A comparison of the structure and composition of montane and lowland tropical forest in the Serranía Pilón Lajas, Beni, Bolivia.

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ABSTRACT

A quantitative inventory is reported for two one hectare permanent plots established in the Serranía Pilón Lajas in Beni, Bolivia. The floristic diversity, as measured by tree species with diameter at breast height greater than 10 cm, was documented at 78 species/ha for the plot established on the piedmont at 270 m above sea level (Río Colorado) and at 146 species/ha for the plot established on the crest of the serranía at 900 m (Cumbre Pilón). The structure of the two plots fall within the range of values reported for mature humid tropical forest associations with 588 and 647 trees/ha and a total basal area of 26.4 and 30.6 m^2/ha for Río Colorado and Cumbre Pilón respectively. The floristic composition between the two sites was moderately similar with 25 species in common, but differences in the abundance of individual species revealed greater differences. The Río Colorado plot was dominated by the palm *Iriartea deltoidea* and a widespread species in the Moraceae, *Pseudolmedia laevis*. The Cumbre Pilón was not dominated by any particular species, but the genus Inga was particularly diverse, as was the Rubiaceae, characteristics typical of the Andean montane forest formations. Both plots showed considerable floristic similarity with other inventories conducted in lowland tropical forest in adjacent regions of Bolivia. Sixty species are identified as being regionally common; these species were shown to be widely distributed taxa with distributions throughout western Amazonia.

INTRODUCTION

Quantitative floristic inventories based on one hectare permanent plots have been used in recent years to characterize forest vegetation throughout the tropics. Typically, investigators are interested in documenting the structure and floristic composition of forest communities. Recently, permanent plots have been used to address changes that may be occurring in tropical ecosystems due to climate change (Phillips and Gentry, 1994) and their value as a tool in environmental monitoring programs is widely recognized. The first such study in Bolivia was conducted by Boom

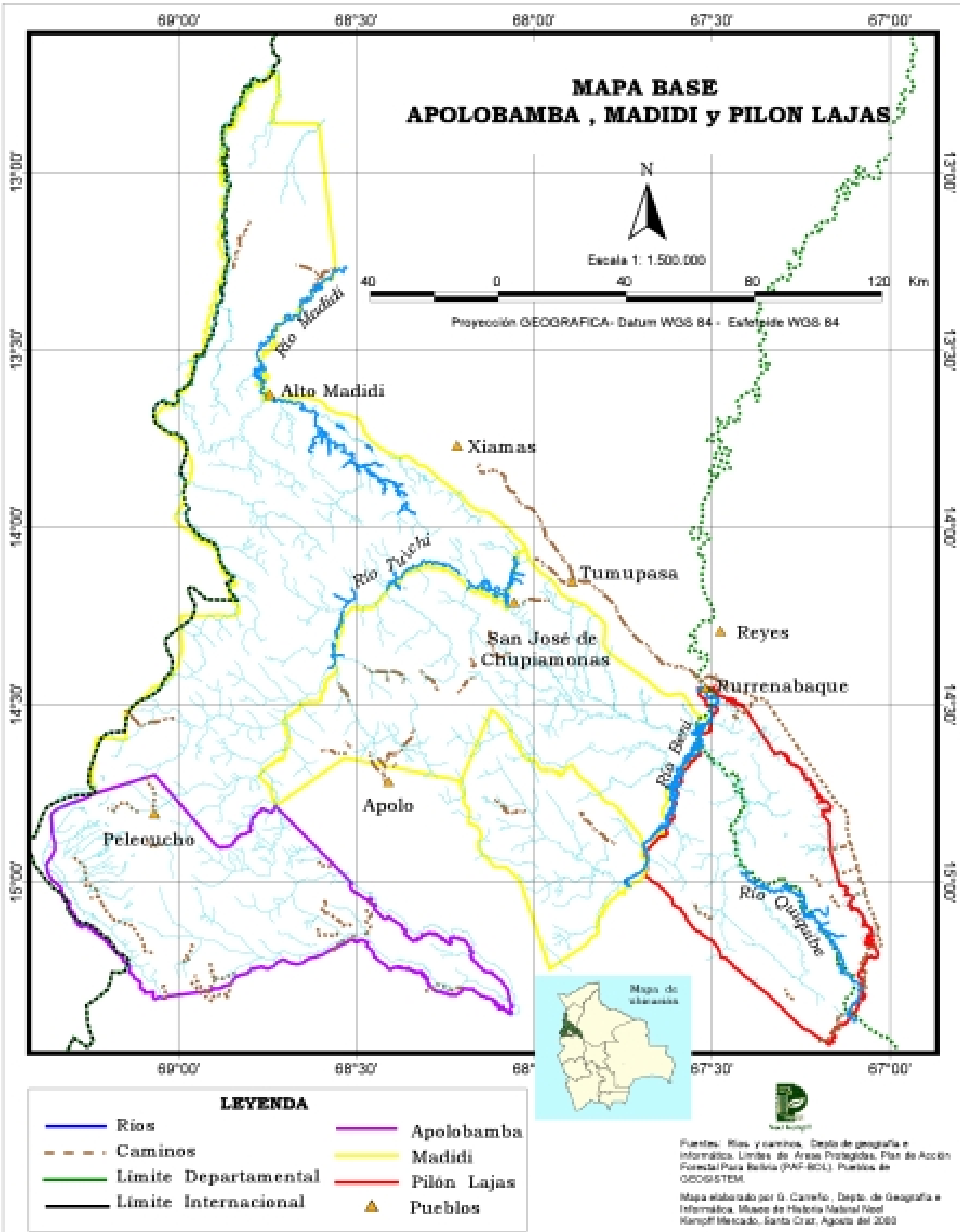
(1986) who sampled a “tierra firme” forest in northern Beni as part of an ethnobotanical study of the Chácobo indigenous group. Subsequent inventories in other parts of the Beni (de Aguila, 1995) and Santa Cruz (Vargas et al. 1994; Vargas, 1995) have contributed to the knowledge of the tropical forest formations in Bolivia. Several other studies are currently underway and the possibility for making biogeographical or phytosociological comparisons based on specimen-based, quantitative inventories is increasingly possible. This report provides data for two permanent plots established on the Serranía Pilón Lajas that was undertaken as part of a dendrological inventory of the region conducted between 1988 and 1992. The structure and composition is documented for a humid montane forest located on the crest of the serranía at 900 m and a humid lowland forest situated on the piedmont at 270 m above sea level (Figure 1).

