FIELD STUDIES OF FAUNA AND FLORA
LA MACARENA, COLOMBIA

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JAPAN - COLOMBIA COOPERATIVE FIELD STUDY

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EDITORS' NOTE

From this edition on, the journal will change the nomenclature of each publication from volumes to numbers, as recommended by ISSN standards. For further reference, the abbreviated name of this journal is: Field Stud. Fauna Flora Macarena Colomb.

Cover: This depiction of a spider monkey was taken from Henri Veyrier's "L'Encyclopedie de Diderot et D'Alembert "

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INTRODUCTION

General Aspects of the Study Site

The study site CIEM (Centro de Investigaciones Ecológicas La Macarena) consists of three research stations on the west margin of Río Duda. The study site is located in a tropical lowland forest on the eastern border of Tinigua National Park, west of La Macarena Mountains, Departamento del Meta, Colombia (2° 40' north and 74° 10' west, 350-400 m over sea level). Tinigua National Park was created in 1989 in an effort to create a biological corridor between two parks already established (La Macarena and Picachos), which were delimited again that year due to increasing human colonization within park limits (Garcés & de La Zerda 1994). Tinigua National Park (201,875 ha) lacks an official control cabin within the park. Forests located around the CIEM stations have not been influenced by human activities.

Rainfall is seasonal in the region, with a 2-3 month dry period occurring between December and March (Fig. 1). Annual rainfall and average temperature estimates at the Chamuza station between 1989 and 1993 were 2622 mm and 25°C (Kimura et al., 1994). Average annual precipitation at Paujil (March 1990-February 1991, August 1996-July 1997, and January-December 2000) was 2782 mm (Table 1).

Table 1. Climate data for three different years at the CIEM (Puerto Paujil station), The table shows total rainfall, the number of months with less than 100 mm of rainfall, mean temperature, average minimum and maximum temperatures, and an index of solar radiation based on a daily estimate on a 0-5 scale.

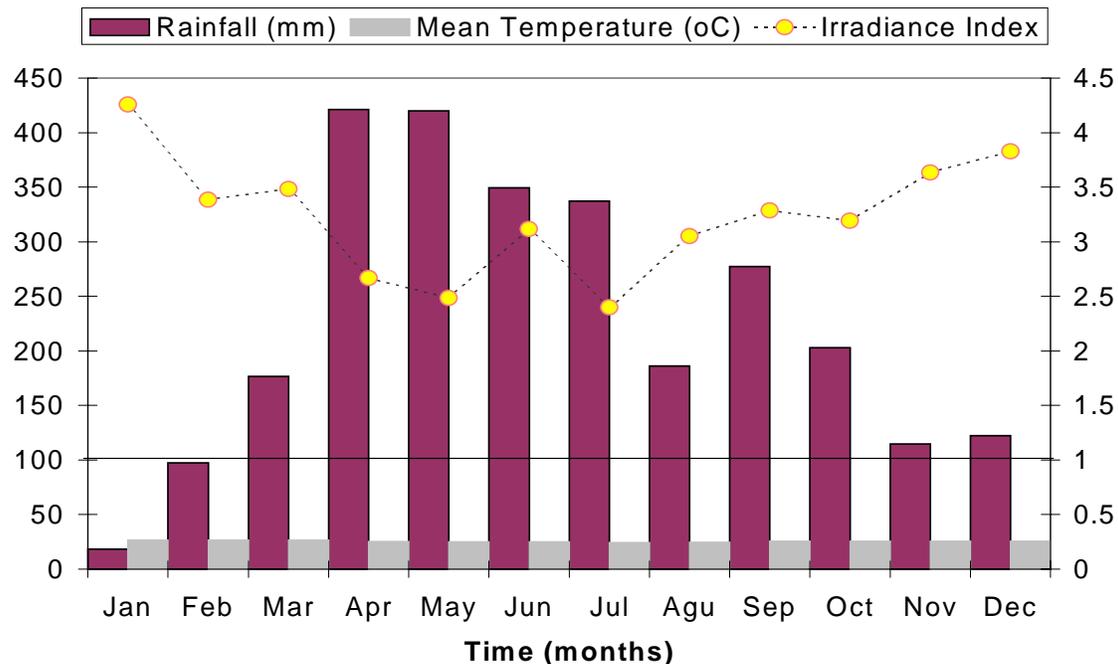| YEAR	Rainfall (mm)	No. dry months	Avg. Temp	Avg. Low	Avg. Max	Radiation Index
1990-1991	2604	2	26.1	21.2	31.1	---
1996-1997	2551	1	25.0	21.4	29.0	3.3
2000	3192	3	25.2	21.3	29.5	3.3
Average	2782	2	25.4	21.3	29.9	3.3

Fig. 1. Annual variation in rainfall, mean temperature, and irradiance (as a 0-5 index) from three years of data collected at Puerto Paujil Station in Tinigua National Park.

The soils in the study area have different geological origins (Botero, 1998). The flat forms along the Duda River were formed very recently in the Holocene by the accumulation of sediments in the usual dynamics of white-water meandering rivers (Terborgh, 1983). These soils are richer in nutrients than in the non-flooded areas. The soils on the high terraces have a complex origin, with some components formed during the Tertiary period and others in the early Quaternary period (Botero, 1998). These soils correspond mainly to Plio-Pleistocene alluvial soils that have been subject to recent tectonic fractures which have produced the differences in height between the river level and the hill crests of up to 65 m (Hirabuki, 1990). These plates have been subject to erosion by water, forming meandering brooks and narrow canyons which are the cause of the undulating topography typical of non-flooded terra firme areas. These sedimentary soils were deposited mainly from periods of the latest Andean uplift, so that they are relatively young and more fertile than the typical soils in central Amazon basin (Botero, 1998)

Previous Vegetation Studies

CIEM consists of plants from four different biomes: the Amazonian forests, the Andean region, the savannas of the Orinoco River, and the Tepuis (on top of La Macarena mountains). Botanical expeditions in La Macarena region began in the 1940's, by the American Museum of Natural History, British Museum of Natural History, University of California, Harvard University, Uni-Mainz, and Universidad Nacional de Colombia (Idrobo, 1967). Later in the 70's and 80's, some studies provided checklist

accounts of the plants found in different areas of the region, including the lowland forests between La Macarena and the Andes (Universidad de Antioquia, 1989; Universidad Nacional de Colombia, 1989; PRORADAM, 1979). We started systematic plant collections in the CIEM in 1988 (Barbosa *et al*., 1990). A. Gentry and M.G.M. van Roosmalen identified the first collections to genus and species in some cases. Botanical collections increased in subsequent years (Barbosa, 1992), an effort that has continued to the present. A significant portion of the plants known to occur in the study site were included in a pictorial fruit guide that includes descriptions, keys, photographs and names for 600 plant species (Stevenson *et al*., 2000). We corroborated the plant identifications for the fruit guide by comparison with specimens in several herbaria (Missouri Botanical Garden, New York Botanical Garden, Museum of Natural History, COAH, and COL), where voucher specimens were deposited.

Patterns of Plant Species Richness

We have collected more than 1,000 vascular plant species in the study site. These plants belong to 109 families and 539 genera. Leguminosae is the richest family, with 105 species (Stevenson, 2002). Fabaceae, with 47 species, would still be the most species-rich family if it were separated from the other legumes. Ferns constitute an important group with 45 species, while Moraceae and Rubiaceae both have 42 species. The richest genus is *Inga* with 28 species; followed by *Ficus*, with 21, *Piper* with 19, and *Psychotria* with 17. Other genera with high numbers of species are *Miconia, Paullinia, Philodendron* and *Ocotea*.

The highest percentage of collected species are corresponds to trees (38%), followed by lianas (20%), herbs (19%), epiphytes (12%) and shrubs (11%). Considering only the trees, legumes are again the most important family (71 spp.), followed by Moraceae (33 spp.). Rubiaceae is the family with the most shrubs, 19 species, followed by Piperaceae and Melastomataceae having 16 and 12 species respectively. Within the lianas, more than 30 species belong to Bignoniaceae. Leguminosae and Cucurbitaceae are also important with 26 and 17 liana species each. The herb community is composed mainly of Graminae, with 37 species, ferns with 27 and Marantaceae with 14 species. Orchids are the richest family of epiphytes (31 spp.), followed by Araceae and ferns, with 25 and 16 species each.

Forest Types

There are relatively few studies on the characterization of forest types in the CIEM study site. Hirabuki (1990) was the first researcher who tried to group vegetation types in terms of physiognomy, by describing the vegetation in several vegetation plots (20-25 x 10-20 m) along two transects of 1,240 and 500 m. He suggested four main vegetation types: *Cecropia*-graminoids open forest, degraded open forest, mature broad-leaved forest, and transitional forest. Based on his classification we grouped the vegetation types in the area in three easily recognized categories (Stevenson *et al*., 1994) because it was difficult to define the transitional forest, and no apparent delimitation of this forest type was possible from the interpretation of aerial photographs. These forest types are: 1). Mature forest, localized on

hill ridges, with trees of 20-25 m in height, and a continuous canopy with emergent trees reaching 30 m; 2). Open-degraded forest, localized on erosion fronts, small valleys and brooklets. This forest was characterized by a high variety of vines, the abundance of bamboo, and with few trees of 20 to 25 m in height, resulting in a discontinuous canopy and a thick understory; and 3). Flooded forest, localized to flatlands formed by the river and characterized by a discontinuous canopy dominated by *Ficus spp., Inga spp.* and *Cecropia sp.* The understory is covered primarily by large herbs (mostly *Heliconia spp*).

We constructed a vegetation map of the study area (426 ha) by superimposing a 50x50 m grid on a trail map and assigning a particular forest type to each cell based on the knowledge of the terrain. The most common vegetation type was mature forest (53%) followed by open degraded forest (34%) and flooded forest (11%). The remaining 2% was composed of riparian forest and a patch of secondary disturbed forest around our campsite.

The forests on the flatland of recent origin (Hara *et al.*, 1999; Stevenson *et al*., 1999) contained at least three different forest types: The first type, riparian forest, is located on recently formed beaches and dominated by *Tessaria integrifolia* (Asteraceae)*, Cecropia membranacea* saplings and several graminoids. This forest type is known to change along a succession to constitute two distinct plant communities, differentiated by the level of the water table. The second forest type occurs on raised bars that flood only on occasional years. The dominant tree species are *Guarea guidonia* and *Cecropia membranacea,* and the understory includes a variety of plants including species of the mature forests and large herbs such *as Heliconia episcopalis*. The third type is found on low-lying areas subject to annual flooding. The trees *Laetia corymbulosa* and *Luehea cf. tessmannii* dominate the plant community, and *Heliconia marginata* dominates the understory.

Several other studies on the structure and floristic composition of the study site have been made (Barbosa & Hirabuki, 1992; Hirabuki & Barbosa, 1992; Stevenson, 1995; Suescún, 2002; Takehara & Stevenson, 1997). Interestingly, some of those studies have produced contradictory results (probably because small and different sample sizes were used), and the floristic affinities, especially concerning the differences among non-flooded forests, are still unclear. For example, Barbosa (1992) proposed several plant associations such as 1. *Phenakospermum-Protium,* 2*. Oenocarpus bataua-Qualea,* 3. *Brosimum guianensis-Ficus* sp., and 4. *Sterculia* sp.-*Gustavia hexapetala* based on a floristic inventory (<1ha). But in a recent study comprising 3 ha (Suescún, 2002), it was demonstrated that some of these species can be abundant in the forest, and their presence is not correlated with the abundance of the other members of the association. Similarly, some plant species reported as very important components of the forest such as *Oenocarpus bataua* and *Theobroma glaucum* (Stevenson *et al*., 2000) were not found to be as frequent in larger plots (Suescún, 2002). We have assumed that mature forest is more diverse than other forest types (Stevenson *et al*., 2000), but quantitative analyses show that the open-degraded forests are at least as diverse as the mature forest (Suescún, 2002).

In order to have a better characterization of the different forests, we collected and compiled floristic and structural data from vegetation plots totaling 7 ha. The purpose of this study was to describe the vegetation of the different forest types in an effort to validate

previous interpretations of forest characterizations. In particular we were interested in addressing the following questions: 1) Are there structural and floristic differences among forest types? 2) Which forests have the most plant species? 3) What habits or growth forms predominate in each forest type? 4) What are the most important species in each forest type? 5) Can different forest types be distinguished from each other based on their floristic composition?

METHODS

A baseline map of forest types was drawn by one of us (M.J.Q) based on an interpretation of aerial photographs taken in the 60's (Fig. 2). She delineated the limits among mature, open-degraded, and flooded forests. The limits of the secondary forests were not taken from the photographs because the clearing was made in the 70's. Similarly, it was impossible to separate the old flooded forests in the interpretation. We introduced the limits of the secondary forest and the flooded forests based on the distribution of trees belonging to species restricted to these habitats. I also adjusted the river course to agree with recent photographs (1995) and my own observations, because the river has changed since the 80's. For example, the river margin most exposed to water erosion has receded at least 50 m in the last ten years. On the other hand the riparian forest that was first colonized by tree seedlings in August 1990 is now a tall *Cecropia membranacea* forest (average DBH of mature trees=34 cm), that began fruiting in 1996.

The core data for the analyses came from five randomly located one-hectare squared vegetation plots: two located on mature forest, one on open-degraded forest, one on flooded forest on a low basin, and one composed mainly of open-degraded forest (with mature forest on two margins). Three of these plots were used previously for a forest characterization (Suescún, 2002). The information for the other two hectares was collected using smaller vegetation plots (100x10m or 10x10 m.) localized on different forest types for similar characterization purposes (e.g. Stevenson, 1995; Stevenson *et al.*, 1999). For all plots, we established sub-quadrants of 100 m^2, where all plants of at least 5 cm DBH were marked and identified. P.R.S identified all the plants in all the 7 ha of vegetation plots. The majority of individuals were identified in the field. For a small proportion of the individuals that were not included in the fruit guide, voucher specimens were collected for further comparison. We measured the DBH of all marked individuals.

We constructed small sub-plots (25m^2) inside the larger plots described above, to quantify the density of saplings and large herbs (DBH between 1 and 5 cm). We included in these medium plots all palms with subterranean stems and large herbs, which technically do not have a trunk, when their height was similar to that of the trees in that category (between 1.7 and 4.5 m.). We measured the density of seedlings, herbs and all small plants (DBH< 1 cm), in smaller plots (4m^2), inside the other quadrants. We did not include recently germinated plants less than a month old. We avoided locating medium and small sub-plots within the one-hectare plot limits or in disturbed areas (next to trails). Thus, the number of small and medium quadrants is less than the number of large plots.
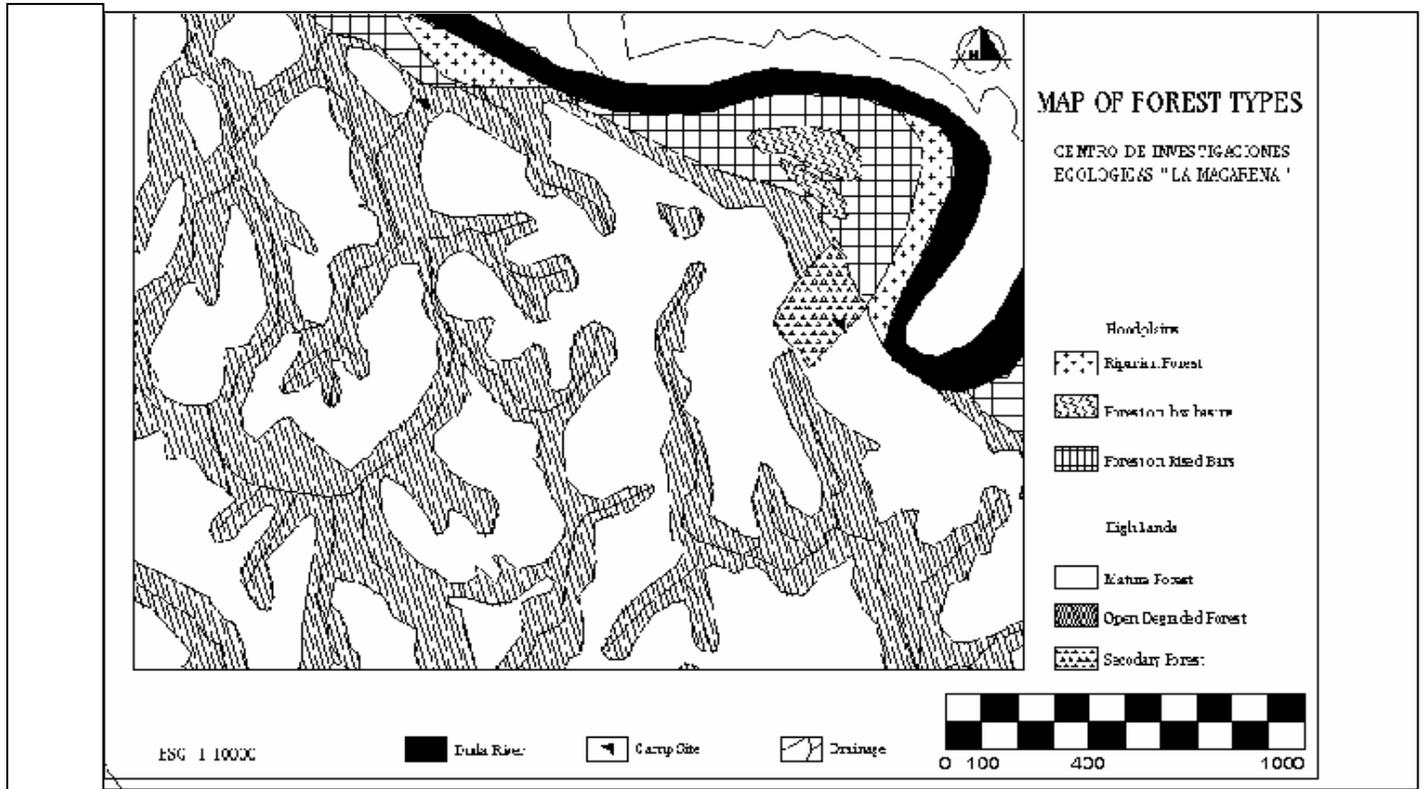
Fig. 2. Map of forest types at the CIEM, Tinigua National Park, Colombia. Three different vegetation forms are currently recognized on the floodplains, and two main forest types occur on the highlands. There is also a small patch of secondary forest around the camp site (see text for more information).

