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ABSTRACT

Enumeration of a one hectare plot at 900 m a.s.l. in Papua New Guinea revealed 693 individuals of 228 tree and liana species $\geq$ 10 cm DBH. A 0.1 hectare subplot contained 302 individuals of 106 species 2.5 $\leq$ DBH $<$ 10 cm. Lauraceae, Moraceae, and Myristicaceae were the most important families in both size classes. This site is very diverse compared with other tropical forests, and like other species-rich sites worldwide, it has high aseasonal rainfall and high rates of natural disturbance.

Key words: forest structure; hectare plot; Papua New Guinea; species diversity; tropical rain forest; vegetation.

Tropical rain forests are among the most species-rich places on earth. Botanical enumerations of forest structure and species diversity have been carried out on 1-ha plots at many sites worldwide (*e.g.*, Boom 1986, Faber-Langendoen & Gentry 1991). Comparisons of these plots have led to refinement of various hypotheses that explain floristic diversity. General ideas about species diversity suggest that habitat heterogeneity is a major factor controlling diversity (Tilman & Pacala 1993). Heterogeneity can result from disturbances, *e.g.* treefalls, or from underlying physical properties, *e.g.* moisture gradients, soil nutrient variation, or slope. Gentry (1988a) thought that rainfall was the most important predictor for plant diversity. Others (*e.g.*, Huston 1980) believe soil nutrient-availability is a crucial determinant. The greater the variety in sites examined and compared, the more robust our hypotheses will be.

Most vegetative studies from New Guinea (NG) are descriptive and are not enumeration-oriented (*e.g.*, Johns 1982, Bowman *et al.* 1990, Hyndman & Menzies 1990); some of the enumeration studies that do exist are not comparable to the standard of $\geq$ 10 cm DBH plants per hectare (*e.g.*, Kiapranis 1991 does not give species diversity for plants $\geq$ 10 cm DBH; Johns 1985 describes only $\geq$ 20 cm DBH plants). However, two comparable studies do exist. Paijmans (1970) reported from 116 to 147 tree species $\geq$ 12 in. girth (9.7 cm DBH) on each of four 0.8 hectare plots in NG. In the Lakekamu Basin in Papua New Guinea (PNG), Oatham and Beehler (in press) found from 97 to 178 species per hectare in three plots of lowland rain forest. Therefore current published data indicate that tree species diversity in NG is moderate. To our knowledge no other comparable enumerations from mature rain forest in NG have yet been published.

Here we report the tree and liana size-class abundance and species diversity for a 1 hectare plot in PNG, compare it with other tropical rain forests, and examine how it fits into current theory regarding floral diversity.

STUDY SITE

We conducted this study at Crater Mountain Biological Research Station (CMBRS) located on the southern scarp of the Central Range of PNG at

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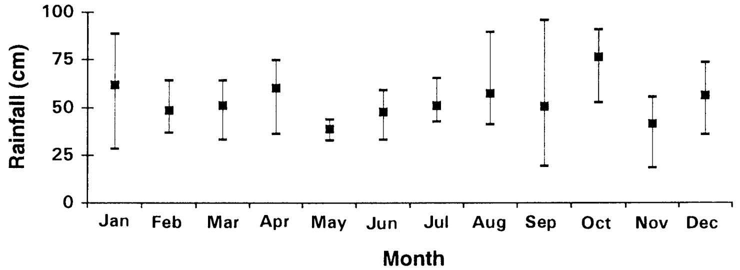

FIGURE 1. Means and ranges for monthly rainfall at CMBRS over a three and a half year period.

6°43′ S and 145°05′E. The station is 10 km east of the village of Haia near the point where the borders of Chimbu, Eastern Highlands, and Gulf Provinces meet. The station is located in the center of the Crater Mountain Wildlife Management Area, a 2600 km^2 area ranging from 300 to 3000 m elevation which is very sparsely populated by subsistence gardeners and hunters. The station has a 4 km^2 main study area which covers an altitudinal range of 850–1350 m and is mostly mature rain forest with some small patches of late secondary growth from old gardens. Local landowners have a moratorium on hunting and cutting over a large area surrounding the study area, which allows long-term study. Over a three and a half year period, rainfall at CMBRS averaged 6.4 m per year, ranged from 18 to 96 cm per month, and was seasonally unpredictable (Fig. 1). In the same period forest temperature ranged from 15°C to 28°C. Topography is extreme with vertical cliffs; landslides and earthquake tremors are fairly common, and treefalls are very common.