STUDY AREA

The Serranía Pilón Lajas consists of a low mountain ridge that has a maximum elevation between 800 and 1200 m; the adjacent piedmont and the intermontane valley are between 300 and 500 m in elevation. Pilón Lajas is part of the geological region designated as the Faja Subandina (subandean strip) and is one of several parallel ridges that are oriented from the southeast to the northwest. These low mountain ranges are composed of Ordovician, Silurian, and Cretaceous sandstone, shale, and mudstone (Oblitas and Brockmann, 1978). The Quiquibey valley located to the southwest of the serranía is a syncline and its eastern escarpment is essentially a truncated anticline that is much more precipitous in comparison to the western slope. The soils on the piedmont are moderately deep, ranging from sandy loam to clay ultisols and entisols that are derived from Quaternary sediments with low to moderate levels of fertility; pH values range from 4.8 to 6.0. The upper soil horizons are generally well-drained, but many sites have a mottled B horizon indicating that these soils are saturated periodically. The soils on the serranía are extremely variable depending upon slope; in general, they are loamy clays that are slightly acidic to alkaline and range from entisols to oxisols (Merlot et al., 1994).

The climate of the area is humid to very humid with a mean annual precipitation of 2550 mm and a mean annual temperature of 25.9° C reported for Rurrenabaque, a small town located on the piedmont just north of the study area on the Beni River (Hanagarth, 1993). The rainy season extends from November to April, while the driest months of the year are July, August, and September. The area, like the rest of lowland Bolivia, experiences strong cold fronts during the austral winter and temperatures as low as 8° C have been recorded during the month of July. Although precise measurements do not exist, precipitation undoubtedly increases with increasing altitude while temperatures decrease.

The natural vegetation of the zone is humid tropical forest that changes in composition and structure according to elevation. The forest on the piedmont has been



classified as a humid lowland forest, while the forest formations on the ridges has been designated as montane humid forest (Beck et al., 1993). These forest formations are composed of different plant associations that relate to changes in soil, humidity, and successional state. On the piedmont, there are examples of forest types with impeded drainage and approximately 25 km to the East are the inundated savannas of San Borja and Reyes which are part of the vast wetland complex of the Llanos de Moxos. The vegetation on the Serranía Pilón Lajas is a patchwork of different communities; landslides are common and a casual observer with the assistance of binoculars can distinguish a patchwork of plant communities in different successional stages. The fauna in the area is both interesting and diverse; although inventories are preliminary, numerous endemic and endangered species are known to exist in the area or in adjacent regions (Emmons, 1991; Merlot et al., 1994).

Land-use in the area is changing due to individuals practicing shifting agriculture. The areas most heavily affected by these activities are adjacent to a highway that was constructed between 1984 and 1991. In 1992 the Bolivian government declared much of the region as an indigenous territory, as well as recognizing the area as a Biosphere Reserve: (Figure 1). Currently, efforts are underway to organize a management framework for the protected area that includes participation of the indigenous groups, colonist communities, and conservation organizations (Merlot et al., 1994).

METHODS

The studies were conducted in two one hectare permanent plots according to the guidelines outlined by Campbell (1989); field work was conducted in 1990 and 1991. In each plot, all trees with a diameter at 1.3 m (diameter breast height or "dbh") greater or equal to 10 cm were tagged, measured, identified, and catalogued. Trees with buttressed trunks or stilt roots were measured 20 cm above these structures. Each tree was marked with a consecutively numbered aluminum tree tag that was nailed 10 cm above the point of measurement. The total height of the tree was estimated visually; trees that straddled the boundaries of subplots were included if the midpoint was situated within the plot. Voucher collections were made for each species; individual trees that could be unequivocally identified in the field were not recollected. Identification of species was made by comparison of voucher specimens to fertile material collected throughout the course of the project. General collections have been distributed to LPB, MO, USZ, and BOLV, as well as a variety of other institutions; voucher specimens are deposited at LPB and MO.

The first plot was established on the piedmont in a forest remnant at the Colegio Técnico Agropecuario Río Colorado, a secondary school situated 35 km north of Yucumo on the highway to Rurrenebaque (Figure 1). The plot is a 100 x 100 m square composed of twenty five 20 x 20 m subplots; it is situated approximately 5 km to the northeast of the school campus facilities on a non-inundated terrace adjacent to the Río Colorado (14°55′S; 67°05′W; 270 m above sea level). According to local sources no previous agricultural or lumber extraction had occurred in the immediate vicinity of the study site in recent memory. The "Río Colorado" plot can be relocated by asking for assistance from the school administrators who have promised to maintain it as a long-term study sight; the boundaries of the plot are the four cardinal directions.

The second plot was located just below and to the northeast of the crest of the Serranía Pilón Lajas near the pass (or "cumbre") between the Quiquibey bridge and the community of Yucumo. The plot has an idiosyncratic design that reflects local topography, but essentially is L-shaped with one leg running downslope along a ridge and a second perpendicular leg that is situated on a terrace below a massive sandstone cliff (15°15′S; 67°00′W; 850-950 m). The soils ranged from superficial and rocky to locally deep in restricted spots; in general they were red and well drained. The "Cumbre Pilón" plot can be relocated by driving 24 km from Yucumo towards the Quiquibey bridge. The plot is situated approximately 1 km to the East of the highest point of the pass; the trail is situated to the left when facing towards the Quiquibey bridge and crosses a field of large boulders. The integrity of this plot as a long term study site has been compromised by subsequent tree felling by colonists; in addition, a large, natural mud-slide occurred during the 1992 rainy season and destroyed the vegetation in approximately 5 subplots.

