species in all tropical forests are a problem for species-sampling, but the problem is accentuated in monodominant African plots.

Monodominance in African forests has been widely discussed (Connell & Lowman 1989, Hart 1990, Newbery *et al.* 2000), but usually in terms of abundance or basal area of large trees. One of the two plot sites in the Congo was chosen to represent monodominance by a large Caesalpinoid tree, *Gilbertiodendron dewevrei* (De Wild.) Leonard. The other site in the Congo (just 40 km from the first) was chosen as “mixed forest”, where *Gilbertiodendron* was much less common. It was not, however, only *Gilbertiodendron* that dominated the Congo plots, indeed, *Scaphopetalum* was numerically far more important. Understorey dominance, and the fact that heavy dominance extends even to the so-called “mixed forests” of the Congo, has not been widely recognized (Hart 1990, Makana *et al.* 2004).

Do monodominance and rarity go hand-in-hand? The Congo example suggests so, and there is a consistent relationship between low dominance and few rare species (Table 2). The Thai plot was exceptional, though, having many rare species – comparable to the Congo – without dominance (Table 2, Fig. 2B). The species-area curve for the Thai plot had a trajectory parallel to those from the Congo, start-

ing with very low richness but exceeding several other plots in the full 50 ha. We conclude that Congo and Thai plots had “inefficient” species-accumulation curves (with poor estimates of diversity in small samples) due to large numbers of rare species, not due to monodominance. The analytical approach of He and Legendre (2002) could be used to further test this assertion.

Diversity of higher taxa

Genus, family, and order accumulation curves closely resembled species-area curves in form: on log-log axes, the slope was initially steep, but quickly declined (data not shown). Species-genus ratios also increased with sample-size, but the form was not consistent (Fig. 3). At some plots, the increase resembled the form of the species-accumulation curve, but in other plots (Philippines and Cameroon), the increase was linear (on log-log axes), and in Sri Lanka, it was asymptotic. In Panama, we also tallied genera in larger areas, and the species-genus ratio continued to increase beyond 50 ha, with the steepest increase at much larger scales; the behavior of the curve within 50 ha did not predict behavior beyond 1000 ha.

The generalization is that species-genus ratios are underestimated in small plots. Interestingly, the species-genus ratio increased within plots between 1 ha and 25 ha along the same line as it increased between plots (Fig. 4); two exceptions were in Sri Lanka and Puerto Rico, where the species-genus ratio barely changed between 1 and 25 ha. Appendices 1-2 show species-genus and genus-family ratios at two scales, along with confidence limits, in all plots.

Richer forests were richer at every taxonomic level (Fig. 5): they had more orders, families, and genera, as well as more genera per family and more species per genus, and these differences were all significant statisti-

cally (see Appendices 1-2 for confidence limits). The correlations were not exact, however, and the number of genera per family, in particular, was only weakly related to species richness (Fig. 5). Weakness of the correlations means that different regions varied in details regarding the source of species diversity. For example, the Borneo and Ecuador plots were similar in family and order richness, but the Ecuador site was richer in genera-per-family while the Borneo plot was richer in species-per-genus (all differences highly significant if measured at the 1-ha scale; see Fig. 5, Appendices 1-2). The reversals just cancelled, so that the two plots were similar in species richness.

Also, African plots were rich in genera-per-family but poor in orders and families relative to other plots with similar species richness (Fig. 5).

Conclusions

One broad result from the large inventories should be heartening – single hectares accurately represented general trends of relative α -diversity. For example, the large and well-known difference in diversity between aseasonal wet forests (Southeast Asia and Amazonia) and seasonal forests (Central America and South Asia) are revealed by small plots as well

