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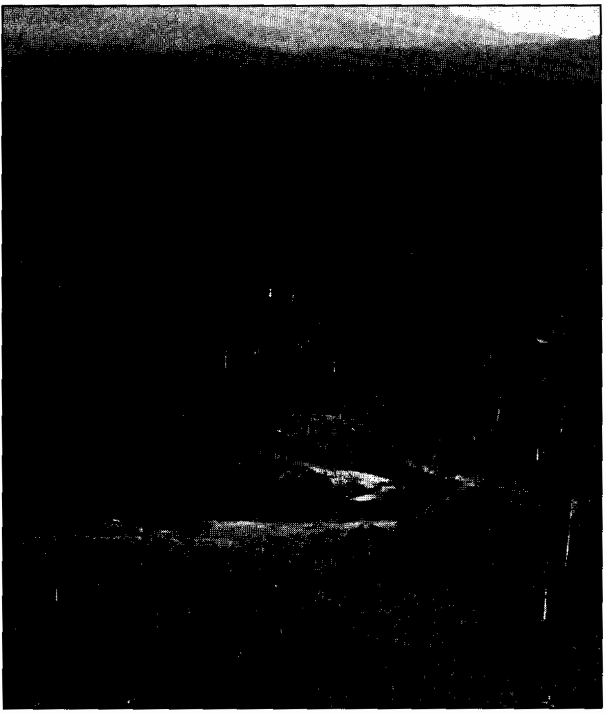

A Biological Assessment of the Lakekamu Basin, Papua New Guinea

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TECHNICAL REPORTS

VEGETATION PART 1: A COMPARISON OF TWO ONE-HECTARE TREE PLOTS IN THE LAKEKAMU BASIN

(J. Alexandra Reich)

Chapter Summary

- We studied forest structure, species diversity and soil characteristics in two one-hectare plots in the IRS study area, one in hill forest and the other in alluvial forest. Plots were 20 m x 500 m with 25 subplots measuring 20 m x 20 m.
- We marked and measured all trees ≥10 cm DBH, and collected voucher specimens from all marked trees for species identification. Lianas were excluded from the study.
- Roughly 253 species were censused: 574 individuals of 182 species on the alluvial plot, and 759 individuals of 156 species on the hill plot. Stem density on the hill plot was significantly higher than on the alluvial plot. Stem size class distributions between the two plots did not differ.
- Most species were "rare." In the alluvial plot, 87.4% of the species had 5 or fewer representatives, and only 1.1% (2 species) had more than 20 individuals. Similarly, 75% of the hill species were represented by 5 or fewer individuals, and 4.5% (7 species) have more than 20 individuals.
- Soil characteristics were essentially typical of tropical rainforests. Soil nutrient contents, pH (4.0 for both), and cation exchange capacities (alluvial = 5.8 and hill = 6.8) were all low; iron and aluminum were high.
- Compared to three other plots in the Basin (Oatham and Beehler 1997), the Ivimka plots had more stems but fewer large trees.
- Through this study we have added to the list of rare species known to occur in the Basin and further demonstrated the heterogeneity within the Basin. The high diversity, rarity and heterogeneity of plant taxa within the Basin testify to the need for conservation. Successful conservation will require broad coverage to encompass the variety of vegetation types occurring within the Basin.

Introduction

In the Asian tropics, PNG is the seventh largest country (out of 19), and holds roughly 450,000 km^2 (12-15%) of the moist and lowland tropical rainforests found in the region; making it second only to Indonesia (Davis 1995a). Considering New Guinea as a biogeographic unit (combining PNG and Irian Jaya) elevates the region to greater prominence: over 800,000 km^2 of forest or roughly 45% of all forest in Malesia (the biogeographic area extending from Malaysia to New Guinea). Thus New Guinea contains more forest than the rest of Indonesia, Malaysia, or Indochina. It is one of the few remaining, large tropical wilderness areas.

Because of its geologic history, New Guinea has a unique flora, combining taxa from the Oriental and Australian biogeographic regions. At least 25,000 species of vascular plants occur in

Thus New Guinea contains more forest than the rest of Indonesia, Malaysia, or Indochina. It is one of the few remaining, large tropical wilderness areas.

New Guinea, the vast majority of which, 20,000 or more, occur in PNG (R. Johns, personal communication, Höft 1992). Thus, roughly half the plant species of the Malesian region are found here. This translates to an astounding figure: roughly 10% of the world's plant species occur in New Guinea.

Among these, most species are found nowhere else in the world. There are 93 endemic genera (Osborne 1995) in PNG and 70-80% of the plant species are thought to be endemic (R. Johns in Davis 1995b). However, these estimates are based on a small number of studies, and a paucity of specimen collections. It is likely that expanded survey work will reveal many new species from PNG and Irian Jaya. Quite likely many of the taxa considered endemic to PNG or Irian Jaya might be found in the other country with adequate survey work. Nonetheless, the global importance of PNG's floral diversity will only increase with further study. Many taxa are shared with Australia's small fragments of rainforests. As these pockets of rainforest degrade, due to the expected consequences of fragmentation (Lovejoy *et al.* 1986), the large intact ecosystems of New Guinea become that much more important.

Few studies have examined the structure and diversity of PNG forests (*e.g.* Paijmans 1970, Johns 1986, Wright *et al.* 1997), and fewer studies have concentrated on the lowland rainforests (Oatham and Beehler 1997, Kiapranis 1991). Nonetheless, it is clear that the rainforests of PNG are similar to other rainforests in that they are very species rich, with many species naturally occurring in low densities (see Discussion). Rainforest trees are vital to many people of PNG, providing many essentials, from food and medicines to construction and fuelwood. Because logging companies are securing timber rights over large areas and forests are being harvested at an alarming rate (Nadarajah 1993), it is urgent that more information be obtained on the structure and ecological functions of PNG's native forests. Such information is a prerequisite for prudent management of forest resources.

Through sampling two one-hectare plots, we intended to investigate forest structure and tree diversity in a portion of the Lakekamu Basin near the Ivimka Research Station. These data will assist future research and conservation activity around the IRS. Information from this study augments previous work in other parts of the Lakekamu Basin (Oatham and Beehler 1997). As more vegetation studies are conducted in the Basin, it will become easier to develop the management priorities and goals for the Lakekamu Conservation Initiative and to manage other rainforest sites in PNG. Finally, the data from this study will help improve our knowledge of the richness of PNG's lowland forests relative to other parts of Asia and the Neotropics that are better-known. Studying rainforests in PNG enhances our knowledge of rainforests worldwide, aiding conservation efforts within and outside of PNG (Oatham and Beehler 1997, Soepadmo 1995).