Plot data was summarized according tothe stantard protocols (Cambpell, 1989): abundance or density is the number of trees registered in the plots, frequency is the number of subplots in which a single species has been recorded, and basal area is the sum of the cross-sectional areas of all the stems for each individual species as calculated from dbh values. These summary statistics are in turn used to calculate percentage values based on the totals for each individual parameter summed over all species. These percentage values are traditionally used for making comparison with other sites and are expressed as relative density, relative frequency and relative dominance. A single summary statistic or "importance value," is calculated by summing the three relative values. A family importance index is calculated in a similar fashion by summing the values for all species within a family; however, frequency data is excluded and a relative diversity value is employed that is based on the number of species for a specific family as a percentage of the total number of species.

RESULTS

The structure of the forest vegetation is represented in Figure 2. The number of individual plants in the different dbh size classes shows that both localities have the typical inverted J curve where abundance decreases with increasing diameter. Nonetheless, the two plots are markedly different with respect to the abundance of trees with different diameters. Although both plots were selected as being representative of "high forest," Río Colorado has more large trees when compared to Cumbre Pilón. This is demonstrated by a larger number of individuals with a dbh greater than 80 cm and, most noticeable, by the presence of a single very large tree (*Hura crepitans*) with a dbh of 162 cm at Río Colorado. Nonetheless, the Cumbre Pilón plot shows greater total basal area due to a higher total density of individual trees (see

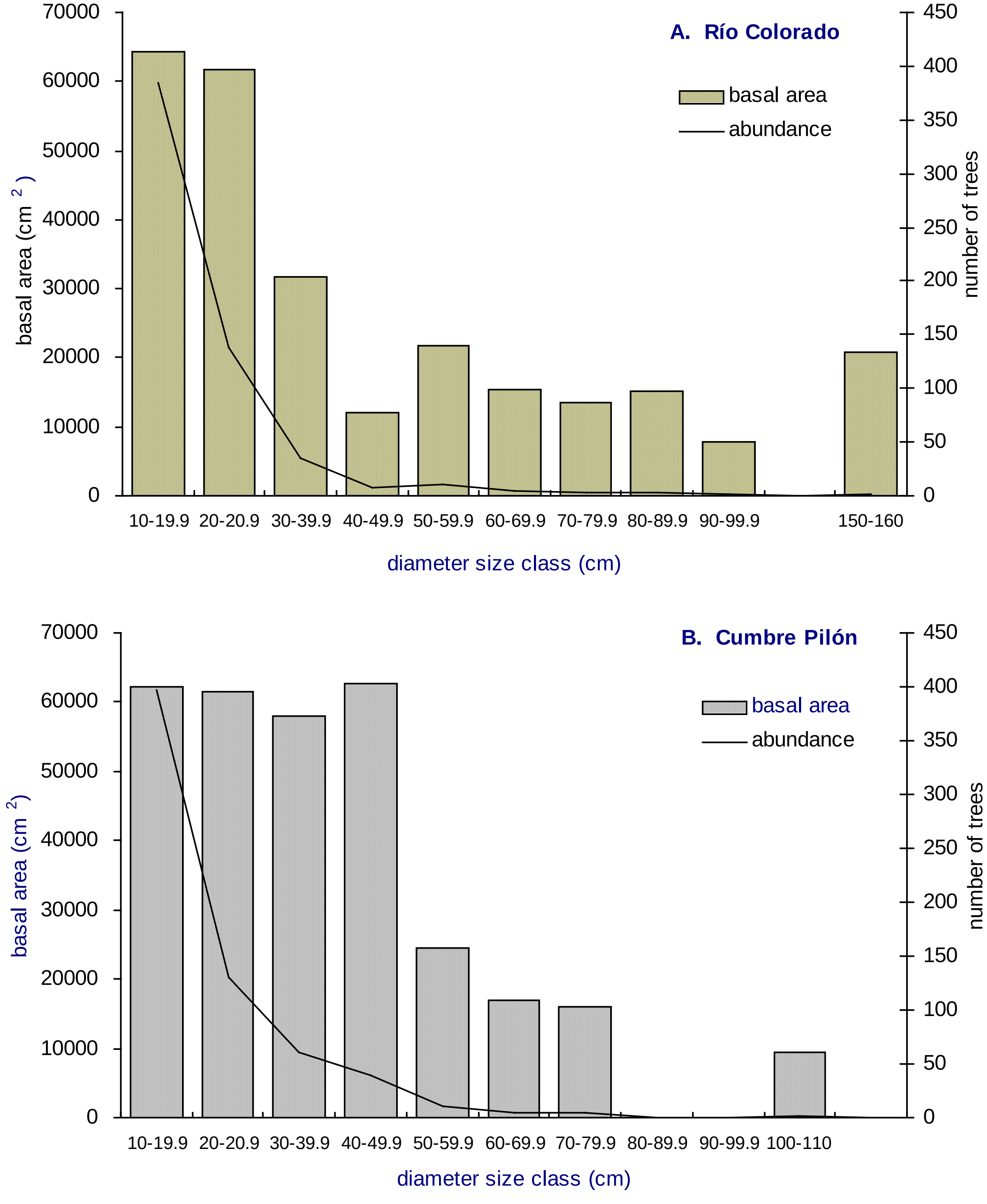


Figure 2. The structure of two one hectare plots on the Serranía Pilón Lajas, Beni, Bolivia. A) Río Colorado at 270 m and B) Cumbre Pilón at 800-900 m elevation. Abundance is represented by the line that is plotted against the right axis; basal area is represnted as a histogram that corresponds to the left axis; x axis values are size class categories based on diameter at breast height (dbh).