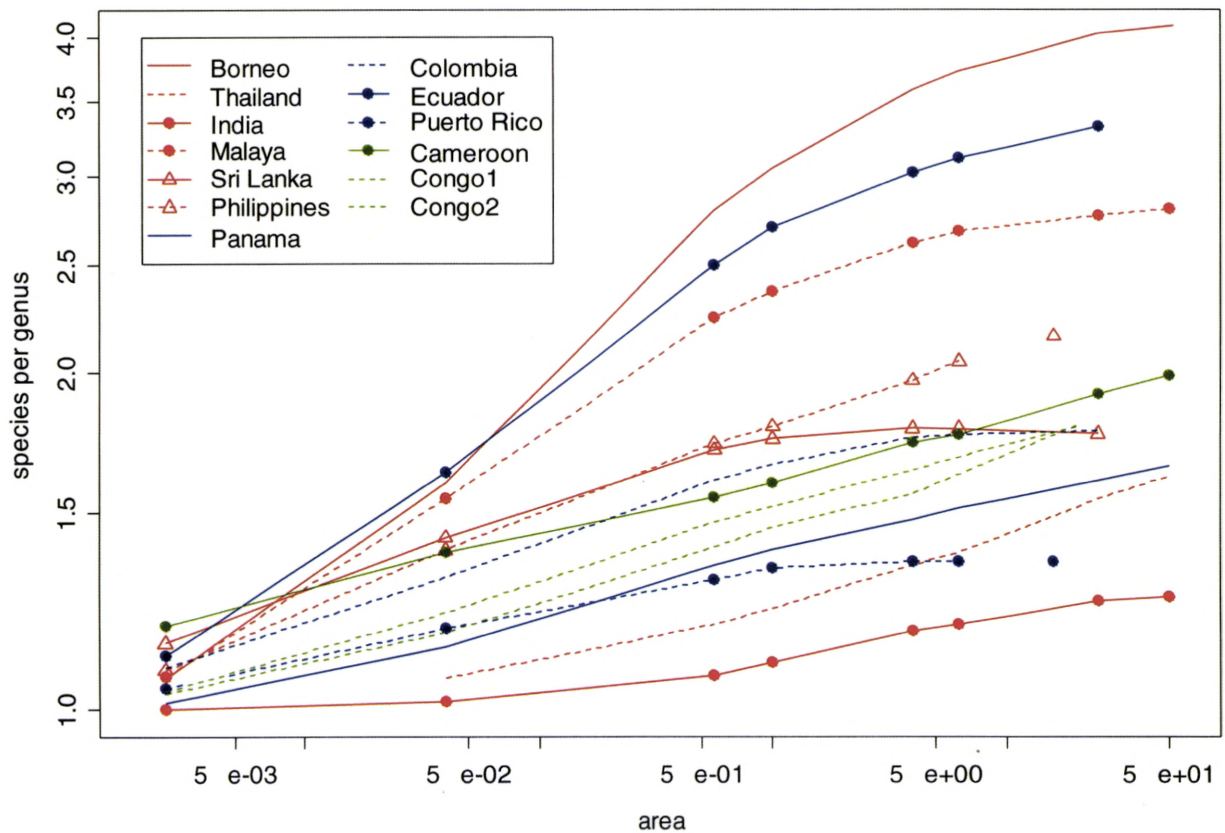


Fig. 3. Species-per-genus as a function of the area of successively larger square subquadrats within tropical forest plots. Asian sites are indicated in red, American in blue, and African in green.