Methods

We randomly selected two sites from previously existing trails (the Bulldog Road and the Ridge Trail, See map page 22) for a one-hectare plot in the alluvial and hill forests, respectively. The alluvial plot is 3 km south, and the hill plot is approximately 0.5 km northeast of the Ivimka Research Station. We delineated belt transects measuring 20 m x 500 m, consisting of 25 subplots (20 m x 20 m) for intra-plot comparisons. Using an altimeter, we recorded the elevation of each subplot, and with a compass/ inclinometer, we measured slope and aspect. From the center of each subplot, we subjectively estimated canopy cover. We permanently marked and measured all trees ≥ 10 cm diameter at breast height (DBH, breast height = 1.4 m above ground). For those trees with large buttresses, we measured diameters just above the buttresses, and recorded the height at which the measurement was taken. In the case of *Pandanus* spp. with multiple stilt roots at 1.4 m high, we measured the diameter of all living prop roots, calculated their total basal area and calculated a measure of diameter from the total basal area (Wright *et al.* 1996).

We collected voucher specimens from all marked trees for identification and storage at the Forestry Research Institute (FRI) in Lae, PNG. In the event of multiple individuals of a positively identified species, we collected one representative specimen for that species. We pressed and stored all specimens in 75% ethanol until transported to a suitable drying facility.

Kippy Demas identified dried specimens to genus or species at FRI. Where identification to species level was not possible, and where sufficient differences were apparent, congeners were divided into morpho-species. We measured species diversity for both plots using the Shannon Diversity Index (Zar 1984). As a measure of the relative contribution of each family to the plots, we calculated Family Importance Values (FIV, Mori *et al.* 1983), an index that incorporates relative diversity, relative density, and relative dominance. Species *vs.* area curves were derived from the cumulative number of species in each 20 m x 20 m subplot.

We collected, dried, and sieved soil samples at 0 cm and 20 cm depths from one random point in each subplot. Soil samples were analyzed for nutrient and mineral content, pH, salinity, and cation exchange capacity by Micro-Macro International, Inc. (Athens, GA). Samples from the 20 cm depth were treated for exchangeable macroelements with 0.5N ammonium acetate and with 0.0005N DTPA for trace metals (Page *et al.* 1982). Extracts were then analyzed with an inductively coupled plasma spectrometer. Nitrogen content was determined with the microkjeldahl technique (Hesse 1972).

We calculated mean tree density per subplot, and tested for a difference between the two plots with a student's t-test. We plotted size class distributions in 5 cm increments, and using the non-parametric Kolmogorov-Smirnov Two-Sample Test, we tested the differences in the size class distributions of the two plots (Sokal and Rohlf, 1995). Where applicable, we made comparisons between our data and published data for PNG, and other tropical sites. Statistical tests were performed with Sigmastat 1.01.

Results

Density and Dominance

We found 575 trees (DBH ≥ 10 cm) in the alluvial plot and 759 trees on the hill plot (Table 1). Stem density (mean number of trees per subplot) was greater on the hill plot than the alluvial plot (Table 1; t= -4.20, df=48, P=0.0001). However, basal areas (dominance) did not differ substantially between the two plots. Total basal area of trees was 28.46 m^2 in the alluvial plot, and 32.04 m^2 in the hill plot (Table 1). Size class distributions between plots did not differ (Figure 1; $KS = 0.062$, $KS^{crit} = 0.075$, $n^1 = 575$, $n^2 = 759$, $P \geq 0.05$). Neither plot had as many large trees as on three other plots in the Lakekamu Basin (Table 1). The stem density and basal area of the Ivimka plots are within the range of what is typical for tropical rainforests around the world (Table 2).

Table 1. Summary statistics for diversity, density and size of woody stems on vegetation plots in the Lakekamu Basin. Alluvial and hill plots from this study at Ivimka, Si and Nagore plots from Oatham and Beehler (1997).

PLOT	SHANNON INDEX **	# OF SPECIES	# OF FAMILIES	# TREES/SUBPLOT (standard deviation)	# TREES ≥ 10 cm DBH	MEAN DBH (cm)	# TREES > 60 cm DBH	# TREES > 100 cm DBH	BASAL AREA (m^2/ha)
Alluvial	4.86	182	52	23.0 (5.62) ***	575	21.1	10	1	28.46
Hill	1.90	156	49	30.4 (6.73) ***	759	19.9	13	0	32.04
Si River*	1.75	93	34	n.a.	392	28.6	43	20	49.32
Nagore N*	1.96	149	42	n.a.	426	23.3	26	1	37.67
Nagore S*	2.01	178	42	n.a.	482	22.1	23	2	28.72

n.a. = not available

* Note: the Oatham and Beehler data include lianas whereas this study did not.

** Note: Shannon Index calculated using Log^{10}.

*** There is a significant difference between the mean number of trees per subplot (t = -4.20, df=48, P=.0001)

Table 2. Tree densities, basal areas, species densities, regions and forest types from studies in comparable tropical forests throughout the world.

REGION	FOREST TYPE	DENSITY #TREES/ha	BASAL AREA (m^2)	DIVERSITY #SPECIES/ha	CITATION
PNG - s	Alluvial/Lakekamu	575	28.5	182	This study
PNG - s	Hill/Lakekamu	759	32.0	156	This study
PNG - s	Lowland/Lakekamu	433	38.6	178	Oatham and Beehler 1997
PNG - n	Low montane	575	29.2	166	Paijmans 1970
PNG - c	Mid montane	693	37.1	228	Wright et al. 1997
Asia	Low/dipterocarp	375	n.a.	134	Poore 1968
Asia	Alluvial	615	28	225	Proctor *et al.* 1982
Asia	Heath	708	43	110	Proctor *et al.* 1982
India	Low montane	635	39.7	91	Pascal and Pelissier 1996
Americas	Alluvial	580	n.a.	300	Gentry 1998
Americas	Alluvial	650	n.a.	204	Gentry 1998
Americas	Alluvial	526	33.5	165	Gentry 1998
Americas	Lowland	446	n.a.	269	Lieberman 1984
Americas	Mid elevation	891	n.a.	200	Mori *et al.* 1983
Americas	Upland	575	29.1	172	Phillips *et al.* 1984
Americas	Terra firma	432	n.a.	179	Pires *et al.* 1953

n = northern, c = central, s = southern, n.a. = not available

Conservation in the Basin that includes adjoining hill forest could preserve a vastly greater range of diversity in a relatively narrow fringe of surrounding hill forest.