Appendix), as well as a greater number of trees in the mid-class size range between 30 and 60 cm in diameter (Figure 2).

The relationship between the area sampled and the number of species encountered is presented in Figure 3. The slope of the species-area curve approaches zero at approximately the 19th subplot for the Río Colorado plot, thus indicating that a one hectare sample was sufficient to characterize the structure and composition of this locality. Nonetheless, like most tropical forest sites continued sampling revealed additional taxa; common widespread species such as _Swietenia_ _macrophylla_ and _Cariniana_ _estrellensis_ were observed within 100 m of the sample plot. The greater species richness of the Cumbre Pilón plot is clearly demonstrated in Figure 3 and this trend was apparent at small sample sizes. The slope of the species-area curve does not approach zero and further sampling would be necessary for a reliable inventory of this forest type. The absolute values for abundance, frequency, and basal area for individual species for the two plots are presented in the Appendix.

The ten most important species at the Río Colorado plot are presented in Table 1. The two most important species are also the two most abundant species, _Iriartea_ _deltoidea_ and _Pseudolmedia_ _laevis_; together these two species represent 28.4% of the total number of trees within the plot. In contrast, a total of 32 species or 41% of the total are represented by a single individual. The relationship between frequency and abundance is pronounced with a r = 0.89, while the correlation between abundance and dominance is r = 0.70. As such, the importance value essentially provides a measure of abundance that is weighted for species with very large trees. Evaluation of the plot data

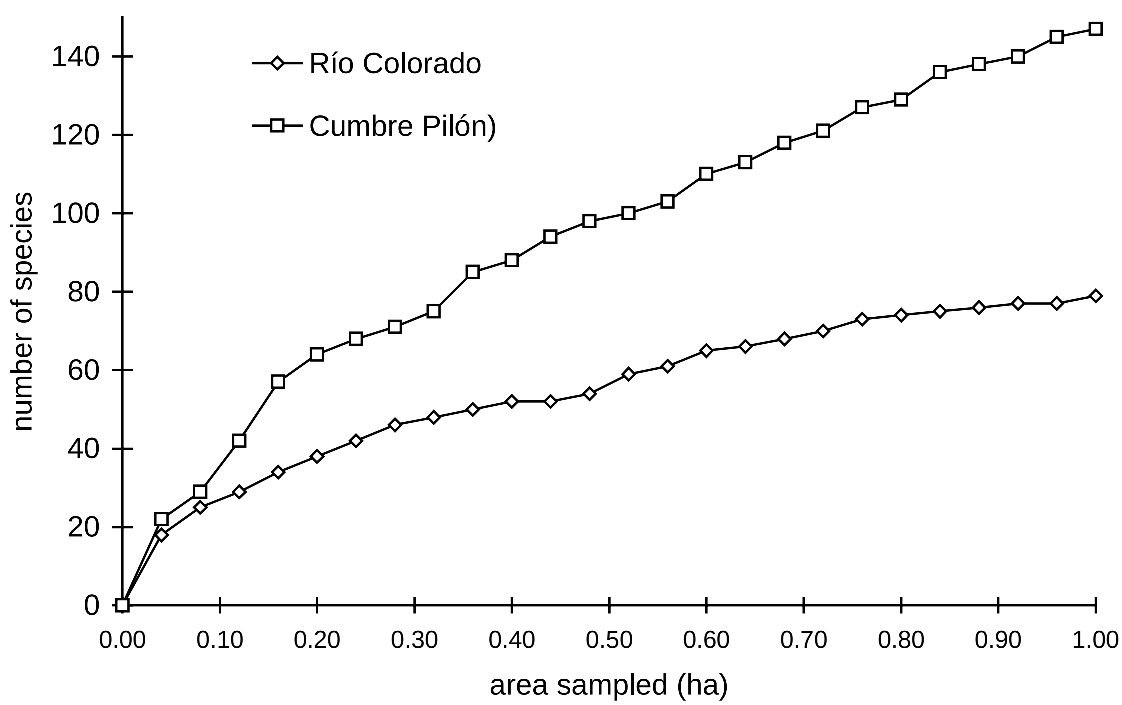


Figure 3. The relationship between tree diversity and sample area for trees with dbh ≥ 10 cm dbh for two one hectare plots on the Serranía Pilón Lajas.

for individual species can, in some cases, permit the classification of specific species into a emergent, canopy, subcanopy, or understory trees. *Hura crepitans*, *Spondias venosa*, *Sapium marmierii*, *Poulsenia armata*, and *Ficus killipii* were emergents species. Most large trees were represented by only a few individuals, but *Sapium marmierii* and *Poulsenia armata* were represented in all class sizes. Palms were the most conspicuous elements of the canopy and subcanopy strata, as well as several species in the Annonaceae, Lauraceae, and Moraceae. Common understory trees were Lunania parviflora and Salacia macrantha; the most common understory plants were shrubs in the Rubiaceae and Melastomataceae that did not meet the measurement criteria of 10 cm dbh. The most important family in the Río Colorado plot was the Moraceae, which was the most diverse of all the families, as well as the most dominant (Table 2). Other diverse families were the Palmae, Lauraceae, and Annonaceae. The Euphorbiaceae was ranked as important due largely to three individuals of *Hura crepitans* with large diameters. This species has been characterized as a pioneer species that requires high light intensity for canopy recruitment (T. Gullison, pers. comm.). Since *H. crepitans* was not recorded in the small diameter size-classes, this provides supporting evidence for the supposition that this study site was a mature forest community with little previous disturbance.

Table 1. The ten most important species in a one hectare permanent plot at the “Cumbre Pilón” in the Serranía Pilón Lajas, Beni Bolivia; the relative values are calculated as a percentage based on the summed values for all species for abundance, frequencies, and basal area; the importance value is a sum of the relative values.