METHODS

The hectare plot was not chosen randomly. The study plot is unlike most other ha-sized sites within the 4 km^2 study area because it contains no large cliffs, large multiple treefalls, or "atypical" vegetation (*e.g.*, overabundance of pandans in flat, wet areas). The plot is at 900 m elevation and ranges in slope from 0 to 80°.

In April 1992 the plot was delineated by walking compass bearings to form a 100 × 100 m square. In April and May 1992 all trees and lianas $\geq$ 10 cm diameter at breast height (DBH) were tagged along 5 m strips within the plot and each plant's position to the nearest 0.5 m was recorded on an X,Y coordinate system. Plant DBH and heights were recorded. All plant heights were estimated by a single observer by extrapolating from a 2 m measure next to the tree. A 10 m strip down the center of the hectare formed a 10 × 100 m subplot where data for all trees and lianas 2.5 cm DBH were recorded. For buttressed trees, DBH was measured just above the highest buttress, with the height of the measurement also recorded; for all other plants DBH was measured at 1.5 m above ground. The DBH of all live stilt roots which reached the ground on *Pandanus* trees were measured, the basal area of each stilt root was determined and summed, and this sum was used to calculate total DBH. For trees with stranglers we took the total DBH of both plants and multiplied the estimated proportional contribution of each to yield DBH of each plant. In June 1994, 20 tree heights were re-estimated using a clinometer at a distance of less than 20 m from the tree base; these trees were scattered throughout the hectare plot. The original estimates varied from the clinometer estimates by 4 ± 2 m for trees up to 35 m in height.

From January to May 1993 voucher specimens were collected and dried from all marked trees and lianas that were not identical to another marked plant that had already been collected. Although we used local tree climbers, climbing spurs, and/or an extendible clipper pole, many lianas were still out of reach and thus species numbers could be underestimated. Specimens were identified to genus or species at the PNG Forestry Research Institute in Lae. Congeners were then sorted into morphospecies, being conservative and splitting only when substantial differences were evident.

We refer to plants $2.5 \leq \text{DBH} < 10$ cm as understory and plants with $\text{DBH} \leq 10$ cm as overstory. Volume was calculated as $V = 0.5 \times$ height basal area, for overstory plants only (Whitmore 1984). This equation gives an estimate of volume of above-ground wood and bark. Species and family diversity were measured by the number of species or families per plot (richness) and by the

Shannon Index which combines evenness with richness (Ludwig & Reynolds 1988). The Family Importance Index (FIV, Mori *et al.* 1983) was used to assess 'the contribution of each family to the stand. FIV combines family richness (number of species), density (number of individuals), and dominance (basal area) into one value. Species-area curves were calculated by dividing the hectare plot into 10 × 100 m strips, adding each strip consecutively, and by dividing the 0.1 hectare subplot into 10 × 10 m sections, adding each consecutively.

In 1993 the entire hectare plot was divided into 20 × 20 m subdivisions marked by PVC pipe and soil samples were collected at one randomly chosen spot within each of these 25 subdivisions. Samples were surface to 20 cm deep 2 cm diameter cores (varied from 10–20 cm; < 20 cm if corer hit rock) and were dried at 30–50°C. A & L Southern Agricultural Laboratories (Pompano Beach, Florida) analyzed samples for pH, water soluble phosphorus, and weak-acid extractable (sodium acetate plus DTPA) nitrogen, potassium, calcium, and aluminum following methods in Wolf (1982). These methods give a better indication of element availability for plants than total digestible methods. In July 1994 slopes for the entire hectare plot were mapped along the 20 × 20 m grid lines using a clinometer. Slopes for each marked plant were extrapolated from these values.

All analyses were carried out on the ten most abundant species in the hectare plot (> ten individuals of (≥ 10 cm DBH). The 20 × 20 m blocks within the hectare plot were used as sampling units. Because our sampling units were not discrete, we could not compare tree distributions with the Poisson probability distribution to see if a species was clumped or uniformly distributed. Because our sampling units were from a square and not a belt transect, we also could not use quadrat-variance methods. Therefore, we used the distance from points on a grid within the hectare plot to the nearest individual of a species to get the distance index of dispersion (I) for each species (Ludwig & Reynolds 1988). Values near 2 show a random pattern, values below 2 show a uniform distribution, and values above 2 show clumping. Pattern significance was then tested with a z-value calculated from the I and the sample size of point distances.

The ground slopes that each species occurred on were compared by Mann-Whitney *U* tests to see if some species tended to occur in steeper areas than other species. An overall ANOVA was used to see if slope alone could account for overall species placement within the hectare plot.

