COMPOSITION AND STRUCTURE OF A ONE HECTARE FOREST PLOT IN THE CRATER MOUNTAIN WILDLIFE MANAGEMENT AREA, PAPUA NEW GUINEA

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ABSTRACT

A one hectare plot transect was established at 550 m above sea level in the Crater Mountain Wildlife Management Area, Simbu Province, Papua New Guinea. All stems ≥ 10 cm in diameter at breast height were enumerated within twenty five contiguous 20 m x 20 m subplots. Overall, the plot contained 615 stems representing 174 species of trees, lianes and hemiepiphytes. The majority of species (63%) were represented by one or two individuals and only 11 species had ≥10 individuals. Myristica subalulata *(Myristicaceae),* Pometia pinnata *(Sapindaceae),* Cryptocarya "depressa-multipaniculata" *spp. group (Lauraceae), and* Chisocheton lasiocarpus *(Meliaceae) were most abundant. The forest canopy was 30-40 m in height with emergent* Pometia pinnata *and showed no indications of recent large-scale disturbance. The results are compared to other PNG forest inventories and suggestions for future surveys are proposed.*

INTRODUCTION

Relatively little is known about the distribution of the 15,000 to 20,000 vascular plant species recorded from New Guinea (Johns, 1993). Significant areas have not been collected botanically and a comprehensive floristic survey is hindered by the poor taxonomic status of many plant groups (Stevens, 1989). Our incomplete floristic knowledge is a real problem in New Guinea forests where increased logging and agricultural activities threaten to erode plant diversity before it has been adequately studied (Sekhran & Miller, 1995). The development of effective conservation strategies for Papua New Guinea (PNG) will be aided, in part, from an understanding of current patterns of floristic diversity and the processes that shape those patterns.

The high species richness of woody plants in wet tropical forests is widely accepted although many competing hypotheses have been proposed to account for the maintenance of this diversity (reviewed in Gentry & Terborgh, 1990; Condit, Hubbell & Foster, 1992). The enumeration of forest plots has become the standard by which forest composition and structure are compared and in which hypotheses about the maintenance of diversity are tested (Condit, 1995). Large, permanent plots (50 ha) have the advantage of providing adequate samples for long term studies of demography and changes in species composition. However, several small plots (1 ha) distributed over a larger area can provide estimates of forest diversity at local scales in the short term.

Earlier descriptions of New Guinea vegetation emphasized forest type classifications (e.g. Paijmans, 1976) and did not estimate the distribution and extent of tree diversity (reviewed in Johns, 1993). Although such estimates are very much needed (Alcorn, 1993), there have been few enumerations of tree diversity in New

Guinea forests. However, Paijmans (1970) surveyed four 0.8 ha plots between 600 and 900 m a.s.l. in the Sibium Range, PNG and there were from 116 to 147 tree species greater than 9.7 cm DBH. Oatham and Beehler (1997) recorded between 97 to 178 tree species ≥ 10 cm DBH in three 1.0 ha plots in lowland alluvial forest in the Lakekamu Basin, PNG. The highest published estimate from PNG is 228 tree and liane species ≥ 10 cm DBH in a 1.0 ha plot at 900 m a.s.l. at Crater Mountain (Wright *et al.*, 1997). Given so few estimates, it is difficult to know if New Guinea forests are more or less diverse than tropical forests elsewhere. We also lack a sufficient understanding of the factors contributing to the patterns of diversity that have been observed.

In contrast to New Guinea, regional changes in tree species composition and forest structure in response to factors such as rainfall, altitude, soils and disturbance have been documented on the island of Borneo (Proctor *et al.*, 1988). In Sarawak, for example, tree species richness was found to be correlated with soil fertility (Proctor *et al.*, 1983). Forest composition differed markedly among soil substrates, although the relationship between soil fertility and forest stature was not predictable (Proctor *et al.*, 1983). In New Guinea, patterns of catastrophic disturbance from fire, earthquakes and volcanos have been implicated as major forces shaping the vegetation (Johns, 1986). Johns (1985) attributed the low diversity of tree species in the lowland forests of Madang Province to the frequency of natural disasters in that region. However, the scarcity of tree diversity estimates from New Guinea has made it difficult to assess the generality of ecological patterns and underlying processes.