Species	Abundance	Frequency	Basal area (cm^2)	Relative density	Relative frequency	Relative dominance	Importance value
Iriartea deltoidea	93	22	27,177	15.82	6.38	10.29	32.48
Pseudolmedia laevis	74	23	21,791	12.59	6.67	8.25	27.50
Poulsenia armata	24	15	22,981	4.08	4.35	8.70	17.13
Astrocaryum murumuru	37	21	8,653	6.29	6.09	3.28	15.66
Sorocea cf. pileata	31	19	8,880	5.27	5.51	3.36	14.14
Sapium marmierii	19	9	21,082	3.23	2.61	7.98	13.82
Hura crepitans	3	3	30,338	0.51	0.87	11.49	12.87
Euterpe precatoria	21	15	4,314	3.57	4.35	1.63	9.55
Celtis schippii	18	13	5,475	3.06	3.77	2.07	8.90
Inga tomentosa	17	11	4,060	2.89	3.19	1.54	7.62
Subtotals	**337**	**151**	**154,752**	**57.31**	**43.79**	**58.59**	**159.67**
Other species	310	195	109,317	42.69	56.99	41.41	140.33
Totals	**588**	**345**	**264,067**	**100.00**	**100.00**	**100.00**	**300.00**

The Cumbre Pilón plot has four species that are ranked as of approximately equal importance (Table 3); together they represent 17.5% of the total number of trees found in that plot. In contrast to the Río Colorado plot, the occurrence of species represented by a single individual was even greater (56%). The four species with a largest basal area (*Poulsenia armata*, *Tetragastris mucronata*, *Dendropanax arboreum*, and *Sapium glandulosum*) are characterized by having numerous stems that also have relatively large diameters. The tallest trees in the plot (i.e., > 35 m tall) were *Poulsenia armata*, *Tetragastris mucronata*, *Terminalia amazonica*, *Terminalia oblonga*, *Myroxylon balsamum*, *Pterocarpus amazonum*, *Inga nobilis*, *Swartzia* cf. *jorori*, *Clarisia* racemosum, Clarisia biflora, Helicostylis sp., Otoba parviflora, Virola peruvianum, Pouteria krukovii, and Ampelocera ruizii. The subcanopy and understory was dominated by Hasseltia floribunda and two species of Allophylus. The most important family in the plot was the Leguminosae with a total of 25 species and large values for abundance and basal area. The most diverse genus was Inga with a total of 11 species. Other diverse families were the Moraceae, Rubiaceae, Sapotaceae, Myrtaceae, Euphorbiaceae, Lauraceae, and Meliaceae, while the Burseraceae, Flacourtiaceae, Sapindaceae and Araliaceae had high importance values due to the relative abundance of one or two species (Table 2).

Table 2. The species diversity and importance values for the families of trees collected in two one hectare permanent plots established in the Serranía Pilón Lajas; the FIV or family importance value is the sum of the relative values for diversity, abundance and dominance (basal areas).

Family	Río Colorado		Cumbre Pilón	
	# Species	FIV	# Species	FIV
Anacardiaceae	1	4.72	1	3.46
Annonaceae	6	16.57	4	7.19
Apocynaceae	-	-	1	2.28
Araliaceae	2	3.54	1	9.27
Bombacaceae	1	1.79	1	0.88
Boraginaceae	-	-	1	0.87
Burseraceae	2	6.53	2	12.46
Caricaceae	1	2.10	-	-
Celastraceae	-	-	1	2.11
Chrysobalanaceae	1	5.38	2	2.19
Combretaceae	-	-	2	3.41
Elaeocarpaceae	1	4.32	2	4.95
Eupborbiaceae	2	25.74	7	17.70
Flacourtiaceae	2	5.12	3	11.87
Guttiferae	-	-	3	5.81
Hippocrataceae	1	2.33	-	-
Lauraceae	8	13.20	9	14.18
Lecythidaceae	-	-	1	0.90
Leguminosae	4	11.14	25	41.90
Mimosoideae	(2)	(7.14)	(14)	(21.06)
Papilionoideae	(2)	(4.01)	(11)	(20.84)
Malpighiaceae	-	-	2	1.91
Melastomataceae	-	-	3	2.78
Meliaceae	5	11.72	8	12.55
Moraceae	12	71.77	13	39.24
Myristicaceae	2	4.59	3	5.04
Myrtaceae	1	1.45	7	7.46
Myrsinaceae	1	1.67	1	1.27
Nyctaginaceae	2	5.63	3	5.58
Palmae	7	57.84	1	3.54
Polygonaceae	2	4.16	3	6.06

Rosaceae	-	-	1	0.98
Rubiaceae	1	1.55	14	18.49
Rutaceae	1	1.45	1	0.93
Sapindaceae	1	2.26	4	11.28
Sapotaceae	-	-	7	15.43
Solanaceae	1	1.93	-	-
Sterculiaceae	2	4.00	1	3.46
Tiliaceae	1	5.45	2	4.89
Ulmaceae	3	10.81	1	6.04
Urticaceae	1	2.41	1	4.92
Verbenaceae	1	2.16	2	2.14
Violaceae	1	1.66	2	2.16
indet	1	1.76	1	1.13
indet	1	1.50	1	0.87
indet	1	1.48	-	-
Total	146		78	

Table 3. The ten most important species in a one hectare permanent plot at the "Cumbre Pilón" in the Serranía Pilón Lajas, Beni Bolivia; the relative values are calculated as a percentage based on the summed values for all species for abundance, frequencies, and basal area; the importance value is a sum of the relative values.