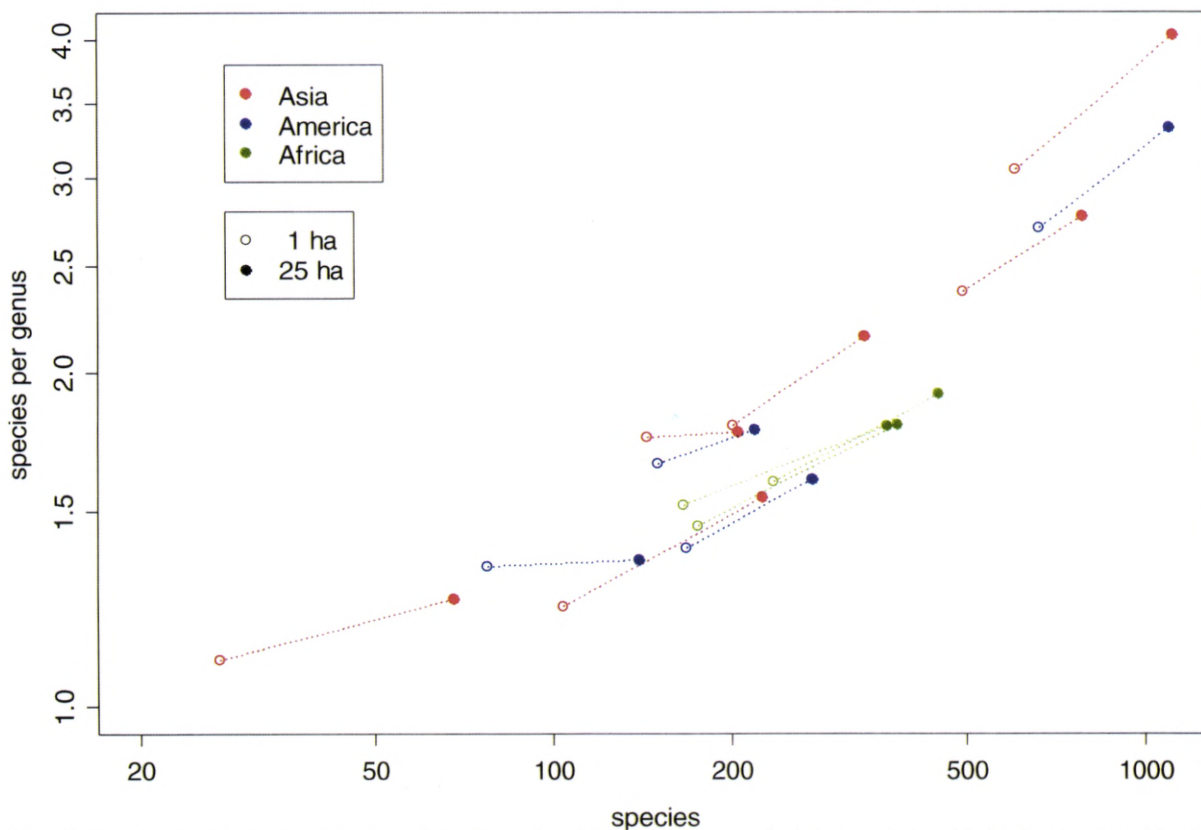


Fig. 4. Species-per-genus as a function of total species richness across tropical forest plots, with both axes logarithmic. Open circles indicate 1-ha samples; closed circles 25 ha (or from the entire plot when smaller than 25 ha). Dashed lines connect the 1-ha and 25-ha points from the same plot. Asian sites are indicated in red, American in blue, and African in green.

as large. Likewise, the low diversity on island plots (Puerto Rico, Sri Lanka, the Philippines) has been widely established by smaller inventories. The assumption that single hectares adequately judge relative diversity underlies nearly all discussions of variation in α -diversity but has seldom been stated.

In Africa, though, single hectare plots are misleading, and ecologists have failed to properly assess α -diversity. African forest diversity has been judged low by tropical forest standards (Richards 1973, Connell & Lowman 1989), but these judgments have been based on small plots. In fact, African forests are per-

fectly respectable in α -diversity when judged by our larger plots (Table 1, Fig. 1). Still, plots in Congo and Cameroon did not approach the very high richness found in Amazonia and Southeast Asia, and we doubt any Africa site will.