In an attempt to document the relationship between New Guinea forest diversity and elevation, four 1.0 ha plots were established in the Crater Mountain Wildlife Management Area (CMWMA). In addition to the 900 m plot described by Wright *et al.* (1997), plots were established at 120 m, 550 m, and 1400 m during a general biological inventory of the CMWMA in 1996. Future plots are also planned for 2000 m and 2800 m sites. A preliminary assessment of forest structure and composition in the 550 m plot is presented in this paper. Subsequent papers will integrate the results from additional plots.

METHODS

Site description

During July 1996, a plot transect was established at approximately 550 m a.s.l. in the CMWMA (Figure 1). The plot was located near the confluence of the O and Pio rivers at 145° 02' 12" E longitude and 6° 47' 19" S latitude in Simbu Province, PNG. The topography of the site was gently inclined to the northeast and strongly dissected by ravines. Soil samples from the nearby Wara Sera Research Station consisted of moderately nutrient-rich clays with considerable aluminum content (Wright *et al.*, 1997). Rainfall at Wara Sera ranged from 5.4 m to 7.4 m per year, averaging 6.7 m per year from 1990 to 1995 (D. Wright, pers. comm.). No months received less than 250 mm on average (Wright *et al.* 1997). The climate is humid and temperatures range from 17° C to 30° C with average daily minima and maxima of 18° C and 24° C, respectively. The vegetation at the O-Pio site is classified as mixed evergreen hill forest (Paijmans, 1976) with minimal evidence of human disturbance. Sago gardening in these forests, however, has been and continues to be an important source of food for local Pawaian landowners.

Field methods

The plot transect consisted of 25 contiguous 20 m x 20 m subplots, marked at each corner with 1 m lengths of plastic pipe. The plot was selected by choosing a random compass bearing between 0° and 180° and a random distance between zero and 1000 m from a base camp located on the bank of the O river. The plot originated at 465 m along a bearing of 88° from the base camp. Demarcation of the plot and all subsequent fieldwork was carried out by trainee students and landowners with supervision (Beehler, 1994). Efforts were made to avoid disturbing any vegetation within the plot, including stems < 10 cm DBH.

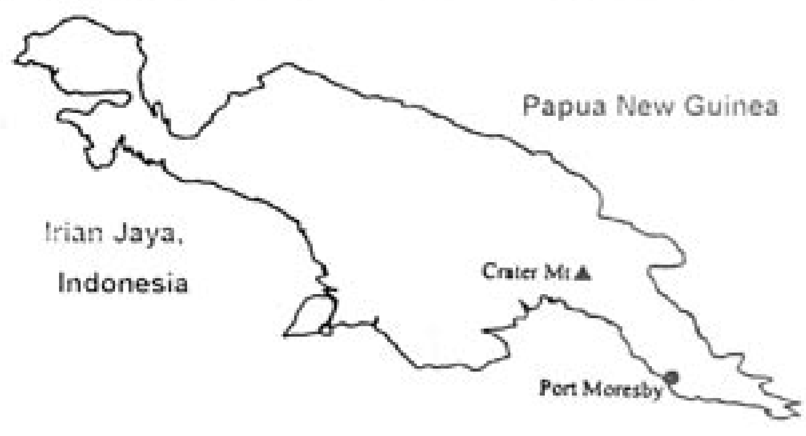

Figure 1. Crater Mountain Wildlife Management Area covers about 2700 km^2 situated near the borders of Simbu, Gulf and Eastern Highlands Provinces in Papua New Guinea.