Species	Abundance	Frequency	Basal area (cm^2)	Relative density	Relative frequency	Relative dominance	Importance value
Tetragastris mucronata	31	16	18,669	4.79	3.21	6.10	14.09
Poulsenia armata	18	13	24,235	2.78	2.61	7.91	13.30
Dendropanax arboreaus	26	19	14,076	4.02	3.81	4.60	12.42
Hasseltia floribunda	38	19	8,236	5.87	3.81	2.69	12.37
Ampelocera ruizii	15	11	9,364	2.32	2.20	3.06	7.58
Sapium cf. glandulosum	12	9	10,628	1.85	1.80	3.47	7.13
Allophylus cf. petiolatus	22	12	3,493	3.40	2.40	1.14	6.95
Clarisia racemosa	11	9	9,391	1.70	1.80	3.07	6.57
Myriocarpus stipitatus	21	11	3,069	3.25	2.20	1.00	6.45
Helicostylis sp.	11	9	8,430	1.70	1.80	2.75	6.26
Subtotals	**205**	**128**	**109,591**	**31.79**	**25.65**	**35.79**	**93.23**
Other species	442	371	196,612	68.31	74.35	64.21	206.87
Totals	**647**	**499**	**306,203**	**100.00**	**100.00**	**100.00**	**300.00**

DISCUSSION

Table 4 shows the total values for the two sites and compares them with selected other localities in the Neotropics. Both forest communities fall within the range of tropical forest associations with respect to tree density and total basal area. The piedmont plot was most notable for the abundance and diversity of palm species, a phenomenon that is not infrequent in lowland forest communities; in contrast, palms are typically less common at higher elevations (Gentry, 1992). Atypical, is the low diversity and abundance of the Leguminosae at Río Colorado, a family that is usually ranked as the most diverse in lowland forest inventories (Gentry, 1988a, 1992). The Moraceae was important on both plots, as were the Annonaceae, Lauraceae, Euphorbiaceae, and Meliaceae. The Rubiaceae was particularly diverse at the Cumbre Pilón plot; several genera were present that are considered to be characteristic of montane forests, particularly *Cinchona*, *Ladenbergia*, *Macrocnemum*, *Coussarea*, and *Alibertia*. The Serranía Pilón Lajas is blanketed in clouds during the rainy season; nonetheless, the forest lacks taxa such as *Weinmannia*, *Podocarpus*, *Juglans*, *Oreopanax*, and *Clethra* that are common at higher elevations in cloud forest formations in other parts of Bolivia (Vargas, 1995; Beck & Smith, 1995). An undescribed species in the genus *Berrya* Roxb. occurred at both sites, but was more common on the piedmont; this species is apparently endemic to premontane forests in this part of Bolivia and adjacent Peru (A. Gentry, pers. com.). *Berrya* was previously thought to be a genus restricted to Asia, but it is closely related and possibly not distinct from the Caribbean and African taxon *Carpodiptera* Burret. The description of this new species awaits the collection of sufficient fertile material to ensure its appropriate classification.

Table 4. A comparison of one hectare forest inventories established in humid tropical forest on well-drained soils at selected localities in South America; only data for trees ≥ 10 cm diameter is presented.

Locality	Source	Number of trees	Basal Area (m^2)	Number of families	Number of genera	Number of species
Bolivia						
Cumbre Pilón	this study	647	30.62	37	92	146
Río Colorado	this study	588	26.40	31	64	78
Bosque Chimanes (Beni)	de Aguila (1995)	582	25.59	32	63	78
Amboró, Río Saguayo (Santa Cruz)	Vargas (1995)	506	39.20	31	58	67
Perseverancia (Santa Cruz)	Vargas et al. (1994)	597	23.38	36	69	90
Noel Kempff Park -1 (Santa Cruz)	Saldias et al. (1994)	653	34.01	32	51	75
Noel Kempff Park -2 (Santa Cruz)	Saldias et al. (1994)	606	25.16	33	61	94
Alto Ivón (Beni)	Boom (1986)	649	21.48	28	63	94
Selected Other Localites						
Añangu (Ecuador)[1]	Balslev et al. (1987)	728	33.70	53	141	228
Jatun Sacha (Ecuador)	Neill & Palacios (ms.)	724	30.53	47	128	246
Yanamono (Peru)	Gentry (1988a)	580		58		283
Mishana (Peru)	Gentry (1988b)	842		50		275
Tambopata (Peru)	Gentry (1988b)	602		42		155
Rio Xingú - 1 (Brazil)	Campbell et al. (1986)	393	27.63	33	76	133
Rio Xingú - 2 (Brazil)	Campbell et al. (1986)	567	32.14	33	83	162
Rio Xingú - 3 (Brazil)	Campbell et al. (1986)	460	28.27	33	72	118

1. Based on point-center transects transformed to hectare values.

Gentry (1995) has shown that montane forest up to 1500 m are similar to lowland forest both in terms of diversity and composition. The data presented here supports that hypothesis in part. A comparison of the species composition of these two plots with recently conducted inventories in humid forest on the Andean piedmont in Santa Cruz (Vargas, 1995) and the adjacent alluvial plain of the Beni (de Aguila, 1995) reveals that 60 species occur at least at two of the four study sites (Table 5). Although the number of shared taxa between the montane sight and the lowland sites are approximately the same, the calculation of an index weighted for unequal sample sizes shows that the lowland plots are more similar to each other than they are to the montane forest plot is (Table 6). The lower values are due to the greater diversity of the montane forest community, which incorporates most of the lowland taxa, as well as a variety of montane forest taxa that are absent from the lowland sites. The differences between the montane and lowland plots are even more pronounced when the abundance values of individual species are used for calculating the similarity index. This reflects the fact that the most abundant species in the montane plots are different from the three lowland plots, while the most abundant species in three lowland plots tend to be the same.