We compared species richness among forest types using standard rarefaction analyses. And we ran an ordination based on the density of different species on 7 plot groupings, using the Canoco program (ter Braak, 1987). Two of them correspond to different one-hectare plots on mature forest (No. 1 and 4), two more to one-hectare plots on open-degraded forests (3 and 6), and one more to flooded forest on low basins (2). The other groupings correspond to small plats summing a total area of one hectare: No. 5 in flooded forest on raised basins and No. 7 a mixture of terra firme forests.

RESULTS AND DISCUSSION

The recent interpretation of aerial photographs revealed a similar proportion of forest types as in previous maps [Mature: 51%, open-degraded: 39%, secondary: 1%, and flooded: 8% (5% on bars, 1% on basins, and 2% riparian)] (Fig. 2).

Diversity and Structural Characteristics

Open-degraded and secondary forests showed the highest plant densities (DBH>5 cm) while the flooded forests showed the lowest densities. However, plant density changes depend on the size of the trees, and the mature and secondary forests showed the highest numbers of plants with more than 20 cm DBH (Table 2). These results agree with previous descriptions that characterized the open-degraded and the flooded forests for their open canopies (Stevenson *et al*. 2000), that are formed usually by trees more than 20 cm in diameter.

We found large structural differences among forest types, as indicated by the frequency of plants in different DBH categories (G=334, p<<0.001, Fig. 3). These differences were very pronounced for small (5-20cm) and large (>40cm) DBH classes (G=227 and 81 respectively, both p<<0.001), but insignificant for intermediate diameters (20-40 cm: G=5.6, p=0.93). The main differences among forest types (Fig. 3) can be summarized as follows: 1). Plants in the smallest diameter categories are at low frequencies in the flooded forests where herbaceous plants dominate the understory. 2) There is a high frequency of small plants (DBH 5-10cm) in the secondary and open-degraded forests, probably because of the high light levels reaching the understory. 3) Relatively large trees (DBH 40-45cm) are most frequent in secondary forests, and trees of this size are the largest trees in this kind of forest (probably the first cohort after disturbance). 4) The frequency of very large emergent trees is higher in the flooded forests than in other forest types (mainly *Ficus* spp.), although some of these trees also occur in the mature forest. 5) The frequency of small plants in the open-degraded forests is higher than in mature forest. The opposite pattern is observed for large plants.

Table 2. Plant density and diversity indices for the different forest types at Tinigua National Park. The number of individuals per hectare is shown for three different diameter classes.

Forest Type	Individuals/Ha			Species /Ha	Shannon Index	Simpson's Index	
	>5 DBH	>10 DBH	>20 DBH			D	I-D
Mature Forest	1293	601	227	115	4.80	0.01	0.99
Open-Degraded F.	1414	609	161	167	4.87	0.02	0.98
Flooded on Bars	799	509	206	124	3.48	0.07	0.93
Flooded on Basins	547	392	180	39	2.17	0.24	0.76
Secondary Forest	1645	902	251	545	3.99	0.05	0.95

None of the diversity indices used indicated that the mature forest is the most diverse (Table 2). The only consistent pattern of diversity among forest types was the low diversity indices for the flooded forests, especially the flooded forest in low basins. Plant diversity in secondary forests was similar to the diversity found in the mature and open-degraded forests (Fig. 4), but it is difficult to assure that the pattern would hold for an increased sample size. The plant diversity in the flooded forest on raised bars turned out to be intermediate between the diversity on low basins and on terra firme forests.

Growth forms also differed among forest types (Fig. 5). The main differences for plants at least 5 cm in diameter were: 1) Low density of all growth forms in the flooded forest on low basins. Trees constitute the main growth form in this kind of forest, but their densities were about half the density of trees in terra firme forests. 2) The density of trees was intermediate for the flooded forest on bars. 3) The abundance of bamboo was highest in open degraded forest. Bamboo was also present in some areas of the secondary forest, but the small sample size precluded me to estimate their densities. 4) Large vines were as frequently observed in the mature forest as in the open-degraded forest, and they were less abundant in flooded forests, especially on low basins. 5) *Phenakospermum guianensis* showed higher abundance in mature forests than in the open-degraded forest, but was absent in flooded forests.
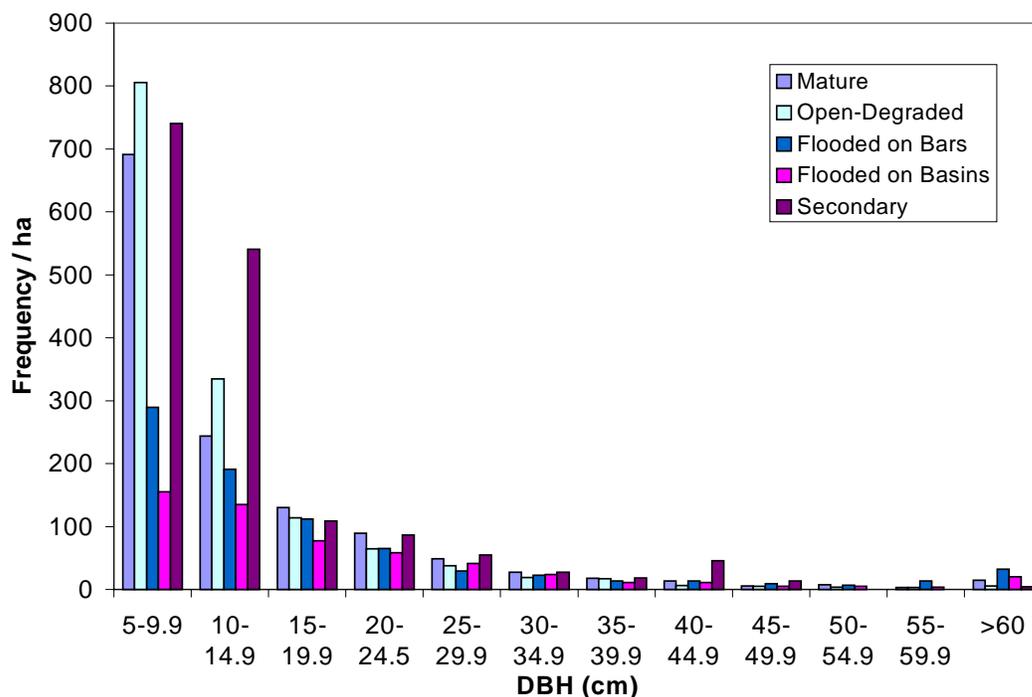

Fig. 3. Density of woody plants in different forest types at Tinigua National Park, according to different DBH (diameter at breast high) categories.
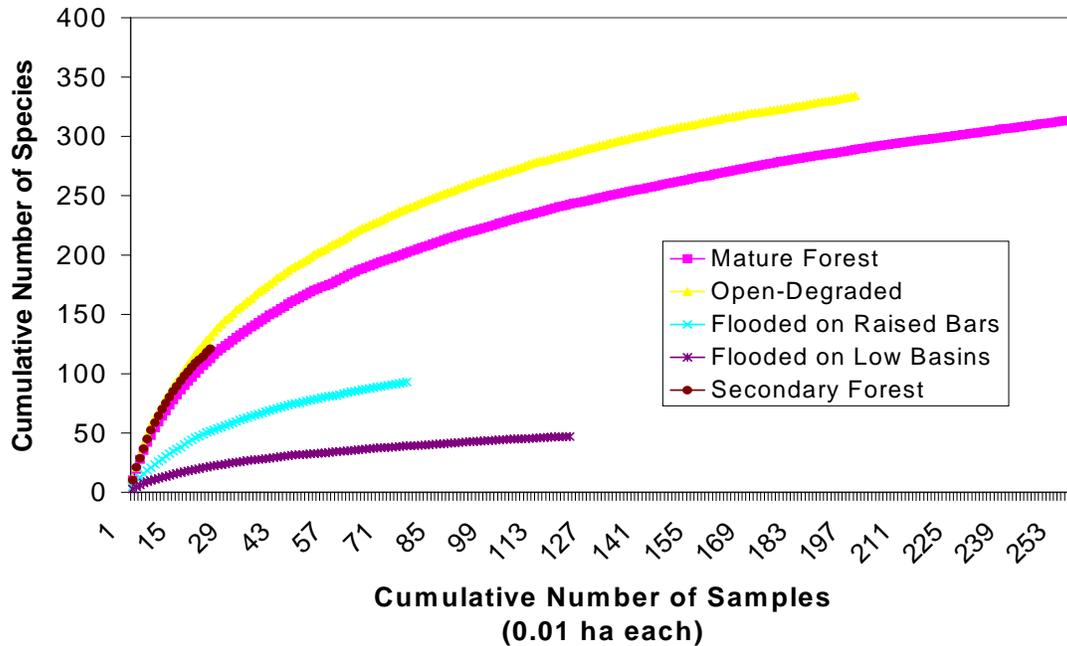
Fig. 4. Rarefaction curves showing the patterns of plant species richness in different forest types at Tinigua National Park.

The main difference in growth forms among forest types in understory vegetation (DBH 1-5cm) was related to the large density of herbs in flooded forests, which corresponded mainly to the abundance of *Heliconia* spp. In fact, *Heliconia marginata* and a few vine species were the only plants common in flooded forests on low basins. Other differences, somehow masked by the huge differences in herb densities, are the high densities of herbs, vines, and even trees in the open-degraded forests compared with the mature forest.

Large differences in the density of various growth forms were also found for small plants (DBH<1 cm). In this category, the major difference was due to the high abundance of shrubs (especially *Psychotria psychotriifolia*) in flooded forests on raised bars, which was rare in other forest types. Once again the general density of plants was lowest in the flooded forest on low basins, regardless of growth form. The density of seedlings from tree species was highest in the mature forest. Vine seedlings were more abundant in terra firme forests than in flooded forests, and the density of epiphytes like *Monstera* spp. and *Syngonium* spp. was highest in the flooded forest on raised bars.
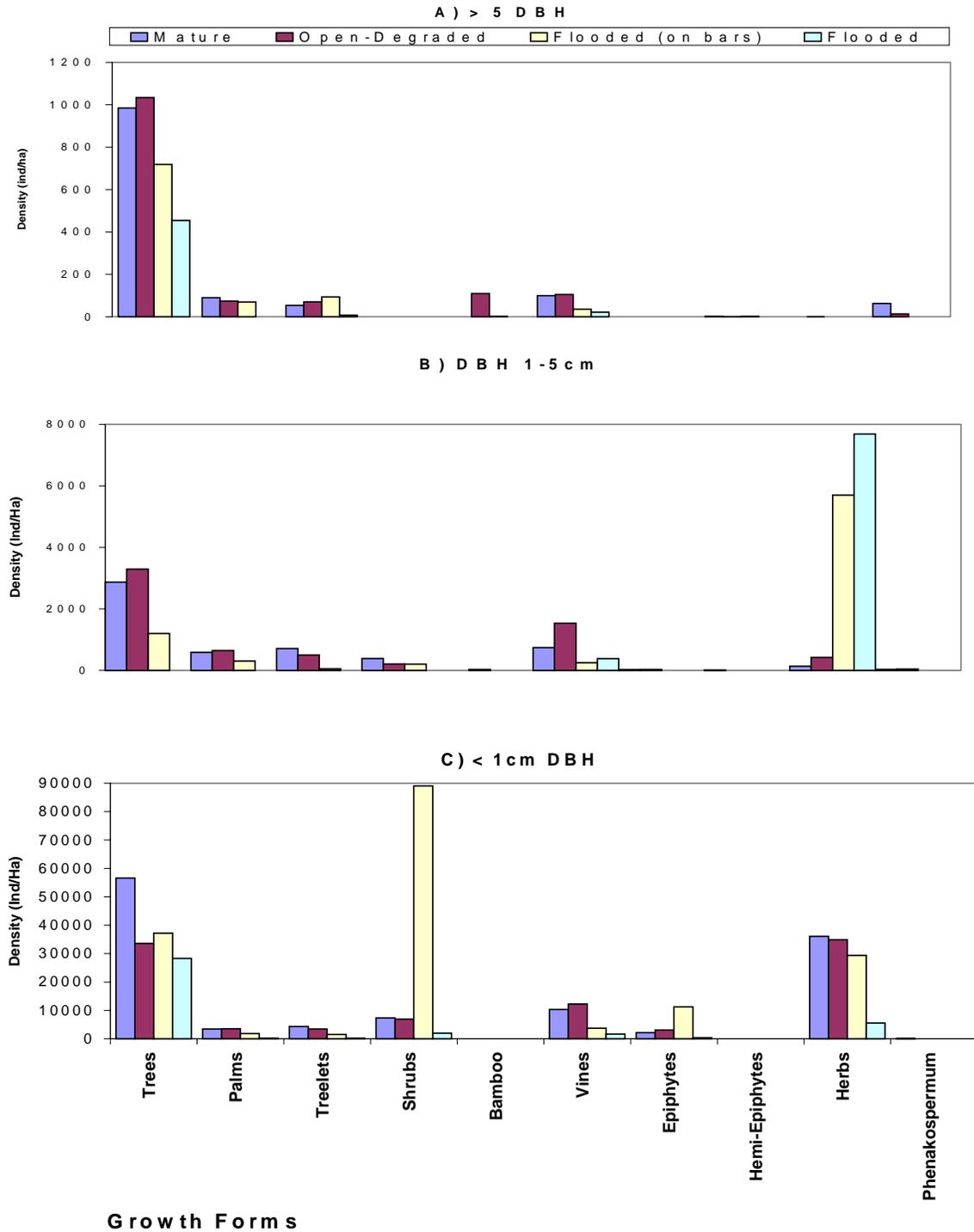
Fig. 5. Comparison of plant growth forms in four different forest types at Tinigua National Park. A) woody plants DBH≥ 5 cm. B) plants DBH >1 and <5 cm. and C) plants up to 1 cm in DBH.

Floristic Characterization

The top twenty species according to the index of importance for each forest type are included in tables 3 to 6. These species varied in importance across forest types. Mature and the open-degraded forests share more than half of the most important species, and some species are equally important in both forest types. For example, *Theobroma glaucum* is the second most important species in both forest types. A small tree that forms large mono-specific stands in the understory, *Rinorea lindeniana* (Violaceae), was the most important species in the open degraded forest. This was caused mainly by the high density of individuals in just one of the hectare plots, but this species also forms stands in mature forest.

An interesting floristic difference between mature and open degraded forest is the higher importance of animal-dispersed species in the former type. In our sample for the mature forest, only 2 of the 20 most important species corresponded to species not dispersed by animals, a tree *Dalbergia* sp. (Fabaceae) and a frequent treelet *Hybanthus prunifolius* (Violaceae). In contrast in the open-degraded forest, 5 out of the 20 most important species did not have animal dispersed seeds (i.e. *Guadua angustifolia*).

The palm, *Oenocarpus bataua*, an important component of the Tinigua flora in previous studies (Stevenson *et al*., 2000), was included within the list of the seven most important species for the terra firme forests. This study also highlights the importance of several species in the Moraceae and Burseraceae families (in particular *Pseudolmedia* spp., *Protium* spp. and *Crepidospermum* spp.), that were among the most important species in both mature and open-degraded forests. In summary, there is so little floristic dissimilarity between the main terra firme forests, that in the absence of clear structural differences it would be difficult to distinguish these forest types.

The abundance of *Henriettella fissanthera* (Melastomataceae), a tree that seems to be restricted to open-degraded forests on high slopes, was only included among the ten most important species in one of the hectares of open-degraded forest. However, its overall abundance does not seem to make it a good indicator species for this kind of forest.

Table 3. Most important plant species in the Mature forest (DBH≥ 5cm), according to the importance index (Index), which is the sum of the relative dominance (R.D), the relative density (R.A), and the relative frequency (R.F.). The relative dominance was calculated based on the basal area (BA). The relative frequency was based on the number of times that each species was present in 283 plots of 100 m^2. To calculate relative values, the raw index for a species was divided by the mean index across all species.

Species	BA (cm2)	R.D.	Density (ind/ha)	R.A.	Freq.	R.F.	Index
Pseudolmedia laevigata	8997	2.72	49	3.80	96	33.92	40.4
Theobroma glaucum	4775	1.45	45	3.45	90	31.80	36.6
Crepidospermum rhoifolium	3394	1.03	40	3.06	92	32.51	36.6
Protium robustum	3854	1.17	40	3.09	84	29.68	33.9
Protium sagotianum	10266	3.11	34	2.60	78	27.56	33.2
Pseudolmedia laevis	5285	1.60	34	2.60	81	28.62	32.8
Oenocarpus bataua	13513	4.09	39	2.98	60	21.20	28.2
Dalbergia sp.	4409	1.33	28	2.13	59	20.85	24.3
Oxandra mediocris	7526	2.28	24	1.83	55	19.43	23.5
Protium glabrescens	3220	0.97	23	1.78	58	20.49	23.2
Phenakospermum guyanense	4060	1.23	63	4.89	42	14.84	20.9
Talisia intermedia	5562	1.68	22	1.70	48	16.96	20.3
Perebea xanthochyma	1731	0.52	19	1.48	45	15.90	17.9
Gustavia hexapetala	14274	4.32	13	1.04	35	12.37	17.7
Crepidospermum goudotianum	1393	0.42	20	1.53	44	15.55	17.5
Brosimum alicastrum	25249	7.64	9	0.68	24	8.48	16.8
Hybanthus prunifolius	481	0.15	17	1.31	40	14.13	15.5
Malmea sp.	3801	1.15	15	1.15	37	13.07	15.3
Pseudolmedia obliqua	4499	1.36	15	1.15	36	12.72	15.2
Aniba hostmanniana	680	0.21	14	1.12	37	13.07	14.4

Actually the difference in bamboo distribution seemed to be the only consistent floristic difference between terra firme forest types. All other species were similarly abundant in both forest types. But even the presence of bamboo (*Guadua angustifolia*) was not homogeneous among open-degraded forest. This may be due to the topographic criteria we used to delimit the forests, which did not include variables such as terrain slope to define the forest types. For example, in the open-degraded hectare surrounding a system of meandric brooks on a flat terrain, there was a very low density of bamboos. This was probably due to the lower light levels reaching the ground in the flat terrain where there is more soil stability, the erosive activity of the creeks is less accentuated, and tree falls are less generalized than in a terrain with steep slopes.