All stems ≥ 10 cm DBH were enumerated. Stems were measured with fiberglass diameter tape to the nearest mm at approximately 1.4 m above the lowest point of ground (DBH). Basal area was calculated for each stem. Irregular trees were measured according to the standard methods used in 50 ha plot enumeration (Manokaran *et al.*, 1990) and the point of measurement was recorded in special cases. For example, trees with buttresses above 1.4 m were measured above the buttresses, noting the height of each measurement. Three stems of *Pandanus* spp. (Pandanaceae) were inaccessible due to numerous prop roots, covered with root spines, and often reaching more than six m in height above ground. Instead, each prop root was measured separately. Aerial roots were also measured in the case of hemiepiphytic strangler figs (*Ficus* subg. *Urostigma*; Moraceae). In one case, it was not possible to measure the diameter of the fused, aerial roots and basal area was instead estimated by subtracting the area of the host tree cavity from the area encompassed by the strangler fig.

Embossed, numbered aluminum tags (Forestry Supplies Inc. Cat. No. 79500) were set at approximately 1.25 m with aluminum nails (8 cm in length). Nails were placed below DBH to avoid inaccurate future measurements due to swelling of stems in response to wounding. Field data were recorded including: DBH, an estimate of tree height to the nearest 2 m, bark characteristics such as color, smell, and exudates, and plant names in the Pawaian language. Botanical vouchers of each tagged individual were collected for distribution to the Harvard University Herbaria (A), the National Herbarium of Papua New Guinea (LAE) and the Botanical Research Institute of Texas (BRIT).

Table 1. Most abundant tree species in the O-Pio transect, Crater Mountain Wildlife Management Area. Species names and Pawaian names follow Takeuchi (1997). Mean height (m), mean DBH (cm), and mean total basal area (cm^2) are listed for each species.

species	family	N	height X±SD	DBH X±SD	total basal area	Pawaian name
Myristica subalulata Miq.	Myristic.	30	11±4	11.7±1.6	3155	e-be
Pometia pinnata Forst.	Sapind.	28	29±13	32.4±14.9	27889	wen-nah
Cryptocarya[1]	Laur.	23	18±7	15.5±5.3	11510	sah-ah
Chisocheton lasiocarpus (Miq.) Valet.	Meliac.	22	18±9	18.6±8.4	7068	mä
Myristica fatua Houtt.	Myrist.	19	17±7	17.6±7.1	5375	we-e, way-e-be
Dysoxylum[2]	Meliac.	17	17±7	23.9±15.4	10606	mä
Endocomia macrocoma (Miq.) deWild.	Myrist.	16	16±6	17.4±6.1	4249	moo-moo
Dysoxylum "brassii " spp. group	Meliac.	14	23±8	23.1±13.5	7773	mä
Dysoxylum cf. excelsum Bl.	Meliac.	13	22±12	21.0±13.9	6340	mä
Pangium edule Reinw.	Flacourt.	11	23±8	31.0±15.9	10294	jae
Alseodaphne "umbelliflora" spp. group	Laur.	11	26±13	27.6±20.4	9851	tö-mä-tai
Pimeleodendron amboinicum Hassk	Euphorb.	10	26±8	24.7±12.2	5834	hoo-le
Microcos grandiflora Burrett	Tiliac.	9	24±7	29.1±11.8	6112	sö-bö
Semecarpus cf. papuanus Laut.	Anacard.	9	23±14	21.4±13.2	4324	hä-ö
Aglaia cf. tomentosa Teijsm. & Binn.	Meliac.	8	20±6	19.1±6.8	2552	ö-rai-may
Microcos sp. A	Tiliac.	8	13±3	14.8±6.9	1649	sö-bö
Garcinia dulcis (Roxb.) Kurz	Clusia.	8	15±4	14.7±2.7	1392	sö-re-ow
Lepidopetalum xylocarpum Radlk.	Sapind.	7	17±7	17.6±6.8	1650	jö-rö
Gomphandra montana (Schellen.)Sleu.	Icacina.	7	12±2	16.3±4.4	1559	swähm-me
Memecylon torricellense Mansf.	Melast.	7	14±3	14.4±4.8	1254	ah-kah-poo
Pisonia longirostris Teysm. & Binn.	Nyctagin.	7	7±2	13.6±2.8	1051	ö-pö
Memecylon cf. schraderbergense Man.	Melast.	7	13±4	13.2±2.0	985	ah-kah-poo
Myristica cornutiflora J. Sinclair	Myristic	6	20±7	22.2±8.8	2627	way-e-be
Endiandra magnilimba Kosterm.	Laur.	6	19±5	18.3±6.8	1766	sah-ah
Aglaia agglomerata Merr. & Perry	Meliac.	6	25±6	20.0±6.7	2066	ö-ri-may; mä; tä-pä-jö-mä;

