

## MATSES INDIAN RAINFOREST HABITAT CLASSIFICATION AND MAMMALIAN DIVERSITY IN AMAZONIAN PERU

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**ABSTRACT.**— The Matses Indians of northeastern Peru recognize 47 named rainforest habitat types within the Gálvez River drainage basin. By combining named vegetative and geomorphological habitat designations, the Matses can distinguish 178 rainforest habitat types. The biological basis of their habitat classification system was evaluated by documenting vegetative characteristics and mammalian species composition by plot sampling, trapping, and hunting in habitats near the Matses village of Nuevo San Juan. Highly significant ( $P < 0.001$ ) differences in measured vegetation structure parameters were found among 16 sampled Matses-recognized habitat types. Homogeneity of the distribution of palm species ( $n=20$ ) over the 16 sampled habitat types was rejected. Captures of small mammals in 10 Matses-recognized habitats revealed a non-random distribution in species of marsupials ( $n=6$ ) and small rodents ( $n=13$ ). Mammal sightings and signs recorded while hunting with the Matses suggest that some species of mammals have a sufficiently strong preference for certain habitat types so as to make hunting more efficient by concentrating search effort for these species in specific habitat types. Differences in vegetation structure, palm species composition, and occurrence of small mammals demonstrate the ecological relevance of Matses-recognized habitat types.

**Key words:** Amazonia, habitat classification, mammals, Matses, rainforest.

**RESUMEN.**— Los nativos Matsés del nordeste del Perú reconocen 47 tipos de habitats de bosque lluvioso dentro de la cuenca del río Gálvez. Combinando sus designaciones vegetativas y geomorfológicas de habitats, los Matsés pueden distinguir 178 tipos de bosque. La base biológica de su sistema de clasificación de habitats fue evaluada documentando características vegetativas y composición de especies de mamíferos por medio de medir vegetación en parcelas, atrapar con trampas, y cazar en habitats reconocidos por los Matsés cerca de la comunidad nativa Matsés Nuevo San Juan. Se encontró diferencias de alto significado ( $P < 0.001$ ) en los medidos parámetros de estructura de vegetación entre los 16 tipos de habitats que fueron muestreados. Homogeneidad en la distribución de especies de palmeras ( $n=20$ ) en los 16 tipos de habitat fue rechazado. Capturas de mamíferos pequeños en diez habitats reconocidos por los Matsés reveló una distribución no-aleatoria en las especies de marsupiales ( $n=6$ ) y roedores pequeños ( $n=13$ ). Mamíferos vistos y señales de mamíferos apuntadas durante cazas con Matsés sugieren que algunas

especies tienen preferencias para ciertos tipos de hábitats reconocidos por los Matsés que son suficientemente fuertes para que la caza sea más eficiente cuando se concentran esfuerzos de busca en específicos tipos de hábitat. Diferencias en la estructura de vegetación, en la composición de especies de palmeras, y en la existencia de mamíferos pequeños demuestra la pertinencia ecológica de estas unidades.

RÉSUMÉ.— Les matses, un groupe amérindien du nord-est du Pérou, reconnaissent 47 types d'habitats (pour lesquels ils disposent de termes spécifiques) de la forêt tropicale dans le bassin hydrographique du fleuve Gálvez. En combinant ces termes pour les différents habitats végétaux et géomorphologiques, les matses arrivent à distinguer 178 types d'habitats. La base biologique de leur système de classification a été évaluée en documentant des caractéristiques de la végétation et des espèces de mammifères à travers l'examen de la végétation dans certaines parcelles-échantillons, la chasse et la prise en piège dans les habitats reconnus par les matses près du village matses de Nuevo San Juan. Des différences très significatives ( $P < 0.001$ ) ont été trouvées dans les paramètres structurels mesurés pour la végétation dans les 16 types d'habitats où des échantillons ont été pris. L'hypothèse d'une distribution homogène des espèces de palmiers ( $n=20$ ) pour les 16 types d'habitats a été réfutée. Des captures de mammifères de petite taille dans dix habitats reconnus par les matses a révélé une distribution non-aléatoire des espèces de marsupiaux ( $n=6$ ) et de petits rongeurs ( $n=13$ ). Des mammifères et des signes rencontrés lors des expéditions de chasse avec les matses suggèrent que certaines espèces de mammifères ont une préférence suffisamment marquée pour certains types d'habitats reconnus par les matses pour que la chasse soit effectivement plus productive si les efforts sont concentrés sur ces habitats. Des différences concernant la structure de la végétation et la composition des espèces de palmiers, ainsi que l'existence de mammifères de petite taille, démontre l'importance écologique de ces unités.

## INTRODUCTION

The ongoing deforestation of the Amazon rainforest presents an urgent need to document its diversity and understand underlying ecological processes. Though it is widely recognized that high species richness in tropical rainforests is associated with habitat heterogeneity, the patterns of habitat diversity within rainforest areas are poorly understood. Vegetation classifications of Brazilian Amazonia based primarily on flooding regimes, water quality, geographic location, and non-forest habitats within the Amazon basin (e.g., Pires 1973; Prance 1978, 1979; Braga 1979; Pires & Prance 1985) are useful for understanding variation on a large scale, but they are not sufficiently detailed to describe habitat types present in a small locality. The classifications of Malleux (1982) and Encarnación (1985, 1993), which are derived from the knowledge of foresters and local residents, respectively, are more detailed and thus more sensitive to variation within large habitat classes. However, these classifications were designed for comparison of habitats throughout the Peruvian Amazon, and still lack detail, especially for *terra firme* habitats. Descriptions of successional stages, initiated yearly by the deposition of sediments along large rivers (e.g., Salo et al. 1986; Lamotte 1990; Kalliola et al. 1991; Campbell et al. 1992), related well to habitat variation on a small scale, but these descriptions

are not applicable to upland rainforest, which covers the vast majority of Amazonia (approximately 85 percent [Prance 1978]).

Some indigenous peoples of Amazonia have extensive knowledge of rainforest communities. This knowledge is reflected in detailed habitat classifications (e.g., Carneiro 1983; Parker et al. 1983; Posey 1983; Alcorn 1984; Posey and Balée 1989; Balée 1994; Shepard et al. in press) which have potential for use in conjunction with scientific surveys, particularly in rapid assessment of rainforest communities for conservation. A case in point is the rainforest habitat classification system of the Matses Indians of Northeastern Peru.

The Matses (also called Mayoruna; Panoan language family) are an indigenous Amazonian society consisting of about 1500 persons living along the Javari River and its tributaries in Peru and Brazil (Figure 1). In 1969 the Matses established peaceful contact with Summer Institute of Linguistics personnel (Vivar 1975), although they reportedly had intermittent contacts with rubber workers between 1920 and 1930 (Romanoff 1984), and it is possible that as early as the fifteenth century some of their ancestors may have been reduced in missions to the east of their present territory (Erikson, 1994). Prior to 1969, the Matses avoided contact by maintaining hostile relations with neighboring non-tribal Peruvians and Brazilians, and by staying far from navigable rivers in the area between the Javari and Ucayali Rivers, and to the east of the Javari (Romanoff 1984). In the 1980's some groups moved away from the inland villages and settled on the banks of the Yaquerana (Upper Javari) and Gálvez Rivers. Acculturation of the Matses to the national culture is proceeding rapidly, but because of their recent isolation, older individuals (>30 years of age) still possess undiminished traditional knowledge.

The Matses meet all their nutritional needs through traditional subsistence activities, including hunting, fishing, trapping, horticulture (primarily manioc, plantains, and corn), and collection of wild foods. They continue to procure the majority of their protein from hunting in upland forests for mammals and birds. The Matses use an elaborate system of rainforest habitat nomenclature and classification to organize their knowledge of resource availability in order to conduct and discuss their subsistence activities more effectively. Their system allows them to identify as many as 104 types of primary rainforest and 74 types of secondary (successional) rainforest within the 8000-km<sup>2</sup> drainage basin of the Gálvez River.

Such narrow definitions of habitat types in Amazonia have limitations, and local plant species composition might be better characterized by broad descriptions of soil and hydrology gradients (Kalliola et al. 1993). However, we present the Matses system as a complementary tool for describing Amazonian habitat diversity, particularly in light of the utility of systems of categorization for establishing conservation policy. The Matses knowledge of rainforest habitats holds potential for description of ecological relationships as well as floristic diversity, considering that some Amazonian animals are known to be largely restricted to minor habitat types; for example, collared titi monkeys (*Callicebus torquatus*) are habitat specialists in creekside forests (Peres 1993) and ichthyomyine rodents are almost never found away from bodies of water (Voss 1988).

This study was designed to provide preliminary biological descriptions of Matses habitat types and to investigate the extent to which Matses habitat designations reflect quantifiable biological factors. To evaluate the ecological basis of

Matses habitat classification, we sampled 16 Matses-recognized habitat types that occurred within a 2 km radius from the Matses village of Nuevo San Juan in northeastern Peru. The objectives of this study were: 1) to describe the Matses system of rainforest habitat identification and classification; 2) to evaluate if Matses-recognized habitat types exhibit distinctive vegetation characteristics with measurements of vegetation density, basal area, and palm species composition; 3) to ascertain if Matses-recognized habitat types exhibit different small mammal composition and abundance with data obtained through systematic trapping; and 4) to see if mammals observed while hunting with the Matses exhibited differential use of Matses-recognized habitat types.

#### STUDY SITE

The study area was located along the Gálvez River (a tributary of the Javari River) at the Matses village of Nuevo San Juan ( $73^{\circ}9'50''\text{W}$ ,  $5^{\circ}17'30''\text{S}$ , 150 m above sea level), in the district of Yaquerana, department of Loreto, in northeastern Peru



FIGURE 1.— Location of Nuevo San Juan study site in northeastern Peru, showing the Gálvez River drainage basin.

(Figure 1). Average annual rainfall (2900 mm) and average annual temperature (25.9°C) were recorded at Jenaro Herrera, the location of the nearest weather station, 100 km west of Nuevo San Juan (Marengo 1983). The period of heavy precipitation extends from late December through mid April; July and August are the driest months. The Gálvez is a blackwater river with a narrow floodplain that seldom extends more than 0.5 km on either side. Although the dry season is not exceptionally dry, the water level in the Gálvez falls impressively, a total of 10 m from April to August.

The area around Nuevo San Juan is primary ("virgin") rainforest except for gaps caused by windfalls and active and abandoned swiddens (0.5-2 ha horticultural plots) that have been cleared since the village was established in 1984. At the time that the Matses moved into the area, no villages had existed in the lower reaches of the Gálvez for at least 25 years (Faura 1964). Woodroffe (1914), who visited the lower Gálvez in 1905-6 reported that there was apparently no human habitation in the area except for a handful of rubber workers. None of the Matses who were interviewed recall there ever having been inhabitants in the Gálvez drainage basin other than at the very headwaters. The Matses recognize some rainforest areas within the Gálvez basin that they identify as villages or swiddens of other tribes through the presence of pot shards, indicator plant species, such as the palm *Elaeis oleifera*, or distinctive vegetation structure; however, no such areas exist within a day's walk from Nuevo San Juan, and so the Matses consider all areas surrounding Nuevo San Juan that were not cleared by them or are visibly the result of a windfall to be primary forest. And we were not able to detect any areas around Nuevo San Juan that appeared to be advanced successional forest (but see Balée [1989] for the possible anthropogenic nature of apparently primary forests in Amazonia). The habitat classification system here includes only rainforest habitats, and so we did not consider beach vegetation or active Matses swiddens, which the Matses classify into at least three types based on the age and/or crop composition of the swidden.

According to Matses informants, over the last 12 years abundance of some game animals has declined and densities of species adapted to secondary forest, such as agoutis (*Dasyprocta fuliginosa*; see Appendix C for mammal species authorities) and pacas (*Agouti paca*), have apparently increased; however, there is no evidence of extirpation of any species from the area.

## METHODS

The data for this study were collected during two field seasons totaling 18 months from 1994 to 1996. From April to July 1994, twelve men from the Matses villages of Nuevo San Juan, Remoyacu, and Buen Perú were individually interviewed about the different habitat types that they recognized. An initial list of Matses names of rainforest habitat types was compiled from interview responses about the natural history of the local mammal fauna (Fleck 1997). Later, informants were asked to list as many rainforest habitat names as they could and to describe them, and then to comment upon habitats listed by other Matses informants. Subsequently, the informants were asked how they identified and classified these habitats and about the ecological relationships between mammals and these

habitats. Only those habitat names that the Matses listed without my help were recorded in the initial listing, but when asked to describe habitats, they were also asked about habitat types mentioned by other informants. Interviews lasted from about 0.5 to 1.5 hours and were carried out without any other adults present. Trade items were exchanged for interviews, but these were given to informants prior to conducting the interview in order to make it clear that receiving the item did not depend upon the nature of their answers. While accompanying Matses on hunting trips, they were asked to name habitats that we passed through and to explain what characteristics they used to recognize them. It is from these interviews and consultations that the final list of habitats was compiled. Habitat type names that were mentioned by only one informant or that were rejected as valid habitat types by more than half of the informants are not included in this paper.