Table 4. Most important plant species in the open-degraded forest, according to the importance index, based on 196 plots of 100 m^2 (see Table 3 for column headings).

Species	B.A. (cm2)	D.R.	Density (ind/ha)	R.A.	Freq.	R.F.	Index
Rinorea lindeniana	3431	1.5	83	5.8	63	32.1	39.5
Theobroma glaucum	4278	1.8	47	3.4	67	34.2	39.4
Protium sagotianum	11705	5.0	45	3.2	60	30.6	38.8
Guadua angustifolia	12550	5.4	110	7.8	33	16.8	30.0
Oenocarpus bataua	11960	5.1	29	2.1	40	20.4	27.6
Crepidospermum rhoifolium	2097	0.9	26	1.8	40	20.4	23.1
Pseudolmedia laevis	4515	1.9	21	1.5	37	18.9	22.3
Dalbergia sp.	2669	1.1	26	1.8	37	18.9	21.8
Quararibea cf. wittii	2096	0.9	30	2.1	36	18.4	21.4
Mabea maynensis	2943	1.3	26	1.8	32	16.3	19.4
Crepidospermum goudotianum	1590	0.7	20	1.4	31	15.8	17.9
Cordia nodosa	41	0.0	2	0.1	33	16.8	17.0
Pseudolmedia laevigata	1414	0.6	17	1.2	29	14.8	16.6
Brownea negrensis	831	0.4	21	1.5	28	14.3	16.1
Siparuna cuspidata	836	0.4	16	1.1	28	14.3	15.8
Pseudolmedia obliqua	2332	1.0	15	1.0	26	13.3	15.3
Perebea xanthochyma	1615	0.7	14	1.0	25	12.8	14.4
Trichilia aff. verrucosa	1715	0.7	15	1.1	24	12.2	14.1
Socratea exorrhiza	2348	1.0	14	1.0	23	11.7	13.7
Protium robustum	1115	0.5	14	1.0	23	11.7	13.2

Flooded forest on raised bars, which are dominated by *Guarea guidonia* and *Cecropia membranacea* (Stevenson *et al.*, 1999), do not share many species with terra firme forests. Only two of the twenty most important species are shared with the open-degraded forest, a palm (*Socratea exorrhiza*) and a small tree (*Quararibea* cf. *wittii*, Bombacaceae). None of the most important species were shared between the mature and the flooded forest on bars.

Less than half of the most important species were shared by the two main flooded forests. Species with a restricted distribution in a particular forest type were more common in flooded forests. For example, *Cecropia membranacea* trees have not been observed in undisturbed terra firme forests, although they can grow on large secondary patches. Similarly, the distribution of *Guarea guidonia* is restricted to flooded forests with very few exceptions. The two most important species in the flooded forest on low basins, *Laetia corymbulosa* (Flacourtiaceae) and *Luehea cf. tessmannii* (Tiliaceae), have only been observed in that kind of forest. Other species that manage to cope with the stressful conditions imposed by the flooding do not seem to be able to colonize other habitats (e.g. *Pseudobombax munguba, Ruprechtia* sp., and *Calycophyllum spruceanum*), a pattern consistently found in other Amazonian sites (e.g. Duivenvoorden 1996).

Table 5. Most important plant species in the flooded forest on raised bars according to the importance index, based on 75 plots of 100 m^2 (see Table 3 for column headings).

Species	B.A. (cm2)	R.D.	Density (ind/ha)	R.A.	Freq.	R.F.	Imp.Ind.
Guarea guidonia	153672	30.7	158	26	37	53.6	110.6
Cecropia membranacea	58268	11.6	135	23	16	23.2	57.3
Socratea exorrhiza	5603	1.1	46	8	21	30.4	39.3
Inga marginata	5931	1.2	30	5	16	23.2	29.5
Alchornea glandulosa	7507	1.5	30	5	13	18.8	25.4
Ficus insipida	73734	14.7	7	1	5	7.2	23.2
Psychotria viridis	2128	0.4	29	5	11	15.9	21.2
Piper tuberculatum	1441	0.3	28	5	10	14.5	19.4
Theobroma cacao	2716	0.5	20	3	9	13.0	17.0
Inga cylindrica	9325	1.9	19	3	8	11.6	16.6
Combretum laxum	2470	0.5	23	4	8	11.6	16.0
Ficus andicola	55771	11.1	1	0	1	1.4	12.8
Bursera inversa	4567	0.9	10	2	7	10.1	12.7
Quararibea cf. wittii	999	0.2	12	2	7	10.1	12.3
Trichilia pleeana	1989	0.4	10	2	7	10.1	12.2
Sapium laurifolium	10025	2.0	17	3	5	7.2	12.1
Ficus maxima	22891	4.6	9	1	4	5.8	11.8
Piper arboreum	1127	0.2	9	1	6	8.7	10.4
Luehea cf. tessmannii	596	0.1	9	1	6	8.7	10.3
Trichanthera gigantea	3431	0.7	13	2	5	7.2	10.1

Secondary forests in the study site also seem to be composed of a set of particular species, but the small sample size did not allow a quantitative analysis. However, all the secondary patches known around the research area are dominated by *Inga edulis* (Mimosaceae), *Spondias mombin* (Anacardiaceae), *Cecropia engleriana, C. membranacea* (Cecropiaceae), *Apeiba tibourbou* (Tiliaceae), *Bellucia pentamera* (Melastomataceae), *Trema* spp. (Ulmaceae), *Aegiphila* spp. (Verbenaceae), *Solanum* spp. (Solanaceae), *Rollinia edulis* (Annonaceae), *Piper* spp.(Piperaceae) or *Sapium* spp. (Euphorbiaceae).

The ordination analysis based on the density of plants larger than 5 cm DBH showed striking differences in floristic composition among forest types (Fig. 6). The most contrasting plot corresponded to the hectare on flooded forest on a low basin, located in the ordination on the opposite side from the terra firme forests. Although the vegetation on flooded forests on raised bars was located in an intermediate position in the ordination, the distance from this type of forest to the forest on low basins and terra firme forests was large, suggesting clear-cut floristic differences. Although all the terra firme forests were grouped on one side of the ordination, there was some differentiation among them in the y axis, the mature forests being located on the lower side and the open-degraded and mixed forests on the middle and upper part (Fig. 6).

The density of the most abundant understory plants (DBH 1-5 cm) in the different forest types (Table 7) indicates that mature and open-degraded forests are very similar due to two palm species (*Attalea insignis* and *Oenocarpus bataua*), which are very abundant in both forest types. Some of the terra firme species included in the lists are locally plentiful (*Capparis frondosa* and *Rinorea lindeniana*), but are not equally abundant in all vegetation plots. In this plant category the main difference among terra firme forests was the inclusion of herb and vine species in the open-degraded forests, which were not as abundant in the mature forest (e.g. *Ischnosiphon* cf. *macarenae, Petrea maynensis, Derris pterocarpus, Combretum laxum,* and *Adenocalymna purpurascens*).

Table 6. .Most important plant species in the flooded forest on low basins, according to the importance index, based on 119 plots of 100 m^2 (see Table 3 for column headings).

Species	BA (cm2)	R.D.	Density (ind/ha)	R.A.	Freq.	R.F.	Imp.Ind.
Laetia corymbulosa	53540	17.5	223	40.7	84	70.6	128.8
Luehea cf. tessmannii	104318	34.1	145	26.6	64	53.8	114.4
Pouteria procera	7740	2.5	18	3.2	17	14.3	20.0
Ruprechtia sp.	8637	2.8	11	2.0	11	9.2	14.1
Ficus maxima	16556	5.4	7	1.2	8	6.7	13.4
Ficus trigona	21609	7.1	6	1.1	6	5.0	13.2
Brosimum lactescens	11743	3.8	8	1.4	9	7.6	12.8
Uncaria guianensis	419	0.1	12	2.2	11	9.2	11.5
Pseudobombax munguba	3597	1.2	10	1.8	10	8.4	11.4
Ficus insipida	26682	8.7	2	0.3	2	1.7	10.7
Inga cylindrica	10859	3.5	5	0.9	5	4.2	8.7
Calycophyllum spruceanum	3196	1.0	8	1.4	7	5.9	8.3
Trichilia pleeana	4043	1.3	6	1.1	7	5.9	8.3
Cecropia membranacea	6686	2.2	13	2.5	4	3.4	8.0
Crateva tapia	3165	1.0	6	1.1	7	5.9	8.0
Pithecellobium cf. inaequale	1442	0.5	6	1.1	7	5.9	7.4
Combretum laxum	476	0.2	8	1.5	6	5.0	6.7
Cydista cf. aequinoctialis	243	0.1	7	1.2	6	5.0	6.4
Gustavia hexapetala	959	0.3	7	1.2	5	4.2	5.7
Guarea guidonia	1175	0.4	6	1.1	4	3.4	4.8

As pointed out in the analysis of growth forms, the most abundant species in the flooded forests corresponded to herbs in the genus *Heliconia*. However, it is important to note that the species are different, suggesting that the most abundant species are adapted to the particular environment within the floodplains.

The floristic similarity between the mature and the open-degraded forest for the smallest plants (DBH<1) is evident because they share about half of the most abundant species (Table 8). Graminoids (e.g. *Pharus virescens*), tree seedlings (*Inga* spp. and *Gustavia hexapetala*), and ferns (*Adiantum* cf. *latifolium*), all contributed to this similarity.

The lowest stratum of flooded forest on raised bars is dominated by a shrub, *Psychotria psychotriifolia* (Rubiaceae) that was also observed in open-degraded forests at a much lower density. *Inga cylindrica* seedlings were common in both kinds of flooded forests, as well as some herbs such as *Heliconia* spp. In fact, the seedling of *Inga cylindrica* seem to be the best adapted to grow in the low light and flooded environment of the forest on low basins, where they are at very high densities compared to all other species. Although this species is able to germinate in mature forests, I have never observed a sapling or an adult tree of *Inga cylindrica* in mature forest, suggesting that there are tradeoffs associated with the success of this species in flooded forests. In general, the diversity of *Inga* seedlings was lowest in flooded forests. The most abundant grasses in terra firme forests were absent in the flooded forests (i.e. *Pharus* spp.).

Table 7. Most important plant species in the understory (DBH 1-5 cm) of the four main forest types at Tinigua National Park, in terms of density of individuals.

Mature Forest		Open-Degraded Forest	
Species	**Density (ind/ha)**	**Species**	**Density (ind/ha)**
Attalea insignis	311	*Rinorea lindeniana*	587
Capparis frondosa	311	*Oenocarpus bataua*	383
Hybanthus prunifolius	260	*Petrea maynensis*	244
Oenocarpus bataua	174	*Hybanthus prunifolius*	165
Trichilia tuberculata	172	*Attalea insignis*	133
Clavija ornata	156	*Derris pterocarpus*	108
Talisia nervosa	140	*Ischnosiphon cf. macarenae*	96
Crepidospermum rhoifolium	132	*Combretum laxum*	91
Pseudolmedia laevigata	102	*Gustavia hexapetala*	85
Aniba hostmanniana	97	*Adenocalymna purpurascens*	79
Flooded Forest (on raised bars)		**Flooded Forest (on low basins)**	
Heliconia episcopalis	5300	*Heliconia marginata*	7550
Costus cf. spiralis	300	*Uncaria guianensis*	257
Inga cylindrica	200	*Calathea comosa*	79
Piper fresnoense	150	*Cissus sp.*	79
Socratea exorrhiza	100	*Heliconia episcopalis*	43
Paullinia bracteosa	100	*Combretum laxum*	21
Syagrus sancona	100	*Tetracera willdenowiana*	21
Genipa Americana	100	*Costus cf. Spiralis*	14
Inga marginata	100		
Trichilia pleeana	100		

CONCLUDING REMARKS

There are structural and floristic differences among the forest types as delineated in

the photographic interpretation. The most marked floristic and structural differences were found when comparing terra firme and flooded forests, and the floristic differences were more accentuated among flooded forest subtypes than among terra firme forest subtypes. In fact, aside from a few examples of species restricted to the open-degraded forest (e.g. *Guadua angustifolia*), almost all terra firme species could be found in both subtypes of forests, and some of the most important species are shared. Even the presence of bamboo is not homogeneous among open-degraded forest as defined by the photo-interpretation. There is no simple way to associate open-degraded forest with the abundance of any particular species. It is possible to use the best candidates such as bamboo, if the slope of the terrain is included in the maps, because bamboo is rarely present in open-degraded forests on flat terrain.

Table 8**.** Most important plant species on the ground (DBH<1cm) in the four main forest types at Tinigua National Park, in terms of density of individuals.

Mature Forest		Open-Degraded Forest	
Species	**Density (ind/ha)**	**Species**	**Density (ind/ha)**
Inga spp.	12850	*Pharus virescens*	12606
Pharus virescens	8567	*Adiantum cf. latifolium*	6525
Gustavia hexapetala	6283	*Inga spp.*	5922
Calathea micans	3367	*Gustavia hexapetala*	3777
Capparis frondosa	3267	*Platypodium elegans*	2535
Adiantum cf. latifolium	3050	*Oenocarpus bataua*	2323
Brosimum alicastrum	2750	*Calathea micans*	2163
Oenocarpus bataua	2367	*Petrea maynensis*	1684
Pharus latifolius	2200	*Rinorea lindeniana*	1649
Castilla ulei	2150	*Hybanthus prunifolius*	1507
Flooded Forest (on bars)		**Flooded Forest (on low basins)**	
Psychotria psychotriifolia	83438	*Inga cylindrica*	20580
Inga cylindrical	11250	*Heliconia marginata*	2991
Sanchezia pennellii	7813	*Cecropia membranacea*	1786
Inga marginata	5313	*Laetia corymbulosa*	1116
Syngonium podophyllum	5000	*Piper fresnoense*	982
Heliconia episcopalis	5000	*Piper phytolaccaefolium*	714
Monstera cf. dilacerata	4375	*Ficus maxima*	625
Trophis racemosa	4375	*Trichostigma octandrum*	580
Acroceras zizanioides	3750	*Brosimum lactescens*	536
Inga cf. marginata	2813	*Panicum sp.*	491

One should be cautious about separating terra firme forests mainly in structural terms because forest dynamics could change a patch of mature forest into an open-degraded forest if there is a high frequency of tree falls. The reverse process could occur in the absence of frequent tree falls, as happens on steep slopes or close to changing watercourses. Therefore, the delimitation of these forests has a dynamic nature and their limits are not expected to be constant through time. In fact, some parts of the

phenological transects that were established ten years ago could now be better classified in a different terra firme forest type.

Contrary to our previous assumptions (Stevenson *et al*., 1994), the open-degraded forests are as or more diverse than the mature forest (Table 2 and Fig. 4). This result supports the intermediate disturbance hypothesis (Connell, 1979), as it has been documented in previous studies in tropical forests (Phillips *et al*., 1994), especially if the hostile conditions associated with flooding are considered large disturbances. It remains to be explored if the differences in diversity are the result of an increased number of stems, as was found for other tropical forest (Hubbell et al. 1999).

We were unable to find any consistent floristic associations in terra firme forests, as were proposed in previous studies (Barbosa and Hirabuki 1992). In contrast, the main floristic differences were well correlated with the different soils and habitat conditions imposed by river dynamics (e.g. flooding level). Such differences could be expected to represent adaptations to soil conditions.
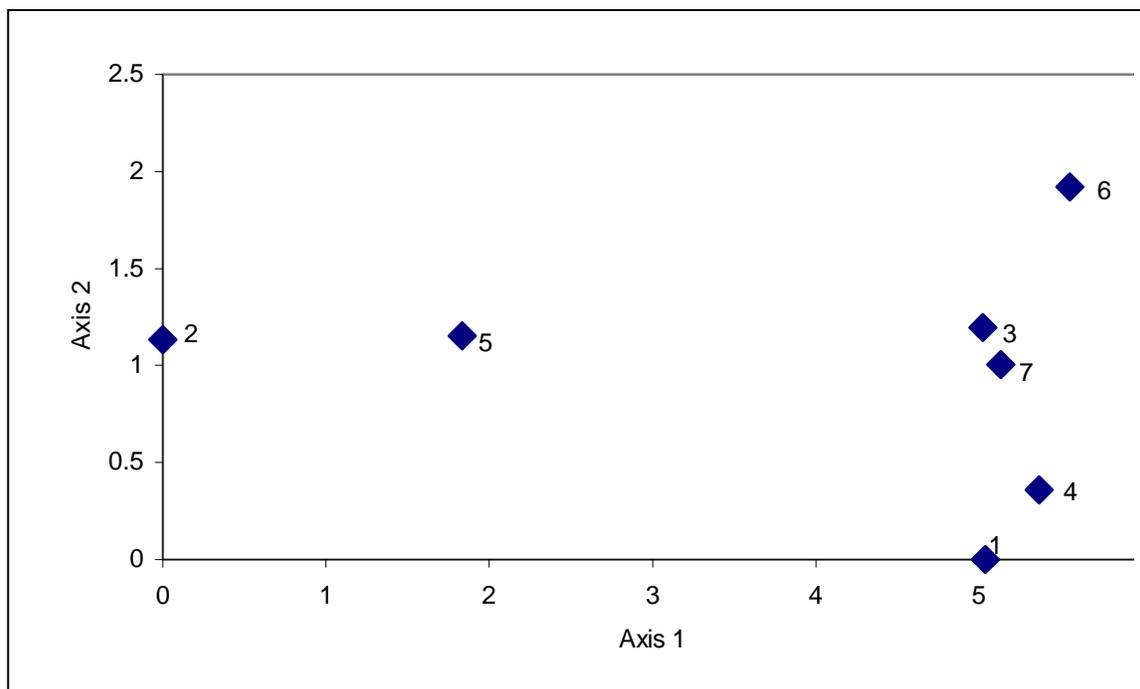

Fig. 6. Ordination of seven one-hectare inventories on different forest types at Tinigua Park, based on the density of individuals of all species greater than 5 cm DBH. 1 and 4= mature forest; 3 and 6= open-degraded; 2=flooded forest on low basins; 5= flooded forest on raised basins, and 7 a mixture of terra firme forests.