Diversity

There were 253 species or morpho-species identified on the plots: 182 species in 104 genera and 52 families in the alluvial plot, and 156 species in 92 genera and 49 families in the hill plot. (Appendix 2). The continued positive slopes in the species-area curves suggest that one hectare is not sufficient for a thorough sampling of the local tree community (Appendix 1A). The Shannon Diversity Index for species in the alluvial plot is 4.86 and for the hill plot is 1.90. There were 86 species (47.25%) in the alluvial plot represented by only one individual, and 64 species (41.03%) in the hill plot (Figure 2). Further, 87.36% of the alluvial species, and 75% of the hill species, have 5 or fewer individuals. Only 2 species (1.1%) in the alluvial plot and 7 species (4.5%) in the hill plot have ≥ 20 individuals (Table 3). Only one species, *Parastemon versteeghii* (Chrysobalanaceae) is among the ten most common species in both plots, with 15 individuals in both plots (Table 3).

Seven families were shared among the ten highest Family Importance Values for both plots (Table 4). Only three of the top ten families at Ivimka are also in the top ten at three other sites in the Lakekamu Basin (Table 5). Eight of 21 dominant plant families are in the top ten of only one of the five inventoried sites in the Lakekamu Basin (Table 5) yet one of these, Datiscaceae on the Si plot, has the fifth highest of fifty top FIV scores in the Basin.

Table 3. Number of individuals for the ten most common species in the alluvial and hill plots.

FAMILY	ALLUVIAL PLOT SPECIES	NUMBER INDIVIDUALS	FAMILY	HILL PLOT SPECIES	NUMBER INDIVIDUALS
Sapotaceae	*Pouteria firma*	24	Myrtaceae	*Syzygium* sp. nov.	58
Verbenaceae	*Teijsmanniodendron bogoriense*	20	Burseraceae	*Haplolobus floribundus*	42
Fagaceae	*Lithocarpus* sp.	18	Myrtaceae	*Xanthomyrtus fusciculata*	41
Clusiaceae	*Calophyllum soulattri*	16	Lauraceae	*Cryptocarya idenburgensis*	25
Chrysobalanaceae	*Parastemon versteeghii*	15	Dipterocarpaceae	*Anisoptera polyandra*	24
Myristicaceae	*Gymnacranthera paniculata*	13	Myrtaceae	*Syzygium accuminatissima*	20
Burseraceae	*Haplolobus pubescens*	13	Verbenaceae	*Teijsmanniodendron ahernianum*	20
Myrtaceae	*Rhodomyrtus* sp.	12	Meliaceae	*Dysoxylum alliaceum*	16
Flacourtiaceae	*Ryparosa javanica*	12	Clusiaceae	*Garcinia hunsteinii*	16
Euphorbiaceae	*Neoscortechinia forbesii*	12	Chrysobalanaceae	*Parastemon versteeghii*	15

Table 4. Number of species, number of stems, and Family Importance Values (FIV, Mori *et al.* 1983) for the ten dominant families in the Alluvial and Hill plots.

	ALLUVIAL PLOT				HILL PLOT		
FAMILY	# SPP. (%)	# INDIVIDUALS (%)	FIV	FAMILY	# SPP. (%)	# INDIVIDUALS (%)	FIV
Euphorbiaceae	16 (8.8)	55 (9.6)	30.65	Myrtaceae	20 (12.8)	200 (26.4)	61.76
Lauraceae	15 (8.2)	37 (6.4)	22.55	Lauraceae	20 (12.8)	121 (15.9)	44.17
Myrtaceae	14 (7.7)	44 (7.7)	22.00	Burseraceae	3 (1.9)	51 (6.7)	19.43
Burseraceae	7 (3.8)	36 (6.3)	13.80	Meliaceae	11 (7.1)	41 (5.4)	18.46
Rutaceae	6 (3.3)	24 (4.2)	12.08	Clusiaceae	7 (4.5)	48 (6.3)	15.32
Fagaceae	2 (1.1)	27 (4.7)	11.77	Euphorbiaceae	8 (5.1)	28 (3.7)	13.16
Myristicaceae	8 (4.4)	25 (4.3)	11.48	Myristicaceae	8 (5.1)	24 (3.2)	9.94
Clusiaceae	5 (2.7)	30 (5.2)	10.03	Verbenaceae	2 (1.3)	23 (3.0)	9.46
Elaeocarpaceae	5 (2.7)	15 (2.6)	9.14	Sapotaceae	6 (3.8)	16 (2.1)	7.37
Sapotaceae	3 (1.6)	27 (4.7)	8.86	Chrysobalanaceae	2 (1.3)	16 (2.1)	7.04

Table 5. Dominant families from the hill and alluvial plots and other lowland sites in PNG (with Family Importance Values; Mori *et al.* 1983.)

SITE	IVIMKA ALLUVIAL	IVIMKA HILL	NAGORE SOUTH*	NAGORE NORTH*	SI RIVER*
Dominant families (FIV)	Euphorbiaceae (30.65) Lauraceae (22.55) Myrtaceae (22.00) Burseraceae (13.80) Rutaceae (12.08) Fagaceae (11.77) Myristicaceae (11.48) Clusiaceae (10.03) Elaeocarpaceae (9.14) Sapotaceae (8.86)	Myrtaceae (61.75) Lauraceae (44.17) Burseraceae (19.43) Meliaceae (18.46) Clusiaceae (15.32) Euphorbiaceae (13.16) Myristicaceae (9.94) Verbenaceae (9.46) Sapotaceae (7.37) Chrysobalanaceae (7.04)	Meliaceae (36.11) Annonaceae (30.06) Lauraceae (26.81) Moraceae (26.22) Sapindaceae (20.09) Rubiaceae (14.44) Nyctaginaceae (12.01) Euphorbiaceae (11.56) Sapotaceae (11.23) Combretaceae (10.14)	Moraceae (47.45) Meliaceae (27.71) Lauraceae (26.76) Sapindaceae (22.82) Annonaceae (17.64) Euphorbiaceae (15.99) Sapotaceae (11.34) Clusiaceae (10.43) Combretaceae (9.98) Rubiaceae (9.83)	Datiscaceae (42.09) Meliaceae (36.42) Moraceae (31.17) Euphorbiaceae (18.98) Anacardiaceae (16.16) Annonaceae (15.42) Myrtaceae (13.38) Combretaceae (10.98) Lauraceae (10.41) Sapotaceae (9.93)

*Data from Oatham and Beehler (1997).