Table 5. Species occurring at two or more plot localities in the premontane or lowland humid forest region of Bolivia; values are the number of trees found in a one hectare plot. Plot localities are as indicated in Table 4; an * indictes the species is known to exist in Ecuador (Neill and Palacios, 1989) or has been cited in unpublished checklists for the indicated region.				
Families—Species	Cumbre Pilón	Río Colorado	Bosque Chimanes	Río Saguayo
Anacardiaceae				
—*Tapirira guianensis*	-	4	7	*
Annonaceae				
—*Cremastosperma leiophyllum*	15	-	-	1
—*Ruizodendron ovale*	1			36
—*Unonopsis mathewsii*	-	7	83	-
—*Xylopia benthamii*	-	1	-	1
Apocynaceae				
—*Aspidosperma rigidum*	5	*	1	2
Araliaceae				
—*Dendropanax arboreus*	26	1	6	1
—*Didymopanax morototoni*	-	1	*	*
Bombacaceae				
—*Chorisia speciosa*	-	*	2	3
Burseraceae				
—*Protium sagotianum*	1	17	26	-
Chysobalanaceae				
—*Hirtella triandra*	1	*	3	*
Combretaceae				
—*Terminalia amazonica*	2	-	1	*
—*Terminalia oblonga*	2	*	2	61
Elaeocarpaceae				
—*Sloanea guianensis*	-	4	8	-
Euphorbiaceae				
—*Alchornea latifolia*	1	-	1	-
—*Hura crepitans*	-	3	2	11
—*Margaritaria nobilis*	-	*	7	3
—*Sapium marmierii*	-	19	17	5
Flacourtiaceae				
—*Hasseltia floribunda*	38	*	7	3
—*Lunania parviflora*	-	11	25	4
Guttiferae				
—*Rheedia acuminata*	6	*	*	1
—*Rheedia gardneriana*	10	*	*	1
Lauraceae				
—*Nectandra* cf.*membranacea*	5	1	?	-
Lecythidaceae				
—*Cariniana estrellensis*	1	*	1	1
Leguminosae				
—*Erythrina poeppigiana*	4	-	-	17
—*Inga marginata*	1	*	1	*
—*Inga tomentosa*	5	17	-	-
—*Swartzia jorori*	4	1	1	2
Meliaceae				
—*Guarea macrophylla*	2	3	11	*
—*Trichilia elegans*	3	-	1	3
—*Trichilia inaequilaterale*	1	-	7	-
—*Trichilia pleeana*	8	13	22	21
Moraceae				
—*Cecropia angustifolia*	2	4	-	-
—*Clarisia biflora*	9	2	1	19
—*Clarisia racemosa*	11	8	*	14
—*Ficus killipii*	2	2	1	*
—*Ficus maxima*	2	1	*	*

—*Poulsenia armata*	18	24	12	41
—*Pourouma cecropiifolia*	-	3	23	1
—*Pseudolmedia laevis*	1	74	16	18
Myristicaceae				
—*Virola flexuosa*	-	-	5	1
—*Virola peruviana*	5	5	9	?
—*Virola sebifera*	-	1	*	1
Myrsinaceae				
—*Stylogyne ambigua*	3	2	-	-
Nytaginaceae				
—*Neea boliviana*	9	2	*	?
—*Neea divaricata*	1	7	*	?
Palmae				
—*Astrocaryum macrocalyx*	13	37	115	63
—*Euterpe precatoria*	-	21	43	*
—*Iriartea deltoidea*	-	93	*	31
—*Scheelea princeps*	-	2	2	15
—*Socratea exorrhiza*	-	17	*	23
Polygonaceae				
—*Triplaris americana*	-	-	3	4
—*Triplaris poeppigiana*	8	3	-	-
Rosaceae				
—*Prunus* cf. *vana*	1	-	2	-
Sapindaceae				
—*Sapindus saponaria*	-	1	*	2
Sterculiaceae				
—*Guazuma ulmifolia*	7	1	20	10
Tiliaceae				
—*Berrya* sp. nov.	7	13	-	-
Ulmaceae				
—*Ampelocera ruizii*	11	1	1	2
—*Celtis schippii*	-	18	20	10
Verbenaceae				
—*Vitex pseudolea*	-	1	-	5
Total	**647**	**588**	**582**	**506**

A comparison with inventories in other Amazonian countries reveals some conspicuous trends. *Pseudolmedia laevis* is ranked within the top twenty important species at Alto Ivon (Boom, 1986), Jatun Sacha (Neill & Palacios, manuscript), Añangu (Balslev et al., 1987), and is present, if not abundant, at Rio Xingu (Campbell et al., 1986). In Bolivia, *P. laevis* generally is considered to be the most abundant species in lowland humid forests in the Pando, Beni, and northern Santa Cruz (Boom, 1986; Saldias et al., 1994; Vargas et al., 1994; Arroyo et al., 1994; de Aguila, 1995). Likewise, several palms are widely distributed and abundant; *Iriartea deltoidea*, *Socratea exorrhiza*, *Euterpe precatoria*, and *Oenocarpus bataua* have been reported for several of the sites in Peru and Ecuador (Balslev et al., 1987; Kahn & Mejia, 1990). In Bolivia, *Iriartea deltoidea* is more common in the forests at the base of the Andes and the adjacent alluvial plain of the Beni, while being absent from the Brazilian Shield region of northern Santa Cruz. *Socratea exorrhiza* and *Euterpe precatoria* are more widely distributed being found commonly throughout the Bolivian orient north of 15° S on the Brazilian Shield and as far south as 17°45′ S on piedmont and foothills of the Andes. A comparison of the common species listed in Table 6 with published checklists from Ecuador (Neill & Palacios, 1989) and Peru (Bracko & Zaruchi, 1993) reveal that 53 of these 60 species are widely distributed taxa that occur throughout western Amazonia.