REFERENCES

Barbosa, C. 1992. Preliminary list of plats collected at the Centro de Investigaciones Primatológicas La Macarena (CIPM), Tinigua National Park, Colombia. *Field Studies of New World Monkeys La Macarena Colombia* 6: 25-41.
--------------- & Y. Hirabuki. 1992. Notas sobre la vegetación y algunas de sus relaciones con primates en la margen derecha del rio Duda, Serranía Chamuza, Macarena (Meta, Colombia). Inderena, Bogotá.
--------------- A. Nishimura, & P. R. Stevenson. 1990. List of plants collected in the study area, La Macarena, Colombia I. *Field Studies of New World Monkeys, La Macarena, Colombia* 3: 49-55.
Botero, P. 1998. Paisajes fisiográficos de la Orinoquia-Amazonia (ORAM), Colombia. *Analisis Geográficos* 27-28: 1-317.
Connell, J. H. 1979. Intermediate-Disturbance Hypothesis. *Science* 204: 1345-1345.
Duivenvoorden, J. F. 1996. Patterns of tree species richness in rain forests of the Middle Caquetá Area, Colombia, NW Amazonia. *Biotropica* 28: 142-158.
Garcés, D. M., & S. de La Zerda. 1994. *Gran Libro de los Parques Nacionales de Colombia*. Intermedio Editores/ Círculo de Lectores, Bogotá.
Hara, M., Y. Hirabuki, A. Takehara, C. Barbosa, & T. Ohba. 1999. Vegetation succession on the floodplain of the Rio Duda, Colombian Amazonia. *Field Stuedies of Fauna and Flora La Macarena Colombia* 13: 311-40.
Hirabuki, Y. 1990. Vegetation and landform structure in the study area of La Macarena: A physiognomic investigation. *Field Studies of New World Monkeys, La Macarena, Colombia* 3: 35-48.
---------------- & C. Barbosa. 1992. Architecture of the hill-crest type forest in the upper Colombian Amazon. *Field Studies of New World Monkeys La Macarena Colombia* 7: 43-53.
Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, & S. L. de Lao. 1999. Light-cap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554-557.
Idrobo, J. M. 1967. Un breve informe sobre las expediciones que han entrado a la Reserva Nacional de La Macarena. : 217-243.
Kimura, K., A. Nishimura, K. Izawa, & C. A. Mejia. 1994. Annual changes of rainfall and temperature in the tropical seasonal forest at La Macarena Field Station Colombia. *Field Studies of New World Monkeys. La Macarena, Colombia* 9: 1-3.

Phillips, O. L., P. Hall, A. H. Gentry, S. A. Sawyer, & R. Vasquez. 1994. Dynamics and Species Richness of Tropical Rain-Forests. *Proceedings of the National Academy of Sciences of the United States of America* 91: 2805-2809.

PRORADAM. 1979. *La Amazonia Colombiana y sus Recursos.* Instituto Geográfico Agustín Codazzi-CIAF, Bogotá.

Stevenson, P. R. 1995. Informe del área muestra Macarena-Llanos. Proyecto ORAM. Instituto Geográfico Agustín Codazzi, Subdirección de Geografía, Bogotá.

-------------------- 2002. Frugivory and seed dispersal by woolly monkeys (Lagothrix lagothricha) at Tinigua National Park, Colombia. PhD. dissertation, SUNY at Stony Brook, New York.

Stevenson, P. R., M. C. Castellanos, & M. P. Medina. 1999. Elementos arbóreos de los bosques de un plano inundable en el Parque Nacional Natural Tinigua, Colombia. *Caldasia* 21: 38-49.

-------------------- M. J. Quiñones, & J. A. Ahumada. 1994. Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at La Macarena, Colombia. *American Journal of Primatology* 32: 123-140.

-------------------- M. J. Quiñones, & M. C. Castellanos. 2000. *Guía de Frutos de los Bosques del Río Duda, La Macarena, Colombia.* Asociación para La Defensa de La Macarena - IUCN, Santafé de Bogotá.

Suescún, M. 2002. Estructura, composición florística y diversidad de tres tipos de bosque en el Parque Nacional Tinigua, La Uribe, Meta, Colombia. Tesis de Pregrado, *Departamento de Ciencias Biológicas.* Universidad de Los Andes, Bogotá.

Takehara, A., & P. R. Stevenson. 1997. Stem Size Data of some Mono-species dominated Forests in La Macarena, Colombia. *Field Studies of Fauna and Flora, La Macarena, Colombia* 11: 57-71.

ter Braak, C. J. F. 1987. CANOCO- a Fortran program for community ordination by partial, detrended, canonical correspondence analysis, principal components analysis and redundancy analysis. Wageningen, The Netherlands.

Terborgh, J. 1983. *Five New World Primates. A study on comparative ecology*. Princeton University Press, Princeton.

Universidad de Antioquia. 1989. Diagnóstico Ambiental del Departamento de Caquetá. Selección viable del trazado de la vía La Uribe-San Vicente del Caguán. Centro de Investigaciones Ambientales, Medellín.

Universidad Nacional de Colombia. 1989. *La Macarena Reserva Biológica de la Humanidad. Territorio de Conflictos.* Centro Editorial, Universidad Nacional de Colombia, Bogotá.

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Sampling methods used to quantify activity patterns and diet: A comparative example using woolly monkeys (*Lagothrix lagothricha*)

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There are several sampling methods that allow the quantification of animal behavior (Altmann, 1974; Lehner, 1979; Martin & Bateson, 1993). Continuous and scan sampling are among the two most frequently used methodologies to quantify activity budgets and the relative proportion devoted to different diet categories. For instance, the diet of woolly monkeys has been described using a variety of methods including stomach contents (Izawa, 1975; Milton & Nessimian, 1984), frequency of feeding observations (Soini, 1986), continuous focal animal sampling (Stevenson, 1992; Stevenson et al., 1994; Dew, 2001), and scan sampling (i.e. Peres, 1994; Defler & Defler, 1996; Di Fiore & Rodman, 2001). However, it is not clear if the results from different protocols are comparable.

Quantification of diet and activity budgets is important for conservation purposes and may provide the base line to test hypothesis about the interaction between ecology and sociality. For example, moving time and daily distance covered by woolly monkeys are known to vary depending on the degree of intra-specific competition, habitat quality, and seasonal fruit production (Stevenson & Castellanos, 2001). Models based on socio-ecological conditions in different study sites might be tested by their predictive power of activity budgets, only if the results obtained by different methods are readily comparable. The main aim of this note is to describe the results of activity patterns and diet composition of woolly monkeys using different sampling methods simultaneously during an intensive sampling period, and to discuss the pros and cons of each sampling regime. An additional goal is to show the degree of variability in diet and activity patterns among consecutive days, which might have implications in data analyses (Jiménez et al. 1998). Finally, we will assess whether consecutive point samples are independent from each other for different time intervals.

METHODS

The observations were made on a group of *Lagothrix lagothricha* (CR12) that had been previously studied by the authors for more than 13 months (Stevenson *et al*., 1994), in Tinigua Natural Park, Colombia. The observations were made during the rainy period (June and July). A total sampling time of 110 hours was completed during 15 days. The daily observations varied from one hour to 9 hours of continuous sampling, depending on weather

conditions. Four main sampling protocols were used as a combination of different sampling and recording rules (Martin & Bateson, 1993).

The following sampling regimes were used:

1. **Continuous focal animal**: The preponderant activity performed by the focal animal was recorded each minute during the sample period. Activities were quantified as events instead of states (as it is usual in continuous focal animal sampling) because we used G test analyses based on frequencies (Sokal & Rohlf, 1995), to allow comparisons with scan and instantaneous scores.

2. **Instantaneous sampling on the focal animal**: Instantaneous observations were recorded for the same focal animal every 5 minutes. When the observer did not have a good visibility over the focal animal no information was recorded. These data were analyzed in three different ways: a set of the total number of observations and two sets of data arranged with alternating observations recorded every 10 minutes.

3. **General scan sampling**: Information on activity patterns and diet was recorded every five minutes, for all visible group members. In this method the position of the observer was not constrained to any particular animal.

4. **Scan sampling following a focal animal**: Instantaneous samples were made on all visible animals every five minutes, while following the same focal animal. The activity of the focal animal itself was not included in the analysis in order to make the results independent from the second sampling regime.

The activities were classified into the following categories: moving, resting, social interactions and feeding (Stevenson et al., 1994). Social interaction results were not included in statistical analysis due to the small sample size. The ingested items were classified in three main categories: arthropods, leaves and fruits.

In order to measure the variation among different sample days, we calculated coefficients of variation (Sokal & Rohlf 1995) for each activity. For this analysis data was extracted from five days, when long sampling periods were achieved.

To determine the sequential independence among sampling points we first generated a null distribution, from one thousand random sequences (maintaining the proportion of scores in each activity constant, as the average for the study period). Then we compared the number of runs from real data, to the distribution of runs from the random bootstrapped data. In this sense, one run corresponds to all contiguous scores recording the same activity (Sokal & Rohlf, 1995). We used a conservative probability for the tests ($p<0.01$), otherwise the lack of independence may be overestimated because adjacent scores in the same activity do not always reflect the same activity bout. The number of samples analyzed was kept constant at 72 (a complete day of samples every 10 min), so that instantaneous samples every ten minutes were complemented with samples from independent adjacent days, and sub-samples were extracted from one day follows of five and one minute sampling intervals.

RESULTS

Table 1 represents the percentages of activities and diet found using the different methods. We found significant differences in activity budgets among different methods (G=20.7, p<0.05). The main differences were found for the values of movement and rest (G=5.7 and G=12.6 respectively, p <0.05 for both). Higher movement estimates were obtained using scan sampling methods that using continuous focal sampling. On the other hand, resting estimates were higher when recorded by the continuous sampling method than when using the scan method. No significant differences were found for overall feeding activities (G=2.4, p>0.05). However, there were differences in the frequencies in which different methods quantified different food types (G=13.7, p<0.05). This was especially due to the differences found for the estimates of arthropod and fruit feeding (G=5.5 and G=6.6 respectively, p<0.05 for both), while the category feeding on leaves did not show significant differences (G=1.7, p>0.05). The scan method without location constraints showed the most extreme estimates (Table 1).

Table 1. Activity budgets and diet composition of Colombian woolly monkeys using different sampling methods. S.I. = Social Interactions, N= total number of observations.

	Moving	Resting	S.I.	Feeding	Arthropods	Leaves	Fruits	N
Continuous	22	51	2	25	26	7	66	6601
Instantaneous	33	27	4	37	26	9	64	1021
Inst. Set 1.	33	30	4	33	28	9	64	511
Inst. Set 2.	31	26	3	40	24	11	65	510
Scan	41	24	7	29	42	5	43	1267
Scan & Focal	49	17	6	28	25	13	62	670

An analysis of variation using instantaneous samples each ten minutes to measure activity budgets and diet showed large amounts of variation among days. The average coefficient of variation was 55% and fruit feeding was the least variable (moving 29%, resting 42%, social interactions 65%, feeding 39%, feeding on leaves 151%, on insects 42%, and fruits 19%).

The five sampling days of continuous sampling showed lack of sequential independence between data points. The number of runs was always less than the critical point expected from a random sequence (14, 21, 24, 23, and 32 << 38). The instantaneous samples every 5 minutes were independent in one case, and clearly not independent in another case. In the three remaining cases the number of runs was close to the critical value (42, 39, 38, 37, and 33;). In contrast, the instantaneous scores every 10 minutes were usually independent. Only once out of the five cases, the number of observed runs was significantly less than the expected according to the bootstrapped distribution (54, 49, 46, 40, and 32; p<0.01 for runs < 38).

DISCUSSION

Continuous focal sampling was very demanding in terms of observational effort in the field. However, it was free from observer attention bias (see below). Another advantage of this method is the possibility to make sequential analyses in order to predict activity patterns along time (Altmann, 1974). It requires attention, training, and ability from the observer to follow one focal animal for long periods, and it demands effort to register data continuously while following a single animal thorough the forest. Using this method, we found high percentages of resting and low values in moving. These differences may be related to the possible bias when we assigned one activity for each minute, because activities within minutes were not measured and thus there was some degree of subjectivity in these records. However this problem can be overcome in the more traditional recording rule when only changes of activity are noted and time is considered as a continuous variable (Altmann, 1974), instead as frequencies as in our analyses. However, this approach may be difficult to carry out for activities of short duration (e.g. feeding on insects, Stevenson, 1992), the use of this method has been recommended in combination with measurements of the feeding rates to quantify primate diets (N.R.C. 1981; Stevenson, 2002). This protocol can be used to estimate actual nutrient intake, if there is information available on food weight and nutritional content.

Instantaneous sampling following a focal animal was less demanding than continuous focal sampling. It requires the ability to follow a focal animal, but at the same time it allows more time to record each observation and to find a good location to register each observation. This type of sampling avoids bias with respect to the location of the observer because it depends on the focal animal's position. This method allows the recording of short activities, and the frequency of such activities can be registered. However, rare activities are difficult to analyze because of the inherent assumptions of statistical analyses based on frequencies (Sokal & Rholf, 1995).

Remarkably, the two independent sets of instantaneous sampling each 10 min. lead to very similar results. This indicates that although the instantaneous samples represent only a small part of the activity of the animals, they provide a very consistent method to record activity budgets. It is important to point out that the time among instantaneous samples depends on the variability of the activities of the species, so that less spacing time between samples is recommended for species with more variation in the behavior (Martin & Bateson, 1993). Furthermore, the sampling points should be spaced enough so each observation is independent of each other.

Scan sampling without a predetermined position was the easiest methodology to carry out. However, it has been suggested that this method can lead to biased estimates because it tends to overestimate the activities that attract the attention of the observer (Altmann, 1974). In this study, moving animals seemed to be more visible to the observer and the activity budget in turn overestimates moving scores. In the same way the high values found for the category of social interactions can be biased because interactions such as mating and playing seemed to attract the observer's attention, producing a systematic bias in the observations.

This method also led to differences in diet composition. According to this technique, the frequency of samples that the monkeys were observed feeding on fruit was very low. Nonetheless, there are difficulties in the observation of this activity due to the preference of woolly monkeys to feed on fruits on the higher crowns in the forest (Stevenson & Quiñones, 1993), animals feeding on fruits can attract the attention of the observer by the noise of falling fruit parts. Interestingly, the studies using scan sampling to measure diet composition showed high percentages of fruit feeding (i.e. Peres, 1994; Defler & Defler, 1996), but we ignore how much these estimates are biased by the mentioned factors.

The only advantage we consider for using this method is it allows direct comparisons among group members. For instance, it has been suggested that both adult woolly monkey males and females with dependent infant (< 1 yr.) consumed more fruit than the other females and the juveniles, and that the latter age/sex classes consume more arthropods than the former classes (Stevenson, 1992). Those results were not conclusive because those observations were made only on focal animals of each age/sex classes in different periods and the differences could also be attributed to changes in the temporal availability of resources. Scan sampling may be useful to answer those kinds of questions. Interestingly, the mentioned trend among age/sex classes was evident in this study (Table 2). However, this potential problem can also be solved by using a rotation protocol to assure that each age/sex class is sampled within the same environmental conditions.

Table 2. Percentage of scan samples devoted by four different age/sex classes of woolly monkeys to ingest different food items (n=366), during an intensive study period at Tinigua Park.

	Arthropods	Leaves	Fruits
Adult male	32	7	51
Female with dependent infant	35	1	65
Adult female without young infant	44	4	41
Juvenile	49	5	35

Scan with focal animal showed the advantage of lowering the problems related to the arbitrary location of the observer, but the results seemed to be biased towards conspicuous activities (i.e. high frequencies of movement and low frequencies of resting), as with *ad libitum* scan sampling.

In summary, it is clear that different observational methods may lead to different results, even looking simultaneously at the same animals and thus results obtained using different methods are not easily comparable. Although focal animal rules require more effort than other methods, it is recommended because it lowers the possibility of systematic biases associated by the observer's attention and location in the field. Instantaneous samplings on focal animals are useful to quantify activity budgets and diet composition. However, in order to determine the accurate composition of the diet, we recommend continuous focal

animal sampling methods in combination with estimates of the feeding rates and the weight of the ingested food. Many of these recommendations have been known for a long time (Altmann, 1974), and we hope that this study will help in the standardization of observational methods that could result in an accurate description and broader use of the results.

It has been pointed out that pooling behavioral data from different days is not adequate in statistical terms if there is significant variation among them (Jiménez et al. 1998). Although we found considerable variation in diet and activity among consecutive days, it is not obvious how we should solve the problem of pooling days to analyze seasonal trends. During the study period for example, woolly monkeys usually crossed at least once a day from mature forest to flooded forest, where they fed on fruits from species specialized on floodable soils such *Laetia corymbulosa* (Flacourtiaceae) and *Cecropia membranacea* (Cecropiaceae)(Stevenson et al. this volume). This pattern implies that there is also variation in diet within a sampling day session, therefore an analysis among days (Jiménez et al., 1998) does not cancel out the issue of pooling variable samples because daily samples are not homogeneous. Unfortunately, ANOVA tests that could help in nesting the variation within samples are not designed for frequency data (like instantaneous points).

Finally, we found that samples recorded one minute and five minutes apart show non sequential independence among data points. This fact can overestimate the degrees of freedom in statistical tests (including the analysis in table 1).The lack of independence may be common in this type of analysis; however, assumptions about independence are rarely tested. Thus, time should be the variable to measure in continuous sampling methods and instantaneous point should be adequately separated in time or degrees of freedom should be corrected. According to our results we should recommend the use of ten minutes instantaneous intervals to measure activity budgets of woolly monkeys, given that only in one fifth of the cases the analysis showed lack of independence. Interestingly, similar analyses with a larger data set collected over three years has shown a larger proportion of non independent day samples for woolly monkeys using instantaneous samples ten minutes apart (37%, n=156, Stevenson in prep.). It seems like there is more chance to find lack of sequential independence for hot seasons and low-fruit availability periods, when resting periods tend to be longer (and the number of runs smaller) than in the middle of the rainy season. If the degree of sequential independence is not known for a species, we recommend bootstrapping techniques before data gathering, in a similar way to the one used in this paper to determine the time interval between instantaneous samples.