The first two axes of a principal components analysis (PCA) of the ten most abundant species were compared with each soil factor via simple linear regression to see if soil factors could be partly responsible for community composition (using the 20 × 20 m blocks as sampling units) (Ludwig & Reynolds 1988).

Spearman correlations were computed for all pairwise species associations, for all pairwise soil factor associations, and for all pairwise species versus soil factor associations on the 20 × 20 m blocks to see if *e.g.*, one species negatively associates with another, or *e.g.*, if a soil factor is positively associated with one species and negatively associated with another. Such associations could lead to increased diversity through specialization on microsite variation. Although some associations could be significant owing to chance alone with this many comparisons, and results could be affected by interaction effects, these analyses can give us an indication of possible associations; multiple regression was not used for these analyses because here we were interested in one on one effects. However, multiple regression was used to detect individual soil factor effects (dependent variables, one per analysis only) on overall species composition, keeping in mind that species abundances may not be independent variables. Statistical analyses were performed with SYSTAT (Wilkinson 1990) and STATMOST (Datamost Corp. 1994).

RESULTS

STRUCTURE.—In the 1 hectare plot we found 693 individuals with DBH ≥ 10 cm; size-class density decreased with each 10 cm rise except in the largest size class (421, 139, 67, 31, 15, 9, 5, 3, 2, 0, 0, 0, 1 individuals, respectively). Only one tree had a DBH over 100 cm (136 cm DBH). Average DBH for the overstory was 21.8 cm (SD = 14.3 cm) and average estimated height was 19 m (SD = 8.5 m). The tallest trees were estimated to be 40 m tall. In the 0.1 hectare subplot we found 302 individuals with 2.5 ≤ DBH < 10 cm; size-class density decreased with each 2.5 cm DBH rise (195, 68, 39 individuals, respectively). Average DBH for the understory was 4.7 cm (SD = 1.9) and average height excluding lianas was 5 m (SD = 2). Understory trees ranged from 2 to 12 m in height.

Total basal area was 37.1 m^2/ha for overstory and 6.1 m^2/ha for understory (extrapolated from

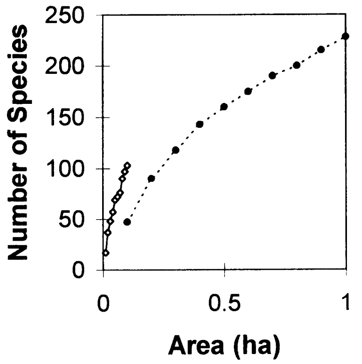

FIGURE 2. Species-area curves for under- and overstory plants. Open diamonds are $2.5 \leq$ DBH < 10 cm and solid circles are DBH ≥ 10 cm.

the 0.1 hectare plot). Volume was 506 m^3/ha for the overstory excluding lianas.

DIVERSITY.—The 1 hectare overstory plot contained 228 species and the 0.1 hectare understory subplot contained 106 species. The understory subplot had 37 species not found in the overstory plot. The Shannon Index for species was 4.91 for the overstory plot and 4.19 for the understory plot. Within the 1 hectare plot, 49 percent of the overstory species (111 of 228 species) had only a single individual and 68 percent (154 of 228 species) had only one or two individuals; eleven species (5%) had over nine individuals (Table 1). Within the 0.1 hectare plot, 60 percent of the understory species (64 of 106 species) had only a single individual and 73 percent (77 of 106 species) had only one or two individuals; four species (4%) had over nine individuals. Neither the overstory nor the understory species area curves approached an asymptote (Fig. 2).

Relative importance values (n_i / n_{total}) for overstory species show an exponential pattern (Fig. 3). The best-fit lognormal curve ($S_o = 68$, $a = 0.44$, $\chi^2 = 3.21$, df $= 6$, $P > 0.5$ to accept H_o of no difference) predicts a total of 274 species (Fig. 4) (Ludwig & Reynolds 1988), supporting the assertion that morphospecies were assigned conservatively (*i.e.*, after fertile material is collected and more time for taxonomic determination is available, species number should increase).