Sixteen Matses-recognized rainforest habitat types (hereinafter, habitat types) that exist within a 2-km radius of Nuevo San Juan were selected for vegetation sampling. The goal of the habitat comparisons in this study was to determine if the basic classification units (named habitat types) of the Matses system were ecologically relevant units. The purpose of our sampling design was not to provide a complete floristic or structural description of each habitat type, but rather to determine if Matses-recognized habitats could be distinguished one from another with data from limited sampling.

From April to July of 1996, eight 0.02-ha vegetation sampling plots (10 x 20 m) were established within each of the 16 habitat types by randomly selecting a starting point and a compass bearing for orientation of the plot. Two to four separate localities of each of the 16 habitat types were sampled; the number of plots per locality was related to the size of the habitat patch. At each plot, eight vegetation density estimates were conducted by using a 1 x 1 m density board marked with a 10 x 10 (10 cm) grid. The board was placed on the ground in a vertical position at a distance of 5 m from the observer and the number of squares more than 50 percent covered by vegetation were counted for the bottom half of the board and again for the top half. Diameter at breast height (DBH; 1.3 m) was measured for each tree within each plot; trees with stilt or buttress roots reaching above 1.3 m were measured just above the roots. From the DBH measurements, mean basal area per ha and mean number of trees >10 cm DBH per ha were calculated for each habitat type.

All identifiable palms (Palmae; palm nomenclature follows Henderson et al. 1995) taller than 1 m were identified and counted within each study plot. Palms were selected for study because they are salient, readily identified components of most Amazon rainforest habitats (Kahn et al. 1988), because Palmae is probably the most economically useful Neotropical plant family (Balick 1984), and because palm fruits and seeds are also important resources for rainforest animals (Zona & Henderson 1989). Other plant species that the Matses indicated as important for identifying habitats were quantified at each plot: the number of *Cecropia* spp. (Moraceae) trees taller than 1 m, the number of *Duroia hirsuta* (Poeppig. & Endl.) Shumann (Rubiaceae) trees taller than 1 m, and the number of lianas >1 cm DBH. The following geomorphological data were also recorded at each plot: distance from the river (during highest water level), relative elevation (estimated elevation above lowest land within 50 m), perceived quality of drainage (during the dry

season), and water regime (maximum number of days a plot remains inundated). Duplicate sets of voucher specimens were deposited at the Instituto de Investigaciones de la Amazonia Peruana herbarium in Iquitos, Peru, at the herbarium at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos in Lima, and at the New York Botanical Garden.

Two dichotomous keys were constructed for identification of Matses-defined habitats in the Nuevo San Juan area, one for geomorphologically-defined habitats and one for vegetatively-defined habitats (Appendices A and B). These keys were developed based on habitat characteristics used by the Matses in teaching DWF how to identify habitats.

Ten of the 16 selected habitat types and a Matses manioc swidden were trapped for small (<1 kg) mammals. The aim of this trapping was not to describe the entire mammalian composition of each habitat or to test for differences in composition with the surrounding habitat, but to determine if the sampled habitats exhibited detectable differences in small mammal composition. At each of the 10 habitats, 30 Sherman live traps, 10 Tomahawk live traps, 40 Victor rat traps, 10 Museum Special snap traps, five pitfall traps with drift fences, and five Matses-constructed deadfall traps (total of 100 traps) were set at each habitat type for 10 nights (total of 1000 trapnights). Traps were spaced evenly over a 1-ha area within each habitat type, at least 10 m away from the edge of the habitat, with half of the Sherman, Victor, and Museum Special traps set 0.5 to 2.5 m above the ground. Two of the eight 0.02 ha vegetation sampling plots were established within each trapping plot. Traps were baited every afternoon with ripe plantain (except for deadfall traps, which were baited with manioc) and checked in the morning. All animals were identified and removed; voucher specimens were prepared for all species and from all animals with questionable identification. Because the number of traps was limited, the 11 areas were not trapped simultaneously, but rather one or two at a time successively over a period of 90 d (20 April to 18 July 1996), a period that coincides with the end of the rainy season and the beginning of the dry season. Voucher specimens are deposited at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos in Lima, and at the American Museum of Natural History in New York.

From April 1995 to July 1996, DWF accompanied Matses on 108 hunting trips for a total of 583 h. The habitat types in which mammals were encountered during each hunt were recorded; two habitat names were recorded for each locality of observation, one for the vegetatively-defined habitat type and one for the geomorphologically-defined habitat type. The location and habitat of signs of mammals, including tracks, dens, beds, scat, and scrapings were also recorded when the sign could be confidently identified to species with the help of Matses.

In order to determine if the frequency of observations of mammalian species per habitat was different than expected by random distribution, the amount of time spent by Matses hunting in each habitat type was estimated by pacing Matses hunting paths for a total distance of 10 km, recording the points at which habitat types began and ended. Pacing data were then mapped by application of a global positioning satellite receiver (Figure 2). Vegetatively- and geomorphologically-defined habitats were calculated separately. Although the sections of the Matses hunting paths that were paced might not represent a random sample of the habi-

tats that the Matses cover on long hunting trips, the path-length estimates provide a rough estimate of the proportion of time that the Matses spend in each habitat type while hunting. Because Matses concentrate search time and hunting effort in selected habitat types, depending on the target species, sampling was not random during hunts. Therefore, these data were not subjected to statistical analysis. Also, this part of the study was not designed to test any mammal-habitat associations put forward by the Matses.

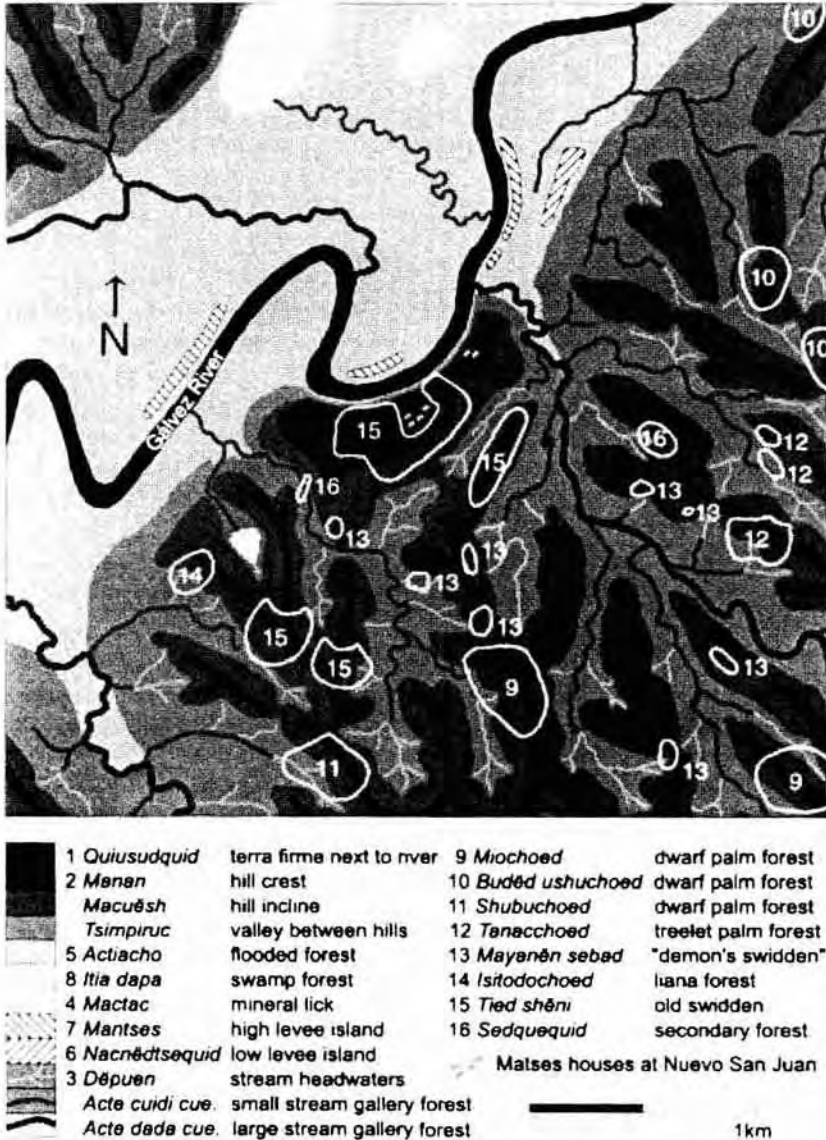


FIGURE 2.-- Geomorphologically-defined (shaded or patterned) and vegetatively-defined (outlined in white) habitat types in the Nuevo San Juan area, showing overlap of the two classification systems.



Vegetation densities, basal area and tree density were compared among the 16 sampled habitat types with one-way ANOVA tests and Tukey multiple comparisons. A Pearson Chi square test was used to test homogeneity of palm species abundances over the sampled habitats. All data recorded at each plot were used to construct classification and regression trees (CART; Brieman et al. 1984). CART analyses were used to see if Matses-recognized habitat types could be predicted using the measured habitat parameters. Three classification and regression trees were constructed, one for the eight sampled vegetatively-defined habitat types, one for the eight sampled geomorphologically-defined habitat types, and one for all 16 sampled habitat types. The dichotomous habitat keys were then compared with the classification trees to see if the two methods produced similar results and to determine if the same habitat characteristics were important distinguishing factors in both. Small mammal species diversity and abundance in the 10 trapped rainforest habitats and one swidden were analyzed using a chi-square test for homogeneity of the distribution of animals (at three levels, family Didelphidae, family Echimyidae, and family Muridae) across the 11 habitats. Exact nonparametric conditional inference was used since the trapping data were sparse--there were many zero values for the number of animals of a species captured in a habitat, making large sample methods invalid.

## RESULTS AND DISCUSSION

The Matses recognize 40 named categories of primary rainforest habitats (of which 38 are terminal categories) and seven named categories of secondary rainforest habitats within the 8000-km<sup>2</sup> drainage basin of the Gálvez River (Table 1). The Matses use different names for floodplain habitats while they are inundated during the rainy season, but these were not counted as different habitat types in this study (Figure 3). The Matses habitat classification system is divided into two separate (but physically overlapping) subsystems: 1) geomorphologically-defined habitat types; and 2) vegetatively-defined habitat types (Figures 2-4).

Vegetation density varied significantly among the 16 sampled habitat types. One-way ANOVA tests revealed highly significant ( $P < 0.001$ ) differences for vegetation density among 16 Matses-recognized habitat types, for both vegetation density below 0.5 m ( $F = 58.90$ ; Figure 5A) and from 0.5 m to 1 m ( $F = 65.52$ ; Figure 5B). Similarly, one-way ANOVA tests revealed highly significant ( $P < 0.001$ ) differences for basal area ( $F = 10.41$ ; Figure 5C) and for tree density ( $F = 9.06$ ; Figure 5D) among the 16 sampled habitat types, though these characteristics were considerably less distinctive than was vegetation density. Significant differences among habitat types in the measured vegetation structure parameters indicate that habitat types are related to vegetation structure and, therefore, of interest for ecological investigation. Moreover, pairwise comparisons of each habitat with each of the other 15 habitats revealed significant differences ( $P < 0.05$  Tukey's pairwise comparisons) in at least one of the four measured vegetation structure parameters in all but three of 28 pairs of geomorphologically-defined habitats and in all but five of 28 pairs of vegetatively-defined habitats. For pairs of geomorphologically- and vegetatively-defined habitats, a higher proportion (12 of 64) did not differ significantly (at 95% C.I) in at least one vegetation structure parameter; however, some

TABLE 1.—Forty-seven named categories of rainforest habitat types recognized by the Matses within the Gálvez River drainage basin in northeastern Peru. The Matses classify habitat types according to criteria of two major types: 1) geomorphological features, and 2) vegetation characteristics. The most important dichotomy in the Matses classification system is between floodplain rainforest along seasonally flooded rivers and upland rainforest that is not subjected to seasonal flooding. Matses also distinguish between primary rainforest and successional habitats. Numbers refer to habitat types sampled in this study and are used in subsequent tables and figures. See Appendix D for linguistic description of Matses habitat terminology.