REFERENCES

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.

Defler, T. R., & S. B. Defler. 1996. Diet of a group of *Lagothrix lagothricha lagothricha* in Southeastern Colombia. *International Journal of Primatoogy.* 17: 161-189.

Dew. 2001. Synecology and Seed Dispersal in Woolly Monkeys (*Lagothrix lagotricha poeppigii*) and Spider Monkeys (*Ateles belzebuth belzebuth*) in Parque Nacional Yasuni, Ecuador. PhD dissertation, *Department of Antrhopology*. University of California, Davis.

Di Fiore, A., & P. S. Rodman. 2001. Time allocation patterns of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in a neotropical terra firma forest. *International Journal of Primatology* 22: 449-480.

Izawa, K. 1975. Foods and feeding behavior of monkeys in the upper Amazon basin. *Primates* 16: 295-316.

Jiménez, I., J. Aldana, D. Cadena, & J. Forero. 1998. How does the diet of a curassow varies within a week? *Field Studies of New World Monkey La Macarena Colombia* 12:33-40.

Lehner, P.N. 1979. Handbook of Ethological Methods. Garland STPM Press. New York.

National Research Council (NRC). 1981. Technics for the study of primate population ecology. National Academy of Sciences. Washington D.C.

Martin, P. & P. Bateson. 1993. Measuring Behaviour: An Introductory Guide. Cambridge University Press, Cambridge.

Milton, K., & J. L. Nessimian. 1984. Evidence for insectivory in 2 primate species (*Callicebus torquatus lugens* and *Lagothrix lagothricha lagothricha*) from Northwestern Amazonia. *American Journal of Primatology* 6: 367-371.

Peres, C. A. 1994. Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagothricha cana*) in Central Amazonia: Comparisons with other Atelines. *International Journal of Primatology* 15: 333-372.

Soini, P. 1986. A synecological study of a primate community in the Pacaya Samiria National Reserve, Peru. *Primate Conservation* 7: 63-71.

Stevenson, P.R. 1992. Diet of Woolly Monkeys (*Lagothrix lagotricha*) in la Macarena, Colombia. *Field studies of New World Monkeys, La Macarena. Colombia.* 6:3-14.

-------------------- 2002. Frugivory and seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colomiba. PhD dissertation. SUNY at Stony Brook, New York.

-------------------- & M. C. Castellanos. 2001. New evidence for large variations in daily path length related to differences in habitat quality in troops of Colombian Woolly Monkeys, *Lagothrix lagothricha* (abstract). Pp. 446. *The XVIII Congress of the International Primatological Society*, Adelaide, South Australia.

-------------------- & M. J. Quiñones. 1993. Vertical stratification of four New World primates, at Tinigua National Park, Colombia. *Field studies of New World Monkeys, La Macarena. Colombia* 8:11-18.

--------------------- M.J. Quiñones & J.A. Ahumada. 1994. Ecological strategies of woolly monkeys (*Lagotrhix lagotricha*) at La Macarena, Colombia. *American Journal of Primatology*. 32:123-140.

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Seed Shadows Generated by Woolly Monkeys (*Lagothrix lagothricha*) within their Home Range

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ABSTRACT

A seed shadow can be defined as the spatial distribution of seeds in the environment, and it is the starting point in a chain of interactions that ultimately determine the distribution of adult plants. The purpose of this study was to describe the seed shadows generated by woolly monkeys (*Lagothrix lagothricha*) and to explore some of the factors that produce them. We carried out observations on focal woolly monkeys during sixty hours per month for two years at a tropical rain forest in Tinigua National Park (Colombia). We tried to collect all fecal samples from the focal animals, dispersed seeds were identified, and the location of droppings and feeding trees was recorded in maps. In general, woolly monkeys disperse seeds over the entire home range. The dispersion patterns of the trees upon which they feed is more clumped than the distribution of dispersed seeds for the great majority of species analyzed. However, they have some potential to generate aggregated regeneration patterns, given that the distribution of droppings is usually clumped. This conclusion varies according to the spatial scale used in the analyses and depends also on sampling size.

Key Words: Seed shadows, seed dispersal, spatial patterns, woolly monkeys (*Lagothrix lagothricha*), Tinigua Park.

INTRODUCTION

It has been postulated that seed dispersal has a profound influence on the demography of plants populations (Schupp *et al*., 1995). The majority of the species in tropical humid forests have fleshy fruits dispersed by endozoochory (Chapman, 1995), and thus animals vectors may influence the spatial distribution of seeds. These seed shadows are the starting point of a chain of processes that finally determine the location of adult plants, which is one of the most important questions in population ecology. The spatial distribution of trees in turn affects the foraging patterns of animals. For these reasons, several factors and hypothesis have been proposed to explain the spatial location of plants and different theories have been formulated. For example, Janzen (1970) predicted a uniform distribution of individuals within plant populations, based on the escape hypothesis. If the seeds with the highest chance of survivorship are the ones dispersed away from parental plants (those that are less subjected to the high predation and competition risks below the parent tree or other trees of the same species), then one could

expect to find the highest recruitment probabilities at intermediate distances between conspecifics. This pattern will ultimately lead to a homogeneous distribution of individuals of each species in the forest. Although it is known that many tropical tree species gain benefits according to the Escape Hypothesis, there is evidence that many others do not fit the expected pattern (Augspurger, 1983; Clark & Clark, 1984; Condit et al., 1992; Terborgh et al., 1993). In fact, there is strong evidence showing that the great majority of tropical tree species have clumped spatial distributions (Condit et al., 2000; Hubbell, 1979). This evidence suggests that besides the possible patterns of mortality near conspecifics (Wills et al., 1997), there are many other factors determining the final location of the trees in the forest.

It has been postulated that the clumped distributions may be the cause of non-homogeneous patterns of ranging and defecation by frugivores (Fleming & Heithaus, 1981; Lieberman et al., 1979; Milton, 1980), or by environmental heterogeneity limiting species distributions to restricted patches with adequate conditions for development (Fowler, 1988). Although there are many studies that demonstrate limited spatial distribution within particular communities, there are very few studies documenting the importance of dispersers as the ultimate factor causing clumped plant distributions (Dinerstein, 1991; Thery & Larpin, 1993; Tutin *et al*., 1991, Fragoso, 1997; Julliot, 1997). The aim of this study was to describe the seed dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) in terms of the distribution of dispersed seeds shadows within the home range of the study group.

On large spatial scales, preliminary studies have shown that the seed shadows generated by a group of woolly monkeys within its home range are highly correlated to the patterns of habitat use (Stevenson *et al*., 1997). This finding is not surprising since woolly monkeys defecate on average more than once each hour (Stevenson, 2000, 2002). Since woolly monkeys usually range widely over the home range, it could be postulated that the seed shadows will be overdispersed in the home range. However, given that the majority of the seeds are deposited in resting places (Stevenson et al., 1997), woolly monkeys might produce clumped spatial distributions. In this paper we test these alternatives, as well as the relationship between the spatial distribution of fruiting trees and seed shadows within the home range of the study group at different spatial scales.

Finally, it has been argued that the distribution of fruiting trees determines the patterns of habitat use in woolly monkeys (Stevenson et al., 1994). Thus it might be expected that the areas with highest densities of fruiting trees during a given season would be the places of highest seed rain. On the other hand, it was found that woolly monkeys rarely (ca. 1%) drop seeds below the parental plant (Stevenson, 2000), thus it is uncertain if they really leave clumps of seeds near parental plants or plants of the same species.

METHODS

The study took place in a humid lowland forest in Tinigua Park, Colombia (for more

information about the study site see Stevenson 2002, and this volume). We carried out behavioral observations on focal individuals of a habituated group of woolly monkeys, CR-12 (initially described in Stevenson et al. 1994). We completed sixty hours of focal samples per month for two years (August 1996-July 1997 and February 2000-January 2001). Observations were evenly distributed across all hours of the day (from 6:00 to 18:00 hr). We noted the location and forest type of the focal animal using instantaneous samples every 30 min. We registered the location of the trees visited for fruit feeding and drew these trees on a map of the study area. Trails marked at least every 50 m, in addition to four years of experience following monkeys in this forest, helped us to determine the location of the focal animal and the route. Whenever possible, we collected all depositions of the focal individual falling to the floor or low vegetation during the sampling periods. We stored feces in marked plastic bags usually for one day before analysis, and then we washed the fecal samples, counted, and identified all seeds.

We plotted the distribution of adult trees and dropping location for the 24 plant species most abundant in defecations on a map with one-hectare grids. Spatial correlations among the number of droppings and the number of trees in each one-hectare plot were calculated, as well as correlations between the number of droppings and the instantaneous scores of habitat use. We carried out a similar analysis using a larger scale, pooling data from plots of similar forest type. In this case the area for each sample was approximately 10 hectares. We used Lloyd's dispersion index (Lloyds, 1967) to characterize the degree of aggregation of both droppings and fruiting trees. Index values close to one indicate random spatial distributions, and greater values indicate clumped distributions.

RESULTS AND DISCUSSION

The seed shadows of the 24 plant species studied were, in general, positively correlated to the overall patterns of habitat use. In fact, I found significant correlation coefficients between the frequency of droppings containing seeds of these species and overall frequency of use in the one-hectare grid for all species but one (Table 1). Using the larger scale, the same analysis showed, in general, larger correlation coefficients, but a lower proportion of the species showed significant coefficients (Table 1). About one-third of these cases correspond to species restricted to the flooded forests (e.g. *Cecropia membranacea, Inga cylindrica,* and *Laetia corymbulosa*).

Given that habitat use seems to be in large part determined by fruit abundance, it is expected that seed shadows would be correlated with the distribution of fruiting trees. However, this pattern was not found for one-third of the species analyzed using the one-hectare grid, and the proportion was even lower for the larger spatial scale (Table 1). It is unlikely that the dispersed seeds will suffer the negative density or distance dependent effects predicted by the escape hypothesis, because these effects are known to occur at small spatial scales (Howe et al, 1985; Wills et al., 1997), and only 7% of the droppings were defecated below crowns of fruiting trees of the same species.

Both the distribution of droppings within the home range and the distribution of fruiting trees were highly clumped. The Lloyd's dispersion indices indicated, however, that the distribution of fruiting trees is more clumped than the distribution of droppings, especially at low spatial scales (e.g. one-hectare quadrants, Table 2). The sample size used to estimate the distribution of droppings was not high (<300, Table 2), considering the droppings could be distributed in 171 ha. the seed shadows on the home range was calculated from a small proportion of dispersed seeds recovered over a two year period with focal animals being followed for 5 days per month.

Table 1. Spatial autocorrelation coefficients between seed shadows and habitat use, and between seed shadows and the distribution of parental trees used by the woolly monkeys during the study. The coefficients are shown in two columns where the analyses were done at different scales: in a grid of one-hectare squares (Ha) and at a larger scale comprising about 10 ha of similar forest types (≈10 Ha).

Species	Droppings vs. Habitat Use		Droppings vs. Parental Trees		Sample Size	
	Ha	≈10 Ha	Ha	≈10 Ha	Droppings	Trees
Apeiba aspera	**0.48**	**0.64**	**0.35**	**0.60**	133	18
Bursera inverse	0.11	0.27	0.00	-0.11	84	9
Castilla ulei	**0.63**	**0.81**	**0.17**	**0.63**	102	36
Cecropia membranacea	**0.49**	0.28	**0.30**	0.51	300	136
Cecropia sciadophylla	**0.44**	**0.77**	0.04	**0.54**	201	12
Crepidospermum rhoifolium	**0.45**	0.50	0.08	0.25	50	52
Garcinia macrophylla	**0.35**	**0.85**	0.09	0.21	40	20
Genipa Americana	**0.37**	0.19	-0.04	-0.18	42	5
Gustavia hexapetala	**0.42**	0.47	**0.40**	**0.64**	184	232
Helicostylis tomentosa	**0.31**	**0.69**	**0.28**	**0.77**	60	16
Hyeronima alchorneoides	**0.47**	**0.63**	0.09	**0.79**	34	6
Hymenaea oblongifolia	**0.28**	0.42	**0.18**	0.20	78	14
Inga alba	**0.38**	0.42	**0.30**	**0.58**	73	17
Inga cf. acreana	**0.49**	**0.75**	**0.44**	**0.87**	47	18
Inga cylindrical	**0.28**	0.42	**0.34**	0.71	116	35
Inga edulis	**0.48**	**0.66**	**0.40**	0.32	105	78
Jacaratia digitata	**0.60**	**0.75**	0.14	0.01	147	18
Laetia corymbulosa	**0.43**	0.45	0.06	-0.01	132	21
Pourouma bicolor	**0.40**	**0.81**	**0.25**	**0.86**	147	65
Protium sagotianum	**0.50**	**0.84**	**0.32**	**0.79**	120	101
Pseudolmedia laevigata	**0.54**	**0.75**	**0.16**	**0.58**	63	40
Simarouba amara	0.18	**0.82**	0.09	**0.67**	28	12
Spondias mombin	**0.46**	**0.55**	**0.29**	0.38	69	27

Thus, given the extensive use of the home range by the study group, it is possible that the actual seed shadows generated by the whole population of woolly monkeys over the years is less clumped than the sampled seed shadow. This suggestion was supported by the fact that the great majority of the plant species analyzed showed more clumped distributions when the data from the first year were analyzed than at the end of the study, using data from

two years (Table 2). Both the distribution of droppings and trees were less clumped when the large spatial scale is considered, except for some species restricted to particular habitat types, such as *Cecropia mambranacea, Inga cylindrica* and *Laetia corymbulosa*, which are confined to some areas of the flooded forest (Stevenson et al., this volume).

Table 2. Spatial distribution of droppings and fruiting trees according to the Lloyd's dispersion index within the home range of the main study group of woolly monkeys at Tinigua. The indices for droppings distribution were calculated twice: at the end of the first year, and at the end of the two-year study.

	Lloyd's Dispersion Index				
	Ha			10 Ha	
Species	Droppings		Trees	Droppings	Trees
	One Year	Total			
Apeiba aspera	12.1	6.4	24.7	2.1	2.6
Bursera inverse	113.5	52.7	44.8	5.0	5.1
Castilla ulei	10.9	6.7	13.2	1.8	2.7
Cecropia membranacea	6.2	6.3	20.3	2.2	10.5
Cecropia sciadophylla	6.5	4.6	32.8	2.1	4.5
Crepidospermum rhoifolium	16.0	11.5	10.6	2.3	1.8
Garcinia macrophylla	27.6	14.1	20.0	3.3	3.0
Genipa Americana	17.4	16.1	87.2	2.6	6.5
Gustavia hexapetala	8.7	5.4	4.2	2.0	1.7
Helicostylis tomentosa	13.8	8.1	25.5	1.8	4.6
Hyeronima alchorneoides	53.8	17.3	60.5	3.0	4.4
Hymenaea oblongifolia	12.2	9.6	27.8	1.6	3.3
Inga alba	18.5	9.8	25.1	2.7	3.2
Inga cf. acreana	72.6	12.5	26.9	2.6	4.6
Inga cylindrical	6.3	6.9	22.5	1.9	8.6
Inga edulis	11.0	8.3	21.5	2.0	5.0
Jacaratia digitata	8.2	6.0	23.5	1.7	3.1
Laetia corymbulosa	13.2	7.1	44.5	2.0	8.9
Pourouma bicolor	6.1	5.6	7.2	2.1	3.2
Protium sagotianum	12.1	5.5	6.0	1.6	2.2
Pseudolmedia laevigata	18.3	11.3	12.0	1.9	2.6
Simarouba amara	19.2	18.5	30.2	2.9	3.3
Spondias mombin	12.9	8.8	21.9	1.9	2.7
Average	21.6	11.3	26.6	2.3	4.3

In conclusion, the distribution of dispersed seeds within the range of the monkeys suggests that the woolly monkeys in this area are playing the role of over-dispersing the seeds, as could be inferred from comparison of the indices of dispersion of both seed shadows and trees. We found, similarly to the preliminary observations on the dispersal behavior of woolly monkeys (Stevenson et al., 1997), that depositions were not distributed at random within the home range of the study group. There was a correlation between the areas most heavily used and the places with high depositions, and that the

areas with the highest seed rain were those used for prolonged resting periods. Therefore, it could be expected that preferred resting places or dormitories should receive the majority of the seeds dispersed by woolly monkeys. So in spite of their general role of over-dispersing seeds, the woolly monkeys could potentially generate clumped distributions of plants, especially at small spatial scales (e.g. preferred trees or branches to rest). More analyses and field studies will be needed to test this hypothesis, as it has been demonstrated for other seed dispersers such as bats, howler monkeys, and gorillas (Fleming & Heithaus, 1981; Julliot, 1997; Rogers et al., 1998). For instance, preliminary results have indicated that in the long term, some of the plant species included in this study have low transition probabilities between seedling and saplings below parental trees than away from them (Stevenson, 2002). Therefore, if these results, suggesting negative density dependent show effects in the long term, are confirmed, then the clumped spatial patterns of the seed rain may not necessarily produce aggregated patterns of adult plants.

REFERENCES

Augspurger, C. K. 1983. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40: 189-196.

Chapman, C. A. 1995. Primate seed dispersal: coevolution and conservation implications. *Evolutionary Anthropology* 4: 74-82.

Clark, D. B., & D. A. Clark. 1984. Spacing dynamics of a tropical rainforest tree, evaluation of the Janzen-Connell model. *American Naturalist* 124: 769-788.

Condit, R., P. S. Ashton, P. Baker, S. Bunyavejchewin, S. Gunatilleke, N. Gunatilleke, S. P. Hubbell, R. B. Foster, A. Itoh, J. V. LaFrankie, H. S. Lee, E. Losos, N. Manokaran, R. Sukumar, & T. Yamakura. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288: 1414-1418.

Condit, R., S. P. Hubbell, & R. B. Foster. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a Neotropical forest. *Am. Nat.* 140: 261-286.

Dinerstein, E. 1991. Seed dispersal by greater one-horned rhinoceros (*Rhinoceros unicornis*) and the flora of rhinoceros latrines. *Mammalia* 55: 355-362.

Fleming, T. H., & E. R. Heithaus. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica* 13 (supl): 45-53.