The 1 hectare overstory plot contained 58 families and the 0.1 hectare plot contained 47 families. The Shannon Index for families was 3.03 for the overstory plot and 3.20 for the understory plot. Within the hectare plot, 33 percent of the overstory families had only one or two individuals and 24 percent had over nine individuals. Within the 0.1 hectare plot, 49 percent of the understory families had only one or two individuals and 17 percent had over nine individuals. The overstory and understory plots both had seven families with FIV values over ten (Table 2). The overstory and the understory shared their three most important fam-

TABLE 1. *Number of individuals and total basal area for the most common species in both overstory (>6 indiv) and understory (>4 indiv) plots.*

Overstory on 1 ha				Understory on 0.1 ha			
Family	Species	# indiv	Basal area (m^2)	Family	Species	# indiv	Basal area (m^2)
Lauraceae	*Cryptocarya* sp. 997	36	1.4541	Myristicaceae	*Myristica subaluata*	27	0.0495
Myristicaceae	*Myristica subaluata*	30	0.3496	Icacinaceae	*Gomphandra montana*	14	0.0207
Lauraceae	*Cryptocarya* sp. 10	25	1.0010	Ochnaceae	*Schuurmania* sp. 1030	13	0.0225
Myristicaceae	*Myristica* sp. 2	19	0.6247	Rubiaceae	*Dolicholobium* sp. 2	12	0.0327
Lauraceae	*Endiandra brassii*	18	1.5813	Clusiaceae	*Mammea* sp. 1	10	0.0178
Sapotaceae	*Planchonella* sp. 1	15	0.5726	Lauraceae	*Cryptocarya* sp. 10	9	0.0150
Myristicaceae	*Horsfieldia spicata*	14	0.7439	Moraceae	*Ficus* sp. 24	8	0.0082
Lauraceae	*Beilschmiedia* sp. 3	11	1.1556	Anacardiaceae	*Semecarpus* sp. 4	7	0.0097
Lauraceae	*Cryptocarya* sp. 6	11	0.3367	Lauraceae	*Cryptocarya* sp. 2	6	0.0182
Lauraceae	*Cryptocarya* sp. 2	11	0.1873	Meliaceae	*Dysoxylum* sp. 6	6	0.0131
Eleaocarpaceae	*Sloanea forbesii*	10	1.0226	Flacourtiaceae	*Casearia* sp. TWA	6	0.0113
Anacardiaceae	*Semecarpus* sp. 2	9	0.3711	Lauraceae	*Cryptocarya* sp. 6	5	0.0146
Malvaceae	*Hibiscus eliptifolia*	9	0.2149	Sapotaceae	*Planchonella* sp. 1	5	0.0121
Rubiaceae	*Dolicholobium* sp. 2	8	0.1722	Myrtaceae	*Syzygium* sp. 12	5	0.0090
Leguminosae	liana sp. 1126	8	0.1658	Lecythidaceae	*Barringtonia montana*	5	0.0088
Meliaceae	*Dysoxylum* sp. 6	7	0.3988	Euphorbiaceae	*Aporusa papuana*	5	0.0074
Urticaceae	*Dendrocnide* sp. 1	7	0.1192	Clusiaceae	*Garcinia hunsteinii*	5	0.0068
Clusiaceae	*Mammea* sp. 1	7	0.0990				

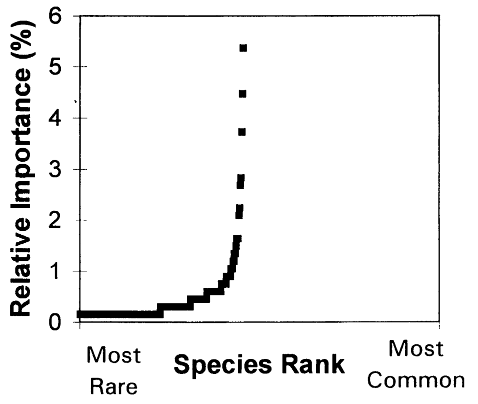

FIGURE 3. The relationship between relative importance values for all overstory species and their rank in the hectare plot (from most rare to most common species). The exponential pattern suggest a log-normal relationship.

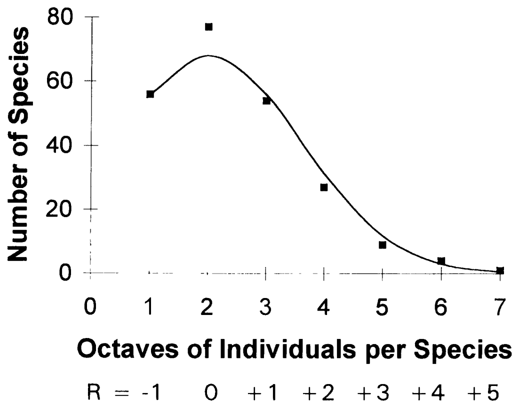

FIGURE 4. Frequency distribution of species count data plotted in octaves. This graph shows the fit of a log-normal curve (the solid line) to the observed data (the points).

ilies; Lauraceae was most abundant in number of species, number of individuals, and basal area in both over- and understory. Moraceae had more species than Myristicaceae, but Myristicaceae had more individuals and greater basal area than Moraceae in both over- and understory (Table 2).