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HABITAT TYPES DEFINED BY GEOMORPHOLOGICAL FEATURES

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	<u>mananucquio</u>	<u>Upland Rainforest</u>
1	<i>quiusudquid</i>	Non-flooding forest adjacent to a river
2	<i>manan</i>	Hill crest (also called <i>manan dadanquio</i> )
	<i>macuësh</i>	Hill incline (also called <i>macuësh potsen</i> )
	<i>tsimpiruc</i>	Valley between upland hills
	<i>acte dada cuëman</i>	Gallery forest along a large stream
	<i>acte cuidi cuëman</i>	Gallery forest along a small stream
3	<i>dëpuen</i>	Ephemeral headwaters of a stream
4	<i>mactac</i>	Poorly-drained muddy mineral lick
	<i>itia*</i>	Upland palm swamp
	<i>anshantuc</i>	Permanently waterlogged swamp
	<u>acte cuëman</u>	<u>Floodplain</u>
5	<i>actiacho</i>	Low seasonally flooded forest (called <i>acte mauan</i> during flooding season)
6	<i>nacnëdtsequid</i>	Levee flooded every year
7	<i>mantse</i>	Levee flooded only on years of exceptionally high water levels (called <i>mashcad</i> during flooding season)
	<i>chian cuëman</i>	Forest along a floodplain lake
	<i>acte mactac</i>	Mineral lick in floodplain forest
8	<i>itia dapa*</i>	Floodplain palm swamp (called <i>itia mauan</i> during flooding season)

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HABITAT TYPES CHARACTERIZED BY VEGETATION CHARACTERISTICS

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	<u>nimëduc<sub>1</sub>**</u>	<u>Primary Rainforest</u>
	<i>isanchoed</i>	Forest dominated by <i>Oenocarpus bataua</i> palms
	<i>nistechoed</i>	Forest dominated by <i>Iriartea deltoidea</i> palms
	<i>shuinte mapichoed</i>	Forest dominated by <i>Attalea tessmanii</i> palms
	<i>budëdchoed</i>	Forest dominated by <i>A. butyracea</i> palms
9	<i>miochoed</i>	Forest with understory dominated by <i>A. racemosa</i> palms
10	<i>budëd ushuchoed</i>	Forest with understory dominated by <i>A. microcarpa</i> palms
11	<i>shubuchoed</i>	Forest with understory dominated by <i>Phytelephas macrocarpa</i> palms
12	<i>tanacchoed</i>	Forest with understory dominated by <i>Lepidocaryum tenue</i> palms
	<i>dapaischoed</i>	Forest with understory and midstory dominated by <i>A. phalerata</i> palms
	<i>cobisanchoed</i>	Swamp dominated by <i>Euterpe precatoria</i> palms
	<i>tiantechoed</i>	Forest dominated by bamboo
	<i>sëntechoed</i>	Forest dominated by <i>Cedrela</i> sp. trees
	<i>pëncadchoed</i>	Forest dominated by <i>pëncad</i> trees
	<i>manipadachoed</i>	Forest dominated by <i>Musa</i> sp. wild bananas

13	<i>mayanën sebad</i>	Forest with open understory, dominated by <i>Duroia hirsuta</i> trees
14	<i>isitodochoed</i> <i>cuëte mampis</i> <i>antinchoed</i> <i>sinadchoed</i>	Forest dense with many large lianas Forest where only thin hardwood trees grow Seasonally flooded forest dominated by <i>A. maripa</i> palms Seasonally flooded forest with understory dominated by <i>Bactris</i> cf. <i>bifida</i> palms
	<i>shiuishchoed</i> <i>cana shëtachoeed</i>	Seasonally flooded swamp forest dominated by <i>Ficus</i> spp. Low floodplain adjacent to the river with dense thorny vegetation

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#### SUCCESSIONAL HABITAT TYPES

15	<i>tied shëni</i>	Secondary forest in abandoned Matses swiddens dominated by <i>Cecropia</i> spp. and <i>Marila</i> spp.
	<i>mayun tied</i>	Secondary forest from abandoned swiddens or villages > 50 yr old
	<i>cuesbudaid</i>	recent blowdown characterized by creeping vines and no trees
	<i>isitodo icsachoeed</i>	Secondary forest thick with vines and young trees
	<i>bucuchoeed</i>	Secondary forest dominated by <i>Cecropia</i> spp.
16	<i>sedquequid</i> ***	Secondary forest from blowdown or river shift with many vines and few <i>Cecropia</i> spp. trees
	<i>cuëteuidquio tabadquid</i>	Secondary forest where hardwood trees are out competing pioneer vegetation and vines

\* *itia* and *itia dapa* are included in both classifications, since they are defined by permanently waterlogged soil as well as being dominated by *M. flexuosa* palm trees

\*\**nimëduc*<sub>1</sub> in the general sense refers to all primary rainforest; in the specific sense (*nimëduc*<sub>2</sub>) it refers only to primary rainforest habitat that does not fall under any of the other named categories

\*\*\**sedquequid* is also used to refer to a *chamizal* (Encarnación 1993), primary forest found on sandy soil where all trees are short and thin. The only *chamizal* in Matses territory is outside the Gálvez drainage basin, far from Nuevo San Juan.

of these pairs were not expected to differ because they often overlap physically in nature.

Twenty species of palms were identified in the sampled plots of the 16 habitat types. Genera that could not be identified with confidence to species in the field (*Geonoma* and *Bactris*) were excluded from analyses. The null hypothesis of homogeneity of the distribution of palm species over the habitats was rejected by the Pearson Chi-square analysis. In fact, some species of palms were present in 100 percent of the eight sample plots of some habitat types and absent in nearly all plots of other habitat types (Table 2; Figure 6). This is not surprising considering that Matses recognize and name many of their vegetatively-recognized habitats after palm species (see Appendix D for linguistic analysis of habitat names). Habitat types that had 100 percent frequency of occurrence of a palm species also had relatively high mean densities of that palm species.

Matses-perceived habitat types could be predicted with classification and regression trees using the measured variables. The classification and regression trees (CART) analysis of the eight geomorphologically-defined habitats correctly classified all (N=64) of the sample plots into their Matses-recognized habitat type

(Figure 7A). In the case of the eight vegetatively-defined habitat types, only four out of 64 sample plots (6.25%) were incorrectly classified (Figure 7B). When all 16 habitats were analyzed simultaneously, 12 of 128 (9.375%) were misclassified (i.e., the CART analysis categorized 12 plots differently than the Matses did). The CART analyses produced trees that were similar to the dichotomous identification keys developed using Matses information (Appendices A and B), with many nodes at the same positions.

The 10 sampled habitats revealed differences in small mammal species composition (Table 3), as well as species richness and abundance (Figure 8). The chi-square test for homogeneity of the distribution rejected the null hypothesis of homogeneity, indicating that the distribution of small mammals varies among the habitat types.

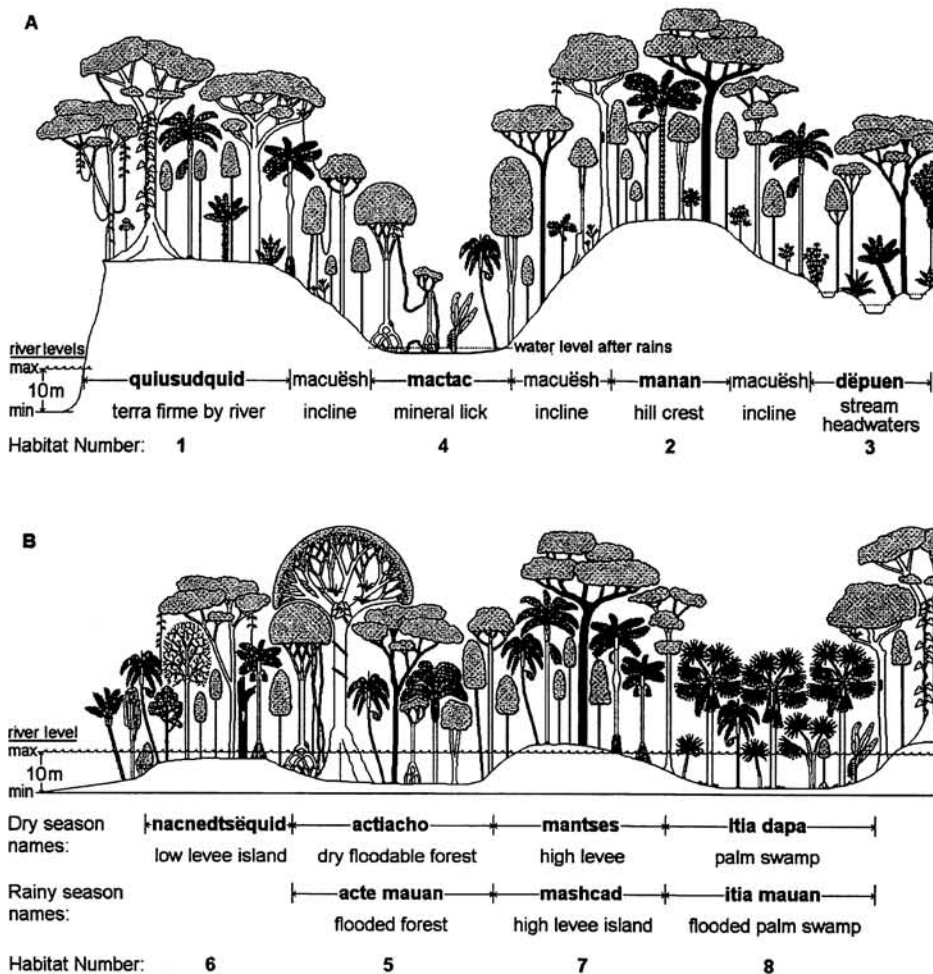


FIGURE 3.-- Profiles of geomorphologically-defined habitat types: A) upland forest habitat types; B) floodplain forest habitat types, showing the annual range of water levels and dry season and rainy season names for the same habitat type.

A large proportion of the observations of some species of mammals were in certain habitat types (Table 4). Many of these values for sightings or signs were more than one order of magnitude higher than would have been expected based on the estimated amount of time Matses spend hunting in each habitat. This suggests that despite the large sampling bias, the listed species might show an actual preference for those habitats.

The Matses system of habitat classification is different from other published rainforest classification systems (e.g., Pires 1973; Prance 1978, 1979; Braga 1979; Malleux 1982; Pires & Prance 1985; Encarnación 1985, 1993) in that it recognizes an exceptionally large number of named habitats for a relatively small area and in that it uses two overlapping subsystems (geomorphological and vegetative), rather than being strictly hierarchical. This study showed that these Matses-recognized habitat types can be recognized based on standard floristic and structural features (Figure 5). Moreover, these habitat types can be correctly predicted by CART analysis (Figure 7) and they can be identified with dichotomous keys (Appendices A & B).

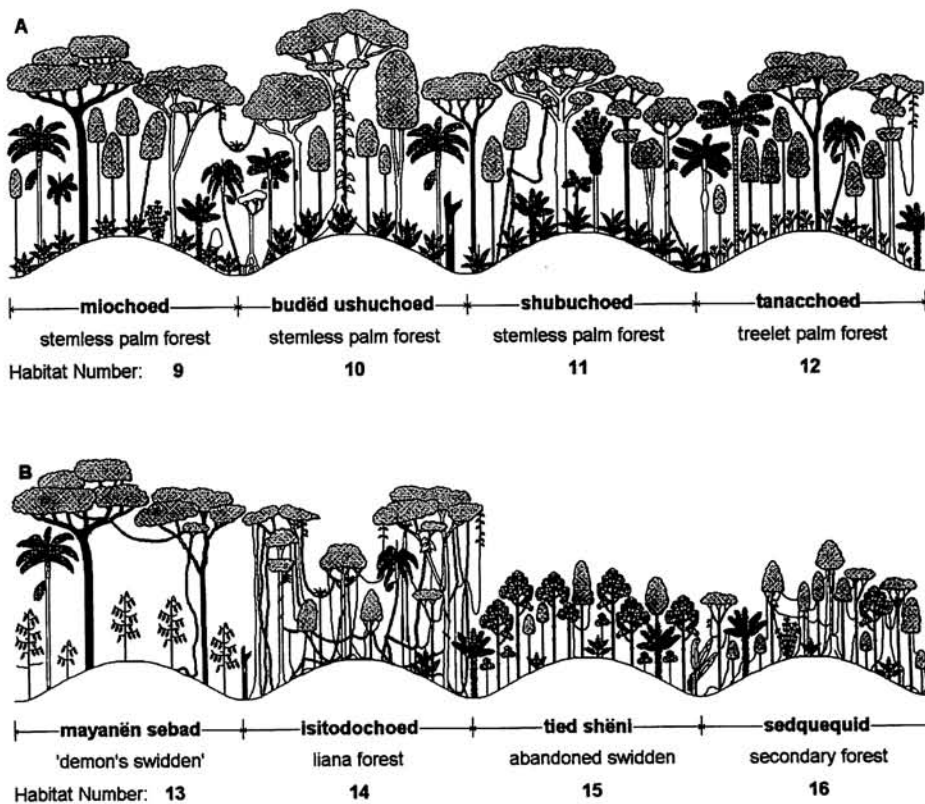


FIGURE 4.— Profiles of vegetatively-defined upland habitat types: A) habitat types dominated by understory palms; B) habitat types with other characteristic vegetation structures.