Fowler, N. 1988. The effects of environmental heterogeneity in space and time on the regulation of populations and communities. Pp. 249-269 in A. J. Davy, M. J. Hutchings, & A. R. Watkinson, eds. *Plant Population Ecology*. Blackwell Scientific, Oxford.

Fragoso, J. M. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology* 85: 519-529.

Howe, H. F., E. W. Schupp, & L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66: 781-791.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203: 1299-1309.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104: 501-528.

Julliot, C. 1997. Impact of seed dispersal by red howler monkeys *Alouatta seniculus* on the seedling population in the understory of tropical rain forest. *Journal of Ecology* 85: 431-440.

Lieberman, D., I. B. Hall, & M. Lieberman. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* 60: 65-75.

Lloyd, M. 1967. Mean crowding. *J. Anim. Ecol.* 36: 1-30.

Milton, K. 1980. *The Foraging Strategies of Howler Monkeys. A Study in Primate Economics*. Columbia University Press, New York.

Rogers, M. E., B. C. Voysey, K. E. McDonald, R. J. Parnell, & C. E. Tutin. 1998. Lowland gorillas and seed dispersal: the importance of nest sites. *Am J Primatol* 45: 45-68.

Schupp, E. W., & M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant-population ecology. *Ecoscience* 2: 267-275.

Stevenson, P. R. 2000. Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: Dispersal distance, germination rates, and dispersal quantity. *American Journal of Primatology* 50: 275-289.

--------------------- 2002. Frugivory and seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colomiba. PhD dissertation. SUNY at Stony Brook, New York.

--------------------- M.C. Castellanos, & L. Barreto 1997. Estudio preliminar de dispersión de semillas por micos churucos (*Lagothrix lagotricha*) en el Parque Tinigua, Colombia. *Universitas Scientiarum* 4: 23-30.

--------------------- M. J. Quiñones, & J. A. Ahumada. 1994. Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at La Macarena, Colombia. *American Journal of Primatology* 32: 123-140.

Terborgh, J., E. Losos, M. P. Riley, & M. Bolanos Riley. 1993. Predation by vertebrates and invertebrates on the seeds of five canopy tree speies of an Amazonian forest. *Vegetatio* 107/108: 375-386.

Thery, M., & D. Larpin. 1993. Seed dispersal and vegetation dynamics at a cock-of-the-rock's lek in the tropical rain forest of French Guiana. *Journal of Tropical Ecology* 9: 109-116.

Tutin, C. E. G., E. A. Williamson, M. E. Rogers, & M. Fernandez. 1991. A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lope Reserve, Gabon. *Journal of Tropical Ecology* 69: 751-763.

Wills, C., R. Condit, R. B. Foster, & S. P. Hubbell. 1997. Strong density- and diversity-
related effects help to maintain tree species diversity in a neotropical forest.
Proceedings of the National Academy of Sciences of the United States of America 94:
1252-1257.

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Preliminary Checklist of the Scarab Community (Coleoptera: Scarabaeidae) at CIEM, Tinigua National Park, Meta-Colombia

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The dung beetles belonging to the family Scarabaeidae, are some of the most important insects in the neotropic, due to their function as bioindicators (Halffter & Favila 1993), organic recycling agents and biological control (Waterhouse 1974), and their significant role as secondary seed dispersal agents (Estrada & Coates 1991). Their importance is associated with feeding habits; they use dung from omnivorous mammals and herbivores to feed the larva and the adults (Halffter & Matthews 1966, Howden & Young 1981, Halffter & Halffter 1989 and Gill 1991).

The knowledge of the diversity of this group in Colombia is poor, and there are very few inventories for these species from long-term studies (Escobar & Medina 1996, Medina & Kattan 1996, Amat *et al*. 1997, Escobar 1997, Amesquita *et al*. 1999, Escobar 2000, Escobar & Ulloa 2000, Medina *et al.* 2001, Medina *et al.* 2002 and Noriega 2002a) and only partial lists have been provided from the study site (Castellanos *et al*. 1999, Laverde *et al*. 2002 and Noriega 2002b). The aim of this paper is to provide the first comprehensive checklist of dung beetles in Tinigua Park.

METHODS

The specimens were collected at CIEM (Centro de Investigaciones Ecologicas de La Macarena), located in a tropical rain forest in the eastern border of Tinigua National Park (for a description of the site see Stevenson *et al.* in this volume). The fieldwork was conducted between June and July of 1994, December and January of 1995, July of 1996 and January of 1998, in all of the habitats described for the zone (Hirabuki 1990).

The specimens were collected using arrays of pitfall traps with human dung and rotting fish as bait (Escobar 1994). Intersection traps were also used, and arrays of elevated traps at different heights were baited with human dung, fish, mushrooms and fruit. In addition, dung from different vertebrates was checked directly in the field for species such as: woolly monkeys (*Lagothrix lagothricha*), red howler monkeys (*Alouatta seniculus*), capybaras (*Hydrochaeris hydrochaeris*), alligators (*Crocodylus intermedius*) and brazilian tapirs (*Tapirus terrestris*) and individuals were manually collected from the vegetation, logs, fungus, litter and fallen fruit along the trail system of the CIEM.

Specimens were conserved in a 70% ethylic alcohol solution and later dried. The specimens were identified to the species level using the existing taxonomical keys (Edmonds 1972, Halffter & Martinez 1977, Howden & Young 1981, Kohlmann 1984, Jessop 1985, Edmonds 1994, Genier 1996, Kohlmann & Solis 1997, Edmonds 2000, Medina & Lopera 2000 and Vitolo 2000),

reference collections and diagnostics from specialists. A reference collection was placed in the entomological room at the University of Los Andes in Bogotá - Colombia.
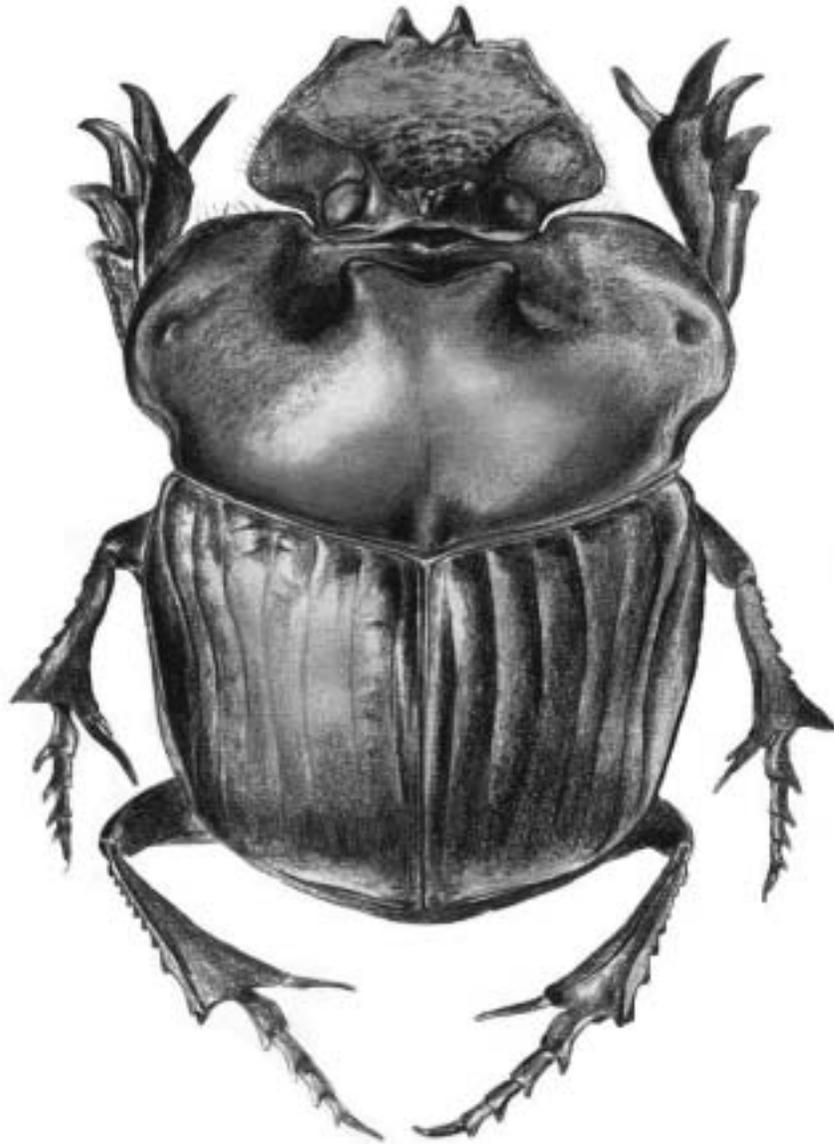
Fig. 1. *Coprophanaeus telamon* (Erichson, 1847), an uncommon species in the CIEM area, near La Macarena, Colombia.

RESULTS AND DISCUSSION

   A total of 57 species were collected, belonging to five tribes and 15 genera (Table 1), with ten of them strictly endemic to the neotropics. The major genus represented in the sample is *Dichotomius* with ten species, followed by the genera *Canthon* with eight species, *Eurysternus* and *Canthidium* with seven species each. In contrast some genus presents only one species as in the case of *Silvicanthon*, *Gromphas* and *Coprophanaeus* with *C. telamon* (Fig. 1).

Table 1. Dung Beetle species collected at the CIEM, Tinigua Park, Colombia.

Subfamily	**Tribe**	
Coprinae		
	Dichotomiini	
		Ateuchus murrayi (Harold, 1868)
		Ateuchus sp.
		Canthidium aurifex Bates, 1887
		Canthidium cupreum (Blanchard, 1843)
		Canthidium esplendidum Harold, 1867
		Canthidium euchalceum Balthasar, 1939
		Canthidium funebre Balthasar, 1939
		Canthidium onitoides (Perty, 1830)
		Canthidium ruficolle (Germar, 1824)
		Dichotomius belus (Harold, 1880)
		Dichotomius boreus (Olivier, 1789)
		Dichotomius compressicollis (Luederwalt, 1929)
		Dichotomius deyrollei (Harold, 1869)
		Dichotomius mamillatus (Felsche, 1901)
		Dichotomius ohausi (Luederwalt, 1922)
		Dichotomius worontzowi (Pereira, 1942)
		Dichotomius cf. *podalirius* (Felsche, 1901)
		Dichotomius cf. *problematicus* (Luederwalt, 1922)
		Dichotomius sp.
		Uroxys bidentis Howden & Young, 1981
		Uroxys micros Bates, 1887
		Uroxys sp1.
		Uroxys sp2.

	Onthophagini	
		Onthophagus buculus Mannerheim, 1829
		Onthophagus curvicornis Latreille, 1811
		Onthophagus haematopus Harold, 1875
		Onthophagus sp.
	Phanaeini	
		Coprophanaeus telamon (Erichson, 1847)
		Gromphas aeruginosa (Perty, 1830)
		Oxysternon conspicillatum (Weber, 1801)
		Oxysternon cf. *smaragdinum* Olsoufieff, 1924
		Phanaeus bispinus Bates, 1868
		Phanaeus cambeforti Arnaud, 1982
		Phanaeus chalcomelas (Perty, 1830)
		Phanaeus hermes Harold, 1868
		Sulcophanaeus faunus (Fabricius, 1775)
		Sulcophanaeus leander (Waterhouse, 1891)
Scarabaeinae		
	Canthonini	
		Canthon aequinoctialis Harold, 1868
		Canthon angustatus Harold, 1867
		Canthon femoralis (Chevrolat, 1834)
		Canthon juvencus (Harold, 1868)
		Canthon lituratus (Germar, 1813)
		Canthon luteicollis (Erichson, 1847)
		Canthon mutabilis Lucas, 1857
		Canthon smaragdulus (Fabricius, 1781)
		Deltochilum amazonicum Bates, 1887
		Deltochilum orbiculare Lansberge, 1874
		Deltochilum parile Bates, 1887
		Deltochilum cf. *problematicus* Bates, 1870
		Scybalocanthon sp.
	Eurysternini	
		Eurysternus caribaeus (Herbst, 1789)
		Eurysternus cayennensis Castelnau, 1840
		Eurysternus foedus Guerin-Meneville, 1844
		Eurysternus hamaticollis Balthasar, 1939
		Eurysternus inflexus (Germar, 1824)
		Eurysternus plebejus Harold, 1880
		Eurysternus velutinus Bates, 1887

Ten species could not be determined and are in process of confirmation, therefore it is possible that new species will be added to the list and the total number in this locality may increase. However, the pattern of species accumulation as a function of sampling time suggest that the list includes the majority of the species in the local community (Fig. 2)

Fig. 2. Cumulative number of scarabid species as a function of sampling effort during the study in the CIEM, Tinigua National Park, Colombia.
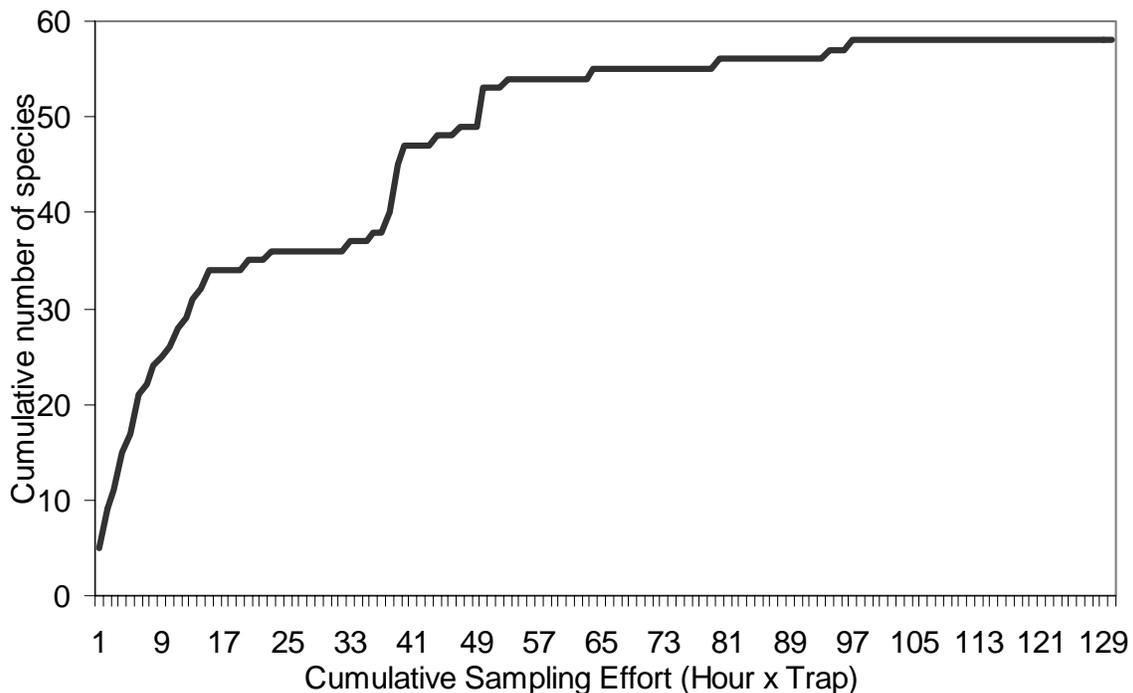
From the collected species it is interesting to note the presence of *Sulcophanaeus leander*, considered a new record for Colombia (Noriega 2002b). The presence of *Phanaeus chalcomelas* and *P. hermes* in this region is considered an expansion on their distribution ranges (Edmonds 1994). Other species with broad distribution like *Canthon aequinoctialis*, *Deltochilum parile*, *Onthophagus haematopus* and specially *Oxysternon conspicillatum*, were frequently found in the study zone.

A more exhaustive collection throughout the year is recommended, as well as the implementation of other kinds of traps (Newton & Peck 1975 and Morón & Terrón 1984), using other types of baits (Matthews 1965 and Howden & Young 1981) and typical faeces of the zone (Martinez 1952, Young 1981 and Janzen 1983).

REFERENCES

Amat, G.G., A.T. Lopera & S. Amezquita. 1997. Patrones de distribución de escarabajos coprófagos en relicto del bosque altoandino Cordillera Oriental de Colombia. *Caldasia*, 19 (1-2): 191-204.

Amezquita, M.S.J., A. Forsyth, A. Lopera & A. Camacho. 1999. Comparación de la composición y riqueza de especies de escarabajos coprófagos (Coleoptera: Scarabaeidae) en remanentes de bosque de la Orinoquía Colombiana. *Acta Zoologica Mexicana* (*n.s.*), 76: 113-126.

Castellanos, M.C., F. Escobar & P.R. Stevenson. 1999. Dung Beetles (Scarabaeidae: Scarabaeinae) attracted to Woolly Monkey (*Lagothrix lagothricha* Humboldt) dung at Tinigua National Park, Colombia. *The Coleopterists Bulletin*, 53(2): 155-159.

Edmonds, W.D. 1972. Comparative skeletal morphology, systematics and evolution of the phanaeine dung beetles (Coleóptera: Scarabaeidae). *U. of Kansas Science Bulletin*. 49: 11-143.

------------------- 1994. Revision of *Phanaeus* Macleay, a new world genus of Scarabaeine dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). *Contributions in Science, Natural History Museum of Los Angeles Country*, 443: 1-105.

------------------- 2000. Revision of the Neotropical dung beetles genus Sulcophanaeus (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Heyrovskyana*, suppl. 6. 60pp.

Escobar, F. 1994. *Excrementos, coprófagos y deforestación en bosques de montaña al sur occidente de Colombia*. Tesis de pregrado Biología-Entomología, Universidad del Valle.

-------------- 1997. Estudio de la comunidad de coleópteros coprófagos (Scarabaeidae) en un remanente de bosque seco al norte del Tolima, Colombia. *Caldasia*, 19(3): 419-430.

-------------- 2000. Diversidad de coleópteros coprófagos (Scarabaeidae: Scarabaeinae) en un mosaico de hábitats en la reserva Natural Nukak, Guaviare, Colombia. *Acta Zoológica Mexicana* (*n.s.*), 79: 103-121.

------------- & C.A. Medina. 1996. Coleópteros coprófagos (Scarabaeidae) de Colombia: estado actual de su conocimiento. 93-116 pp. In: G. Amat, G. Andrade y F. Fernández (eds.). *Insectos de Colombia*. Academia Colombiana de Ciencias Exactas Físicas y Naturales y Pontificia Universidad Javeriana, Bogotá.