Physical Parameters

The two plots differed in several characteristics beside the obvious difference in elevation (Table 6). The alluvial plot was essentially level whereas the hill plot traversed steep and varied topography. The subplots in the alluvial forest were more varied in canopy openness (Table 6), perhaps due to more or larger treefalls. The relative humidity of the hill forest was noticeably lower than in the alluvial forest; breezes unnoticeable in the alluvial forest cooled and dried the hill forest despite the relatively minor difference in elevation (personal observation).

Soil samples from the two plots exhibited some differences (Table 7). The color of soil from the hill plot was a homogeneous ferrous red, whereas in the alluvial plot, colors ranged from ferrous yellow to bluish gray. The surface of the soil in the alluvial plot was bare, and no horizon line was apparent between 0 - 50 cm depth. However, the hill plot had a surface layer 10-30 cm thick of mosses and leaf litter. Magnesium and sodium contents were both significantly higher in the alluvial soil samples, while copper content was significantly higher in the hill plot soil samples (Table 7). Soil characteristics and nutrient content of both plots were consistent with other tropical lowland silty clay soils (Gentry 1988). Generally nutrients, notably nitrate, ammonium, and phosphorus contents were low, while iron, and aluminum were high (Table 7). Cation exchange capacity (CEC) and pH were predictably low in both plots, and did not differ between plots.

Table 6. Characteristics of study plots.

PLOT	ELEVATION (M ASL)	LENGTH ORIENTATION	SLOPE	ASPECT	% CANOPY (MEAN)
Alluvial	100 - 120	069°	0° - 5°	none	55 -99 (82)
Hill	175 - 260	031°	25° - 50°	variable	70 - 95 (83)

Table 7. Soil analysis results from the Lakekamu Basin for nutrients (ppm), pH, and cation exchange capacity (CEC). The arithmetic means and standard errors of the means (SEM) are reported for the Hill and Alluvial plots. The test statistics from the Mann-Whitney U-test (T-statistic) and probability values (P) are reported for comparisons between sites. Bold faced P values indicate significant differences.

	HILL PLOT (SEM)	ALLUVIAL PLOT (SEM)	(T-STATISTIC)	P
NO_3	5.67 (0.52)	6.13 (2.16)	82	.161
NH_4	0.04 (0.03)	0.0 (0.0)	49	.463
P	0.0 (0.0)	0.71 (0.485)	60	.442
K	17.84 (9.93)	14.17 (2.13)	85	.083
Ca	7.51 (3.98)	9.37 (1.68)	51	.083
Mg	5.64 (1.95)	9.15 (1.59)	48	**.038**
Fe	167.77 (11.57)	126.92 (25.92)	58	.328
Mn	6.25 (3.17)	2.14 (0.69)	51.5	.083
B	0.17 (0.05)	0.11 (0.01)	74.5	.505
Cu	1.12 (0.21)	0.27 (0.05)	40	**.002**
Zn	0.73 (0.29)	0.44 (0.03)	70	.879
Mo	0.13 (0.13)	0.0 (0.0)	64	.721
Na	11.41 (0.35)	13.42 (0.69)	47	**.028**
Al	1198.79 (84.60)	1157.61 (62.47)	70	.879
pH	4.0 (0.05)	4.03 (0.05)	65.5	.798
CEC	6.75 (0.44)	5.80 (0.34)	81	.195

* All values for ammonium in the alluvial plot were zero, with the exception of one sample (25.13 ppm), which is not included in the analysis.

Discussion

Overall IRS Flora

Certainly two hectares are inadequate to describe the flora of the IRS study site. The steep increase of the species area curves (Appendix 1A) indicates that the woody flora was not completely sampled. The slight leveling of the species area curve for the hill plot (Appendix 1A) midway along the transect coincides with where the transect crested a ridge. This emphasizes the importance of randomly placing transects; a transect that followed a ridgetop might have underestimated the species richness of this site.

The plot data, combined with the general survey data (Takeuchi and Kulang, next section) yields a more complete picture of the flora. Neither method alone (plots or general collecting) produced a complete flora. The plot enumerations added eleven families and roughly 174 species to those found by general collecting (Appendices 2 and 3). Combined, the RAP survey revealed the presence of over 600 plant species in 130 plant families. Such high diversity apparent in such a small portion of the Basin in such a short time period substantiates the overall finding of the RAP survey that this is an area of rich biodiversity. It is indicative of the high diversity of the Basin to compare our results from two hectares: 253 species among 1,334 stems > 10 cm DBH, to the results of a fifty hectare plot in Panama: 303 species among 235,895 stems > 1 cm DBH (Hubbell and Foster 1992).

The creation of two marked plots with representative specimens in the nearby collections at FRI enhances the attractiveness of the IRS to scientists considering research in PNG.

Density, Dominance and Diversity

The hill forest had substantially more stems than the alluvial plot, but not disproportionately more in any size category. The hill forest plot had only a nominally greater total basal area and only two more very large trees (DBH ≥ 60 cm) (Table 2). Likewise, the stem size class distributions of both plots were remarkably similar (Figure 1).

Despite having more trees, the hill forest had lower diversity than the alluvial forest both in terms of alpha diversity and the Shannon Index (Table 1). The hill forest was dominated by two families—Myrtaceae and Lauraceae. These two families contained over 25% of the species and over 40% of the stems found on the hill plot whereas the alluvial plot had no such dominant families (Table 4). Interestingly, of the four families Takeuchi and Kulang (next section) list as dominants, three were dominant on the hill plot, but one they reported, Elaeocarpaceae, did not rate in the top ten hill families (Table 4) nor did the botanical survey team report Lauraceae as a dominant family. This emphasizes the importance of combining quantitative and qualitative assessments.

Both plots exhibited the pattern expected in tropical rainforests: many rare species and a few fairly common species. More than forty percent of the species on both plots were only represented by a single individual. Over 86% of the species on the alluvial plot were represented by 5 or fewer individuals compared to 64% on the hill plot. The higher diversity of the alluvial forest was characterized by a greater number of rare species. Whereas most species were represented by rare taxa, a substantial number of the stems were represented by a few common species. The top ten species comprised 26.9% of stems in the alluvial plot and 36% of the stems in the hill plot (Table 2). For the two plots combined, 7.5 % of the species accounted for 32.4 % of the stems.

Although the two Ivimka plots shared seven of the top ten families (FIV), they shared only 28.5% of their species (Appendix 2), shared only one domainant species (Table 3), and were strikingly dissimilar in terms of general floristics (next section). The two plots were separated by less than 5 km, had similar soils (Table 7) and only a small elevational difference (Table 6). Quite likely, the differences in ground slope (and hence drainage), and disturbance regimes (Table 6) between the two plots has a profound effect on vegetation. Conservation in the Basin that includes adjoining hill forest could preserve a vastly greater range of diversity in a relatively narrow fringe of surrounding hill forest.