Geomorphologically-defined habitats are identified by abiotic features including distance from a river, relative elevation, drainage quality, and water regime. Habitat types such as *manan*<sup>2</sup> 'hill crest', *actiacho* 'seasonally flooded forest', and *quijsudquid* 'terra firme next to a river' are identified using geomorphological features (Figure 3). All the rainforest in the Gálvez River drainage basin is included in the geomorphologic classification system (Figure 2). Floristic composition and vegetation structure can be affected by water regime, drainage, topography, and

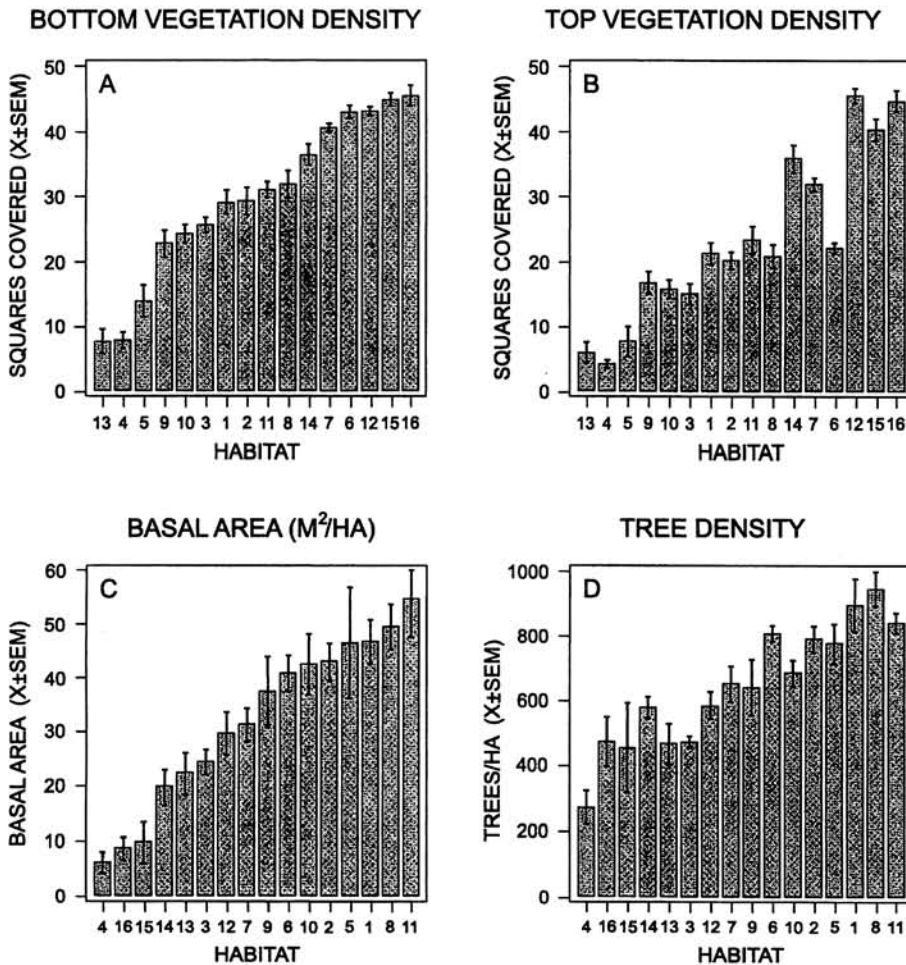


FIGURE 5.— Mean ( $\pm$ SEM) vegetation density, basal area ( $m^2/ha$ ) and trees ( $>10$  cm DBH) per ha for 16 Matses-recognized habitat types. Habitats in panel A are listed in order of increasing mean number of squares covered; habitats in panel B are listed in the same order as in panel A to illustrate differences in horizontal vegetation density between the lower level (0-0.5 m) and the higher level (0.5-1 m). Habitats in panel C are presented in order of increasing mean basal area; in panel D habitats are in the same order as in panel C to illustrate differences between basal areas and trees per ha in the same habitat types.

TABLE 2.— Frequency of occurrence of 20 palm species in Matses-recognized habitat types. Values represent the number of 0.02-ha plots, out of eight sampled per habitat type, in which a species was recorded (values appear in **bold** type when the palm species is part of the name of the habitat type). Numbers preceding palm species (1-20) correspond to numbered drawings in Figure 6. Habitat type numbers (1-16) correspond to numbered habitats in Table 1 and Figures 2-4).

PALM SPECIES	HABITAT TYPES															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 <i>Astrocaryum chambira</i>	1	3							1	3	4		1	3	2	
2 <i>Astrocaryum jauari</i>					2											
3 <i>Astrocaryum murumuru</i>	6	5	7		2				5	3	5	5		4	4	1
4 <i>Attalea butyracea</i>					3	1	1								2	
5 <i>Attalea insignis</i>			2						2							3
6 <i>Attalea microcarpa</i>	5									8		1		1		1
7 <i>Attalea racemosa</i>			5						8		5	3	1		2	3
8 <i>Attalea tessmanii</i>			1						1		5					1
9 <i>Euterpe precatoria</i>			1	3	6	8	8	8	3		2	3		3		
10 <i>Hyospathe elegans</i>		3	1						1		2	1				
11 <i>Iriartea deltoidea</i>	4	2	1				4	3			3		1			
12 <i>Iriartella stenocarpa</i>		2								1						
13 <i>Lepidocaryum tenue</i>		1										8				
14 <i>Mauritia flexuosa</i>								8								
15 <i>Oenocarpus bataua</i>	7	6	6				3		5	4	3	4	1			2
16 <i>Oenocarpus mapora</i>					1		2	2	1							
17 <i>Pholidostachys synanthera</i>		3									2					
18 <i>Phytelephas macrocarpa</i>			3						3		8					2
19 <i>Socratea exorrhiza</i>						2	7	6		3		2				
20 <i>Wettenia augusta</i>		1	1									1				

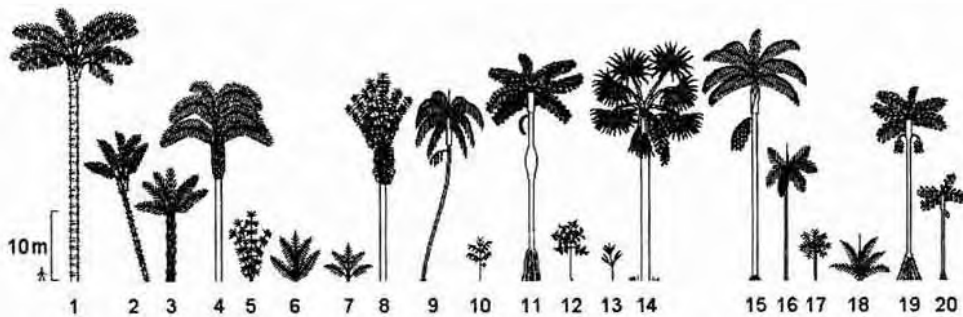


FIGURE 6.— Drawings (to scale) of palms species identified in Matses-recognized habitats. Numbers correspond to numbered palm species in Table 2.

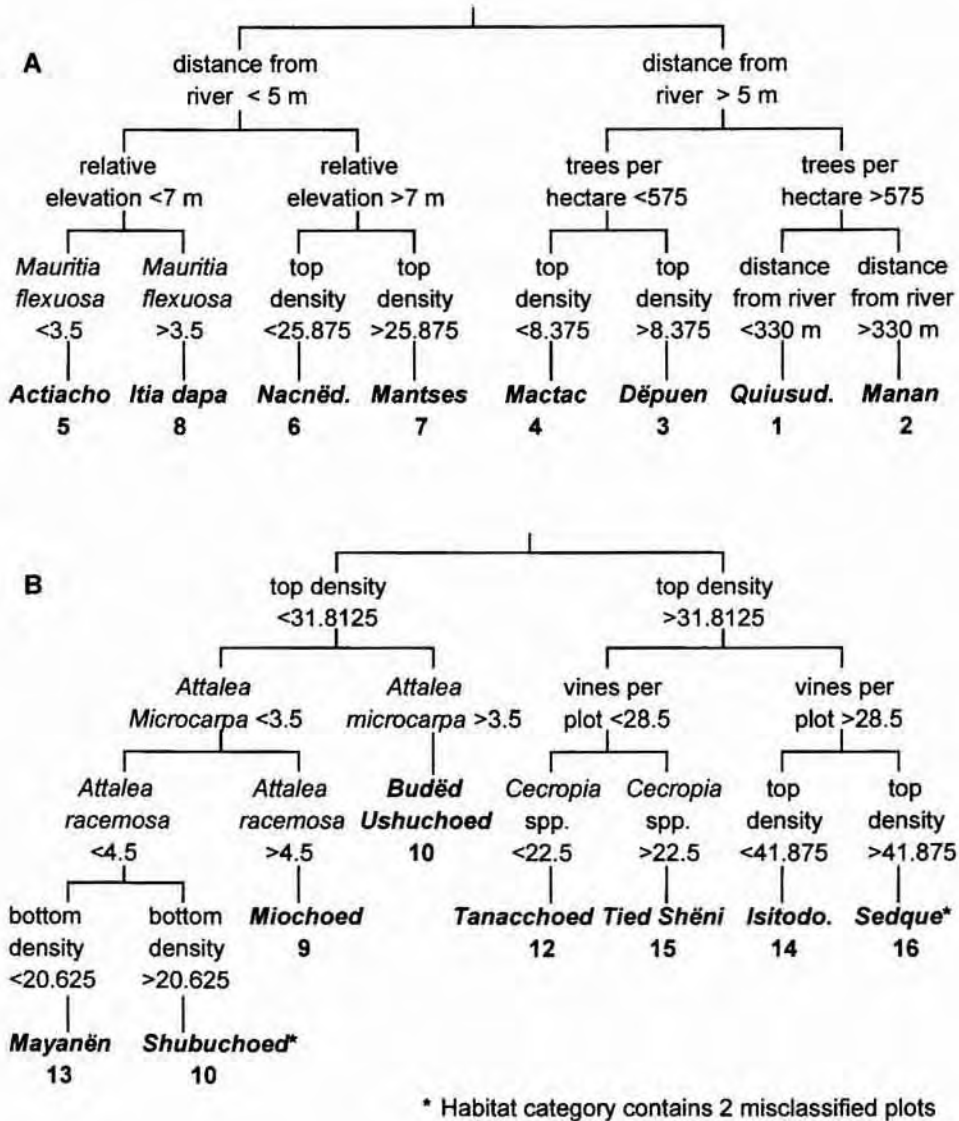


FIGURE 7.— A) Classification and regression tree for eight geomorphologically-defined habitat types. Misclassification error rate was 0% for the 64 plots. Measured habitat characteristics used to construct the tree included distance of the plot from the Gálvez river, relative elevation above lowest land within 50 m, number of trees per ha, number of *Mauritia flexuosa* palms in the plot, and horizontal vegetation density 0.5 to 1 m above the ground. B) Classification and regression tree for eight vegetatively-defined habitat types. Misclassification error rate was 6.25 percent (4 of 64 plots). Measured habitat characteristics used to construct the tree included horizontal vegetation density 0.5 to 1 m above the ground, number of *Attalea microcarapa* palms in the plot, number of vines, number of *Attalea racemosa* palms, number of *Cecropia* spp. trees, and horizontal vegetation density below 0.5 m.



distance from the river, and other physical factors (Duivenvoorden 1996), so geomorphologically-defined habitats generally contain a circumscribed range of species and predictable structures.