------------- & P. Chacón de Ulloa. 2000. Distribución espacial y temporal en un gradiente de perturbación de la fauna de coleópteros coprófagos (Scarabaeidae, Aphodiinae) en la Reserva Natural La Planada, Nariño, Colombia. Revista de Biología Tropical, 48 (4): 961 - 975.

Estrada, A. & E.R. Coates. 1991. Howler monkey (*Alouatta palliata*), dung beetles and seed dispersal: Ecological interactions in the tropical rain forest of Los Tuxtlas. *Journal Tropical Ecology*, 7: 475-490.

Genier, F. 1996. A revision of the neotropical genus *Ontherus* Erichson (Coleoptera: Scarabaeidae, Scarabaeinae). *Memoirs of The Entomological Society of Canada*, 170: 168 pp.

Gill, B.D. 1991. Dung beetles in tropical American forests. Cap. 12, pags. 211-230 In: I. Hanski and Y. Cambefort (eds.), *Dung Beetle Ecology*. Princeton University Press, Princeton, NJ.

Halffter, G. & E.G. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomológica Mexicana*, 12-14: 1-312.

------------- & A. Martinez. 1977. Revision monografica de los Canthonina americanos, IV parte. Clave para géneros y subgeneros. *Fol. Entomol. Mex.* 38: 29-107.

------------- & M.E. Favila. 1993. The Scarabaeidae (Insecta: Coleoptera) an animal group for analysing, inventoryng and monitoring biodiversity in tropical rainforest and modified landscapes. *Biology International*, No. 27. 21 pp.

------------- & V. Halffter. 1989. Behavioral evolution of the nonrolling roller beetles. *Acta Zoológica Mexicana* (*n.s.*), 32: 1-53.

Hirabuki, Y. 1990. Vegetation and Land form structure in the study area of La Macarena. A Physionomic investigation. *Field Studies of New World Monkeys, La Macarena, Colombia*, 3: 35-55.

Howden, H.F. & O.P. Young. 1981. Panamenian Scarabaeinae: taxonomy, distribution and habits (Coleoptera: Scarabaeidae). *Contributions of the American Entomological Institute*, 18(1): 1-204.

Janzen, D. 1983. Insects at carrion and dung. 640-42I pp. In: D.H. Janzen (ed.). *Costa Rican Natural History*. Univ. Of Chicago Press, Chicago.

Jessop, L. 1985. An identification guide to Eurysternine dung beetles (Coleoptera, Scarabaeidae). *J. Nat. Hist*. 19: 1087-1111.

Kohlmann, B. 1984. Biosistematica de las especies Norteamericanas del Genero *Ateuchus* (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Entomológica Mexicana* No. 60: 3-81.

------------------ & A. Solis. 1997. El genero *Dichotomius* (Coleoptera: Scarabaeidae) en Costa Rica. *Gior. Ital. Di Entom.* 8: 343-382.

Laverde, L.J., M.C. Castellanos & P.R. Stevenson. 2002. Dispersión secundaria de semillas por escarabajos coprófagos (Scarabaeidae) a partir de heces de churucos (*Lagothrix lagothricha*) en el Parque Nacional Tinigua, Colombia. *Universitas Scientiarum*, 7(1): 17-29.

Martínez, A. 1952. Scarabaeidae nuevos o poco conocidos III. *Mis. Est. Pat. Reg. Argentina*, 81-82: 53-118.

Matthews, E.G. 1965. The taxonomy, geographical distribution, and feeding habits of the Canthonines of Puerto Rico (Coleoptera: Scarabaeidae). *Transactions of the American Entomological Society*, 91: 431-465.

Medina, C.A., F. Escobar & G.H. Kattan. 2002. Diversity and Habitat Use of Dung Beetles in a Restored Andean Landscape. *Biotropica*, 34(1): 181-187.

------------------ & G.H. Kattan. 1996. Diversidad de coleópteros coprófagos (Scarabaeidae) de la reserva forestal de Escalerete. *Cespedesia*, 21(68): 89-102.

------------------ & A. Lopera. 2000. Clave ilustrada para la identificación de los géneros de escarabajos coprófagos (Coleoptera: Scarabaeinae) de Colombia. *Caldasia*, 22 (2):299-315.

------------------ A. Lopera, A. Vitolo, & B.D. Gill. 2001. Escarabajos coprófagos (Coleoptera: Scarabaeidae) de Colombia. *Biota Colombiana*, 2(2): 131-144.

Moron, M.A. & R.T. Terron. 1984. Distribución altitudinal y estacional de los insectos necrofilos en la Sierra Norte de Hidalgo, México. *Acta Zoologica Mexicana* (n.s.) 3: 1-47.

Newton, A. & S.B. Peck. 1975. Baited pitfall traps for beetles. *The Coleopterist Bulletin*, 29(1): 45-46.

Noriega, J.A. 2002a. First report of the presence of the genus *Digitonthophagus* (Coleoptera: Scarabaeidae) in Colombia. *Caldasia*, 24(1): 213-215.

------------------. 2002b. Aportes a la biología del escarabajo sudamericano *Sulcophanaeus leander* (Waterhouse, 1891) (Coleoptera: Scarabaeidae). *Acta Zoologica Mexicana* (*n.s.*), 87: 67-82.

Vitolo, A. 2000. Clave para la identificación de los géneros y especies Phanaeinas (Coleóptera: Scarabaeidae: Coprinae: Phanaeini) de Colombia. *Rev. Acad. Colomb. Cienc.*, 24(93): 591-601.

Waterhouse, D.F. 1974. The biological control of dung. *Scientific American*, 230: 100-109.

Young, O.P. 1981. The attraction of Neotropical Scarabaeinae (Coleoptera: Scarabaeidae) to reptile and amphibian fecal material. *The Coleopterist Bulletin*, 35(3): 345-348.

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Preliminary study of the bat community at the CIEM, Tinigua National Park, Colombia

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ABSTRACT

The bat community at CIEM (Centro de Investigaciones Ecológicas La Macarena) was studied during six months, using mist nets in the understory. In this tropical rain forest at Tinigua National Park (Colombia), we captured individuals of three different families: Phyllostomidae (29 species from 6 subfamilies), Vespertilionidae (4 species) and Noctilionidae (1 species). Phyllostominae was the richest subfamily, and this pattern of species richness corresponds to the expectations for undisturbed Neotropical forests. The most abundant species were frugivore species (i.e. *Carollia brevicauda, Artibeus lituratus,, A. jamaicensis, A. obscurus* and *Carollia castanea*).The majority of the species and individuals in the community are mainly frugivores (50% and 90% respectively). The most important plants providing fruits belong to just three genera (*Piper, Cecropia* and *Ficus*). According to germination rates of seeds dispersed by bats and their patterns of habitat use, the bat community seems to play an important role in plant regeneration of some species through seed dispersal.

INTRODUCTION

In terms of species richness, Chiroptera is the most important mammal order in Neotropical rainforests. About 39% of all mammal species in this region are bats, and this group includes 22.4% of all mammal species in South America (Cabrera, 1958; Emmons & Feer, 1990; Kalko, 1998). Furthermore, they have been proposed as indicator species because their diversity tends to decrease in disturbed areas (Fenton *et al*., 1992). The relative representation of species of different families has been suggested as a proxy to infer forest disturbance (Medellin *et al.*, 2000). In particular, it has been proposed that a large number of Phyllostominae species indicates low levels of disturbance; therefore, the first purpose of this study is to test that generalization for an undisturbed site.

Bats play an important role in plant-animal interactions, as pollinators and seed dispersers (Linares, 1987; Fleming *et al.*, 1993; Duncan & Chapman, 1999). Faunivorous species may control insect population densities (Romano *et al.*, 1999). In spite of their ecological importance, these
mammals have not been studied at the site; therefore the aim of this paper is to describe the bat community in different habitats found at CIEM. In particular, we tried to answer the following questions for bats foraging or commuting trough in the understory of different forest types: 1). What species are present at the site, and what is the relative abundance of each species? 2) Are there differences in community assemblage for different forest types? 3) Are there short-term differences in their abundance and reproductive cycles? 4) What plant species do bats consume? and 5) How does seed dispersal by bats affect germination rates?

METHODS

The study took place at the CIEM in Tinigua National Park (see details in Stevenson *et al.*, this number). Bats were captured using mist nets (12 x 2 m) in the understory of three different forest types (*terra firme*, flooded, and secondary forest). Each forest type was sampled four nights per month during the study period (January-June 1997), and four different places were used for each forest type. We used two nets each sampling night, which remained open between 18:00 and 22:00 h. The nets were inspected once an hour. Additionally, we set up nets in riparian forest and beaches to increase the chances of capturing bat species associated with these habitats.

For each bat captured, we recorded the species, time of capture, net location, sex, reproductive status, forearm length, weight and approximate age (i.e. adult, subadult, or juvenile; based on bone development at joints of the phalanx). We assigned species names based on nomenclature proposed by Cuervo *et al*. (1986). We classified female reproductive condition in four categories: 1) pregnant, when it was possible to recognize a well developed embryo. 2) Lactating, when females were secreting milk. 3) Females carrying infants and 4) Inactive, when the females did not show any of the above characteristics. Furthermore, we distinguished parous from nulliparous females based on the shape of the pubic bones.   For males we recorded sexual period based on testicle size.

We collected fecal material from captured bats to identify plants included in their diets. Seeds of the most common species were set for germination trails in petri dishes. Plant nomenclature was based on (Stevenson *et al.*, 2000).

In order to describe diversity patterns we used rarefaction analyses and Shannon`s diversity index (Magurran, 1988). We used nested ANOVA tests to compare diversity patterns and capture rates (individuals/hour.net).

RESULTS

We captured 612 bats in 738 h (0.83 bats/h.net). Capture rates were on average higher in *terra firme* forests (1.15 ind/h.net) than in secondary (0.85) and flooded forests (0.64)(Table 1). However, capture rates were variable within those forests, and we found no significant differences between forests (F=0.36, p>0.05). Capture rates in riparian forest and beaches were similar to those found in older forest in the floodplain (0.66).

We recorded 34 bat species, belonging to three different families: Phyllostomidae, Noctillionidae, and Vespertilionidae. Phyllostomidae was the richest family and within it, Phyllostominae was the subfamily with the highest number of species (Table 2). The rarefaction
curve for our study indicates that we should expect to find more species with more sampling effort (Fig. 1). The most abundant species were frugivorous species such as *Carollia brevicauda* (30.7%)*, Artibeus lituratus* (18.7)*, A. jamaicensis* (12.1)*, A. obscurus* (9.6) and *Carollia castanea* (7.8). In fact, we found that the trophic guild best represented in this community corresponds to fruit eaters (50% of the species), followed by omnivores (15%), insectivores (15%), and carnivores (9%). The proportion of frugivores is even greater when looking at the percentage of individuals in each trophic level (90.4% frugivores, 4.6% omnivores, 2.0% carnivores, and 1.8% insectivores). We did not find differences in species diversity estimates between forests (Table 1). The most common

Table 1. Capture rates and species diversity estimates of bat species in three different forest types during the study period at CIEM, Tinigua National Park, Colombia.

Month	Jan	Feb	Mar	Apr	May	Jun	Average
Terra Firme **Forest**							
Individuals Captured	28	32	40	27	40	53	
Monthly Average	7.0	8.0	10.0	6.8	10.0	13.3	9.3
SD.	5.2	2.9	4.8	2.6	3.4	5.9	4.4
Capture rates	0.88	1.00	1.25	0.84	1.25	1.66	1.15
Shannon H`	2.14	1.77	2.42	1.83	1.55	2.05	1.96±0.31
Secondary Forest							
Individuals Captured	40	32	29	27	29	7	
Monthly Average	10.0	8.0	7.3	6.8	7.3	1.8	4.0
SD.	7.1	4.1	4.0	2.2	5.3	1.3	6.8
Capture rates	1.25	1.00	0.91	0.84	0.91	0.22	0.85
Shannon H`	1.05	1.24	1.17	1.32	1.82	1.55	1.36±0.28
Flooded Forest							
Individuals Captured	42	8	12	13	26	21	
Monthly Average	5.1	2.0	3.0	3.3	6.5	5.3	4.2
SD.	3.5	0.8	2.2	2.6	3.1	1.5	1.7
Capture rates	1.31	0.25	0.38	0.41	0.81	0.66	0.64
Shannon H`	1.71	1.39	1.33	1.52	1.93	2.00	1.65±0.28

species were found in all three forest types. The main pattern of habitat use was the high representation of *Carollia brevicauda* and *C. castanea* in secondary forests, and the preponderance of *Artibeus* spp. in *terra firme* forests (Fig. 2).

Table 2. Bat species captured using mist nets in the understory of different forest types at CIEM, Tinigua National Park, Colombia. The relative abundance of each species based on 612 individuals captured is shown in the last column.

| Family	Subfamily	Species	Relative Abundance % of captures
Phyllosthomidae	**Carollinae**	*Carollia brevicauda*	30.56
		Carollia castanea	7.84
		Carollia perspicillata	0.82
		Rhinophylla pumilio	1.14
		Rhynophylla fischerae	0.33
	Glossophaginae	*Anoura geoffroyi*	0.16
		Glossophaga soricina	0.49
	Phyllosthominae	*Chrotopterus auritas*	0.16
		Mimon crenulatum	0.16
		Mycronycteris nicefori	0.16
		Phyllosthomus discolor	0.16
		Phyllosthomus elongatus	1.63
		Phyllosthomus hastatus	1.47
		Tonatia bidens	0.49
		Tonatia silvícola	0.82
		Trachops cirrhosus	0.98
		Vampyrum spectrum	0.16
	Stenoderminae	*Uroderma bilobatum*	3.92
		Uroderma magnirostrum	2.45
		Artibeus jamaicensis	12.09
		Artibeus lituratus	18.3
		Artibeus obscurus	9.64
		Artibeus phaeotis	0.65
		Chiroderma salvini	0.49
		Ectophylla macconelli	0.65
		Vampyrops infuscus	0.16
	Sturnirinae	*Strunira luisa*	0.49
		Sturnira tildae	0.16
Vespertilionidae		*Eptesicus brasilensis*	0.33
		Eptesicus diminutus	0.16
		Myotis oxyotus	0.16
		Saccopteryx bilineata	0.33
Noctilionidae		*Noctilio albiventris*	0.33
Desmodidae		*Desmodus rotundus*	0.16

Fig. 1. Cumulative number of species (based on rarefaction methods), as a function of sampling size, for the bat community at the CIEM, Tinigua National Park Colombia.
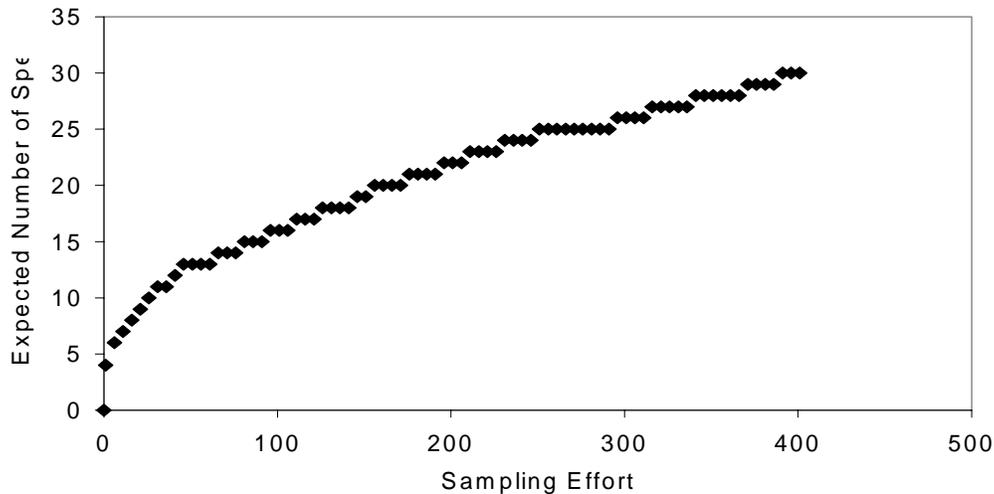
Some species seemed to have habitat preferences. In particular, *Carollia perspicillata* and *Anoura geoffroyi* were captured exclusively in flooded forests and *Noctilio albiventris* and *Vampyrum spectrum* in beaches. *Sturnira luisi, S. tildae, Myotis oxyotus*, and *Rhynophylla fisherae* were found only in secondary forest. Ten species were captured only in terra firme forests (*Tonatia bidens, Desmodus rotundus, Glossophaga soricina, Micronycteris nycefori, Mimon crenulatum, Saccopteryx bilineata, Eptesicus diminutus, Chiroderma salvini, Phyllostomus discolor* and *Chrotopterus auritus*).

Although it is difficult to detect reproductive cycles in a short term study, some species seemed to show birth peaks at the rainy period (i.e. *Artibeus lituratus*). Reproductively active individuals of the most common species such as *Carollia brevicauda, Artibeus lituratus* and *A. jamaicensis* were found along the study period, and it remains uncertain if these levels of reproductive activities are present all year around at the study site.