We believe that high family and genus diversity in Amazonia and Southeast Asia demonstrates that some of the extraordinary richness there is ancient. On the other hand, the species-per-genus ratio was also consistently related to species richness, suggesting that some of the diversity variation in the tropics is due to recent speciation. Both the museum

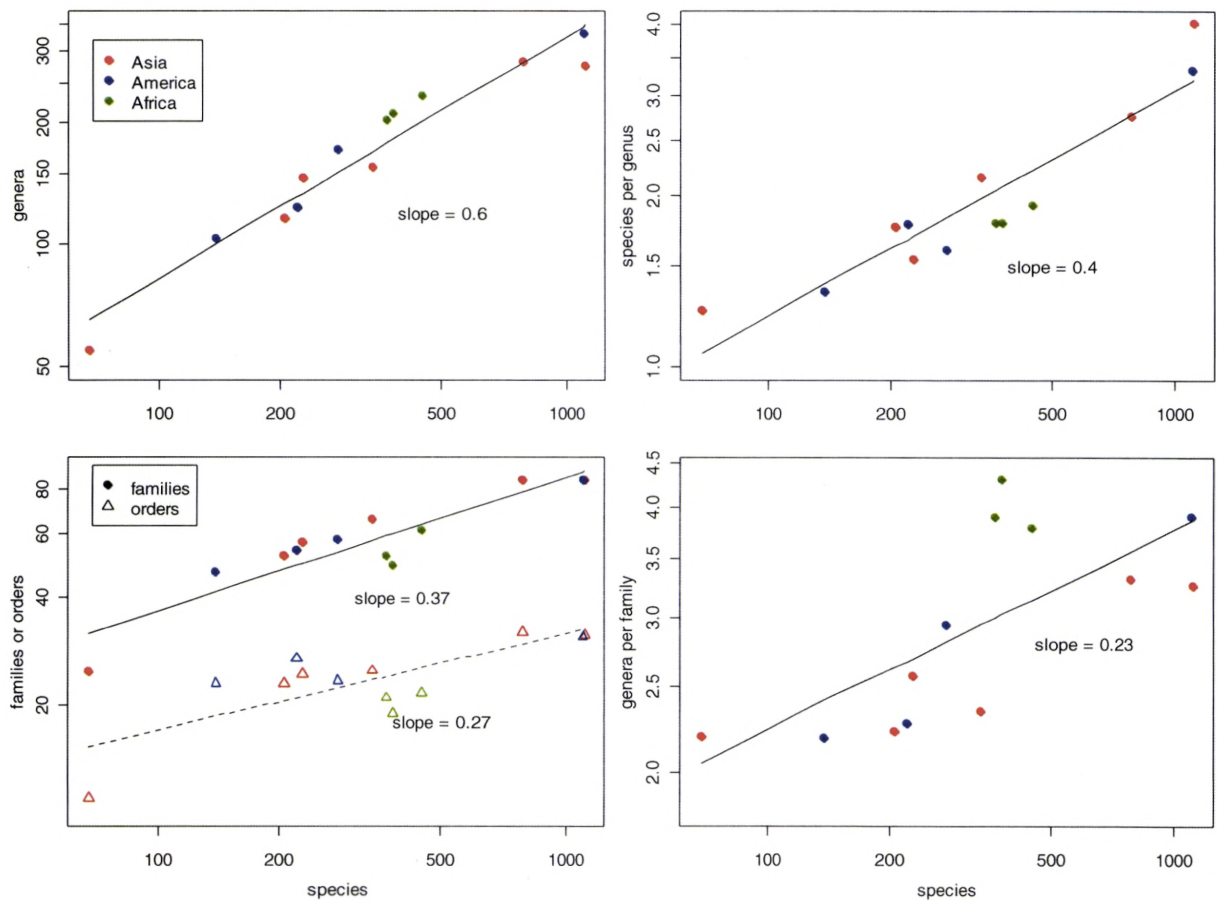


Fig. 5. Richness of higher taxonomic levels as a function of species richness across large tropical forest plots. Both axes are logarithmic. The horizontal axis is identical in all 4 panels. All five of the relationships have a regression line (from log-transformed variables) drawn; all five regressions were significantly positive.

hypothesis and the recent-speciation hypothesis are supported (Richardson *et al.* 2001, Bermingham & Dick 2001). The fact that the species-genus ratio increases with sample size within plots along the same line as it does between forests suggests that extinction has been blind to genus-level taxonomy, randomly removing species without regard to their genus affiliation. The results do not prove random extinction, but they are consistent with it.