Vegetatively-defined habitats are identified primarily by the presence of an obvious dominance by a plant species (e.g., certain palms) or plant life form (e.g., lianas) throughout the habitat. *Miochoed* 'forest characterized by *Attalea racemosa* (an understory species of stemless palm)' and *isotodochoed* 'forest characterized by lianas' are examples of habitat types defined this way (Figure 4). Named vegetatively-defined habitats cover only 10-15 percent of the rainforest (Figure 2). The remainder of the area, called *nimëduc* is not differentiated in the Matses classification.

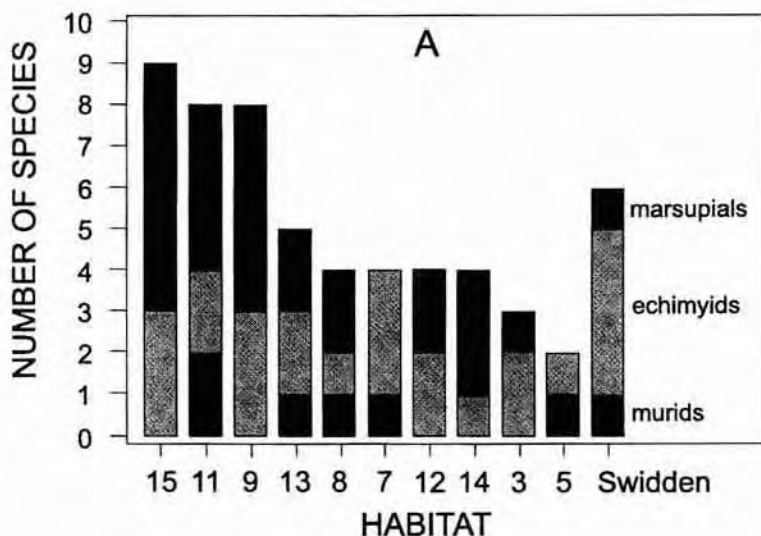
Because the entire rainforest is divided into both geomorphologically defined habitats and vegetatively-defined habitats, the two must overlap (Figure 2). Some vegetatively-defined habitat types can occur in several different geomorphologically-defined habitat types, so there is not a one-to-one correspondence between the two subsystems. By combining the geomorphological and the vegetative habitat classifications, the Matses can refer to any locality with more detail and efficiency (Table 5). This seems to be a very practical solution considering that it would re-

TABLE 3.- Captures of mammal species during 1000 trapnights in each of 10 Matses-recognized rainforest habitat types. (Common names in Appendix C.)

MAMMAL SPECIES	TRAPPED HABITATS										TOTAL OCCUR- RENCE	CAP- TURES
	3	5	7	8	9	11	12	13	14	15		
<i>Didelphis marsupialis</i>				1		2				1	3	4
<i>Marmosa murina</i>					1					1	2	2
<i>Marmosops noctivagus</i>					2		3	1	4	1	5	11
<i>Metachirus nudicaudatus</i>					1	1			1	2	4	5
<i>Micoureus</i> spp.				1	3	1	1		1	1	6	8
<i>Philander mcilhennyi</i>	1				1	2				1	4	5
<i>Oecomys bicolor</i>			1			1					2	2
<i>Oecomys</i> cf. <i>trinitatis</i>		3									1	3
<i>Oryzomys perenensis</i>				1							1	1
<i>Oryzomys macconnelli</i> cf.								1			1	1
<i>Scolomys ucayalensis</i>						1					1	1
<i>Mesomys ferrugineus</i>						1					1	1
<i>Proechimys cuvieri</i>	1									1	2	2
<i>Proechimys</i> sp. 1			2								1	2
<i>Proechimys</i> sp. 2			2	1	1					2	4	6
<i>Proechimys</i> sp. 3			1		1			1			3	3
<i>Proechimys</i> sp. 4	3				6	4	2	3	2	1	7	21
<i>Proechimys</i> sp. 5							1	2			2	3
<i>Proechimys</i> sp. indet.*	4	2	1	1	2	2	6	4	7	10	10	39
Total Species (20)	3	2	4	4	8	8	4	5	4	9		
Total Captures	9	5	7	5	18	15	13	12	15	21		120

\* Unidentifiable because captured animals were juveniles or skulls were crushed by kill bar.

### SPECIES RICHNESS



### ABUNDANCE

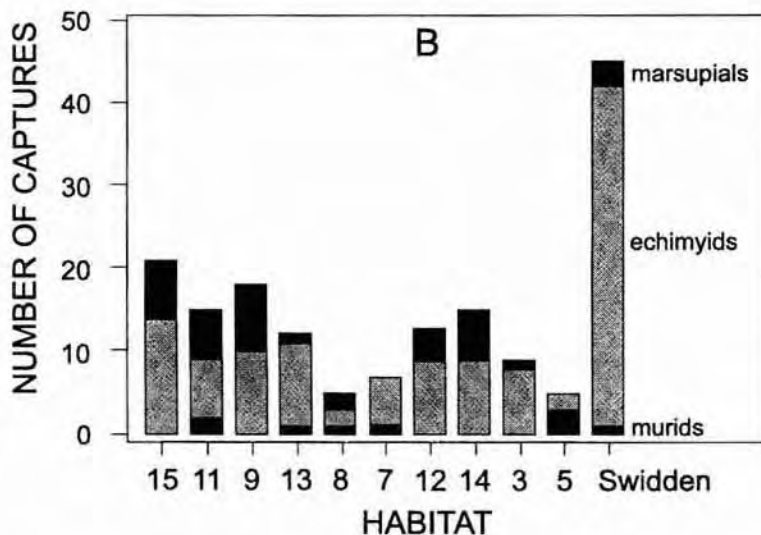


FIGURE 8.— Species richness (A) and abundance (B) of marsupials, echimyid rodents, and murid rodents based on data from 1000 trapnights in 10 Matses-recognized habitat types (and in a Matses manioc swidden). Data are presented for three groups (taxa): marsupials (family Didelphidae); echimyid rodents (family Echimyidae); and murid rodents (family Muridae).

quire much repetition to include such detail in a strictly hierarchical system. It should be noted that lexemes for the two classes of habitat designations are not combined by forming compounds or lexicalized phrases, but rather may simply be mentioned in the same conversation to designate a more specific habitat type or to describe a particular locality.

The Matses system is also useful because habitats belonging to a particular habitat type have several attributes in common (i.e., the categories are polythetic or logically natural). Because traditional societies rely heavily upon the environment for subsistence, a habitat classification system that is useful for multiple subsistence activities (hunting, trapping, and gathering of food, medicines and construction material) would be useful and therefore more likely to be maintained in a culture.

TABLE 4.— Mammal species that were frequently detected in Matses-recognized habitat types. The percentages of time spent in habitat types while hunting were calculated based on paced trail lengths. Sightings include animals killed or observed while hunting. Signs include fresh tracks and new dens. Proportions of sightings/signs were calculated as the number of times a species was recorded in a habitat type, divided by the total number of times that species was recorded while hunting. Calculations are separate for geomorphologically-defined (1-8) and vegetatively-defined (9-16) habitat types.

HABITAT TYPE	TIME IN HABITAT	MAMMAL SPECIES	SIGHTINGS IN HABITAT	SIGNS IN HABITAT
1 <i>quijsudquid</i>	1-2%	<i>Saimiri sciureus</i>	19%(5/26)	
2 <i>manan</i>	30-40%	<i>Priodontes maximus</i>	0% (0/1)	79%(31/39)
3 <i>dëpuen</i>	3-5%	<i>Dasypus kappleri</i>	70%(7/10)	65%(30/46)
4 <i>mactac</i>	<1%	<i>Ateles chamek</i>	43%(9/21)	
		<i>Tapirus terrestris</i>	33%(2/6)	49%(23/47)
		<i>Tayassu pecari</i>	40%(6/15)	52%(22/42)
5 <i>actiacho</i>	5-10%	<i>Allouata seniculus</i>	89%(16/18)	
		<i>Saimiri sciureus</i>	62%(16/26)	
		<i>Isothrix bistrata</i>	81%(18/22)	
6 <i>nacnëdtsequid</i>	<1%	<i>Dasypus novemcinctus</i>	50%(2/4)	53%(9/17)
7 <i>mantse</i>	<1%	<i>Dasypus novemcinctus</i>	25%(1/4)	29%(5/17)
		<i>Agouti paca</i>	20%(1/5)	23%(7/30)
8 <i>itiadapa</i>	2-3%	<i>Cacajao calvus</i>	52%(11/2)	
		<i>Tapirus terrestris</i>	33%(2/6)	26%(12/47)
9 <i>miochoed</i>	5-10%	<i>Dasypus kappleri</i>	40%(4/10)	39%(18/46)
10 <i>budëdushuchoed</i>	1-2%			
11 <i>shubuchoed</i>	3-5%	<i>Mazama americana</i>	20%(1/5)	27%(3/11)
12 <i>tanacchoed</i>	2-3%	<i>Pecari tajacu</i>	29%(2/7)	25%(15/59)
		<i>Myrmecophaga tridactyla</i>	33%(1/3)	28%(5/18)
13 <i>mayanën sebad</i>	2-3%			
14 <i>isitodochoed</i>	1-2%	<i>Choloepus hoffmanni</i>	36%(4/11)	
		<i>Cabassous unicinctus</i>	0% (0/1)	48%(14/29)
15 <i>tied shëni</i>	5-10%	<i>Agouti paca</i>	40%(2/5)	37%(11/30)
		<i>Dasyprocta fuliginosa</i>	60%(9/15)	44%(4/9)
16 <i>sedquequid</i>	2-3%	<i>Saguinus fuscicollis</i>	38%(10/26)	
		<i>Saguinus mystax</i>	26%(8/31)	

TABLE 5.--Relationship between named rainforest habitat types, showing which vegetatively-characterized habitat types are found on which geomorphologically-defined habitat types. By using two names, the Matses can describe as many as 104 types of primary rainforest and 74 types of secondary rainforest.

VEGETATIVELY-DEFINED HABITAT TYPES.	GEOMORPHOLOGICALLY-DEFINED HABITAT TYPES.																
	<i>Mananucquio</i>				<i>Acte cuëman</i>												
	1	2	3	4	5	6	7	8									
	<i>q</i>	<i>m</i>	<i>m</i>	<i>t</i>	<i>a</i>	<i>a</i>	<i>d</i>	<i>m</i>	<i>i</i>	<i>a</i>	<i>a</i>	<i>n</i>	<i>m</i>	<i>c</i>	<i>a</i>	<i>i</i>	
	<i>u</i>	<i>a</i>	<i>a</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>ë</i>	<i>a</i>	<i>t</i>	<i>n</i>	<i>c</i>	<i>a</i>	<i>a</i>	<i>h</i>	<i>c</i>	<i>t</i>	
	<i>i</i>	<i>n</i>	<i>c</i>	<i>i</i>	<i>t</i>	<i>t</i>	<i>p</i>	<i>c</i>	<i>i</i>	<i>s</i>	<i>t</i>	<i>c</i>	<i>n</i>	<i>i</i>	<i>t</i>	<i>i</i>	
	<i>u</i>	<i>a</i>	<i>u</i>	<i>m</i>	<i>e</i>	<i>e</i>	<i>u</i>	<i>t</i>	<i>a</i>	<i>h</i>	<i>i</i>	<i>n</i>	<i>t</i>	<i>a</i>	<i>e</i>	<i>a</i>	
	<i>s</i>	<i>n</i>	<i>ë</i>	<i>p</i>	<i>d</i>	<i>c</i>	<i>e</i>	<i>a</i>		<i>a</i>	<i>a</i>	<i>ë</i>	<i>s</i>	<i>n</i>			
	<i>u</i>		<i>s</i>	<i>i</i>	<i>a</i>	<i>u</i>	<i>n</i>	<i>c</i>		<i>n</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>c</i>	<i>m</i>	<i>d</i>	
	<i>d</i>		<i>h</i>	<i>r</i>	<i>d</i>	<i>i</i>				<i>t</i>	<i>h</i>	<i>t</i>	<i>s</i>	<i>u</i>	<i>a</i>	<i>a</i>	
	<i>q</i>			<i>u</i>	<i>a</i>	<i>d</i>				<i>u</i>	<i>o</i>	<i>s</i>		<i>ë</i>	<i>c</i>	<i>p</i>	
	<i>u</i>			<i>c</i>	<i>i</i>					<i>c</i>		<i>ë</i>		<i>m</i>	<i>t</i>	<i>a</i>	
	<i>i</i>			<i>c</i>								<i>q</i>		<i>a</i>	<i>a</i>		
	<i>d</i>			<i>u</i>	<i>c</i>							<i>u</i>		<i>n</i>	<i>c</i>		
				<i>ë</i>	<i>u</i>							<i>i</i>					
				<i>m</i>	<i>ë</i>							<i>d</i>					
				<i>a</i>	<i>m</i>												
				<i>n</i>	<i>a</i>												
				<i>n</i>													
Primary Forest																	
	<i>nimëduc<sub>2</sub></i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	<i>isanchoed</i>	X	X														
	<i>nistechoed</i>				X	X	X										
	<i>shuinte mapichoed</i>		X														
	<i>budëdchoed</i>				X	X											
9	<i>miochoed</i>	X	X	X	X	X	X	X									
10	<i>budëd ushuchoed</i>	X	X	X	X		X	X									
11	<i>shubuchoed</i>	X	X	X	X	X	X	X			X	X	X	X			
12	<i>tanacchoed</i>		X	X	X	X	X	X									
	<i>dapaischoed</i>	X	X	X	X	X	X	X									
	<i>cobisanchoed</i>				X					X							
	<i>tiantechoed</i>				X	X	X										
	<i>sëntechoed</i>	X	X	X	X	X	X	X									
	<i>pëncadchoed</i>		X	X	X	X	X	X									
	<i>mani padachoed</i>		X	X	X	X	X	X									
13	<i>maynën sebad</i>	X	X	X	X		X	X									
14	<i>isitodochoed</i>		X	X													
	<i>cuëte mampis</i>		X														
	<i>itia</i>								X								
	<i>antinchoed</i>									X					X		
	<i>sinadchoed</i>									X	X				X		
	<i>shuiishchoed</i>									X					X	X	
	<i>canashëtachoed</i>									X					X		
	<i>itia dapa</i>																X
Secondary Forest																	
15	<i>tied shëni</i>	X	X	X													
	<i>mayun tied</i>	X	X	X		X	X										
	<i>cuesbudaid</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	<i>isitodochoed</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	<i>bucuchoed</i>	X	X	X	X	X	X	X			X	X	X	X			
16	<i>sedquequid</i>	X	X	X	X	X	X	X	X			X	X	X	X		
	<i>cuëteuidquio tabad.</i>	X	X	X	X	X	X	X			X	X	X	X			