Lianas comprised a higher proportion of individual plants in the understory (11%) than in the overstory (2%). A smaller proportion of understory (0.3%) than overstory (1.2%) plants were *Pandanus* (Pandanaceae). The understory contained no palms or tree ferns, and the overstory plants were 0.7 percent palms and 0.4 percent tree ferns.

SOILS.—Soil appearance ranged from a dark brown loam to a gray and orange clay. Aluminum levels ranged from 12 to 54 ppm; nitrogen ranged from 15 to 85 ppm; and calcium ranged from 270 to 1560 ppm. Phosphorus levels were 2 to 6 ppm and potassium levels were 2 to 67 ppm; pH was consistently acidic (Table 3). No spatial patterns or gradients were evident for any of these factors within the 1 hectare plot. Aluminum and pH were negatively correlated (Spearman $r = -0.4$, $P = 0.05$); phosphorus and potassium were also negatively correlated (Spearman $r = -0.44$, $P = 0.03$); nitrogen and potassium were positively correlated

TABLE 2. *Number of species and individuals, basal area, and Family Importance Values (FIV) for the ten most important overstory and understory families.*

	DBH ≥ 10 on 1 ha				10 > DBM ≥ 2.5 on 0.1 ha			
Family	# sp	# indiv	Basal area (m^2)	FIV	# sp	# indiv	Basal area (m^2)	FIV
Lauraceae	33	179	10.6096	68.9	8	36	0.1025	36.2
Myristicaceae	9	85	2.6158	23.3	5	32	0.0639	25.7
Moraceae	24	42	1.5024	20.6	15	24	0.0353	27.9
Meliaceae	16	36	2.1870	18.1	7	16	0.0356	17.7
Myrtaceae	16	31	1.2278	14.8	5	11	0.0167	11.1
Elaeocarpaceae	7	28	2.1735	13.0				
Rubiaceae	10	27	0.9015	10.7	4	21	0.0609	20.7
Clusiaceae	8	17	0.7340	7.9	3	15	0.0266	12.1
Sapotaceae	3	18	1.1435	7.0				
Anacardiaceae	3	15	0.4843	4.8	3	9	0.0112	7.6
Icacinaceae					1	14	0.0207	9.0
Ochnaceae					1	13	0.0206	8.6
Others	99	215	13.5594	110.9	54	111	0.2194	123.4
Total	228	693	37.1388	300.0	106	302	0.6134	300.0

TABLE 3. *Soil nutrient contents from 25 10–20 cm deep 2 cm diameter core samples spatially separated within the hectare plot. Phosphorus is water soluble and other elements are weak-acid extractable. Scale refers to a standard generic rating criteria used by commercial soil-testing laboratories based on what an average plant needs to maintain health (Wolf 1982).*

Element	Mean	SD	Range	Scale
Water (%)	46	8	34–73	
pH	5.1	0.2	4.7–5.5	
Nitrogen (ppm)	29	16	15–85	fair to high; mean is good
Phosphorus (ppm)	4	1	2–6	all poor
Potassium (ppm)	27	18	2–67	poor to fair; mean is poor
Calcium (ppm)	635	311	270–1560	poor to good; mean is fair
Aluminum (ppm)	28	10	12–54	good to excessive; mean is high

(Spearman $r = 0.47$, $P = 0.02$); there were no other statistically significant correlations among the soil factors tested.

TREE DISPERSION.—The distance index of dispersion (I) for each of the ten most abundant species on the hectare plot ($\geq$ 10 cm DBH) ranged from 1.48 to 2.45; none of the indices were significant (all $P > 0.15$) showing that tree distributions for each species did not differ from random.

ABIOTIC EFFECTS ON SPECIES COMPOSITION.—Pairwise Mann-Whitney U tests between the ten most abundant species (> ten individuals/ha) showed that *Horsfieldia spicata* occurred on steeper slopes than *Myristica subaluata* ($Z = 2.18$, $P < 0.05$) and *Cryptocarya* sp. 2 ($Z = 2.02$, $P < 0.05$). An ANOVA with the ten most abundant species showed that slope alone could not account for overall species distribution ($F_{9,\ 180} = 1.44$, $P = 0.17$).

The first component of a PCA analysis of species abundances in the 20 × 20 m blocks accounted for 28.8 percent of the variation in species abundances; the second component accounted for 19.5 percent. No obvious species groupings were revealed. Although the graph did show nonlinearity, a regression of PCA1 and PCA2 was not significant, and so a DPC axis could not be created. Simple linear regression of PCA1 against soil pH, N, P, K, Ca, and Al and of PCA2 against soil pH, N, K, Ca, and Al showed no significant values; however, regression showed that PCA2 tended to associate negatively with phosphorus ($r = -0.39$, $P = 0.00004$).