Physical Parameters

The soil samples were typical of poor tropical soils (Gentry 1988), with a Ca^+ content less than 100ppm. Both plots had very low pH, which leads to decreased bio-availability of phosphorus, calcium, copper and magnesium, especially in the presence of ferrous and aluminum oxides and calcium ions (Barber 1995). Phosphorus and nitrogen were both limited in our soils, suggesting that nutrients are very tightly cycled between detritus and live material. Low phosphorus content in the alluvial plot could limit litter fall, and contribute to the near absence of leaf litter in the alluvial plot (Vitousek 1984). The flat terrain in the alluvial forest apparently does not limit leaching rates relative to the steeper hill forest (where the moss layer might help slow erosion). Only magnesium and sodium were significantly higher in the alluvial plot and copper was significantly lower (Table 7). CEC was low, which limits plants' abilities to uptake nutrients. Quite likely, the native flora is well-adapted for low nutrient soil but exotic taxa (*e.g.* oil palm plantations proposed as a development project) would not flourish in the Basin. The Basin's poor soils could also limit or impede forest regeneration after logging.

During the one-month period of data collection, we observed eight treefalls in and around the alluvial plot. Treefalls are common and often large in the study area (B. Gamui and A. Sitapa, unpublished data). This creates heterogeneity of seral stages in the alluvial forest and probably contributes the elevated high diversity of the alluvial forest. Indeed our estimates of canopy cover varied more in the alluvial forest (Table 6), largely due to the presence of more canopy openings due to treefalls. Many factors, such as shallow, water-logged soils or high wind velocities could contribute to high treefall rates which in turn could limit tree size. Interestingly, the other plots in the Basin (Oatham and Beehler 1997) had more large trees (Table 1). It would be rewarding to compare disturbance rates at different sites in the Basin and the effect on tree size and diversity.

Vegetation in the Lakekamu Basin

Oatham and Beehler (1997) studied three one-hectare plots in the Nagore-Si region of the Lakekamu Basin, and reported a range of 392 - 482 woody stems per plot (Table 1). Due to the inclusion of lianas in their study, these data are not directly comparable to ours. However, as both Ivimka plots had more stems and more species (except the hill plot which had fewer than the Nagore South plot), the exclusion of lianas from the Nagore-Si plots would only widen the differences (Table 1). The greater basal areas and mean DBH at the Nagore-Si plots is probably not due to the inclusion of lianas, but rather the greater number of large trees. The Nagore-Si plots had more than twice the number of trees ≥ 60 cm DBH than on the Ivimka plots (Table 1).

Although the complete species composition data of the other three Lakekamu vegetation plots were not available, it is obvious the species composition of the three Nagore-Si plots differed substantially from the two Ivimka plots. Only three families were in the top ten in terms of family importance values in all five plots (Table 5), and eight were in the top ten in just one of the five plots. Among the top ten in each plot, there is no consistency in rank. Datiscaceae is the dominant family at the Si River plot and not in the top ten on any of the other four plots, Meliaceae ranked high in the Nagore-Si plots but was not in the top ten on the Ivimka alluvial plot.

Oatham and Beehler (1997) emphasized the heterogeneity among the Nagore-Si plots. Addition of the two Ivimka plots further emphasizes the heterogeneity in the Basin. None of the 23 top species in the Nagore-Si plots (Oatham and Beehler 1997) rank in the top ten in this study (Table 3). Furthermore of the 23 top species in the Nagore-Si plots, only three occurred (but were not dominant) in the alluvial plot and only one occurred in the hill plot. If we assume that undetermined species of one plot were equivalent to undetermined congeners in the other plot there could be as many as 12 of the dominant 23 Nagore-Si species on the alluvial plot and eight on the hill plot.

The Nagore-Si plots and Ivimka hill and alluvial plots all exhibited dramatic differences in species composition and structure. The two most separated sites are only about 20 km apart in continuous, closed forest. From the air, the forest of the Basin appears to be a complicated mosaic of different forest types (A. Mack, personal communication). Given the spatial variety of forest types in the Basin, it is clear that a successful conservation initiative will require coverage of most or the entire Basin. The causes and means of maintaining this heterogeneity are still speculative. Revealing these relationships would greatly assist conservation planning throughout New Guinea. Future research that combines remote sensing, by satellite or aircraft with additional ground survey of plots would be richly rewarding. The five one hectare plots in the Basin create a good beginning for such an initiative.

Comparison to Other Rainforests and Conservation Implications

Because the hill forest had some taxa characteristic of lower montane forests (*e.g.*, Podocarpaceae, Winteraceae), it is interesting to compare to site at the transition from hill to lower montane forest 250 km away in the Crater Mountain Wildlife Management Area (CMWMA) at 900 m elevation (Wright *et al.* 1997). The CMWMA plot had fewer stems per hectare, but substantially more species (Table 2). The Lakekamu plots are not as diverse as the CMWMA plot and all but the hill plot had substantially fewer stems. The two Ivimka plots each shared five top families with the CMWMA plot (Wright *et al.* 1997).

From a partial survey of rainforest vegetation studies (Table 2) the Ivimka plots lie within the range of values for species richness, number of stems and basal area per hectare. The basal areas in the hill (32.04 m^2) and alluvial (28.46 m^2) plots are somewhat below the estimated pantropical mean basal area (36 m^2, Dawkins 1959), but the tree density on the hill plot is somewhat high (Table 2). A large number of small trees might make these forests less attractive to commercial loggers, though the threat from logging is real. Of nineteen major timber export species (Sekhran and Miller 1995), at least seven occurred in the hill forest. However, only four occurred in the alluvial plot and only three timber species had ten or more stems ≥ 10 cm DBH on the pooled Nagore-Si plots (Oatham and Beehler 1997). Thus it appears the hill forest adjoining the Basin might be attractive to commercial loggers, but the timber in the Basin itself is probably less valuable. The shallow rivers of the Basin and road-building in the muddy, often-flooded alluvial Basin could make timber extraction difficult in the Basin.