[1]*"depressa-multipaniculata"* spp. group; [2]*"parasiticum-pettigrewianum"* spp. group;

Taxonomic methods

Plant names are adopted from Takeuchi (1997), who resurveyed the O-Pio plot in March 1997 to verify identifications made by Paul Katik and Pawaian names recorded by Debra Wright. Determinations reported by Takeuchi and those made by P. F. Stevens agreed in 95% and 82% of cases at family and generic ranks, respectively. Takeuchi rejected ten erroneous vouchers from the original survey and supplied names for 23 individuals that were not collected in the initial survey. In the majority of cases, individuals were identified to species. Individuals were assigned to morphospecies in cases where it was not possible to assign a species name due to the sterile condition of the vouchers. Morphospecies are hereafter referred to as species for the sake of brevity. The broad species concept of Takeuchi establishes a lower limit on the number of species in the plot and species richness may increase as additional fertile collections are made. In a single case, *Arcangelisia* sp. (Menispermaceae) from the initial survey is accepted instead of *Piper* cf. *caninum* (Piperaceae) from the second survey, based on DBH and bark characters.

RESULTS

Forest composition

The transect included a total of 615 stems ≥ 10 cm DBH comprising 174 species in 95 genera and 46 families. Although higher taxonomic ranks are not comparable indicators of diversity (see Discussion), families including Meliaceae, Myristicaceae, Lauraceae were well represented in the O-Pio transect, with at least 15 species in each family. Sapindaceae, Myrtaceae, and Annonaceae had ≥ 10 species per family. Genera including *Aglaia* (Meliaceae), *Chisocheton* (Meliaceae), *Dysoxylum* (Meliaceae), *Myristica* (Myristicaceae), *Cryptocarya* (Lauraceae), *Syzygium* (Myrtaceae), *Ficus* (Moraceae), and *Garcinia* (Clusiaceae) were also well represented, with at least five species per genus.

The relationship between abundance (the number of individuals per species) and species richness (Figure 2) showed an inverse relationship that is characteristic of diverse tropical forests. The majority of species are locally rare while a few species are relatively common. Sixty-five species (38%) were represented in the transect by a single individual. One hundred and ten species (63%) had fewer than three individuals in the transect. Twenty-five species (14%) were represented by more than five individuals (Table 1). *Myristica subalulata* (Myristicaceae), a common subcanopy tree throughout PNG, was most abundant with 30 individuals/ha. *Pometia pinnata* (Sapindaceae), a canopy species and a valuable source of timber, was the second most abundant species with 28 individuals. Other abundant canopy trees included *Cryptocarya "depressa-multipaniculata"* spp. group (Lauraceae), *Chisocheton lasiocarpus* (Meliaceae), 3 species of *Dysoxylum* (Meliaceae), 2 species of *Aglaia* (Meliaceae), *Pangium edule* (Flacourtiaceae), *Alseodaphne "umbelliflora"* spp. group (Lauraceae), *Pimeleodendron amboinicum* (Euphorbiaceae), *Microcos grandiflora* (Tiliaceae), *Semecarpus* cf. *papuanus* (Anacardiaceae) and *Myristica cornutiflora* (Myristicaceae).