One hectare is probably not enough to show associations between species and soil factors, especially as microsites were more fine-grained than our one soil sample per 400 m^2. However, of 60 pairwise Spearman correlations between species abundances and soil factors, three were significant (*Cryptocarya* sp. 997 and nitrogen, $r = -0.39$, $P = 0.055$; *Beilschmiedia* sp. 3 and potassium, $r = -0.37$, $P = 0.07$; and *Cryptocarya* sp. 6 and potassium, $r = 0.51$, $P = 0.01$). This indicates that microsite soil nutrients may be determining species presence in some cases. Multiple regressions of abundances of the ten most abundant species on each of the six soil factors (dependent variables) in the 20 × 20 m blocks showed only one significant case—potassium levels affected overall species composition ($P = 0.018$); some species were positively associated with potassium and others were negatively associated.

INTERSPECIES EFFECTS.—A Spearman correlation matrix with 45 species by species comparisons showed that six were significant with either positive or negative associations between species (*Myristica subaluata* and *Cryptocarya* sp. 997, $r = 0.42$, $P = 0.04$; *Cryptocarya* sp. 10 and *Horsfieldia spicata,* $r = 0.54$, $P = 0.01$; *Cryptocarya* sp. 10 and *Cryptocarya* sp. 2, $r = -0.4$, $P = 0.05$; *Endiandra brassii* and *Beilschmiedia* sp. 3, $r = -0.42$, $P = 0.04$; *Planchonella* sp. 1 and *Horsfieldia spicata,* $r = -0.41$, $P = 0.05$; and *Beilschmiedia* sp. 3 and *Cryptocarya* sp. 6, $r = -0.35$, $P = 0.08$).

DISCUSSION

STRUCTURE AND DIVERSITY COMPARISONS WITH OTHER SITES.—The average basal area of trees over 0.3 m girth (about 10 cm DBH) for virgin lowland rain forests pantropically is estimated to be 36 m^2/ha (Dawkins 1959). Thus our plot, at 37.1 m^2/ha, has typical basal area for a lowland rain forest (though it is officially classified as hill forest, Paijmans 1976). The number of stems per hectare was high compared with other forests overall, but similar to more species-rich rain forests (Table 4). Our plot is among the most diverse worldwide (Table 4).

TABLE 4. *Forest structure and diversity in tropical forest 1-ha plots worldwide, with an emphasis on the most diverse sites. Soil types (poor, medium, good) were gleaned from the literature for each site.*

Site	No. of species	No. of stems ≥ 10 DBH	Rain (m)	Type	Soil	Elev. (m)	Source
Amazonia, Ecuador	307	693	3.5	aseasonal	med	260	Valencia *et al.* 1994
Mishana, Peru	289	858	3.7	aseasonal	poor	140	Gentry 1988b
Choco, Colombia	258	675	7	aseasonal	poor	100	Faber-Langendoen and Gentry 1991
CMBRS, PNG	228	693	6.4	aseasonal	med	900	This study
Gunung Mulu, Sarawak	214	778	5.1	aseasonal	poor	200	Proctor *et al.* 1983
Pasoh, Malaysia	210	530	2	aseasonal	good	200	Kochummen *et al.* 1990
Cocha Cashu, Peru	201	673	2	seasonal	good	100	Gentry and Terborgh 1990
Queensland, Australia	108	957	2	seasonal	poor	730	Phillips *et al.* 1994
La Selva, Costa Rica	96	447	4	aseasonal	good	100	Lieberman *et al.* 1985
BCI, Panama	93	414	2.5	seasonal	med–good	10	Gentry 1990
Amazon, Venezuela	83	744	3.5	aseasonal	poor	100	Uhl and Murphy 1981

In addition, the smaller size-class plants (2.5–10 cm DBH) are also comparable with other very diverse sites; CMBRS is similar to the Choco Region in Colombia with 106 and 138 species respectively per 0.1 hectare, and 297 and 282 individuals respectively per 0.1 hectare (Faber-Langendoen & Gentry 1991).

Other NG sites studied to date have fewer species per hectare than our site (Paijmans 1970; Oatham & Beehler, in press). Those sites have relatively seasonal rainfall and are in relatively flat areas (maximum slope 40°); our site has aseasonal rainfall and much more relief (up to 80° slope). We believe that topography and aseasonality are major determinants of diversity (see below). Additionally, our site has greater stem density than other NG sites studied; Oatham and Beehler (in press) found a positive correlation between stem number and species number among their three lowland plots.