Nearly one quarter of the world's lowland tropical rainforests is already gone with much of the rest of it existing in only small fragments (often on the order of 1 km^2; Turner and Corlett 1996). Conserving the remaining large, undisturbed areas of the world must be ranked among the highest priorities in biological conservation. The Lakekamu Basin is one outstanding candidate for conservation. The data indicate extraordinary diversity and heterogeneity within the Basin. The Basin comprises a logical conservation unit—a major watershed that is currently sparsely inhabited and devoid of roads or other major development projects. The area may have some valuable timber. However the data suggest timber species are scattered in their distribution and often small in stature, making extraction expensive especially in light of the limited options for road-building or log-rafting in much of the Basin.

The pristine quality of the Lakekamu ecosystem, its high diversity, its ready access by small aircraft and the newly-constructed Ivimka Research Station present an ideal environment for expanding research and possibly ecotourism in the area. The permanent plots, voucher plant series and other assets contributed by the RAP team should increase the area's attractiveness to scientists and tourists.

Figure 1. Size-class distributions of trees in the alluvial and hill plots. Size classes begin with trees ≥ 10 cm DBH in each plot. Labels indicate the upper limit of each size class. The size class distributions for the two plots did not differ statistically significantly.

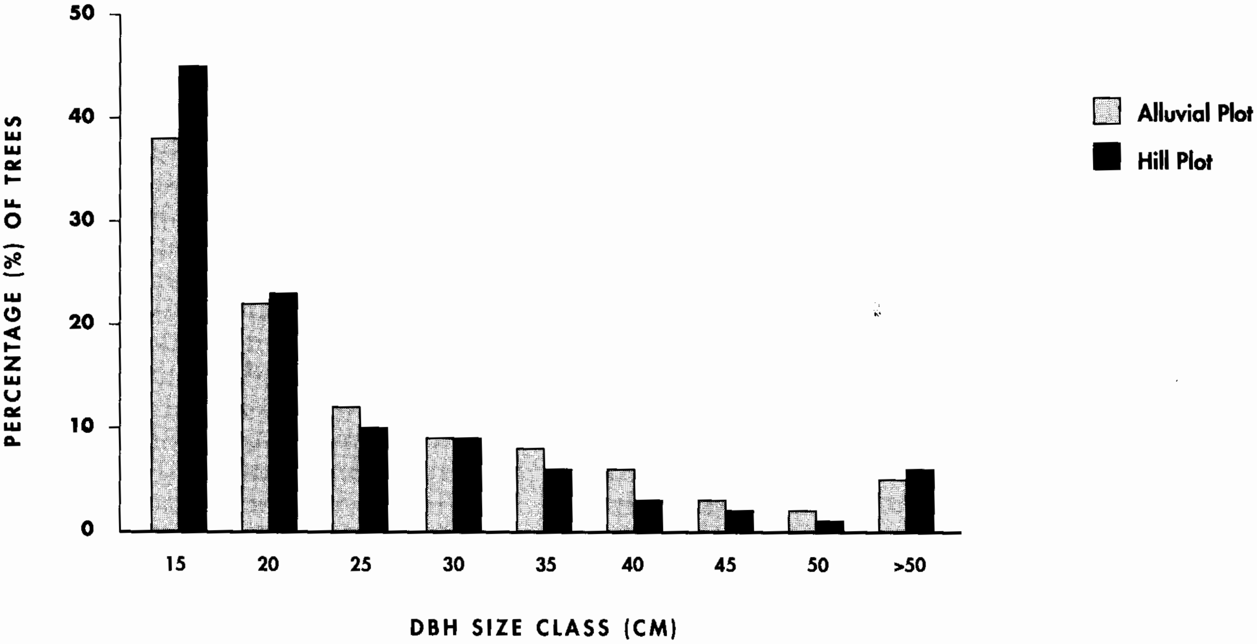
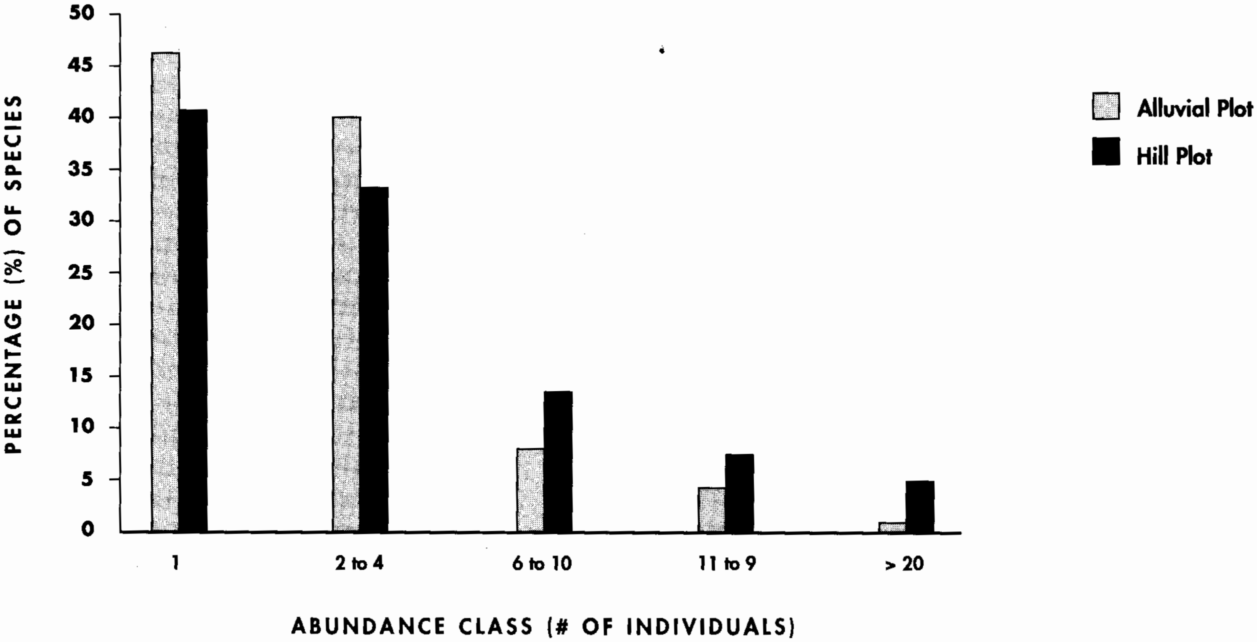


Figure 2. The percent of total species within a plot according to abundance classes. Abundance classes numbers of individuals ≥ 10 cm DBH representing a species within each plot. The two distributions did not differ significantly.