The species accumulative curve (Figure 3) gives an indication of the completeness of the transect as a sample of overall tree diversity at the O-Pio site. The number of new species encountered rises without limit if individuals are sampled according to their location within the subplots. A randomized sampling sequence yields a more asymptotic curve (see Discussion). The total number of woody species at the O-Pio site was estimated using the non-parametric method of Chao (reviewed in Colwell and Coddington 1994). The total number of species is:

$$S_{tot} = S_{obs} + (L^2/2M)$$

where S_{obs} is the number of species sampled, L is the number of species known from single individuals (singletons), and M is the number of species represented by two individuals (doubletons). The variance of this estimate of overall species richness is:

$$var(S_{tot}) = M[\frac{(L/M)^4}{4} + (L/M)^3 + \frac{(L/M)^2}{2}]$$

The total number of woody species ≥ 10 cm DBH at O-Pio was estimated at 221 with a variance of 160. However, this figure underestimates regional woody species richness given the pre-asymptotic shape of the species accumulation curve (Figure 3 and see Discussion).

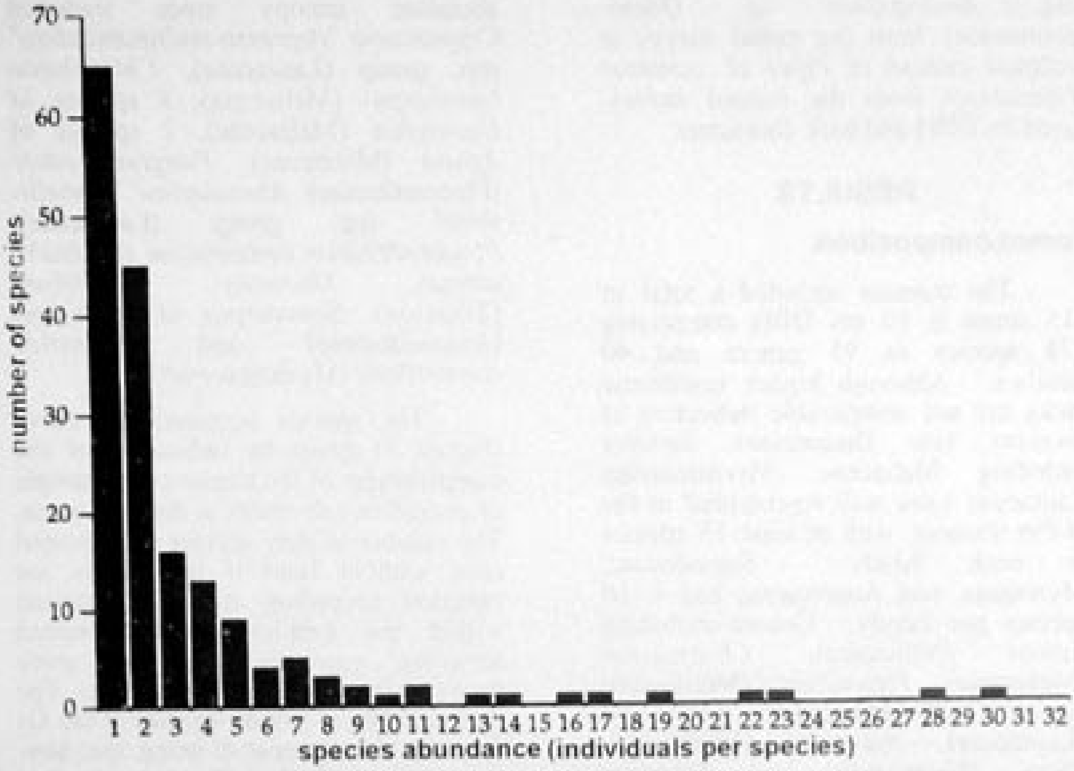

Figure 2. Frequency distribution for the number of individuals per species in the 1 ha O-Pio transect, Crater Mountain Wildlife Management Area.