Fig. 2. Patterns of habitat use for the most abundant bat species at CIEM, Tinigua National Park (Colombia), according to the number of captures in three different forest types. Each forest type was sampled 192 h evenly distributed during six months.
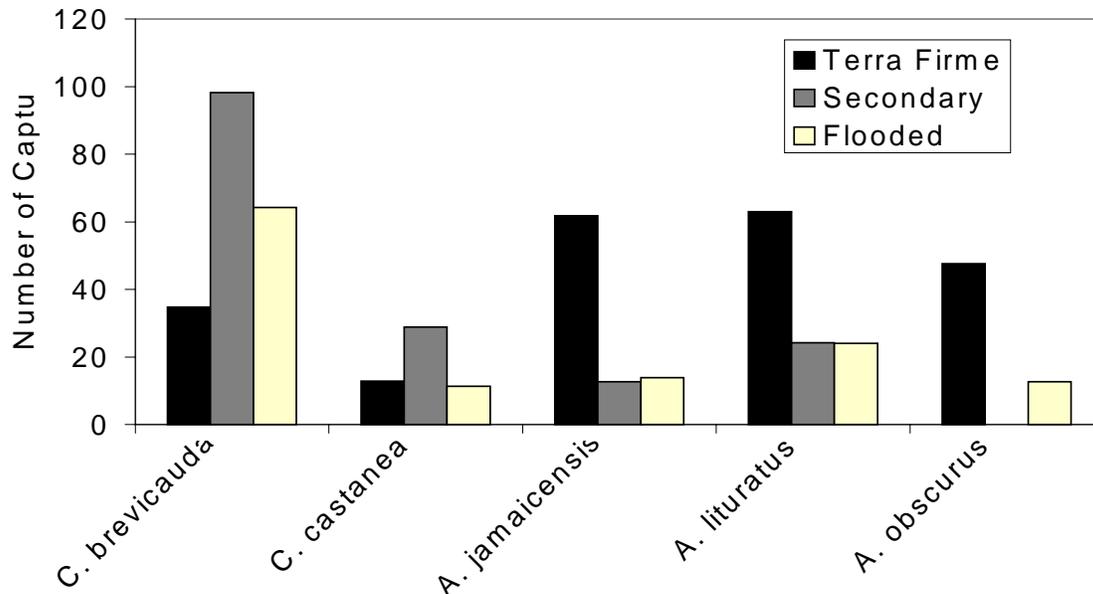
The main plant species consumed by bats for their fruits included three genera: *Piper, Cecropia,* and *Ficus*. Nine *Piper* species were recorded as fruit sources (*P. hispidum, P. phytholacaefolium, P. aequale, P. peltata, P. arboretum, P. cumanense, P. consanguineum, P. laevigatum* and *P. tuberculatum*). *Cecropia* species identified in fecal samples included *C. engleriana, C. membranacea*, and *C. ficifolia*. Four fig species were identified (*F. maxima, F. nymphaeifolia, F. insipida* and *F. trigonata*). The relative importance of these plants varied for each bat species. For instance, it was found that *Carollia brevicauda* defecated more often *Piper* seeds (55.2%) than *Cecropia* (31.0%) and *Ficus* (5.2%). Seeds of Solanaceae were also detected in their depositions. A similar pattern was found for *Carollia castanea* (*Piper*: 66.7%, *Cecropia*: 5.0%, and *Ficus*: 8.3%). In contrast, *Artibeus jamaicensis* defecated seeds of *Ficus* and *Cecropia* (both 40%) more frequently than *Piper* seeds (13.3%). *Artibeus lituratus* defecated seeds of *Cecropia, Piper* and *Ficus* in similar proportions (38.5, 34.6 and 26.9% respectively). The pattern for *Artibeus obscurus* showed a higher proportion of *Cecropia* (61.5%) and *Ficus* (30.8%), compared to *Piper* (7.7%). Seeds dispersed by the most common bat species germinated at similar or higher rates than non-dispersed seeds (Fig. 3).

Fig. 3. Germination rates of undispersed (control) seeds in three plant genera and seeds dispersed by different bat species at Tinigua National Park, Colombia. Error bars represent a standard deviation.

A) *Piper* spp.

B) *Cecropia* spp.

C) *Ficus* spp.
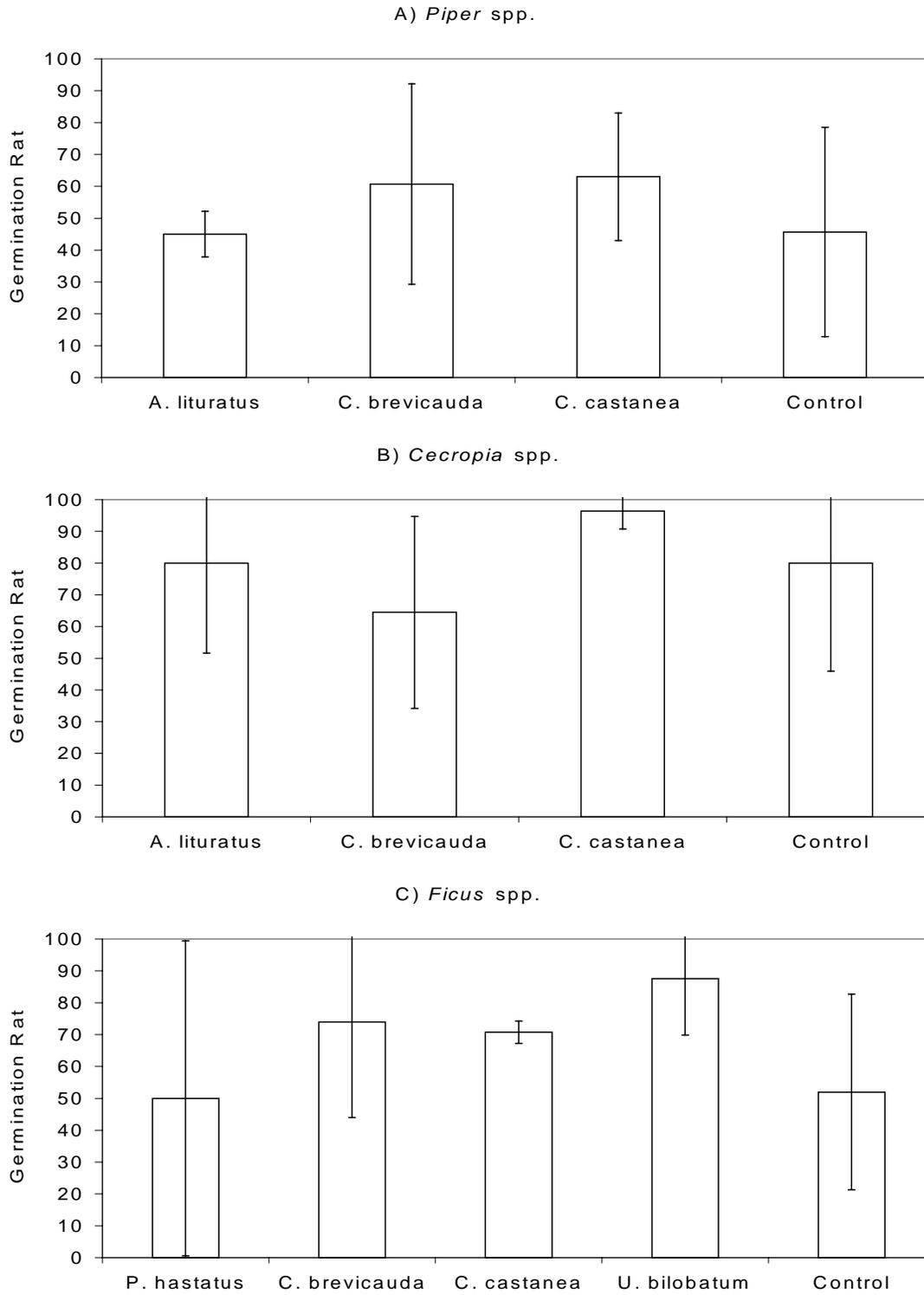
DISCUSSION

The capture rates found in this study are similar to those found in other studies [0.83 in CIEM vs. 1.05 in La Selva (Lavall & Fitch 1977), 0.87 in La Macarena (Sánchez *et al.,* 1996), and 0.74 in undisturbed central Amazon forests (Bernard & Fenton, 2002)]. The total number of bat species found in Tinigua and their diversity patterns fall within the range of estimates found for other Neotropical sites (Table 3). However, species richness values from this study should be taken as underestimates. First of all, sample size was small and the cumulative number of species did not get saturated (as a rule of thumb 1000 captures are required Bergallo *et al.*, 2003). Second, we did not sample the canopy, and it is well documented that a large proportion of bat species are exclusive canopy dwellers (Bernard, 2001). In spite of this limitation, some patterns seem strong enough to make certain generalizations. There is a large contribution of phyllostominae species in the area, and this was expected because this family tends to be rich in species in the understory of undisturbed areas (Medellin *et al.*, 2000). The community at Tinigua shares a large number of species with close-by areas in La Macarena (20 species), which is expected according to neutral models of community assemblage (Hubbell, 2001). However, Tinigua also shares many species (23) with a distant place in Manu National Park in southern Peru, a region with similar climate and soil origin. This pattern has been found for other groups of organisms such as plants and birds (see references in Link & Stevenson, 2004) and supports the theory that similar macro-ecological conditions in western Amazonia (i.e. climate and soil fertility) are major determinants of the patterns of community composition in the region (Gentry, 1988).

Table 3. Species richness and diversity indices for bat communities in different Neotropical sites.

Habitat Type	Locality, Country	Species	H	Captures	Source
Humid Forest	Selva Lacaonda, Mexico	28	2.43	445	Medellin *et al.*, 2000
	Quintana Roo, Mexico	14	1.85	129	Fenton *et al.*, 1992
	La Selva, Costa Rica	57	2.69	1865	Laval & Fitch, 1977
	Cristobal, Panamá Z.C.	31	1.97	1128	Fleming *et al.*, 1972
	Tinigua Park, Colombia	34	2.29	612	This study
	Saul, French Guiana	40			Simmons *et al.*, 2000
	Amazonas, Brasil	32	2.08		Marques, 1979**
	Belem, Brasil	49	2.36	1853	Kalko & Handley, 2001
	Manú, Perú	44			Ascorra *et al.*, 1991
Savanna-Forest	La Macarena, Colombia	39	1.97	919	Sánchez *et al.*, 1996
	Espiritu, Bolivia	38	2.88		Aguirre, 2002
Dry Forest	Balboa, Panamá Z.C.	27	1.89	1048	Fleming *et al.*, 1972
	El Frío, Venezuela	36		797	Ibañez, 1981
	La Pacífica, Costa Rica	27	2.07	964	Fleming *et al.*, 1972
	La Tatacoa, Colombia	23		518	Ruiz *et al.*, 1997
	Lagunillas, Venezuela	18			Sosa,1991 *

* cited in Ruiz 1997, ** in Sanchez et al., 1996.

The dietary preferences found for the common species agrees with the findings of other studies. For example, it has been shown that species in the genus *Artibeus* feed mainly on *Ficus* species, while *Carollia* spp. tend to base their diets on *Piper* fruits (Gardner 1977, Fleming & Heithaus, 1981). These results suggest that it might be possible to generate models to predict the relative abundance of these bats based on the abundance of their main feeding sources, as it has been done for some primate taxa (Stevenson, 2001). These models might be used for management plans, either to propose conservation areas with adequate resources for particular species or for reintroduction programs. Finally, our estimates indicate that the bat community at CIEM includes at least 20% of the species registered for Colombia (Rojas, 1997), and this area should remain protected in order to maintain its biodiversity.

Germination rates of dispersed seeds were either higher or similar to control seeds. This pattern seems very consistent for different plants dispersed by other bat species (Defigueiredo & Perin, 1995; Izhaki *et al.*, 1995; Iudica & Bonaccorso, 1997; Godinez-Alvarez & Valiente-Banuet, 2000; Lobova *et al.*, 2003; Naranjo *et al.*, 2003). Furthermore, it has been shown that bats can disperse seeds far from parental trees, and individual bats can use a variety of environments were viable seeds can be deposited (Fleming and Heithaus, 1981; Estrada & Coates-Estrada, 2002). Given these aspects of seed dispersal quality, and the high proportion of seeds deposited by bats in the center of canopy gaps (Gorchov *et al.*, 1993), it is very likely that bats play very important roles in the regeneration of some plant species such as *Piper* and *Cecropia* (Fleming, 1981; Lobova *et al.*, 2003).

ACKNOLEDGMENTS

REFERENCES

Aguirre, L. F. 2002. Structure of a Neotropical savanna bat community. *Journal of Mammalogy* 83:775-784.

Ascorra, C., E. Wilson & M. Romo. 1991. Lista anotada de los quirópteros de Parque Nacional Manu, Perú. *Publ. Mus. Hist. Nat.* (A) 42:1-14.

Bergallo, H. G., Esberard, C. E. L., Mello, M. A. R., Lins, V., Mangolin, R., Melo, G. G. S. & Baptista, M. 2003. Bat species richness in Atlantic forest: What is the minimum sampling effort? *Biotropica* 35:278-288.

Bernard, E. 2001. Vertical stratification of bat communities in primary forests of Central amazon, Brazil. *Journal of Tropical Ecology* 17:482-482.

-------------- & Fenton, M. B. 2002. Species diversity of bats (Mammalia: Chiroptera) in forest fragments, primary forests, and savannas in central Amazonia, Brazil. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 80:1124-1140.

Cabrera, A. 1958. Catálogo de los mamíferos de América del Sur. Vol.1. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Zoologia. Buenos Aires.

Cuervo, A., J. Hernández & A. Cadena. 1986. Lista actualizada de mamíferos de Colombia, anotaciones sobre su distribución. *Caldasia* 15:71-75.

Defigueiredo, R. A. & Perin, E. 1995. Germination Ecology of *Ficus luschnathiana* drupelets after bird and bat ingestion. *Acta Oecologica-International Journal of Ecology* 16:71-75.

Duncan R. S. & C. A. Chapman. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications* 9(3):998-1008.

Emmons, L. & Feer, F. 1990. Neotropical rainforest mammals: a field guide. University of Chicago Press, Chicago. xiv, 281.

Estrada, A. & Coates-Estrada, R. 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. *Biological Conservation* 103:237-245.

Fenton, M., L. Acharya, D. Audet, M. Hickey, C. Merriman, M. Obrist, D. Syme & B. Adkins. 1992. Phyllostomid bats (Chiroptera: Phyllostomydae) as indicators of habitat disruption in the Neotropics. *Biotropica* 24:440-446.

Fleming, T. H. 1981. Fecundity, fruiting pattern, and seed dispersal in *Piper amalago* (Piperaceae), a bat dispersed tropical shrub. *Oecologia* 51:42-46.

-------------------- & Heithaus, E. R. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica* 13 (supl):45-53.

-------------------- E.T. Hooper & D. E. Wilson. 1972. Three Central American bat communities: Structure, reproductive cycles, and movement patterns. *Ecology* 53:653-670.

-------------------- Venable, D. L. & Herrera, L. G. 1993. Opportunism Vs Specialization - the Evolution of Dispersal Strategies in Fleshy-Fruited Plants. *Vegetatio* 108:107-120.

Gardner, A. L. 1977. Feeding habits. In: Biology of bats in the New World family Phyllostomatidae. Part II. Baker, R. J., K. Jones Jr., & D.C. Carter (eds.). Spec. Publ. Mus. Texas Tech. Univ. Lubbock, 13:1-364.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75:1-34.

Godinez-Alvarez, H. & Valiente-Banuet, A. 2000. Fruit-feeding behavior of the bats *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight cage experiments: Consequences for dispersal of columnar cactus seeds. *Biotropica* 32:552-556.

Gorchov, D. L., Cornejo, F., Ascorra, C. & Jaramillo, M. 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. *Vegetatio* 108:339-349.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, N.J. xiv, 375.

Ibañez, C. J. 1981. Biología y ecología de los murciélagos del hato "El Frío", Apure, Venezuela. *Doñana, Acta Vertebrata. Sevilla, España* 8-4:1-271.

Iudica, C. A. & Bonaccorso, F. J. 1997. Feeding of the bat, *Sturnira lilium*, on fruits of *Solanum riparium* influences dispersal of this pioneer tree in forests of northwestern Argentina. *Studies on Neotropical Fauna and Environment* 32:4-6.

Izhaki, I., Korine, C. & Arad, Z. 1995. The effect of bat (*Rousettus aegyptiacus*) dispersal on seed germination in Eastern Mediterranean habitats. *Oecologia* 101:335-342.

Kalko, E. K. V. 1998. Organisation and diversity of tropical bat communities through space and time. *Zoology-Analysis of Complex Systems* 101:281-297.

------------------- & Handley, C. O. 2001. Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology* 153:319-333.

Laval, R. K. & H. S. Fitch. 1977. Structure, movements and reproduction in three Costa Rican bat communities. *Occ. Paper Mus. Nat. Hist., University of Kansas* 19:1-28.

Linares, O. J. 1987. Murciélagos de Venezuela. Cuadernos Lagoven. Caracas, Venezuela.

Link, A. & P. R. Stevenson. 2004. Fruit syndromes in animal dispersed plants at Tinigua National Park, Colombia. Revista Chilena de Historia Natural (en prensa).

Lobova, T. A., Mori, S. A., Blanchard, F., Peckham, H. & Charles-Dominique, P. 2003. Cecropia as a food resource for bats in French Guiana and the significance of fruit structure in seed dispersal and longevity. *American Journal of Botany* 90:388-403.

Magurran, A. E. 1988. Ecological Diversity and Its Measurements. Princeton University Press, Princeton. Capt. 2, pp. 7-45.

Medellin, R. A., Equihua, M. & Amin, M. A. 2000. Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. *Conservation Biology* 14:1666-1675.

Naranjo, M. E., Rengifo, C. & Soriano, P. J. 2003. Effect of ingestion by bats and birds on seed germination of Stenocereus griseus and *Subpilocereus repandus* (Cactaceae). *Journal of Tropical Ecology* 19:19-25.

Romano, M. C., Maidagan, J. I. & Pire, E. F. 1999. Behavior and demography in an urban colony of *Tadarida brasiliensis* (Chiroptera: Molossidae) in Rosario, Argentina. *Revista de Biologia Tropical* 47:1121-1127.

Ruiz, A., Santos, M., Soriano, P. J., Cavelier, J. & Cadena, A. 1997. Mutualistic relations between the bat *Glossophaga longirostris* and the columnar cacti in the arid region of La Tatacoa, Colombia. *Biotropica* 29:469-479.

Sánchez-P., P., P. Rivas & A. Cadena. 1996. Diversidad biológica de una comunidad y su relación con la estructura del hábitat de bosque de galería, Serranía de La Macarena, Colombia. *Caldasia* 18:343-353.

Simmons, N. B., Voss, R. S. & Peckham, H. C. 2000. The bat fauna of the Saul region, French Guiana. *Acta Chiropterologica* 2:23-36.

Stevenson, P. R. 2001. The Relationship between fruit production and primate abundance in Neotropical forests. *Biological Journal of the Linnean Society* 72:161-178.

-------------------- Quiñones, M. J. & Castellanos, M. C. 2000. Guía de Frutos de los Bosques del Río Duda, La Macarena, Colombia. Asociación para La Defensa de La Macarena - IUCN (The Netherlands), Santafé de Bogotá.

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