VEGETATION PART 2: BOTANICAL SURVEY (Wayne Takeuchi and Joel Kulang)

Chapter Summary

- About 450 species and morpho-species of vascular plants were recorded during the survey.
- Alluvial forest in the Basin is very species rich and comprised of a heterogeneous mosaic of different communities and various seral stages, with no strongly dominant species.
- The hill forest adjoining the Basin is less diverse than the alluvial forest and contains a suite of about ten dominant species.
- The frequency of natural disturbances in the alluvial forest, from windthrows and changes in river course contribute to the high diversity, heterogeneity and lack of dominance in the Basin, whereas the greater stability in the hill forest leads toward the opposite.
- There is an anomalous component of normally montane species descending to low elevations where they interface with the alluvial forest.
- The flora of the area has a strong component of local endemism and taxa confined to the Papuan (southern PNG) subregion; these taxa are poorly known, making the RAP collections particularly significant.
- There is little evidence of anthropogenic disturbance and few weedy, large-disturbance specialist species. The Lakekamu Basin has pristine wilderness vegetation, a condition that will soon be very rare globally.

Introduction

A botanical reconnaissance of the IRS study area was conducted between Oct. 14 and Nov. 12, 1996 by the principal author and two survey trainees. The team's primary responsibilities included species checklisting, collection of herbarium specimens, and *ad libitum* exploration. Our taxonomically-oriented activities were designed to complement the vegetation plots censused by a counterpart team and generate a preliminary floral description of the area.

Methods

Exploration and collections were made in all directions from the Ivimka Research Station sited on the Sapoi River. The reconnaissance followed established trails and the many stream channels in the study area. We spent 19 days working in alluvial and riverine forest and 9 days in the hill forest. Gatherings of fertile specimens were obtained for taxonomic study and field-pressed in 70% surgical alcohol for subsequent processing and determination at the Lae National Herbarium. Materials for exsiccatae were accompanied by numerous bottled, carpological, and xylarium accessory collections. Specimens were typically secured in multiple sets (up to 10) for principal distribution to Lae Herbarium (LAE), Botanical Research Institute of Texas (BRIT), Kew, Harvard University Herbaria, and Leiden. Residual duplicates will be distributed in accordance with the exchange protocols of LAE and BRIT. Common taxa already well-known to the lead botanist were simply checklisted as sight records.

Results and Discussion

Vegetation Description

Appendix 3 is a compilation of all sight enumerations and of species documented by actual collections. A total of about 450 morphospecies was recorded among vascular plants within the investigated elevational range from 100 m to 370 m.

From daily reconnaissance and collecting, a general impression was obtained of the vegetation around the base camp that corroborates the general findings from the vegetation plots. At the most basic level, there is a very obvious distinction between the alluvial forest on the Avi Avi-Sapoi flood plain and the foothill forest on the slopes above. The differences between the formations are structural as well as compositional. In comparative terms, the hill communities have lesser understory development and canopy stratification. Although there is noticeable intermixing of plant taxa, the hill forest seemed decidedly less rich than alluvial communities. At least on a local basis, hill canopies often exhibit frequency dominance by a suite of about 10 species (primarily a

Calophyllum complex with *C. euryphyllum, C. goniocarpum*, and *C. papuanum, Garcinia* sp., *Teijsmanniodendron ahernianum, Syzygium* spp., *Elaeocarpus sepikanus* and *E. blepharoceras*) and evoke a perception of homogeneity relative to the alluvial forest, where dominance relationships were not particularly apparent.

On the recent Hammermaster and Saunders (1995) forest classification, the Lakekamu mature-growth alluvial forests are primarily assignable to large to medium crowned forest, and open forest (structural codes Pl and Po respectively). Both forest types are low altitude (<1000 m) formations on plains and fans. Seral communities within the survey area are consistent with mixed riverine successions (code Fri). This latter category is represented by heterogeneous forest with many seral stages, and species composition is typically highly variable. Changes in streamcourse along meandering rivers are the major factor determining the character of such communities. Lowland forest classes Pl and Po are currently under consideration by the PNG Dept. of Environment and Conservation (DEC) for designation as logging exclusion zones, on account of the habitat value and damage susceptibility to logging of such forests (DEC 1996). The forest type represented by the Lakekamu successional communities are not regarded as requiring any sort of special designation or protection (ibid).

A conspicuous aspect of the Lakekamu regrowth phase is the collective rarity of plants usually common in disturbed environments. Taxa such as *Gouania, Mussaenda, Homalanthus, Commersonia, Melochia, etc.*, ordinarily prolific in anthropogenic habitats were typically present only as isolated individuals in the surveyed area, even in otherwise disturbed sites such as windthrows and riverbanks. Their infrequent occurrence suggests that disturbance conditions are spatially restricted and ephemeral, so that the recovery process ensues rapidly and the seral phases are quickly reset. Under such conditions, the weedy species characteristic of repetitively disturbed habitats never have an opportunity of becoming spatially dominant. When considered in conjunction with the structural characteristics of the forest, the image which emerges of this vegetation is that of a highly dynamic flora moving rapidly through maturational stages. The numerous treefalls and canopy opening events observed during the expedition support the notion of a latent ecosystem conditioned by unpredictable events.

The Lakekamu hill forest can be considered primarily medium-crowned forest on low altitude uplands (<1000 m) under Hammermaster and Saunders forest code Hm. Such communities are characterized by gradual transitions in floristic composition, with the interval below 500 m resembling large-to-medium crowned and open-forests (types like Pl and Po), and the elevations above 500 m being more similar to montane formations. This is probably the situation at the survey sites. However a significant permutation at Ivimka is the otherwise unexpected occurrence of montane genera such as *Rhododendron, Dimorphanthera, Rapanea, Zygogynum, Levieria, etc.* at descending elevations to the interface with alluvial plain. These seemingly anomalous occurrences may be indicative of some peculiarity in the Quaternary vegetational history of the Lakekamu flora, or alternatively, it may indicate just how little we know about the real ecological amplitude of these taxa.

In both the alluvial and hill environments, tree stocking densities and canopy heights varied considerably irrespective of forest type. Heavy rains were experienced during most of the expedition, but the amount of epiphytic growth was much less than what would otherwise be expected from such an apparently high-rainfall habitat. The fern and orchid flora was actually somewhat depauperate of species. Although hill substrates were consistently overlain with litter accumulations much thicker than the alluvial counterpart, this was likely a seasonal distinction rather than a characteristic structural feature.

The Lakekamu alluvial zone is clearly a composite of floristically differentiable communities. Forest sections immediately adjacent to rivers have species frequencies distinct from interior stands, in spite of the commonly shared taxa. Even within the forest proper however, there is discernable fragmentation in community structure. The large number of windthrows seen during

A conspicuous aspect of the Lakekamu regrowth phase is the collective rarity of plants usually common in disturbed environments.

the survey indicate that seral clusters of even-aged cohorts are typically establishing in scattershot fashion throughout the forest matrix. With maturation of the gap communities, a rotating spatial mosaic is collectively composed by the various cohort populations, each in its own particular dynamic phase.