For example, the Matses habitat *shubuchoed* 'Phytelephas microcarpa stemless palm forest' is notable to the Matses for containing palms for thatch (*P. microcarpa*), being located on good soil that is ideal for making swiddens, and having high densities of trees with edible fruits, which can be harvested seasonally and attract game.

Although the Matses habitat classification system is not entirely hierarchical, each of the two subsystems is. Geomorphologically-defined habitat types are classified into two major categories: *mananucquio*, upland rainforest that is not affected by seasonal flooding of a river (Table 1; Figure 3A), and *acte cuëman*, floodplain forest along a river that is subjected to seasonal flooding (Table 1; Figure 3B). Vegetatively-defined habitats are arranged in a very shallow hierarchy and are placed into two general categories: *nimëduc* 'primary rainforest' and an unnamed category for secondary rainforest habitats (Table 1; Figure 4). Thus, *nimëduc* has both a general and a specific definition (i.e., it is polysemous with referents at two taxonomic levels). In the general sense it means all primary rainforest (*nimëduc*<sub>1</sub>), and in the specific sense it refers to all primary rainforest excluding the other named vegetatively-defined habitats (*nimëduc*<sub>2</sub>). The Matses do not have a named category for "secondary forest", but interview responses clearly show that they place successional forest habitat types into a category that is separate from the named category for primary rainforest, *nimëduc*<sub>1</sub> (i.e., "secondary forest" is a covert category [Berlin et al. 1968]).

Primary rainforest is characterized by high diversity and infrequent clumping of one plant species (Gentry 1992), so the Matses habitat types that are characterized by a dominant species of plant are the exception. The occurrence of vegetatively defined habitat types cannot be predicted by geomorphological factors alone, but their distribution is probably related to some combination of edaphic, historical, and biological factors which favor dominance of some species. For example, higher densities of *Lepidocaryum tenue*, (the colonial treelet palm that dominates *tanacchoed*) were found in yellow ferralitic soil in higher densities than in poorly-drained gleyic soil (Kahn & Mejia 1987). The high densities of *Duroia hirsuta* and the dearth of understory vegetation in Devil's gardens (called by Matses *mayanën sebad* 'demon's swidden'; Figure 4B) may be the result of a potentially allelopathic iridoid lactone (plumericin) produced by *D. hirsuta* (Page et al. 1994). The scarcity of pioneer species (e.g., *Cecropia* spp.) in *sedquequid* 'natural secondary forest' (Figure 4B) compared to *tied shëni* 'secondary forest from abandoned swiddens' (Figure 4B) is likely due to advanced regeneration in natural treefall gaps from preexisting small trees in arrested growth stages that are not killed by treefalls (Uhl et al. 1988).

*Miochoed* 'Attalea racemosa stemless palm forest' and *budëd ushuchoed* 'Attalea microcarpa stemless palm forest' (Figure 4A) have not been described as rainforest habitat types in the literature (although Henderson [1994] noted that *Attalea racemosa* sometimes forms dense colonies). Perhaps *P. macrocarpa* and *L. tenue* palm forest habitats are more likely to find their way into the literature because they are very important sources of thatch in the Peruvian Amazon, while *Attalea* spp. are not. *Miochoed* and *budëd ushuchoed* (and *shubuchoed*, 'Phytelephas macrocarpa stemless palm forest'; Figure 4A), however, are important to the Matses because great long-nosed armadillos, *Dasypus kappleri*, an important game species, are found frequently in these habitats. *Shubuchoed* and *miochoed* had relatively high small

mammal abundance and species richness, especially for marsupials, compared to other trapped habitats. This may be due to large numbers of macroinvertebrates that thrive in the leaf litter collected in the bases of stemless palms (de Vasconcelos 1990) which may provide food for marsupials. *Mayanën sebad* 'demon's swidden' is not an economically useful habitat for Matses, but these anomalous open zones in otherwise dense tropical forest are too obvious to go unrecognized.

Kahn (1987) found that in eastern Amazonia, differences in palm species composition and abundance exist among hill plateaus, hill crests, hill slopes (inclines) and depressions between hills; these differences were attributed to differences in declivity (angle of slope) among the sites, which affected the drainage and canopy structure, thereby creating different abiotic and biotic conditions for palms. Similarly, relatively small variation in elevation (39 m) can affect rainforest tree species composition (Lieberman et al. 1985); hills in the Nuevo San Juan area can rise up to 60 m above adjacent gullies. These studies lend credibility to the Matses perception that hill crests and hill inclines differ vegetatively.

Knowledge of rainforest habitats is important not only for describing floristic diversity, but also for understanding the ecology of animals in those areas. Capybara (*Hydrochaeris hydrochaeris*) in Amazonian Peru used beaches, *Cecropia* forests, and low levees more often than swamps, low flooded forests, and high levees (Soini & Soini 1992). Woolly monkeys (*Lagothrix lagotricha*) used *colinas* (inland hilly forest) and *igapó* (seasonally flooded blackwater forest) more often than expected in Amazonian Colombia (Defler 1996). Squirrel monkeys (*Saimiri sciureus*) in Surinam showed a preference for liane forests and were found most often in that formation (Mittermeier & van Roosmalen 1981). Results of habitat-mammal associations recorded while hunting with Matses reflect too much sampling bias to reliably determine habitat preferences by game mammals, but the high proportion of time that game species were found in certain habitats illustrates the importance to Matses hunters of recognizing many habitat types in order to hunt more efficiently.

Very poor drainage and perhaps toxic levels of some minerals in the soil seem to inhibit growth of trees so that a conspicuously low basal area and tree density exist in *mactac* 'muddy mineral lick' (Figure 3A). *Mactac* habitats are important to the Matses for hunting and they intentionally make their paths through *mactac* because of the high likelihood of finding game there. Tapirs (*Tapirus terrestris*), white-lipped peccaries (*Tayassu pecari*), and spider monkeys (*Ateles chamek*) were found very often in this habitat, as well as howler monkeys (*Alouatta seniculus*), collared peccaries (*Pecari tajacu*), and brocket deer (*Mazama americana*, *M. gouazoubira*).

The vegetation in *dëpuen* 'stream headwaters' is neither conspicuously different from that in the surrounding habitats nor does this habitat type contain a high concentration of economically important plant species, but it is important for hunting armadillos (*Dasypus kappleri*). *D. kappleri* make burrows in the eroded sides of *dëpuen* gullies and the Matses have become quite skilled at detecting occupied burrows and flooding out the armadillos. The preferred location for searching for *D. kappleri* is in *dëpuen* that overlaps *miochoed*, *budëd ushuchoed*, or *shubuchoed*. According to the Matses, armadillo paths are very common in these vegetatively-defined habitats because they contain good soil with large numbers of soil invertebrates. In fact, the preferred location for Matses to make swiddens is on *shubuchoed*, *miochoed*, or *budëd ushuchoed*, but not where these overlap *dëpuen*,

but rather where they occur on *manan* 'hill crests' and *macuësh* 'hill incline' or on *quiusudquid* 'terra firme next to a river'. Thus, it can be seen that Matses subsistence activities and knowledge of natural history knowledge are sensitive to habitat types that are not lexicalized, but that they can, nevertheless, refer to with precision using a combination of names from the two habitat classification subsystems.

The Matses utilize their knowledge of habitat types to understand seasonal movements of animals. Folk natural history information from the Matses describes the movements of frugivores across several habitat types in response to habitat-specific seasonal availability of fruit and secondary foods (Harder & Fleck 1997). Many animals move between rainforest habitats during the course of the year (e.g., ungulates: Bodmer 1990), and utilize seasonally available resources in different habitat types within the upland and floodplain rainforests (e.g., primates: Peres 1994; Stevenson et al. 1994; Defler 1996).

Species richness of trapable small mammals was lower in *actiacho* 'seasonally flooded forest' than in any of the upland habitats, a trend similar to that found in upland rainforest and blackwater seasonally flooded rainforest habitats near the Ucayali River in Loreto, Peru (Fleck & Harder 1995). An important difference between two types of successional forest recognized by the Matses is that *tied shëni* had the highest abundance of small mammals of the 10 sampled rainforest habitats, while auxiliary trapping in *sedquequid* (350 trapnights) produced zero captures. Second to active swiddens, *tied shëni* is the Matses' favorite habitat type for trapping *Proechimys* rats.

Use of local habitat classifications of indigenous people is not a substitute for extensive regional surveys as in Terborgh and Andresen (1998) or for broader descriptions based on gradients in soil types and hydrology. Nevertheless, there are several applications of indigenous classification systems for diversity inventories and management planning. For example, a researcher could consult locals about the habitat types they recognize and ask to be led to the different habitats, thus efficiently finding some habitat types that might contain fauna or flora that is rare elsewhere, and would otherwise be detected only by chance. One innovative application of folk classification systems is Shepard et al.'s (in press) utilization of the rainforest habitat classification system of the Matsigenka Indians of Amazonian Peru to interpret LANDSAT images. Another use of indigenous habitat classification and resource knowledge is in designing, implementing and managing communal reserves, national parks and other natural protected areas with indigenous populations. A case in point is the use of Matsigenka ecological knowledge described by Shepard (in press) to form a baseline for implementing a recently-approved Conservation International project in the Vilcabamba Cordillera of Peru that engages the local indigenous groups as primary stewards of two communal reserves and as stakeholders in a proposed national park.

In order to develop effective conservation policy in Amazonian countries, it is essential to have an understanding of habitat heterogeneity in Amazonia, but unfortunately at present there is not a habitat classification system for Amazonia available to scientists and policy makers that considers all minor habitat types such as those described in this paper. One way to develop a comprehensive habitat classification system for Amazonia would be to compile descriptions of habitat types recognized by locals and biologists throughout the Amazon basin, deter-

mining which described habitats are similar enough to be considered a single habitat type, and determining whether habitats are geomorphologically or vegetatively-defined. The fact that Shepard et al. (in press) found a comparable classification system for the Matsigenka (more than 40 named habitat types in independent geomorphological and vegetation classifications) suggests that compiling a classification of Amazonian habitats in this way would be practicable. The problem with this approach is time. Indigenous knowledge of habitat classification is passed in an oral natural history that depends upon active hunting in traditional ways. These ways are being threatened by the onslaught of western culture. As young men move to cities or adopt western methods of hunting with shot guns and flashlights, fewer will learn or become skilled in traditional ways that depend heavily upon the indigenous habitat classification. Thus, it is important to study native habitat classifications before they are lost to cultural change along with their potential value to ecology and conservation.