Forest structure

Vegetation in the O-Pio transect consists of primary lowland rain forest with no evidence of recent, catastrophic disturbance. Canopy height ranged from 30 to 40 m with scattered emergent trees to an estimated 60 m in height (e.g. *Pometia pinnata*; Sapindaceae). Subcanopy trees ranging from 5 to 20 m in height were most abundant and there were no divisible subcanopy layers or strata. Trees and saplings of ≤ 10 cm DBH were also abundant and it is likely that some species were not represented in larger diameter classes. Epiphytic ferns and orchids were relatively common in the canopy, along with climbing rattan (*Calamus*; Arecaceae), herbaceous pipers (Piperaceae) and aroids (Araceae). The herbaceous understory consisted of ferns, *Sellaginella*, *Cyrtandra* (Gesneriaceae), and ground gingers (Zingiberaceae and Commelinaceae).

The distribution of diameter size classes for trees ≥ 10 cm DBH is indicative of mature-phase forest. The majority of trees (66%) were less than 20 cm DBH but 54 trees (9%) were more than 40 cm DBH and 16 trees (2%) were more than 60 cm DBH. A combined basal area of 31.5 m^2 was calculated for all 615 stems ≥ 10 cm DBH. All stems were woody with the exception of a single herbaceous *Musa* sp. (Musaceae). Trees comprised 602 of the 615 stems with lianes and hemiepiphytes making up the remainder. Buttresses and prop roots were noted for 34 and 19 trees, respectively. Lianes included two individuals of *Entada phaeseoloides* (Fabaceae), one *Arcangelisia* sp. (Menispermaceae) and four *Gnetum latifolium* (Gnetaceae). Hemiepiphytes included two individuals of *Ficus microcarpa* (Moraceae), one *Ficus glaberrima* and one *Schefflera* sp. (Araliaceae). Five individuals cauliflorous *Ficus* were also recorded.

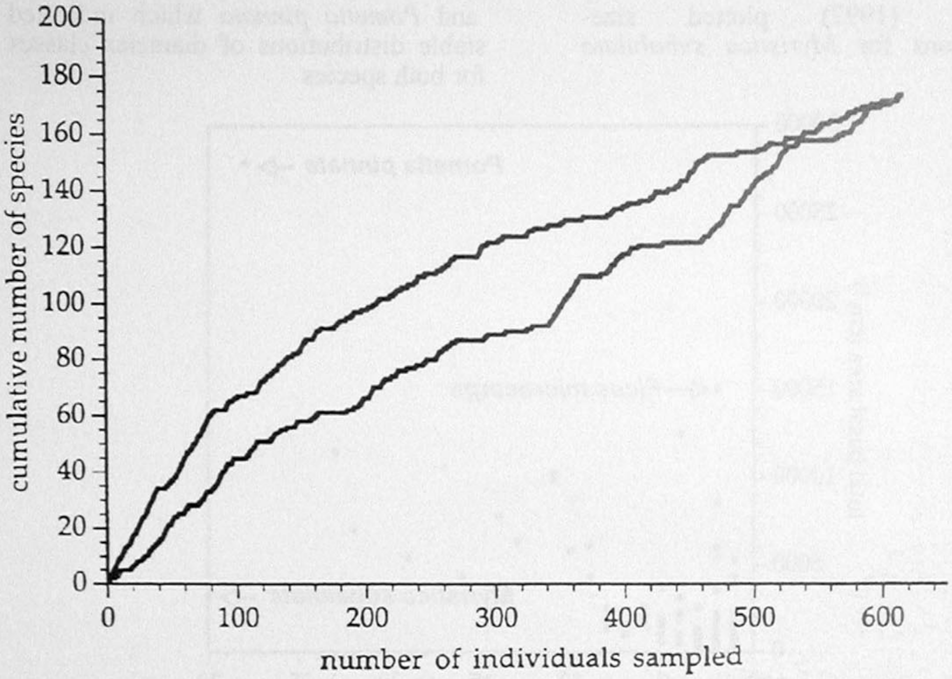

Figure 3. Species accumulation curves for the 1 ha O-Pio transect, Crater Mountain Wildlife Management Area. The lower curve is derived from sampling of individuals based on their location within the subplots. The upper curve is based on a randomized sample sequence.