Increasing species-genus ratio with increasing generic richness is consistent with two alter-

native hypotheses about diversity: increased speciation in rich sites, or increased extinction in low-diversity sites. There is one major hypothesis not consistent with these results: that the high speciation rate has been entirely recent. If speciation rate has been higher at some sites, it must have been going on for more than 70 million years, which is the age of many angiosperm families.

Classification schemes at all taxonomic levels, from species to orders, whether based on DNA or morphology, reflect taxonomists'

biases as well as true relationships. It is possible, for instance, that African forests are poor in families and rich in genera per family solely because African taxonomists split genera more often than American taxonomists do. We doubt, though, that biases in classification account for the overall patterns in diversity of higher taxa shown in Fig. 5. It seems clear that species-rich forests are also richer at deeper phylogenetic divisions. Better-resolved molecular phylogenies of more angiosperm genera and families will soon provide more precise estimates of deep diversity (Webb *et al.* 2002).

Fortunately, variation in generic richness and the species-genus ratio were (mostly) correctly judged in smaller plots. For this reason, a much larger study of species-genus ratios and generic and family diversity across continents could be done with the large number of 0.1- and 1-ha plots now assembled (Enquist *et al.* 2002). We emphasize, though, that the large plots have allowed us to check assumptions about how well small plots assess diversity.

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Appendix 1. Diversity per ha (mean \pm 95% confidence limits) at several taxonomic levels in 13 large forest plots; all individuals \geq 1 cm dbh included.

plot	species/1 ha	genera/1 ha	families/1 ha	orders/1 ha	spp/gen 1 ha	gen/fam 1 ha
Lambir	606.3 \pm 13.3	198.4 \pm 3.0	68.8 \pm 0.9	25.7 \pm 0.4	3.05 \pm 0.04	2.88 \pm 0.03
HKK	103.9 \pm 3.0	84.4 \pm 2.4	37.6 \pm 1.1	17.7 \pm 0.5	1.23 \pm 0.01	2.25 \pm 0.03
Mudumalai	27.4 \pm 1.5	24.9 \pm 1.3	15.4 \pm 0.7	9.7 \pm 0.2	1.10 \pm 0.01	1.62 \pm 0.04
Pasoh	495.6 \pm 5.8	209.5 \pm 2.4	69.7 \pm 0.8	26.5 \pm 0.3	2.37 \pm 0.02	3.01 \pm 0.02
Sinharaja	144.1 \pm 3.9	82.6 \pm 2.6	43.2 \pm 1.3	20.9 \pm 0.4	1.75 \pm 0.02	1.91 \pm 0.02
Palanan	200.8 \pm 4.6	112.0 \pm 1.9	52.4 \pm 0.9	21.2 \pm 0.5	1.79 \pm 0.03	2.14 \pm 0.03
BCI	167.6 \pm 2.5	120.3 \pm 1.5	49.6 \pm 0.6	22.0 \pm 0.3	1.39 \pm 0.01	2.43 \pm 0.03
La Planada	150.0 \pm 3.0	90.5 \pm 1.7	44.3 \pm 0.8	24.6 \pm 0.5	1.66 \pm 0.02	2.04 \pm 0.03
Yasuni	663.3 \pm 10.2	245.3 \pm 3.0	73.4 \pm 0.9	28.0 \pm 0.4	2.70 \pm 0.03	3.34 \pm 0.04
Luquillo	77.6 \pm 2.2	57.9 \pm 1.7	34.5 \pm 1.1	18.3 \pm 0.6	1.34 \pm 0.02	1.68 \pm 0.05
Korup	236.03 \pm 6.1	147.7 \pm 2.9	47.4 \pm 0.8	18.9 \pm 0.3	1.60 \pm 0.02	3.12 \pm 0.05
Lenda	165.6 \pm 13.1	108.7 \pm 4.9	37.5 \pm 0.9	14.8 \pm 0.6	1.52 \pm 0.02	2.90 \pm 0.09
Edoro	174.7 \pm 5.2	120.2 \pm 3.9	39.7 \pm 1.1	14.5 \pm 0.5	1.45 \pm 0.02	3.03 \pm 0.08