Family comparisons to other sites.—PNG and the Neotropics share Moraceae as a dominant family and Lauraceae is plentiful in all regions examined (Table 5). Fruits of Lauraceae are typically nutrient-rich and fruits of Moraceae (*Ficus*) are available year-round–important features for tropical frugivores; this may help to explain their pantropical abundance. Australia and NG do not share Fabaceae as a common family with Neotropical and Asian sites; faunal dispersal agents or historical factors could be responsible for this. All the other PNG sites shared Euphorbiaceae as an important family with Asia; our site did not. Our site was unusual in its abundance of Myristicaceae.

SOILS—Soils at CMBRS were moderately fertile compared to other tropical sites. Gentry (1988b) stated that if calcium is below 100 ppm the soil should be considered poor; calcium levels averaged 635 ppm, well above this figure. Calcium concentration should correlate with overall fertility (Jordan & Herrera 1981). Furthermore, our samples were taken up to 20 cm deep; some studies use only the top 5–10 cm which are more nutrient laden than lower horizon soils (often clays); thus our samples may be even richer than they appear in comparison to other sites. The soil acidity led to high aluminum levels (hence the negative correlation), which exacerbates calcium, phosphorus, and potassium deficiencies in non-tolerant plant species (Sanchez 1976). Phosphorus was most limiting, as is typical of mature rain forest (Vitousek 1984), but aluminum-tolerant species are usually also tolerant of low phosphorus levels (Sanchez 1976). Because there was a negative correlation between phosphorus (which is held in the soil and not easily leached) and potassium (easily leached) and a positive correlation between nitrogen and potassium (both easily leached), microsite drainage seems to play a role in relative nutrient abundance. Owing to the high rainfall at our site, we would expect low nitrogen and potassium levels due to leaching. However, in places nitrogen levels were moderate to high, suggesting that soil nitrogen is being replenished. When taking soil samples, the 30 cm corer often hit rock. This mountainous site has a shallow soil and thus the parent rock may rejuvenate soil nutrients (see Whitmore 1989), which could explain the moderate nutrient levels despite the soil acidity, excessive rainfall and consequent leaching. Furthermore, the area is tectonically active, with frequent tremors and landslips, which allows surfacing of parent material, *i.e.*, fresh

TABLE 5. *Dominant families from tropical rain forest sites worldwide.*

Neotropical	Asian	Queensland	PNG			
Gentry 1990	Proctor *et al.* 1988 Whitmore 1984 Kochummen *et al.* 1990	Connell *et al.* 1984 Williams and Tracy 1984	This study	Paijmans 1970	Kiapranis 1991	Oatham and Beehler, in press
Fabaceae	Dipterocarpaceae	Sapotaceae	Lauraceae	Lauraceae	Euphorbiaceae	Moraceae
Moraceae	Euphorbiaceae	Lauraceae	Myristicaceae	Meliaceae	Moraceae	Meliaceae
Annonaceae	Fabaceae	Myrtaceae	Moraceae	Moraceae	Meliaceae	Lauraceae
Lauraceae	Myrtaceae	Elaeocarpaceae	Meliaceae	Myrtaceae	Lauraceae	Eupohorbiaceae
Sapotaceae	Lauraceae	Meliaceae	Myrtaceae	Euphorbiaceae		Sapindaceae
	Burseraceae	Clusiaceae	Eleaocarpaceae			
	Anacardiaceae		Rubiaceae			

material, and thus soil enrichment. Nutrients could also be supplied in the plentiful rainfall through ash fall from volcanic eruptions in the neighboring areas (Jordan 1982, Johns 1986).

CAUSES OF DIVERSITY—Our one hectare plot had 228 species ≥ 10 cm DBH making it the richest site yet sampled in NG and among the most diverse worldwide (Table 4). Why is it so diverse?

NG's original flora was Gondwanan, but with the meeting of the Australian and southeast Asian plates about 10 million years BP, Laurasian floras began their immigration onto the island (Walker & Hope 1982). Therefore, NG has components from both supercontinents, which could increase diversity. Since then, continual uplifting of the island has led to environmental instability and isolation, which has caused rapid speciation; 55 percent of NG's plant species are endemic (Walker & Hope 1982).

During the Quaternary glacial periods, the tree-line in NG was depressed by 1500 m (Whitmore 1984) to 2300 m a.s.l. (Walker & Hope 1982). Since our site is at 900 m elevation, it would not have lost as many species during this time period as higher elevation sites would have; thus historic glaciation would not have decreased species diversity at our site.