The relationship between species abundance and combined basal area is shown in Figure 4. In general, the most abundant species have the highest basal area (see also Table 1), although there are noteworthy exceptions. *Pometia pinnata* is exceptionally common and is a large canopy emergent, so that this species alone comprises 9% of the basal area in the transect. On the other hand, *Myristica subalulata* (Myristicaceae) is more common than *Pometia pinnata*, but this species is restricted to the subcanopy and never attains diameters greater than 17 cm. *Ficus microcarpa* (Moraceae) is another interesting exception to the general relationship between abundance and combined basal area. Although this species is represented by only two individuals, their elaborate aerial root systems contribute to an overall basal area of 15138 cm^2, second only to *Pometia pinnata*. Four individuals with ≥ 10 cm DBH were excluded from these analyses because exact DBH measurements were lost or missing. These trees included one individual each of *Myristica subalulata*, *Lepidopetalum xylocarpum*, *Microcos* cf. *grandiflora*, and *Cryptocarya* sp. "*depressa-multipaniculata* group".

The initial census in July 1996 and the second census in March 1997 provide a glimpse of tree mortality rate in the plot. During the nine month interval between surveys, 6 trees (0.975%) died of apparent damage to their crowns and one tree was felled (Takeuchi, 1997). Extrapolating over a 12 month period, the annual mortality rate would be 1.3%. Fifty trees (8%) showed evidence of broken crowns suggestive of damage resulting from falling trees and one large tree fall gap was located within the plot. There was no other evidence of major catastrophic or historical disturbance within the plot. Few species are present in the transect at densities high enough to permit the examination of demographic patterns.

These findings rank O-Pio among the most species-rich tropical forests in the world.

It is difficult, however, to compare the taxonomic composition of the O-Pio plot to other plots due to the severe problem of estimating higher taxonomic diversity and endemism. Studies of ecological diversity have generally not appreciated the fact that taxa of the same rank are not equivalent evolutionary units (Doyle & Donoghue, 1993). Given that most families are either not sister groups or not monophyletic, numerical comparisons of families do not enhance our understanding of diversity. The problem is well illustrated by "Tiliaceae", "Sterculiaceae", and Malvaceae, all families that occur at O-Pio. "Tiliaceae" and "Sterculiaceae" are polyphyletic within the order Malvales (Alverson *et al.*,1998) and a monophyletic circumscription would alter the number of recognizable families at O-Pio. Statements about richness and endemism of families will be arbitrary and even misleading unless supported by a phylogenetic classification or by comparisons of sister groups. In recognition of this problem, family importance values are not reported.

The problem of estimating diversity at the species level may be more tractable, given a consistent and conservative notion of species. We would like to know the extent to which the O-Pio transect represents woody plant diversity at the site. Species-area curves are the standard means of inferring the completeness of a sample from a community, however, the order in which samples are accumulated affects the shape of the curve (Colwell & Coddington, 1994). When individuals are surveyed according to their location within subplots, the species accumulation curve rises without limit (Figure 3). However, if the sampling sequence is randomized to remove spatial patterns, the accumulation curve is more asymptotic. The comparison of these curves illustrates the effect of spatial patterning in species distributions on overall species richness.

It is not possible to accurately estimate regional species richness from the O-Pio data because of the constant increase in the number of new species as more individuals were sampled. Most new species were represented by fewer than three individuals and the rate of rare species accumulation did not decrease with the sampling of more subplots. In this situation, Chao values will consistently underestimate species richness (Colwell & Coddington 1994). The O-Pio transect results illustrate that future studies of tree diversity in New Guinea and elsewhere should take into consideration both the problem of higher taxonomic comparisons and the effect of sampling when estimating species richness. Forest enumerations of larger areas will be required to estimate regional species richness in New Guinea.

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