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#### NOTES

<sup>1</sup> The first author's current address, to where correspondence should be sent, is:  
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<sup>2</sup> The orthography used here is the practical orthography developed by SIL personnel for Bible translation and pedagogical materials, which has become the official writing system for the Matses (Kneeland 1979). The alphabet is phonemically-based and modeled after Spanish orthography. To produce a pronunciation that approximates Matses, words written in this orthography may be pronounced as if reading Spanish, with the following exceptions: *ẽ* is a high central unrounded vowel [ɨ]; *c* (spelled *qu* preceding *e*, *ẽ* and *i*) is pronounced as a glottal stop word-finally and preceding consonants, and as [k] elsewhere; *d* is pronounced as a flap [ɾ] between vowels, and as a [d] elsewhere; and *ts* should be read as an unvoiced alveolar affricate. Word-level stress is on even-numbered syllables (counting from left to right) unless otherwise marked.



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APPENDIX A.— Key for identification of Matses-named geomorphologically-defined rainforest habitat types found within 2 km of Nuevo San Juan

- 1 More than 3 m above normal peak river level, near or far from a river, never flooded by seasonal rise of a river ..... Go to 2
- 1' Less than 3 m above normal peak river level, always near a river, subject to seasonal flooding of a river ..... Go to 9
- 2 Elevation rising 10-60 m above surrounding land ..... Go to 3
- 2' In a valley between hills ..... Go to 5
- 3 Adjacent to river, (up to 100 m from river) *quiúsudquid*, terra firme adjacent to a river
- 3' At least 100 m from river ..... Go to 4
- 4 Top of hill with incline <15° ..... *manan*, hill crest
- 4' Side of hill with incline >15°, 10 m above lowest point of valley ..... *macuësh*, hill incline
- 5 Along a stream ..... Go to 6
- 5' Not along a stream ..... Go to 8
- 6 Among several headwater gullies, gullies contain running water only during and immediately after rains ..... *dëpuen*, stream headwaters
- 6' Along a stream >1 m wide, stream contains water all year ..... Go to 7
- 7 Along a stream >3 m wide, stream floods during heavy rains *acte dada cuëman*, gallery forest along large stream
- 7' Along a stream >1 m and <3 m wide, stream swells during rains, but does not overflow banks during heavy rains .. *acte cuidi cuëman*, gallery forest along small stream
- 8 Very poor drainage, ground always waterlogged or muddy ..... *mactac*, mineral lick
- 8' Area between gallery forest and hill inclines, fair drainage, ground damp, but never waterlogged ..... *tsimpiruc*, valley
- 9 "Island" elevated 7-13 m above surrounding land, does not flood during most of rainy season ..... Go to 10
- 9' Relatively flat land, floods during most of rainy season ..... Go to 11
- 10 0-3 m below normal peak river level, flooded yearly, but only for a few weeks during highest water ..... *nacnëdtsequid*, low levee island
- 10' 0-3 m above normal peak river level, only floods on years of exceptionally high river levels ..... *mant ses*, high levee island
- 11 Adjacent to a river or higher than land separating it from a river, drains well during dry season ..... *actiacho*, seasonally flooded forest
- 11' Never adjacent to a river, lower than land separating it from the river, ground remains waterlogged during rainy season, dominated by *Mauritia flexuosa* palms ..... *itia dapa*, palm swamp

APPENDIX B.– Key for identification of Matses-named vegetatively-defined rainforest habitat types found within 2 km of Nuevo San Juan

- 1 Primary rainforest vegetation, trees at least 40 m high, some trees with thick (DBH > 0.6 m) trunks ..... Go to 2
- 1' Secondary rainforest vegetation, trees not reaching 40 m, no trees with thick trunks  
Go to 8
  
- 2 Forest understory dominated by palms ..... Go to 3
- 2' Forest understory not dominated by palms ..... Go to 6
  
- 3 Forest understory dominated by treelet palms (*Lepidocaryum tenue*) ..... **tanacchoed**,  
*Lepidocaryum tenue* treelet palm forest
- 3' Forest understory dominated by stemless palms (*Attalea* or *Phytelephas*) ..... Go to 4
  
- 4 Forest understory dominated by *Phytelephas* sp. palms ..... **shubuchoed**, *Phytelephas macrocarpa* dwarf palm forest
- 4' Forest understory dominated by *Attalea* sp. palms ..... Go to 5
  
- 5 Forest understory dominated by *Attalea racemosa* palms .... **miochoed**, *Attalea racemosa* dwarf palm forest
- 5' Forest understory dominated by *Attalea microcarpa* palms ... **budëd ushuchoed**, *Attalea microcarpa* dwarf palm forest
  
- 6 Forest understory and midstory with low vegetation density and dominated by *Duroia hirsuta* (small dicot trees) ..... **mayanën sebad**, *Duroia hirsuta* 'demon's swidden'
- 6' Forest not dominated by *Duroia hirsuta* ..... Go to 7
  
- 7 Forest dominated by numerous large and small lianas, high vegetation density  
**isitodochoed**, liana forest
- 7' Forest not dominated by any salient form of vegetation ... **nimëduc<sub>2</sub>**, undifferentiated primary forest
  
- 8 Forest dominated by *Cecropia* spp. *Marila* spp. and other pioneer tree species, relatively few lianas, few primary forest species; from an abandoned Matses swidden  
**tied shëni**, abandoned swidden
- 8' Forest containing a wide variety of primary forest species that have sprouted vegetatively from stumps and roots of fallen trees, mixed with pioneer tree species, contains many small lianas and creeping vines; not from an abandoned swidden . **sedquequid**, natural secondary forest

Note: The keys in Appendices A and B can be used to describe any locality within 2 km of Nuevo San Juan, Peru using two habitat names, one geomorphologically-defined habitat name and one vegetatively-defined habitat name.

APPENDIX C.— List of 84 non-flying mammal species captured, observed (\*), or reported by Matses (\*\*) in the Nuevo San Juan area in 1995-1996.

LATIN NAME <sup>a</sup>	ENGLISH NAME <sup>b</sup>	MATSES NAME <sup>c</sup>
<b>DIDELPHIMORPHIA</b>		
<i>Caluromys lanatus</i>	western woolly opossum	<i>abuc checa</i>
<i>Didelphis marsupialis</i>	common opossum	<i>mapiocos</i>
<i>Gracilinanus kalinowskii</i> <sup>1</sup>	Kalinowski's gracile mouse opossum	<i>checampi</i>
<i>Marmosa murina</i>	murine mouse opossum	<i>checampi</i>
<i>Marmosops noctivagus</i>	White-bellied slender mouse opossum	<i>checampi</i>
<i>Marmosops impavidus</i>	Andean slender mouse opossum	<i>checampi</i>
<i>Metachirus nudicaudatus</i>	brown 4-eyed opossum	<i>checa dëuisac</i>
<i>Micoureus demerarae</i>	Long-furred woolly mouse opossum	<i>checampi</i>
<i>Micoureus regina</i>	Short-furred woolly mouse opossum	<i>checampi</i>
<i>Monodelphis adusta</i>	Sepia short-tailed opossum	<i>yama</i>
<i>Monodelphis emiliae</i>	Emilia's short-tailed opossum	<i>yama</i>
<i>Philander mcilhennyi</i> <sup>2</sup>	Anderson's gray four-eyed opossum	<i>checa dëuisac</i>
<b>XENARTHRA</b>		
<i>Bradypus variegatus</i>	Brown-throated three-toed sloth	<i>mëincanchush</i>
<i>Choloepus cf. hoffmanni</i>	Southern two-toed sloth	<i>shuinte</i>
<i>Cabassous unicinctus</i> *	Southern naked-tailed armadillo	<i>mencludu</i>
<i>Dasybus kappleri</i>	Great long-nosed armadillo	<i>tsaues</i>
<i>Dasybus novemcinctus</i>	nine-banded armadillo	<i>sedudi</i>
<i>Priodontes maximus</i>	giant armadillo	<i>tsauesamë</i>
<i>Cyclopes didactylus</i>	pygmy ant eater	<i>tsipud</i>
<i>Myrmecophaga tridactyla</i>	giant ant eater	<i>shaë</i>
<i>Tamandua tetradactyla</i>	collared tamandua	<i>bëui</i>
<b>PRIMATES</b>		
<i>Callithrix pygmaea</i>	pygmy marmoset	<i>madun sipi</i>
<i>Saguinus fuscicollis</i>	saddleback tamarin	<i>sipi cabëdi</i>
<i>Saguinus mystax</i>	Black-chested mustached tamarin	<i>sipi ësed</i>
<i>Callimico goeldii</i> *	Goeldi's monkey	<i>sipi chëshë</i>
<i>Alouatta seniculus</i>	red howler monkey	<i>achu</i>
<i>Aotus nancymae</i>	night monkey	<i>dide</i>
<i>Ateles chamek</i>	black spider monkey	<i>chëshëid</i>
<i>Cacajao calvus</i>	red uakari monkey	<i>senta</i>
<i>Callicebus cupreus</i>	titi monkey	<i>uadë</i>
<i>Cebus albifrons</i>	white-fronted capuchin monkey	<i>bëchun ushu</i>
<i>Cebus apella</i>	brown capuchin monkey	<i>bëchun chëshë</i>
<i>Lagothrix lagotricha</i>	common woolly monkey	<i>poshto</i>
<i>Pithecia monachus</i>	monk saki monkey	<i>bëshuicquid</i>
<i>Saimiri sciureus</i>	common squirrel monkey	<i>tsanca</i>
<b>CARNIVORA</b>		
<i>Atelocynus microtis</i> **	short-eared dog	<i>mayanën opa</i>
<i>Speothos venaticus</i> *	bush dog	<i>achu camun</i>
<i>Herpailurus yaguarondi</i> *	jaguarundi	<i>bëdi chëshë</i>
<i>Leopardus pardalis</i>	ocelot	<i>bëdimpi</i>
<i>Leopardus wiedii</i> **	margay	<i>tëstuc mauequid</i>
<i>Panthera onca</i> *	jaguar	<i>bëdi</i>
<i>Puma concolor</i> *	puma	<i>bëdi piu</i>
<i>Eira barbara</i>	tayra	<i>batachoed</i>
<i>Galictis vittata</i> **	grison	<i>bosen ushu</i>
<i>Lontra longicaudis</i>	southern river otter	<i>bosen</i>

<i>Mustela africana</i> **	Amazon weasel	<i>opampi</i>
<i>Pteronura brasiliensis</i>	giant river otter	<i>onina</i>
<i>Bassaricyon gabbii</i>	olingo	<i>shēmēin</i>
<i>Nasua nasua</i>	South American coati	<i>tsise</i>
<i>Potos flavus</i>	kinkajou	<i>cuichic</i>
<i>Procyon cancrivorus</i> **	crab-eating raccoon	<i>tsise biecuador</i>
<b>CETACEA</b>		
<i>Sotalia fluviatilis</i> *	gray dolphin	<i>chishcan chēshē</i>
<i>Inia geoffrensis</i> *	pink river dolphin	<i>chishcan piu</i>
<b>PERISSODACTYLA</b>		
<i>Tapirus terrestris</i>	Brazilian tapir	<i>nēishamē</i>
<b>ARTIODACTYLA</b>		
<i>Pecari tajacu</i>	collared peccary	<i>shēcten</i>
<i>Tayassu pecari</i>	white-lipped peccary	<i>shēctenamē</i>
<i>Mazama americana</i>	red brocket deer	<i>senad piu</i>
<i>Mazama gouazoupira</i>	gray brocket deer	<i>senad tanun</i>
<b>RODENTIA</b>		
<i>Microsciurus flaviventer</i>	Amazon dwarf squirrel	<i>capa cudu</i>
<i>Sciurillus pusillus</i>	Neotropical pygmy squirrel	<i>cacsi</i>
<i>Sciurus ignitus</i>	Bolivian squirrel	<i>capampi</i>
<i>Sciurus igniventris</i>	northern Amazon red squirrel	<i>capa</i>
<i>Sciurus spadiceus</i>	southern Amazon red squirrel	<i>capa</i>
<i>Nectomys apicalis</i> <sup>3</sup>	water rat	<i>maca tanun</i>
<i>Oecomys bicolor</i>	arboreal rice rat	<i>shubu pecquid</i>
<i>Oecomys cf. trinitatis</i>	arboreal rice rat	<i>abuc macampi</i>
<i>Oryzomys cf. macconnelli</i>	rice rat	<i>tacbid umu</i>
<i>Oryzomys perenensis</i> <sup>3</sup>	common rice rat	<i>tacbid umu</i>
<i>Oryzomys yunganus</i>	rice rat	<i>tacbid umu</i>
<i>Scolomys ucayalensis</i>	gray spiny mouse	<i>tacbid umu</i>
<i>Coendou prehensilis</i>	Brazilian porcupine	<i>isa</i>
<i>Dinomys branickii</i>	pacarana	<i>tambis biecuador</i>
<i>Hydrochaeris hydrochaeris</i>	capybara	<i>memupaid</i>
<i>Dasyprocta fuliginosa</i>	black agouti	<i>mēcueste</i>
<i>Myoprocta pratti</i> <sup>4</sup>	green acouchi	<i>tsatsin</i>
<i>Agouti paca</i>	paca	<i>tambis</i>
<i>Isothrix bistrriata</i>	yellow-crowned brush-tailed tree rat	<i>abuc maca</i>
<i>Makalata didelphoides</i> <sup>5</sup>	red-nosed tree rat	<i>abuc maca</i>
<i>Mesomys ferrugineus</i> <sup>4</sup>	spiny tree rat	<i>abuc maca</i>
<i>Proechimys brevicauda</i>	spiny rat	<i>tambisēmpi</i>
<i>Proechimys cuvieri</i>	spiny rat	<i>tambisēmpi</i>
<i>Proechimys kulinae</i> <sup>6</sup>	spiny rat	<i>tambisēmpi</i>
<i>Proechimys simonsi</i>	spiny rat	<i>tambisēmpi</i>
<i>Proechimys steerei</i>	spiny rat	<i>tambisēmpi</i>

<sup>a</sup> Nomenclature follows Wilson & Reeder (1993) unless otherwise noted.