As our site is between lowland and montane forests, it has species from both forest types, which could increase overall diversity. For example, Proctor *et al.* (1988) found that species-area curves had the greatest slope (*i.e.*, more species per area) at mid elevations of 600–700 m that were between two major habitat types.

In addition to these more general causes of high species diversity, there are two main ways more species can co-exist in an area: 1) if there are no dominants, *i.e.*, if all species are equal competitors with continued existence depending on stochastic factors, and/or 2) if there are lots of micro-niches (spatially and temporally) with different dominants in each (Tilman & Pacala 1993).

Gentry (1988b) believed that sites with high aseasonal rainfall and fertile to moderately infertile soils supported the most diverse floras (our site has high aseasonal rainfall and has low to moderately fertile soils). These ideas fit well with the argument for an absence of the ability to dominate and thus exclude other species. For example, species that can differentially survive dry periods cannot derive benefit from this advantage in aseasonal environments. Species that are differentially able to prosper without various nutrients cannot dominate in environments that do not lack those nutrients. Note that these arguments take a coarse-grained view, *i.e.*, species cannot dominate the entire habitat.

Mycorrhizae can also reduce chances of competitive exclusion (Janos 1987); *e.g.*, a species requiring little phosphorus may dominate in a low phosphorus area unless mycorrhizal associations allow other species in the area to get the phosphorus they need. Sharing of assimilates and nutrients via non-host-specific vesicular-arbuscular mycorrhizal fungal mats could also decrease competitive advantage (Grime *et al.* 1987). Abundant year-round water availability at our site might enhance mycorrhizal function.

The second factor leading to increased diversity, spatial and temporal heterogeneity, is perhaps the easiest way to see how many species can co-exist. If selection creates specialists on each habitat patch or temporal niche, then β-diversity will rise (see below). The resultant habitat mosaic will allow spillover from one community type to the other, increasing α-diversity.

Owing to microsite heterogeneity, soil nutrient availability and texture (clay versus loam) at our site was extremely patchy and variable which should increase species diversity (Gentry 1988b). Combinations of soil fertility and mycorrhizal availability could determine seedling establishment and dominance at each microsite (Alexander 1989). Also, the heavy rainfall at our site causes stream rivulets on the hillsides which result in leaching gradients, further increasing nutrient heterogeneity. Our results show that microsite levels of soil nutrients do affect which species will exist at that microsite, supporting this argument.

CMBRS has extreme and varied topography. Different tree species demonstrated preferences for different slopes; this topographic variance in species composition may reflect soil differences (Ashton 1964). Either way, the great diversity in topographic features should increase tree diversity by enhancing habitat heterogeneity. The topography and high rainfall account for the abundance of rivers and streams surrounding the plot which also increases habitat heterogeneity. Heavy rainfall can wash away establishing seedlings on steep slopes, increasing stochastic effects as well as microsite competitive advantage. The rain also makes the few level areas in the study area swampy, increasing habitat heterogeneity.

Phillips *et al.* (1994) have recently shown that tree turnover rate (a measure of disturbance dynamics) is the best predictor of species richness when comparing many sites; more dynamic forests have more species. NG has very high rates of natural disturbance (Johns 1986). The topography, heavy rainfall, earthquake tremors, and lightning make our site extremely dynamic. For example, two out of 42 0.1 hectare phenology plots (5%) were taken out by landslides within four years (D. Wright, pers. obs.); this is a conservative indication as plots were not located on the steepest ground. Treefalls are extremely common at CMBRS (D. Wright, pers. obs.). These disturbances lead to the presence of many successional phases, with different species specializing in each phase, increasing diversity (Grubb 1977). Additionally, local people have historically worked small garden patches in the area; these anthropogenic disturbances are also in different states of succession.

In their many site comparison, Phillips *et al.* (1994) found that aseasonality was the second best predictor for high species diversity. In addition to producing a more benign environment that may inhibit competitive exclusion as discussed above, aseasonality can increase variety in temporal strategies; phenology and seed germination and establishment can be staggered year-round, thus decreasing competition for seed dispersers, pollinators, resources, and germination sites and allowing more species to co-exist (Gentry 1989). Our site is aseasonal and at any time of the year several species are in each of the reproductive phases.

In summary, this 900 m a.s.l. site is among the most diverse worldwide with 228 species ≥ 10 cm DBH; its common families include Lauraceae, Myristicaceae, Moraceae, and Meliaceae. We speculate that the high diversity of this site results from: historical processes of two major floras coming together ; mountainous isolation leading to endemism and speciation; topographic and soil habitat heterogeneity; high turnover/disturbance rates; and abundant aseasonal rainfall allowing year-round reproduction and establishment.

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