The variation in spatial scale of community organization (as evidenced from tree densities, canopy development, species composition, *etc.*) suggests the parallel existence of disturbance mechanisms of complementary scale to the floristic variation. At one end of the spectrum are small-area successions resulting from individual windthrows and the breakage of large tree limbs. However, storms of progressive intensity would be expected to produce gaps of increasing size and continuity. Large shifts in streamcourse could also produce area-extensive displacements. The forest section along the trail/trapline opposite the 3k transect might be an example of such larger-scale past disturbance. Over time, the sequential occurrence of forest upsets with differing extension would be expected to superimpose on each other in random fashion. The cumulative result would be a heterogeneous forest with a confusing successional mixture of component parts. This may be the etiology for the Lakekamu alluvial mosaic, especially if substrate patterns cannot be linked to the aboveground patterns.

In contrast to the flood plain vegetation, hill forest within the surveyed area (to 370 m elevation) does not show signs of dynamic turnover to the same extent as the flatland. This comparative stability is accompanied by an apparent reduction in overall richness.

Supposed distinctions in forest quality derived from casual observation need to be confirmed empirically with systematic sampling. The two one-hectare plots of the RAP survey corroborate many general impressions, but more extensive sampling is recommended. A study program preceded by extensive reconnaissance and community entitation is suggested, to be followed by central placement of various releves or hectare plots within the entited units. Community separations could be thereby defined more closely, though the dynamic relationship between forest units can only be resolved by long-term tracking.

Phenological Patterns

Mass and synchronized flowering was noted during the survey for taxa in *Barringtonia, Calophyllum, Dimorphanthera, Dysoxylum, Garcinia, Grenacheria, Metrosideros, Neisosperma, Pternandra, Syzygium,* and *Timonius.* Periods of peak flowering and anthesis were typically very brief, sometimes lasting only a few days. Most plant species exhibited erratic flowering phenology, with populations exhibiting a full range of unsynchronized states. However even with the apparent randomly-behaving taxa, a commonly seen pattern was the occurrence of flowering trees in clusters, though conspecific individuals short distances away might be entirely sterile.

Extensive germinant and seedling crops were noted for *Calophyllum* in hill forest. With the exception of *Calophyllum*, mature understories were largely clear of germinant flushes, suggesting that canopy opening is otherwise necessary for germination of tree taxa.

Phenological patterns were difficult to assess on an impressionistic basis due to the selectivity of human observation. Attention is naturally drawn to fertile specimens, so the perceived proportion of fertile individuals from a population can be easily overstated. Objective sampling protocols need to be established to provide reliable data for ecological applications such as animal-plant interactions.

Botanical and Conservation Significance of the Lakekamu Tract

Botanists on rapid-format surveys work at a unique disadvantage relative to their zoological-study counterparts. Faunistic enumerations can occur by visual or auditory record, and captures need not be gravid to be identifiable but botanical specimens typically require fertile structures in order to be reliably named. This distinction applies especially to species-rich plant groups. Unfortunately, the large families are exactly where botanical records of greatest conservation and biological significance are likely to be secured.

The percentage coverage which the survey has achieved of the Lakekamu flora is of course unknown. Many taxa with unfamiliar vegetative features were seen throughout the survey, but could not be collected in fertile condition. Our gatherings probably encompass only a minor percentage of the aggregate flora, but it is worth noting that a substantial number of new taxa and records were nonetheless obtained. If such a comparatively small sample can yield significant results, the potential for further discovery is certainly even greater. The best finds have yet to be made, and there is much scope for future exploration.

Approximately 400 exsiccatae numbers were made during the RAP survey, and the most significant discoveries have been summarized in Appendix 4. Plants previously unknown to science, rare taxa, distributional and range extension records have all been documented by the collections.

A curious aspect of the discoveries from Lakekamu is that most of the new records represent taxa common in the survey area. This circumstance is a reflection of the low botanical collection density for PNG in general and for the Papuan territories specifically, a situation allowing even high-visibility taxa to remain undetected. At Lae Herbarium, the number of specimens from Gulf Province is among the lowest from any district. In the post-Independence period, concentration of the national infrastructure in forestry and botany to Morobe Province has indirectly contributed to a comparative neglect of the Papuan flora. The selection of Lakekamu as a survey site was thus especially appropriate, and further efforts directed to the southern side should continue to produce disproportionate returns.

Ecologically, the Lakekamu tract shows considerable promise as a research venue due to its natural-growth status and the rich mixture of closely juxtaposed seral communities. This area would be very suitable for investigations into the dynamics of the Papuan lowland forest and for evaluating connections between environmental latency and floristic diversity. The unusual elevational occurrences are also rather provocative and deserving of further inquiry.

The Lakekamu flora could support intensive taxonomic study on a number of plant groups. From impressions obtained during the survey, families Annonaceae, Euphorbiaceae and Clusiaceae (Guttiferae) are appropriate subjects for specialist examination, being composed of diverse and numerically prominent representatives. Generic limits are inadequately defined in Annonaceae (only Sapotaceae and Lauraceae are in comparable disarray), and the species rich Lakekamu assemblage would serve as an excellent subject for detailed study.

INSECTS PART 1: THE SOCIAL HYMENOPTERA (Roy R. Snelling)

Chapter Summary

- Social Hymenoptera (Apidae, Formicidae, and Vespidae) were surveyed 20 October to 8 December, 1996 using a variety of techniques (active searching for individuals and nests, Malaise traps, litter sifting, and baiting).
- A total of 281 species of social Hymenoptera were collected, represented by approximately 3000 specimens; 254 of these species belong one family, the Formicidae (ants).
- About twenty-two species collected represent new, undescribed species and one represents a new genus.

Introduction

The social Hymenoptera (ants, bees, and wasps) are an influential part of the biotic environment in New Guinea, as they are in most tropical rain forests. In both absolute numbers and biomass the social Hymenoptera, especially ants, often dominate arthropod faunas of tropical rainforests, both in the canopy and on the ground (Davidson 1997; Wilson 1987). It is estimated that about one-third of the entire animal biomass of the Amazonian *terra firme* rain forest is composed of ants and termites and that, along with bees and wasps, these insects comprise more than 75% of the total insect biomass (Fittkau and Klinge 1973). Other studies have suggested that much the same is true