Appendix 2. Diversity (mean \pm 95% confidence limits) at several taxonomic levels in 16-25 ha within large forest plots. For plots with \leq 25 ha, no confidence limits could be calculated. Figures from sites marked with an asterisk are based on $<$ 25 ha; otherwise, figures are based on exactly 25 ha (Table 1); all individuals \geq 1 cm dbh included.

plot	species/25 ha	genera/25 ha	families/25 ha	orders/25 ha	spp/gen 25 ha	gen/fam 25 ha
Lambir	1118.49 \pm 52.00	277.15 \pm 13.16	84.84 \pm 4.78	31.44 \pm 3.60	4.04 \pm 0.03	3.27 \pm 0.07
HKK	225.91 \pm 12.22	146.28 \pm 6.88	56.83 \pm 7.07	24.42 \pm 2.97	1.54 \pm 0.04	2.58 \pm 0.22
Mudumalai	68.28 \pm 6.69	54.55 \pm 6.75	24.82 \pm 1.18	11.00 \pm 0.00	1.25 \pm 0.09	2.20 \pm 0.19
Pasoh	779.50 \pm 7.22	281.87 \pm 6.32	84.82 \pm 1.90	31.89 \pm 1.36	2.77 \pm 0.06	3.32 \pm 0.10
Sinharaja	205 \pm .	116 \pm .	52 \pm .	23 \pm .	1.77 \pm .	2.23 \pm .
Palanan *	335 \pm .	155 \pm .	66 \pm .	25 \pm .	2.16 \pm .	2.35 \pm .
BCI	274.79 \pm 8.73	171.34 \pm 5.66	58.10 \pm 2.82	23.43 \pm 1.51	1.60 \pm 0.03	2.95 \pm 0.11
La Planada	219 \pm .	123 \pm .	54 \pm .	27 \pm .	1.78 \pm .	2.28 \pm .
Yasuni	1104 \pm .	332 \pm .	85 \pm .	31 \pm .	3.33 \pm .	3.91 \pm .
Luquillo *	140 \pm .	103 \pm .	47 \pm .	23 \pm .	1.36 \pm .	2.19 \pm .
Korup	446.94 \pm 22.92	232.74 \pm 9.26	61.32 \pm 1.98	21.61 \pm 1.61	1.92 \pm 0.03	3.80 \pm 0.23
Lenda *	364 \pm .	203 \pm .	52 \pm .	21 \pm .	1.79 \pm .	3.90 \pm .
Edoro *	379 \pm .	153 \pm .	45 \pm .	18 \pm .	1.60 \pm .	3.40 \pm .

Appendix 3. Diversity (mean \pm 95% confidence limits) of species \geq 10 cm dbh in both 1 ha and 25 ha within large plots. Sites marked with an asterisk did not have 25 ha, and the second column is based on the full 16 ha in those cases.

plot	species/1 ha	species/25 ha
Lambir	245.70 \pm 5.92	854.46 \pm 137.49
HKK	65.62 \pm 2.91	182.78 \pm 26.53
Mudumalai	22.04 \pm 0.88	60.44 \pm 6.57
Pasoh	207.32 \pm 4.75	609.66 \pm 13.35
Sinharaja	71.20 \pm 5.04	167.00 \pm
Palanan *	98.86 \pm 6.43	262.00 \pm .
BCI	90.68 \pm 1.73	210.10 \pm 11.59
La Planada	84.98 \pm 2.38	172.00 \pm
Yasuni	253.56 \pm 6.65	820.00 \pm
Luquillo *	42.20 \pm 2.30	87.00 \pm .
Korup	85.42 \pm 3.44	259.76 \pm 35.40
Lenda *	49.09 \pm 8.65	211.00 \pm .
Edoro *	66.98 \pm 2.69	212.00 \pm .