<sup>b</sup> Most common names from Emmons and Feer (1997).

<sup>c</sup> Only lexicalized terms are listed. For the many mammal species that are lexically overdifferentiated by the Matses (see Fleck *et al.* 1999 for primate overdifferentiation by the Matses), the Matses name given represents the non-terminal lexeme that corresponds most closely to the scientific species. Also, many of the game species have multiple synonymous names, in this list the most common synonyms used at Nuevo San Juan are presented here.

<sup>1</sup> Hershkovitz (1992)

<sup>2</sup> Patton & da Silva (1997)

<sup>3</sup> Patton *et al.* (2000)

<sup>4</sup> Voss *et al.* (in press)

<sup>5</sup> Emmons (1993)

<sup>6</sup> da Silva (1998)

## APPENDIX D.– Linguistic analysis of habitat terminology.

Here all the habitat types listed in Table 1 are analyzed linguistically. Habitats are listed and discussed in three sections based on their analyzability. The first and second categories include terms that are not synchronically segmentable, and correspond to Conklin's (1962:123) "unitary simple lexemes" and Berlin et al.'s (1973:217) "(unanalyzable) primary lexemes." The first category includes lexemes that have a single meaning in Matses, and the second category includes polysemous lexemes. The third category includes names with more than one morpheme, corresponding to Conklin's (1962:123) "unitary complex lexemes" and Berlin et al.'s (1973:217) "unproductive (analyzable) primary lexemes." None of the habitat names include morphemes that refer to a superordinate category, so there are no terms corresponding to Conklin's (1962:123) "composite lexemes" or Berlin et al.'s (1973:123) "secondary lexemes."

One notable trend in Matses habitat nomenclature is that all of the synchronically unanalyzable terms (category 1) are for geomorphologically-defined habitats, suggesting that these habitat names are older than those designating vegetatively-defined habitats. If indeed the geomorphological habitat classification subsystem is older, it is notable that plot it was this sub-system that was more easily classified by the CART analyses.

1) Non-polysemous monomorphemic terms:

<i>tsimpiduc</i>	'valley between hills'
<i>anshantuc</i>	'permanently waterlogged swamp'
<i>nimëduc</i>	'primary forest/undifferentiated primary forest'
<i>mananuc</i>	'upland forest' (usually used with the emphatic <i>-quio</i> )
<i>manan</i>	'hill crest'
<i>macuësh</i>	'hill incline'
<i>mantses</i>	'high levee'
<i>mashcad</i>	'levee island (flooding season term for <i>mantses</i> )'
<i>actiacho</i>	'low seasonally flooded forest'
<i>dëpuen</i>	'stream headwaters'

*Possible historical analyses.*– The form *uc* appears to be a historical locative postposition. The only nouns in Matses that can appear in a locative phrase without a locative postposition are those ending in *uc* (these happen to all be habitat terms); so the term *mananuc* 'upland forest' is almost certainly historically derived from *manan* 'hill crest' and possibly once could be analyzed as 'in the hills'. The term *actiacho* 'low seasonally flooded forest' obviously contains the word *acte* 'water/river/stream', but the form *acho* is not found elsewhere in the language (like *cran-* in English *cranberry*), so it is debatable whether this word is synchronically segmentable.

Matses has a productive but apparently very old process of noun incorporation using abbreviated forms of body part terms prefixed to noun, verb, and adjective roots. The prefix provides a locative orientation in reference to an actual or metaphorical body part. The words listed above are no longer synchronically



segmentable, but the form *ma* in elevated topographical terms may be related to the prefix *ma-* 'head.' Similarly, the form *tsi* in *tsipiruc* 'valley' may be the prefix *tsi-* 'hips.' And finally, the form *dē* in *dēpuen* 'stream headwaters' may be the prefix *dē-* 'nose' (cf. "upstream" is *dēbiate-mi* 'nose-Directional.')

## 2) Polysemous monomorphemic names

*mactac* 'mineral lick' also means 'mud'

*itia* 'upland palm swamp' also refers to the palm species, *Mauritia flexuosa*

The reason for separating these terms from those in one is that it is not clear which of the meanings for these terms is the older one, making it questionable whether these are old lexemes or recent coining of new habitat names through metonymy. Note that *nimēduc* is polysemous in the sense that it refers to categories at two levels of habitat classification ('primary forest' and 'undifferentiated primary forest'), but this polysemy does not bring into question whether this is a recently-introduced term for designating a habitat type.

## 3) Synchronically analyzable names:

Geomorphologically-defined habitat terms are mostly nominalizations and locative phrases, while vegetatively-defined habitat terms, especially for primary forest, mostly involve the noun phrase enclitic *-choed* 'characterized by,' which is a very productive morpheme that can be used to describe any animate or inanimate entity besides rainforest habitats (e.g., the name for the tayra is *batachoed* 'sweet-characterized.by' because it eats fruits and steal papayas; or a man with a large belly may be teased by calling him *chichanchoed* 'stomach.parasite-characterized.by'). However, all the terms listed below represent lexicalized terms (they are used consistently, they have restricted meanings, and they are treated differently grammatically from *ad hoc* descriptive phrases).

<i>quiusud-quiv</i> rise.above-Agt.Nzr <sup>1</sup>	'non-flooding forest next to a river' (lit. 'one that rises above')
<i>nacnēd-tsē-quiv</i> stick.out-Dim-Agt.Nzr	'low levee that is flooded every year' (lit. 'one that sticks out a bit')
<i>sedque-quiv</i> shine-Agt.Nzr	'secondary forest from blowdown or river shift with many vines and few <i>Cecropia</i> spp. trees' (lit. 'one that shines/is bright [due to sun shining through the open canopy]')
<i>cuēte-uid-quio tabadquiv</i> only-Emph stand-Agt.Nzr	'secondary forest where hardwood trees tree-are-out competing pioneer vegetation and vines' (lit. 'one where only dicot trees stand')
<i>cuesbud-aid</i> fall.over-Pat.Nzr	'recent blowdown characterized by creeping vines and no trees' (lit. 'fallen over')

<i>acte cuëma-n</i> river edge-Loc	'floodplain forest' (lit. 'beside a river')
<i>acte dada cuëma-n</i> stream body edge-Loc	'gallery forest along a large stream' (lit. 'beside the body of a stream')
<i>acte cuidi cuëma-n</i> stream branch edge-Loc	'gallery forest along a small stream' (lit. 'beside the branch of a stream')
<i>chian cuëma-n</i> lake edge-Loc	'forest along a floodplain lake' (lit. 'beside a lake')
<i>acte mauan</i> river flooded.place	'flooding season term for <i>actiacho</i> ' (lit. 'flooded place by a river')
<i>tied shëni</i> swidden old	'secondary forest in abandoned Matses swiddens dominated by <i>Cecropia</i> spp. and <i>Marila</i> spp. trees' (lit. 'old swidden')
<i>mayu-n tied</i> nonMatses-Gen swidden	'secondary forest from abandoned swiddens or villages >50 yr old' (lit. 'non-Matses Indians' swidden')
<i>mayan-n sebad</i> demon-Gen swidden	'forest with open understory, dominated by <i>D. hirsuta</i> trees' (lit. 'demon's swidden')
<i>cuëte mampis</i> dicot.tree ?small	'forest where only thin hardwood trees grow' (lit. 'small dicot trees')
<i>isan-choed</i> Oenocarpus.mapora-char	'forest dominated by <i>O. bataua</i> palms' (lit. one characterized by <i>O. bataua</i> palms')
<i>niste-choed</i> Iriartea.deltoidea-char	'forest dominated by <i>I. deltoidea</i> palms'
<i>shuinte mapi-choed</i> sloth head-char	'forest dominated by <i>A. tessmanii</i> palms' ("sloth head" is the name for <i>A. tessmanii</i> )
<i>budëd-choed</i> Attalea.butyracea-char	'forest dominated by <i>A. butyracea</i> palms'
<i>mio-choed</i> Attalea.racemosa-char	'forest with understory dominated by <i>A. racemosa</i> palms'
<i>budëd ushu-choed</i> Attalea.butyracea white-char the name for <i>A. microcarpa</i> )	'forest with understory dominated by <i>A. microcarpa</i> palms' ("white <i>A. butyracea</i> " is the name for <i>A. microcarpa</i> )

<i>shubu-choed</i> Phytelephas macrocarpa-char	'forest with understory dominated by <i>P. macrocarpa</i> palms'
<i>tanac-choed</i> Lepidocaryum.tenuе-char	'forest with understory dominated by <i>L. tenuе</i> treelet palms'
<i>dapais-choed</i> Attalea.phalerata-char	'forest with understory and midstory dominated by <i>A. phalerata</i> palms'
<i>cobisan-choed</i> Euterpe.precatoria-char	'swamp dominated by <i>E. precatoria</i> palms'
<i>tiantе-choed</i> bamboo-char	'forest dominated by bamboo'
<i>sēnte-choed</i> Cedrela-char	'forest dominated by <i>Cedrela</i> sp. trees'
<i>pēncad-choed</i> tree.species-char	'forest dominated by <i>pēncad</i> trees'
<i>mani pada-choed</i> plantain flat-char	'forest dominated by <i>Musa</i> wild banana plants' (lit. 'characterized by having flat [leaved] plantains')
<i>isitodo-choed</i> liana-char	'forest dense with many large lianas'
<i>antin-choed</i> Attalea.maripa-char	'seasonally flooded forest dominated by <i>A. maripa</i> palms'
<i>sinad-choed</i> Bactris-char	'seasonally flooded forest with understory dominated by <i>Bactris</i> cf. <i>bifida</i> palms'
<i>shiuish-choed</i> Ficus-char	'seasonally flooded swamp forest dominated by <i>Ficus</i> sp. trees'
<i>cana shēta-choed</i> macaw beak-char	'low floodplain adjacent to the river with dense thorny vegetation' ("macaw beak" is the name for a species of waterside shrub)
<i>isitodo icsa-choed</i> vine thicket-char	'secondary forest thick with vines and young trees' (lit. 'characterized by vine thickets')
<i>bucu-choed</i> Cecropia-char	'secondary forest dominated by <i>Cecropia</i> sp. trees'

<i>acte mactac</i> river mineral.lick	'mineral lick in floodplain forest' (lit. 'mineral lick by a river')
<i>itia dapa</i> palm.swamp large	'floodplain palm swamp' (lit. 'big palm swamp')
<i>itia mauan</i> palm.swamp flooded.place	'flooding season term for <i>itia dapa</i> ' (lit. 'flooded place in a palm swamp')

The last three terms listed in this section contain words that are identical to other habitat terms; however, *mactac* and *itia* are not superordinate categories, but rather occur at the same taxonomic level (and therefore are not "composite lexemes"/ "secondary lexemes."

<sup>1</sup> Morpheme gloss abbreviations:

Agt.Nzr	'Agent Nominalizer'
Gen	'Genitive'
char	'characterized by'
Loc	'Locative'
Dim	'Diminutive'
Pat.Nzr	'Patient Nominalizer'
Emph	'Emphatic'