In contrast, there is little floristic overlap between the forests situated at the base of the Andes and the lowland humid forests in northern Bolivia (Table 6) or on the Brazilian Shield in eastern Bolivia (Killeen, unpublished data). The importance of ongoing botanical inventory in the region is highlighted by comparing the list of trees from this study with the recently published Guía de Arboles de Bolivia (Killeen et al., 1993). Twenty nine species not cited in this treatment of Bolivia trees are reported, or 14.3% of the total of 203; undoubtedly, the list would be greater if the undetermined specimens were identified.

Table 6. A comparison of the floristic similarities of five one hectare plots established in humid forest in eastern Bolivia; only those plots with more than 85% of the taxa determined to the species level were selected for comparison; values are the number of species found in both plots (n_c), Sorensen's coefficient of similarity based on presence vs. abscence (S_c), and Sorensen's coefficient of similarity based on quantitative data (S_q); locality data is as in Table 4.

	Cumbre Pilón			Río Colorado			Bosque Chimanes			Río Saguayo			Alto Ivon		
	n_c	S_c	S_q	n_c	S_c	S_q	n_c	S_c	S_q	n_c	S_c	S_q	n_c	S_c	S_q
Cumbre Pilón	-	-	-	23	0.20	0.15	24	0.23	0.14	23	0.22	0.18	1	0.04	0.01
Río Colorado				-	-	-	22	0.28	0.36	25	0.32	0.35	8	0.09	0.10
Bosque Chimanes							-	-	-	24	0.33	0.31	7	0.06	0.12
Río Saguayo										-	-	-	5	0.06	0.04
Alto Ivón													-	-	-
Total species	146			78			78			67			94		

$S_c = 2c / a + b$, where c is the number of species in common between two localities; a and b are the total number of species found in each of the two localities A and B.

$S_q = 2n_c / n_{a} + n_{b}$, where n_c is the sum of the lower of the two abundance values (i.e., number of stems) for each species that occurs at both of the two localities; $n_{a} + n_{b}$, is the sum of the total abundance values for the two localities A and B (Magurran, 1988).

The moderate levels of tree species diversity recorded for lowland humid forest communities in Bolivia (Table 7) and the abundance of species that are widely distributed can be interpreted in a variety of ways. Such characteristics would support the assumption that these forests have only recently become established in a biogeographical time frame and would conform to the hypothesis that Amazonian forest vegetation has expanded southward during the Holocene (Ratter, 1992; Prado & Gibbs, 1993). Likewise, there is widespread evidence that much of lowland Bolivia has been subject to recurrent catastrophic disturbance caused by the fluvial dynamics of both the major and secondary river systems (Hanagarth, 1993; Gullison et al., 1995). Such disturbance has resulted in the formation of a diverse assemblage of habitats, particularly wetland plant communities; however, it has not been conducive to the development of rich forest communities typically found on well-drained soils throughout the Neotropics. Finally, the data from these plot studies support the generally accepted hypothesis that tree species richness is correlated with latitude and precipitation (Gentry, 1988a).

Table 7. Tree diversity values for 24 one hectare plots established in Bolivia since 1980; only data for trees greater than 10 cm dbh is presented; precipitation data are approximate values in mm.

Locality	Coordinates	Elevation in m	Precipitacion in mm	Number of species/ha
Lowland Forests				
Humid Forests				
Alto Ivon [1]	11°45′S 66°02′W	200	1550	94
Ríos Blanco y Negro [2]	14°33′S 62°45′W	300	1400	90
Noel Kempff , Los Fierros-1[3]	14°35′S 66°50′W	300	1500	94
Noel Kempff , Los Fierros-2[3]	14°35′S 66°50′W	300	1500	75

Noel Kempff, Las Gamas [4]	14°48′S 60°23′W	700	1500	75
Pilón Lajas, Río Colorado[5]	14°55′S 67°05′W	270	2500	79
Bosque Chimanes[6]	15°00′S 66°30′W	200	1700	78
Amboro, Río Saguayo[7]	17°45′S 63°44′W	360	1700	67
Riverine or Flooded Forests				
Noel Kempff, Las Torres 3[4]	13°39′S 60°49′W	250	1500	76
Estación Biológica del Beni , Maniqui[8]	14°30′S 66°50′W	200	1800	49
Estación Biológica del Beni -01[9]	14°46′S 66°40′W	200	1800	51
Estación Biológica del Beni -02[9]	14°44′S 66°40′W	200	1800	52
Deciduous Forests				
Noel Kempff, Las Torres 1[11]	13°39′S 60°49′W	350	1500	40
Noel Kempff, Las Torres 2[11]	13°39′S 60°49′W	350	1500	34
Bajo Paraguá, Cerro Pelao 1[11]	14°32′S 61°30′W	400	1500	46
Bajo Paraguá, Cerro Pelao 2[11]	14°32′S 61°30′W	400	1500	62
Jardin Botánico de Santa Cruz[10]	17°47′S 63°04′W	375	1150	34
Montane Forests				
Humid Forests				
Pilón Lajas, Cumbre Pilón [5]	15°15′S 67°00′W	900	3000	146
Alto Beni, Sapecho 1[12]	15°30′S 67°25′W	700	1600	118
Alto Beni, Sapecho 2[12]	15°30′S 67°25′W	600	1600	116
Alto Beni, Sapecho 3[12]	15°30′S 67°25′W	700	1600	115
Cloud Forests				
Amboró, Cerro Bravo[7]	17°49′S 64°32′W	2500	1000	43
Amboró, Río Amparo[7]	17°50′S 63°20′W	1000	1000	35
Amboró, San Rafael[7]	18°23′S 63°52′W	1500	1500	50

1. Boom, 1986. 2. Vargas et al., 1994 3. Saldias et al., 1994 4. Arroyo et al., 1994	5. this study 6. de Aguila, 1995. 7. Vargas, 1995 8. W. Palacios et al. (unpublished data)	8. Dallmeier et al., 1991 9. Saldias, 1991 10. Jardim et al. 1994 11. R. Seidel (unpublished data)

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